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A New Species and Two New Subspecies of *Hipposideros* (Chiroptera) from Western Papua New Guinea

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ABSTRACT. *Hipposideros edwardshilli* n.sp., *H. wollastoni parnabyi* n.subsp. and *H. w. fasensis* n.subsp. are described on the basis of electrophoretic and morphological analysis. All are members of the *Hipposideros cyclops* group of Hill (1963). *Hipposideros edwardshilli* is closely related to *H. corynophyllus*. Additional material of *H. corynophyllus* (previously known from a single specimen with broken forearms) is described.

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Hill (1963) considered that several highly distinctive species of *Hipposideros* belonged within a supraspecific grouping that he called the *Hipposideros cyclops* group. The group as then defined consisted of *H. cyclops* and *H. camerunensis*, both very large species from Africa, and *H. semoni*, *H. stenotis*, *H. wollastoni* and *H. muscinus* from Australia and New Guinea. Hill suggested that it was "...a relict group of remote origin, a view supported by the profound differences between its Ethiopian representatives and its remaining representatives in the Australasian region...". Hill (1963) characterises the Australasian members of the group by their small size, large ears, complex noseleaves and broad skull. Among the distinctive features of the noseleaf Hill (1963) notes the following: the presence of two lateral supplementary leaflets, the intermediate part has a median tubercle and the posterior noseleaf is moderately developed with three supporting septa, its upper edge being more or less semicircular, thickened, and usually having a median club-like process. At the time of Hill's revision the various species were very poorly represented in Museum collections. Hill (1963) had available for study a single specimen each of *H. muscinus*, *H. wollastoni* and *H. stenotis* as well as nine *H. semoni*.

Hill (1985) described *Hipposideros corynophyllus*, based upon a single specimen with both forearms broken. He assigned this new species to the *H. cyclops* group and suggested that it was a close relative of *H. semoni*. He also described three additional specimens of *H. wollastoni* from Telefomin and the nearby Tabubil area, western Papua New Guinea (Fig.1). He noted that the additional *H. wollastoni* specimens all possess a club-like eminence in the middle of the posterior noseleaf, a feature that is lacking in the holotype, until then the only known specimen, which was collected in what is now Irian Jaya, approximately 480 km to the west of Telefomin (Fig.1).

During a survey of the mammals of West Sepik Province T.F.F. was able to collect relatively large numbers of bats referable to the *H. cyclops* group. These included 33 individuals of a new subspecies of *H. wollastoni*, and 24 *H. corynophyllus*, all from the Telefomin area; a single specimen of another apparently new subspecies of *H. wollastoni*, and six individuals of an apparently new species related to *H. corynophyllus*, all from the North Coast Ranges some 200 km north of the Telefomin area. These specimens form the basis of this work. Additionally, four specimens of *H. semoni*, four of *H. stenotis* and one of *H. muscinus*, which had not previously been reported upon, were available for study.

Materials and Methods

Colours where capitalised refer to Smythe (1974). The following prefixes for registration numbers of specimens are used. AM M – Australian Museum; BMNH – Natural History Museum, London; CM – Australian National Wildlife Collection; WAM – Western Australian Museum. The holotypes of *Hipposideros corynophyllus* and *H. wollastoni* were examined by T.F.F during a visit to the Natural History Museum in November 1989. Other specimens examined during this study are listed in Appendix II. Tables 1-4 are included in Appendix I.

Electrophoresis was performed for one hour with a constant 200v potential drop between electrodes on Titan 111 cellulose acetate plates according to standard procedures and stained using agarose overlays following recipes given in Harris & Hopkinson (1977), Richardson *et al.* (1986) and Colgan (1986). Details of running buffers are given in Table 1. Portions of liver were ground in two volumes of homogenising buffer (Colgan, 1986) in hand held glass grinders. The homogenate was centrifuged and the supernatant stored (for up to two weeks) at -75°C until required for electrophoresis. The allozymes identified in this study are designated by numerals in order of decreasing (anodal) mobility. Distance analyses and measures of genetic variability were calculated using BIOSYS-1 (Swofford & Selander, 1981) or by hand. Duplicate loci present in *H. edwardshilli* and *H. corynophyllus* but not in other taxa were included in the calculation of the distance between this one pair but were not used in other calculations. All distance measures available in BIOSYS-1 were examined. The values for the standard Nei distance and Wright's modification of Roger's distance are given in Table 2 (Nei's unbiased estimate cannot be calculated for heterozygotes in single specimen samples, i.e., for *H. w. fasensis* here, so the standard Nei measure is given for distances where one or both taxa have only one specimen).

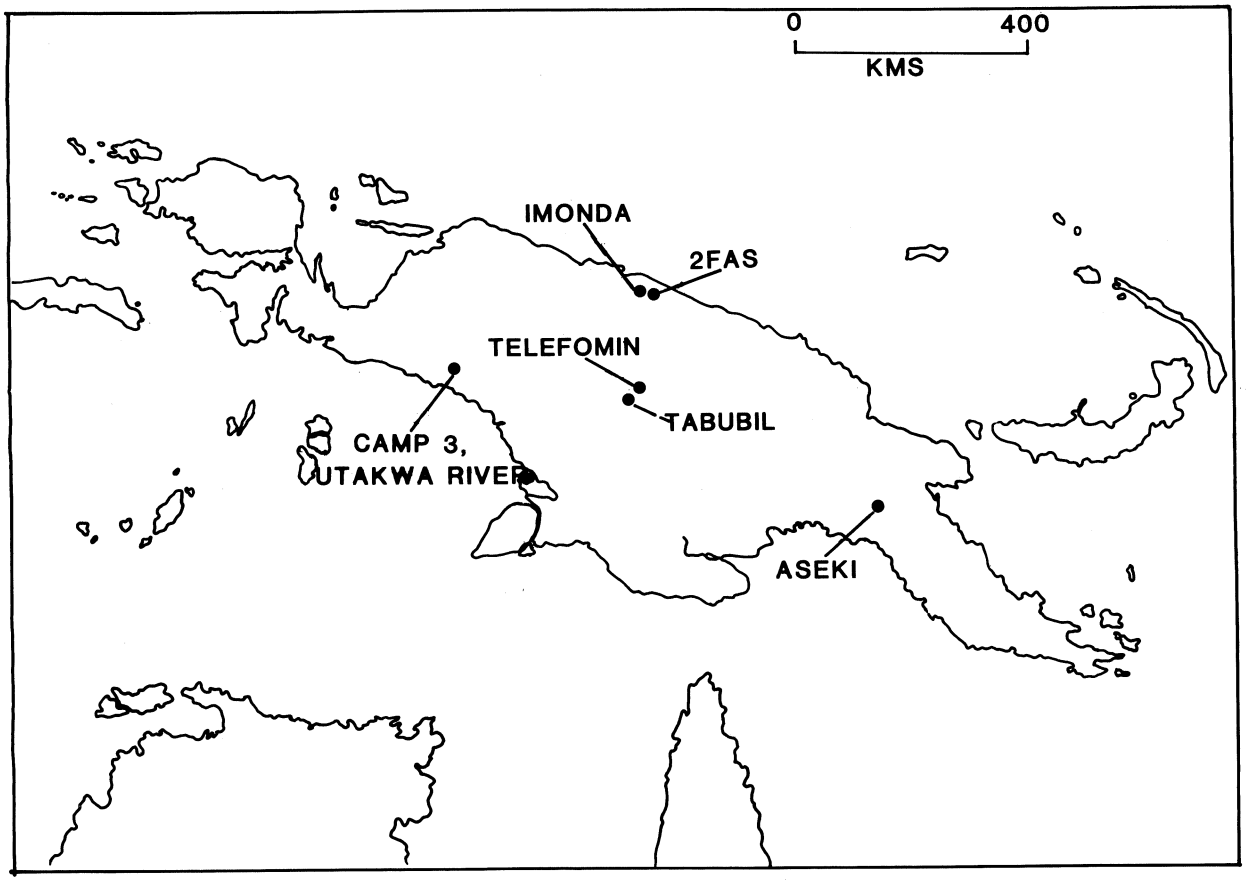

Fig.1. Map of New Guinea showing localities and areas mentioned in text.

Results

Electrophoresis. Genetic studies were made of the following specimens: *H. edwardshilli*, *H. corynophyllus*, *H. w. parnabyi* and *H. w. fasensis*. Studies of 34 presumptive loci show that *H. edwardshilli* and *H. corynophyllus* are distinguished by fixed differences for three isoenzymes (AK-1, MPI-1 and 6-PGDH) and a large frequency difference at another (G-6-PDH-2). The Nei genetic distance between these taxa is relatively small compared to their distances from *H. w. parnabyi* and *H. w. fasensis* and, indeed, if taken at face value, would not strongly suggest that two distinct species are being analysed. However, it may be noted that there is a very low level of genetic polymorphism within both *H. edwardshilli* and *H. corynophyllus*. This would tend to minimise the effect of the variation which is observed between the taxa (owing to the use of the squares of identities within taxa in the denominator of Nei's metric). The factor should not be so apparent in Roger's distance calculations, and as can be seen from Table 2, the value for this distance between *H. edwardshilli* and *H. corynophyllus* is higher than the Nei metric when compared to the measurements between the other taxa. When viewed in this light, the genetic evidence provides support for the separation of *H. edwardshilli* and *H. corynophyllus* into distinct species.

Genetic studies of 31 presumptive loci show that *H. w. parnabyi* and *H. w. fasensis* are distinguished by four fixed differences (FDP, GPI, LDH-1, and UDPG). Examination of more specimens of *H. w. fasensis* might reduce this number but it is more probable that large frequency differences would remain for these isozymes. Further studies could also reveal that the allozymes (IDH-1 2 and PGM 1) which are found in the present sample in *H. w. fasensis* but not *H. w. parnabyi* are actually restricted to the former taxon. In any case the genetic data strongly support the discrimination of these taxa at least at the sub-specific level.

Systematics

Hipposideridae

Hipposideros Gray, 1831

***Hipposideros edwardshilli* n.sp.**

Figs 2-5, Table 3

Type material. HOLOTYPE, AM M21752, adult female in spirit, skull extracted. Collected from a mistnet set at Imonda Station (3°20'S 141°10'E), Bewani Mountains, Papua New Guinea at an altitude of 240 m, 1 Mar. 1990, P. German & L. Seri.

PARATYPES, AM M21753, adult male skin and skull, same data as for holotype; AM M21749, adult female in spirit, skull extracted, AM M21750-51, adult males entire in spirit, all from cave 150 m south-west of Imonda Airstrip, 28 Feb. 1990, P. German & L. Seri; AM M22841, adult female in spirit (skull extracted but not fully cleaned), collected while flying by local people at Pou Village near Imonda by V. Kula, 8 June 1990.

Etymology. In honour of John Edwards Hill, in recognition of his outstanding contributions to bat taxonomy, and the help he has extended over the years to researchers investigating chiropteran taxonomy.

Diagnosis. Differing from all *Hipposideros* except members of the *H. cyclops* group of Hill (1963) in possessing two club-like projections on the noseleaf. The two African members of the *H. cyclops* group are very large and markedly different from the Australasian

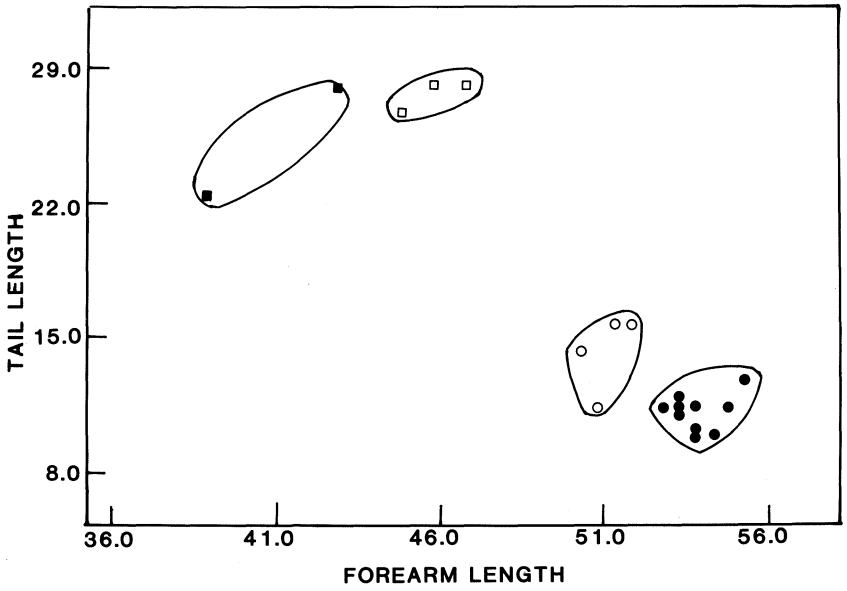

Fig.2. Bivariate plot of tail length over forearm length (in mm) for *Hipposideros corynophyllus* (dot), *H. edwardshilli* (circle), *H. semoni* (hollow square) and *H. stenotis* (square).

species (Hill, 1963) and they are not further discussed here. Differing from all Australasian members of the *H. cyclops* group except *H. corynophyllus* Hill (1985) in having a forearm length greater than 49.6 and a tail less than 15 mm long, in having the postmetacrista of M^3 reduced, and in having the talonid of M_3 reduced and laterally displaced. Further differing from *H. semoni* and *H. stenotis* in lacking the thin web of bone connecting the articular and angular processes on the mandible, in having C^1 and P^4 separated by P^2 (a feature that also distinguishes it from *H. wollastoni*). Further differing from *H. muscinus* and *H. wollastoni* in having the club-like projections of the noseleaf very prominent, and from *H. wollastoni* in lacking an accessory posterior noseleaf. Differing from *H. corynophyllus* in being Prout's Brown dorsally and Cinnamon Rufus ventrally as opposed to Hair Brown overall, and in that: i) the fur and forearm are shorter and the tail on average longer (Fig.2, Table 3); ii) the rostral swellings are more inflated; iii) the frontal concavity is deeper in profile; iv) the postorbital region is more constricted; v) the bulla are on average larger; and vi) the ventral projection of the noseleaf is

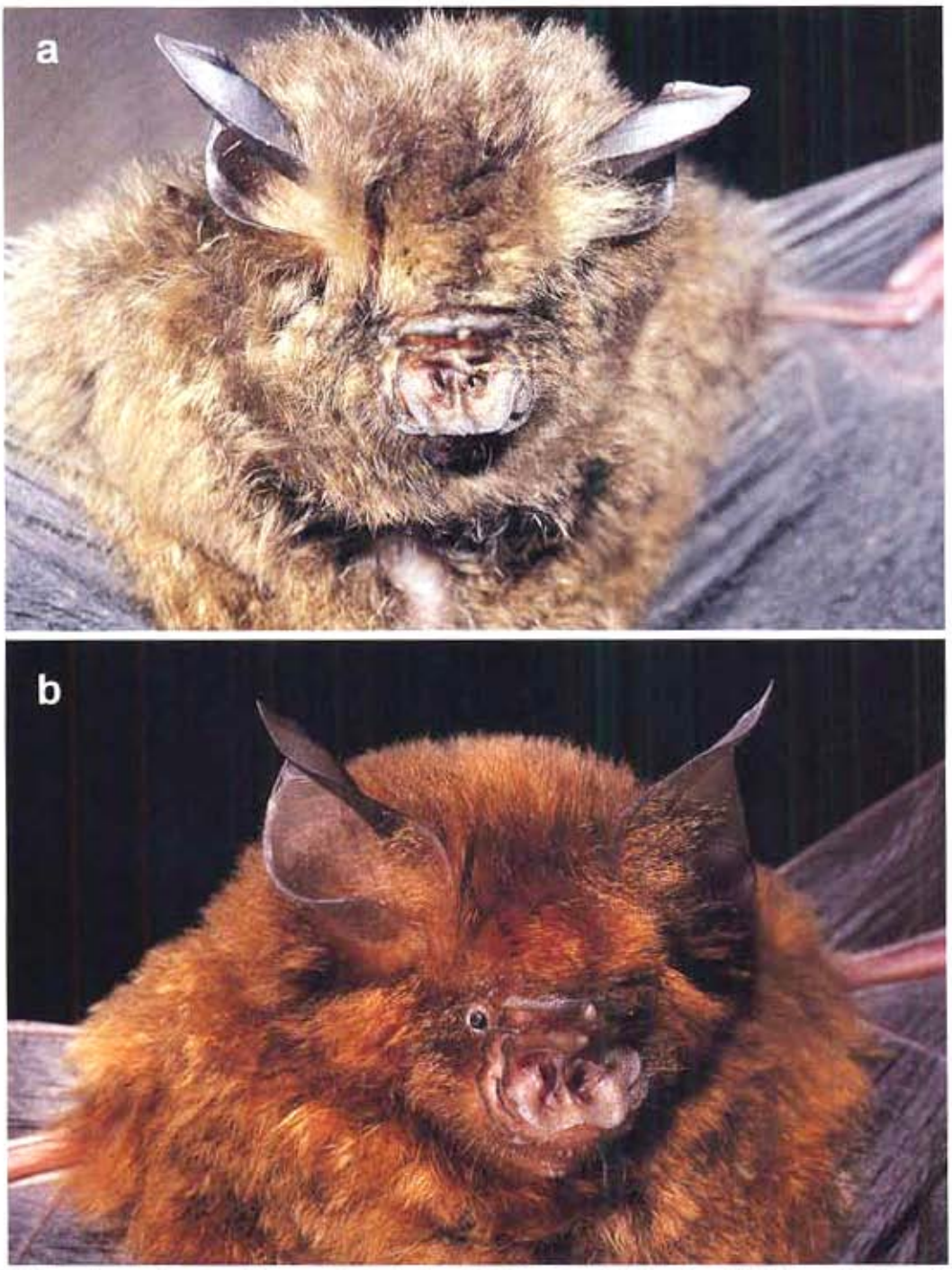

Fig.3. Colour photographs of a, *H. corynophyllus* (photo H. Cogger) and b, *H. edwardshilli* (photo P. German).

shorter and laterally compressed (Fig.3).

Description. Externally most similar to *H. corynophyllus* Hill (1985), but differing in that the fur is Prout's Brown dorsally with a reddish tinge in life, and the venter is Cinnamon Rufus (Fig.3). This presents a marked contrast to *H. corynophyllus* which is close to Hair Brown all over, but with silver tipping ventrally. The fur is also markedly shorter: around 8.7 mm long on the midback on a study skin of *H. edwardshilli*, as

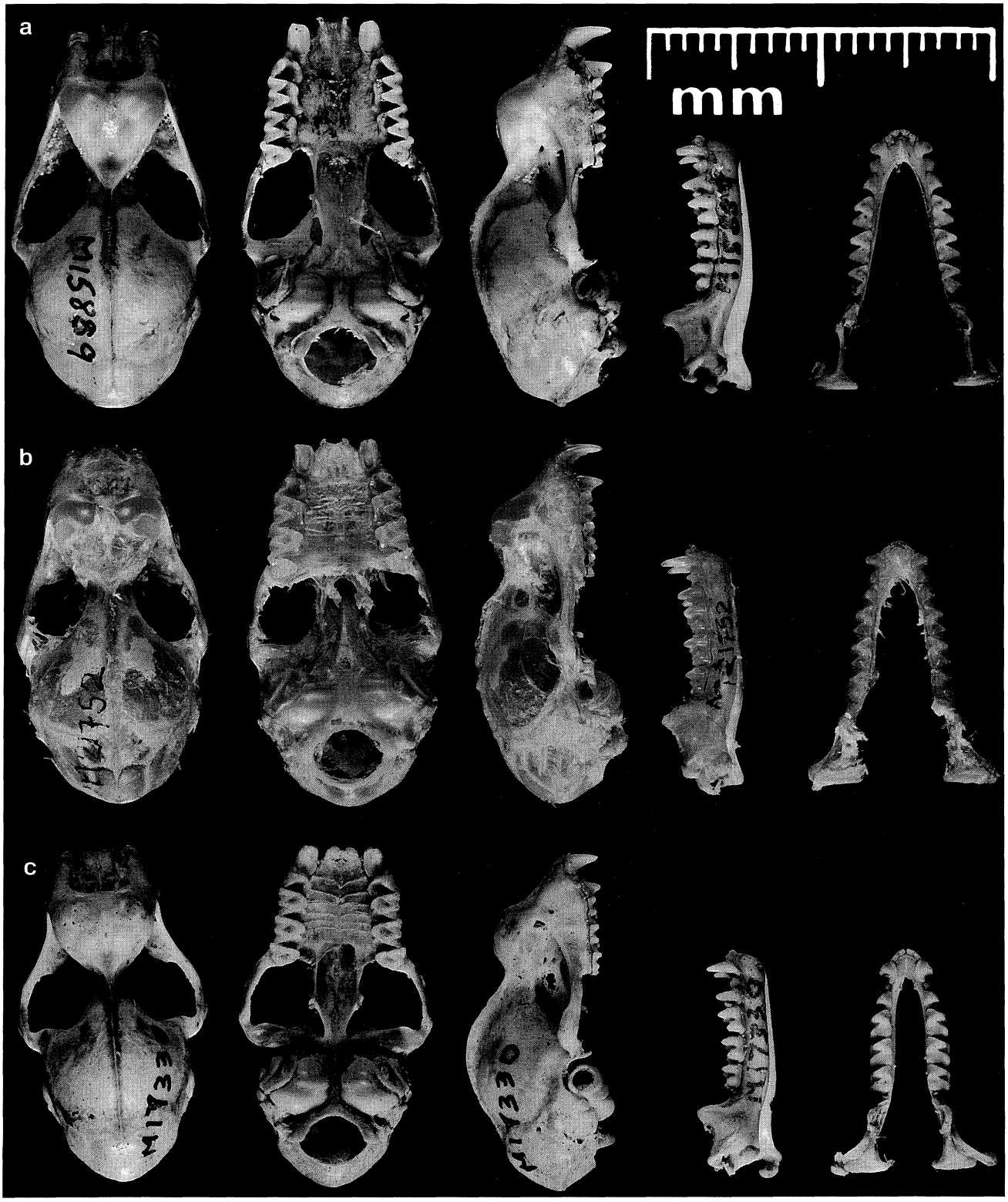

Fig.4. Photographs of the skulls of a, *Hipposideros corynophyllus* (AM M15889); b, *H. edwardshilli* (AM M21752 holotype); and c, *H. semoni* (AM M17330).

opposed to 14.2 mm in the same position in a study skin of *H. corynophyllus*. The claws of the feet of the new species are smaller than in *H. corynophyllus*. The tail is very short (11.1-15.0 mm long). The noseleaf is largely similar to that of *H. corynophyllus*, differing primarily in the shape of the lower club. In *H. corynophyllus* this club is very long and tubular; in *H. edwardshilli* it is shorter and laterally flattened (Fig.3).

In many regards the skull of *H. edwardshilli* is intermediate in morphology between the conditions seen in *H. semoni* and *H. corynophyllus*. The rostral swellings are intermediate in size between the condition seen in these species (Fig.4). Partly as a consequence of this the frontal concavity is in profile deeper than in *H. corynophyllus* but shallower than in *H. semoni* (Fig.4). The anteorbital foramen is elongate and similar in shape to that of *H. corynophyllus*. The bulla are larger than in either species (Figs 4-5). The dentary lacks the thin web of bone that connects the angular and articular processes, as in *H. corynophyllus*. The P^2 prevents contact between the C^1 and P^4, also as in *H. corynophyllus*. The posterior end of the molar dentition is also reduced in a similar manner to *H. corynophyllus*, the postmetacrista of M^3 being minute, while the talonid of M_3 is reduced and laterally displaced (Fig.4).

Discussion. The recovery of a large sample of *H. corynophyllus* has allowed for a re-assessment of the diagnosis of this species as given by Hill (1985) which was based upon a single specimen with both forearms broken. A statistical summary for this sample is given in Table 3. Hill (1985) estimated that the forearm length might have been around 48 to 49 mm. The sample now available indicates that forearm length ranges from 52.0 to 54.6 mm (mean = 53.0 mm). The dental, cranial and facial features as described by Hill (1985) are confirmed by the larger series, but an additional important feature, tail length, has been identified. Tail length ranges from 9.0 to 12.0 mm, which is far shorter than in any other Australasian species in the *Hipposideros cyclops* group. Both forearm length and average tail length distinguish *H. corynophyllus* from *H. edwardshilli* (Fig.2). The inverse relationship between tail and forearm length in the four species in Figure 2 is curious. Such a relationship is not evident in other members of the *H. cyclops* group.

Hipposideros edwardshilli is known from six individuals, of which two are subadult. The subadults are greyish in colouration, while all four adults are brownish red, as described above for the holotype. Three of these specimens were taken from a limestone cave at an altitude of 240 m, and others were caught while flying in the vicinity. *Hipposideros corynophyllus* also inhabits limestone caves, but it is only known from elevations above 1,400 m in the Telefomin area, approximately 200 km to the south (Flannery & Seri, 1990). *Hipposideros corynophyllus* shares caves with *H. wollastoni parnabyi* in the Telefomin area. No *H. wollastoni* were collected in the cave that shelters *H. edwardshilli* near Imonda.

It seems likely than the nearest relative of *H. edwardshilli* is *H. corynophyllus*. Both species have reduced the posterior ends of the molar rows and have very short tails. Both features are unique within Australasian members of the *Hipposideros cyclops* group, and are unusual within *Hipposideros* as a whole. They are also both large species (the largest of the Australasian members of the *H. cyclops* group), and both have very well-developed club-like projections in the centre of the posterior and intermediate noseleaves. It is interesting that in so many aspects of cranial morphology *H. edwardshilli* is intermediate between the condition seen in *H. semoni* and *H. corynophyllus*. These three species,

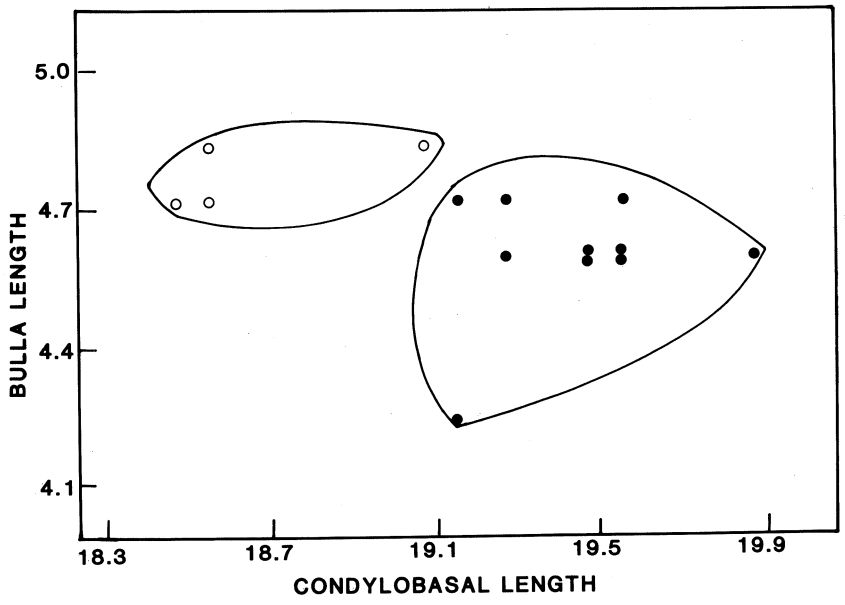

Fig.5. Bivariate plot of bulla length over condylobasal length (in mm) for *Hipposideros corynophyllus* (dot) and *H. edwardshilli* (circle).

along with *H. stenotis* of Australia, clearly form a cluster of closely related species within the *H. cyclops* complex, as all possess very prominent club-like projections on the posterior and intermediate noseleaves. These are either smaller or absent in other members of the *H. cyclops* group in Australasia.

One further record, which may relate to this species, needs discussion. McKean (1968) reports upon a single bat from Aseki, Morobe Province that he refers to *H. semoni*. However, the forearm length (51.8 mm) suggests that this bat was not *H. semoni*, but either *H. corynophyllus* or *H. edwardshilli*. The exact identity of the specimen will probably never be resolved, as it remained in McKean's personal collection until it was destroyed during Cyclone Tracy in 1974 (J. Calaby, personal communication). The record is of potential great importance, however, as it is much further east than other records for these species.

Hipposideros wollastoni Thomas, 1913

Diagnosis. *Hipposideros wollastoni* can be distinguished from all other species of *Hipposideros* in its possession of a posterior accessory noseleaf. This structure is joined to the posterior leaf by two external and two intermediate septa.

Discussion. Examination of the three specimens reported upon by Hill (1985) from Telefomin and Tabubil, 33 obtained by T.F.F. from Telefomin and other localities within a 30 km radius, and a single specimen from the North Coast Range, has revealed considerable variability within this taxon. The Telefomin and North Coast Range samples are sufficiently different to recognise them as distinct subspecies, which are described below. The question as to whether these three taxa should be recognised at the specific or subspecific level is a vexed one. There is little doubt that all three are close relatives, as they are the only *Hipposideros* to possess an accessory posterior noseleaf, an undoubted synapomorphy. The biochemical data, however, suggests that at least *H. w. parnabyi* and *H. w. fasensis* are quite distinct, the data being concordant with recognition at species level. There are also several morphological and colour differences between these taxa. If, however, these two taxa were to be recognised as distinct species at present, problems concerning the nominotypical form would arise. The only known specimen of the nominotypical form cannot be compared with the other taxa biochemically. Furthermore, it is faded and its original colour is uncertain. It can, however, be adequately diagnosed from the other two forms on the basis of its cranium and noseleaf structure. Even if it is accepted, on the basis of biochemistry and morphology, that *H. w. parnabyi* and *H. w. fasensis* are distinct species, it cannot be adequately demonstrated that one or the other is not a subspecies of *H. wollastoni*. To add to the uncertainty, two of the three forms are known from a single specimen. Given these difficulties, it is our decision that, until further data are forthcoming, it is best to regard these as samples representing very distinct subspecies of a single species.

Hipposideros wollastoni wollastoni Thomas, 1913

Table 4

Type material. HOLOTYPE, BMNH 13.6.18.4, adult female in spirit, skull extracted, collected by Dr Wollaston in January 1912 at an elevation of around 750 m at Camp 3 (4°27'S 137°14'E) on the Utakwa River, southern slopes of the Central Cordillera, in what is now Irian Jaya.

Diagnosis. Differing from *H. wollastoni parnabyi* in its shorter ear and cheektooth row length, and lack of a club in the middle of the posterior noseleaf. Differing from *H. wollastoni fasensis* in its shorter forearm and cheektooth row length, broader rostrum, in having the accessory posterior noseleaf shorter than the posterior noseleaf, and in its lesser bizygomatic width.

Discussion. The noseleaf is figured in Hill (1963). No additional material has been reported upon since the discovery of the holotype. The holotype is so badly faded that its original colour cannot be determined, and the colour is not recorded in the type description.

Hipposideros wollastoni parnabyi n.subsp.

Figs 6-10, Table 4

Type material. HOLOTYPE, AM M15892, adult female in spirit, skull extracted, collected from a cave in the Nong River valley adjacent to Miptigin, Telefomin area (5°11'S 141°35'E), 9 July 1985 by T.F. Flannery.

PARATYPES, 32 (see Appendix II).

Etymology. For Harold Edwin Parnaby, in recognition of his contribution to bat taxonomy and conservation.

Diagnosis. Differing from *H. wollastoni wollastoni* in its longer ear (Table 4), greater condylobasal length (Fig.6), possession of a small club in the middle of the posterior noseleaf, and in lacking the fringe of hairs along the posterior margin of the posterior accessory noseleaf (Fig.7). Differing from *H. wollastoni fasensis* n.subsp. in colour, having a brownish (see below) dorsum and Drab Grey venter, as opposed to being black overall; in its longer ear (Fig.8), larger rostral eminences (Table 4, Figs 9,10), in having the accessory noseleaf lower than the posterior noseleaf and in having fewer hairs along the dorsal margin of the accessory posterior noseleaf.

Description. The description of the pelage is taken from a dry skin not discoloured by alcohol (AM

M21745). The flight membranes, noseleaf and ears are close to Sepia (119), but in some specimens (most of which are subadults) the ears can be speckled with pink. The tips of the dorsal fur are close to Hair Brown, but for the basal two thirds the fur is close to Drab-Gray. This underfur shows through in life, giving the animal a pale appearance. The fur of the venter is close to Drab-Gray also, but is several shades lighter than the base of the dorsal fur. This gives the bat a strongly bicoloured appearance, the dorsum appearing darker than the venter. The noseleaf of this subspecies has been described in Hill (1985), and our sample confirms the features noted by him. Hill (1985) describes the differences between the cranium in this subspecies and the nominotypical form. The larger series of skulls now available does not reveal any more significant variability. A statistical summary for the sample is given in Table 4. See Figure 10 for the holotype skull.

Discussion. The Australian Museum holds 33 individuals from the Telefomin, Nong River and Tifalmin areas (see Flannery & Seri, 1990), while the British Museum (Natural History) holds two individuals from Telefomin and one from Tabubil to the South. The town of Tabubil lies at approximately

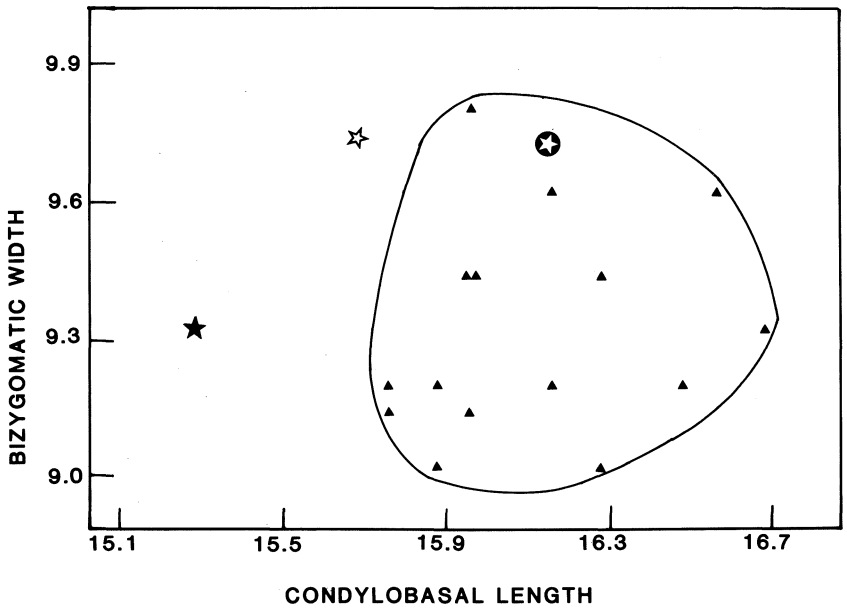

Fig.6. Bivariate plot of bizygomatic width over condylobasal length (in mm) for *H. w. parnabyi* (triangle), *H. w. fasensis* (star in circle), *H. w. wollastoni* (star) and *H. muscinus* (hollow star).

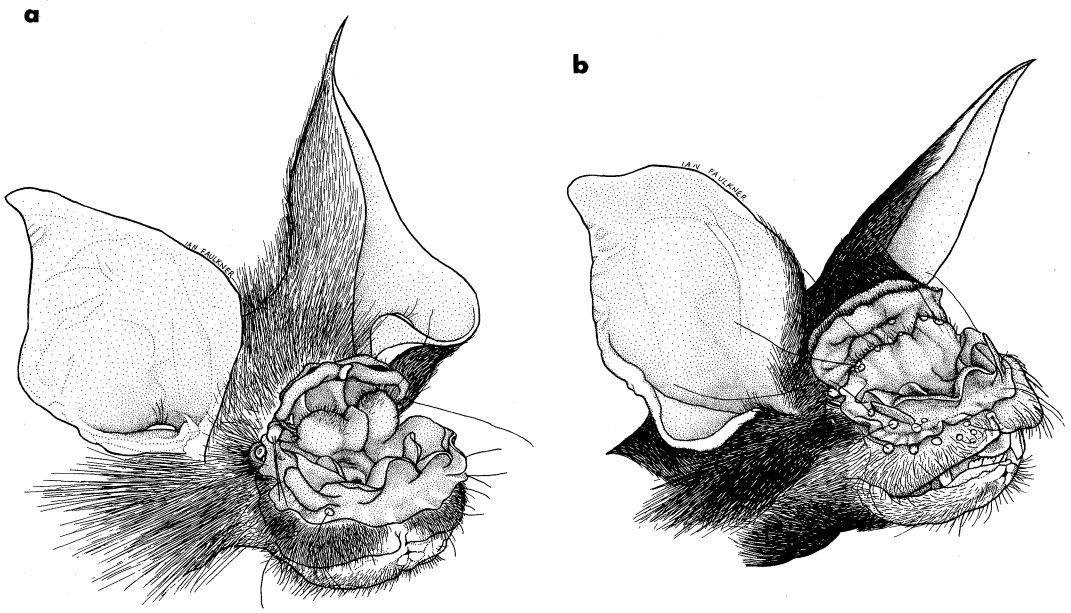

Fig.7. Drawings of the face of a, *H. w. fasensis* and b, *H. w. parnabyi.*

580 m elevation. Vegetational zonation is markedly depressed in the Tabubil area, probably due to near continuous cloud cover and extremely high rainfall. Species typical of forest above 2,000 m elevation in the Telefomin area occur as low as 800 m in the Tabubil area (Flannery & Seri, 1990). This may account for the occurrence of *H. w. parnabyi* at such a low elevation in this region. The Museum of Victoria also holds a single individual (NMV C25494) from Kavorabip (elevation 1500 m) in the Tabubil area. The remaining subspecies of *H. wollastoni* are known from a single specimen each. There is very little morphological variability within the large sample of *H. wollastoni parnabyi* available for study. Juveniles have fur similar in colour to adults, although the ears may have pinkish blotches, and all individuals have a small club-like structure on the posterior noseleaf. There is no sexual dimorphism in size or morphology. All likewise differ from *H. w. fasensis* in having the fringe of hair less well developed on the dorsal margin of the accessory posterior noseleaf. The skulls of 19 individuals (of which 15 are complete adult skulls) have been removed and measured, and they reveal the kind of variability typical of a microchiropteran species that lacks sexual dimorphism.

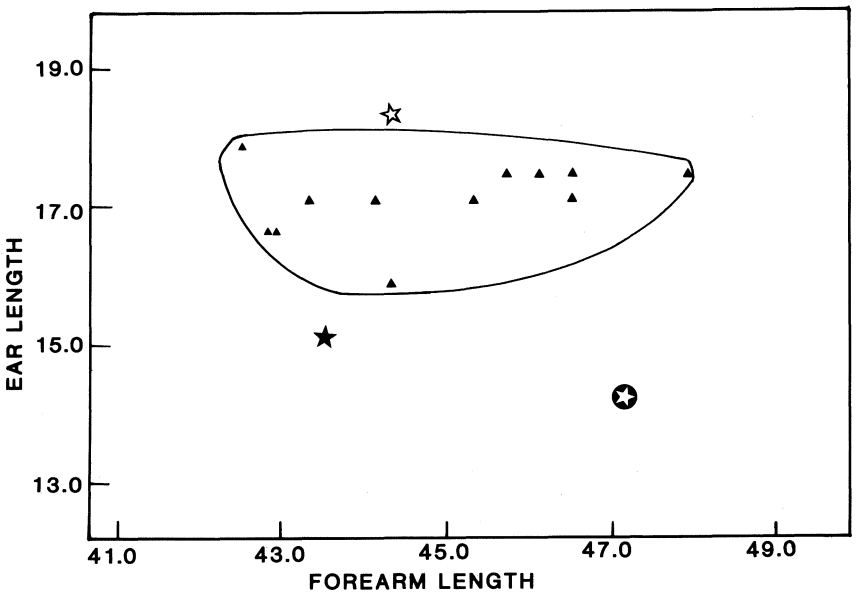

Fig.8. Bivariate plot of ear length over forearm length (in mm) for *H. w. fasensis* (star in circle), *H. w. parnabyi* (triangle), *H. w. wollastoni* (star) and *H. muscinus* (hollow star).

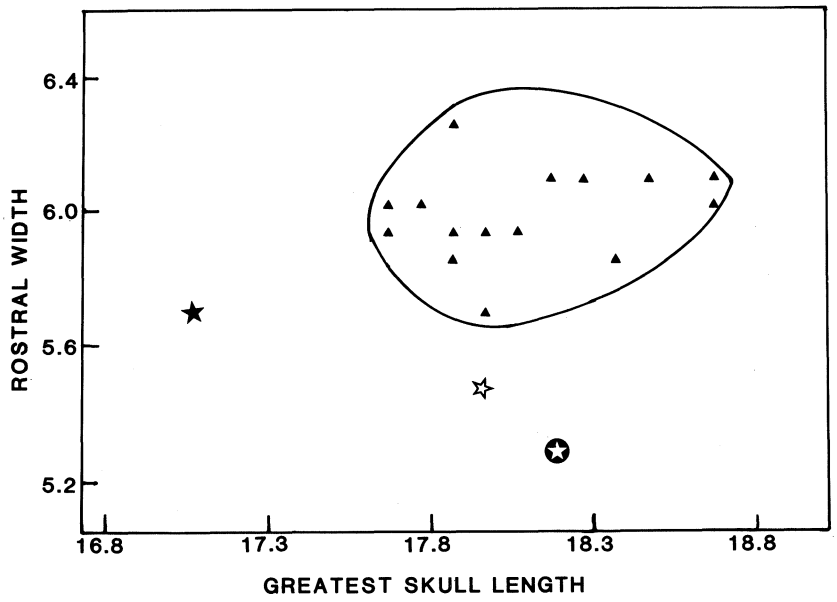

Fig.9. Bivariate plot of rostral width over greatest skull length (in mm) for *H. w. parnabyi* (triangle), *H. w. fasensis* (star in circle), *H. w. wollastoni* (star) and *H. muscinus* (hollow star).

Hipposideros wollastoni fasensis n.subsp.

Figs 6-10, Table 4

Type material. HOLOTYPE, AM M21876, young adult female (basilar suture fused but wing joints still unfused) caught hanging under a small landslip at an elevation of 400-450 m on the hill south of 2Fas Airstrip (3°13'S 141°30'E) West Sepik Province, Papua New Guinea, acquired by T. Flannery, 26 Feb. 1990.

Etymology. After the Fas villages; Sowarnafas (also known as 1Fas), 2Fas and 3Fas. It was due to confusion caused by these names that T.F.F. was stranded in 2Fas Village for a week, when he had planned to work at 3Fas. During this interlude he acquired the holotype of *H. w. fasensis.*

Diagnosis. Differing from *H. wollastoni wollastoni* in its narrow rostral eminences (Fig.9), in that the accessory posterior noseleaf is taller than the posterior noseleaf, the median projection of the intermediate noseleaf is not as pronounced, and the fringe of hairs along the posterior margin of the accessory posterior noseleaf is very well developed (Fig.7a). Differing from *H. wollastoni parnabyi* n.subsp. in being black all over rather than brown and fawn, in having narrow and low rostral eminences, shorter ears (Fig.8a), the accessory posterior noseleaf taller than the posterior noseleaf, in lacking such a prominent median eminence in the centre of the intermediate noseleaf, in lacking a club in the middle of the posterior noseleaf, and in possessing a well-developed fringe of hairs along the posterior margin of the accessory posterior noseleaf (Fig.7a).

Description. The pelage is approximately 5.5 mm long over the midback. Differing from *H. w. parnabyi* in that the dorsum is black, and in that the venter is also black, but with very slight pale tipping. The ears, noseleaf and wing membranes are all black. The left forearm is broken, and the joints of the phalanges of the wings are slightly swollen, which is another indication that the individual was not fully adult. The skin of the noseleaf is black, and the noseleaf differs from that of other *H. wollastoni* in a number of ways. The accessory posterior noseleaf is marginally taller than the posterior noseleaf itself, while in other subspecies the posterior noseleaf is the taller of the two structures (Fig.7). The fringe of hairs along the dorsal margin of the accessory posterior noseleaf is dense, although individual hairs are short. There is no median prominence (club) on the posterior noseleaf (also seen in *H. w. wollastoni).* The median projection of the intermediate noseleaf is small relative to other forms of *H. wollastoni.* The lateral leaflets do not differ (except in colour) from *H. w. parnabyi.*

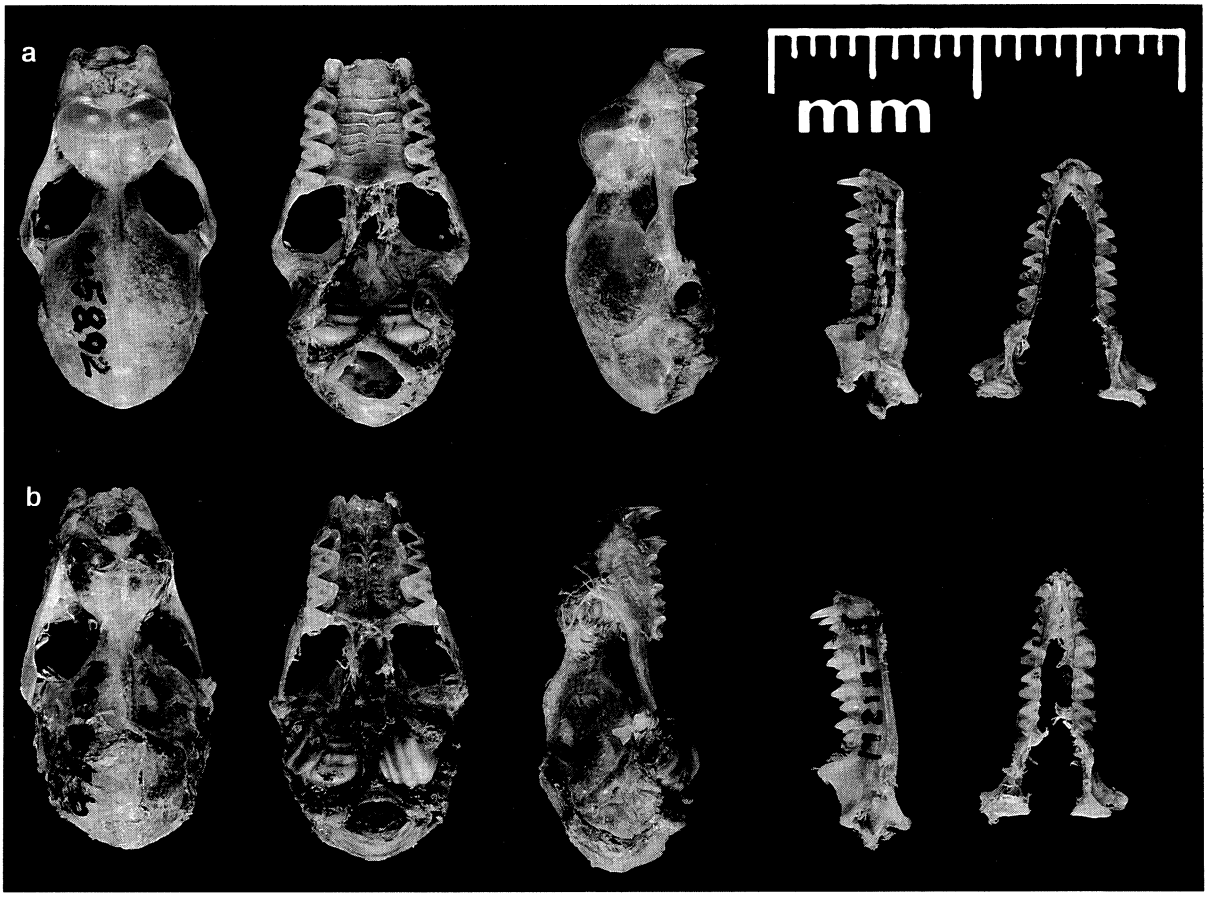

Fig.10. Photographs of the skulls of a, *Hipposideros wollastoni parnabyi* (AM M15892, holotype) and b, *H. w. fasensis* (AM M21876, holotype).

The rear of the skull is cracked and slightly distorted (which probably happened at the time of capture, see Fig.10). The anterior right moiety of the braincase has a depressed fracture. The skull evidently is from a young adult as the basilar suture is fused, the adult dentition erupted, but the teeth are little worn. The teeth are large relative to condylobasal length (Table 4), which may also indicate that it was not fully grown. In overall shape very similar to *H. w. parnabyi*, but differing in the following: rostral swellings and supraorbital crests not as prominent, the sagittal crest tapers off more rapidly posteriorly. The basicranial region is fractured, and as a result cannot be fully cleaned, dried tissue thus obscures some morphology.

Discussion. The single known specimen of *H. w. fasensis* was caught by a man from Fugere Village near 2Fas Airstrip. There were two bats roosting together under the small overhang left in a bank by a small landslip, one of which escaped. This roost site is very different from that used by *H. w. parnabyi* in the Telefomin area. In several years work, which resulted in the collection of 33 individuals, *H. w. parnabyi* was only encountered at roost in deep, moist limestone caves. Only a single small cave was located in the 2Fas area. It was inhabited by a large colony of *Hipposideros massigtaylorae*.

Although the noseleaf, ear and pelage of *H. w. parnabyi* are distinctive, the skull reveals few differences from other *H. wollastoni*. The teeth are relatively large, and the skull had clearly not reached its full adult size. Forearm length would probably have increased a little by the time growth ceased.

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APPENDIX I

Table 1. Enzymes scored, E.C. Numbers, electrophoretic conditions and inferred genotype for four *Hipposideros* taxa. Enzymes are identified by the abbreviations given in Harris & Hopkinson (1977). Buffer compositions are given in Colgan (1986). Taxa were monomorphic for the stated genotype except that the *H. corynophyllus* (FB96) was heterozygous for a variant G-6-PDH allozyme. Genotypes have been inferred on the supposition that the loci are not sex-linked.

Enzyme	E.C. No.	Buffer	Locus	Inferred Genotypes			
				H. wollastoni parnabyi	*H. wollastoni fasensis*	*H. edwardshilli*	*H. corynophyllus*
AAT	2.6.1.1	TC 100	1	11	11	11	11
			2	11	11	11	11
AK	2.7.4.3	TC 100	1	22	11	22	22
			2	11	11	11	11
ALD	4.1.2.13	TEM 50	1	11	11	11	11
ENOL	4.2.1.11	TEM 50	1	11	11	22	22
EST	3.1.1.1	TEM 50	1	11	11	22	22
FDP	3.1.3.11	TEM 50	1	11	11	33	22
FH	4.2.1.1	TC 100	1	11	11	11	11
GA-3-PDH	1.2.1.12	TEM 50	1	11	11	11	11
GPD	1.1.1.8	TEM 50	1	11	11	11	11
			2	11	11	11	11
General		TEM 50	1	22	22	11	11
Protein			2	22	22	11	11
			3	11	11	11	11
G-6-PDH	1.1.1.49	TEM 50	1	11	11	22	22
			2	22	11, 12	null	null
GPI	5.3.1.9	TEM 50	1	11	11	22	11
IDH	1.1.1.42	TEM 50	1	33	33	11	12
			2	11	11	11	11
LDH	1.1.1.27	TC 100	1	22	22	33	11
			2	11	11	11	11
MDH	1.1.1.37	TEM 50	1	11	11	11	11
			2	11	11	11	11
MPI	5.3.1.8	TEM 50	1	22	11	22	22
			2	11	11	null	null
6-PGDH	1.1.1.44	TEM 50	1	33	11	22	22
PGM	2.7.5.1	TEM 50	1	22	22	22	12
SDH	1.1.1.14	TEM 50	1	22	22	11	11
SOD	1.15.1.1	TEM 50	1	11	11	22	22
			2	11	11	null	null
TPI	5.3.1.1	TEM 50	1	11	11	11	11
			2	11	11	11	11
UDPG	2.7.7.9	TC 100	1	11	11	33	22

Table 2. Genetic distances between four *Hipposideros* taxa. The figures below the diagonal refer to Wright's modification of Rogers' distance and those above to Nei's standard distance. Distances are based only on those loci which are represented in both members of the relevant pair.

Taxon	*H. e.*	*H. c.*	*H. w. p.*	*H. w. f.*
H. edwardshilli	–	0.115	0.544	0.500
H. corynophyllus	0.330	–	0.661	0.614
H. wollastoni parnabyi	0.648	0.696	–	0.159
H. wollastoni fasensis	0.622	0.672	0.381	–

Table 3. Summary of measurements for *Hipposideros edwardshilli*, *H. corynophyllus*, *H. stenotis* and *H. semoni*. Measurements are as follows: 1) forearm length, 2) tail length, 3) ear length, 4) condylobasal length, 5) greatest skull length, 6) bizygomatic breadth, 7) width across rostral swellings, 8) bimastoid breadth, 9) C^1-M^3 length (alveolar), 10) M^2-M^2 breadth (alveolar, external), 11) bulla width.

	Variable	Mean	S.D.	N	Median	Minimum	Maximum
H. edwardshilli	1	50.25	.66	4	50.20	49.60	51.00
	2	13.57	1.80	4	14.10	11.10	15.00
	3	20.45	1.00	4	20.60	19.30	21.30
	4	18.60	.27	4	18.50	18.40	19.00
	5	21.02	.29	4	21.00	20.70	21.40
	6	11.07	.19	4	11.15	10.80	11.20
	7	6.95	.06	4	6.95	6.90	7.00
	8	10.07	.05	4	10.10	10.00	10.10
	9	7.93	.09	4	7.95	7.80	8.00
	10	8.00	.08	4	8.00	7.90	8.10
	11	4.75	.06	4	4.75	4.70	4.80
H. corynophyllus	1	53.03	.81	10	52.80	52.00	54.60
	2	10.58	1.06	10	10.85	9.00	12.00
	3	20.67	1.13	11	20.50	18.90	22.60
	4	19.35	.22	11	19.40	19.10	19.80
	5	21.88	.75	11	21.90	19.80	22.60
	6	11.45	.18	11	11.50	11.10	11.60
	7	6.68	.23	11	6.70	6.40	7.00
	8	10.26	.14	11	10.30	10.00	10.50
	9	8.30	.11	11	8.30	8.10	8.40
	10	8.21	.17	10	8.15	8.10	8.60
	11	4.59	.15	10	4.60	4.20	4.70
H. stenotis	1	45.00	1.00	3	45.00	44.00	46.00
	2	26.67	.58	3	27.00	26.00	27.00
	3	20.00	1.00	3	20.00	19.00	21.00
	4	17.05	.57	4	16.80	16.70	17.90
	5	18.95	.81	4	19.05	17.90	19.80
	6	10.67	.30	4	10.70	10.30	11.00
	7	6.03	.36	4	6.15	5.50	6.30
	8	8.38	.43	4	8.50	7.80	8.70
	9	7.05	.33	4	6.95	6.80	7.50
	10	7.30	.28	4	7.20	7.10	7.70
	11	4.05	.37	4	4.10	3.60	4.40
H. semoni	1	40.53	2.20	3	41.50	38.00	42.10
	2	25.00	4.20	2	25.00	22.00	28.00
	3	19.23	1.10	3	19.70	18.00	20.00
	4	15.25	.79	4	15.05	14.60	16.30
	5	17.05	.79	4	17.05	16.20	17.90
	6	9.35	.26	4	9.30	9.10	9.70
	7	5.65	.38	4	5.50	5.40	6.20
	8	7.30	.56	4	7.20	6.80	8.00
	9	5.83	.31	4	5.90	5.40	6.10
	10	6.30	.27	4	6.40	5.90	6.50
	11	3.50	.22	4	3.45	3.30	3.80

Table 4. Summary of measurements for the three subspecies of *Hipposideros wollastoni* and *H. muscinus*. See Table 3 for explanation of measurements.

	Variable	Mean	S.D.	N	Minimum	Maximum
H. w. fasensis	1	46.80	–	1	–	–
	2	23.60	–	1	–	–
	3	14.30	–	1	–	–
	4	16.10	–	1	–	–
	5	18.10	–	1	–	–
	6	9.70	–	1	–	–
	7	5.30	–	1	–	–
	8	7.80	–	1	–	–
	9	6.90	–	1	–	–
	10	6.50	–	1	–	–
	11	3.80	–	1	–	–
H. w. parnabyi	1	44.67	1.70	15	42.30	47.50
	2	25.27	1.60	12	23.00	28.00
	3	17.06	.49	12	15.90	17.70
	4	16.05	.29	15	15.70	16.60
	5	18.02	.33	15	17.60	18.60
	6	9.30	.23	15	9.00	9.80
	7	5.97	.14	15	5.70	6.20
	8	7.75	.42	15	7.10	8.40
	9	6.67	.15	15	6.50	7.00
	10	6.66	.18	13	6.20	6.90
	11	3.77	.11	13	3.60	4.00
H. w. wollastoni	1	43.20	–	1	–	–
	2	27.00	–	1	–	–
	3	15.00	–	1	–	–
	4	15.20	–	1	–	–
	5	17.00	–	1	–	–
	6	9.30	–	1	–	–
	7	5.70	–	1	–	–
	8	8.00	–	1	–	–
	9	6.40	–	1	–	–
	10	6.80	–	1	–	–
	11	–	–	-	–	–
H. muscinus	1	44.00	–	1	–	–
	2	28.00	–	1	–	–
	3	18.00	–	1	–	–
	4	15.60	–	1	–	–
	5	17.90	–	1	–	–
	6	9.70	–	1	–	–
	7	5.40	–	1	–	–
	8	8.00	–	1	–	–
	9	6.50	–	1	–	–
	10	6.70	–	1	–	–
	11	3.70	–	1	–	–

APPENDIX II

Specimens examined in Australia for this analysis, excluding type specimens (see text). Specimens marked with an asterisk were used in the metric analysis.

Hipposideros corynophyllus – AM M15889*, 17889, 17890*, 17971, 17972*, 17973, 17974, 17975, 17976, 17977, 17978*, 17979, 17980, 17981, 17982*, 17983*, 17984*, 17985, 17986*, 17987, 17988*, 17989*, 19985, 21742*, all Telefomin and Tifalmin areas, West Sepik Province, PNG.

Hipposideros wollastoni parnabyi – AM M15885*, 15886*, 15887, 15888*, 15890*, 15891*, 15892*, 15893*, 15894*, 15895*, 15896*, 15897*, 16721, 17917, 17918, 17919*, 17920, 17921, 17922, 17923, 17924, 17925*, 17926*, 17927, 17928, 17929*, 17930, 17931*, 21743*, 21744*, 21745*, 21875, 23203, all Telefomin and Tifalmin areas, West Sepik Province, PNG.

Hipposideros muscinus – AM M17331* near Noru Village, Chimbu Province, PNG.

Hipposideros semoni – AM M16614*, 16616* Iron Range, Qld, 17330* Varirata National Park, Central Province, PNG, WAM18055* Helenvale, Qld

Hipposideros stenotis – CM10020* Pine Creek, NT, WAM10471* Bonaparte Archipelago, WA, 19391* Koolan Island, WA, 19893* no locality.