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Revision of the Genus *Melonycteris* (Pteropodidae: Mammalia)

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ABSTRACT. The genus *Melonycteris* consists of three species: *M. melanops* Dobson, 1877, *M. woodfordi* (Thomas, 1887), and *M. fardoulisi* n.sp. *Melonycteris melanops* is monotypic and widespread in the Bismarck Archipelago. It is orange in colour, and is unique in the genus in retaining a claw on digit two of the wing and in having P^1 and M_3 reduced. *Melonycteris woodfordi* is an orange-coloured species also, which is found in the northern and eastern Solomon Islands, and consists of two subspecies (the smaller *M. w. woodfordi*, found on the islands from Buka to Ysabel, and the larger *M. w. aurantius* on the Nggela Group). *Melonycteris w. aurantius* is unique in the genus in that females are usually larger than males, while in *M. w. woodfordi* the sexes are similar in size. *Melonycteris fardoulisi* n.sp. is a predominantly brownish species in which the sexes differ in colour and where males are markedly larger than females. It is distributed in the western and southern islands of the main Solomons chain, and includes four subspecies (*M. f. fardoulisi* n.subsp. from Makira, *M. f. maccoyi* n.subsp. from Malaita, *M. f. schouteni* n.subsp. from Guadalcanal and *M. f. mengermani* n.subsp. from Western Province). The subspecies differ in size, colour and degree of sexual dimorphism.

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Species of the genus *Melonycteris* are endemic to the Bismarck Archipelago and Solomon Islands, Melanesia. They are brightly-coloured bats, often having profuse pink spotting on their black wing membranes. The dorsal fur can be bright orange, and white 'epaulettes' may be present. They are members of the subfamily Macroglossinae and are nectar feeders, Kress (1985) demonstrating that on Guadalcanal at least the blossoms of *Heliconia solomonensis* are visited. The first of these distinct bats to be described was *Melonycteris melanops* Dobson, 1877 (syn. *Pteropus* (*Cheiropteruges*) *alboscapulatus* Ramsay, 1877). This species is now known to occur on many islands of the Bismarck Archipelago (Fig.1). In 1887 Thomas described a new genus and species, *Nesonycteris woodfordi*, from Alu Island (the type locality) and nearby Fauro Island in the Shortland Group, northern Solomons. Pohle (1953) recognised the close similarity between species of *Nesonycteris* and *Melonycteris*, and suggested that *Nesonycteris* should be placed in synonymy with *Melonycteris*, the older and thus correct generic name. All subsequent workers have accepted this synonymy.

A third species of *Melonycteris*, *M. aurantius* was

described by Phillips (1966), based upon one adult female (the holotype) from Florida Island in the Nggela Group and five subadult female paratypes from Choiseul, Solomon Islands. Phillips suggested that *M. woodfordi* and *M. aurantius* occurred in sympatry as both species were supposedly taken in the same net on Choiseul. Phillips (1968) listed four specimens of *Melonycteris woodfordi* which were also supposedly from Choiseul.

The only other primary literature records for species of *Melonycteris* are those of McKean (1972) who described nine specimens of *M. woodfordi* from various locations on Bougainville; Sanborn (1931) who notes a specimen from the Russell Islands; and Smith & Hood (1981), who mention that *M. melanops* was localised but relatively abundant in their study areas on New Britain and New Ireland. They mention the capture of 13 individuals in a single net at one locality.

This research is based primarily upon material collected by myself and others in the Bismarck Archipelago and the Solomon Islands during 1987-1991. The Australian Museum now holds 129 specimens of *Melonycteris*, most of which were collected during this period. Examination of this material revealed that existing taxonomic concepts are incorrect, and that both taxonomic diversity was greater, and zoogeographic patterns quite different, from that previously described.

Materials and Methods

In addition to the holdings of the Australian Museum I borrowed extensively from the collections of the Bishop Museum and the Australian Nation Wildlife Collection during the course of this study. During an overseas study tour in 1989 I also examined all *Melonycteris* specimens available in the American Museum of Natural History; Bishop Museum; British Museum (Natural History); and Los Angeles County Museum. Thus most, if not all, world museum holdings of *Melonycteris* were examined.

All of the AM M specimens collected during the 1987, 1990 and 1991 expeditions to the Solomon Islands were captured in mistnets. Despite considerable efforts neither hunting nor searching by local people were successful in obtaining *Melonycteris* specimens.

Measurements throughout are given in millimetres and weights in grams. Specimen number prefixes are as follows AM – Australian Museum; AMNH – American Museum of Natural History; BM – Bishop Museum; BMNH – Natural History Museum (London); CM – National Wildlife Collection (Canberra); LACM – Los Angeles County Museum. Specimens used in the morphometric analysis are marked with an asterisk. Colours where capitalised follow Smithe (1974). The STATISTIX package was used for statistical analysis, and results of 't' tests were considered significant at the level given assuming unequal variances unless otherwise stated. Primary data will be supplied upon request to the

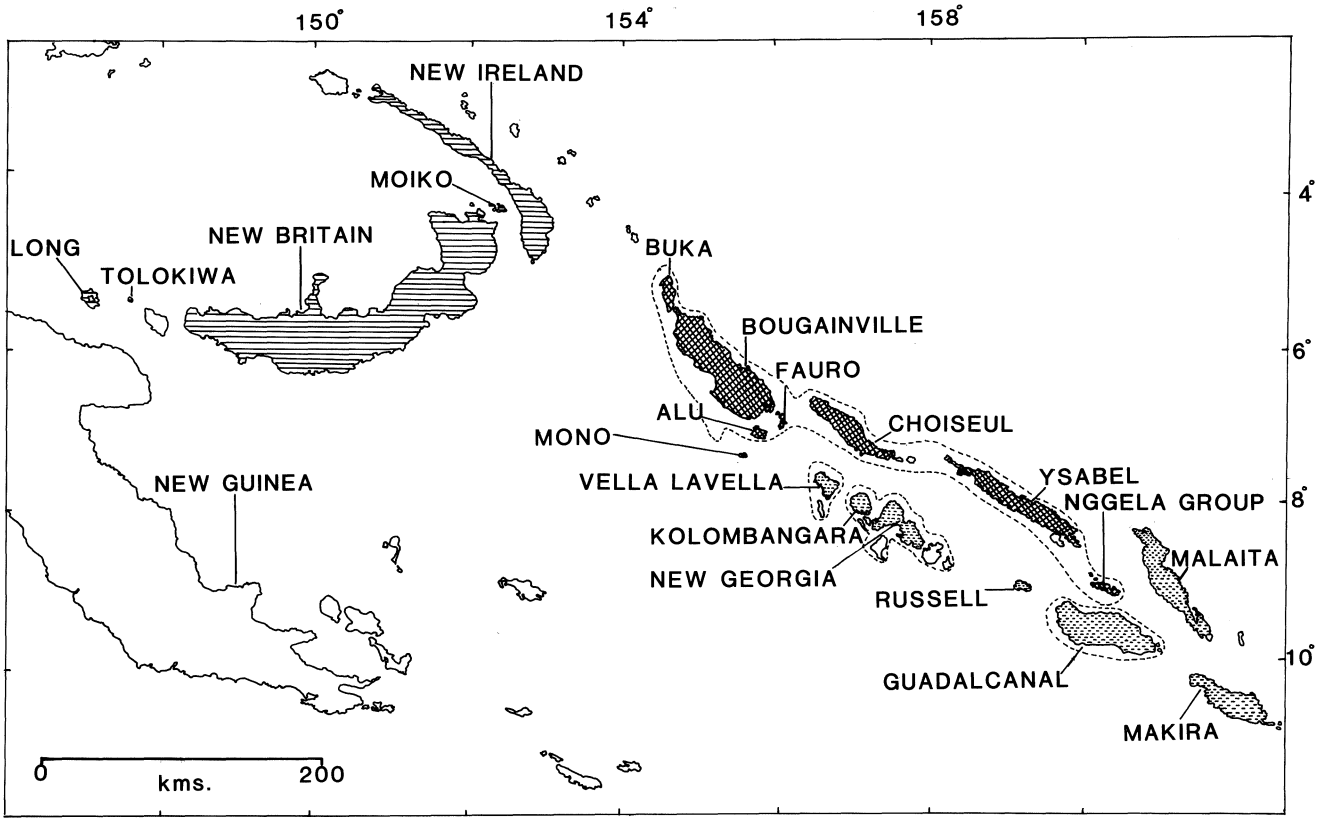

Fig.1. The distribution of the species of *Melonycteris*, including localities mentioned in the text. Horizontal bar = *M. melanops*, hatching = *M. woodfordi*, spotting = *M. fardoulisi*.

author.

Tables 1-5 are included in the Appendix.

Systematics

Pteropodidae

Macroglossinae

Melonycteris Dobson, 1877

Melonycteris melanops Dobson, 1877

Figs 2,4, Table 1

Type material. HOLOTYPE, BM 77.7.18.10, skin and skull of an adult male collected on New Ireland by the Rev. G. Brown.

Synonym. *Pteropus* (*Chieropteruges*) *alboscapulatus* Ramsay, 1877. Holotype AM P1271* (Palmer register), adult male skin with skull inside. The locality given by Ramsay (in the title of the paper only) is Duke of York Island. A label accompanying the specimen marked as the holotype reads as follows "Loc. New Ireland, Bismarck Archipelago. Hab. Duke of York and New Ireland, Bismarck Arch." The specimen was collected by the Rev. George Brown. The specimen marked as the holotype matches in colour and measurements the specimen described by Ramsay.

Other specimens examined. New Ireland; AM M19638*, AM M19933*, AM M20061*, AM M20114*, LACM67048, LACM67054, LACM67062, LACM67065. New Britain; AM M20063*, AM M20064*, AM M20163, AM M201644*, LACM65777. Locality unknown AM M2417*. Long Island AMNH 237311, Tolokiwa Island AMNH 237312.

Diagnosis. *Melonycteris melanops* can be distinguished from other species of *Melonycteris* in possessing the following features: shoulders with white epaulettes; base of fur black, and venter darker; digit 2 of wing clawed; P^1 rudimentary, M_3 is greatly reduced in size (Fig.4).

It further differs from *M. fardoulisi* in that the dorsum is more rufescent, and the sexual dimorphism in the canine and sagittal crest is not as great. It differs further from *M. woodfordi* in that males usually possess a larger sagittal crest.

Distribution. Confined to the Bismarck Archipelago, where it has been recorded from the islands of New Ireland, New Britain, Long, Tolokiwa, and Moiko (in the Duke of Yorks, and possibly other islands in that group). Recent surveys of Manus Island and northern New Guinea by the author have confirmed the absence of this species and indeed any other members of the genus at these localities.

Discussion. Although only small numbers are available, it appears that there is little morphological variation between the New Britain, Duke of York and New Ireland samples of *M. melanops*. Some specimens from New Ireland have a less brilliant orange dorsum and a smaller white epaulette than New Britain animals, but populations from the two islands do not differ consistently in these or other features. Table 1 indicates that New Ireland animals may be slightly smaller in interorbital and postorbital width, but larger in C^1-M^2 length. These differences however may simply reflect age differences and small sample size (the postorbital width at least decreases with age in *M. woodfordi*, the only species for

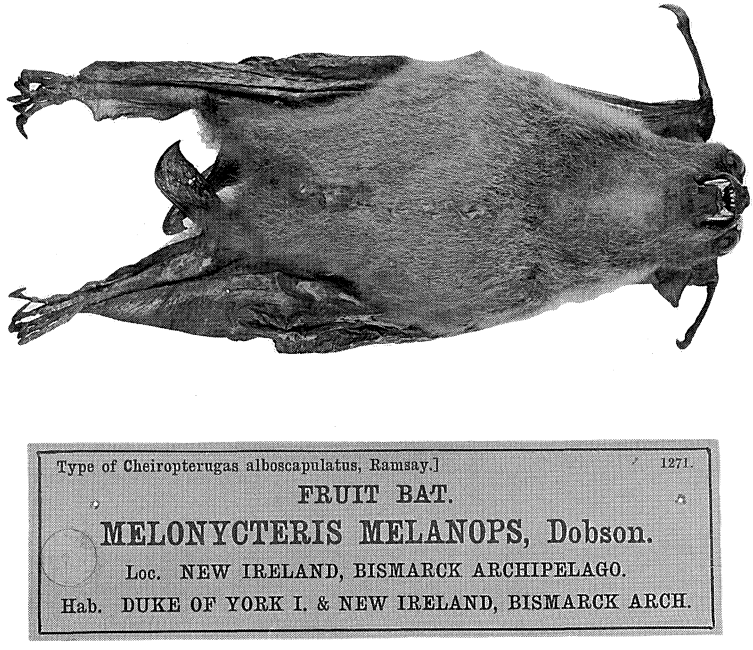

Fig.2. Holotype (AM P1271) of *Cheiropteruges alboscapulatus* Ramsay.

which large samples are available, see below). The single specimen examined from Tolokiwa Island is small in condylobasal length and bizygomatic width relative to animals from elsewhere. However, it is typical of the species in its pelage and morphology. The single skin without skull from Long Island is also typical in colour for the species. Further samples are necessary to determine if the metric differences discussed here are typical for the various island populations. However, the differences appear slight and do not seem to warrant taxonomic recognition.

I have found *Melonycteris melanops* to be uncommon both on New Ireland and New Britain, with a total of only eight specimens being taken during extensive mammal surveys of both islands. Smith & Hood's (1981) observations, however, suggest that the species can sometimes be locally abundant.

Melonycteris woodfordi (Thomas, 1887)

Figs 3,6-8, Table 2

Type material. HOLOTYPE, BM 87.1.18.9*, adult male skin and skull collected at Alu, Shortland Islands by C.M. Woodford.

Diagnosis. *Melonycteris woodfordi* differs from *M. melanops* in possessing larger P^1 and M_3 and in lacking white epaulettes, black underfur, and a claw on digit 2. It differs from *M. fardoulisi* n.sp. in being orange rather than brownish dorsally and having no difference in colour between the sexes, sagittal crest less well developed in adult males (except for some *M. w. aurantius*), males not significantly larger than females (at P less than 0.10) in condylobasal length and cheektooth length, and sexual dimorphism in bizygomatic width, canine length, and canine morphology less pronounced (Tables 2-4, Fig.3).

Discussion. *Melonycteris woodfordi* is known from many islands in the northern part of the Solomon Island chain, and is presumably widespread throughout that region. It has been recorded from the islands of Buka, Bougainville, Mono, Oblari, Alu, Fauro, Choiseul, Ysabel, Russel, Nggela and Florida. (Fig.1). Within this distribution two distinct subspecies can be distinguished: *M. w. woodfordi* of Buka, Bougainville, Mono, Alu, Fauro, Choiseul, and Ysabel; and *M. w. aurantius* from Nggela and Florida.

Melonycteris woodfordi woodfordi (Thomas, 1887)

Figs 3-5, Table 3

Other specimens examined. Buka: AM M19816*.

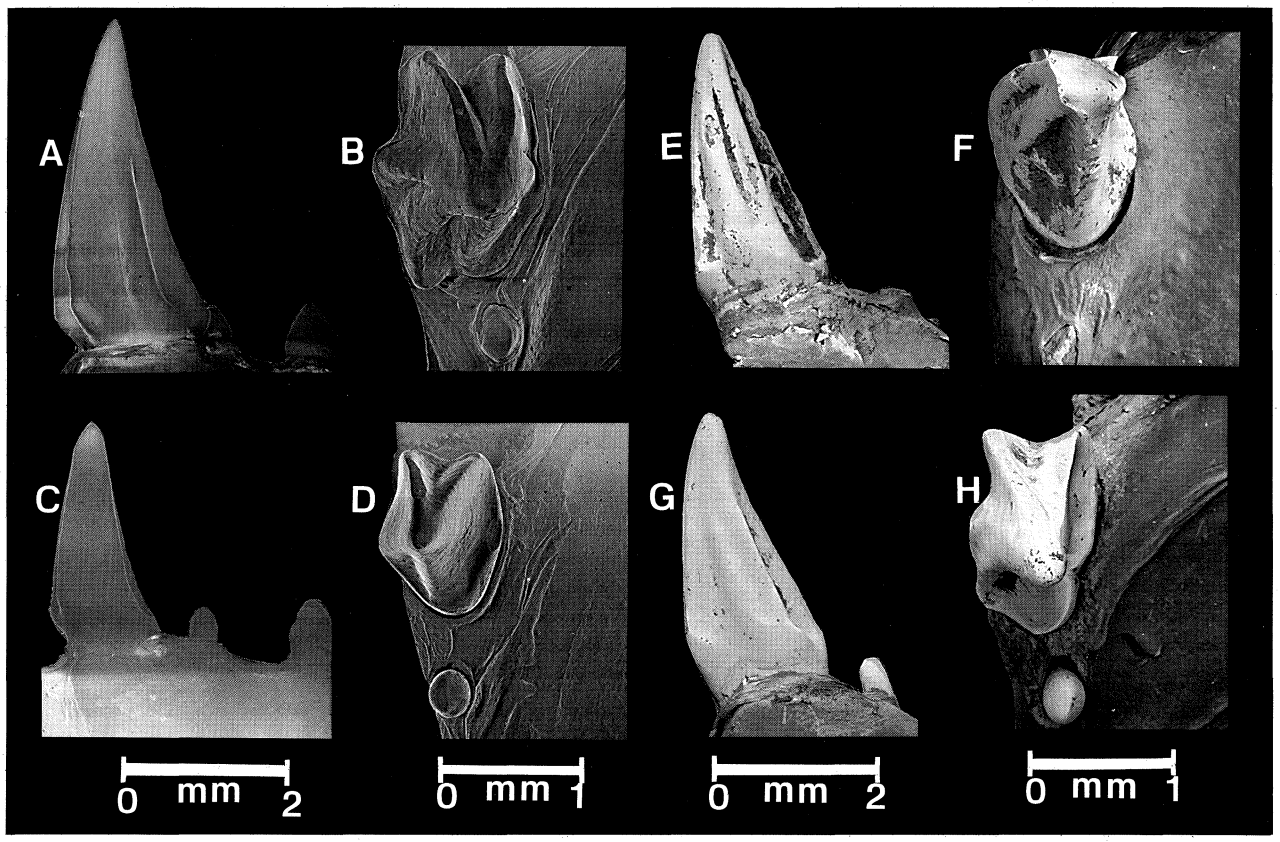

Fig.3. The canines of *Melonycteris fardoulisi fardoulisi*: A, B – AM M18833 male, and C, D – AM M18849 female. Canines of *Melonycteris woodfordi woodfordi*: E, F – AM M6576 male, G, H – AM M6298 female.

Bougainville: AM M6289*, AM M6532, AM M6576*, AM M6577, AM M6653, AM M6654, AM M6655, AM M6656; CM583*, CM584*, CM585*, CM586*, CM587*, CM588*, CM589, CM590*, CM591*; BM22357, BM61083, BM61085, BM61087*, BM61105, BM61167*, BM61160*, BM61276*, BM61303*. Mono: AM M23185, AM M23816, AM M23787, AM M23788, AM M23790*, AM M23791*, AM M23792, AM M23793, AM M23809*, AM M23810*, AM M23811*, AM M23812*, AM M23815*, AM M23816*, AM M24194, AM M24195, AM M24196, AM M24197, AM M24198, AM

Fig.4. A, the cranium of a male (AM M20061), and B, female (AM M20114) *Melonycteris melanops*, C, cranium of a male (AM M6576), and D, female (AM M6289) *Melonycteris woodfordi woodfordi*.

M24199, AM M24200, AM M24201, AM M24202, AM M24203, AM M24204, AM M24205, AM M24026, AM M24027, AM M24028, AM M24029, AM M24210, AM M24211, AM M24212, AM M24213, AM M24214, AM M24215, AM M25055, AM M25216. Oblari Island (Shortlands): AM M23784, AM M23785*, AM M23786*, AM M23789*, Choiseul: AM M18828*, AM M18829*, AM M18844*, AM M18845*, AM M18846*, AM M21807*, AM M21808*, AM M21809*, AMNH 99916; BM23615, BM23617, BM23558, BM23681, BM23694. Ysabel: AM M18837*, AM M18838*, AM M18839, AM M18840, AM M18842*, AM M18847*, AM M18868, AM M21810, AM M21811, AM M23794* AM M23813*; AM M24216, AM M24217, AM M24218, AM M24219, BM24255*

Diagnosis. *Melonycteris w. woodfordi* differs from *M. w. aurantius* in being significantly smaller (P less than 0.10) in all parameters measured except upper cheektooth row length and upper canine length in males, and postorbital width in females. It further differs in lacking a sagittal crest in males, and in that females are not significantly larger (P less than 0.10) than males in condylobasal length, postorbital width and cheektooth row length.

Distribution. This subspecies has been recorded from the islands of Buka, Bougainville, Alu, Fauro, Mono, Oblari, Choiseul and Ysabel (Fig.1).

Discussion. There is some slight variation in size between populations of *M. w. woodfordi*. Individuals from the Shortlands tend to be the largest as reflected by forearm length (Fig.5), while those from Choiseul are smallest. This pattern is rather curious, as the Shortlands and Choiseul are separated by less than 40 km, and the majority of the Shortland Islands were joined with Choiseul during periods of lowered sea level in the late Pleistocene. Despite these differences there are extensive overlaps in size between various island populations, and no important morphological differences exist between samples from the various islands. Colour varies only slightly between individuals. The most sombre orange individuals tend to be from the Shortlands, while some individuals from Choiseul are the brightest, including the specimens that Phillips (1966) designated paratypes of *M. aurantius*. These specimens, however, are clearly subadult *M. woodfordi* and conform closely in morphology, size and colour with the Australian Museum sample from Choiseul (see below).

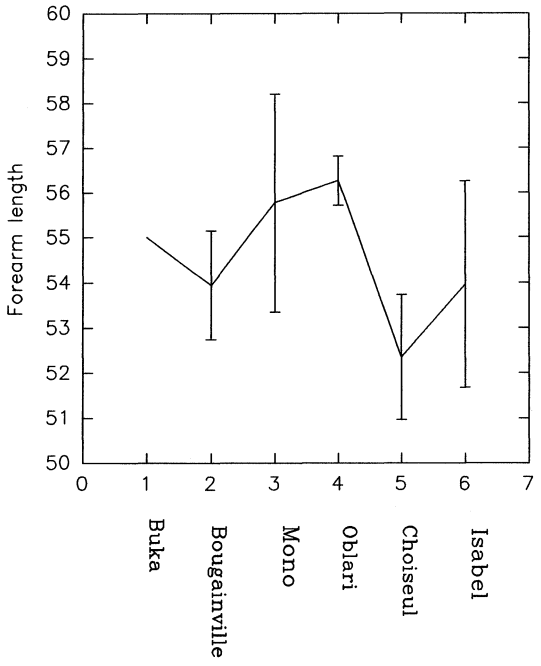

Fig.5. A, forearm length (mean and 95% confidence limits) of adults of various populations of *Melonycteris woodfordi woodfordi*.

Melonycteris woodfordi woodfordi shows the least sexual dimorphism of any of the forms of *Melonycteris*. The only statistically significant differences between the sexes (P less than 0.10) are bizygomatic width and canine length (Table 2, Fig.6). Both are however highly significant differences (P less than 0.0010). There are also some non-metric differences in cranial morphology between the sexes. In females the lines of insertion of the temporals remains widely separated over most of the calvarium. They gradually converge posteriorly and may meet near the occipital crest. Although there is never a sagittal crest in males, the lines of insertion of the temporals converge and join in about the middle of the calvarium. This suggests that temporal muscle mass is greater in males, which is probably related to the greater width of the zygomatic arches and generally larger canines in males.

The locality given by Phillips (1968) for his *M. woodfordi* sample is incorrect. He reported that all four specimens were from Choiseul. In fact, BM 23413, BM 23414, and BM 23434 are from Kolombangara Island, while BM 23275 is from Vella Lavella Island, both in Western Province. These specimens are all assigned here to a new species (see below).

I have had no experience of this subspecies in the field, although judging from museum records it can be locally abundant. It has been captured in some numbers in coconut plantations on Ysabel and Choiseul. Although most records of *M. w. woodfordi* are from near sea level there is a series in the Bishop Museum from Mutahi Village, 18 km south-west of Tinputz, Bougainville, that come from an altitude of 700 m. They are indistinguishable in morphology from individuals from lower altitudes and represent the highest altitudinal record for this taxon.

Melonycteris woodfordi aurantius Phillips, 1966

Figs 7,8, Table 2

Type material. HOLOTYPE, BM24440*, adult female skin and skull, collected at Haleta, Florida Island (9°07'S 160°27'E), Nggela Group, Solomon Islands, 11 Oct. 1964, P.J. Shanahan.

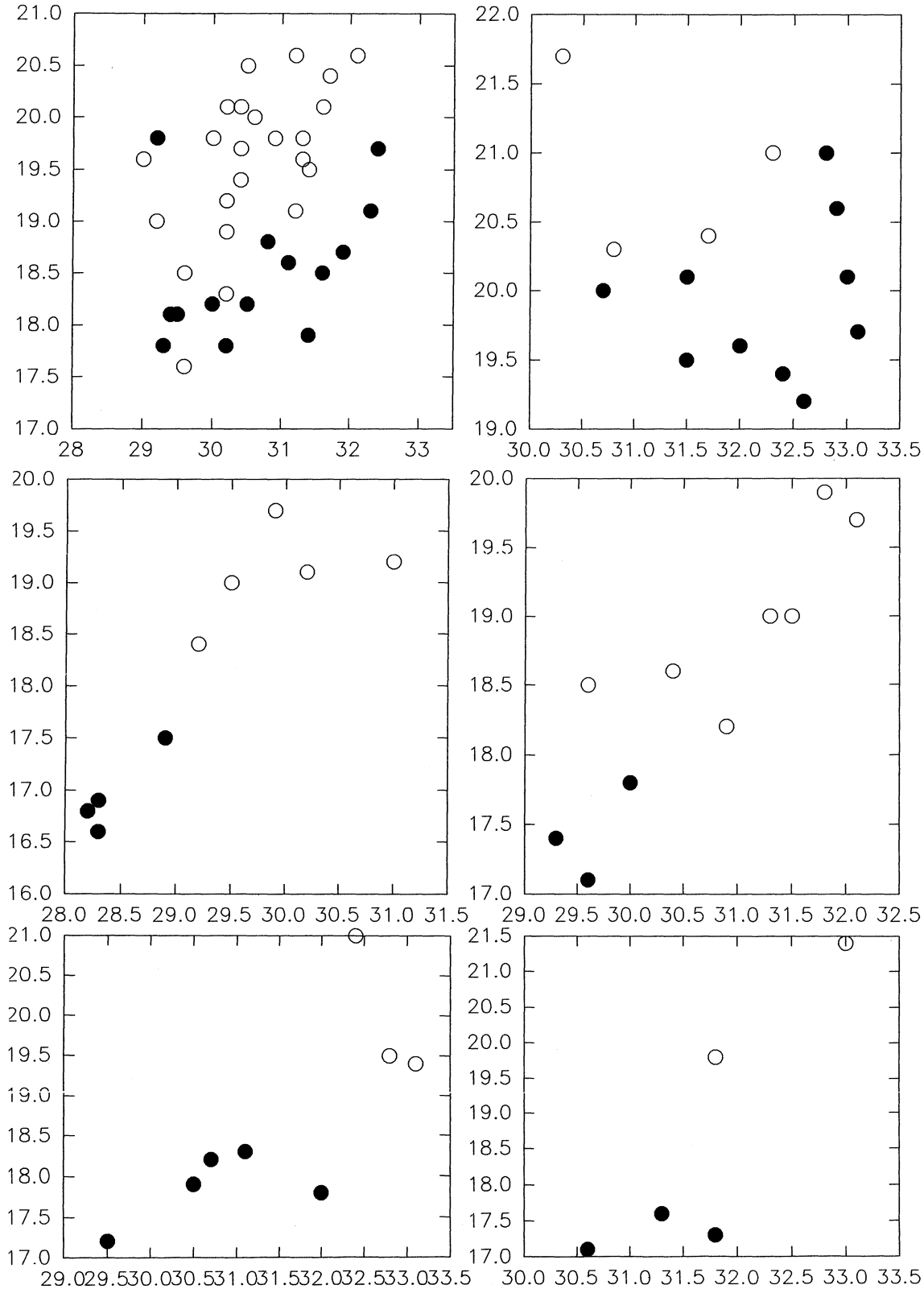

Fig.6. Bivariate plot of bizygomatic width (vertical axis) over condylobasal length (horizontal axis) for adult males and females of the Solomon Islands subspecies of *Melonycteris*. From upper left to lower right, *Melonycteris woodfordi woodfordi*, *M. w. aurantius*, *M. fardoulisi mengermani*, *M. f. schouteni*, *M. f. maccoyi*, *M. f. fardoulisi*.

Other specimens examined. Nggela: AM M18832*, AM M18835*, AM M18843*, AM M18869, AM M24044, AM M24047*, AM M24048*, AM M24049*, AM M24050*, AM M24051*, AM M24052*, AM M24053*, AM M24054*, AM M24055*, AM M24056*, AM M25023, AM M25024, AM M25025, AM M25026, AM M25027, AM M25028, AM M25029, AM M25030, AM M25031, AM M25032, AM M25033, AM M25034, AM M25035, AM M25037, AM

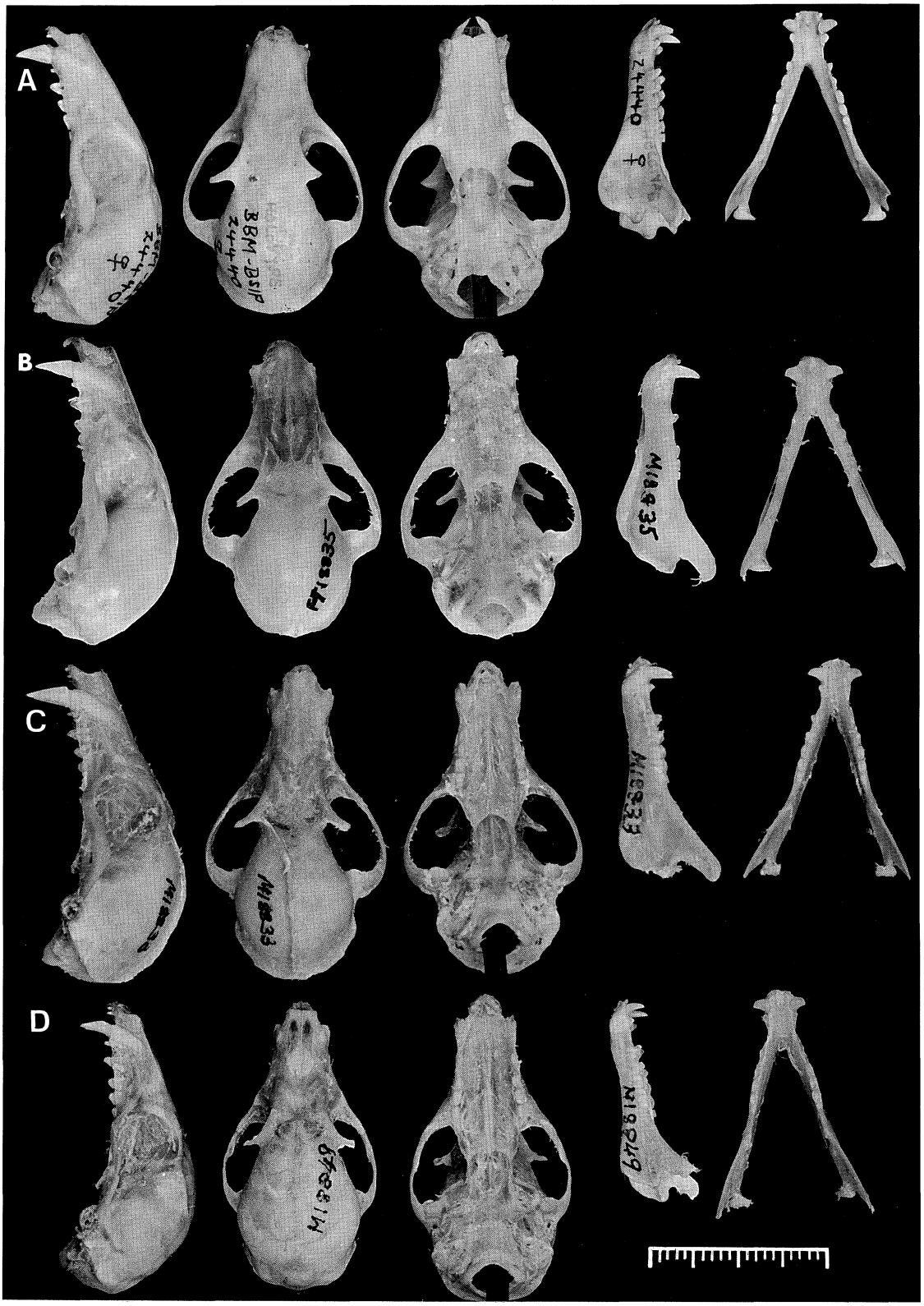

Fig.7. A, cranium of the holotype of *Melonycteris woodfordi aurantius* (BM24440, female); B, cranium of male *M. w. aurantius* (AM M18835); C, cranium of holotype male *Melonycteris fardoulisi fardoulisi* (AM M18833); and D, cranium of female paratype *M. f. fardoulisi* (AM M 18849).

M25050, AM M25051, AM M25054, AM M24055.

Diagnosis. *Melonycteris w. aurantius* differs from *M. w. woodfordi* in being significantly larger (P less than 0.10) in all variables measured except upper cheektooth row length and upper canine length in males, and in postorbital width in females. It further differs in that females are significantly larger than males (P less than 0.10) in postorbital breadth and upper cheektooth row length.

Distribution. Nggela and Florida Islands, Nggela Group, Solomon Islands.

Discussion. The concept of the taxon *aurantius* developed here is quite different from that of Phillips (1966). I regard it to be a subspecies of *M. woodfordi* that is restricted to the Nggela group. It differs from *M. w. woodfordi* primarily in its larger size and in that females are larger than males in most measurements. This latter condition is most unusual in *Melonycteris*, where the majority of taxa show marked sexual dimorphism with males being larger than and morphologically different in cranial morphology from females. The difference in insertion lines for the temporals as described for the sexes of *M. w. woodfordi* however holds true for this subspecies also, with the difference that the males can develop a sagittal crest on the posterior part of the cranium. This may be a function of larger size.

The holotype of *M. w. aurantius* is described in detail by Phillips (1966). He regarded it as being somewhat atypical of his new species, and many of the features that he mentioned in his diagnosis and discussion in fact represent the condition of the paratypes only. This has led to some confusion, as these paratypes differ in important ways from the holotype. Indeed I consider that the paratypes represent a different taxon (*M. w. woodfordi*), from the holotype. The holotype of *M. w. aurantius* is clearly adult. The basilar suture is fused and the animal was lactating when captured. The length of the forearm is given both on the label and by Phillips (1966) as 53.8 mm. However, this cannot be correct. Even as a dry skin the left forearm (the only one easily measurable) is 58.9 mm long, and the right appears to have been of a similar length. Before shrinkage associated with drying out, the forearm would perhaps have been 1 to 2 mm longer. The error in measuring forearm length probably occurred in the field, or it may be a transcriptional error. The correct forearm length of the dry skin is concordant with the forearm lengths of other specimens of this taxon from the Nggela group reported upon here, but differs markedly from that of Phillips' paratypes. These latter are from Choiseul, and the two specimens measured by me have forearm 49 and 51 mm in length. To judge from Phillip's (1966) metrical summary (mean = 49.3, N = 6, R = 42.9-53.8, the largest being the holotype), the forearms of the remaining specimens must be of a similar length or

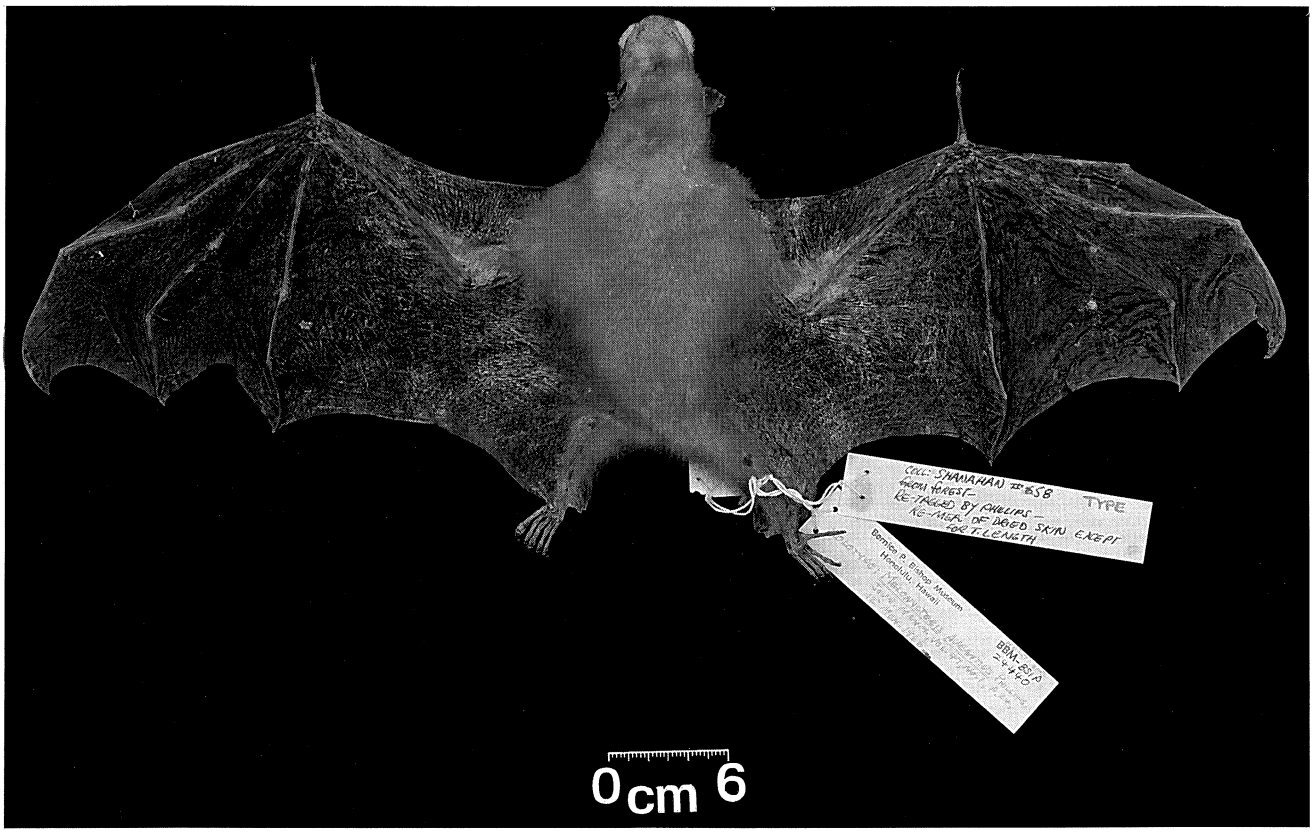

Fig.8. Study skin of the holotype of *Melonycteris woodfordi aurantius* (BBM 24440).

shorter. The paratypes are all subadult and, to a large extent, the features mentioned by Phillips as being diagnostic for *M. aurantius* are juvenile features seen in all species of *Melonycteris*.

Foremost among these features is postorbital width, which Phillips (1966) gives as being 8 to 9 mm in *M. aurantius*, as opposed to 7 to 7.5 mm in *M. woodfordi*. Postorbital width is typically larger in juvenile *Melonycteris* than in adults. For example, in the sample of *M. w. woodfordi* from Bougainville held in the Australian Museum, postorbital width ranges from 7.0 to 9.3 mm (N = 25), and those with the largest widths are juvenile. This is because the supraorbital process and calvarium separate as the skull lengthens with age, and a constriction is created between these structures, thus forming a narrower postorbital width. Phillips' misunderstanding of this feature was further compounded as he was comparing (in part) individuals of *M. f. mengermani* from Western Province, for which the sexes had been misrecorded, (and which he took to be typical *woodfordi*, see above and below).

A second diagnostic feature mentioned by Phillips is that the premaxillaries do not contact in *M. aurantius*, being separated by a gap of three to four mm, while in *M. woodfordi* they supposedly do contact. Phillips' estimate of the interpremaxillary gap is impossible, for the purported distance is far too great. Three to four mm is the distance between the canines in most *M. woodfordi*; the premaxillae, where they have not yet contacted, are never separated by more than 1 mm. In all species of *Melonycteris* the maxillaries are held only loosely in place, and either abut (in many adults) or are slightly separated but connected by soft tissue anteriorly (in juveniles). This latter condition is seen in the material assigned to *M. aurantius* by Phillips, and thus is a further juvenile feature.

A third feature mentioned by Phillips is that the posterior portion of the skull is deflected ventrally at a more acute angle than in *M. woodfordi*. This again is typical of all juvenile *Melonycteris*, but is not as evident in adults. It is worth emphasising that none of these features are well expressed in the adult holotype of *M. aurantius*, but are evident in the juvenile paratypes.

Finally, Phillips notes that in *M. aurantius* the dorsum is a more bright orange than in *M. woodfordi*. The holotype (which Phillips says is duller than the paratypes), is indistinguishable in colour from specimens that I have referred to *M. w. aurantius* from Nggela, and indeed from the majority of *M. w. woodfordi* specimens examined by me. The paratypes (from Choiseul) are about as bright as the most rufescent individuals of *M. w. woodfordi* in the collections of the Australian Museum, which are from Choiseul and Ysabel. Phillips may have been misled in his comparisons in that the material that he considered to be typical *M. woodfordi* in fact represents *M. f. mengermani* from Western Province, which is less orange in dorsal colouration than *M. woodfordi*.

Melonycteris fardoulisi n.sp.

Figs 7,9-12, Tables 2-5

Etymology. For Mr Emmanuel Fardoulis, whose generosity in supporting mammal research at the Australian Museum has allowed important studies to be carried out into the biology of the mammals of the Solomon Islands, which otherwise could never have been done.

Diagnosis. *Melonycteris fardoulisi* differs from all other species of *Melonycteris* in that dorsum is brownish rather than orange, in that sexes differ in colour, males being darker than females. Further differing from *M. melanops* in lacking white epaulettes, in having brown rather than black fur bases, in lacking claw on digit 2, and in having larger P^1 and M_3. It further differs from *Melonycteris woodfordi* in that males are significantly larger than females (P less than 0.10) in all samples except *M. f. fardoulisi* where the sample size is very small (see below), in condylobasal length and upper cheektooth row length. The disparity between the sexes (with males being larger) in condylobasal length relative to bizygomatic width, and in canine size and morphology, is also greater (Figs 3, 6). A prominent sagittal crest is present in most adult males (in some *M. f. mengermani* it is less prominent).

Discussion. *Melonycteris fardoulisi* occurs as distinctive populations on the larger islands of the eastern Solomons chain, as well as in Western Province. It almost certainly does not occur on Rennell or Belona, nor on the islands of Temotu Province, as our survey, as well as the work of Hill (1956) failed to reveal it there. The populations of Western Province, Malaita, Guadalcanal and Makira are each very distinctive, and that from the Russells may prove to be distinctive when more specimens are forthcoming. These first four populations are here named as subspecies: they are *M. f. fardoulisi* from Makira, *M. f. maccoyi* from Malaita, *M. f. schouteni* from Guadalcanal, and *M. f. mengermani* from Western Province and, tentatively, the Russells.

Melonycteris fardoulisi fardoulisi n.subsp.

Figs 7,10, Table 3

Type material. HOLOTYPE, AM M18833*, adult male skin and skull, caught in a mistnet in secondary forest near Sesena Village (8°31'S 162°05'E), altitude 100-200 m, Makira, Solomon Islands, T. Flannery, 16 Nov. 1987.

PARATYPES, AM M18834, subadult male skin and skull collected, 17 Nov. 1987; AM M18849*, young adult female skin and skull collected, 17 Nov. 1987; AM M18848, juvenile female body in spirits, skull cleaned; AM M20112, entire juvenile female in spirits. Other data as for the holotype.

Additional specimens examined. Makira: AM M23304*,

Fig.9. A, cranium of the holotype male *Melonycteris fardoulisi maccoyi* (AM M18836); B, cranium of paratype female *M. f. maccoyi* (AM M18831); C, cranium of the holotype male of *Melonycteris fardoulisi schouteni* (AM M18841); D, cranium of the paratype female *M. f. schouteni* (AM M18830).

AM M23305, AM M23306, AM M23637*, AM M23638*.

Diagnosis. *Melonycteris f. fardoulisi* differs from *M. f. maccoyi* in abundant pink spotting on the ears, flight membranes and feet. Differs from *M. f. schouteni* and *M. f. mengermani* in that males are significantly larger (P less than 0.10, width across M^1 could not be tested for because of small sample size) in forearm length, condylobasal length (equal variances), zygomatic width (equal variances) canine length, and

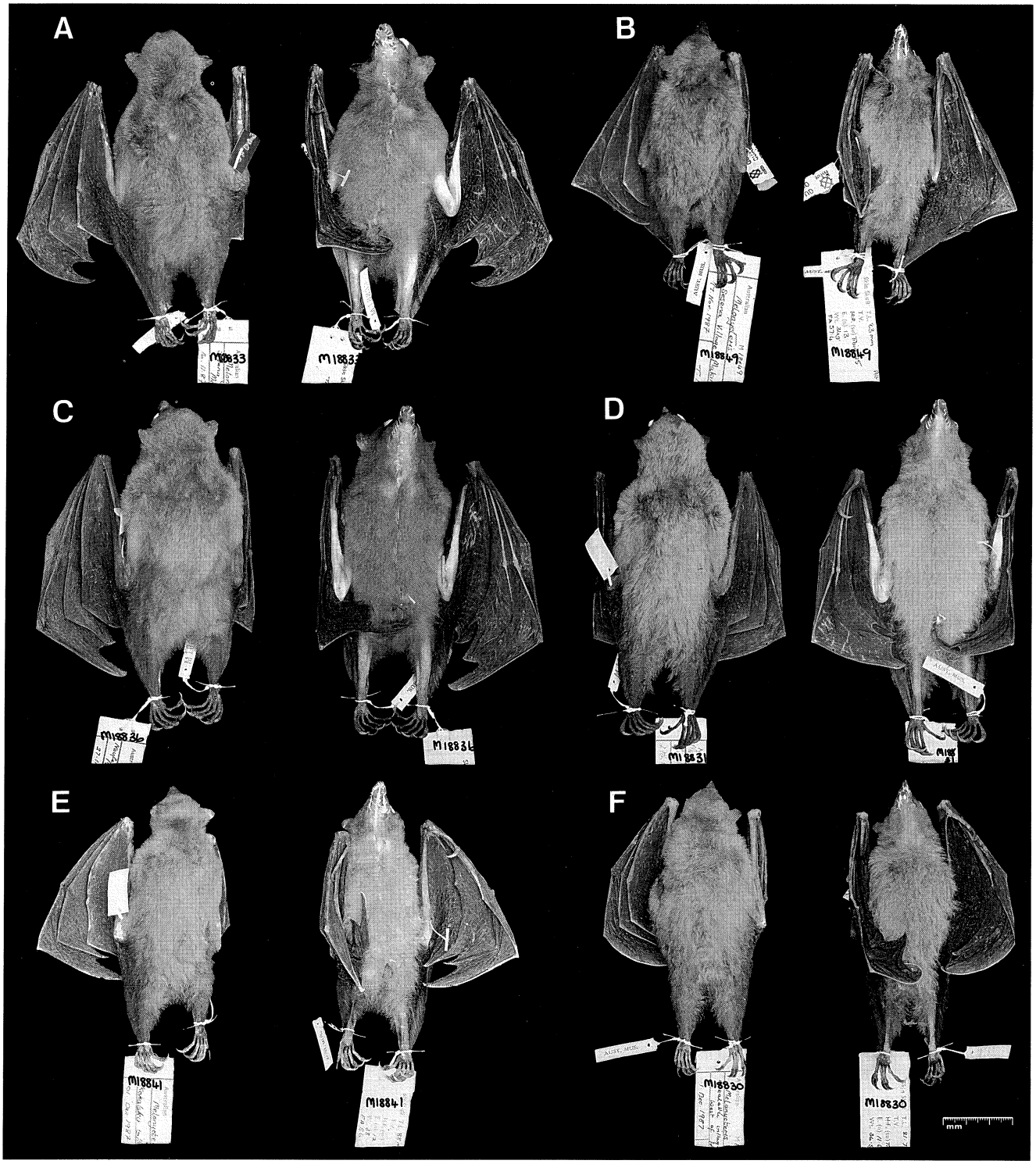

Fig.10. Study skins in dorsal and ventral views of A, holotype male (AM M18833) and B, paratype female (AM M18849) of *Melonycteris fardoulisi fardoulisi*; C, holotype male (AM M18836) and D, paratype female (AM M18831) of *M. f. maccoyi*; E, holotype (AM M18841) and F, paratype female (AM M18830), of *M. f. schouteni*.

from *M. f. mengermani* only in upper cheektooth row length. Females are significantly larger than those of *M. f. schouteni* and *M. f. mengermani* in condylobasal length, and larger than females of *M. f. mengermani* only in forearm length, upper cheektooth row length and (equal variances) width across M^1. Females of *M. f. schouteni* however have a significantly broader interorbital region than in *M. f. fardoulisi*.

Distribution. Makira (San Christobal) Island, Solomon Islands.

Description. *Pelage.* The dorsum and head of the holotype is close to Cinnamon Brown. The venter is Drab. A narrow band of dark hairs is present round the eyes. The ears and feet are black with conspicuous pink spotting. The flight membranes are black, with pink spotting concentrated along the forearm and phalanges. There is no pink spotting on the undersurface of the wings. The claws are dark brown and the muzzle thinly furred. Males are a darker shade of brown than females, being close to Cinnamon Brown or Fuscous, while females are close to Drab or Russet.

Skull. The skull of the holotype is large for a species of *Melonycteris*. There are extremely well-developed sagittal and occipital crests. It differs from the holotype of *M. woodfordi aurantius* (a taxon close in size and geographic location) in the following ways. The rostrum is more elongate and the premaxillaries extend further beyond the canines. The sagittal and occipital crests are extremely well developed. These crests are all but absent in *M. w. aurantius*. The canine is much larger.

The oldest paratype female (AM M18849) of *M. f. fardoulisi*, which still has the basilar suture slightly open, differs from the holotype of *M. w. aurantius* in the following ways. The bizygomatic breadth is much narrower and the occipital crests are even less well developed. The supraorbital processes are extremely poorly developed, and the zygomatic arches are thin by comparison. The braincase is more globose, and the canines are smaller and more gracile.

Discussion. This remains the most poorly known of the subspecies of *M. fardoulisi*. The small sample size (two adult males and three adult females, one of the latter being a young adult) has made statistical comparisons difficult, and it is possible that further differences will emerge as a larger sample becomes available.

The holotype male and a juvenile female paratype (AM M18833, 18848) were taken in a mistnet set in a new garden by a small river situated about 1 km to the east of Sesena Village. The garden contained ripening Papaw, and was backed by dense but disturbed forest. Other Megachiroptera taken on the same night at this location were *Dobsonia inermis* and *Nyctimene* sp. The other specimens of this new taxon were taken in mistnets set on cleared ridgetops and along tracks in disturbed forest. Specimens of *Melonycteris* were rare relative to other Megachiroptera obtained by mistnetting on Makira during 1987; only *Nyctimene* sp. (of which four individuals were obtained) was taken less frequently.

Melonycteris fardoulisi maccoyi n.subsp.

Figs 9,10, Table 3

Type material. HOLOTYPE, AM M18836*, skin and skull of an adult male, collected at Naufe'e Village (10°31'S 161°03'E), altitude 400 m, Malaita, Solomon Islands, T. Flannery, 27 Nov. 1987.

PARATYPE, AM M18831*, skin and skull of adult female, collected at Sinalaggu Harbour, 4 km north of Naufe'e Village, sea level, Malaita, Solomon Islands, T. Flannery, 27 Nov. 1987.

Other specimens examined. Malaita; AM M23457, AM M23577, AM M23814, AM M23817, AM M23818*, AM M23819*, AM M23820*, AM M23821*, AM M23822*, AM M24576, AM M24578, AMNH 99950*. BM24051*.

Etymology. For Mr Mike McCoy of Honiara, without whose help I would have been unable to visit Naufe'e Village, the type locality.

Diagnosis. *Melonycteris f. maccoyi* differs from *M. f. fardoulisi*, and indeed all other *Melonycteris* except some individuals from the Russells, in lacking pink spotting on the ears, feet and wing membranes. It differs from *M. f. schouteni* and *M. f. mengermani* in that both sexes are significantly larger (P less than 0.10) in forearm length and condylobasal length. In addition, males of *M. f. schouteni* are significantly smaller in upper cheektooth row length, canine length, zygomatic width and width across the canines, while males of *M. f. mengermani* are significantly smaller in upper cheektooth row length and upper canine length, and females are significantly smaller in bizygomatic breadth and cheektooth row length.

Distribution. Malaita Island, Solomon Islands.

Description. *Skin.* The skins of the holotype, paratype and referred specimens are similar in morphology. The holotype (a male) is slightly darker in dorsal and ventral colouration than the paratype (a female). Except for some fine pink speckling on the ears, the skin is entirely black in the holotype male. Other specimens are similar except that the paratype has three to four small pink flecks on the forearm, and the additional specimens have between none and eight such tiny flecks on the forearm. The dorsum of the male is close to Drab, but has a less marked brownish suffusion than in *M. f. fardoulisi*. The venter is similar in colouration to that of *M. f. fardoulisi*. Males tend to be darker than females, varying in colour between Drab and Fuscous, while females are close to Russet, but may have Drab underfur.

Skull. The skull of the holotype (male) is similar in morphology to that of the holotype of *M. f. fardoulisi*.

That of the female paratype and referred specimens have the basilar suture fully fused, indicating that they are fully adult.

Discussion. Statistical and non-metric analysis indicates that sexual dimorphism is greater in *M. f. maccoyi* than in *M. f. schouteni*. This dimorphism is a result of the larger size and exaggerated characteristics of males, particularly enlargement of the canine and temporal muscle mass and its associated changes in cranial morphology. The most obvious of these cranial changes are the development of a prominent sagittal crest acting as a firm anchor point for the temporals, and a broadening of the zygoma, allowing for attachment of these large muscle masses to the dentary.

The holotype was taken in a mistnet set near a fruiting forest tree by Sias, a Kwaio assistant. Other Megachiroptera taken in the same mistnet on the same night include *Rousettus amplexicaudatus*, *Dobsonia inermis*, *Macroglossus minimus*, *Nyctimene malaitaensis* and *N. major*. The paratype was taken in a mistnet set near ripening Papaw at sea level. Other species taken in the net included *D. inermis* and *R. amplexicaudatus*. My experience suggests that *Melonycteris fardoulisi maccoyi* is rare relative to other Megachiroptera on Malaita; only *N. major* (of which I obtained but a single specimen) was taken less frequently. *Nyctimene major* usually inhabits small oceanic islands, and its rarity on the mainland of Malaita may be due to competition with *N. malaitaensis*. The rarity of *M. f. maccoyi* on Malaita may be due to forest disturbance, as the species is more common on islands with extensive tracts of primary forest. Malaita is the most heavily populated island in the Solomons chain. Little undisturbed forest remains, and what there is restricted to small patches. Indeed *M. f. maccoyi* was found to be more common in eastern Malaita by Mr P. German in 1990, in an area which is closer to some less disturbed forest.

Melonycteris fardoulisi schouteni n.subsp.

Figs 9,10, Table 4

Type material. HOLOTYPE, AM M18841*, skin and skull of an adult male from Kokaleku Village (9°28'S 159°53'E), altitude 400-500 m, northern Guadalcanal, Solomon Islands. Collected by T. Flannery, 1 Dec. 1987.

PARATYPES, AM M18830*, skin and skull of an adult female; AM M20133, entire female in spirits. Locality and collecting details as for the holotype.

Other specimens examined. Mount Makarakomburu, Guadalcanal; AM M22185*, AM M22186*, AM M22193, AM M22194, AM M22203, AM M22207, AM M22218, AM M22219, AM M22230, AM M22233*, AM M22235, AM M22236, AM M22239, AM M22240, AM M22247*, AM M22251*, AM M22421*, AM M25217, AM M25218: Guadalcanal; BM23831*. BMNH 88.1.5.15*

Etymology. For Mr Peter Schouten, who has, through his art work, so enhanced our understanding of the beauty and diversity of the mammals of Melanesia.

Diagnosis. *Melonycteris fardoulisi schouteni* can be distinguished from *M. f. maccoyi* and *M. f. fardoulisi* in that males are significantly smaller (P less than 0.10, width across M^1 could not be compared with *M. f. fardoulisi* because of sample size) in forearm length, (equal variances) condylobasal length, (equal variances) zygomatic width, and canine length, and from *M. f. maccoyi* alone in upper cheektooth row length. Females are significantly smaller than these subspecies in forearm length and condylobasal length, but are larger than *M. f. fardoulisi* alone in postorbital width. It differs from *M. f. mengermani* in that males are significantly larger in forearm length, condylobasal length and cheektooth row length, while females are significantly larger in condylobasal length, upper cheektooth row length and width across M^{1-1}.

Distribution. Guadalcanal Island, Solomon Islands.

Description. *Skin.* The colour of the dorsum of the holotype male is close to Cinnamon Brown, and very similar to that of *M. f. fardoulisi*. However, the puppet skin of the paratype (female) is markedly lighter, close to Amber. The venter of the paratype female skin is also brighter than that of the holotype male. Males are almost always a darker shade of brown than females, the darkest being close to Fuscous, paler ones being close to Cinnamon Brown. The darkest females approach Cinnamon Brown in colour, and range through to the lightest individuals which are close to Amber in colour. Other aspects of the pelage and external morphology are as in *M. f. fardoulisi*.

Skull. The skull of the holotype (male) is very similar in most respects to that of *M. f. fardoulisi*. However, it differs in its lesser development of the sagittal and occipital crests, and in its smaller size. The canines are not as hypertrophied as in males of *M. f. fardoulisi* and *M. f. maccoyi*, but are still markedly larger than in females. The cleaned skull of the paratype (female) is only slightly smaller than that of the male, and it lacks any suggestion of a sagittal crest, the insertion points for the temporals being separated by almost 6mm in the middle of the calvarium. The occipital crests are barely noticeable. The canines are relatively small and gracile.

Discussion. The three type specimens were taken in mistnets set in newly made gardens near Kokaleku Village, in an area surrounded by largely undisturbed forest. *Nyctimene albiventer*, *Rousettus amplexicaudatus* and *Dobsonia inermis* were taken in the same nets. Other specimens were taken in undisturbed primary montane forest on Mount Makarakomburu, at altitudes of between 380 and 1,270 m. *Melonycteris f. schouteni* is not uncommon on Guadalcanal, but is nonetheless not as commonly caught as species of *Macroglossus*, *Rousettus* and *Nyctimene*.

Melonycteris fardoulisi mengermani n.subsp.

Figs 11,12, Tables 4,5

Type material. HOLOTYPE, AM M22331*, adult male skin and skull, collected 18 Sept. 1990, Vanga Point (7°54'S 156°58'E), Kolombangara Island, Western Province by H. Parnaby.

PARATYPES, AM M22330*, AM M22332*, AM M22333* all adult female skins and skulls, AM M22690* adult male in spirit, skull extracted, AM M22691 female in spirit, skull extracted. Locality and other data same as for the holotype, but collected between 17 and 18 Sept.

Additional specimens examined. Kolombangara: BM23413, BM23414*, BM23434, BM23343, BM23387, BM24423, BM23425, BM23422: Vella Lavella BM23257: New Georgia AM M22325*, AM M22326*, AM M22328*, AM M22334*, AM M22770, AM M22771, AM M22772, AM M22773, AM M22774, AM M22775.

Etymology. A euphonius combination of the surnames of Dr Gregory Mengden and Mr Pavel German, who participated in the 1987 Australian Museum expedition to the Solomon Islands, and contributed greatly to its success.

Diagnosis. *Melonycteris fardoulisi mengermani* differs from all other subspecies in that males are significantly smaller (P less than 0.10) in forearm length, condylobasal length and (equal variances) cheektooth row length, and from *M. f. fardoulisi* and *M. f. maccoyi* in canine length, and from the former alone in zygomatic width. Females are significantly smaller than other subspecies in condylobasal length and cheektooth row width, from all except *M. f. maccoyi* in width across M^{1-1}, and from all except *M. f. schouteni* in forearm length. The sagittal crest of males is usually less well developed than in other subspecies, while the zygomatic breadth is great relative to the condylobasal length in males.

Distribution. *Melonycteris fardoulisi mengermani* has been found on Vella Lavella, Kolombangara, and New Georgia Islands in Western Province (Fig.1). It may also occur in the Russell Group (see below).

Description. *Pelage.* The fur of the venter of the holotype is close to Raw Umber. The skin itself is brown, and the fur of the dorsum of the holotype is close to Cinnamon Brown. In general, individuals are not as dark as they can be in other subspecies of *M. fardoulisi.* Males are usually close to Cinnamon Brown, and females are light in colour, close to Amber or Clay. Although pale, none approach the orange colour of *M. woodfordi.* At

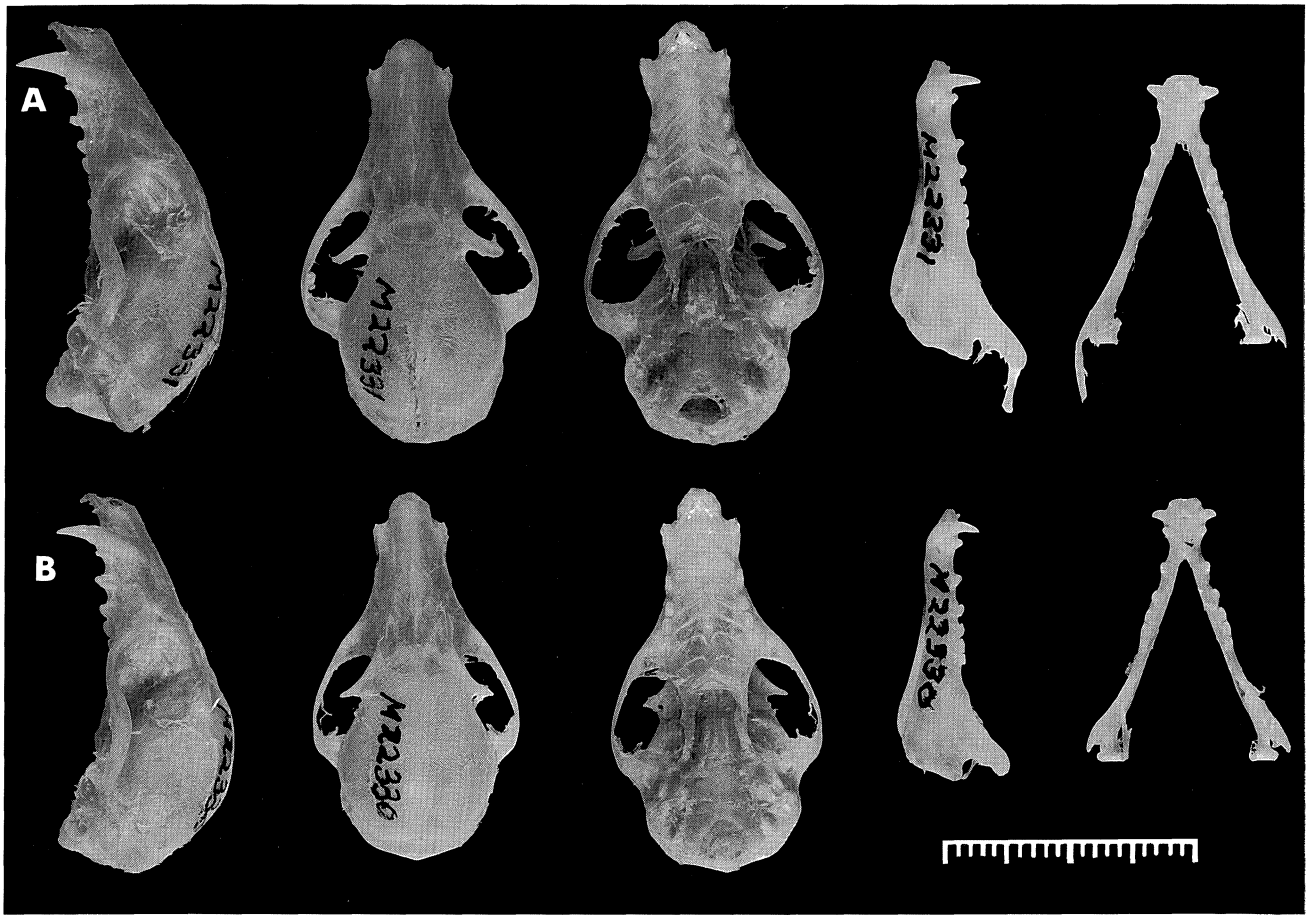

Fig.11. A, cranium of holotype male *Melonycteris fardoulisi mengermani* (AM M22331); B, cranium of paratype female *M. f. mengermani* (AM M22330).

the extremes the colour variants of the sexes approach each other, but in the present samples do not overlap.

Skull. The complete fusion of the basilar suture of the skull shows that the holotype is adult. Apart from its smaller size and more gracile construction, it is similar in morphology to the holotype skull of *M. w. aurantius*. It differs however in the presence of a very slight sagittal crest.

Discussion. Unfortunately there has been some confusion regarding the identity of some of the skulls referred to this new taxon. The confusion centres around two skulls that apparently lost their identification during preparation, and a third which appears to be a female skull associated with a male skin. This latter specimen is BM23434. A note accompanying the remaining two skulls suggests that one is probably the skull of BM23883, the other BM23275 (possibly meant to read BM23257). Whatever the case, these three skulls have been excluded from this analysis, as it is now not possible to be confident about their sex or origin. Indeed, the entire Bishop Museum sample of *M. f. mengermani* should be treated with caution. It appears that considerable confusion between skulls and skins or bodies arose at the time of preparation, and the association of skulls with other remains cannot not be assumed to be correct.

Phillips (1966, 1968) mentions four of the specimens (BM23413-4, 23434, 23275) described here. He regarded them as being *M. woodfordi* from Choiseul. It is unclear how this confusion regarding locality arose, as the specimens are all accompanied by tags bearing the correct locality data. As mentioned elsewhere this misunderstanding contributed to Phillip's misinterpretation of *M. aurantius*.

This subspecies has a wide altitudinal distribution. The Australian Museum expedition to Western Province found it to be common near sea level on Kolombangara and New Georgia, while the Bishop Museum specimens from Kolombangara were collected at an elevation of around 700 m at a location called Gollifer's Camp.

Fig.12. A, study skin in dorsal and ventral view of A, holotype male *Melonycteris fardoulisi mengermani* (AM M22331) and B, paratype female *M. f. mengermani* (AM M22330).

Russell Islands Population. Five specimens (AMNH 79912; BMNH 33.11.11.1, AM M24046, AM M25021, AM M25022) have been collected in the Russell Group. They are tentatively referred to *Melonycteris fardoulisi mengermani*, although their morphology is unusual. There are two distinct colour morphs in the sample. Two of the individuals (AMNH79912, AM M24046) are a uniform dark brown, close to Fuscous, and lacking any pink spotting. Except for their small size, they resemble the darkest individuals of *M. f. maccoyi*. The others are brownish but with pink spots, resembling closely in colour typical *M. f. mengermani*. The sample includes three adult males and one adult female with skulls extracted, all of which could be measured (Table 5). The male sample does not differ significantly (at 0.10) from *M. f. mengermani*. The single female cannot be compared using 't' tests, but it falls outside the range of variability (being larger) of female *M. f. mengermai* (N = 4) in condylobasal length, zygomatic width, upper cheektooth row length and width across M^{1-1}.

Although there are differences in colour in some individuals, and the only known female is clearly larger than any of the measured *M. f. mengermani*, the Russell Islands population is tentatively retained within *M. f. mengermani*. It clearly shows the greatest similarity to that subspecies, although additional material, particularly more females, may well show that it warrants independent subspecific rank. The British Museum specimen was collected on Yandina by Mr Lever in June 1932, and bears a tag stating that it had fallen from a Coconut tree. The American Museum specimen was collected on Pavuvu during the Whitney Expedition by R.H. Beck on 6 August 1927, while the three Australian Museum specimens were collected on Pavuvu by Ian Aujare in April 1991.

Discussion

Phylogenetic relationships. The relationships of the genus *Melonycteris* within the Macroglossinae remain uncertain, which makes it difficult to determine the polarity of many characters within the group. However, because of their distribution and nature, the polarity of some key features is clear. *Melonycteris woodfordi* and *M. fardoulisi* share at least one unquestionably derived feature not seen in *M. melanops*. This is the loss of the claw from digit 2 of the forearm. Contrary to Phillips' (1966) view, this claw is not a mere rudiment that can be easily rubbed off. It is, in my experience a firmly attached claw, invariably present in *M. melanops* but absent in all other taxa. This synapomorphy (claw loss) for *M. woodfordi* and *M. fardoulisi* suggests that they are sister taxa. *Melonycteris melanops* possesses some derived features not seen in other species of *Melonycteris*. These include reduction in the size of M_3 and P^1 (Fig.4) and the presence of a white epaulette on the shoulder (a feature unique within the subfamily). *Melonycteris woodfordi* is unique in the genus in having no sexual dimorphism in most dimensions (*M. w. woodfordi*), or in females being larger (*M. w. aurantius*).

Zoogeography. None of the three species of *Melonycteris* occur in sympatry. The distribution of the various species and subspecies accords well with expectations based upon geography and geological history. The dentally most distinctive member of the genus (*Melonycteris melanops*) is found throughout the Bismarck Archipelago, which is the most isolated part of the range of members of the genus. No subspecies can be recognised at present within this species.

All of the islands known to support *Melonycteris w. woodfordi* are fragments of a much larger landmass that existed when the sea level was lowered during Pleistocene glacial maxima. Diamond (1974) has named this palaeo-landmass Greater Bukida (Fig.1). Thus it seems likely that *M. w. woodfordi* was present throughout most of this landmass during the late Pleistocene, and that since its fragmentation the subspecies has not differentiated greatly morphologically. The only Greater Bukidan fragments that do not support *M. w. woodfordi*, (but which support a closely related taxon) are Nggela and Florida Islands in the Nggela Group, where *M. w. aurantius* is endemic. The Nggela Group have had the most tenuous connection of any of the Greater Bukidan fragments. Seabed topography suggests that the Nggelas would have been the first part of Greater Bukida to have been isolated after the last glacial, around 15,000 ybp. The other islands began to separate between 14,000 and 8,000 ybp. This earlier separation, and the tenuous link between Nggela and the rest of Greater Bukida, may be the reason why *M. w. aurantius* has been able to differentiate there.

Melonycteris fardoulisi is distributed on the long isolated southern and eastern islands of the Solomons chain. There is no evidence that these islands have ever been connected to each other or to any other large landmass. On each of the major islands within its distribution a highly distinctive subspecies has developed.

At the generic level the distribution of *Melonycteris* is unusual in that it is the only mammalian genus to be restricted to both the Solomon Islands and Bismarck Archipelago. Its distribution suggests that the species of *Melonycteris* are not easily able to cross large water barriers as is, for example, the macroglossine species *Macroglossus minimus*, which is distributed throughout the entire region inhabited by species of *Melonycteris* and beyond, but with no evidence of speciation within Melanesia. Some *Melonycteris* are, however, clearly sufficiently vagile for individuals to have crossed the 170 km water gap separating New Ireland and Buka at some time in the past.

Sexual dimorphism. The degree and nature of sexual dimorphism in the species of *Melonycteris* is remarkable. Among bats sexual dimorphism usually takes the form of subtle differences in colouration, body size, or the presence/absence of dermal glands (Hill & Smith, 1984). However, where males are larger than females the males can have greater temporal muscle mass and larger

canines. These latter differences are, however, again usually subtle. Hill & Smith (1984) note that this area of chiropteran biology has received little attention, but that such sexual differences may be related to differing roost and feeding preferences for the sexes.

The pattern of sexual dimorphism described by Hill & Smith (1984) as being most common in bats (slight differences in body size, canine length and temporal muscle mass) is indeed the pattern seen in *M. melanops*. The other species and subspecies however show somewhat different patterns. *Melonycteris woodfordi woodfordi* shows the fewest differences between the sexes, there being no difference in overall size or colour, but males have larger canines and masseter muscle mass (which is reflected in greater zygomatic width and the shape of the parietal ridging on the skull). *Melonycteris woodfordi aurantius* differs from all other *Melonycteris* (and indeed most other pteropodids) in that the usual sexual dimorphism in certain features is reversed, with females being significantly larger than males in condylobasal length, cheektooth row length and postorbital width, but with males still maintaining significantly larger canines and greater zygomatic width. In all populations of *Melonycteris fardoulisi* the sexes differ in colour (the males being darker), males are significantly larger than females in most cranial dimensions and in overall body size; and differences in canine morphology and size, and cranial architecture, are taken to an extreme. Overall, *M. f. schouteni* and *M. f. mengermani*, the subspecies with the smallest body size, show the least degree of sexual dimorphism (although it is still significant), while *M. f. fardoulisi* and *M. f. maccoyi* show the greatest difference between the sexes of any *Melonycteris*. Indeed, so striking is the difference that when I first encountered *M. f. fardoulisi* in the field, differences in colour, size and head shape initially convinced me that males and females represented two different species. This great degree of sexual dimorphism is due to the hypertrophy of male characteristics, the males being larger, having greater sagittal crest development, and larger canines than in the other subspecies. Differences among females of the various subspecies are generally less striking. These general patterns of sexual dimorphism do not seem related to overall size however, and body size bears no relationship to island size in *Melonycteris*.

The varying degrees and nature of sexual dimorphism in the species of *Melonycteris* offer an ideal opportunity to examine the function and significance of sexual dimorphism among bats. For example, a detailed study of the natural history of *Melonycteris woodfordi aurantius* (in which the female is larger) and *M. fardoulisi maccoyi* (where the male is larger), and which occur on similar islands a mere 40 km apart, may go far in answering such questions.

Limited field observations suggest that the sexes of *Melonycteris fardoulisi* may forage separately. For example, during an expedition I undertook to high elevation undisturbed rainforest on the slopes of Mount Makarakomburu in May 1990, 16 *Melonycteris* were obtained. Of these 13 were males and three were females, only one of which was adult. A similarly striking situation was encountered on near Su'u Harbour, Malaita by P. German during the 1991 Australian Museum Solomon Islands Expedition. In secondary forest and garden he collected nine adult *Melonycteris fardoulisi maccoyi*, all of which were female. Further investigations into the capture frequency of the sexes of *M. fardoulisi* may reveal whether these sex ratios are typical of the respective habitats.

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APPENDIX I

Table 1. Forearm length and cranial measurements for island populations of *Melonycteris melanops* (adults only). X = mean, R = range, St = standard deviation, N = sample size, l = length, w = width. * upper cheektooth row length, from anterior of canine to posterior of last molar.

	New Britain		New Ireland		Duke of York
	male	female	male	female	male
Forearm					
X	62	60	64.4	62.2	59.2
R	–	59-61	–	61-63	54.7-63.6
N	2	2	1	3	2
Condylobasal l.					
X	33.6	31.8	33.4	32.3	–
R	–	31.2-32.3	–	31.5-32.7	–
N	1	2	1	3	–
Bizygomatic w.					
X	21.5	18.8	21.1	18.7	19.1
R	–	18.1-19.5	–	18.5-18.9	–
N	1	2	1	3	1
Interorbital w.					
X	7.4	7.2	7.1	6.7	6.2
R	–	6.9-7.4	–	6.5-6.8	–
N	1	2	1	3	1
Postorbital w.					
X	7.6	8.7	7.1	8.3	6.7
R	–	8.6-8.7	–	8.1-8.5	–
N	1	2	1	3	1
Cheekteeth l.*					
X	10.8	11.0	11.6	11.6	11.0
R	–	10.6-11.3	–	11.2-12.1	–
N	1	2	1	3	1
M^{1-1} w.					
X	8.5	8.4	8.4	8.2	8.1
R	–	8.3-8.4	–	8.1-8.4	–
N	1	2	1	3	1
Canine l.					
X	4.7	4.0	4.5	3.8	3.6
R	–	3.9-4.0	–	3.5-4.0	–
N	1	2	1	3	1

Table 2. Forearm and selected cranial measurements for the subspecies of *Melonycteris woodfordi* (adults only). See Table 1 for key.

	M. w. woodfordi		*M. w. aurantius*	
	male	female	male	female
Forearm				
M	54.2	55.2	59.2	59.6
R	50.0-59.2	51.0-60.0	57.7-61.1	58.3-61.8
St	2.11	2.46	1.48	1.27
N	29	14	4	10
Condylobasal l.				
M	30.5	30.7	31.3	32.3
R	29.0-32.1	29.2-32.4	30.3-32.3	30.7-33.1
St	0.84	1.13	0.90	0.80
N	26	14	4	10
Zygomatic w.				
M	19.5	18.5	20.8	19.9
R	17.4-20.6	17.8-19.8	20.0-21.7	19.2-21.0
St	0.86	0.65	0.73	0.56
N	28	15	4	10
Postorbital w.				
M	7.6	7.8	7.0	8.0
R	6.5-8.6	7.0-8.8	6.7-7.4	7.3-9.1
St	0.52	0.52	0.30	0.52
N	30	15	4	10
Cheekteeth l*				
M	10.9	11.0	10.9	11.5
R	10.1-11.6	10.2-12.0	10.6-11.1	10.9-12.3
St	0.38	0.48	0.25	0.49
N	29	14	4	9
M^{1-1} w.				
M	7.9	7.9	8.6	8.6
R	7.1-8.6	7.2-8.4	8.4-8.9	8.2-9.1
St	0.34	0.37	0.24	0.27
N	29	14	4	10
Upper canine l.				
M	4.1	3.5	4.2	3.8
R	3.4-4.5	2.6-4.0	3.6-4.5	3.4-4.2
St	0.34	0.40	0.44	0.26
N	31	15	4	10

Table 3. Forearm and selected cranial measurements for *Melonycteris fardoulisi fardoulisi* and *M. f. maccoyi* (adults only). See Table 1 for key.

	M. f. maccoyi		*M. f. fardoulisi*	
	male	female	male	female
Forearm				
M	61.2	57.8	60.7	57.4
R	57.9-64.6	56.4-59.0	60.6-60.7	56.9-57.8
St	3.35	1.11	0.07	0.45
N	3	5	2	3
Condylobasal l.				
M	32.8	30.8	32.4	31.2
R	32.4-33.1	29.5-32.0	31.8-33.0	30.6-31.8
St	0.35	0.91	0.85	0.60
N	3	5	2	3
Zygomatic w.				
M	20.0	17.9	20.6	17.3
R	19.4-21.0	17.2-18.3	19.8-21.4	17.1-17.6
St	0.90	0.43	1.13	0.25
N	3	5	2	3
Postorbital w.				
M	7.2	7.7	7.6	7.8
R	6.4-8.1	6.9-9.0	6.9-8.3	7.7-7.9
St	0.85	0.81	0.99	0.12
N	3	5	2	3
Cheekteeth l.*				
M	11.4	10.7	11.3	11.0
R	11.1-11.5	10.0-11.5	11.0-11.5	10.5-11.6
St	0.23	0.53	0.35	0.57
N	3	5	2	3
M^{1-1} w.				
M	8.1	7.6	7.8	7.7
R	8.0-8.3	7.3-7.8	7.8	7.5-8.0
St	0.17	0.21	- 0.26	
N	3	5	2	3
Upper canine l.				
M	5.0	3.6	4.9	3.5
R	4.8-5.2	3.3-4.0	4.8-5.0	3.5-3.6
St	0.21	0.30	0.14	0.06
N	3	5	2	3

Table 4. Forearm and selected cranial measurements for *Melonycteris fardoulisi mengermani* and *M. f. schouteni* (adults only). See Table 1 for key.

	M. f. mengermani		*M. f. schouteni*	
	male	female	male	female
Forearm				
M	55.1	53.5	56.9	55.6
R	53.6-57.5	52.4-55.5	55.7-60.0	53.0-58.0
St	1.43	1.42	1.60	2.51
N	6	4	6	3
Condylobasal l.				
M	29.9	28.4	31.1	29.6
R	29.2-31.0	28.2-28.9	29.6-32.1	29.3-30.0
St	0.66	0.32	0.86	0.35
N	6	4	7	3
Zygomatic w.				
M	19.1	17.0	19.0	17.4
R	18.4-19.7	16.6-17.5	18.2-19.9	17.1-17.8
St	0.47	0.39	0.63	0.35
N	5	4	7	3
Postorbital w.				
M	7.2	8.1	7.4	8.0
R	6.8-7.6	7.7-8.7	5.9-8.1	7.9-8.1
St	0.35	0.44	0.77	0.10
N	6	4	7	3
Cheekteeth l.*				
M	10.5	9.9	11.0	10.3
R	10.2-10.7	9.6-10.1	10.5-11.3	10.2-10.4
St	0.24	0.22	0.34	0.12
N	6	4	7	3
M^{1-1} w.				
M	7.7	7.4	7.7	7.8
R	6.9-8.2	7.2-7.5	7.4-8.2	7.7-7.9
St	0.47	0.15	0.29	0.10
N	6	4	7	3
Upper canine l.				
M	4.1	3.3	4.2	3.2
R	3.7-4.4	3.2-3.6	3.9-4.4	2.9-3.7
St	0.27	0.19	0.24	0.46
N	7	7	4	3

Table 5. Forearm and selected cranial measurements for *Melonycteris fardoulisi* cf. *mengermani* (adults only) from the Russell Islands. See Table 1 for key.

	BMNH33.11.11.1	AMNH 79912	AM M24046	AM M25022
Sex	M	M	M	F
FA	54.5	53.3	54.8	54.6
Condylobasal l.	29.4	30.1	29.7	30.5
Zygomatic w.	19.2	19.5	19.2	18.3
Postorbital w.	6.6	6.3	7.5	7.9
Cheekteeth l.*	10.3	9.9	9.5	10.5
M^{1-1} w.	7.8	7.5	7.4	7.7
Upper canine l.	3.9	–	3.5	3.4