NOTES ON COLLECTIONS OF FRUIT BATS FROM SULAWESI AND SOME OFF-LYING ISLANDS (MAMMALIA, MEGACHIROPTERA)

by

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Notes are given on the taxonomy, reproductive biology, ecology and ectoparasites of 20 species of – mostly recently collected – Megachiroptera from Sulawesi, Indonesia. The occurrence of one species on Sulawesi is considered doubtful and a further three species are deleted from the Sulawesian faunal list. A key based on externally visible characters and a gazetteer of the collecting localities of Sulawesian bats are appended.

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INTRODUCTION

The fruit bat fauna of Sulawesi (Celebes) as presently known numbers 21 species, including three endemic species, two of which belong to endemic, monotypic genera; a number of other taxa is restricted to Sulawesi and one or a few other island groups in the region (cf. Van Strien, 1986). A number of these have remained poorly known until today, as only very few specimens seem to have been collected and deposited in museum collections, and even fewer have been reported in the literature. References from before 1912 have been reviewed extensively by Andersen (1912); since then, odd specimens have been mentioned or described in reports on random collections from much larger regions (e. g. Tate, 1942; Hill, 1974 and 1983) or in revisions or reviews of certain taxonomic sections (e. g. Hayman, 1946; Peterson & Fenton, 1970; Rookmaaker & Bergmans, 1981; De Jong & Bergmans, 1981; Musser, Koopman & Califia, 1982; Rozendaal, 1984).

Over the last few years several new collections of fruit bats have been made in Sulawesi and most of these have for the greater part been deposited in the Rijksmuseum van Natuurlijke Historie at Leiden and the Zoölogisch Museum in Amsterdam. Some Macroglossinae from these collections have been dis-

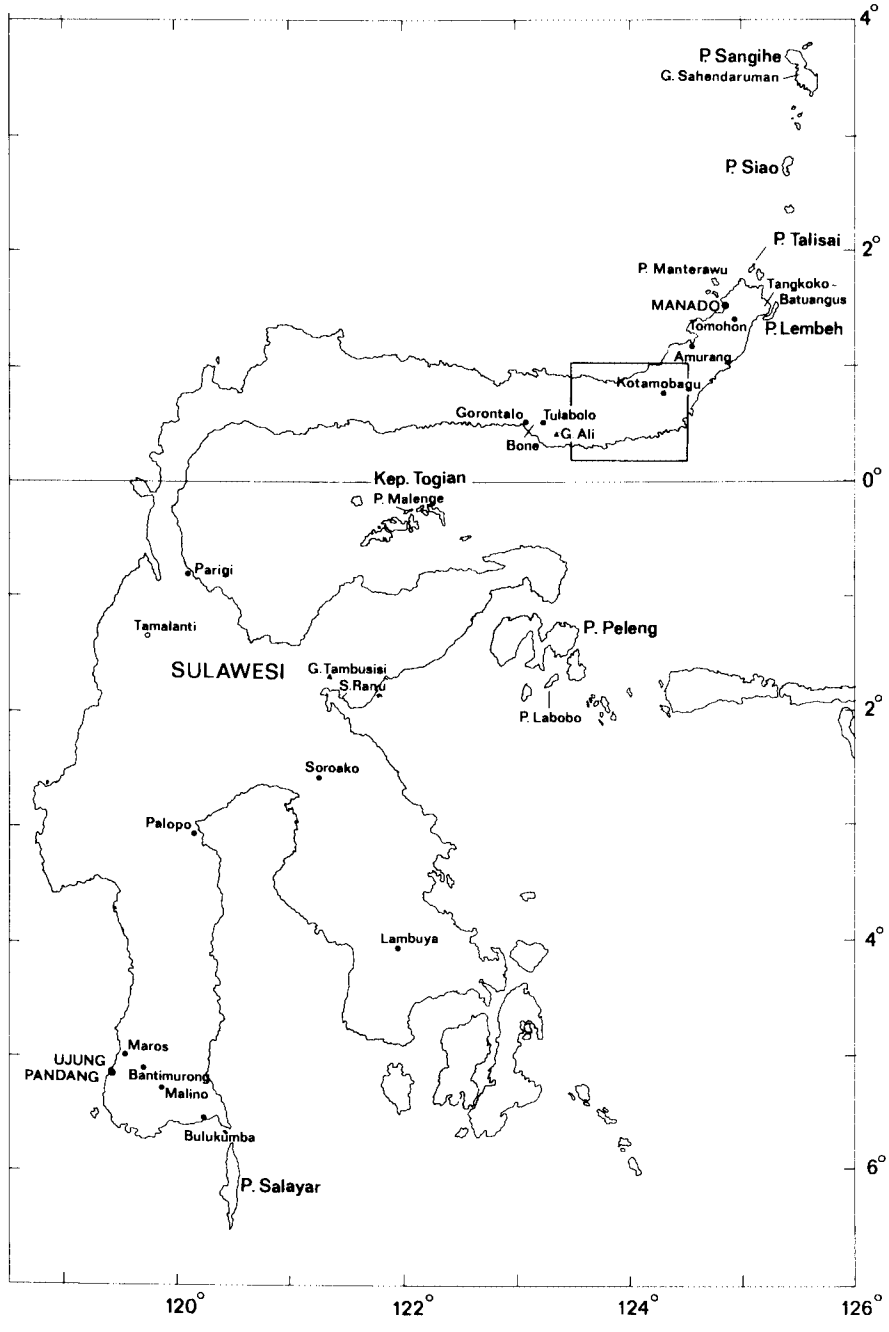

Fig. 1. Map of Sulawesi showing collecting localities mentioned in the text. For a more detailed map of the outlined area in North Sulawesi, see fig. 2.

cussed by Rozendaal (1984) but the remainder, later augmented by new sendings, contains many interesting specimens, including some of the least known species, and provide new insights into taxonomic questions as well as some zoogeographic considerations, which are presented in this paper. Apart from the recent collections, both museums possess some of the oldest Sulawesian fruit bat specimens on record, and in a number of cases it was considered useful to include some of this older material as well.

MATERIAL AND METHODS

Unless stated otherwise in the species accounts, the fruit bats are adult (based upon examination of skull ossification) and have been preserved in alcohol. Ectopararasites have been collected in the field and during examination of the bat specimens for this report; they are deposited in the same collections as their host specimens.

Important synonyms are listed only when changes in current taxonomy or nomenclature are proposed. In the case of some old specimens incorrectly identified in earlier publications, the relevant references have been included.

Sulawesian localities mentioned in the text appear on the maps (figs. 1 and 2) or in the gazetteer (p. 71); some localities have not been traced.

Specimens have been measured with vernier callipers; teeth with a binocular microscope with micrometer disc. All measurements are given in millimetres and all weights in grammes. Drawings of palatal ridge patterns and skulls were made by the senior author using a binocular microscope with drawing-attachment.

The following abbreviations have been used:

alt. – altitude
BMNH – British Museum (Natural History), London
imm. – immature
MZB – Museum Zoologicum Bogoriense, Bogor
NAMRU – United States Naval Medical Research Unit 2, Jakarta
NMB – Naturhistorisches Museum, Basel
N. P. – National Park
RMNH – Rijksmuseum van Natuurlijke Historie, Leiden
SMF – Senckenberg Museum, Frankfurt
ZMA – Zoölogisch Museum, Amsterdam
ZMB – Zoologisches Museum, Berlin

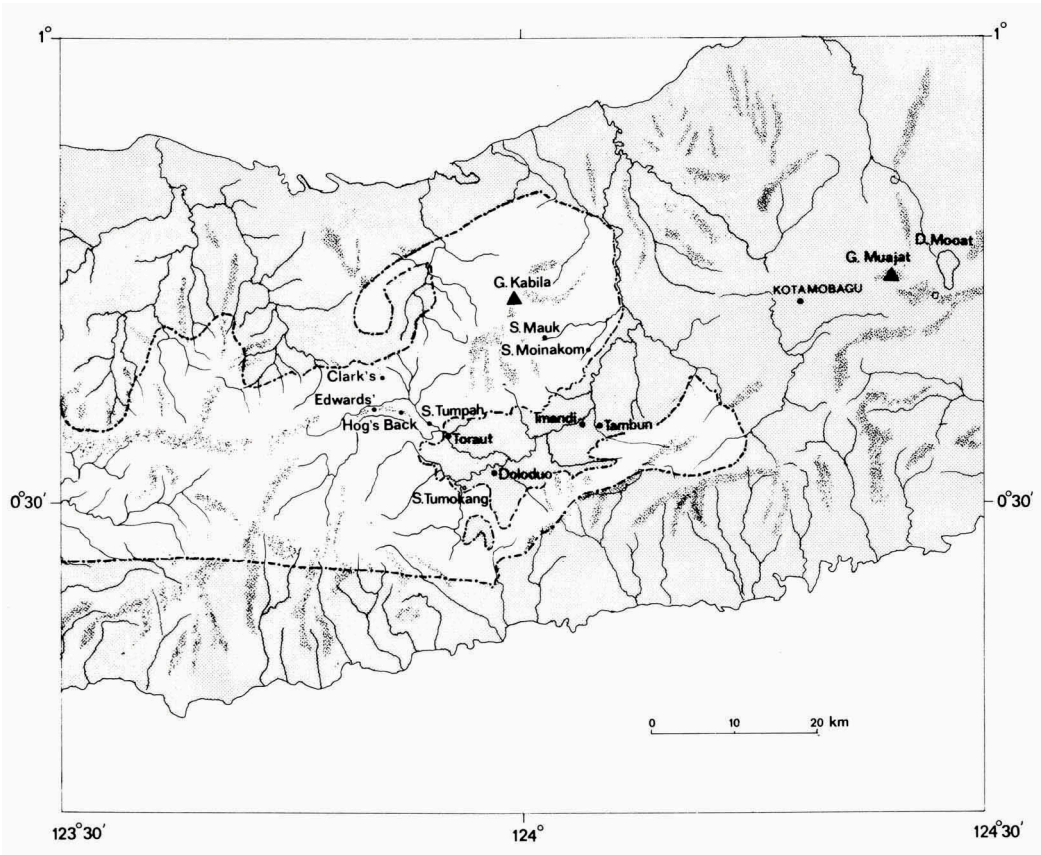

Fig. 2. Map of the eastern section of the Dumoga-Bone N. P. in northern Sulawesi, showing collecting localities mentioned in the text. Unshaded area depicts territory within the boundaries of the Dumoga-Bone National Park; principal mountain ranges are stippled. 'G' denotes 'Gunung' (= Mount, indicated by solid triangles); 'D' denotes 'Danau' (= Lake); 'S' denotes 'Sungei' (= River).

SPECIES ACCOUNTS

PTEROPODIDAE
PTEROPODINAE

Rousettus amplexicaudatus amplexicaudatus (Geoffroy)

Pteropus amplexicaudatus Geoffroy, 1810: 96-97, pl. 4 – Timor.

Specimens examined. — NAMRU 3445, 3444, 3453, 1 ♂, 2 ♀ (skins and skulls), 24.ix.1972, Wasupondo, leg. NAMRU-2; NAMRU 3458, ♂ (skin and skull), 24.ix.1972, Wawondula, leg.

NAMRU-2; NAMRU 5097, ♀ (skin and skull), 22.v.1975, Kosio, leg. NAMRU-2; NAMRU 11182, imm. ♀ (skin and skull), 7.viii.1977, Mario, Iuwu, leg. M. Sibula; ZMA 21.444, ♀ (skull extracted), early xii.1980, Ujung Pandang, leg. H. Moll; NAMRU 6712, 6714, ♂, imm. ♀ (skins and skulls), 20.vii.1981, Lembeh I., leg. NAMRU-2; RMNH 33201-33202, ♂, imm. ♀ (skulls extracted), 18.i.1982, Imandi market, leg. W. F. Rodenburg & J. Wind; RMNH 33199-33200, 2 ♀ (skulls extracted), 24.iii.1982, Imandi market, leg. W. F. Rodenburg & J. Wind; ZMA 22.141, imm. ♀, 22/23.i.1983, Sungei Tumokang Lama, near Doleduo, leg. F. G. Rozendaal.

Measurements and weights. — See table 1.

Discussion. — In their review of *R. amplexicaudatus*, Rookmaaker & Bergmans (1981: 20-21) did not allocate Sulawesian specimens to subspecies. In cranial dimensions their specimens generally agreed with Javanese representatives of *R. a. infumatus* (Gray, 1870), although in two males the skull length was rather as in nominate *amplexicaudatus* from Timor, and lengths of metacarpals and phalanges were somewhat greater than in *infumatus*. Including their specimens from Sulawesi, Peleng and Talisai in the present review, measurements of 13 males and 10 females from Sulawesi and nearby islands are available. Forearm lengths in males range from 77.3 to 85.6 (n = 13; mean 81.5) and in females from 73.7 to 84.9 (n = 9; mean 79.3). Greatest skull lengths in males range from 35.2 to 38.5 (n = 10; mean 36.8) and in females from 32.9 to 36.3 (n = 10; mean 35.0); condylobasal lengths in males range from 34.2 to 37.2 (n = 10; mean 35.4) and in females from 33.3 to 35.4 (n = 10;

	males			females		
	n	mean	min - max	n	mean	min - max
forearm length	12	81.55	77.3-85.6	9	79.35	73.7-84.9
3rd metacarpal length	13	51.1	46.8-54.2	8	49.9	45.2-53.9
5th metacarpal length	13	47.6	43.2-52.6	8	46.5	42.8-49.6
greatest skull length	10	36.85	35.2-38.5	10	35.2	33.9-36.3
condylobasal length	10	35.4	34.2-37.2	10	34.0	32.9-35.4
zygomatic width	14	22.3	20.7-23.3	10	20.7	20.2-21.6
C^1-M^2 (over crowns)	13	13.1	12.1-13.6	11	12.3	11.8-12.7
C_1-M_3 (over crowns)	12	14.45	13.4-15.0	9	13.85	13.3-14.2
M_3 length	8	1.38	0.9- 1.6	10	1.35	1.2- 1.48
weight	1		80	3		50 -70

Table 1. Selected measurements, and weights, of adult *Rousettus a. amplexicaudatus* (Geoffroy, 1810) from Sulawesi, Peleng, Lembeh and Talisai Islands (including specimens listed by Rookmaaker & Bergmans, 1981).

mean 34.2). When compared to the measurements in tables 1 and 2 of Rookmaaker & Bergmans (1981: 14-15) it is apparent that specimens from Sulawesi average distinctly higher in forearm and skull measurements than Javan specimens and that especially males agree to a greater extent with specimens from Timor. We therefore tentatively assign Sulawesian populations to the typical subspecies.

Hill (1983: 106) concluded from measurements given by Rookmaaker & Bergmans (1981: 19) that the Sulawesian populations would "in some ways" be intermediate between *R. a. infumatus* and Timorese *R. a. amplexicaudatus*, and suggested that the latter could be associated with the former at least as well as with populations from New Guinea and the Philippines, as Rookmaaker & Bergmans (1981: 13) had done.

R. a. infumatus is only poorly known from its type locality Flores. The three specimens from that island studied by Rookmaaker & Bergmans (1981: 3) are smaller in most dimensions than *amplexicaudatus* from Timor and agree better with the Javan sample, which in almost all dimensions averages lower than the sample from Timor, and which because of its relatively large sample size was considered by these authors as their best example of *infumatus*. Three previously unreported (dry) specimens from Flores, collected by NAMRU-2 in 1973 at Ruteng (NAMRU 4103, 4116 and 4117), strongly suggest that the species' dimensions average larger on this island than on Java. A male has a forearm length of 83.4; two females have forearm lengths of 81.3 and 81.0 respectively; greatest skull length and condylobasal length in the male are 38.5 and 36.7, and in the females 35.9 and 34.1, and 35.5 and 33.8 respectively. Thus *infumatus* from Flores may be identical with typical *amplexicaudatus*, but according to us Sulawesian populations of *amplexicaudatus* do not seem to connect those from Timor with Javan populations. In a forthcoming study (Bergmans & Boeadi, in prep.), recently collected Indonesian material of *Rousettus* – mainly from Java and Sumatra – in the collection of the Museum Zoologicum Bogoriense will be reviewed; this will offer a better opportunity to re-examine the views regarding Javan *amplexicaudatus* as expressed by Rookmaaker & Bergmans (1981).

Remarks. — Specimen NAMRU 3445 has a small M^3 on both sides.

Reproductive biology. — Adult females RMNH 33199-33200, collected 23 or 24 March, were pregnant: their (single) embryos have forearm lengths of 29.5 and 27.8 respectively. An adult female (ZMA 21.444) caught early December appears to have been lactating at the time of capture.

Ectoparasites. — Specimen ZMA 21.444 was infested with the nycteribiid fly *Eucampsipoda inermis* Theodor, 1955.

Rousettus bidens (Jentink)
(fig. 3)

Boneia bidens Jentink, 1879, 117 – Bone, North Sulawesi; Matschie, 1899: 69; Miller, 1907: 62; Andersen, 1912: 58; Laurie & Hill, 1954: 32.
Boneia menadensis Thomas, 1896: 242 – Menado; Miller, 1907: 62.

Specimens examined. — NAMRU 6707-6708, ♀, ♂ (skins and skulls), 20.vii.1981, Lembeh I., cave, leg. S. Sarbini; RMNH 33197-33198, 2 ♀ (skulls extracted), 24.iii.1982, Imandi market, leg. W. F. Rodenburg & J. Wind; ZMA 22.690-22.695, 3 ♂, 2 ♀, 1 ♂ (four skulls extracted), 10.iv, 8.v (two specimens), 25.v, 17.vi and 22.vi.1985, Imandi market, leg. R. Dekker; ZMA 22.759-22.765, 2 ♂, 2 ♀, 3 imm. ♂ (five skulls extracted), 17.vii (three specimens), 22.vii and 7.ix.1985 (three specimens), Imandi market, leg. R. Dekker.

Measurements and weights. — See table 2.

Discussion. — In his original description of the genus *Boneia* and its type species *B. bidens*, Jentink (1879) did not compare either genus or the at that

	males			females		
	n	mean	min - max	n	mean	min - max
forearm length	5	97.9	94.3 -103.5	6	99.4	96.9 -101.7
greatest skull length	5	44.9	43.9 - 46.3	5	45.0	43.8 - 45.8
condylobasal length	5	42.5	41.6 - 43.9	5	43.5	42.6 - 44.5
rostrum length	5	16.5	15.3 - 17.7	5	17.1	16.4 - 17.7
palatal length	5	22.1	21.7 - 23.3	5	22.7	21.6 - 23.6
mandible length	5	33.4	32.6 - 34.3	5	33.5	32.6 - 34.0
mandible height	5	12.3	11.6 - 12.7	5	12.0	11.4 - 12.8
cranium width	4	18.5	18.1 - 19.0	4	18.4	17.8 - 18.9
interorbital width	5	8.0	7.5 - 8.3	5	7.9	7.2 - 8.4
postorbital width	5	8.4	8.1 - 8.7	5	9.7	9.2 - 10.9
zygomatic width	4	27.0	25.3 - 27.8	4	25.0	24.3 - 25.8
width over crowns of:						
C^1 - C^1	5	10.9	10.8 - 11.0	5	10.3	10.1 - 10.8
C^1 - M^2	5	15.2	14.7 - 15.9	5	15.3	14.8 - 16.0
M^1 - M^1	5	12.5	12.3 - 12.8	5	12.8	12.5 - 13.0
M^2 - M^2	5	12.3	12.1 - 12.5	4	12.6	12.1 - 13.0
C_1 - M_3	5	17.4	16.9 - 18.1	5	17.3	16.4 - 18.8
weight	5	171	156 - 184	5	171	150 - 194

Table 2. Measurements and weights of adult specimens of *Rousettus bidens* (Jentink, 1879).

time unique specimen of the new species with any other megachiropteran taxon. The second specimen to become known to science, from Gorontalo, was listed without descriptive notes (Jentink, 1887: 264; 1888: 152). Thomas (1896: 242), dealing with the third known specimen, from Manado, suggested a resemblance to *Xantharpyia* Gray, 1843 – a nomen nudum of *Rousettus* Gray, 1821 (see Andersen, 1912: 16; see also Thomas' remarks on this matter in his description of the new genus *Harpyionycteris* in the same paper (Thomas, 1896: 243)). Matschie (1899: 69) did not comment on the affinities of the genus but on account of the characters used in his key, *Boneia* follows immediately after *Rousettus*, which order is maintained in his treatment of the genera. Miller (1907: 47) placed *Rousettus* in his key with genera having the "posterior portion of the occiput not distinctly elongated and tubular" and *Boneia* with those having the "posterior portion of the occiput distinctly elongated and tubular"; from his descriptions of the two genera it does not appear that he has considered their possible relationship. Andersen (1912: 55), to be considered as the first critical reviser, described *Boneia* as "closely allied to *Rousettus*, with which it accords in most of its cranial and dental and practically all external characters...". He agreed with Miller (1907: 47) that in *Boneia* braincase deflection is greater than in typical *Rousettus*, but explicitly stated that its occiput is not tubular as in *Pteropus* Brisson, 1762, which he described as having the "occiput produced backward and downward, as a short tube" (Andersen, 1912: 61). According to Andersen, the differential characters of *Boneia*, when compared to *Rousettus* are: palate much broader anteriorly; premaxillae separated in front; upper and lower canines excessively heavy at base; lower canines directed strongly outward; inner pair of incisors lost (at least in adults); outer pairs of lower incisors larger than inner; crowns of molariform teeth flatter.

Boneia indeed bears a striking resemblance to *Rousettus*. When compared with the sympatric species *Rousettus amplexicaudatus* and *R. celebensis* Andersen, 1907, the only immediately apparent external difference is the relatively large size of *Boneia*.

Since Andersen wrote, several other species of *Rousettus* have been described, the inclusion of which has considerably enlarged the concept of the genus: *R. shortridgei* Thomas & Wroughton, 1909 (studied by Andersen after completion of his text on *Rousettus*; see his "Addenda" (Andersen, 1912: 811); *R. madagascariensis* Grandidier, 1929; *R. obliviosus* Kock, 1975 and *R. spinalatus* Bergmans & Hill, 1980. As Andersen (1912: 56) already observed, the degree of braincase deflection in *Boneia* is intermediate between that in what he called "typical *Rousettus*" (*R. aegyptiacus* (Geoffroy, 1810); *R. amplexicaudatus*; *R. leschenaultii* (Desmarest, 1820) and *R. celebensis*) and

Rousettus (Stenonycteris) lanosus Thomas, 1906. We have compared the skulls of the present specimens of *Boneia* with some of *R. lanosus* from Kenya in the ZMA collection and found that the angle of deflection is hardly different. The occipital region in *Boneia* is certainly somewhat more elongated than in *R. lanosus*, due to a slightly greater angle between the dorsal part of the braincase just above the occipital ridge and the occipital part just below it. The palate in *Boneia* is relatively broader anteriorly than in the *Rousettus* species mentioned before, due to the relatively heavier build of the rostrum in the former. However, this difference is of a gradual nature: when compared to the West and Central African subspecies, *R. aegyptiacus unicolor* (Gray, 1870), the difference in rostrum morphology is hardly noticeable and in this respect there is much more variation between *R. aegyptiacus* and species like *lanosus* and *madagascariensis* (see also Andersen, 1912: 811, on the relatively heavy rostrum and broad palate in *R. shortridgei*). The separated premaxillae in *Boneia*, possibly related to the broadening of the anterior part of the rostrum, and the loss of the first upper incisors (I^1), which in turn may be connected with the separated premaxillae (which, by their separation, have lost in strength for functional support of the incisors), are not found in any species of *Rousettus* but, as Andersen (1912: 22) observed, premaxillaries in *Rousettus* are rarely co-ossified, except sometimes in *R. aegyptiacus* (and in *Lissonycteris* Andersen, 1912, a 'subgenus' not included in *Rousettus* by the present authors), and upper incisors are minute in all species of *Rousettus* and, as the recently collected specimens of *Boneia* show, not absent in all specimens of that taxon: specimen NAMRU 6707 shows traces of alveolar cavities of I^1 on both sides; specimen ZMA 22.693 has an I^1 on the right side; specimen ZMA 22.690 has an I^1 on both sides. Thus it seems that both conditions are not very different from those in *Rousettus*. The differences in dental characters which Andersen (1912: 56-57) noticed may all be found – to a greater or lesser extent – to exist between species of *Rousettus* as well. Canines in females of *Boneia bidens* are not or not much heavier than in *Rousettus aegyptiacus unicolor* and *R. leschenaultii shortridgei*. In males of *B. bidens* they are relatively higher and basally longer (not wider) than in those species. *R. l. shortridgei* has the lower canines directed strongly outward and the outer lower incisors distinctly larger than the inner (a weaker state of the latter condition is found in all species of *Rousettus*). The crowns of the molariform teeth in *Boneia* are generally less modified than in *Rousettus*, but a sharp difference does not exist. P^3 and P_3 are generally only slightly higher in *Rousettus*, but P^4 and P_4 are more modified than in *Boneia*. M^1 and M_1 in *Rousettus* are at best but weak reflections of P^4 and P_4 respectively, and M^2, M_2 and M_3 are not very different from their counterparts in *Boneia*.

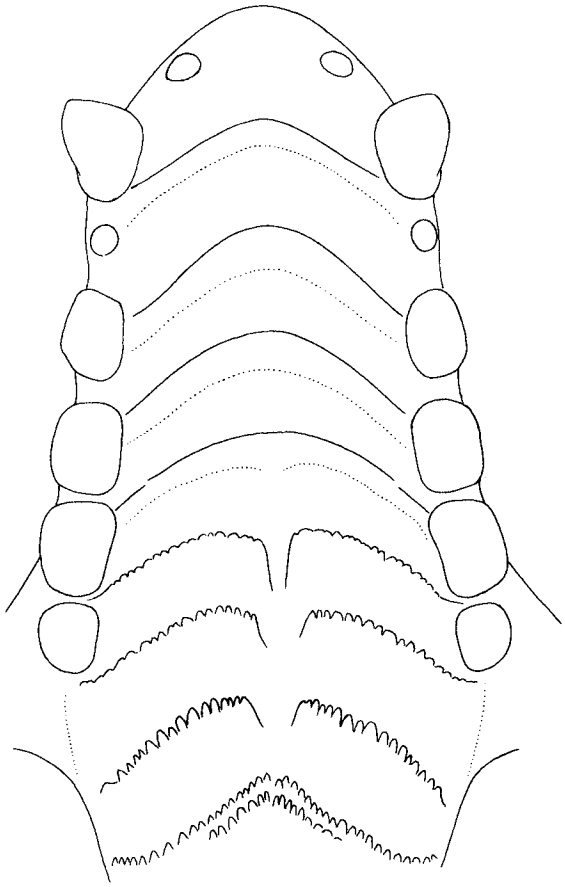

Fig. 3. Palatal ridge pattern of *Rousettus bidens* (Jentink, 1879), specimen ZMA 22.762.

The palatal ridge pattern in *Boneia* (fig. 3) is essentially as in *Rousettus*, except that in *Boneia* there are usually two instead of one finely denticulated ridges near the posterior margin of the palate; the posterior of these two ridges is not always complete, but if it is complete there may even be the median part of a third.

The chin and – in some specimens – the throat are thinly furred, as in many specimens of *Rousettus*.

Boneia bidens lives gregariously in caves, just like *Rousettus* does (Mr. Sukaeri Sarbini, pers. comm. to the senior author, 21.xii.1981) and probably possesses the faculty of echolocation which within the Megachiroptera is restricted to *Rousettus*.

The above-mentioned considerations have led us to consider *Boneia* as a

synonym of *Rousettus*. A thorough revision of the genus *Rousettus* might possibly result in the retention of *Boneia* as a valid subgenus, but is outside the scope of the present paper.

Andersen (1912: 59) could study males of *Boneia* only and mentioned a forearm length range of 95 – 95.5, which is now extended to 94.3 – 103.5 (n = 5: mean 97.9); in six females it ranges from 96.9 to 101.7 (mean 99.4). Greatest skull lengths in five males range from 43.9 to 46.3 (mean 44.9) and in five females from 43.8 to 45.8 (mean 45.0). It appears as if females have, on average, slightly longer forearms. Furthermore, males have distinctly narrower postorbital widths, larger canines and thus larger widths over C^1-C^1, and slightly smaller widths over the last upper molars (table 2).

In adult males the mantle – including the lateral tufts – is roughly as Andersen (1912: 59) described it. Contrary to what he wrote, the throat is not furred as the other ventral parts, but with aberrant, longer hairs, which appear as a weak extension of the mantle. The colour of the mantle in our series is variable, from light "golden buffy" (Andersen, 1912: 59) to much darker brownish shades. A curious character – not observed by Andersen – is formed by a few dozen extremely long hairs, in one specimen up to 47 mm long, scattered over the median part of the nape in adult males. Subadult males lack these characters. Adult females have only slightly longer and paler hairs around the neck; they have neither lateral tufts nor the very long neck hairs observed in the males.

The new localities, Lembeh Island and the Dumoga-Bone National Park area, are located within the known range of the species, which stretches from Gorontalo to Manado.

Reproductive biology. — Two males (ZMA 22.691 and 22.760), bought 8 May and 17 July, had rather large, descended testes. Two females, bought on 17 June (ZMA 22.694) and 17 July (ZMA 22.761), were pregnant (one small embryo each) and had rather large nipples; a female bought 24 March (RMNH 33198) had rather large nipples; females bought 25 May (ZMA 22.693) and 22 July (ZMA 22.762), and one collected 20 July (NAMRU 6707) had large nipples.

Ecology. — Tambun, from where the RMNH specimens were reported to originate, is located in an area with a primary forest/farm bush mosaic. As mentioned earlier, *Rousettus bidens* is a cave-dweller. The Tambun area lies at an altitude of 200-500 m; the type specimen of *Boneia menadensis* was collected at an elevation of c. 1060 m (3500 feet: Andersen, 1912: 59). From this information, the species may be expected to be a lowland forest bat, possibly restricted in its distribution by the presence of suitable caves (or substitutes), and foraging in partly cultivated areas as well.

Ectoparasites. — The following nycteribiid flies were collected: *Eucampsipoda* spec. nov. from ZMA 22.691, *Leptocyclopodia* spec. nov. from ZMA 22.694 and *Archinycteribia curvistyla* Maa, 1975, from ZMA 22.694 and 22.759. Specimen ZMA 22.694 also yielded two fleas of the species *Thaumapsylla breviceps* Rothschild 1907.

Rousettus celebensis Andersen

Rousettus celebensis Andersen, 1907: 509-510 – Mt. Masarang, Celebes, 3500 feet.

Specimens examined. — ZMA 18.571, ♂ (skin and skull), xi.1975, Kuala Navusu, near Parigi, alt. 50 m, leg. C. P. Groves; ZMA 21.445-21.446, ♀, imm. ♀ (skulls extracted), xii.1980, Ujung Pandang, leg. H. Moll; ZMA 21.527, imm. ♂ (skull extracted), 20.x.1981, Sungei Moinakom (southern foothills Gunung Kabila), alt. 725 m, leg. K. D. Bishop, F. G. Rozendaal & W. F. Rodenburg; RMNH 33224, 2 imm. ♂, 8.xi.1981, desa Luksagu, Pulau Peleng and RMNH 33219, 1 ♂, 3 imm. ♂, 8/9.xi.1981, same locality, leg. W. F. Rodenburg & K. D. Bishop; RMNH 33220, 1 ♂, 4 imm. ♂, 3 imm. ♀, 18.i.1982, Imandi market, leg. W. F. Rodenburg & J. Wind; ZMA 21.754, ♂, 19/20.i.1982, Bantimurong, leg. W. Bergmans; RMNH 33221, ♂, ♀, 6.iii.1982, southern slopes of Gunung Ali, alt. 650 m, leg. W. F. Rodenburg & J. Wind; RMNH 33222, 3 imm. ♀, 13/14.iii.1982, southern slopes Kabila range, Sungei Moinakom, leg. W. F. Rodenburg & J. Wind; RMNH 33223, ♂, 24.iii.1982, Imandi market, leg. W. F. Rodenburg & J. Wind; RMNH 33311, imm. ♀, 20/21.i.1983, Sungei Kosinggolan, near Doleduo, alt. 200 m, leg. F. G. Rozendaal; ZMA 22.136-22.139, 22.141, ♂, ♀, imm. ♂, 2 imm. ♀, 22/23.i.1983, Sungei Tumokang Lama, near Doleduo, leg. F. G. Rozendaal; RMNH 33423, imm. ♀, 26/27.i.1983, Sungei Moinakom, alt. 625 m, leg. F. G. Rozendaal; RMNH 33310, 33431, ZMA 22.140, RMNH 33312, ♂, imm. ♂, imm. ♀, 9/10.ii.1983, Tangkoko Batuangus and one ♀, 10/11.ii.1983, same locality, leg. F. G. Rozendaal; ZMA 22.219- 22.223, 2 ♂, ♀, imm. ♂, imm. ♀, 27.iii.1983, Ujung Pandang, leg. R. Mayai; ZMA 22.482, ♂, 31.i.1985, Toraut base camp, alt. 220 m, leg. T. W. Harman; RMNH 35703-35707, 35721, 2 ♂, 4 ♀, 21/22 and 22/23.iii.1985, rentis area, Toraut, Dumoga-Bone N. P., alt. 225 m, leg. F. G. Rozendaal; RMNH 35708-35717, 3 ♂, 6 ♀, 27/28 and 28/29.iii.1985, Sungei Tumpah, Toraut, Dumoga-Bone N. P., alt. 225 m, leg. F. G. Rozendaal; RMNH 35122, ♀, Clark's camp, Dumoga-Bone N. P., alt. 1140 m, leg. F. G. Rozendaal; RMNH 35718, ♀, 16.iv.1985, summit Gunung Muajat, alt. 1780 m, leg. F. G. Rozendaal; RMNH 35719-35720, 19/20.iv.1985, 2 ♀, Danau Mooat, alt. 1080 m, leg. F. G. Rozendaal; RMNH 35666-35671, 3 ♂, 3 ♀, 13/14 and 14/15.v.1985, NW slope of Gunung Sahendaruman, Sangihe I., alt. c. 600 m, leg. F. G. Rozendaal.

Measurements. — Rookmaaker & Bergmans (1981: 23) and Hill (1983: 107-108) recorded ranges of measurements for this species. The present specimens fall completely within these ranges: 11 adult males have forearm lengths from 72.0 to 78.0 (mean 74.9) and five adult females range from 72.3 to 76.8 (mean 73.2).

Remarks. — The collecting localities of the specimens examined do not extend the known range of the species.

Ecology. — Fieldwork in the Tangkoko-Batuangus nature reserve has shown this species – with *Cynopterus brachyotis* (Temminck) – to be the most

numerous fruit bat mistnetted, examined and released along the forest edge and in coastal bush in that area: of c. 70 bats netted, examined and released on 7/8 February 1982, 40 were *Rousettus celebensis* and 20 *Cynopterus brachyotis*. Within primary forest it was netted in smaller numbers. In the Tangkoko-Batuangus reserve the species was observed to roost in numbers in a shallow, low coastal cave at Tanjung Mandera.

Reproductive biology. — An adult female caught early December (ZMA 21.445) has very small nipples; specimens captured 22/23 January (ZMA 22.139) and 6 March (RMNH 33221) had fairly large nipples; a female collected 10/11 February (RMNH 33312) had large nipples; of five females collected 27/28 March, three (RMNH 35712, 35713, 35717) had large nipples, as had female RMNH 35721, collected 21/22 March. An adult female caught on 27/28 March 1985 over Sungei Tumpah (Dumoga-Bone N. P.) and released the next day had given birth to a single young when kept overnight in a holding bag. The adult female caught 27 March (ZMA 22.222) had an embryo with a forearm length of 28 mm; on 13 April 1983 a female nursing a young was observed in a roost in a shallow cave at Tanjung Mandera, Tangkoko-Batuangus reserve; in lowland forest in that reserve two females carrying a single young each were caught, examined and released on 12/13 April. An adult male collected 27 March (ZMA 22.219) has large testes. A juvenile female taken on 26/27 January (RMNH 33423) had a forearm length of 61.0.

Ectoparasites. — Specimens ZMA 21.527, ZMA 22.136-22.137 and RMNH 33310 and 33312 were infested with the batfly *Leptocyclopodia (Leptocyclopodia) ferrisiana* Maa, 1966.

Pteropus hypomelanus macassaricus Heude

Pteropus macassaricus Heude, 1896: 177, pl. 5, fig. 4 – Macassar.
Pteropus hypomelanus, Jentink, 1890-91: 125; partim: specimens 457, 467 and 468 from Makassar – no. 466 not traced.

Specimens examined. — ZMA 3082-3083, 3088, 1 immature ♀, 2 ♂ (skulls extracted), (ix?).1888, Ujung Pandang, leg. M. Weber.

Remarks. — The specimens collected by Weber have been identified as belonging to the subspecies *macassaricus* by Dr. H. Felten. The immature female (sutures of skull basis not completely fused; dentition complete but cheek teeth crowded) has a forearm length of 111.6 and a greatest skull length of 55.0. The fur in this specimen generally agrees with Andersen's description (1912: 124) of the bright phase; the mantle hairs of the neck have very dark

brown basal halves; ventrally, a longitudinal patch of fur on the centre of breast and belly consists of uniformly ochraceous buff hairs. The two males are fully adult; some measurements (ZMA 3083/3088 respectively) are: forearm length 135.5/128.2; greatest skull length 62.4/58.9; condylobasal length 59.8/57.6; zyogmatic width -/33.0; length of upper tooth row, over crowns 22.8/22.5. The pelage colours of these specimens fall within the variation of what Andersen (1912: 124) described as the bright phase, with the exeption of the fur on breast and belly, which is rather darker.

The measurements given by Andersen (1912: 125-126) for this subspecies are those of three males from North Sulawesi and Sangihe and one female from Ujung Pandang; forearm lengths range from 131 to 145.5 and the single greatest skull length given is 64. Other measurements given by Andersen (1912: 125-126) also indicate that specimens from northern Sulawesi may average larger than south-western ones.

Ectoparasites. — Specimen ZMA 3083 yielded two nycteribiid flies, *Cyclopodia horsfieldi* De Meijere, 1899.

Pteropus hypomelanus Temminck, 1853, subspecies?

Pteropus chrysoproctus (not of Temminck), Jentink (1887: 258, specimen *f*; 1888: 144, specimen *v*; both references apply to the same single specimen from the Sangihe Is.).

Pteropus hypomelanus macassaricus (not of Heude), Andersen (1912: 124-126; partim: the specimens from North Sulawesi, Manado and the Sangihe Is.).

Pteropus melanopogon (not of Peters), Jentink (1888: 142-143; partim: the specimens from Siao and Sangihe Is.)

Discussion. — The type locality of *Pteropus macassaricus* Heude, 1896 is Makassar, now Ujung Pandang. Andersen (1912: 125) agreed with Matschie (1899: 26) that this species represented *P. hypomelanus*, but retained it as a valid subspecies and included specimens from North Celebes, Manado, Sangihe Islands and Lirung (Salebabu, Talaud Is.). The measurements given by Andersen (1912: 125-126) are from three males from northern localities and one female from Ujung Pandang. They are rather larger than those of our Ujung Pandang males assigned to *hypomelanus macassaricus*, as discussed in the account of that subspecies (considering that the lower values given by Andersen will be those of his Ujung Pandang female). The same apparent difference in size is shown by the male specimen from the Sangihe Islands and formerly identified by Jentink (1887: 258; 1888: 144) as *Pteropus chrysoproctus* Temminck, 1837. The naked dorsal tibia of that specimen clearly identifies it as belonging to the *hypomelanus* group distinguished by Andersen (1912: 98-99); the skull of the specimen – although incomplete – is much larger than those of our southern males. Some measurements are (with those of specimens

ZMA 3083/3088 from Ujung Pandang following in parentheses): rostrum length 26.0 (24.1/21.4); mandible length 53.7 (49.6/47.1); C^1-M^2 25.7 (22.9/22.5); C_1-M_3 28.4 (25.1/25.2); M^2-M^2 17.0 (15.2/13.8). These measurements indicate that specimens from northern Sulawesi are not identical with the south-western specimens representing the subspecies *macassaricus*, and that their taxonomic status should be reviewed on the basis of more extensive material than available to us for this study.

Pteropus griseus mimus Andersen

Pteropus griseus mimus Andersen, 1908: 364 – Macassar.
Pteropus hypomelanus (not of Temminck), Jentink, 1890-91: 125; partim: one of five ♀.

Specimens examined. — ZMA 3087, ♀ (skull extracted), xi.1888, Salayar, leg. M. Weber, field number 538.

Remarks. — This specimen confirms the occurrence of the species on Salayar, as recorded by Andersen (1912: 91) in his key, but questioned by the same author (1912: 139) in his description because he had not seen any specimen from that locality himself. For no apparent reason, Laurie & Hill (1954: 33) suggested that Salayar might be inhabited by the typical subspecies; they are followed in this by Van Strien (1986: 12). In fact, the specimen's fur is quite as Andersen (1912: 133) described it for *mimus* – then considered a full species – and its measurements do at least not contradict its allocation to that taxon. The specimen is apparently quite old, with canines worn to about halfway the cingula. The teeth cannot be measured properly and unfortunately the skull is incomplete, with part of the occipitum missing.

Reproductive biology. — The specimen has large nipples and was probably lactating at the time of capture.

Ectoparasites. — Two nycteribiid flies, identified as *Cyclopodia horsfieldi* De Meijere, 1899, were still clinging to the fur on the lower back.

Pteropus caniceps Gray

Pteropus caniceps Gray, 1870: 107 – Batchian.

Remarks. — Andersen (1912: 194) listed the specimens from Siao, mentioned by Jentink (1887: 262; 1888: 148-149) under *Pteropus hypomelanus* Temminck, 1853, under *Pteropus caniceps*. The old labels with these three specimens bear Andersen's handwritten re-identifications, added during his studies in the collections in Leiden in November 1907. However, we found all

three specimens to represent *Acerodon celebensis* (Peters, 1867) (cf. the account of that species in this study). The references to *Pteropus caniceps* from Siao by Laurie & Hill (1954: 34) and Van Strien (1986: 11) are most likely based on Andersen's error and consequently this species should be deleted from the list of Chiroptera occurring in the Sangihe Islands.

The alleged occurrence of *Pteropus caniceps* in Sulawesi is based on the single type specimen of *Pteropus dobsoni* Andersen, 1908, a species later considered a subspecies of *caniceps* (Laurie & Hill, 1954: 34; Hill, 1983: 109; Van Strien, 1986: 11). This specimen had been purchased from the dealer Frank and was labelled "Celebes" only (Andersen, 1912: 193). To our knowledge the only material referred to *dobsoni* after its description is a series of seven specimens recorded – but unfortunately not described – from the island of Peleng by Tate (1942: 336). Thus, the actual occurrence of *caniceps* or *caniceps dobsoni* in Sulawesi needs confirmation by additional material. A detailed study of Tate's Peleng series and a comparison with the type specimen of *dobsoni* and material of typical *caniceps* is desirable. For the time being we prefer to regard the provenance of the type specimen of *dobsoni* and the identification of the Peleng series as *dobsoni* with some reservation. Musser, Koopman and Califia (1982) figured occlusal views of the cheek teeth of a specimen from Peleng Island identified as *caniceps dobsoni* (probably of Tate's series referred to above), without discussing its identification. The teeth are different, in some respects, from those of *caniceps* specimens from the North Moluccas (ZMA 21.433, 22.134).

Pteropus alecto alecto Temminck

Pteropus alecto Temminck, 1837: 75 – Menado.

Specimens examined. — ZMA 9191-9192, ♀, ♂ (skull of ♂ extracted), 24.ix/6.x.1888, Maros, leg. M. Weber; ZMA 9193, ♂, xi.1888, Ujung Pandang, leg. M. Weber; ZMA 21.435-21.436, ♂, ♀ (skulls extracted), about 15.x.1980, Ujung Pandang market, leg. H. Moll; RMNH 33205-33206, imm. ♀, 5/6.xi.1981, Pulau Manterawu, leg. W. F. Rodenburg; ZMA 21.635- 21.636, ♂, ♀, 15.i.1982, Ujung Pandang (said to originate from Bulukumba), leg. W. Bergmans; RMNH 33207-33208, 33212, ♂, 2 imm. ♂, 18.i.1982, Imandi market, leg. W. F. Rodenburg & J. Wind; ZMA 22.769, imm. ♀ (skull extracted), 20.iv.1985, Imandi market, leg. R. Dekker; RMNH 35724-35725, ♂, ♀, 24.iv.1985, Imandi market, leg. F. G. Rozendaal.

Measurements and weights. — Five adult males have forearm lengths of 172.4, 172.2, 171.2, 165.7 and 162.6 (ZMA 21.435, 9193, 21.635, 9192 and RMNH 33212 respectively); three adult females have forearm lengths of 170.6, 169.7 and 168.0 (ZMA 9191, 21.636 and 21.436 respectively). An adult male weighed 700 g (ZMA 21.635), an adult female 725 g (including an embryo

of 90 g; ZMA 21.636) and a nearly adult female 495 g (ZMA 22.769).

Remarks. The whole series, including the immature specimens, is suggestive of a difference in body size between northern, typical specimens and south-western specimens, but the number of adult specimens is too small to be conclusive; the specimens from south-west Sulawesi would on the average be somewhat larger.

Other possible differences are to be found in the skull and teeth: south-western specimens appear to have an anteriorly slightly narrower mandible, with a longer symphysis, slightly more differentiated cheek teeth and slightly larger incisors, P_1 and M_2.

Fur colours are generally in accordance with the description by Andersen (1912: 367). Specimen ZMA 9191 has a reddish brown mantle and specimen RMNH 33205 has a golden brown nape and mantle with a darker reddish brown central patch.

Reproductive biology. — Males collected on 15 and 17/18 January had large testes, measuring 19 x 16 mm in specimen ZMA 21.635. The pregnant female ZMA 21.636 was collected on 15 January.

Ectoparasites. — The four ZMA specimens bought at Ujung Pandang were infested with the nycteribiid fly *Cyclopodia horsfieldi* De Meijere, 1899.

Acerodon celebensis (Peters)

Pteropus celebensis Peters, 1867: 333 – Celebes.

Pteropus hypomelanus (not of Temminck), Jentink (1887: 262; partim: specimens *m*, *n* and *o*); Jentink (1888: 149; partim: specimens *o-r*; Jentink (1890-91: 125; partim: 4 of the 5 specimens with field number 538, from Salayar).

Pteropus macklotii (not of Temminck), Jentink (1890-91: 126; partim: specimens 319, 320 from Maros, and 584b-c from island opposite Palopo; specimen 584a and another, not listed by Jentink, presumably in BMNH: see Andersen, 1912: 418).

Pteropus caniceps (not of Gray), Andersen (1912: 194; partim: in the synonymy under *Pteropus hypomelanus* specimens *m*, *n* and *o* quoted from Jentink, 1887 and specimens *o*, *p* and *r* quoted from Jentink, 1888).

Specimens examined. — RMNH, Jentink, 1887: 262, specimen *n* of '*Pteropus hypomelanus*' / Jentink, 1888: 149, specimen *p* of '*Pteropus hypomelanus*', ♂, mounted, skull extracted, 22.x.1865, Siao, leg. D. S. Hoedt; RMNH, Jentink, 1887: 262, specimens *m* and *o* of '*Pteropus hypomelanus*' / Jentink, 1888: 149, specimens *o* and *r* of '*Pteropus hypomelanus*', ♀, immature ♀, mounted specimens with extracted skulls, 10.xi.1865, Siao, leg. D. S. Hoedt; ZMA 3089-3091, 16.501, 2 ♀, 2 immature ♀ (2 made into skins), all skulls extracted, xi.1888, Salayar, leg. M. Weber; ZMA 16.357-16.358, immature ♂, ♂ (skins and skulls), 24.ix/6.x.1888, Maros, leg. M. Weber; ZMA 16.359, 16.361, ♀, immature ♀ (skins and skulls), ii(/iv?).1888, island opposite Palopo, leg. M. Weber; RMNH 35723, ♂, 24.iv.1985, Imandi market, leg. F. G. Rozendaal.

Measurements. — Specimen ZMA 16.358 has a forearm length of 140.8;

forearm lengths in three adult females (ZMA 3090, 16.501, and 16.359) are 133.4, 138.2 and c. 138 respectively. Andersen (1912: 424) gave as range for this measurement in three adults 130 – 140. Greatest skull lengths, ranging from 62.5 to 63 in five adults examined by Andersen (1912: 425), are 64.4 in male specimen ZMA 16.358 and 62.4, 63.0 and 63.4 in females ZMA 3090, 16.501 and 16.359 respectively. The immature male RMNH 35723 has a forearm length of 126.6, a greatest skull length of 63.1 and a condylobasal length of 61.4. From its skull base sutures – which are nearly fully fused – the specimen appears to be nearly adult.

Remarks. — The fur colours are as Andersen (1912: 418) described them; in some specimens these colours are somewhat faded. Of the mounted specimens from Siao – apparently the first to be recorded from that island (see Van Strien, 1986: 13) – the forearm lengths cannot be taken accurately and the skulls of the adult specimens are incomplete.

Andersen (1912: 417) observed that the dentition in *A. celebensis* is weaker than in any other species of the genus, while from his text it is also evident that the dental features which characterize the genus are relatively poorly pronounced in this species: consequently specimens of *A. celebensis* have frequently been misidentified as belonging to *Pteropus* (cf. Musser, Koopman & Califia, 1982). Among the specimens examined, the single northern specimen (RMNH 35723) differs from southern ones in having smaller upper and lower incisors, narrower and shorter upper canines with weaker secondary "cusps", and P_4 and M_1 with less distinct inner basal ledges, which do not extend as far forward as in most other specimens.

Reproductive biology. — The three adult females, collected in November and February (to April?) had large nipples; the latter specimen carried a large embryo with a forearm length of 20.2. The immatures taken in November have forearm lengths of 121.9 and 113.5 (females ZMA 3089 and 3091 respectively) and one obtained in February (ZMA 16.361) has a forearm length of 109.1.

Ectoparasites. — Specimens ZMA 3091 and ZMA 16.501 yielded one nycteribiid fly each, identified as *Cyclopodia horsfieldi* De Meijere, 1899; the latter specimen furthermore yielded one flea *Thaumapsylla breviceps* Rothschild, 1907.

	female BMNH 40.691.k holotype	female RMNH 34939	male RMNH 34940	male ZMA 22.770 imm.
forearm length	110	110.6	104.9	96.1
thumb length (with claw)		49.3	46.7	45.9
3rd metacarpal length	75	80.6	76.1	72.3
5th metacarpal length	82	85.9	78.0	74.8
ear length	20	18.6	19.4	17.8
hindfoot length (with claws)	33°	30.5	33.3	30.2
tibia length		45.0	41.7	39.7
greatest skull length	54	55.8	55.3	50.7
condylobasal length	53	54.8	53.7	47.3
rostrum length	19.5	21.5	21.1	19.4
palatal length		33.6	32.7	
cranium width	22	19.5	20.5	21.0
interorbital width	8	6.6	7.2	6.4
postorbital width	9	8.5	9.8	10.0
zygomatic width	28	27.8	27.6	26.4
mandible length	42	42.3	41.4	38.3
mandible height	19	20.0	18.8	15.8
C^1-C^1 (over crowns)		8.9	8.7*	8.6
C^1-M^2 (over crowns)	17	18.4	17.3*	16.4
M^2-M^2 (over crowns)		16.2	17.9*	15.3
C_1-M_3 (over crowns)	18.5	21.0	19.9*	18.8
weight		250+	190	164

° without claws; * strongly worn; + pregnant

Table 3. Measurements and weights of *Neopteryx frosti* Hayman, 1946. Those of the holotype are cited from the original description.

	female BMNH 40.691.k holotype	female RMNH 34939	male ZMA 22.770
length x width of C^1		2.2 x 1.7	2.5 x 2.0
P^3	2 x 2.5	1.8 x 2.2	1.75 x 2.1
P^4	2.5 x 3	2.3 x 2.3	2.4 x 2.5
M^1	2.5 x 2.8	2.35 x 2.2	2.6 x 2.6
M^2	2 x 2.2	1.7 x 1.95	2.0 x 2.1
C_1		1.7 x 1.65	1.8 x 1.75
P_1	1 x 1	0.85 x 0.75	0.9 x 0.9
P_3	2 x 2	1.6 x 1.5	1.8 x 1.6
P_4	2.8 x 2.8	2.6 x 2.1	2.6 x 2.1
M_1	2.8 x 2.5	2.45 x 2.2	2.5 x 2.2
M_2	2.2 x 2.2	2.0 x 2.0	1.95 x 1.9
M_3	2 x 2	1.5 x 1.6	1.6 x 1.6

Table 4. Teeth measurements of *Neopteryx frosti* Hayman, 1946.

Neopteryx frosti Hayman
(figs. 4-8)

Neopteryx frosti Hayman, 1946: 571 – Tamalanti, West Celebes, 3,300 ft.

Specimens examined. — ZMA 22.770, immature ♂ (skull extracted), 14.ix.1985, bought at Imandi market by R. Dekker; RMNH 34939-34940, ♀, ♂ (skulls extracted), 27/28.iii.1985, mistnetted high over Sungei Tumpah, near Toraut rentis area, Dumoga-Bone N. P., alt. 225 m, leg. F. G. Rozendaal.

Measurements and weights. — See tables 3 and 4.

Discussion. — The type and hitherto unique specimen of this species, an adult female, was collected in 1938 or 1939 at Tamalanti, western Central Sulawesi, at an altitude of about 1000 m (3300') (Hayman, 1946: 571).

The recently collected specimens represent the first records of the species since its description and extend the known distribution to include northern Sulawesi.

In addition to Hayman's detailed description, with which our specimens

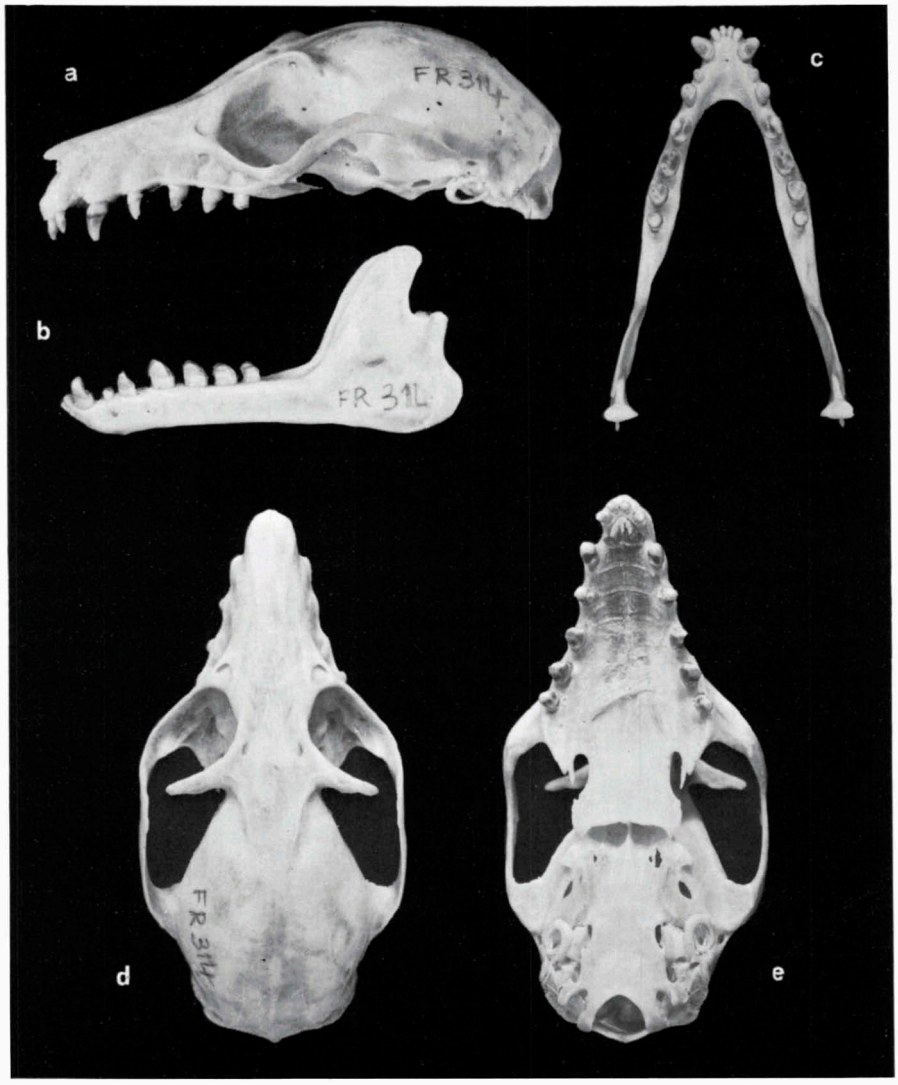

Fig. 4a-e. Skull of *Neopteryx frosti* Hayman, 1946, ♂ specimen RMNH 34940; a: lateral aspect of skull (left side); b: lateral aspect of mandible (left side); c: dorsal aspect of mandible; d: dorsal aspect of skull; e: ventral aspect of skull. Photoghraphs by E. L. M. van Esch (RMNH).

generally agree, the following complementary remarks can be made. It should be borne in mind that the type specimen consists of a dry skin – with folded wings – and a skull (see photographs in Walker et al., 1964: 202) whereas the present specimens are preserved in spirit, with extracted skulls. This will

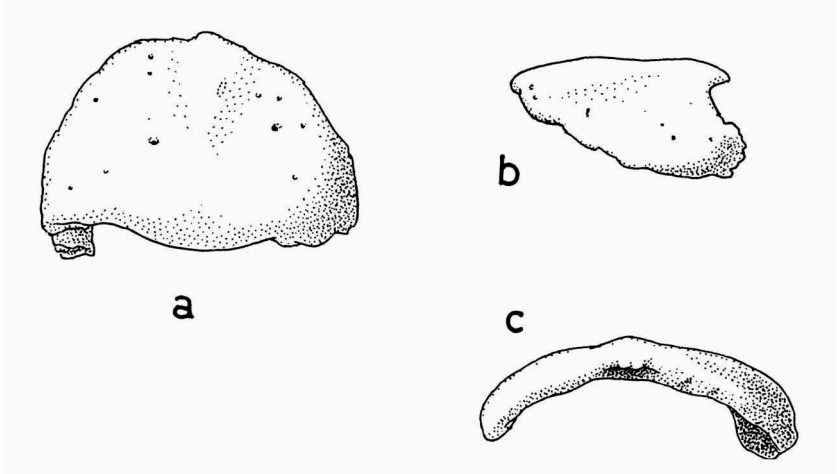

Fig. 5a-c. Baculum of *Neopteryx frosti* Hayman, 1946, specimen RMNH 34940; a: dorsal aspect (distal side above); b: lateral aspect (left side); c: distal view.

probably account for some of the observed differences.

Table 4 shows that the female RMNH 34939 is somewhat larger in most respects than the type specimen. The adult male has a shorter forearm, but larger skull dimensions. The immature male has the skull sutures all clearly visible, with those in the skull basis only recently fused and not yet ossified, but its dentition is complete, with interdental spaces almost as wide as in the others, except between P^3 and P^4 and between P_4 and M_1 (compare fig. 4 with the photograph in Walker et al., 1964: 202) rather than with Hayman's original drawings).

As in *Pteropus*, the males have an external penis of some length, about 12 mm in both specimens, thickest and dark brown (vs. medium brown) in the adult male.

The basal half of the ear is furred, contra Hayman (1946: 571). In the males, the wing membrane is inserted at about 3 mm from the median line of the back, leaving a 6 mm wide part of the back exposed; this, as well as a band of about 8-9 mm width of each adjoining wing membrane, is furred. In the female the wing membranes practically meet on the lower back, and the width of the dorsal median furred band is about 27 mm (30 mm in the type, according to Hayman, 1946: 571). The pelage on the forepart of the body, especially dorsally, is more woolly and less adpressed than the fur on the lower parts. Dorsally the mantle is distinctly paler than the fur on the lower part of the back; individual hairs of the mantle are brownish white with very short brown tips (longest in the adult male), whereas the hairs of the remainder of the back are uniformly brown, with at most a slightly paler base. When submerged, the

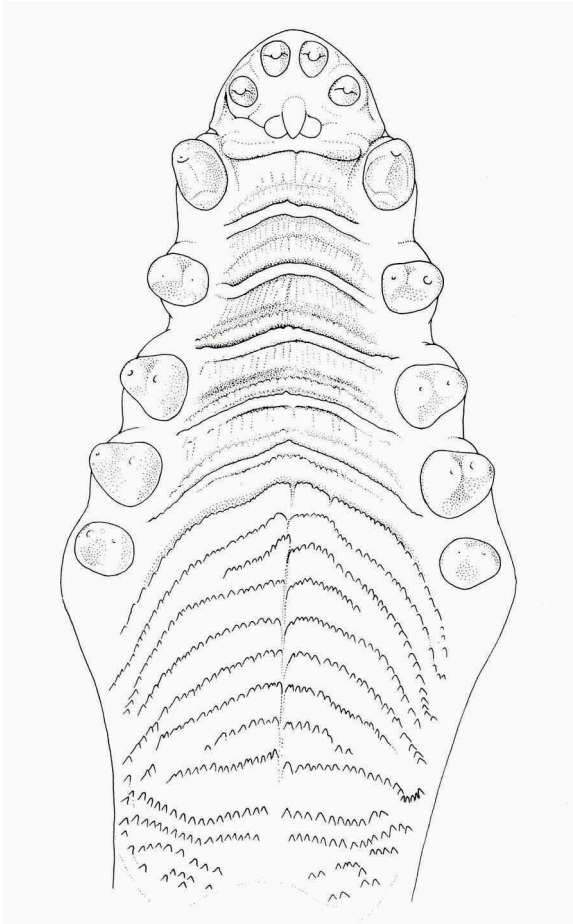

Fig. 6. Palatal ridge pattern of *Neopteryx frosti* Hayman, 1946, specimen ZMA 22.770.

woolly structure of the mantle becomes apparent, with all hairs standing out, while those on the rest of the back remain adpressed. Ventrally, this woolly collar is much less distinct, with uniformly light brown hairs. Hidden in the fur in the angle between neck and shoulder, the males have two or three small transverse skin ridges, strongest in the adult male. The stripe running from the muzzle to the forehead is less conspicuously white in front of the eyes than in the type specimen. The same holds for the 'stripes' along the upper and lower lips, which consist of a few lines of white hairs. The white is most distinct between the eyes and behind the mouth. The contrasting brown fur of the head is quite light, especially between the muzzle stripe and the upper lips; it is lightest in the female and darkest in the adult male (fig. 7). The wing membranes are medium to light brown, darkest in the immature male. The pattern

Fig. 7. Head of *Neopteryx frosti* Hayman, 1946, showing distinctive facial pattern (♂; RMNH 34940); Sungei Tumpah, Toraut, Dumoga-Bone National Park; reproduced from a colour transparency by F. G. Rozendaal, 28 March 1985.

of blackish brown – black according to Hayman (1946: 572) – lines (fig. 8) is of course more easily studied in spirit specimens than in dry skins. Apart from the fasciae described by Hayman, the dark colour is also found in numerous small, thickened spots along the dorsal side of the index and third finger and – mostly merged into narrow, interrupted lines – along the fourth and fifth fingers; furthermore, dark brown dots merged into longitudinal bands of variable extent are also found along the dorsal side of forearm, femur and tibia, especially in the immature male and least prominent in the female. Ventrally, some dark spots are scattered over the forearm (males only) and metacarpals (males and female). Dorsally, a dark brown band runs along the anterior side of the antebrachial membrane, at 1-2 mm from the margin; this band is very distinct in the immature male, weak in the adult male and hardly present in the female. Near its insertion on the back, the wing membrane is also dark brown, over the whole length, and connected with the bands on upper arm and leg in the immature male, only on the lower part of the back in the adult specimens. Caudally, dark brown stripes run along the margin of the wing membrane between the fourth and fifth finger (1-2 mm wide, least distinct in the female) and between the fifth finger and foot (up to 5 mm wide). All dark stripes and bands appear to consist of concentrations of spots and have irrigular margins.

The skull (fig. 4) is of a pteropine type but differs from each of the three types within *Pteropus* as distinguished by Andersen (1912: figs. 7, 8). The rostrum is elongate and strongly tapering. The alveolar line is concave: its projection backwards in order to assess the braincase deflection is not possible, but in adult specimens this deflection is still considerable. All three specimens lack the postorbital processes on the zygoma as figured by Hayman (1946: 573) for the type specimen. The zygoma is rather slender in the adult male and somewhat heavier in the other two specimens. The postdental palatal vacuities described and figured by Hayman are present in all three specimens, but differ from those in the type specimen: they interrupt the posterior lateral palate margins and are thus indentations rather than real foramina. The adult male differs from the adult female by its greater width over M^2-M^2; its width over the upper canines is slightly less than in the female and hence its toothrows converge more strongly. The rami of the mandible are narrow, quite unlike those in Andersen's pteropine skull types. In the female the posterior part of the mandible is similar to that of the type specimen, although the coronoid process is somewhat more slender and higher. In both males this process is distinctly more slender than in the female and – as in the adult male – lower.

The teeth of the adult specimens (fig. 4) are considerably worn. The following description applies to the dentition of the immature male. The first

Fig. 8. Dorsal aspect of *Neopteryx frosti* Hayman, 1946, showing distinctive wing pattern (♂; RMNH 34940); Sungei Tumpah, Toraut, Dumoga-Bone National Park; reproduced from a colour transparency by F. G. Rozendaal, 28 March 1985.

upper incisors are slightly larger than the second, and closer to each other than to the second. (This condition exists also in the adult male; in the female the first and second upper incisors stand less far apart). The upper canines have a narrow posterior basal shelf, with a weak but quite distinct inner margin and a small posterior cusp. There is no P^1 (following Hayman's denomination of the teeth). Even in this immature specimen the crowns of premolars and molars are smooth and rounded. P^3 is distinctly higher and shorter than P^4 and M^1 and M^2; its outer cusp is distinctly higher than its inner cusp, and although its posterior slope is less steep than its anterior slope, the posterior basal shelf is rudimentary. P^4 and M^1 are quite alike, with their outer cusps longer than the inner; in P^4 the cusps are slightly higher and shorter and the basal shelf is also shorter. M^1 is directed much more outward than P^4. In M^2 the outer and inner cusps are merged into a broad external-anterior ledge, from which the surface gradually slopes backwards, towards the posterior basal shelf. The first lower incisors (I_1) are not as small when compared to the second lower incisors (I_2) in our specimens. The distances between I_1 and I_1 and between I_1 and I_2 are about equal. P_3, P_4, M_1 and M_2 all have an inner and outer cusp and a vestige of a posterior basal shelf; the cusps are most distinct in P_4 and M_1 and situated

anteriorly in P_3, and just anterior to the middle in P_4, M_1 and M_2. The outer cusps are higher (hardly so in P_4) and shorter (except in P_3) than the inner: the lingual sides of these teeth are the longest. The rather flat M_3 shows weak traces of an inner and outer cusp.

The palatal ridge pattern of the immature male is depicted in fig. 6. There are six flat, undivided interdental ridges; nine denticulated and medially divided ridges, for the most part postdental; and a third group consisting of two rows of denticulations, also divided in the middle, and some irregular incomplete rows or groupings of denticulations on the left and right of the posterior soft palate. The soft palate of the adult female is also almost complete but dry: it is not much different from that of the immature male. The tongue – preserved only in the immature male – is covered with small papillae on the sides and large trident ones on the median part, backwards from about 2 mm behind the tip to circa 11 mm from the tip; at about 15 mm from the tip the median papillae are smaller and bear two teeth; the lateral papillae are also (bi-)toothed and approach the median ones in size.

Baculum. — The baculum of the adult male (figs. 5a-c) is a small concave bony structure, its greatest width 5.9 mm and its outline roughly a half circle, with a thickened outer margin (ending on one side in an irregular outgrowth) and some minute holes through the thinner median part.

Reproductive biology. — The adult male has testes with a length of about 16 mm, measured externally. The adult female carried an embryo with a total length of 45 mm.

Ecology. — Specimens RMNH 34939-34940 were caught simultaneously in three mistnets strung above each other (with the lowest shelf at c. 20 metres height) over Sungei Tumpah, which runs through lowland primary forest.

Styloctenium wallacei (Gray)
(fig. 9)

Pteropus wallacei Gray, 1866: 65, fig. 1 – Makassar.

Specimens examined. — All specimens enumerated below were purchased at the market of Imandi. RMNH 33214, ♂, imm. ♂, ♀, 24.iii.1982, leg. W. F. Rodenburg & J. Wind. ZMA 22.704-22.706, 2 ♂, ♀ (skulls extracted), 1.iv.1985; ZMA 22.710, ♂ (skull extracted), 20.iv.1985; ZMA 22.711, imm. ♀, 27.iv.1985; ZMA 22.707-22.709, 3 ♂ (skulls extracted), i.v.1985; ZMA 22.712, imm. ♂, 10.vi.1985; ZMA 23.084-23.085, ♀, imm. ♀, 9.ix.1985; ZMA 23.086-23.088, imm. ♀, imm. ♂, ♀, 14.ix.1985, all leg. R. Dekker.

Measurements and weights. — See tables 5 and 6.

Remarks. — Since Gray's description, based on an immature specimen from Ujung Pandang (formerly Makassar), new specimens have been reported from near Amurang (Jentink, 1883: 172); Masarang, Tomohon (Meyer, 1899: 5; Andersen, 1912: 446); Malenge (Tate, 1942: 338); River Ranu, Tambusisi Damar on Mount Tambusisi, and Titaeli (Hill, 1983: 109).

At least 35 specimens have been reported so far, but the species' dimensional variation is poorly known. Published forearm lengths in males are 95.5 and 96.6 (Andersen, 1912: 446; Hill, 1983: 110) and in females 90 and 95.5 (Jentink, 1883: 173; Hill, 1983: 110); known greatest skull lengths are 49 for a male (Andersen, 1912: 447) and 51.8 for a female (Hill, 1983: 110). Our seven

	males			females		
	n	mean	min - max	n	mean	min - max
forearm length	8	98.8	96.3 - 103.2	4	99.0	97.3 - 101.3
ear length	7	22.7	21.0 - 24.8	4	21.7	19.8 - 24.1
greatest skull length	6	51.1	50.0 - 52.1	2		52.0 - ±54.3
condylobasal length	6	48.7	47.7 - 50.4	2		50.3 - ±51.6
rostrum length	6	19.1	18.4 - 20.0	2		19.6 - 20.5
palatal length	6	27.6	27.1 - 28.0	1		27.8
cranium width	6	18.8	18.1 - 19.8	2		18.6 - 19.5
interorbital width	6	6.6	5.6 - 7.2	2		6.4 - 7.4
postorbital width	6	6.4	5.5 - 7.2	1		5.4
zygomatic width	6	27.4	26.0 - 28.8	1		27.0
mandible length	6	38.5	38.0 - 40.0	1		40.2
mandible height	6	19.4	17.9 - 20.8	1		21.8
C^1-C^1 (over crowns)	6	9.8	9.3 - 10.1	2		9.8 - 10.2
C^1-M^2 (over crowns)	6	19.6	19.0 - 20.1	2		19.7 - 20.2
M^2-M^2 (over crowns)	6	13.3	12.4 - 14.0	2		13.5 - 13.9
C_1-M_3 (over crowns)	6	20.1	19.9 - 20.5	2		20.3 - 20.6
weight	6	191	174 - 202	1		218

Table 5. Body and skull measurements and weights of adult specimens of *Stylocteníum wallacei* (Gray, 1866), purchased at Imandi market.

	males			females		
	n	mean	min - max	n	min	- max
C^1 length	5	3.05	2.9 - 3.25	2	2.8	- 2.9
width	5	2.4	2.3 - 2.5	2	2.3	- 2.5
P^1 length	4	0.85	0.8 - 0.9	2	0.7	- 1.0
width	4	0.75	0.7 - 0.9	2	0.9	- 1.1
P^3 length	5	2.8	2.6 - 3.1	2	2.9	- 3.2
width	5	2.5	2.4 - 2.6	2	2.3	- 2.5
P^4 length	5	3.4	3.3 - 3.75	2	3.3	- 3.4
width	5	3.3	3.2 - 3.4	2	3.2	- 3.2
M^1 length	5	3.6	3.4 - 3.7	2	3.3	- 3.4
width	5	3.2	3.0 - 3.3	2	3.0	- 3.0
M^2 length	5	2.3	2.0 - 2.4	2	2.4	- 2.5
width	5	2.3	2.0 - 2.5	2	2.2	- 2.2
C_1 length	5	2.3	2.15 - 2.5	2	2.0	- 2.4
width	5	2.2	2.0 - 2.3	2	2.0	- 2.2
P_1 length	5	1.3	1.0 - 1.5	2	1.3	- 1.5
width	5	1.4	1.2 - 1.5	2	1.2	- 1.5
P_3 length	5	2.8	2.7 - 2.9	2	2.5	- 3.0
width	5	2.05	2.0 - 2.1	2	1.9	- 2.2
P_4 length	5	3.2	3.0 - 3.4	2	3.1	- 3.3
width	5	2.8	2.7 - 2.9	2	2.6	- 2.9
M_1 length	5	3.6	3.5 - 3.7	2	3.5	- 3.6
width	5	3.3	3.2 - 3.3	2	3.3	- 3.3
M_2 length	5	3.2	3.0 - 3.3	2	3.1	- 3.1
width	5	2.9	2.7 - 3.0	2	2.9	- 3.0

Table 6. Teeth measurements of adult specimens of *Styloctenium wallacei* (Gray, 1866), purchased at Imandi market.

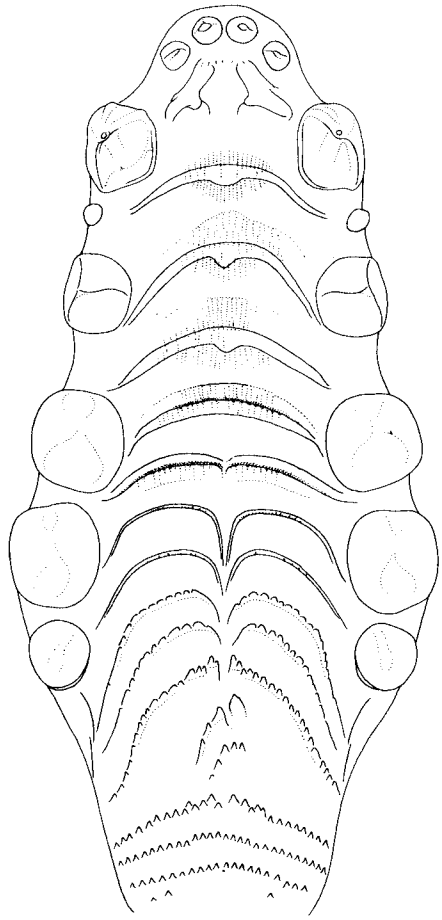

Fig. 9. Palatal ridge pattern of *Styloctenium wallacei* (Gray, 1866), specimen ZMA 22.709.

adult males have forearm lengths of 96.3 – 103.2 (mean 98.6) and six of them have greatest skull lengths of 50.0 – 52.1 (mean 51.1); four adult females have forearm lengths of 97.3 – 101.3 (mean 99.0) and two have greatest skull lengths of 52.0 and c. 54.3. The latter measurements suggest that females attain larger average skull dimensions than males, which would be quite unusual within the Pteropodidae.

Andersen (1912: 442-447, fig. 23) published an excellent description and skull figures for the species, to which a few notes are added here. The upper canines in the specimen figured by Andersen (1912: 443) have distinct postero-internal basal ledges. In specimen ZMA 23.087 this ledge forms a small but distinct cusp, in some others it is only slightly raised. In specimens with worn

teeth incisors, canines and third premolars may be distinctly worn, whereas fourth premolars and molars show hardly any wear; the latter have light or dark reddish brown crowns, while the other teeth are coloured normally or are only partly brownish. One specimen (ZMA 22.704) lacks P^1 on both sides.

The palatum bears – from front to back – four interdental ridges, six centrally divided ridges (still largely interdental – the first sometimes not or only weakly divided – and the last three of four with denticulations), two postdental denticulated ridge fragments in the middle and three or four postdental, whole or slightly divided denticulated ridges (fig. 9).

Dobsonia crenulata Andersen

Dobsonia crenulata Andersen, 1909: 532 – Ternate.

Specimens examined. — RMNH 33203-33204, 2 ♂ (skull of RMNH 33203 extracted), 8/9 and 8.xi.1981, desa Luksagu, Pulau Peleng, Banggai Is., leg. W. F. Rodenburg & K. D. Bishop.

Measurements. — Forearm length 116.7 in RMNH 33203 and 117.6 in RMNH 33204; the following measurements were taken from RMNH 33203: greatest skull length 50.8; condylobasal length 48.1; rostrum length 15.9; palatal length 26.6; cranium width 18.9; interorbital width 8.5; postorbital width 7.2; zygomatic width 30.7; mandible length 39.2; mandible height 20.7; $C^1 - C^1$ (over crowns) 10.2; $C^1 - M^2$ (over crowns) 20.5; $M^1 - M^1$ (over crowns) 15.5; $M^2 - M^2$ (over crowns) 13.5; $C_1 - M_3$ (over crowns) 21.5; length x width of: C^1 4.6 x 3.0; P^3 4.1 x 3.2; P^4 4.3 x 3.1; M^1 5.4 x 2.9; M^2 2.5 x 1.8; C_1 3.3 x 2.7; P_1 1.7 x 1.6; P_3 4.0 x 2.7; P_4 4.3 x 2.7; M_1 4.4 x 2.4; M_2 3.6 x 2.3; M_3 2.0 x 1.6.

Discussion. — The genus *Dobsonia* was long thought to be represented in Sulawesi by a single species, *D. exoleta* Andersen, 1909. De Jong & Bergmans (1981: 217) recorded *D. crenulata* – previously known from the North Moluccas only – from the Sangihe and Togian Islands. The Sangihe specimens examined were all too damaged to be measured reliably, but appeared to be rather small. The specimens from the Togian Is. extended the known measurement ranges of *crenulata*, to overlap with that of the smaller *D. viridis* (Heude, 1896) from the southern Moluccas, especially in the females. But, as De Jong & Bergmans (1981: 222) stated: " Of *viridis*, hardly ever more than two or three of one sex per population are known: uniting *crenulata* with it seems premature".

D. viridis averages smaller in body, skull and teeth dimensions. Hill (1983: 110) assigned two specimens from Central Sulawesi (River Ranu) to *viridis* mainly because of their "on the whole (.....) slightly narrower cheek teeth

similar in width to those of *viridis*. They have smaller canines than the subadult holotype of *crenulata*, corresponding closely to those of *viridis*". On this basis Hill (1983: 111) provisionally synonymized *crenulata* with *viridis*. The forearm lengths of his specimens are given as 113.5 (female) and 125.4 (male), $C^1 - M^2$ lengths as 18.8 (female) and 19.8 (male), and greatest skull lengths as 48.2 (female) and 50.1 (male). The present specimens have forearm lengths of 116.7 and 117.6 respectively; the greatest skull length of RMNH 33203 is 50.8 and its $C^1 - M^2$ length is 20.5. From these and the teeth measurements it appears that the Peleng males are not very different from the six males from the Togian Is. assigned to *crenulata* by De Jong & Bergmans (1981: 217); their forearm lengths are below the minimum value in that small sample as are, in RMNH 33203, zygomatic width, width over upper canine crowns, and widths of P^3, P^4 and M^1; the latter approach those of Hill's male specimen. The forearm lengths of the Peleng males fall within the range of typical *viridis* (Kei Is.: 114.5 – 118.5 in four specimens; SMF 5604; ZMB 4702; BMNH 10.3.1.57 and BMNH 10.3.1.90/92); the skull of RMNH 33203 is larger and agrees with typical (North Moluccan) *crenulata* skulls, and the teeth – in particular M^1, M_1 and M_2 – are all larger than those in four typical males of *viridis* from the Kei Is. and within the range of four *crenulata* males from Halmahera (MZB 2979-2980), Ngele Ngele Besar (an islet west of Morotai; ZMA 21.432) and Bacan (ZMA 22.129).

These data may be interpreted as a further indication that *crenulata* is conspecific with *viridis*, as Hill assumes, but in our opinion synonymization should be based on a revision of as many specimens as possible and not from the necessity to allocate a few odd ones. If *crenulata* is to be considered a subspecies of *viridis*, new diagnoses of the subspecies to be recognized are needed. Within populations of *Dobsonia*, the variation in teeth dimensions may be considerable; to start with, the sexes should be treated separately. Between populations there may be variation in teeth morphology which should also be taken into account: for instance, in the species under consideration the notches in the longitudinal ridges of some premolars and molars may vary from very distinct to very weak.

Reproductive biology. — Specimen RMNH 33203 had very large testes at the time of capture.

Ecology. — Both specimens were mistnetted over brackish water in partially disturbed, tall mangrove forest, within 100 m from the sea.

Ectoparasites. — Specimen RMNH 33203 is heavily infested with an unidentified species of mite (Acari), hundreds of which are attached to its flight membranes where these cover the lower back.

Dobsonia exoleta Andersen

Dobsonia exoleta Andersen, 1909: 531, 533 – Tomohon, Minahassa

Specimens examined. — RMNH 33211, ♀, imm. ♀, 18.i.1982, Imandi market, leg. W. F. Rodenburg & J. Wind; RMNH 33209-33210, imm. ♀, ♀, 24.iii.1982, Imandi market, leg. W. F. Rodenburg & J. Wind; ZMA 22.126, imm. ♀ (skull extracted), 24.i.1983, Imandi market, leg. F. G. Rozendaal; ZMA 22.127, imm. ♀ (skull extracted), 25/26.i.1983, Sungei Moinakom, Dumoga-Bone N. P., alt. 625 m; RMNH 35693, imm. ♀, 28/29.iii.1985, Sungei Tumpah, Toraut rentis area, Dumoga-Bone N. P., alt. 225 m, leg. F. G. Rozendaal.

Measurements. — The adult females have forearm lengths of 114.0 and 120.3 respectively, falling within the range given by De Jong & Bergmans (1981: 215).

Remarks. — The specimens from Dumoga-Bone are the first to be recorded from the National Park.

Dobsonia minor (Dobson)

Cephalotes minor Dobson, 1879: 875 – Amberbaki, north-west New Guinea.

Remarks. — Boeadi & Bergmans (1987) recorded the first specimen of *Dobsonia minor* from Sulawesi; previously the species was known from New Guinea and the geologically related islands of Yapen and Bagabag only. The Sulawesian specimen, from Londa Cave near Rantepao (2° 59′ S, 119° 54′ E) differs from specimens from the New Guinean region in its relatively short ears, longer lower tooth rows, and generally larger teeth – except M^2 which is smaller. The aforementioned authors emphasize the rather exceptional distribution pattern as it is known at present and suggest that the species should be looked for on the islands between Sulawesi and New Guinea.

Cynopterus brachyotis (S. Müller)

Pachysoma brachyotis S. Müller, 1838: 146 – Dewei River, Borneo.
Cynopterus minor Revilliod, 1911: 517 – Lambuja, Southeast Sulawesi. New synonymy.
Cynopterus brachyotis brachyotis, Andersen, 1912: 614; Hill, 1983: 116.

Specimens examined. — NMB 1734, immature ♂ (skull in situ, 2.iii.1903, Lambuja, donated by P. Sarasin (the holotype of *Cynopterus minor* Revilliod, 1911); RMNH 33195, imm. ♂, 8/9.xi.1981, desa Luksagu, Pulau Peleng, leg. W. F. Rodenburg & K. D. Bishop; RMNH 33193-33194, ♂, imm. ♀, 18.xi.1981, desa Lipulalongo, Pulau Labobo, leg. W. F. Rodenburg & K. D. Bishop; ZMA 21.528-21.529, 2 ♂ (skull of ZMA 21.528 extracted), 28.x.1981, Sungei Moinakom, Dumoga-Bone N. P., alt. 625 m, leg. K. D. Bishop, F. G. Rozendaal & W. F. Rodenburg; ZMA

21.791-21.792, ♀, ♂, 14.i.1982, Malino, alt. c. 1100 m, leg. W. Bergmans; RMNH 33170, 33183, 33185, 2 ♀, imm. ♀, 18.i.1982, Imandi market, leg. W. F. Rodenburg & J. Wind; ZMA 21.793-21.812, 9 ♂, 4 imm. ♂, 8 ♀, 1 imm. ♀, 18 and 18/19.i.1982, Bantimurong, leg. W. Bergmans; RMNH 33171, 33182, imm. ♂, ♂, 13/14 and 13.iii.1982, Sungei Moinakom, Dumoga-Bone N. P., alt. 530 m, leg. W. F. Rodenburg & J. Wind; RMNH 33424, 33422, ♀, imm. ♂, 26/27 and 27/28.i.1983, Sungei Moinakom, Dumoga-Bone N. P., alt. 625 m, leg. F. G. Rozendaal; ZMA 22.145-22.149, 3 ♂, 1 ♀, 1 imm. ♀, 10/11.ii.1983, Tangkoko-Batuangus, leg. F. G. Rozendaal; ZMA 22.215-22.218, 2 ♂, 1 ♀, 27.iii.1983, Ujung Pandang, leg. R. Mayai; RMNH 35686-35691, 3 ♂, 3 ♀, 21/22.iii.1985, rentis area, Toraut, Dumoga-Bone N. P., alt. 225 m, leg. F. G. Rozendaal; RMNH 35692, ♂, 27/28.iii.1985, Sungei Tumpah, Toraut, Dumoga-Bone N. P., alt. 225 m, leg. F. G. Rozendaal; RMNH 35680-35681, 2 ♂, 13/14 and 14/15.v.1985, NW slope of Gunung Sahendaruman, Sangihe I., alt. c. 600 m, leg. F. G. Rozendaal.

Measurements and weights. — See table 7.

Remarks. — Revilliod (1911: 517) described a new species *Cynopterus minor*, based on a single small male specimen from Lambuja, Southeast Sulawesi. His description of its colours is suggestive of an immature specimen. Apparently, no throat collar is present, the brown of the head and back is mixed with pale grey (individual hairs have mouse grey, nearly white bases and light brown tips) and the underside is grey, even whitish on the throat. No other specimens have been assigned to this species since its description. Andersen (1912: 617), unaware of Revilliod's description, found two immature females from northern Sulawesi "in every respect typical *C. b. brachyotis*". Hill (1983: 116-117), who had many more Sulawesian specimens before him, confirmed this.

The senior author had the opportunity to study the holotype of *Cynopterus minor* and to compare it with a number of other *Cynopterus* specimens, including the Sulawesian specimens discussed here. The specimen has a greatest skull length of about 26 and a forearm length of 53.9. Judging from its virtually unworn teeth, rather narrow interdental spaces, developmental stage of the finger joints and greyish brown fur, the specimen is immature. Andersen (1912: 612) gave as greatest skull length range in *C. b. brachyotis* 27 – 30.7, and as forearm length range 57 – 66. In size and morpholopgy of the cheek teeth, the specimen agrees completely with what Andersen (1912: 597) described for typical *brachyotis*: relatively narrow, oval in outline and with surface cusps in P_4 and M_1 small or entirely absent (lacking in P_4 in this particular specimen). Surprisingly, one of the labels with the specimens revealed that Andersen studied the specimen himself in April 1913, after his revision of the genus had been published (Andersen, 1912). Apparently Andersen also failed to find any character which would justify separation from *brachyotis*, since he had identified the specimen as nominate *brachyotis*. We cannot but agree with Andersen and consequently relegate *Cynopterus minor* Revilliod to the synonymy of *C. b. brachyotis* S. Müller.

		males			females		
		n	mean	min - max	n	mean	min - max
Southwest Sulawesi	forearm length	10	64.7	62.5 - 67.6	10	66.2	63.4 - 68.8
(Bantimurong, Malino,	ear length	10	15.8	14.8 - 16.7	10	15.6	14.1 - 16.6
Ujung Pandang)	weight	9	34	31 - 39	5	36	31 - 39
	weight*				3	44	38.5 - 48
North Sulawesi	forearm length	7	61.5	60.0 - 64.0	5	61.7	60.5 - 63.5
	ear length	3	16.5	15.5 - 17.0	2		14.5 - 16
	weight	7	27	24 - 30	4	27	23.5 - 34
	weight*				1		39
Sangihe Islands	forearm length	2		68.5 - 72.0			
	weight	2		36 - 41			
Banggai Islands	forearm length	1		61.3			
(Labobo Island)	ear length	1		15.5			

* pregnant females

Table 7. Selected measurements and weights of adult *Cynopterus b. brachyotis* (Müller, 1838) from Sulawesi and off-lying islands (collectors' measurements).

Table 7 shows that the present specimens, with a combined forearm length range of 59.5 – 68.8, average rather large. They obviously represent more than one population, with larger specimens in the south-west and on the Sangihe Islands, and smaller representatives in the north (and possibly on the Banggai Is.). Sexual dimorphism in forearm length (longest in females) is evident from the largest – south-western – sample.

Reproductive biology. — Five females, collected on 14 and 18 January and 21/22 March carried one embryo each. Four males collected on 18 and 10/11 January had fairly large testes; one taken on 27 March had very large testes. Immature but rather large specimens, with forearm lengths of 57.6 and more, and weights of 23.5 and over, have been collected in January, February and March, and in October and November. One smaller specimen, a male with a forearm length of 53.7 and a weight of 16.7, was taken on 1 April.

Ecology. — *Cynopterus brachyotis* is probably originally a species of the lowland rainforest, but very well able to adapt to other environments and can in fact be found in almost any type of habitat. The series reported upon here has been collected in: primary forest; disturbed primary forest; partly disturbed mangrove forest, over brackish water less than 100 m from the sea; coastal alang-alang/secondary forest mosaic; plantations/secondary forest mosaic; a solitary fig tree (*Ficus* sp.) in a deforested village area; grass plain with scattered trees in a limestone area; and among fruit trees in a garden in

Ujung Pandang. Collecting heights vary from sea level to about 1100 m.

Ectoparasites. — A nycteribiid fly *Eucampsipoda* spec. nov. was collected from specimen RMNH 33422. Two as yet unidentified Streblidae were collected from specimen ZMA 21.529, and one specimen of the nycteribiid fly *Leptocyclopodia (Leptocyclopodia) ferrisiana* Maa, 1966, was taken from specimen ZMA 22.147, but as the latter three flies were discovered only during our later examinations they may have been stragglers.

Thoopterus nigrescens (Gray)
(fig. 10)

Cynopterus marginatus var. *nigrescens* Gray, 1870: 123 – Morty.

Specimens examined. — ZMA 21.608-21.610, ♂, 2 ♀ (2 skulls extracted), 21/22.x.1981, Sungei Moinakom, Dumoga-Bone N. P., alt. 725 m, leg. K. D. Bishop, F. G. Rozendaal & W. F. Rodenburg; ZMA 21.611-21.612, 2 ♀ (one skull extracted), 22.x.1981, upper tributary of Sungei Mauk, Dumoga-Bone N. P., alt. 960 m, leg. K. D. Bishop, F. G. Rozendaal & W. F. Rodenburg; ZMA 21.614-21.615, 2 ♀ (one skull extracted), 25.x.1981, ridge leading to Gunung Kabila, Dumoga-Bone N. P., alt. 1350 m, leg. K. D. Bishop, F. G. Rozendaal & W. F. Rodenburg; RMNH 33218, ♂, 11/12.xii.1981, south slopes of Gunung Ali, Dumoga-Bone N. P., alt. 500 m, leg. W. F. Rodenburg & J. Wind; RMNH 33215, 3 ♂, 10 ♀ (three skulls extracted), 18.i.1982, Imandi market, leg. W. F. Rodenburg & J. Wind; ZMA 21.616-21.617, ♂, ♀ (skull of 21.616 extracted), 14.i.1982, Malino, alt. c. 1100 m, leg. W. Bergmans; ZMA 21.618-21.620, 2 ♂, 1 ♀ (two skulls extracted), 18.i and 19.i.1982, along Bantimurong river, leg. W. Bergmans; RMNH 33216, 2 ♀, 13 and 13/14.iii.1982, Sungei Moinakom, alt. 530 m, leg. W. F. Rodenburg & J. Wind; RMNH 33216, 33229, ♂, ♀, 14 and 14/15.iii.1982, upper tributary of Sungei Mauk, alt. 960 m, leg. W. F. Rodenburg & J. Wind; RMNH 33217, ♀, 24.iii.1982, Imandi market, leg. W. F. Rodenburg & J. Wind; ZMA 22.105, ♀ (skull extracted), 24.i.1983, Imandi market, leg. F. G. Rozendaal; RMNH 35694, ♀, 27/28.iii.1985, Sungei Tumpah, Toraut, Dumoga-Bone N.P., alt. 225 m, leg. F. G. Rozendaal; RMNH 35695, imm. ♀, 8/9.iv.1985, Clark's camp, Dumoga-Bone N. P., alt. 1180 m, leg. F. G. Rozendaal; RMNH 35696, ♀, 17.iv.1985, summit of Gunung Muajat, Dumoga-Bone N. P., alt. 1780 m, leg. F. G. Rozendaal; RMNH 35697, ♂, 19/20.iv.1985, Danau Mooat, alt. 1080 m, leg. F. G. Rozendaal; RMNH 35661-35664, 4 ♀, 13/14 and 14/15.v.1985, NW slope of Gunung Sahendaruman, Sangihe I., alt. c. 600 m, leg. F. G. Rozendaal; RMNH 35665, ♀, 31.v/1.vi.1985, NE slope of Gunung Sahendaruman, Sangihe I., alt. c. 750 m, leg. F. G. Rozendaal.

Measurements and weights. – See table 8.

Discussion. — *Thoopterus nigrescens* is a relatively little – known species which has previously been recorded from Morotai (North Moluccas), the vicinity of Amurang (Jentink, 1888: 155 as from Menado, s. n. *Cynopterus latidens* Dobson, but see Jentink, 1883: 170 and Meyer, 1899: 7 about the Von Faber collection), the provinces of Laguna and Batangas, Luzon (Elera, 1895: 7; doubted by Taylor, 1934: 189-190), Tomohon and "Minahassa" (Meyer, 1899: 7), Manado (Matschie, 1899: 77; as this locality is based on a specimen collected by Von Faber, the specimen could possibly also originate from 'near

	North Sulawesi						Southwest Sulawesi				all combined	
	males			females			males		female		males	females
	n	mean	min - max	n	mean	min - max	n	min - max	n		mean	mean
forearm length	4	73.9	72.6 - 75.3	13	74.2	71.5 - 78.3	2	76.7 - 81.6	1	81.0	75.65	74.3
greatest skull length	3	36.4	34.9 - 37.3	7	35.5	33.7 - 37.1	2	37.8 - 39.7	1	36.9	37.3	35.3
condylobasal length	3	35.1	34.1 - 35.8	6	34.2	32.8 - 35.7	2	36.9 - 38.2	1	34.9	36.0	33.9
rostrum length	3	11.6	11.5 - 12.0	7	11.4	10.8 - 12.0	2	12.5 - 12.6	1	12.0	12.0	11.3
palatal length	3	19.1	18.3 - 19.6	7	18.6	17.5 - 19.4	2	20.1 - 20.6	1	19.2	19.6	18.4
mandible length	3	27.9	27.3 - 28.4	7	26.8	25.5 - 27.7	2	28.9 - 30.2	1	28.0	28.5	26.6
mandible height	3	14.3	13.7 - 15.1	7	14.0	12.8 - 14.6	2	14.6 - 16.6	1	14.8	14.8	13.8
cranium width	3	14.3	13.8 - 14.7	7	14.1	13.1 - 14.7	2	14.6 - 15.1	1	13.6	14.5	14.1
interorbital width	3	8.3	7.7 - 8.9	7	7.9	6.7 - 8.4	2	8.7 - 8.9	1	8.0	8.5	7.8
postorbital width	3	7.2	6.9 - 7.3	7	7.0	6.5 - 7.5	2	7.0 - 7.4	1	7.4	7.2	7.1
zygomatic width	3	23.8	22.0 - 25.8	7	23.0	20.8 - 24.2	2	24.5 - 26.4	1	23.8	24.4	22.8
width over crowns of:												
$C^1 - C^1$	3	7.6	7.2 - 7.9	7	7.1	6.6 - 7.6	2	7.9*- 8.0	1	7.35	7.7	7.0
$C^1 - M^1$	3	12.7	12.1 - 13.0	7	12.0	11.3 - 12.7	2	13.7*- 13.7	1	12.7	13.1	12.0
$M^1 - M^1$	3	12.4	11.1 - 13.2	7	11.8	10.7 - 12.6	2	12.7 - 12.9*	1	12.0	12.5	11.6
$C_1 - M_2$	3	14.0	13.1 - 14.6	7	13.1	12.2 - 14.0	2	15.0*- 15.0	1	14.0	14.4	13.1
weight							2	67 - 99	1	86		

* teeth strongly worn

Table 8. Measurements and weights of adult *Thoopterus nigrescens* (Gray, 1870) from Sulawesi.

Amurang') and River Ranu and Tambusisi Damar (Hill, 1983: 126).

The specimens recorded by Hill (1983: 126) were the first to be reported from Central Sulawesi; those collected by Bergmans and reported here represent the first record from Southwest Sulawesi. Specimens RMNH 35661-35665 represent the first record of the species from the Sangihe Islands.

Gray (1870: 123), who described the species as a variety of *Cynopterus marginatus* Lesson, 1827 – a junior synonym of *C. sphinx* (Vahl, 1797) – published no measurements. Meyer (1899: 7) recorded forearm lengths of 70, 71, 72 and 76 in four females. Matschie (1899: 77) studied one specimen with a forearm length of over 65. Andersen (1912: 665) studied the adult female type specimen (with incomplete skull) in the BMNH collection, an adult female with broken skull and a juvenile male, both from near Amurang (RMNH; reported by Andersen as from Manado, but both collected by F. von Faber); only measurements of the type specimen were given: its forearm length was 73.5. Hill (1983: 126) studied an additional 17 specimens: the forearm length range in four specimens (sex not stated) was 76.5 – 78.9.

The present series of 41 specimens, including at least 21 adults (a number of specimens listed above, including those from Sangihe I., were not available in time for inclusion in our analysis of sexual, taxonomic and geographical variation) , extends the known size variation, shows sexual dimorphism in skull and body size and strongly suggests body and skull size differences within Sulawesi, with northeastern specimens averaging smaller and southwestern larger. The forearm lengths in six adult males range from 72.6 to 81.6 and in 15 females from 69.2 to 81.0; the greatest skull lengths in five adult males varies from 34.9 to 39.65 and in eight females from 33.7 to 36.9. Canines in males are stronger and higher than in females. The palatal ridges of ♀ specimen ZMA 22.105 are shown in fig. 10. A comparison of northern and southern specimens shows that within populations females tend to have – on average – longer forearms and smaller skulls than males and that southwestern specimens average larger than northern ones (table 8).

Apart from body and skull size, some other arguments tend to support a possible distinctness of southwestern specimens. Firstly, their teeth are morphologically slightly different: upper canines are longer at their bases, PM^2 is slightly larger, PM^4 is relatively longer, both M_1 and M_2 are slightly larger. The lower incisors are generally smaller, PM_2 is larger, the anterior slope of PM_3 is less steep; PM_4 is wider at its posterior side and both lower molars are slightly larger. Secondly, *Thoopterus nigrescens* apparently is a lowland forest species and the forests of SW Sulawesi have been isolated from those in other parts of the island during the Pleistocene inundation of the Tempe Depression, which has probably also been responsible for (sub)speciation in Sulawesian monkeys

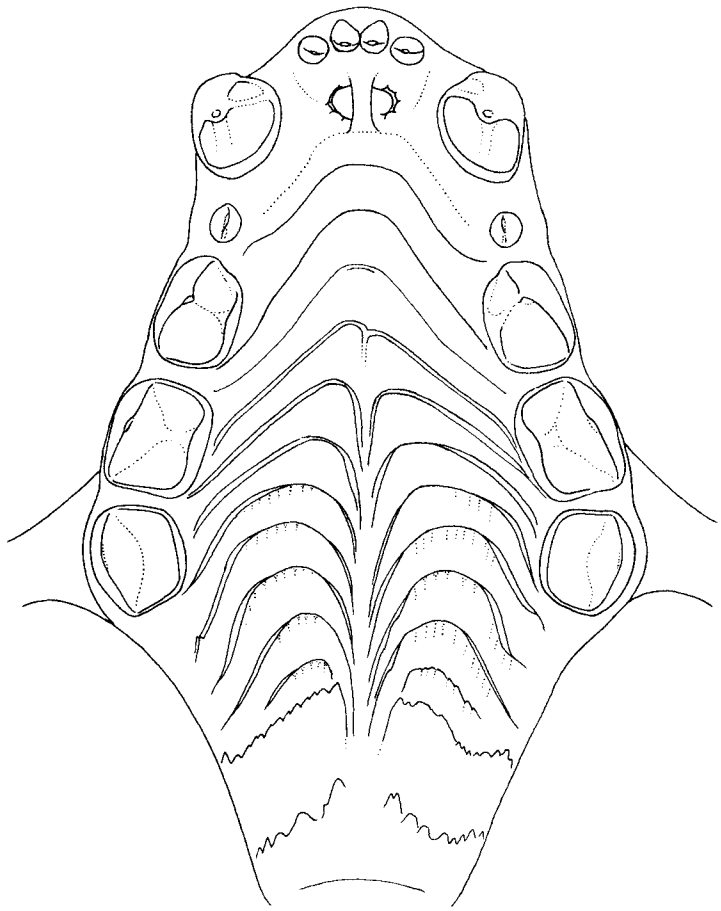

Fig. 10. Palatal ridge pattern of *Thoopterus nigrescens* (Gray, 1870), specimen ZMA 22.105.

(Fooden, 1969). At present the forest remnants in SW Sulawesi are isolated from the remaining forests in Central Sulawesi by agricultural fields covering nearly all of the southwestern peninsula, but this is probably of a relatively recent date. As more information on specimens from Central Sulawesi and larger samples from SW Sulawesi may show that size and other variation is clinal it seems best, for the present, not to distinguish the southwestern specimens taxonomically.

Ecology. — The species has been collected in forest between altitudes of c. 50 m (Bantimurong) and 1780 m (summit of Gunung Muajat). At Malino, specimens ZMA 21.616 and 26.617 were collected while feeding in an isolated fig tree (*Ficus* sp.) in the village area, together with *Cynopterus b. brachyotis*.

At Bantimurong specimens were collected in a small patch of woodland on a narrow river plain wedged between limestone hills. Nearly all specimens examined were infested with bat flies (Nycteribiidae; see below), with up to three different species per specimen (ZMA 21.617). This suggests communal roosting and possibly the use of the same roosts over long periods of time.

Reproductive biology. — Subadult specimens were collected in January, March, October and December. Adult males with small to rather small testes were taken on 18 January (exterior length 14 mm) and 14 March (11 mm). Females with small nipples were caught in January and October, with fairly large nipples in January and March; pregnant females on 19 January (total length of single embryo c. 36 mm) and 24 January (forearm length of single embryo c. 22.5 mm). The fur in immature specimens is darker and greyer than in adults.

Ectoparasites. — The following Nycteribiidae were collected: *Leptocyclopodia (Leptocyclopodia) analis* Maa, 1968, from specimens ZMA 21.608-21.610, 21.611-21.612, 21.615, 21.616-21.617 and 21.618. Specimens ZMA 21.617 and 21.620 yielded specimens of *Leptocyclopodia (L.) ferrisiana* Maa, 1966. *Leptocyclopodia (Oncoposthia) laminata* Maa, 1968, was collected from ZMA 21.616- 21.617.

Chironax Andersen, 1912

This genus is based on four specimens of *Pteropus melanocephalus* Temminck, 1825, obtained by J. C. van Hasselt in the mountainous regions of Bantam, West Java, between his arrival on Java in 1820 and his death on 8 September 1823. Andersen examined the syntypes and at that time only known specimens for his Catalogue (Andersen, 1912), in which he gave a detailed description but no figures. The original figures of skeleton and skull provided by Temminck (1825) are rather schematic and not very accurate.

Not much has been published on *Chironax*. Hill (1974: 127-129; 1983: 123-124) surveyed the literature; since then, the first specimen from Borneo was described by Hill & Francis (1984: 307) and figured in colour by Payne, Francis & Phillips (1985: pl. 7).

The genus is now known from Thailand, peninsular Malaysia, Sumatra, Java, Borneo and Sulawesi.

Hill (1974: 127-129; 1983: 123-124) discussed the apparent geographic variation within the genus, of which all representatives are considered to belong to the type species. A first specimen from Sulawesi differed from Malayan specimens in colour, wing structure, skull characters, teeth dimensions and morphology of the third upper molar (Hill, 1974: 127-129); because he had no

typical Javan specimens at his disposal, Hill left the question of the taxonomic status of the Sulawesian population to be resolved later, when more material from both Sulawesi and Java would be available. In 1983 Hill had studied a small series from Java and a number of data on two other specimens from Sulawesi in the ZMA collection (21.638, 21.639). The latter specimens had been identified as *Chironax melanocephalus* by Bergmans (who had no other specimens of the genus at hand); Hill (1983: 123-124) found that they confirmed the earlier observed differences between Sulawesian and Malaysian specimens, while typical Javan specimens appeared to conform to Malaysian rather than Sulawesian examples. Malaysian specimens seem to be larger, on the average, than either Javan or Sulawesian specimens. Hill (1961: 640) measured forearm lengths of 42.5 – 47.5 (mean 45.5) in 12 Malaysian specimens and greatest skull lengths of 23.0 – 23.7 (mean 23.4) in six.

For the present study ten specimens from Sulawesi were available, which have been compared with the syntype series of *Pteropus melanocephalus*. Moreover, ten other Javan specimens and three from unknown – but probably Javan – origin in the RMNH collection have been studied.

Taxonomically the Sulawesian specimens appear to represent a quite distinct entity, for which a new subspecies is proposed below.

Chironax melanocephalus melanocephalus (Temminck)
(figs. 11, 14)

Pteropus melanocephalus Temminck, 1825: 190, pls. 12, 16, figs. 3-4 – Bantam, Java.

Specimens examined. — RMNH 35728, ♀ (mounted skeleton, skull), 1823, Bantam, Java, leg. J. C. van Hasselt (syntype; Jentink, 1887: 266, specimen *a*); RMNH 35729, ♀ (mounted, skull extracted), 1823, Bantam, Java, leg. J. C. van Hasselt (syntype; skull: Jentink, 1887: 266, specimen *b*; skin: Jentink, 1888: 155, specimen *a*); RMNH 35731, sex unknown (skull only), 1823, Bantam, Java, leg. J. C. van Hasselt (syntype; Jentink, 1887: 266, specimen *c*); RMNH 35730, ♀ (mounted, skull in situ), 1823, Bantam, Java, leg. J. C. van Hasselt (syntype; Jentink, 1888: 155, specimen *b*); RMNH 14788, ♂ (skin and skull), 28.iv.1933, Situ Gunung, S slope of Gunung Pangrango, 1350 m, W Java, leg. M. Bartels; RMNH 14789, 14790, 14792, 14793), imm. ♂, 2 ♀, imm. ♀ (skins and skulls), 30.x.1933, Cibodas, S slope Gunung Pangrango, W Java, leg. M. Bartels; RMNH 14802, ♂ (skin and skull), 20.xi.1933, Cibodas, S slope of Gunung Pangrango, W Java, leg. M. Bartels; RMNH 14791, 14794, 14803, imm. ♂, ♂, imm. ♀, 26.ii.1934, Cibodas, S slope of Gunung Pangrango, W Java, leg. M. Bartels; RMNH 32599, imm. ♀ (skin and skull), undated, Situ Gunung, S slope Gunung Pangrango, W Java, leg. H. J. V. Sody; RMNH 35732-35734, unsexed (skins and skulls), undated, no locality, leg. M. Bartels /H. J. V. Sody.

Measurements and weights. — See tables 9 and 10.

Remarks. — To date, the best account of the syntype series of nominate *Chironax melanocephalus* is that by Andersen (1912: 658-661). Hill (1983: 123-

	male	male	male	male	male	female	female
RMNH reg. no.	14788	14789	14791	14794	14802	35128*	35129
Age	ad.	imm.	imm.	ad.	ad.	ad.	ad.
forearm length (label)	44.2	43.2	43.8	45.0	42.6		
forearm length (dry)	43.4	42.6	39.8	43.5	41.65		±44.3
greatest skull length	22.4	21.6	20.9	23.35	22.2	22.15	
condylobasal length	21.3	20.4	19.7	21.8	21.4	20.7	
rostrum length	6.75			7.1	6.6	6.7	7.0
palatal length	11.0			11.2	10.8	10.9	11.3
cranium width	10.0			10.2	9.65	9.7	
interorbital width	4.3	4.15	3.8	4.1	4.2	4.1	4.4
postorbital width	4.6	4.8	4.85	4.55	4.7	4.7	4.6
zygomatic width	14.3	13.8	12.9	14.85	14.45	14.0	
mandible length	16.45			17.2		15.6	16.0
mandible height	8.45			8.4	8.1	7.4	
C^1-C^1 (over crowns)	4.6			4.7	4.5	4.4	
C^1-M^1 (over crowns)	6.9	6.55	6.6	7.4	7.25	6.75	
M^1-M^1 (over crowns)	6.6			6.8		6.4	
C_1-M_2 (over crowns)	7.3			7.9		7.3	
interspace C^1-P^3	0.7			0.7	0.65	0.45	
weight		17			12		

* lectotype

Table 9. Body and skull measurements and weights of *Chironax m. melanocephalus* (Temminck, 1825) from Java; specimens RMNH 35732-35734 are of uncertain, but likely, Javan origin. All specimens prepared as dry skins and skulls.

126) provided data on some additional specimens from Java – although in part mixed with data on Sumatran specimens. For the purpose of further revisory work we have selected a lectotype specimen (RMNH 35728; Jentink, 1887: 266, specimen *a*) – the same specimen of which skeleton and skull were figured with the original description – and give new illustrations of its skull (figs. 11a-e). This specimen is the best example among the four syntypes. The two other extracted skulls are damaged and incomplete, with heavily worn teeth; the skull which has remained inside one of the two mounted specimens is most probably also incomplete. The skins of the two mounted specimens are strongly faded and have little value compared with the almost complete skeleton of the specimen chosen as the lectotype. It should be added that, to judge from the stage of tooth wear, the skulls or mandibles of two syntype

female	female	female	female	female	female	female	?	?	?
35131	35130	14790	14792	14793	14803	32599	35132	35133	35134
ad.	ad.?	ad.	imm.	ad.	imm.	imm.	ad.	ad.	ad.
		46.0	44.5		43.7	41.3			
	±42.8	44.5	43.9	39.9	41.4		>42	43.3	43.8
≥22.4		23.3		≥23	20.1		≥21.9	22.9	22.7
		22.3			18.7			21.9	21.7
7.1		7.0					7.0	6.9	6.9
11.1		11.25					11.3	11.4	11.0
		10.4		9.9				9.8	10.1
4.5		4.4	4.15	4.2	3.75		4.4	4.7	4.45
4.55		5.1	4.7	4.9	4.95		5.3	5.1	5.0
				15.0	12.6			14.3	14.1
16.3		16.85		16.0			16.5	16.5	16.8
8.0		8.0		7.7			7.5	8.4	8.0
4.6		4.7		4.5			4.7	5.0	4.8
7.0		6.9	6.6	6.8	6.2		7.0	6.9	7.1
6.7				6.6			6.7	6.7	6.7
7.7								7.7	7.6
0.7		0.65		0.55			0.6	0.6	0.5
		17	14	13					

specimens (*b* and *c* of Jentink, 1887: 266) have been exchanged in Temminck's time; as it is impossible to reconstruct what has happened and to know which of the two skulls belongs with the single skin, we have left the combination unaltered.

Unfortunately all other Javan specimens and also those of uncertain provenance which we have studied consist of skulls and dry skins with folded wings. For these reasons, it is not well possible to measure and compare their wing bone dimensions with those of the spirit specimens from Sulawesi. An assessment of possible intraspecific variation in fur colours will only be possible when Javan spirit specimens become available for comparison. Therefore, we have concentrated on skull and teeth characters. As there is little need to repeat Andersen's account, the information given here on nominate *melanocephalus* is restricted to measurements (tables 9 and 10) and figures (figs. 11a-e). A number of details of skull and teeth will be referred to in the discussion of the next taxon.

Restriction of type locality. — In a letter dated 14 March 1823, written during his exploration of the Bantam district in West Java, Van Hasselt refers

sex	male	male	male	female
RMNH reg.no.	14789	14791	14802	35128*
C^1	1.5 x 1.3	1.6 x 1.3	1.65 x 1.3	1.4 x 1.3
P^1	0.55 x 0.5	0.5 x 0.5	0.5 x 0.5	0.45 x 0.45
P^3	2.1 x 1.35	2.0 x 1.3	2.25 x 1.4	2.0 x 1.4
P^4	1.9 x 1.3	1.75 x 1.3	2.1 x 1.4	1.8 x 1.3
M^1	1.2 x 1.1	1.15 x 1.1	1.3 x 1.15	1.3 x 1.1
C_1	1.1 x 1.1	1.1 x 1.3		1.2 x 1.1
P_1		0.65 x 0.7	0.8 x 0.9	0.7 x 0.7
P_3	1.85 x 1.35	1.7 x 1.4	1.9 x 1.35	1.9 x 1.3
P_4	1.8 x 1.35	1.8 x 1.4	1.85 x 1.35	1.9 x 1.35
M_1	1.5 x 1.1	1.45 x 1.1	1.6 x 1.1	1.5 x 1.1
M_2	0.7 x 0.55	0.7 x 0.5	0.7 x 0.6	0.7 x 0.65

* lectotype

Table 10. Teeth measurements (length x width, over crowns) of *Chironax m. melanocephalus* (Temminck, 1825) from Java.

to 'three bats of a genus that was previously unknown from Java', which were amongst the mammals collected in primary forest on Gunung Karang (Van Hasselt, 1823). Although the number mentioned does not exactly match the number of specimens in the syntype series, it seems justified to assume that this reference concerns *Chironax*, since Temminck (1825: 190) stated that the specimens were collected in 'mountainous parts of the district Bantam', 'in the most remote parts of Java'. We therefore restrict the type locality of nominate *melanocephalus* to Gunung Karang, Bantam, West Java.

Chironax melanocephalus tumulus subspec. nov.
(figs. 12-14)

Chironax ?melanocephalus, Hill, 1974: 127 (specimen BMNH 73.1802, from Soroako, Central Sulawesi).

Chironax melanocephalus, Hill, 1983: 122 (partim: specimens ZMA 21.638-21.639, from North Sulawesi, also listed below).

Holotype. — ZMA 22.101, adult ♂ (in alcohol, skull extracted), 25/26.i.1983, Sungei Moinakom, Dumoga-Bone National Park, North Sulawesi, Indonesia, alt. 625 m, leg. F. G. Rozendaal.

female 14792	female 14803	female 32599	? 35133	? 35134
1.4 x 1.2	1.35 x 1.2	1.4 x 1.3	1.4 x 1.4	1.4 x 1.4
0.5 x 0.5	0.4 x 0.5	0.5 x 1.45	0.5 x 0.5	0.5 x 0.6
2.0 x 1.3	1.85 x 1.3	2.0 x 1.4	2.05 x 1.5	2.0 x 1.25
1.85 x 1.3	1.7 x 1.3	1.75 x 1.35	1.85 x 1.35	1.7 x 1.3
1.3 x 1.1	1.1 x 1.05	1.25 x 1.0	1.2 x 1.0	1.35 x 1.0
	1.05 x 1.2	1.1 x 1.1	1.15 x 1.3	1.0 x 1.3
	0.6 x 0.75	0.65 x 0.7	0.75 x 0.85	0.65 x 0.9
1.7 x 1.2	1.6 x 1.3	1.9 x 1.45	1.85 x 1.4	1.6 x 1.35
1.85 x 1.4	1.8 x 1.35	1.8 x 1.45	1.85 x 1.45	1.7 x 1.4
1.6 x 1.15	1.4 x 1.05	1.35 x 1.05	1.35 x 1.1	1.5 x 1.1
0.8 x 0.6	0.65 x 0.5	0.7 x 0.6	0.7 x 0.6	0.7 x 0.6

Paratypes. — ZMA 21.638, MZB 14510, 2 ♀ (in alcohol, one skull extracted), 22 and 23.x.1981 respectively, upper tributary of Sungei Mauk, Dumoga-Bone N. P., alt. 960 m, leg. K. D. Bishop, F. G. Rozendaal & W. F. Rodenburg; RMNH 33167-33168, 2 ♀ (skulls extracted), 14/15 and 15/16.iii.1982, upper tributary of Sungei Mauk, Dumoga-Bone N. P., alt. 960 m, leg. W. F. Rodenburg & J. Wind; ZMA 22.102, ♂ (skull extracted), 25/26.i.1983, Sungei Moinakom, Dumoga-Bone N. P., alt. 625 m, leg. F. G. Rozendaal; RMNH 33263-33264, ♂, ♀ (skulls extracted), 26/27.i.1983, Sungei Moinakom, Dumoga-Bone N. P., alt. 625 m, leg. F. G. Rozendaal; RMNH 35726-35727, ♀, ♂ (skulls extracted), 11/12.iv.1985, Hog's Back, Dumoga-Bone N. P., alt. 480 m, leg. F. G. Rozendaal. Referred material. — BMNH 73.1802, ♀ (skin and skull), 20.ix.1972, Soroako, alt. 385 m, leg. S. Sarbini; NAMRU DJM-5028, ♀ (skin and skull), 19.v.1975, Lake Iloloi, alt. 870 m, leg. S. Sarbini.

Measurements and weights. — See tables 11 and 12.

Diagnosis. — A distinct *Chironax* of about normal size, with long metacarpals, delicate skull, long rostrum, wide interorbital region, large postorbital width, and small teeth without much differentation.

Description. — A very small fruit bat with strongly contrasting dorsal and ventral fur colours, short tubular nostrils, and small, rounded ears. Fur soft and dense. Back fur very dark brown, tinged with grey (this grey stronger in young adults and possibly a juvenile character); hairs slightly lighter and greyish at their bases; hairs on middle of back up to 10 mm in length. Fur on top of head a minimal shade darker at most, about 4.5 mm in length, and much shorter fur on rostrum and sides of head. Area around nostrils naked but for scattered dark, thick tactile hairs (4 mm long). Area around eyes thinly furred, with two (sometimes three) dark tactile hairs (7 mm long) above each eye. Short, dark tactile hairs on upper lip and some longer ones (4.5 mm long)

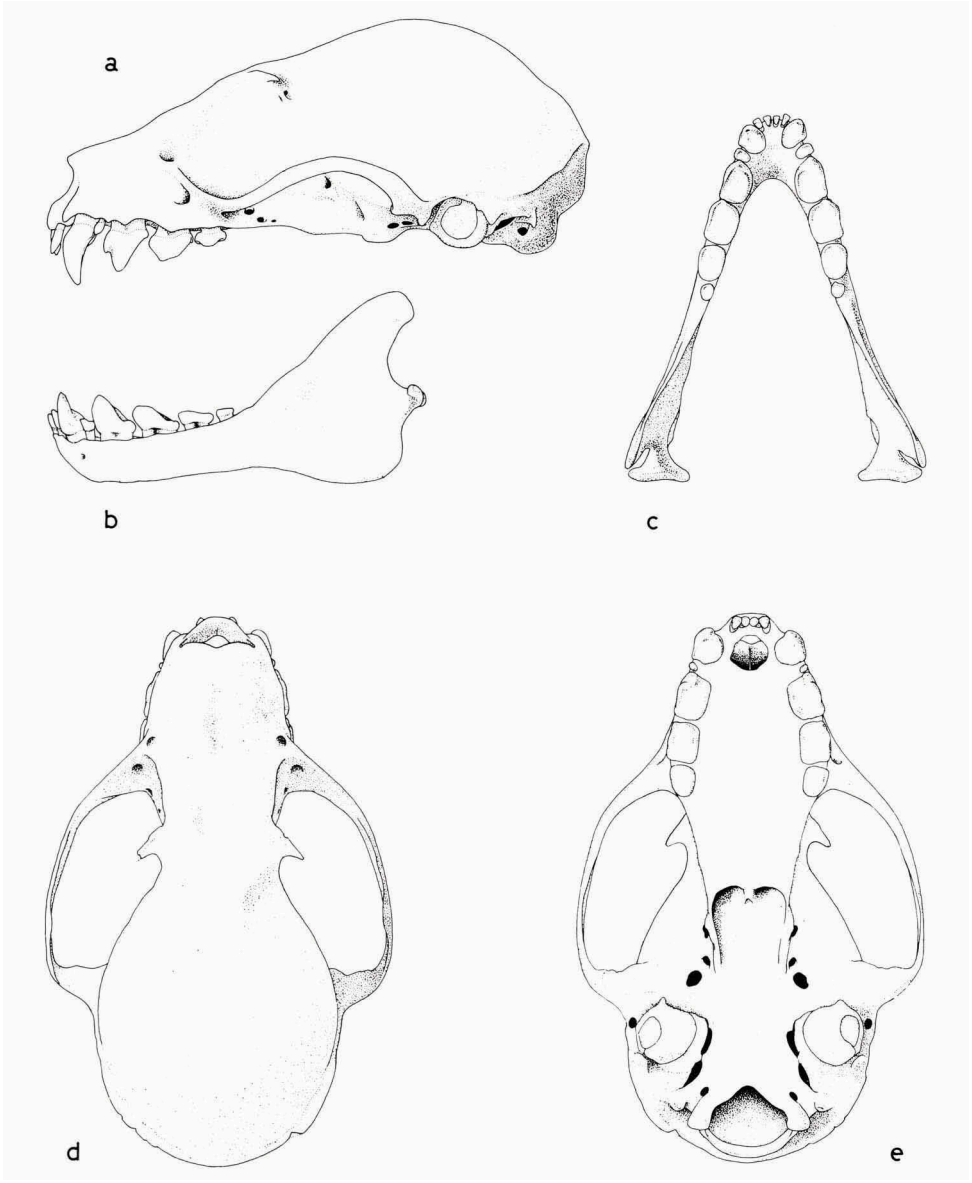

Fig. 11a-e. Skull of lectotype of *Chironax melanocephalus melanocephalus* (Temminck, 1825) (specimen RMNH 35728); small foramina coloured black; a: lateral aspect of skull (left side); b: lateral aspect of mandible (left side); c: dorsal aspect of mandible; d: dorsal aspect of skull; e: ventral aspect of skull (damaged auditory region partly reconstructed).

behind corner of mouth. Light-coloured bristle- like, short adpressed hairs on upper lip; the same type of hairs, but somewhat longer, behind the anterior naked part of the chin. Ventral fur essentially whitish; lateral and caudal fur darker. Demarcation between dorsal and ventral fur colours along a rather sharp line from corner of mouth to anterior ear-base, and from back of ear across shoulder to wing insertion. Chin and centre of throat with thinly scattered, short hairs. Fur on shoulders, breast and belly generally light yellowish white, but rather greyish in some specimens and with yellowish orange tipped hairs in a very narrow collar in one male (RMNH 35727). In none of the ten specimens the hairs on the shoulders grow as tufts or crowns. Fur on sides and postgenital area greyish yellow or – in young adults – almost completely grey. The amount of grey in the ventral pelage is correlated with the extent of that colour on the base of the hairs.

The forearm length range in four males is 44.3 – 45.5 (mean 44.9). If the forearm length is put at 1000, the index range of the third metacarpal length (sexes combined) is 710 – 740 and the index range of the fifth metacarpal length 716 – 745.

Skull delicately built; greatest length 22.1 – 22.8 (mean 22.45) in four males and 21.8 – 22.9 (mean 22.25) in five females. Rostrum length relatively greater than in nominate subspecies (fig. 12a). Anterior rostral width small; width over crowns of upper canines 4.3 – 4.5 (mean 4.4) in three males and 4.1 – 4.25 (mean 4.2) in five females, against 4.5 – 4.7 (mean 4.6) in three males and 4.4 – 4.7 (mean 4.55) in four females of the nominate subspecies. Dorsal aspect of sides of rostrum straight to weakly concave, against convex – caused by larger volume of dental roots, especially of P^3 – in nominate subspecies. Median pair of paranasal air sinuses formed by frontal (and possibly nasal and maxillary) bones less swollen than in nominate subspecies, resulting in weaker median dorsal depression and less undulating lateral outline of rostrum. Lacrimal foramen generally oriented caudally, vs. dorsally in nominate subspecies. Infraorbital foramen relatively small. Interorbital region wider and postorbital width absolutely larger than in nominate subspecies (figs. 12b-c). Basis of postorbital process generally broad, although not in all specimens as broad as in holotype; concurring with this basal width, bony support at ventral side of process more voluminous; this supporting bone not pierced by a narrow canal as in 11 out of 12 specimens of the nominate subspecies. Bony bar separating optic foramen and anterior lacerate foramen generally wider than in nominate subspecies. Caudal margin of bony palate slightly concave, with a small median projection in seven out of nine specimens; this margin variable in nominate subspecies: either slightly concave or nearly straight, with or without a median projection, and in some specimens with a median notch. Caudal end

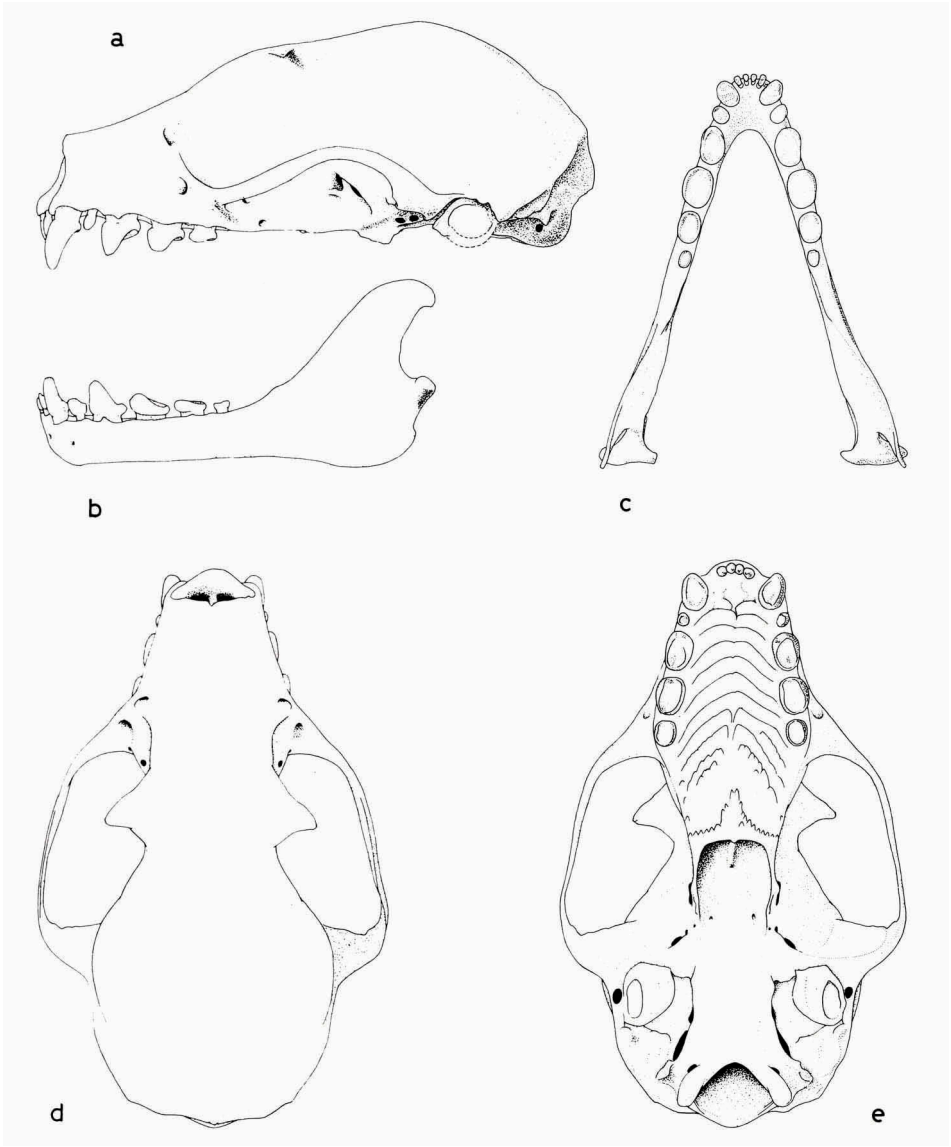

Fig. 12a-e. Skull of holotype of *Chironax melanocephalus tumulus* subspec. nov. (adult ♂; ZMA 22.101); small foramina coloured black; a: lateral aspect of skull (left side); b: lateral aspect of mandible (left side); c: dorsal aspect of mandible; d: dorsal aspect of skull; e: ventral aspect of skull (damaged auditory bullae region restored, after paratype ZMA 22.102; palatal ridges drawn from wet specimen).

sex collection reg. no.	male* ZMA 22.101	male ZMA 22.102	male RMNH 33263	male RMNH 35127	female MZB 14510	female RMNH 33167	female RMNH 33168	female RMNH 33264	female RMNH 36126	female ZMA 21.638
forearm length	45.3	44.3	44.6	45.5	45.6	46.5	43.8	45.4	45.2	45.6
3rd metacarpal length	32.9	31.6	32.1	32.4	33.0	33.2	31.4	32.8	33.5	33.4
5th metacarpal length	33.4	31.7	32.9	32.7	34.0	34.1	31.7	33.3	33.8	33.6
ear length				9.7	10.0				10.0	10.4
foot length				9.6	10.2				9.2	10.0
tibia length				15.8	15.9				16.5	16.2
greatest skull length	22.8	22.1	22.5	22.35	22.2	22.9	21.8	21.95	22.3	
condylobasal length	22.0	21.4	21.5	21.2	21.6	22.1	20.85	21.0	21.55	
rostrum length	7.3	6.9	7.2	7.05	7.1	7.4	7.05	7.05	6.9	
palatal length	11.3	10.9	10.75	10.8	11.1	11.4	10.8	10.7	10.85	
cranium width	10.05	9.9	10.15	10.0	10.1	10.3	9.75	9.65	9.8	
interorbital width	4.9	4.6	5.25	4.85	5.1	5.1	5.05	5.0	4.8	
postorbital width	5.25	5.5	5.7	5.5	5.5	5.7	6.3	5.8	5.6	
zygomatic width	14.25	13.8	14.35	13.9	13.9	14.45	13.8	13.5	14.4	
mandible length	16.65	15.3	15.95	15.9	15.9	16.15	15.9	15.75	16.25	
mandible height	7.45	7.1	6.9	7.3	7.0	7.3	6.85	7.0	7.5	
C^1-C^1 (over crowns)	4.3	4.4	4.45		4.1	4.25	4.15	4.2	4.2	
C^1-M^1 (over crowns)	7.0	6.65	6.9		6.6	6.8	6.7	6.7	6.7	
M^1-M^1 (over crowns)	6.2	6.1	6.55		6.3	6.4	6.5	6.2	6.3	
C_1-M_2 (over crowns)	7.8	7.3	7.7		7.4	7.65	7.45	7.4	7.55	
interspace C^1-P^3	1.0	0.95	1.0		0.95	0.9	0.8	0.9	1.0	
weight	13	12	12	13.9				11.5	17 (pregnant)	

* holotype

Table 11. Body and skull measurements and weights of *Chironax melanocephalus tumulus* subspec. nov. from Sulawesi. All measurements were taken from adult specimens preserved in alcohol.

of nasal septum variable, very thin or rather solid and partly hollow, and not in all specimens extending beyond palate. Palatine part of palatine-pterygoid wings solid; in nominate subspecies either with oval apertures level with optic and anterior lacerate foramina – these apertures in some specimens wholly or partly closed by an opaque sheet of bone –, or solid. (In lectotype of nominate subspecies there are apertures, but these are irregular in outline and may be

sex collection reg. no.	male* ZMA 22.101	male ZMA 22.102	male RMNH 33263	female MZB 14510	female RMNH 33167	female RMNH 33168	female RMNH 33264
C^1	1.35 x 1.05	1.45 x 1.15	1.4 x 1.1	1.35 x 1.05	1.35 x 1.1	1.5 x 1.05	1.5 x 1.05
P^1	0.6 x 0.5	0.5 x 0.5	0.5 x 0.45	0.5 x 0.35	0.55 x 0.5	0.55 x 0.45	0.55 x 0.45
P^3	1.6 x 1.0	1.6 x 1.1	1.55 x 1.0	1.6 x 1.0	1.65 x 1.0	1.65 x 1.05	1.65 x 1.05
P^4	1.55 x 1.15	1.5 x 1.1	1.5 x 1.15	1.5 x 1.0	1.5 x 1.1	1.45 x 1.1	1.45 x 1.1
M^1	1.1 x 0.85	1.25 x 0.9	1.15 x 0.9	1.0 x 0.8	1.15 x 0.9	1.2 x 0.9	1.2 x 0.9
C_1	1.1 x 0.95	1.1 x 1.05	1.15 x 1.0	1.0 x 0.9	1.25 x 0.9	1.15 x 0.9	1.15 x 0.9
P_1	0.8 x 0.7	0.7 x 0.75	0.75 x 0.65	0.7 x 0.6	0.8 x 0.65	0.9 x 0.7	0.9 x 0.7
P_3	1.7 x 1.1	1.55 x 1.1	1.6 x 1.0	1.55 x 1.0	1.7 x 1.1	1.7 x 1.0	1.7 x 1.0
P_4	1.7 x 1.15	1.55 x 1.2	1.6 x 1.2	1.6 x 1.1	1.7 x 1.15	1.65 x 1.2	1.65 x 1.2
M_1	1.3 x 0.9	1.25 x 0.95	1.3 x 0.95	1.3 x 0.9	1.35 x 0.9	1.3 x 0.95	1.3 x 0.95
M_2	0.7 x 0.55	0.75 x 0.65	0.8 x 0.7	0.8 x 0.6	0.8 x 0.65	0.8 x 0.6	0.8 x 0.6

* holotype

Table 12. Teeth measurements (length x width, over crowns) of *Chironax melanocephalus tumulus* subspec. nov. from Sulawesi.

Fig. 13. Habitus of *Chironax melanocephalus tumulus* subspec. nov. (adult ♀; ZMA 22.102), primary forest, Sungei Moinakom, Dumoga-Bone N.P., alt. 625 m. Reproduced from a colour transparency taken by F. G. Rozendaal, 26 March 1983.

artefacts, and have been omitted from the figures.) Pterygoid wings relatively thin. Round and oval foramina generally small; round foramen even absent in one specimen (MZB 14510) and present on one side only in another (ZMA 22.102). Orientation of oval foramen less horizontal than in nominate subspecies; oval foramen in some specimens partly covered in ventral view by a thin bony sheet protruding from a proximal extension of the posterior margin of the glenoid fossa. Postglenoid foramen normal. Basioccipital rather elongate and flat. Anterior part of basicochlear fissure narow; posterior lacerate foramen not visible in lateral view. Orientation of hypoglossal foramina less horizontal than in nominate subspecies, generally relatively small, and in some specimens present as one or two minute apertures only. Occipital foramen with weakly convex dorsal margin; in nominate subspecies the dorsal margin of this foramen is rather more angular.

Teeth smaller in length, width and height and morphologically less differentiated than in nominate subspecies. Upper canines with only a trace of an antero-internal longitudinal groove, and a very narrow lingual shelf. P^3 without an additional antero- external cusp and with a mere trace of a precingular basin (cf. Slaughter, 1970: 56, fig. 1). P^4 without trace of precingular basin. Lower canines relatively narrow at their bases; P_3 with faint trace of precingular basin. Abnormal dention found in two specimens: one male (RMNH 35727) has no second molars; another male (ZMA 22.102) has an additional upper incisor, located next to the left I^2 in an almost 'natural' position, which suggests an atavism and as such lends support to the theory that in Megachiroptera the lost upper incisor is I^3; see also Slaughter (1970: 56-57). Palatal ridge pattern: one medially divided ridge between canines; six interdental ridges which may or may not be divided; three or four not wholly interdental divided ridges with, from anterior to posterior, weak to distinct denticulations; and one denticulated ridge near the posterior border of the bony palate.

Etymology. — Mr. J. E. Hill first recognized that this fruit bat might represent a new taxon; the Latin subspecific epithet *tumulus*, with as first meaning "little hill", alludes both to that fact and to the small size of the bat.

Distribution. — Northeast Sulawesi (Dumoga-Bone National Park and Lake Iloloi) and E Central Sulawesi (Soroako).

Ecology. — Specimens have been taken in primary forest at altitudes of up to 960 m, in a number of cases near or over small streams; in Sulawesi, the species is apparently restricted to lowland forest.

Reproductive biology. — A female caught on 14/15 March (RMNH 33168) had an embryo with a total length of 17.3 and a forearm length of 11.3 ; another female, caught on 11/12 April (RMNH 35726), had an embryo with a total length of 22 and a forearm length of 13.8. A male collected on 11/12 April

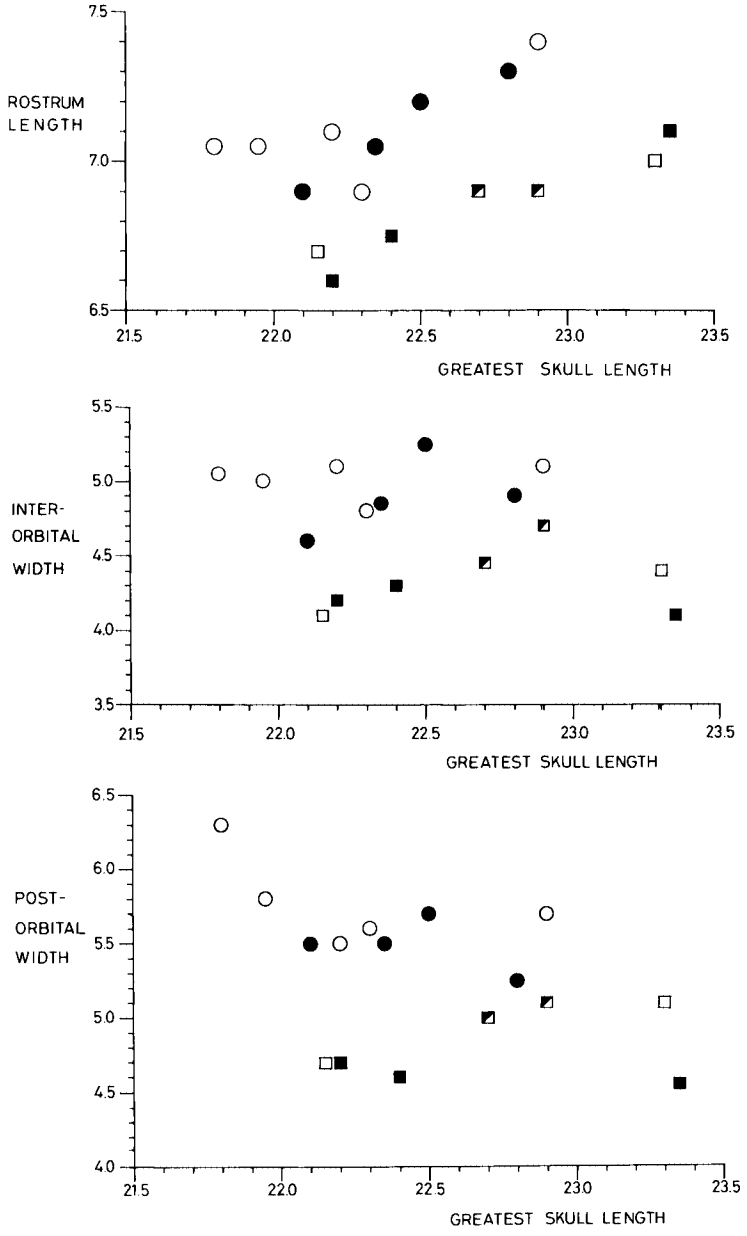

Fig. 14a-c. Relative skull measurements in *Chironax melanocephalus tumulus* subspec. nov. (black dots: ♂; open circles: ♀) and *Chironax melanocephalus melanocephalus* (Temminck, 1825) (black squares: ♂; open squares: ♀; black and white squares: sex unknown and Javan provenance uncertain). a: rostrum length in relation to greatest skull length; b: interorbital width in relation to greatest skull length; c: postorbital width in relation to greatest skull length.

(RMNH 35727) had large, descended testes; testes of males caught towards the end of January (ZMA 22.101-22.102; RMNH 33263) were rather small.

Ectoparasites. — Three specimens yielded one to three as yet unidentified mites (Acari) each, collected from the ventral fur and adjoining wing membranes.

Remarks. — Two specimens (ZMA 21.639; RMNH 33263) had a tiny splinter of presumably vegetable material (tips of thorns?) embedded in the bone of their nasals, about midway between the anterior sides of their eyes.

Discussion. — The many diagnostic characters of this new taxon indicate a number of developmental trends which diverge from their equivalents in the nominate subspecies and might justify distinction at species level. However, we prefer to let this question rest until sufficient numbers of – preferably spirit – specimens from Thailand, peninsular Malaysia, Sumatra and Borneo have become available for study.

NYCTIMENINAE

Nyctimene cephalotes cephalotes (Pallas)

Vespertilio cephalotes Pallas, 1767: 10, pl. 1, 2 – "Moluccas"; type locality restricted to Amboina by Andersen (1912: 707).

Specimens examined. — ZMB 83870, immature ♂ (skull only), 6.viii.1938, Pulau Peleng, leg. J. J. Menden; ZMA 21.544, ♀ (skull extracted), 28.x.1981, Sungei Moinakom, Dumoga-Bone N. P., alt. 625 m, leg. K. D. Bishop, F. G. Rozendaal & W. F. Rodenburg; RMNH 33186-33190, 4 ♂, 1 ♀, 18.i.1982, Imandi market, leg. W. F. Rodenburg & J. Wind.

Measurements. — The males have forearm lengths of 65.3, 67.7, 64.2 and 68.3 respectively; females have forearm lengths of 69.5 and 70.4 respectively.

Remarks. — Apparently on account of its small size, the skull of ZMB 83870 had been identified as *Nyctimene minutus* Andersen, 1910 by K. F. Koopman in 1978 and therefore has drawn our attention. Having examined the skull we conclude that it is an immature specimen of *cephalotes*. Its skull base sutures are not completely fused and its premolars and molars are still somewhat more crowded than in adult *cephalotes*. It is nevertheless larger in almost all dimensions than the holotype and only known specimen of *minutus*, and approaches or falls within the ranges given for *cephalotes* by Andersen (1912: 719); some measurements are: greatest skull length 29.1, palation to incisive foramina 11.9, zygomatic width 19 or more, $C^1 - M^1$ (crowns) 10.1. *N. cephalotes* has previously been recorded from Peleng I. by Tate (1942: 343).

Andersen (1912: 687) described the palatal ridge pattern in the genus, which he had studied in three species, including *cephalotes*. However, his illustration

depicts an incomplete soft palate, probably only the part that covers the bony palate. In specimen ZMA 21.544 there are up to 25 ridges (instead of 13 to 15 as stated by Andersen), consisting of (from front to back) eight undivided ridges – the last of which, and all those behind it, with rather sharply pointed 'teeth' -, three almost or only just divided, five irregularly interrupted, six undivided and six divided ridges (of the latter, the median divisions widen towards the posterior end of the palate and the last few ridges are little more than lateral remnants, with only a few 'teeth').

Reproductive biology. — One male collected on 18 January (RMNH 33187) has large descended testes; the females were both pregnant: total length of the embryo of ZMA 21.544, collected 28 October, is 18 mm, measured in situ; the embryo of RMNH 33190, collected 18 January, measures 30.8 mm.

MACROGLOSSINAE

Eonycteris spelaea rosenbergii (Jentink)

Eonycteris spelaea variété insulaire, Jentink, 1888: 158.
Callinycteris rosenbergii Jentink, 1889: 210, pl. 9 figs. 1-4 – Gorontalo (restricted to Tulabolo by Rozendaal (1984: 195).
Callinycteris rosenbergi, Matschie, 1899: 91; Miller, 1907: 70; Tate, 1942: 343.
Eonycteris rosenbergi, Andersen, 1910: 625; Andersen, 1912: 737; Hill, 1983: 33.
Eonycteris bernsteini, Tate, 1942: 345.
Eonycteris rosenbergii, Rozendaal, 1984: 189.

Specimens examined. — All specimens were purchased at Imandi market by R. Dekker: ZMA 22.714, juvenile ♀, 8.vii.1985; ZMA 22.715, ♀, 15.vii.1985; ZMA 22.716-22.717, ♀, juvenile ♀, 17.vii.1985; ZMA 22.758, ♂, 22.vii.1985; ZMA 23.079-23.080, imm. ♀, ♀, 25.ix.1985. Comparative material examined. — Thailand: ZMA 21.405, ♀ (skin and skull), 25.v.1977, cave 20 km SE of Chantaburi, leg. H. Felten. West Malaysia: ZMA 22.059-22.060, 2 ♀, 13.x.1982, Bentong, leg. F. S. Lukoschus. Sumatra: ZMA 2406, an incomplete skull, unsexed, undated, cave near Pajakumbuh (Ngalau), collector unknown; ZMA 16.698, ♂, 1905-1917, Deli, leg. L. P. le Cosquino de Bussy; ZMA 21.892-21.894, ♂, 2 ♀, 21 and 22.x.1982, near Parapat, leg. P. J. H. van Bree. Java: ZMA 2046, ♀ (skin and skull), iii.1928, Gua Lalaj, near Cineam, leg. F. Kopstein; ZMA 19.299-19.303, 3 ♂, 2 ♀, 7.vii.1977, Ciampea, leg. P. J. H. van Bree & Boeadi. Bali: ZMA 21.543, ♀, 8.i.1982, Goa Lawa, leg. W. Bergmans. Philippines: ZMA 14.415, ♀ (skin and skull), 7.iii.1971, Initiao, Mindanao, leg. D. S. Rabor.

Measurements and weights. — (Adult male specimen ZMA 22.758 and females 22.715 and 22.716 respectively; of the latter only forearm length, ear length and weight): forearm length 73.7, 71.4, 76.9; ear length 18.1, 16.5, 17.5; weight 80, 69, 82; greatest skull length 35.9, 34.7; condylobasal length 33.9, 32.5; rostrum length 13.7, 13.5; palatal length 18.4, 17.9; mandible length

26.7, 25.9; mandible height 10.5, 9.8; cranium width c. 14.8, 14.5; interorbital width 6.7, 7.1; postorbital width 7.5, 7.8; zygomatic width —, 20.0; mastoid width —, 13.2; width/length (over crowns) of: C^1-C^1 7.3, 7.3, C^1-M^2 12.4, 12.0, M^2-M^2 8.0, 8.3, C_1-M_3 14.0, 13.0; length x width (over crowns) of: P^3 2.1 x 1.1, 2.1 x 1.1, P^4 2.2 x 1.4, 2.1 x 1.5; M^1 2.3 x 1.3, 2.4 x 1.4; P_3 1.6 x 0.9, 1.7 x 1.0, P_4 2.0 x 1.2, 2.0 x 1.2, M_1 2.3 x 1.25, 2.2 x 1.3, M_2 1.4 x 0.95, 1.5 x 1.1. Furthermore, see table 13 for a comparison of measurements and weights of extralimital populations of *E. spelaea* and those of *E. s. rosenbergii*.

Discussion. — Jentink (1889: 209) mentioned three characters in which he found the new genus *Callinycteris* to differ from *Eonycteris*: attachment of the wing membrane to the second instead of the first toe, five instead of six lower cheek teeth, and anal glands level with – instead of posterior to – the anus. Matschie (1899: 90) doubted the value of the first two characters: a specimen in the Berlin museum, identified as *Eonycteris spelaea*, had its wing inserted between the first and second toe, and other specimens identified as such had led him to conclude an enlargement of the anal glands during the mating season, changing their relative position so as to coincide with the position observed in *Callinycteris*. On the other hand, Matschie noted from the figures in Jentink (1889: pl.9 fig. 2) that the palatal ridge pattern and tongue papillae in *Callinycteris* seemed to differ from their counterparts in *Eonycteris* and that in the former genus P^4 would be the longest upper cheek tooth instead of M^1 as in the latter.

Miller (1907: 70), who studied a skull photograph of the holotype, noted that the teeth in *Callinycteris* were "throughout more robust than those of *Eonycteris*" and that the crowns of P^4 and M^1 were "distinctly broader in proportion to their length". Andersen (1910: 625) anticipated his revision of *Callinycteris* in his Catalogue (Andersen, 1912) by stating that "*E. rosenbergi*" had "hitherto, without sufficient reason, been placed in a distinct genus, *Callinycteris*.". Andersen (1912: 734) found that in *Eonycteris* the wing membrane was often inserted on the first toe, or between first and second, and sometimes on the second toe. The absence of M_3, a rudimentary tooth in *Eonycteris*, was in Andersen's opinion an invalid reason for the generic separation of *rosenbergii*. In two specimens of *E. spelaea* examined by him this tooth was missing on one side. After studying the holotype of *rosenbergii*, Andersen simply diagnosed it "As *E. spelaea*, but m_3 absent" and could not confirm any of the differences suggested by Matschie (1899: 90-91) and his teeth measurements of the specimen fell within the ranges he had found for *spelaea* (except that P^4 was 0.1 mm longer than the maximum measured in that species), which refuted Miller's remark on the presumed heavy dentition in *rosenbergii*. The only difference that Andersen (1912: 737) observed was the

slightly smaller size of all types of tongue papillae in *rosenbergii*. Tate (1942: 343) pointed out that the posterior molars in many fruit bat genera are obsolescent and agreed with Andersen that the absence of M_3 would possibly not justify the separation of *Callinycteris* from *Eonycteris*. Hill (1983: 132-133) identified three specimens of *Eonycteris* from southeast Sulawesi, apparently all with M_3 present on both sides, as *E. spelaea*, constituting the first record of the species for that island. This author furthermore suggested that the specimens could be referable to the subspecies *glandifera* Lawrence, 1939 (type locality Luzon, Philippines), a large form with a strong rostrum. In the same context Hill (1983: 133) remarked that the holotype of "*Callinycteris rosenbergi* Jentink, 1889 (= *Eonycteris rosenbergi*)", if it were proved to be an M_3-less example of *Eonycteris spelaea*, might on the basis of its supposedly heavy dentition (Miller, 1907) represent the same subspecies as his specimens from southeast Sulawesi, in which case the name *rosenbergii* would have priority over *glandifera*. Rozendaal (1984) re-examined the two southeast Sulawesian specimens of *E. spelaea* and found a third – from Raha, Muna Island – in the RMNH collection. These were compared with two Philippine specimens of *glandifera* and measurements of six others, and the southeast Sulawesian specimens referred to *glandifera*. In the same paper Rozendaal described two additional specimens of *rosenbergii*: an adult female collected by him in North Sulawesi and an immature male of unknown Sulawesian provenance from the collections of the Zoologisches Museum, Berlin. Lacking third lower molars on both sides, the specimens seemed to confirm the diagnostic value of this character. For all practical purposes Rozendaal (1984: 200) tentatively retained *rosenbergii* as a valid species.

The additional specimens are undoubtedly referable to a single species; although their collecting localities are not exactly known, they can safely be assumed to originate from the Dumoga-Bone National Park, where Rozendaal (1984: 189) collected a specimen.

Of the three adults, one specimen (ZMA 22.716) lacks both M_3, another (ZMA 22.715) has one M_3, and in the third and fourth (ZMA 22.758 and 23.080) M_3 is present on both sides. Apparently this population is characterized by a relatively high incidence of the lack of the third lower molar, but as such this character is evidently not of diagnostic value. Rozendaal (1984: 196) quotes Sody on the doubtful taxonomic value of the – even constant – lack of last molars and we agree that if *rosenbergii* is retained as a valid taxon, there should be other differential characters, but first its possibly synonymy with *glandifera*, as suggested by Tate (1942) and Hill (1983), should be investigated.

When compared to nominate *spelaea*, *glandifera* would be distinguished by shorter and less dense fur, larger size and more heavily built skull, less tapering

region and source		males						females						sexes combined or unknown			
		fal		gsl		weight		fal		gsl		weight		fal		gsl	weight
		n	min - max	n	min - max	n	min - max	n	min - max	n	min - max	n	min - max	n	min - max	n	n min - max
Burma	1	5	67.4-77.7	5	34.2-36.6												
	2															1	36.1
Laos	3							1	67.8								
Thailand	4													-	60 -75*		- 37 -82*
	5							1	70.5	1	34.8						
Malaya	6													-	62 -71		
	1	4	63.8-70.9	4	32.0-34.7	4	51.0-56.3	7	63.8-66.5	7	32.3-35.3	7	34.0-45.2				
Sumatra	7													14	63.8-71.2		
	5	2	68.8-73.5	1	34.4												
Borneo	8													-	61 -70		
Java	1	5	66.7-70.0	5	33.0-35.4			5	62.0-71.6	5	32.7-35.7						
	5	2	71.3-72.9	1	35.7	2	70 -80	1	65.7	1	33.3						
Bali	7													15	64.7-74.0		
	1	6	65.0-74.8	6	33.2-35.6			2	67.5-68.9	2	33.2-33.8						
Timor	7							1	73.7	1	36.9						
SE Sulawesi	1	1	74.3	1	35.9			2	72.0-76.1	2	33.9-34.6						
N Sulawesi	1							1	70.2	1	33.9						
	5	1	73.7			1	80	2	71.4-76.9	1	34.7	2	69 -82				
Philippines	9	2	72 -76	2	35 -35.1			7	71 -74	2	35 -36						
	2	1	76														
	1	3	70.7-72.4	3	35.0-36.6			3	67.7-71.9	3	33.0-33.6						

* range apparently includes immatures

Table 13. Forearm lengths (fal), greatest skull lengths (gsl) and weights of *Eonycteris spelaea* (Dobson, 1871), including *E. spelaea rosenbergii* (Jentink, 1889); source codes: 1 = Rozendaal, 1984; 2 = Lawrence, 1939; 3 = Phillips, 1967; 4 = Lekagul & McNeely, 1977; 5 = ZMA collection; 6 = Medway, 1969; 7 = Goodwin, 1979; 8 = Medway, 1977; 9 = Taylor, 1934 (recorded as *E. robusta* Miller, 1913).

rostrum, much greater width across the occipital crests and mastoid region, and smaller molariform teeth – except for the last molars (Lawrence, 1939: 39). Tate (1942: 344) suggested that the aberrant throat fur colour as described for adult male *glandifera* is absent in typical *spelaea* (cf. also Rozendaal, 1984: 198, 200). Published measurements (see table 13) do not confirm that Philippine specimens would be larger in body and skull dimensions than Burmese specimens (the type locality of *spelaea* is Moulmein, Burma). Hill (1983: 133) confirmed the above-mentioned skull characters for the southeast Sulawesian specimens. The present North Sulawesian specimens also have a relatively strong rostrum in comparison with specimens from Thailand, Sumatra and Java in the ZMA collection. Tackling the problem of subspecific limits within *spelaea* should start with a direct comparison of a larger Philippine representation with series from Burma. If *rosenbergii* is found to differ subspecifically from *spelaea*, it may be synonymous with *glandifera*, over which the name *rosenbergii* has priority. Pending a more extensive review of the genus, we now prefer to treat *rosenbergii* as a subspecies of *spelaea*, characterized by a relatively heavy rostrum, a high incidence of the loss of M_3, slightly smaller tongue papillae and possibly darker, greyer fur, darker wing membranes and darker claws (see also Rozendaal, 1984: 192).

Ectoparasites. — Specimens ZMA 22.715, 22.716 and 22.758 were infested with the nycteribiid fly *Eucampsipoda lieftincki* Maa, 1975; specimen ZMA 22.715 furthermore yielded seven fleas, *Thaumapsylla breviceps* Rothschild, 1907; the caudal membrane of specimen ZMA 22.758 is infested with mites of an unidentified species.

Macroglossus minimus lagochilus Matschie

Macroglossus lagochilus Matschie, 1899: 96 – Buru.

Specimens examined. — RMNH (uncatalogued), ♀ (skull extracted), 8.xi.1981, 21.00 hrs, desa Leksagu, Pulau Peleng, leg. W. F. Rodenburg & K. D. Bishop; RMNH 33418, ZMA 22.113, ♂, 26/27- and 28/29.i.1983, Sungei Moinakom, Dumoga-Bone N. P., alt. 625 m, leg. F. G. Rozendaal; RMNH 33417, ♀, 10/11.ii.1983, Tangkoko-Batuangus, leg. F. G. Rozendaal; ZMA 22.214, ♀, 27.iii.1983, Ujung Pandang, leg. R. Mayai; RMNH 35682, ♂, 25/26.iii.1985, rentis area, Toraut, Dumoga-Bone N. P., alt. 225 m, leg. F. G. Rozendaal; RMNH 35683, ♀, 27/28.iii.1985, Sungei Tumpah, Toraut, Dumoga-Bone N. P., alt. 225 m, leg. F. G. Rozendaal; RMNH 35684, ♂, 10/11.iv.1985, Hog's back, Dumoga-Bone N. P., alt. 480 m, leg. F. G. Rozendaal; RMNH 35685, ♂, 19/20.iv.1985, Danau Mooat, alt. 1080 m, leg. F. G. Rozendaal; RMNH 35673, ♂, v.1985, Gunung Sahendaruman, Sangihe Is., leg. F. G. Rozendaal; RMNH 35674-35679, 4 ♂, ♀, imm. ♀, 14/15-17/18.v.1985, NW slope of Gunung Sahendaruman, Sangihe I., alt. c. 600 m, leg. F. G. Rozendaal; RMNH 35672, ♀, 29/30.v.1985, NE slope of Gunung Sahendaruman, Sangihe I., alt. 750 m, leg. F. G. Rozendaal.

Remarks. — Hill (1983) published an excellent review of the present state of the taxonomy of this genus and is followed in assigning the specimens from Sulawesi, Peleng and Sangihe to the subspecies *lagochilus*. Forearm lengths of adult specimens are 41.6 in male ZMA 22.113 and 39.9, 38.7 and 40.7 in females RMNH (uncatalogued), RMNH 33417 and ZMA 22.214 respectively. Greatest skull length in female RMNH (uncatalogued) is 24.3.

Reproductive biology. — Sulawesian females collected 10/11 February and 27 March were pregnant, with one embryo each, measuring 15.2 and 17.5 mm in length in situ, respectively. A third female, caught 8 November, had large nipples. The Sangihe female RMNH 35676 (14/15 May) carried an embryo.

Ecology. — Males RMNH 33418 and ZMA 22.113 were mistnetted over a stream in dense primary forest at c. 625 m altitude; female RMNH (uncatalogued) was taken over brackish water in tall mangrove forest, about 100 m from the shoreline. Female ZMA 22.214, from Ujung Pandang, was collected in a garden in the town centre.

HARPYIONYCTERINAE

Harpyionycteris celebensis Miller & Hollister

Harpyionycteris celebensis Miller & Hollister, 1921: 99 – Gimpoe, C Sulawesi.

Specimens examined. — RMNH 33192, immature ♂ (skull extracted), 18.i.1982, Imandi market, leg. W. F. Rodenburg & J. Wind; ZMA 22.106, immature ♀ (skull extracted), 24.i.1983, Imandi market, leg. F. G. Rozendaal; RMNH 33434, ♀ (skull extracted), 26/27.i.1983, Sungei Moinakom, Dumoga-Bone N. P., alt. 625 m, leg. F. G. Rozendaal; RMNH 35698-35699, ♂, ♀, 27/28.iii.1985, Sungei Tumpah, Toraut, Dumoga-Bone N. P., leg. F. G. Rozendaal; RMNH 35700-35702, 2 ♀, ♂, 4/5.iv.1985, Clark's camp, Dumoga-Bone N. P., alt. 1140 m, leg. F. G. Rozendaal; the following specimens were all purchased at Imandi market by R. Dekker: ZMA 22.696-22.703, 22.766-22.768, 22.967, 22.968, ♂ (skull extracted), 20.iv.1985; immature ♀, 27.v.1985; 2 ♀, 1 ♂, 2 ♀ (all skulls but one extracted), 17.vi.1985; ♀, 15.vii.1985; 2 ♀ (skull of one extracted), 20.vii.1985; ♀ (skull extracted), 9.ix.1985; ♂ (skull extracted), 14.ix.1985.

Measurements and weights. — See table 14.

Discussion. — Hill (1983: 127-130) reviewed the literature on the genus *Harpyionycteris* and described a series of nine newly collected specimens – among which six adults – from Central Sulawesi. The present series of 21 specimens – all from North Sulawesi – includes at least seven adults (specimens RMNH 35698-35702 were not available in time for closer examination), which have greatest skull lengths of 39.5 – 42.4 and forearm lengths of 83.8 – 89.8, slightly enlarging the respective size ranges given by Hill, but smaller than the

	males		females				
	ZMA 22.696	ZMA 22.968	RMNH 33434	ZMA 22.699	ZMA 22.766	ZMA 22.768	ZMA 22.967
forearm length	85.7	89.8	83.8	85.0	87.9	84.0	87.6
thumb length (with claw)	36.0	37.0	35.0	34.4	36.4	35.0	35.7
third metacarpal length	64.3	64.5	61.2	62.5	63.7*	61.8	64.9
fifth metacarpal length	61.0	62.5	59.6	60.4	60.7*	59.5	61.8
tibia length	30.8	30.6	29.5	29.3	29.3	29.6	29.2
hindfoot length	24.7	22.5	19.2	21.9	21.9	22.2	23.4
ear length	17.8	18.6	17.1	16.4	17.9	18.7	17.7
greatest skull length	41.8	42.4	39.5	41.5	41.0	40.8	41.3
condylobasal length	40.4	41.3	38.0	39.4	39.4	39.3	39.9
rostrum length	14.3	14.8	14.2	14.6	13.8	14.2	13.9
palatal length	21.6	22.2	20.6	21.2	20.9	20.9	20.7
cranium width	16.3	16.9	16.5	16.6	15.8	15.8	-
interorbital width	7.6	7.4	6.4	7.1	6.9	7.6	7.0
postorbital width	5.9	6.1	6.1	6.1	6.1	5.9	6.0
zygomatic width	24.8	25.0	23.8	24.3	-	23.9	-
mandible length	32.7	34.0	31.2	32.9	32.0	32.4	32.0
mandible height	15.1	17.5	14.9	17.1	14.7	15.5	16.0
width over crowns of							
$C^1 - C^1$	8.2	8.3	8.3	8.1	8.2	8.4	7.7
$C^1 - M^2$	17.3	⩾17.2	16.7	17.0	16.5	17.1	16.4
$M^2 - M^2$	11.9	12.0	11.5	11.5	11.2	11.7	11.0
$C_1 - M_3$	18.6	18.1	17.8	18.1	17.8	18.3	17.2
weight	119	133	83	130	126	115	142

* metacarpals deformed, with curved proximal ends

Table 14. Measurements and weights of adult specimens of *Harpyionycteris celebensis* Miller & Hollister, 1921, from Sulawesi.

measurements mentioned for the holotype from Central Sulawesi and a specimen from Southeast Sulawesi (see Peterson & Fenton, 1970: 10). Hill (1983: 130) retained *celebensis* as specifically distinct from *whiteheadi* Thomas, 1896 (type locality Mindoro I., Philippines), although with strong reservations. Lack of sufficient topotypical material of *whiteheadi* prevented a proper assessment of some possibly quite variable characters in nominate *whiteheadi* and hence the taxonomic value of the characters claimed to distinguish *celebensis*. For the same reason we also prefer to retain *celebensis* as a full species.

Several of the specimens examined have numerous small – and occasional larger – unpigmented spots scattered over their wing membranes. The palatal ridge pattern normally consists of – from front to back – five undivided and three divided ridges and one thin, serrated ridge. In some specimens there are six undivided and two divided ridges; the central one of the the divided ridges may be a mere rudiment. One specimen (ZMA 22.766) has deformed metacarpals with rather strongly curved proximal ends.

Reproductive biology. — Two adult males (ZMA 22.696 and 22.968), purchased on 20 April and 14 September, have large testes. The female RMNH 33434, collected 26/27 January, carried an embryo with a forearm length of c. 15, another, purchased on 8 or 9 September (ZMA 22.967), an embryo with a forearm length of 25. A female mistnetted and released by FGR over Sungei Moinakom (Dumoga-Bone N. P.) on 27/28 January 1983 nursed a young. Immature but rather large specimens were bought on 18 and 24 January, 27 May, 17 June and 15 and 20 July. Two females bought on 17 June were nearly full-grown, with almost fused skull base sutures but with forearm lengths of 88.0 and 86.1 respectively.

REJECTED RECORDS

Pteropus melanopogon Peters, 1867

Pteropus melanopogon Peters, 1867: 330 – Amboina.

Discussion. — Jentink (1888: 142-143) listed three mounted specimens (*p*, *q* and *r*) from Sangihe and Siao under *Pteropus melanopogon*. Laurie & Hill (1954: 34) referred to Jentink's record; previously, the occurrence of the species on the Sangihe Islands was questioned by Andersen (1912: lxvi).

Only one skull can be located, which is referable to *P. hypomelanus*; all three skins are identified with that species. Consequently, *P. melanopogon* should be deleted from the list of Megachiroptera occurring in the Sangihe Islands.

Pteropus chrysoproctus Temminck

Pteropus chrysoproctus Temminck, 1837: 67, pl. 35 fig. 2; pl. 36 figs. 7, 8 – Amboina.

Remarks. — Jentink (1887: 258, specimen *f*; 1888: 144, specimen *v*) recorded *Pteropus chrysoproctus* from the Sangihe Islands ('Iles Sanghi'). The single specimen in question is a mounted adult male with a very incomplete skull. Andersen (1912: 263) possibly did not study the specimen himself but – although questioning the occurrence of *chrysoproctus* on Sangihe (see Andersen, 1912: lvi) – mentioned 'Sanghir Islands (Siao)' under the species' range as 'recorded in the literature'. Laurie & Hill (1954: 36) also mention 'Siao Island, Sanghir Islands', with Jentink (1887) as source. Van Strien (1986: 11) includes 'Sangir' in the range of the species.

We are not aware of other records of this species from Sulawesi or one of the off-lying islands under consideration. Hill (1983: 109) does not list the species in his short summary of Sulawesian *Pteropus* species on record. We examined the specimen identified by Jentink as *P. chrysoproctus* and found it to represent *Pteropus hypomelanus* Temminck, 1853; for details, see the account of that species in this paper. Consequently, *Pteropus chrysoproctus* should be deleted from the faunal list of Sulawesi and off-lying islands.

Pteropus personatus Temminck

Pteropus personatus Temminck, 1825: 189 – Ternate.

Specimens examined. — ZMB 4884, adult male, skull extracted, undated, 'Gorontalo, Celebes', leg. J. G. F. Riedel; ZMB 5387, adult female (skull only), undated, 'Celebes', leg. Schneider.

Discussion. — The above-listed specimens allegedly collected on Sulawesi agree in all repects with typical *personatus* from the North Moluccas, and were identified as such by Matschie (1899: 32; 1900: 270)*. However, as for the provenance of these two specimens it should be noted that both specimens are not adequately labelled; specimen ZMB 3587 was procured from a dealer who had 'ausgedehnte Geschäftsverbindungen bis in den Molukken' (Gebhart, 1964: 321); at present the accompanying skin cannot be located in the collections of the Zoologisches Museum Berlin (Dr. R. Angermann, in litt., 13.ii.1986). Riedel, although resident at Gorontalo between 1853 and 1878

[Footnote]* A previous reference '(und Celebes)' under *Pteropus personatus* in Peters (1867: 329) refers to an erroneous synonymization of *Styloctenium wallacei* with *Pteropus personatus*.

(Meyer & Wiglesworth, 1898: 4) may well have obtained specimen ZMB 4884 from another locality since he had collectors working for him in various parts of the Moluccas. In view of these considerations we consider the provenance of the two specimens questionable and propose to delete the species from the list of Sulawesian Megachiroptera.

FIELD KEY TO ADULT SPECIMENS OF SULAWESIAN MEGACHIROPTERA, BASED ON EXTERNALLY VISIBLE CHARACTERS

1 a. Upper side of muzzle with contrasting stripe or band of white fur . 2
b. Fur on upper side of muzzle not strongly contrasting with surrounding fur 3
2 a. Wing membranes from sides of back; first finger with claw; 2 lower incisors; forearm length 96-104 ..... *Styloctenium wallacei*
b. Wing membranes from near middle of back; first finger without claw; 4 lower incisors; forearm length about 100-110 ..... *Neopteryx frosti*
3 a. Forearm length more than 105 4
b. Forearm length less than 105 10
4 a. First finger with claw; wing membranes from sides of back 5
b. First finger without claw; wing membranes from spinal line, covering back fur completely 9
5 a. M^1 with distinct antero-internal cusp; M_1 and M_2 with inner basal ledges; forearm length 130-141 ..... *Acerodon celebensis*
b. M^1 without antero-internal cusp; M_1 and M_2 without inner basal ledges 6
6 a. Forearm length 160-175 ..... *Pteropus alecto*
b. Forearm length less than 155 7
7 a. Ear relatively long and pointed, reaching back of eye when laid forward; forearm length 135-144 ..... *Pteropus caniceps*
b. Ear relatively short and not pointed, not reaching back of eye when laid forward; forearm length 118-146 8
8 a. Forearm length 128-146 ..... *Pteropus hypomelanus*
b. Forearm length 118-128 ..... *Pteropus griseus*
9 a. M_1 with distinct antero-internal cusp or ledge ... *Dobsonia crenulata*
b. M_1 without antero-internal cusp or ledge ..... *Dobsonia exoleta*
10 a. Forearm length 38-42; rostrum and tongue long and narrow ..... *Macroglossus minimus*
b. Forearm length 43 or more; if less than 60, then rostrum and tongue short and broad 11

11 a. External tail distinctly present 12
b. External tail rudimentary (a mere knob) or absent 19
12 a. First finger without claw 13
b. First finger with claw 14
13 a. Wing membranes from spinal line, covering back fur completely; forearm in single known Sulawesian specimen 78.5; (at most) 2 upper and 2 lower incisors ..... *Dobsonia minor*
b. Wing membranes from sides of back; forearm length 65-77; 4 upper and 4 lower incisors ..... *Eonycteris spelaea*
14 a. Nostrils projecting as cylindrical tubes from upper surface of muzzle; ears and wing membranes spotted with yellow; no lower incisors . 15
b. Nostrils not projecting as cylindrical tubes; ears and wings wholly dark; 4 lower incisors 16
15 a. Forearm length 60-70 ..... *Nyctimene cephalotes*
b. Forearm length about 50 ..... *Nyctimene minutus*
16 a. Rostrum short and broad; ear margin (and often phalanges) marked with white; forearm length 59-69; tail 6-11; 4 upper and 5 lower cheek teeth ..... *Cynopterus brachyotis*
b. Rostrum long; ears and phalanges wholly dark; forearm 72 or more; tail 12 or more; 5 upper and 6 lower cheek teeth 17
17 a. Forearm length 94-104 *Rousettus bidens* b. Forearm length 85 or less 18
18 a. Tail membrane dorsally naked; forearm length 73-85 .... *Rousettus amplexicaudatus*
b. Tail membrane dorsally densely furred; forearm length 72-78 .....
19 a. Forearm length 43.8-46.5; fur of breast and belly yellowish .... *Chironax melanocephalus*
b. Forearm length 71 or more; fur of breast and belly very dark 20
20 a. Forearm length 71-82; 4 upper and 4 lower incisors; cheek teeth relatively simple ..... *Thoopterus nigrescens*
b. Forearm length 83-93; 2 upper and 2 lower incisors; cheek teeth multicuspidate ..... *Harpyionycteris celebensis*

DISCUSSION

Most of the recently collected fruit bats reported here originate from the eastern part of the northern peninsula of Sulawesi; in fact, the majority was collected inside or bought just outside the boundaries of the Dumoga-Bone National Park. Altogether 26 fruit bat species have been recorded from Sulawesi (see the taxonomic section in this paper). Three of those are not tenable: records of *Pteropus melanopogon* and *Pteropus chrysoproctus* appeared to be based on misidentified specimens and that of *Pteropus personatus* on two specimens of doubtful provenance. The latter species is known to be quite common in those areas where it does occur (personal observation by FGR on Ternate, Bacan and Halmahera) and the fact that it has never been collected in Sulawesi since that first doubtful record renders it unlikely that it really occurs there. Until new and irrefutable evidence becomes available, we prefer to delete *Pteropus personatus* from Sulawesi's faunal list. Two other taxa of the list of 26 have been synonymized: *Cynopterus minor* with *C. brachyotis*, and *Eonycteris rosenbergii* with *E. spelaea*. Of the remaining list of 21 Sulawesian fruit bat species, 14 are known to occur in the Dumoga Bone National Park area – among which two Sulawesian endemic genera and at least six endemic species and subspecies –, while six others have not been found there yet. The latter six are *Pteropus caniceps dobsoni* of which the occurrence in Sulawesi is in need of confirmation; *Pteropus griseus mimus*, a quite poorly known species recorded from Luzon and Ujung Pandang (Andersen, 1912) and therefore not unlikely to occur in northern Sulawesi; *Pteropus hypomelanus*, recorded from northern Sulawesi (Andersen, 1912; this paper) but possibly restricted to coastal areas and smaller islands; *Dobsonia crenulata* (recorded as subspecies of *D. viridis* by Hill, 1983: 111) and *Dobsonia minor*, both only recently discovered in Sulawesi and to be expected at other than the known localities, possibly also in northern Sulawesi; and *Nyctimene minutus* Andersen, 1910, based on a single specimen collected in 1859 by A.R. Wallace in Tondano, northeast Sulawesi, and never rediscovered on that island. Thus, with its recorded megachiropteran fauna, the Dumoga-Bone National Park is obviously very important for the conservation of this segment of the unique natural heritage of Sulawesi and, in view of the role fruit bats play in the reproduction and dispersal of a considerable number of trees and other plant species, for the conservation of the Sulawesian rain forest at large.

Many of the fruit bats on which this report is based were bought on the food market of the village of Imandi, situated on the edge of the Tambun forest where no doubt many of them were caught. The local people have hunted and eaten fruit bats for many years – if not centuries. Heinrich (1943: 106-107,

figure) reports on an encounter, in 1931, with a bat hunter in northeast Sulawesi who told him that on favourable nights he netted as many as 50 specimens, or even more. Today, hunting seems still to be carried out exclusively with nets (R. Dekker, pers. obs.). The bats in the market are always freshly killed from the preceding night, apparently never shot but netted and killed by hitting them on the back of the head (which renders a number of them less suitable for taxonomic work because it may break their skulls quite badly). On the market of Ujung Pandang, on 15 January 1982, one of us (WB) counted about a hundred live *Pteropus alecto*, offered for sale by a single trader who told they were from Bulukumba, which for the most part were virtually undamaged and thus had apparently also been netted. The market in Imandi occasionally also yielded insectivorous bats, such as the relatively large *Cheiromeles parvidens* Miller & Hollister, 1921. In the streets of Manado, FGR regularly observed numbers of *Acerodon celebensis* offered for sale alive. (In the North Moluccas, hunters regularly visit large roosts of *Pteropus* species, e.g. those of *P. conspicillatus* Gould, 1850, on small islands of Bacan, and large numbers are shot with air rifles for consumption, with the aid of powerful torches. On a smaller scale, numbers of *Dobsonia* are netted when visiting fruiting trees in gardens; these are also collected in numbers from accessible caves).

Most, if not all, fruit bat populations in the region have apparently survived this steady human predation until today. Yet, with the area of essentially undisturbed rain forest steadily shrinking and the pressure from the increasing human population mounting, there must come a moment when this demand will become a threat to the survival of the more vulnerable species. The apparent rarity of some *Pteropus* species, not only in this area but also in other islands where the forest is under pressure from cultivation and where fruit bats are hunted, e.g. Bali, may in part be due to overhunting. (An extralimital example is offered by Wheeler, 1980, who lists overhunting, loss of habitat and typhoons as factors contributing to the decline of *Pteropus mariannus* Desmarest, 1822, in the Marianas). In the particular case of the Dumoga-Bone National Park, some endemic Sulawesian species believed to be generally uncommon or of restricted distribution are involved, such as *Neopteryx frosti* and *Rousettus bidens*. Therefore it seems worthwhile to include such potential fruit bat conservation problems explicitly in management guidelines and practices for such valuable national parks as Dumoga-Bone.

Although the collections reported upon in this paper have contributed to a better knowledge of a number of hitherto poorly known Sulawesian fruit bats, many questions remain. Most of the bats were collected in northern Sulawesi

and on the Sangihe Islands, and some dozens in south-west Sulawesi. In some species differences were found between northern and south-western representatives: northern *Pteropus hypomelanus* are larger than south-western specimens, and south-western *Cynopterus brachyotis*, *Thoopterus nigrescens* and perhaps *Pteropus alecto* average larger than their northern counterparts. Prolonged isolation of south-western forests may be an explanation but it seems wise to await the results of current work on a large collection of fruit bats from central Sulawesi by G. G. Musser (American Museum of Natural History) before elaborating on this. Central Sulawesian populations may turn out to be similar to northern ones, which would support the above suggestion; alternatively they may be intermediate, indicating clinal variation.

Finally, few fruit bats have hitherto been collected in, or at least reported from the eastern and southeastern peninsulas of Sulawesi. Collecting efforts in those parts would be worthwhile, as these would help establish a more complete view of the Sulawesian fruit bat fauna, and contribute to the study of the affinities with the bat fauna of the islands to the east of Sulawesi.

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GAZETTEER

Gazetteer of Sulawesian collecting localities mentioned in the text (see also maps, figs. 1-2).

The spelling of localities is in accordance with that adopted in the 'Gazetteer of Indonesia and Portuguese Timor' (2nd edition), issued by the Office of Geography, Department of the Interior, Washington (1968); co-ordinates of subcamps used during Project Wallace 1985 in the Dumoga-Bone National Park were established by British Army surveyors; other localities in the National Park (marked with an asterisk) were plotted from a detailed map (approximate scale 1: 100.000), prepared by the Project Wallace Survey Team (October 1985). Some localities have not been traced.

0°24′ N	123°22′ E	Ali, Gunung (Mount Ali)
1°11′ N	124°35′ N	Amurang
5°02′ S	119°40′ E	Bantimurong
0°32′ N	123°08′ E	Bone
4°48′ S	119°40′ E	Bulukumba
0°37′ N	123°51′ E	Clark's camp
1°38′ S	120°03′ E	Gimpoe (Laurie & Hill, 1954: 145)
0°31′ N	123°03′ E	Gorontalo
0°35′ N	123°51′ E	Edwards' camp
0°35′ N	123°52′ E	Hog's Back
0°35′ N	124°04′ E	Imandi*
0°52′ N	124°25′ E	Iloloi, Danau (Lake Ililoi)
0°43′ N	123°59′ E	Kabila, Gunung (Mt. Kabila), ridge to*
0°31′ N	123°56′ E	Kosinggolan, Sungei* (River Kosinggolan)
0°07′ N	124°05′ E	Kosio
1°45′ S	123°20′ E	Labobo, Pulau (Labobo I.)
		Lambuya (Lambuja)
0°26′ N	125°13′ E	Lembeh, Pulau (Lembeh I.)
		Lotta, Masarang: see Masarang
1°16′ S	123°26′ E	Luksagu, desa (Luksagu village)
0°20′ N	122°05′ E	Malenge, Pulau (Malenge I.)
5°15′ S	119°51′ E	Malino
1°30′ N	124°50′ E	Manado (Menado)
1°44′ N	124°44′ E	Manterawu, Pulau (Manterawu I.)
3°49′ S	119°15′ E	Mario, Iuwu
5°06′ S	120°05′ E	(or) Mario, Iuwu
5°00′ S	119°34′ E	Maros
5°28′ S	120°04′ E	Masarang
0°41′ N	124°02′ E	Mauk, Sungei (Mauk River), upper tributary of*

0°40′ N	124°04′ E	Moinakom, Sungei (Moinakom River)*
0°22′ N	123°59′ E	Mooat, Danau (Lake Mooat)
0°45′ N	124°25′ E	Muajat, Gunung (Mt. Muajat)
		Navusu, Kuala: see Parigi
3°00′ S	120°12′ E	Palopo
0°49′ S	120°01′ E	Parigi
1°20′ S	123°10′ E	Peleng, Pulau (Peleng I.)
1°51′ S	121°30′ E	Ranu, Sungei (Ranu River)
6°05′ S	120°30′ E	Salayar, Pulau (Salayar I.)
3°35′ N	125°32′ E	Sangihe, Pulau (Sangihe I.)
3°32′ N	125°32′ E	Sahendaruman, Gunung (Mt. Sahendaruman)
2°42′ N	124°24′ E	Siao, Pulau (Siao I.)
2°33′ S	121°22′ E	Soroako
1°50′ N	125°04′ E	Talisai, Pulau (Talisai I.)
1°20′ S	119°46′ E	Tamalanti
0°35′ N	124°05′ E	Tambun*
1°39′ S	121°22′ E	Tambusisi Damar
1°29′ N	125°09′ E	Tangkoko-Batuangus reserve
		Titaeli
0°20′ S	122°00′ E	Togian, Kepulauan (Togian Is.)
1°19′ N	124°49′ E	Tomohon
0°34′ N	123°54′ E	Toraut base camp and rentis area
0°31′ N	123°16′ E	Tulabolo
0°31′ N	123°56′ E	Tumokang Lama, Sungei (Tumokang Lama River)*
5°08′ S	119°24′ E	Ujung Pandang (formerly Makassar)
2°35′ S	121°16′ E	Wasupondo
2°38′ S	121°21′ E	Wawondula

REFERENCES

Andersen, K., 1907. On Pterocyon, Rousettus, and Myonycteris. Ann. Mag. nat. Hist. (7) 19: 501-515.

Andersen, K., 1908. Twenty new forms of Pteropus. Ann. Mag. nat. Hist. (8) 2: 361-370.

Andersen, K., 1909. On the fruit bats of the genus Dobsonia. Ann. Mag. nat. Hist. (8) 4: 528-533.

Andersen, K., 1910. Ten new fruit-bats of the genera Nyctimene, Cynopterus and Eonycteris.— Ann. Mag. nat. Hist. (8) 6: 621-625.

Andersen, K., 1912. Catalogue of the Chiroptera in the collection of the British Museum. I. Megachiroptera: i-ci, 1-854. London.

Boeadi & W. Bergmans, 1987. First record of *Dobsonia minor* (Dobson, 1879) from Sulawesi, Indonesia (Mammalia, Megachiroptera). — Bull. Zool. Mus. Univ. Amsterdam 11: 69-74, table 1.

Dobson, G. E., 1879. Notes on recent additions to the collection of Chiroptera in the Muséum d'Histoire Naturelle at Paris, with descriptions of new and rare species. Proc. Zool. Soc. Lond. for 1879: 873-880.

Elera, R. P. Fr. Casto de, 1895. Catálogo sistemático de toda la fauna de Filipinas conocida hasta el presente, y á la vez el de la colección zoológica del museo de p. p. dominicos del colegio-universidad de Santo Tomas de Manila, escrito con motivo de la exposición regional Filipina. Manila. Vol. 1: vertebrados. i-viii, 1-701. Manila.

Fooden, J., 1969. Taxonomy and evolution of the monkeys of Celebes (Primates: Cercopithecidae): i-vii, 1-148. Basel & New York.

Gebhart, L., 1964. Die Ornithologen Mitteleuropas. 1-403. Giessen.

Geoffroy, E., 1810. Description des rousettes et des cephalotes, deux nouveaux genres de la famille des chauve-souris. Ann. Mus. Hist. Nat. Paris 15: 86-108, 4 pls.

Goodwin, R. E., 1979. The bats of Timor: systematics and ecology. — Bull. Amer. Mus. Nat. Hist. 163: 75-122, figs. 1-4.

Gray, J. E., 1866. A revision of Pteropine bats (Pteropidae), and the descriptions of some apparently undescribed species. Proc. Zool. Soc. Lond. for 1866: 62-67, figs. 1-2.

Gray, J. E., 1870. Catalogue of monkeys, lemurs and fruit-eating bats in the collection of the British Museum: i-viii, 1-137. London.

Hayman, R. W., 1946. A new genus of fruit-bat and a new squirrel, from Celebes. — Ann. Mag. nat. Hist. (11) 12: 569-578.

Hasselt, J. C. van, 1823. [Abstract of letter.] — Algemeene Konst- en Letter-Bode voor het jaar 1823, no. 48: 341-342.

Heinrich, G., 1943. Der Vogel Schnarch. Zwei Jahre Rallenfang und Urwaldforschung in Celebes. Zweite Auflage. 1-198, 63 figs. Berlin.

Heude, P. M., 1896. Etudes odontologiques. Seconde partie. Mammifères carnassiers. Chapitre 4. Mammifères volants. — Mém. Hist. nat. Emp. Chin. 3: 175-187, pl. 5; Chang-Hai.

Hill, J. E., 1961. Fruit-bats from the Federation of Malaya. — Proc. zool. Soc. Lond. 136: 629-642, fig. 1, tabs. 1-4.

Hill, J. E., 1974. New records of bats from southeastern Asia, with taxonomic notes. — Bull. Br. Mus. nat. Hist. (Zool.) 27: 127-138.

Hill, J. E., 1983. Bats (Mammalia: Chiroptera) from Indo-Austra lia. — Bull. Brit. Mus. nat. Hist. (Zool.) 45: 103-208, tabs. 1-14.

Hill, J. E. & C. M. Francis, 1984. New bats (Mammalia: Chiroptera) and new records of bats from Borneo and Malaya. — Bull. Br. Mus. nat. Hist. (Zool.) 47: 305-329,figs. 12, tabs. 1-4.

Jentink, F. A., 1879. On a new genus and species of bat from Celebes. — Notes Leyden Mus. 1: 117-119.

Jentink, F. A., 1883. List of species of mammals from West-Sumatra and North-Celebes, with descriptions of undescribed or rare species. — Notes Leyden Mus., 1: 170-181.

Jentink, F. A., 1887. Catalogue ostéologique des mammifères. — Muséum d'Histoire Naturelle des Pays-Bas 9: 1-360, 12 pls. Leiden.

Jentink, F. A., 1888. Catalogue systématique des mammifères. — Muséum d'Histoire Naturelle des Pays-Bas 12: 1-280. Leiden.

Jentink, F. A., 1889. On a new genus and a new species in the macroglossine-group of bats. — Notes Leyden Mus. 11: 209-212, pl. 9, figs. 1-4.

Jentink, F. A., 1890-1891. Rodentia, Insectivora, Chiroptera. In: Weber, M., Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien. I, 4: 115-130. Leiden.

Jong, N. de, & W. Bergmans, 1981. A revision of the fruit bats of the genus *Dobsonia* Palmer, 1898 from Sulawesi and some nearby islands (Mammalia, Megachiroptera, Pteropodinae).— Zool. Abh. Staatl. Mus. Tierk. 37: 209-224.

Laurie, E. M. O., & J. E. Hill, 1954. List of land mammals of New Guinea, Celebes and adjacent islands 1758-1952: 1-175, 1 map, 3 pls. London.

Lawrence, B., 1939. Collections from the Philippines Islands. Mammals.— Bull. Mus. comp. Zool. Harvard 86: 28-73.

Lekagul, B. & J. A. McNeely, 1977. Mammals of Thailand. i-li, 1- 758, figs, map. Bangkok.

Matschie, P., 1899. Die Megachiroptera des Berliner Museums für Naturkunde: i-viii, 1-102, errata, maps I-II, pls. 1-14. Berlin.

Matschie, P., 1900. Die Säugetiere der von W. Kükenthal auf Halmahera, Batjan und Nord-Celebes gemachten Ausbeute.— Abh. Senckenb. naturf. Ges. 25: 247-295, pls. 11-13.

Medway, Lord, 1969. The wild mammals of Malaya and offshore islands including Singapore. i-ix, 1-127, figs. Kuala Lumpur.

Medway, Lord., 1977. Mammals of Borneo. i-xii, 1-172, figs. Kuala Lumpur.

Meyer, A. B., 1899. Säugetiere vom Celébes und Philippinen-Archipel. 2. Celebes-Sammlungen der Herren Sarasin.— Abh. Ber. Zool. Anthrop.- Ethnogr. Mus. Dresden 7: 1-55.

Meyer, A. B. & L. W. Wiglesworth, 1898. The birds of Celebes and neighbouring islands 1: i-xxxii, 1-392, 7 maps, pls. 1-17. Berlin.

Miller, G. S., 1907. The Families and Genera of Bats.— U. S. nat. Mus. Bull. 57: i-xvii, 1-282, pls. I-XIV.

Miller, G. S. & N. Hollister, 1921. Twenty new mammals collected by H. Raven in Celebes. Proc. Biol. Soc. Wash. 34: 93-104.

Müller, S., 1838. Over eenige nieuwe zoogdieren van Borneo. Tijdschr. Natuurl. Gesch. Physiol. 5: 134-150.

Musser, G. G., K. F. Koopman & D. Califia, 1982. The Sulawesian Pteropus arquatus and P. argentatus are Acerodon celebensis; the Philippine P. leucotis is an Acerodon.— J. Mammal. 63: 319-328.

Pallas, P. S., 1767. Spicilegia Zoologica. Berlin.

Payne, J., C. M. Francis & K. Phillips, 1985. A field guide to the mammals of Borneo: 1-332, pls. Kota Kinabalu and Kuala Lumpur.

Peters, W., 1867. Über die Flederhunde, Pteropi, und insbesondere über die Arten der Gattung Pteropus s. s..— Monatsber. Königl. preuss. Akad. Wiss. Berlin 1867: 319-333.

Peterson, R. L., & M. B. Fenton, 1970. Variation in the bats of the genus Harpyionycteris, with the description of a new race.— Life Sci. Occ. Pap. Roy. Ont. Mus. 17: 1-15, figs. 1-4, tabs. 1-3.

Phillips, C. J., 1967. A collection of bats from Laos.— J. Mammal. 48: 633-636.

Revilliod, P., 1911. Über einige Säugetiere von Celebes.— Zool. Anz. 37: 513-517.

Rookmaaker, L. C. & W. Bergmans, 1981. Taxonomy and geography of Rousettus amplexicaudatus (Geoffroy, 1810) with comparative notes on sympatric congeners (Mammalia, Megachiroptera).— Beaufortia 31: 1-29, figs. 1-3, tabs. 1-6.

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. Med. Leiden 58: 187-212, figs. 1-5, tabs. 1-7.

Slaughter, B. H., 1970. Evolutionary trends of chiropteran dentitions. In: B. H. Slaughter & D. W. Walton (eds.), About bats: 51-83, figs. 1-5. Dallas.

Strien, N. J. van, 1986. Abbreviated checklist of the mammals of the Australasian Archipelago: i-vii, 1-91. Bogor.

Tate, G. H. H., 1942. Pteropodidae (Chiroptera) of the Archbold collections. – Bull. Amer. Mus. nat. Hist. 80: 331-347.

Taylor, E. H., 1934. Philippine land mammals. — Philippine Bur. Sci. Monogr. 30: 1-548, pls. 1-25.

Temminck, C. J., 1824-1841. Monographies de Mammalogie, ou description de quelques genres de mammifères, dont les espèces ont été observées dans les differens musées de l'Europe. (Vol. I 1824-1827; vol. II 1835-1841). Paris.

Thomas, O., 1896. Mammals from Celebes, Borneo, and the Philippines recently received at the British Museum. — Ann. Mag. nat. Hist. (6) 18: 241-250.

Walker, E. P., F. Warnick, K. I. Lange, H. E. Uible, S. E. Hamlet, M. A. Davis & P. F. Wright, 1964. Mammals of the world. I: i-xlviii, 1-644, figs, 5 tables. Baltimore.

Wheeler, M. E., 1980. The status of the Marianas fruit bat on Saipan, Tinian, and Rota. – J. Hawaii Audubon Soc. 40: 109- 113.