

**A revision of the genus *Zaglossus*
(Monotremata, Tachyglossidae), with description
of new species and subspecies**

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Summary. – A systematic revision of monotremes of the genus *Zaglossus* has revealed unexpected morphological diversity. Statistical and non-metric analysis indicate that three species can be recognised: *Zaglossus bruijnii* (Peters and Doria, 1876), which inhabits the Vogelkop, Fak Fak and possibly the Charles Louis Mountains regions; *Zaglossus bartoni* Thomas, 1907a, which occurs on the central cordillera between the Paniai Lakes and the Nanneau Range, as well as the Huon Peninsula; and *Zaglossus attenboroughi* n. sp. from the Cyclops Mountains. Four distinct subspecies of *Z. bartoni* can be discerned. The three subspecies inhabiting the central cordillera increase in size from east to west: *Z. b. smeenki* n. ssp. of the Nanneau Range being the smallest, the nominotypical form intermediate in size, and *Z. b. diamondi* n. ssp. the largest. *Zaglossus b. clunius* inhabits the Huon Peninsula.

Résumé. – Une révision systématique des Monotrèmes du genre *Zaglossus* a montré une diversité morphologique inattendue. L'analyse statistique et non métrique indique qu'on peut reconnaître trois espèces: *Zaglossus bruijnii* (Peters et Doria, 1876) qui habite dans les régions de Vogelkop, Fak Fak et les Montagnes de Charles Louis; *Zaglossus bartoni* (Thomas, 1907) qui se trouve dans la cordillère centrale entre les Lacs Paniai et la chaîne de montagnes Nanneau, ainsi que dans la Péninsule Huon; et *Zaglossus attenboroughi* n. sp. qui vit dans les Montagnes Cyclops. Quatre sous-espèces distinctes de *Zaglossus bartoni* sont discernées. La taille des trois sous-espèces qui habitent la cordillère centrale augmente d'est en ouest. *Zaglossus bartoni smeenki* n. ssp. de Nanneau est la plus petite, la forme nominale est intermédiaire en dimension, et *Zaglossus bartoni diamondi* n. ssp. est la plus grande. *Zaglossus bartoni clunius* habite la Péninsule Huon.

INTRODUCTION

The living monotremes are classified in three genera; *Ornithorhynchus* (the platypus), *Tachyglossus* (the short-beaked echidna) and *Zaglossus* (the long-beaked echid-

nas). Previously, these genera have usually been regarded as monotypic. Members of the genera *Zaglossus* and *Tachygllossus* are clearly closely related, but they differ in the morphology of their beak (long and downcurved in *Zaglossus*, short and straight in *Tachygllossus*), as well as other details of cranial architecture (Griffiths *et al.* 1991).

Great geographic variability has long been recognised within *Zaglossus*. Variation in size gives some indication of this. Some *Zaglossus* are the largest living monotremes, the skins of the largest individuals (perhaps stretched) measured approximately a metre long from the tip of the beak to the tip of the tail (Rothschild 1913), and captive specimens have been known to attain approximately 17 kilograms in weight (Dawson *et al.* 1978). Others, however, are no larger than average *Tachygllossus* (30–45 cm long, and 2–7 kilograms in weight, Augée 1995). In contrast to *Tachygllossus aculeatus*, which eats ants and termites, *Zaglossus* appear to feed primarily on worms (Van Deusen and George 1969).

Extant species of *Zaglossus* are restricted to New Guinea and Salawati, a Pleistocene land bridge island off New Guinea's western tip (Fig. 1). They may also possibly occur on Waigeo and/or Supiori, but voucher specimens are lacking (Flannery 1995b). Australian fossils previously assigned to the genus are now placed in the genus *Megahibgwilia*, or are of uncertain generic status (Griffiths *et al.* 1991).

The long-beaked echidna was first described as *Tachygllossus bruijnii* by Peters and Dona (1876), from a trophy skull from the Arfak Mountains. The following year it was given generic status by Gill (1877) as *Zaglossus*, and independently six months

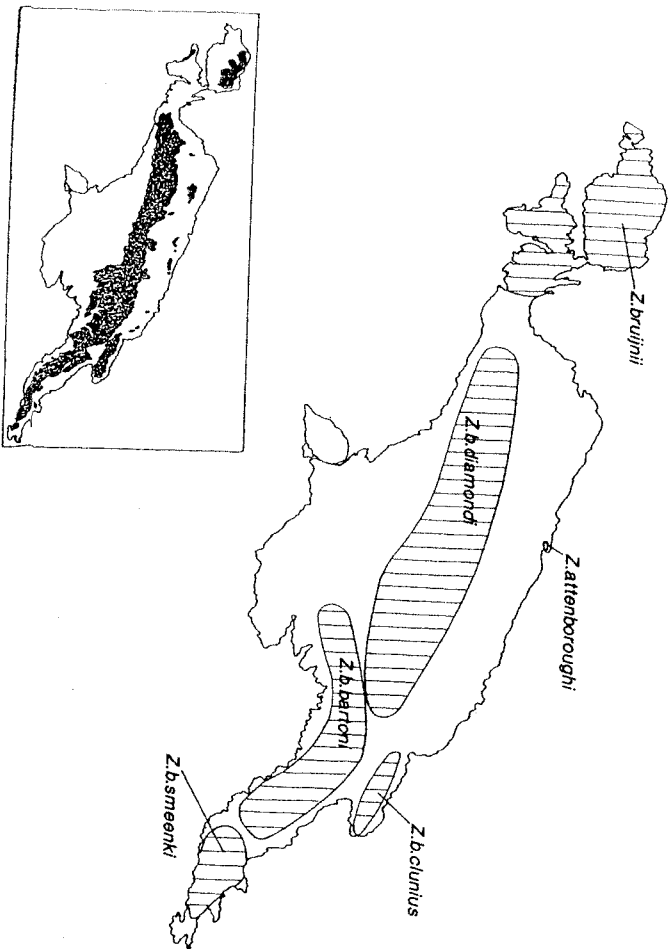


Fig. 1. — Map of New Guinea showing the approximate distribution of the species and subspecies of *Zaglossus*.

later by Gervais (1877) as *Acanthoglossus*. Three years later DuBois (1882), unaware of Gill's name, noted that *Acanthoglossa* had previously been given to a beetle, and unsure whether the difference in termination would be sufficient to prevent what in today's terminology is called homonymy, proposed a provisional replacement generic name *Brynumia* (sic.). Apparently under the impression that a new generic name required a new specific name as well, he suggested renaming the species *Brynumia triadactyla*. He listed the features supporting its generic status, by whatever name it were to be eventually designated.

A new species *Proechidna villosissima*, said to be distinguished by its extremely thick fur with shorter spines barely protruding through it, was named by DuBois (1884) from a specimen known only to have come from "New Guinea", meaning somewhere in the then Dutch (now Indonesian) part.

Rothschild (1892) described *Proechidna nigro-aculeata* from the Charles Louis Mountains, as a species with sparser pelage than *Proechidna bruijnii*, and spines tending to be black. Later (1913) he came to doubt the type locality, considering that it was more likely that the specimen came from Sorong.

Toldt (1906), who was the first author to establish the priority of *Zaglossus*, considered the description of different taxa premature; the variability in spines and hair covering could as well be ascribed to age and seasonal variation, and much more material was needed, from different localities, before the question could be addressed.

Despite this cautious note, other authors, especially Rothschild and Thomas, continued to add to the list of *Zaglossus* species and subspecies. Thomas (1907a) described a new subspecies — the first specimen from what is now Papua New Guinea, the thick-furred *Acanthoglossus bruijnii bartoni* from Mt Victoria in the Owen Stanley range. In a later paper Thomas (1907b) described *Acanthoglossus goodfellowi* from Salawati (the first record of a long-beaked echidna from beyond the mainland of New Guinea). This was another form said to have relatively sparse hair. It is curious that Thomas did not believe that the number of claws in *Zaglossus* was of any taxonomic significance; in his 1907a paper he did not mention this character at all, and although in the 1907b paper he corrected the omission, noting that the type of *A. b. bartoni* had five claws on both fore and hindfeet, he cautioned that "considerable variation in this respect has already been recorded".

Allen (1912) revived Toldt's skepticism of the reality of different species and subspecies of *Zaglossus*. He reviewed the material in the Harvard collection, claiming that variation at some localities (Fak Fak, Arfaks) encompassed the characters attributed to all the taxa described by DuBois, Rothschild and Thomas. Rothschild (1913) strenuously disputed Allen's conclusions; Allen's Fak Fak specimens were "bought from natives by the collector, and have an element of doubt as to the place of origin"; eight living specimens from Kaimana in the Charles Louis Mountains, recently seen by him, varied from *bartoni*-like to *nigroaculeata*-like not because of enormous intraspecific variability, but because Kaimana is in an intergrade zone between them; and so on. Rothschild (1913) defended the validity of all five taxa proposed up to that time, listing them as subspecies of *Zaglossus bruijnii*.

Kerbert (1913) again expressed doubt about the value of pelage thickness and colour, or spine length and colour, for taxonomy, but instead relied upon claw number. Recounting the presence of *Z. b. bartoni* over the whole of the eastern (then British and German) half of New Guinea, he specified that this form consistently had five claws on fore and hindfeet, while those further west has only three, quoting also a letter from Walter Rothschild to that effect. On this basis he separated the two at species level, and even proposed giving the eastern species its own generic status, as *Prozaglossus bartoni*.

In 1922 Thomas and Rothschild revised the genus, accepting *Z. bartoni* as a full species, and described *Zaglossus bartoni chinus* from the Saruwaged Mountains, on the Huon Peninsula. In the same paper Rothschild alone took responsibility for naming two further taxa: *Zaglossus bruijini gularis* from the southern flanks of the Charles Louis Mountains, and *Zaglossus bruijini pallidus* from Geelvink Bay.

Laurie (1952) described a further species, *Zaglossus bubuensis*, from the Babu River district at 7,800 feet, where *Z. bartoni* had also been taken. The new species was said to be five-clawed like *Z. bartoni*, but browner, with the hair not quite covering the spines, and the feet being light brown.

Finally, Van Deusen and George (1969) offered a preliminary revision of the genus, in which they provisionally recognised a single species "until such time as a taxonomist can examine and evaluate [the] material personally" (p. 22).

Ideally, systematic revisions of extant mammal groups should be accompanied by some sort of biochemical analysis. Allozyme electrophoresis of frozen or fresh tissues is currently the most popular of these techniques. Regrettably, in the case of *Zaglossus*, such a study may never be possible. All *Zaglossus* are rare and endangered. They are listed on Appendix I of CITES and, over 15 years of intensive mammal research in New Guinea, T.F.F. has encountered them as living animals just once. DNA analysis of museum specimens may be possible, but at present morphological studies of museum collections, as sparse and unsatisfactory as they are, must suffice for the needs of the systematist.

MATERIALS AND METHODS

All specimens of *Zaglossus* which could be located in world museum collections were examined and measured (see Appendix 1). These include the holotypes of *bartoni*, *bruijini*, *bubuensis*, *chinus*, *goodfellowi*, *gularis*, *nigrocauleatus* and *pallidus*. Only the holotype of *villosissima* (Du Bois 1884), which is a well-illustrated juvenile specimen from the Vogelkop area, could not be examined.

Details of pelage, claw number and non-metric variability in cranial morphology were noted. A series of measurements were then taken on each skull (Appendix 1). *Zaglossus* skulls are delicate, and many museum specimens were damaged and/or lack their extremely fragile mandibles. Where a skull was slightly broken (e.g. a condyle or the tip of the bill was missing) a measurement would be estimated. Cases where this has occurred are indicated in Appendix 1 with the annotation^{es}. With the exception of Figure 5, only adults (individuals with the cranial sutures obscured or nearly so) were used in the statistical analysis. Measurements are given in millimetres and weights in grams. Discriminant Analyses were performed using SPSS Windows, "Direct" Method.

RESULTS

Determining age and sex

Adult *Zaglossus* can readily be distinguished from juveniles by possessing the following characteristics:

1) The sutures of the cranial bones are unfused. In adults these sutures tend to close completely and become obliterated, traces of the naso-frontal suture being among the last to disappear.

2) The major basicranial foramina tend to stay widely open into adulthood, and then narrow slowly with age.

3) The rostrum lengthens and becomes more robust anteriorly.

4) The bones of the posterior palate become more robust, and their margins become visible below the basicranium when viewed from behind.

5) The narial opening becomes rounded posteriorly and shorter with age (12.5-17.3 in adults, 18.1-20.0 in subadults).

Determining sex in museum specimens of *Zaglossus* is difficult. Monotremes lack external genitalia, so dissection or close examination of the cloacal area is necessary in order to provide unequivocal evidence of an individual's sex. Living animals can be sexed by everting the penis (in males) or by palpation of the penial sack.

A spur is present on the ankle of males, but is usually absent in females. It seems likely that many museum specimens were sexed on the basis of the presence or absence of the spur alone. Van Deusen and George (1969) note that "The anatomy of the spur and its gland, and the question of their presence or absence in female specimens will be the subject of a later note. At present we would say that the sexing of *Zaglossus* using only the presence or absence of the spur as a criterion, may lead to error" (p. 12). The "later note" was never published. Griffiths (1978) observed, however, that all males have a spur, and that some juvenile females may have one also. Insufficient adult female *Zaglossus* were examined by him to determine whether the spur ever persists into adulthood. Despite the clear difficulties in determining the sex of museum specimens, data pertaining to sex was accepted as it was written on the specimen label, or recorded in a museum register, as there was no real alternative.

Sexual dimorphism in *Zaglossus*

As skewed sex ratios were present in some samples, it was important to determine whether sexual dimorphism in cranial dimensions or body weight existed in *Zaglossus*. Only one sample (sample 2) of the six which we recognised in *Zaglossus* had a sufficient number of identified, wild-caught males and females to undertake statistical analysis. T-tests reveal that body weight (see Table 1) did not differ significantly (at 0.05) between the sexes, nor did any of the 9 cranial measurements taken on museum specimens. We conclude from this that significant sexual dimorphism does not exist in the population from which sample 2 is drawn.

We also ran a Discriminant Analysis on the entire adult sample we ascribe to *Z. bartoni* (see below). There is a slight separation between the sexes, but much overlap (Fig. 2). Palate Length (PAL) contributes most to the separation; this, and to a lesser degree Interorbital Width (IOW) and Rostrum Height (RH) load positively on the vector (i.e. tend to be greater in females) and contrast with Beak Length (B), Bizygomatic Width (BZW) and Bimastoid Width (BIMAST), which load negatively (i.e. tend to be larger in males). We conclude that for multivariate and univariate purposes, any sexual difference that does exist in this larger sample is not likely to obscure taxonomic difference. There is no *prima facie* evidence for sexual dimorphism in the remaining samples.

TABLE 1. - Weights (in kilograms) for specimens of wild caught *Zaglossus* and sex.

reg. no.	male	female
<i>Zaglossus bartoni bartoni</i> (Sample 2)		
BM 50.1452	5.9	
BM 50.1454	7.9	
BM 50.1453		9.9
AMNH190682		7.3
AMNH190863	4.9	
Griffiths (1978)	8.0	
"	6.0	
"	6.6	
"	7.6	
"	7.0	
"	7.0	
"		7.4
<i>Zaglossus bartoni smeetki</i> (Sample 1)		
CM 6055	5.6	
AMNH157072	3.3	
<i>Zaglossus bartoni diamondi</i> (Sample 4)		
AMNH7998		9.1
AMNH190859		6.6

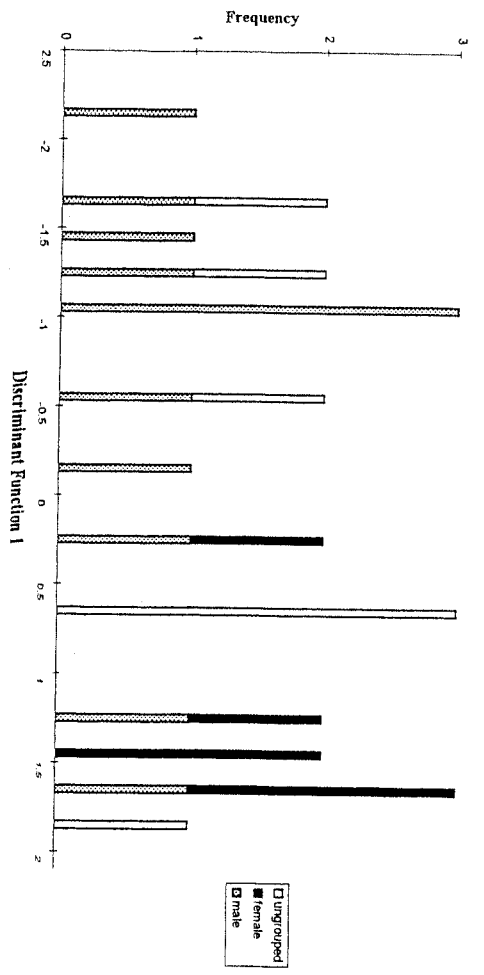


Fig. 2. - Discriminant Analysis of the sexes in *Zaglossus bartoni* (all samples combined). Shaded = males, black = females, blank = ungrouped cases.

Analysis of geographic variability

The living monotremes pose an especially difficult problem for taxonomists. All are edentulous as adults, the echidnas lacking even a dental lamina. Furthermore, the cranium is variable in morphology. Both age and sex play some role in this variability, as do individual differences. Despite this high degree of variability, and the difficulties imposed by their edentulous nature, some geographically related variability could be distinguished within *Zaglossus*.

Analysis of the data began with a broad survey of the available material, to determine whether there were *prima facie* grounds for division into two or more groups. Our initial research suggested that seven geographically separate groups existed. These were categorised as coming from the following areas: Sample 1, the Nanneau Range, far eastern Papua New Guinea; 2, the Owen Stanley Range between about Efogi and Wau; 3, the Huon Peninsula; 4, the central cordillera east of the Paniai Lakes to the Krake Mountains; 5, New Guinea west of the Paniai Lakes; 6, the Cyclops Mountains, northeastern Irian Jaya; and 7, the lowlands of south Chimbu Province (see Appendix 1). The names *bartoni* and *bubensis* are available for sample 2, *clunius* for sample 3, and *bruijini*, *villossissimus*, *nigroculcata*, *goodfellowi*, *gularis* and *pallidus* for sample 5.

Claw number

Our testing of the hypothesis that these samples were distinct began with an examination of Kerbert's (1913) assertion that *Zaglossus* from "eastern" and "western" New Guinea represented two distinct species which differed in claw number. We started by identifying where the supposed disjunction between "eastern" and "western" populations lay, and found to our surprise that it lay well to the west of the centre of the island, in the Lake Paniai area. Samples from west of there share a constellation of features absent in more easterly populations, and were classified by us as sample 5, the easterly ones from the main cordillera being divided between samples 1 and 4.

The key difference noted by earlier authors between eastern and western *Zaglossus* is that western ones normally have three claws on each foot, while more easterly ones have five. Allen (1912) noted that 25 specimens which he examined from western New Guinea (many of which were poorly localised) had three claws on each foot. He also recorded five specimens from "western New Guinea" which had more than three claws on one or more feet. One had an additional claw on digit five on all four feet, a second, a claw on digit five of the hindfoot only, a third a claw on digit one of the right forefoot, and a fourth a claw on digit one of the right forefoot. None of the anomalous specimens reported by Allen is accompanied by precise locality data, and many lack such data entirely. In the absence of precise locality data, and these specimens with anomalous claw numbers for *Zaglossus* taxonomy is uncertain.

A specimen described by Weber (1888), which was held in Amsterdam, reportedly had five claws on both forefeet, but lacked claws on digit 1 of the hindfoot. One of us (T.F.) has examined all *Zaglossus* held in the Institute voor Taxonomie, Amsterdam, and cannot find a specimen with such a claw number. This claw number is, however, consistent with specimens we place in sample 4 (Paniai Lakes to the Krake Mts), but not those from west of Lake Paniai (sample 5).

Griffiths (1978) examined claw number in more easterly populations. Of 10 animals which he examined which had originated from east of Wau (our samples 1 and 2), nine had five claws on each foot, while one (from Mt Tafra) lacked a claw on digit five

on the left hindfoot. Two out of three specimens from Pangia in the Southern Highlands (sample 4) lacked a claw on the same digit, while one had claws on all digits.

Results of our examination of claw number in museum specimens world-wide is given in Appendix 2. These data confirm the work of Kerbert (1913), Griffiths (1978) and Van Deusen and George (1969), the latter of whom note that "a large majority of western specimens (our sample 5) lack claws on digits one and five", while eastern specimens usually have claws on these digits.

The situation in *Zaglossus* from east of the Paniai Lakes is complicated, as five sub-populations have been discerned. For all of these except one, five claws are usually present on each foot. The exception is the *Zaglossus* population from the central part of the central cordillera, eastwards from the Paniai lakes through to the Central Highlands of Papua New Guinea (sample 4). The small sample of museum skins (five) available from this population reveal that five claws are invariably present on the forefoot, but that the claw on digit five of the hindfoot is often absent (three out of five cases).

We conclude that claw number is a consistent and useful characteristic for distinguishing members of our sample 5 (the population living west of Lake Paniai) from all other *Zaglossus*. Individuals assigned to our sample 5 all have three, or very occasionally four, claws on the forefoot. All specimens assigned to other samples had five claws on each forefoot. We therefore propose to separate samples 5 and 1/2/3/4 at the specific level: they differ absolutely, as required under the Phylogenetic Species Concept. The names for these two species are *Zaglossus bruijnii* and *Zaglossus bartoni*, respectively.

Claw number on the hindfoot is more variable. Of the anomalous animals listed by Allen, three had a claw on digit five of the hindfoot. Interestingly, claw number on the hindfoot seems to vary most in our sample 4, three (including two noted by Griffiths (1978)) lack claws on digit five of the hindfoot, while one specimen lacks one such claw only. Only two of the five skins examined had five claws on each hindfoot. This appears to represent a relatively consistent difference between sample 4 and samples 1-3 and possibly 6; we suggest recognising sample 4 subspecifically and propose a new name for it below.

Cranial characters

Having demonstrated that differences in claw number, on the forefoot at least, is a consistent diagnostic characteristic which differentiates between *Zaglossus* living to the east and west of the Paniai Lakes, attempts were made to define other differences. There is a slight suggestion that bizygomatic width is narrower relative to basicranial length in sample 5 (Fig. 3), but further data are necessary before this can be tested. Unfortunately most skulls assigned to sample 5 are broken so that either CBL or BZW cannot be measured.

Examination of cranial measurements of samples 5 and 4 (drawn from the populations living immediately to the east (4) and west (5) of the Paniai Lakes) reveals significant differences (at 0.05) in CBL, BZW, PAL, and B (Table 2). Significant differences are also evident between sample 5 and the other samples (1-3) drawn from the five clawed form (see Table 2). All this reinforces our conclusion (above) that sample 5 is distinct at the specific level (as *Z. bruijnii*) from other samples.

Discriminant Analysis of samples 1/2/3/4, of the eastern species *Zaglossus bartoni*, using all measurements except the often unavailable *Mandibular Length (M)*, separates them cleanly (Fig. 4). They form an east-west cline along the first Discriminant Function, and the two central forms (samples 2 and 3) differ on Function 2. On

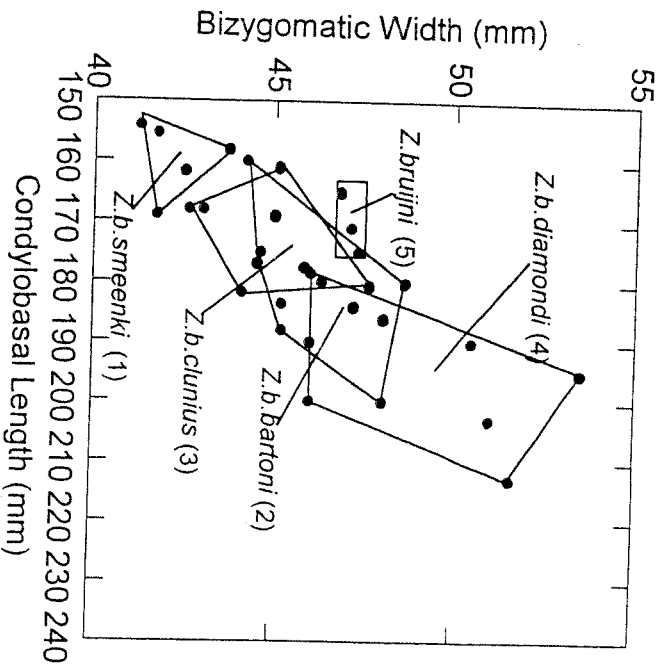


Fig. 3. - Bivariate plot of Condylobasal Length over Bizygomatic Width for *Zaglossus*.

function 1, CBL and BZW load strongly positively (i.e. the samples increase in size, but have relatively shorter palates, from east to west). On Function 2, PAL and CBL load positively, while B, in particular, loads very strongly negatively (i.e. sample 3 has a shorter beak for its size compared to sample 2).

When the western species, *Zaglossus bruijnii*, is included in a Discriminant Analysis, it differs from *Z. bartoni* on Function 2, even with juveniles included (Fig. 5), while the subspecies of the latter are strung out mainly along Function 1. The loadings for the two Functions are much as in the analysis based upon *Z. bartoni* alone, except note (Appendix 1) that in *Z. bruijnii* CBL is extremely variable; this presumably accounts for its reduction in value and the consequent compression of the *Z. bartoni* samples along a single axis.

A few nonmetrical characters vary between samples. *Zaglossus bartoni* crania usually have a dorsal depression between braincase and rostrum, which is lacking in *Z. bruijnii*, but this is not invariably the case, especially *Z. bartoni* from west of the Wau area (sample 4) tend to lack the depression. The orbitotemporal fossa in *Z. bartoni* tends to be smaller than in *Z. bruijnii*, and the thin plate that encloses its posterior end extends well forward, so that it is easily visible in ventral view, whereas it is barely visible ventrally in *Z. bruijnii*. The posterior end of the palate (between the orbitotemporal fossae) in *Z. bartoni* is flattened, whereas in *Z. bruijnii* the deep median channel of the palate continues well back into this region. Finally, the braincase in *Z. bartoni* is often as high as it is long (sometimes assuming a curious pyramidal shape), which is never the case in *Z. bruijnii*.

TABLE 2. - Table of t-test results for five samples of *Zaglossus*. 1 = *Z. bartoni smeenkii*, 2 = *Z. bartoni bartoni*, 3 = *Z. bartoni chinii*, 4 = *Z. bartoni diamondi*, 5 = *Z. bruijnii*. Results in bold are significant at 0.05.

		BZW				
CBL	0	1	2	3	4	5
	1	0.00	0.00	0.00	0.00	0.00
	2	0.00	0.06	0.00	0.00	0.20
	3	0.01	0.11	0.00	0.00	0.02
	4	0.00	0.00	0.00	0.00	0.04
IOW	0	1	BIMAST			
	1	0.01	2	3	4	5
	2	0.12	0.00	0.00	0.00	0.00
	3	0.00	0.69	0.01	0.19	0.04
	4	0.00	0.26	0.15	0.00	0.08
RH	0	1	0.93	0.01	0.57	0.29
	1	0.01	RBR			
	2	0.00	2	3	4	5
	3	0.01	0.01	0.10	0.00	0.04
	4	0.00	0.00	0.07	0.04	0.78
PAL	0	1	0.89	0.00	0.16	0.60
	1	0.02	0.17	0.33	0.33	0.08
	2	0.00				
	3	0.00				
	4	0.00				
J	0	1				
	1	0.00				
	2	0.02				
	3	0.05				
	4	0.00				

Pelage

A careful examination of pelage revealed no consistent diagnostic features for the populations living to the east and west of the Paniai Lakes, although some unusual features (such as sparse fur and the presence of black spines), are common in individuals from *Z. bruijnii* (see below), but unknown in other *Zaglossus*.

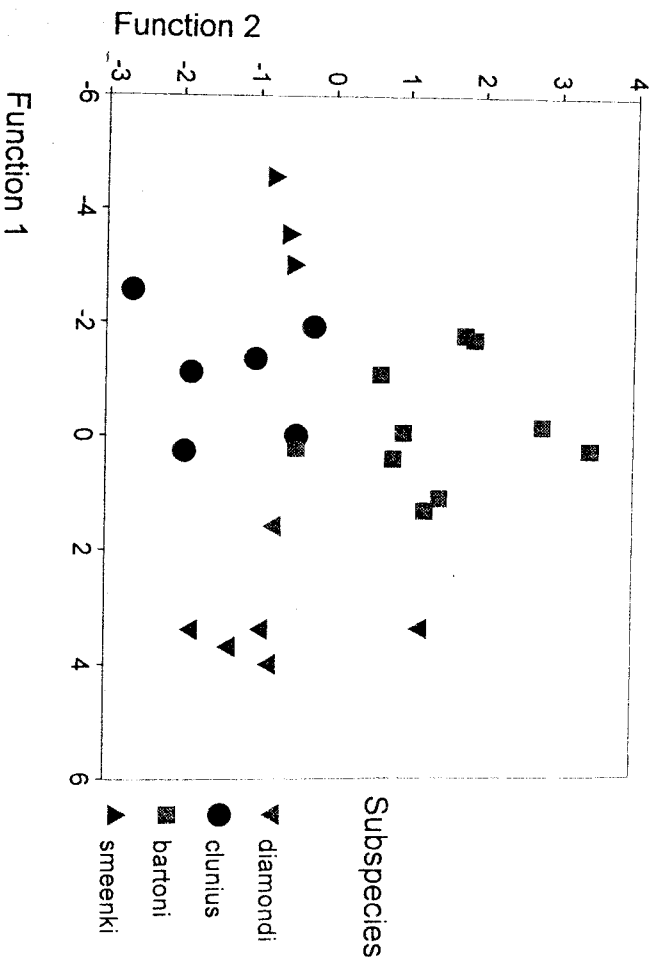


Fig. 4. - Discriminant Function Analysis for the subspecies of *Zaglossus bartoni*.

Conclusions

We consider that the differences in claw number and cranial morphology identified above provide clear evidence that *Zaglossus* living to the west and east of the Paniai Lakes represent distinct species. These species do not presently occur in sympatry, but are restricted to the mountain summits (and in the case of *bruijnii* possibly to lower elevation forests as well) to the east (*bartoni*) and west (*bruijnii*) of the lakes system. The Paniai Lakes region is one of the most heavily populated regions in New Guinea. Forest has been cleared from a huge area around the lakes, and game animals have been largely exterminated locally. It seems possible that the two *Zaglossus* species once occurred in sympatry or parapatry in this region, but until an adequate fossil record is recovered, this will remain uncertain.

Taxonomic treatment of allopatric populations is difficult, for they can be validly recognised as subspecies or species. In this case, we recognise the populations as full species, both because they are readily and consistently distinguishable morphologically, and because one population can itself be divided into what we recognise as subspecies (see below). Complexes of allopatric species have been commonly recognised among New Guinean mammals (e.g. *Dendrolagus goodfellowi* complex, *Thylogale bruijnii*

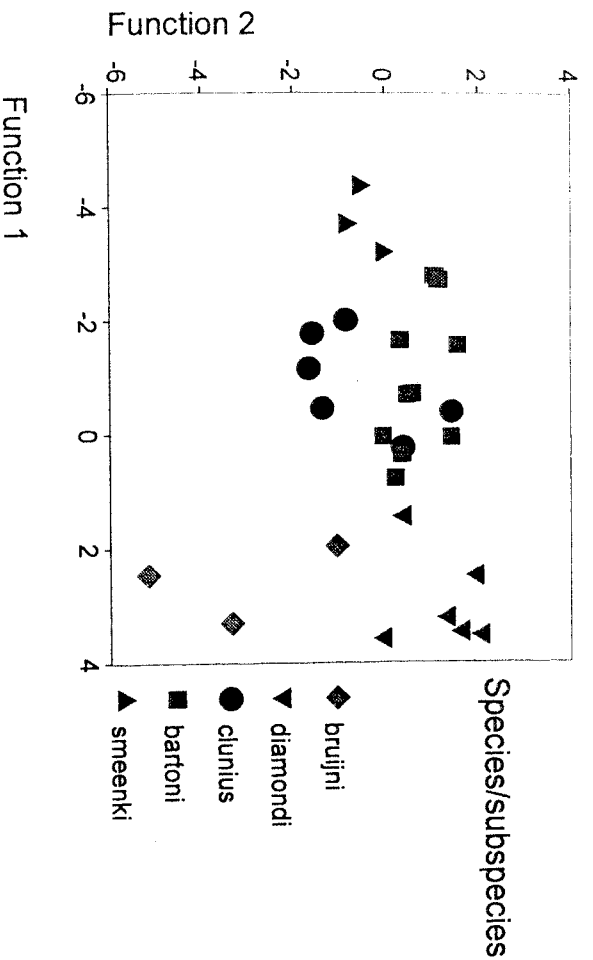


Fig. 5. – Discriminant Function Analysis for all *Zaglossus*, juveniles included.

complex, *Dorcopsis* complex; see Flannery 1995a), so our treatment of *Zaglossus* here is consistent with the species concept used in many previous works.

Having established that our sample 5 is a distinct species (*Z. bruinjini*) from all other samples, we went on to examine variability within sample 5, and between the remaining samples.

Zaglossus bruinjini, the species living to the west of Lake Paniai proved to display very little geographic variability. Condylobasal length varied considerably within the sample, however, as did external characters such as spine colour and the density and colour of the fur. There is, especially given the relatively small sample of complete crania, no basis at present for recognising subspecies within *Z. bruinjini*.

Samples of *Z. bartoni*, the species living to the east of the Paniai Lakes, however, displayed considerable geographic variation. All samples recognised in our initial sort could be differentiated statistically, except for samples 2 and 7 (where there were no significant differences at 0.05). As a result, sample 7 was merged into sample 2.

The Nanneau Range sample (1): This sample possessed the smallest cranial size of any *Zaglossus*, except for the poorly known Cyclops sample (6). It was significantly smaller (at 0.05) than any other sample examined in all dimensions, except for RBR and IOW, which were not significantly different from sample 3 (Huon Peninsula, see Table 2). No subspecific name is available for this population, and we propose one below.

The Owen Stanley Range and south Chimbu sample (2): This sample represents *Zaglossus* of moderate cranial size. It is significantly larger than sample 1 (at 0.05) in all cranial dimensions measured, and significantly larger than sample 3 (at 0.05) in BIMAST, RH and PAL. It is significantly smaller (at 0.05) than sample 4 in CBL, BZW, RBR, PAL, B and J. Differences were not as marked with sample 5, which was significantly different (at 0.05) in IOW only (Table 2). The names *bartoni* and *buhuenis* are available for the subspecies represented by this sample.

The Huon Peninsula sample (3): These *Zaglossus* were of small cranial size. They were significantly larger (at 0.05) than sample 1 in all dimensions except RBR and IOW, and significantly smaller than sample 2 (at 0.05) in BIMAST, RH and PAL. They were significantly smaller (at 0.05) than sample 4 in CBL, BZW, BIMAST, RBR, RH, PAL and B and significantly smaller (at 0.05) than sample 5 in BZW and IOW. The name *clunius* is available for this sample.

The Kraike Mts to Lake Paniai sample (4): These *Zaglossus* had the largest cranial dimensions of any measured, being significantly larger (at 0.05) in all cranial dimensions than sample 1, in all but IOW, BIMAST and RH than sample 2, and all but IOW and J (where sample size was insufficient) than sample 3. This sample was significantly larger (at 0.05) than sample 5 in CBL, BZW and PAL (sample size being insufficient for B). There is no name available for this sample, which we describe as a new subspecies below.

The Cyclops Mts sample (6). This sample is represented by a single damaged specimen, which is nevertheless very distinctive in morphology. It is the smallest of all *Zaglossus*, but because of the small sample size, t-tests could not be carried out (see below). We argue (below) that this sample represents a third species of *Zaglossus*.

Systematics

Family Tachyglossidae Gill, 1872

Genus *Zaglossus* Gill, 1877

Synonyms: *Acanthoglossus* Gervais, 1877

Bryunia Dubois, 1882

Prozaglossus Kerbert, 1913

Zaglossus bruinjini (Peters and Doria, 1876)

Holotype: GE 1623. Skull only, Arfak Mountains, collected by A.A. Brujin.

Synonyms: *Bryunia triactyla* Du Bois, 1882

Proechidna villosissima Du Bois, 1884

Proechidna nigrocuticula Rothschild, 1892

Acanthoglossus goodfellowi Thomas, 1907a

Zaglossus bruinjini guttatis Rothschild, 1922

Zaglossus bruinjini pallidus Rothschild, 1922

Diagnosis: A medium-sized species of *Zaglossus*, differing from all other taxa in possessing three (rarely four) claws on the fore and hindfeet. It is sharply and significantly smaller (at 0.05) in CBL, BZW and PAL than the *Z. bartoni diamondi*, which abuts it to the east, and differs significantly from other *Z. bartoni* in some cranial

dimensions (see Table 2). The orbitotemporal fossa is large, and the plate terminating it posteriorly is poorly visible in ventral view. The median palatal groove extends back to the posterior of the palate. The brain-case tends to be low-crowned. It further differs from the species based on sample 6 in the colour of its pelage and larger size (see below).

Specimens examined: 16 adult and 3 juvenile skulls, 19 skins.

Distribution: New Guinea west of the Paniai Lakes (Fig. 1). Rothschild's (1913, 1922) records of specimens from Kaimana on the southern side of the Charles Louis Range is problematic. Rothschild himself doubted the veracity of the location, suggesting that the specimens might have come from Sorong. Further, the present day Kaimana is located on the western tip of the Vogelkop neck (3°40'S, 133°45'E), far to the west of the Charles Louis Ranges (135°30'E). The easternmost limit of the species is still in doubt. There is no doubt, however, that *Zaglossus* (probably this species) occurs as far east as the mountains fringing the western side of Etna Bay (134°50'E) (Flannery 1995a). There are no undoubted records of *Zaglossus* from the Weyland and Charles Louis Ranges, and it is possible that the species has been hunted to extinction there as well as in the region of the Paniai Lakes. It has broad elevational range, from near sea-level (on Salawati) to at least 2,250 m in the Arfak Mountains (e.g. AM M17891).

Description: *Zaglossus bruijnii* is a medium sized species which is highly variable in colour and the density of its fur. Most individuals are black in overall fur colour, but some (possibly including the majority of specimens which have been kept in captivity) are dark brown. The holotype of *pallidus* is even lighter brown in colour. Short-beaked echidnas (*Tachylossus aculeatus*) can be very pale, with almost white individuals being reported; *Zaglossus bruijnii* may be similarly variable. Many *Z. bruijnii* have pale fur on the head and feet, which is variable in extent and intensity. In some, the face and feet can appear white.

Spine colour varies between almost entirely white (e.g. MCZ 12,414), black with a white tip (MCZ 7,389), or almost entirely black (the type of *nigroaculeata*). We could discern no geographic pattern to this variability. It should be noted, however, that black spines are entirely absent in other species of *Zaglossus*.

The amount of fur present between the spines is also more variable in this species than in any other. This probably reflects the fact that its distribution can extend down to sea-level, whereas all other *Zaglossus* are restricted to higher elevations. Specimens from lower elevation areas (e.g. the Fak Fak Peninsula and Salawati) have very little fur, while those from the higher peaks of the Arfaks can be so densely furred as to obscure the spines of the back. Again, similar variability in fur density is seen in *T. aculeatus*, with individuals from cold regions being more densely furred.

Discussion: This is the type species of *Zaglossus*. It is a variable species in pelage and, to some extent size, and it inhabits a broader elevational range than most other *Zaglossus*, which, with the exception of *Z. bartoni bartoni* and *Z. b. smeetki*, restricted to elevations above about 1,300 metres.

Allen (1912) examined the characters used to distinguish the forms *goodfellowi*, *villosissima*, and *nigroaculeata*, and concluded that none provided a reliable means to diagnose these from *bruijnii*. The presence of spines on its belly and the sparseness of its fur were the characteristics used by Thomas (1907) to distinguish his new form *goodfellowi*. Allen showed, however, that Thomas' assertion that individuals referable to the taxon *bruijnii* lacked spines on the belly was incorrect. The variability in fur

density observed in this study further indicates that the forms *goodfellowi* and *villosissima* are not distinguishable from *bruijnii*. The colour of the spines, their density, and the robustness of the claws (all used to distinguish *nigroaculeata*) are likewise too variable to be reliable.

Rothschild (1922) distinguished the subspecies *pallidus* as having a white head and pale pelage. Individuals of *Z. bruijnii* are not infrequently seen with both of these characteristics, as are a few *Z. bartoni*. He also distinguished the form *gularis* on the basis that it lacked spines on the undersurface (a feature variably present in *bruijnii*), its large claws, and the concavity of the skull. These last two features vary with age.

The area from the Vogelkop east to Paniai Lakes has a number of endemic mammals whose distributions are similar to those of *Zaglossus bruijnii*. These include *Dendrolagus urinus*, *Microperoryctes murinus*, *Pseudochinus schlegelii* and *Pseudochirops coronatus*. Together these taxa represent an old, endemic and largely montane element in far west New Guinea.

Zaglossus bartoni Thomas, 1907

Diagnosis: Distinguishable from *Z. bruijnii* by invariably possessing five claws on the forefeet, and at least four (usually five) on the hindfeet. The orbitotemporal fossa is reduced, with an anteriorly extensive plate at its posterior end. The palate is flattened posteriorly. The brain-case tends to be high crowned. Differs from the species based on sample 6 in the colour of the fur and its larger size.

Four subspecies are recognised: *Z. b. bartoni*, *Z. b. clunius*, *Z. b. smeetki* subsp. nov., and *Z. b. diamondi* subsp. nov.; these are differentiated mainly by size and proportional differences.

Zaglossus bartoni has a distribution which is virtually identical with that of a number of other mammal species, including *Phalanger camelliae*, *Pseudochirops corinnae*, *Uromys anak*, and *Anisomys imitator*. These are all moderately large mammals which inhabit the mid to upper montane forest.

Zaglossus bartoni bartoni Thomas, 1907

Holotype: BMNH 7.7.17.5, an old female skin and skull collected at an elevation of about 2,400 m on Mt Victoria, Wharton Range, Papua New Guinea.

Synonyms: *Zaglossus hubbentis* Laurie, 1952

Diagnosis: A medium-sized subspecies, significantly larger (at 0.05) in all cranial dimensions measured than *Z. b. smeetki*, and significantly larger (at 0.05) than *Z. b. clunius* in BIMAST, RH and PAL. It is significantly smaller (at 0.05) than *Z. b. diamondi* in CBL, BZW, RBR, PAL, B and J.

Specimens examined: 17 adult and 2 juvenile skulls, 12 skins.

Distribution: The Papua New Guinea central cordillera between the Efofi area (147°42'E) to around Wau (146°44'E) including the Wharton Range and the Wau-Bulo area, at elevations between about 2,000 and 3,200 metres. A population, provisionally referred to this taxon, occurs in the lowlands of southern Chimbu Province, at about 600 metres elevation in the Haha area (Fig. 1).

Description: This taxon is less variable in fur density and colour than *Z. bruijnii*. Most of the specimens we have examined (e.g. AM M5993) have long, dense blackish

fur which obscures the spines over the dorsum, although they are visible on the sides. Some specimens have dark brown rather than blackish fur, and one (AM M3212) has spines which are clearly visible all over the back. The spines are invariably white.

Specimens from the Hata area (600 metres elevation) of southern Chimbu Province are tentatively referred to this taxon as they could not be distinguished on the basis of available material. They appear to be somewhat less well-furred than others, the spines being visible through the fur of the back. This population is poorly-known, a single photograph of an adult female (see Flannery 1995a, p. 66) providing the only evidence for its external appearance.

Discussion : This taxon is well represented in world museum collections. Aspects of the biology of the Mount Tafa population have also been studied by Griffiths (1978). Most museum specimens are from the Wharton Range and the Wau area, where it occurs at altitudes above about 2,000 metres. In subalpine grassland, such as that in the Neon Basin, Mt Albert Edward at 3,200 metres elevation, where hunting pressure is low, it may be relatively common.

Laurie (1952) distinguished *bubuensis* from *bartoni* (with which it was supposedly sympatric), on the basis of its shorter, brown (rather than black) fur, light brown feet and less curved rostrum. All of these features vary within the sample of *Z. b. bartoni* available to us, and the condition seen in *bubuensis* falls within this variation.

No other mammal species has a distribution which overlaps precisely with that of *Z. b. bartoni*. The New Guinean population of *Nyctophilus timorensis* however, coincides with it. The zone of potential contact between *Z. b. bartoni* and *Z. b. diamondi* is extensive, but it lies in an area of dense human population (the Eastern Highlands and Chimbu), where there are no records of living *Zaglossus*. The westernmost records of *bartoni* are from unusually low elevation, while all the eastern records of *diamondi* are from high elevations. It seems possible that these populations once replaced each other elevationally, but the middle elevation zone (where parapatry may have occurred) is now heavily populated and its forests grossly modified or cleared. There is no evidence of intergradation of these subspecies.

Zaglossus bartoni clunius Thomas and Rothschild, 1922

Holotype : BMNH 28.10.1.33, an adult female skin and skull from the Rawlinson Mountains, Huon Peninsula.

Diagnosis : A small *Zaglossus* which invariably has five claws on each foot. Significantly larger than *Z. b. smeenki* in all dimensions except RBR and IOW. It is significantly smaller than *Z. b. bartoni* (at 0.05) in BIMAST, RH and PAL. The beak is shorter relative to the braincase than in *Z. b. bartoni*. It is significantly smaller (at 0.05) than *Z. b. diamondi* in CBL, BZW, BIMAST, RBR, RH, PAL and B.

Distribution : The mountains of the Huon Peninsula (Fig. 1). Specimens collected by Van Deusen during the Seventh Archbold Expedition came from elevations of between about 2,100 m and 2,700 metres in the Saruwaged Mountains. He reported (in Van Deusen and George 1969) that in this region *Zaglossus* was "an inhabitant of humid montane forests that are almost continually blanketed by cloud cover" (p. 14). Specimens seen : 12 adult, 1 juvenile skulls, 10 skins.

Description : The fur is long and black. It usually all but obscures the spines in the middle of the back. The spines are white. Colouration seems to be uniform in this subspecies.

Discussion : *Zaglossus bartoni clunius* is geographically isolated from other *Zaglossus* by the dry lowlands of the Markham River Valley. The Huon Peninsula is an isolated and mountainous region which is home to a number of other endemic mammalian subspecies, including *Mallomys aroaensis hercules*, *Hyomys goldiath strobilurus*, *Abomalomys sevia sevia*, *Pseudochitrops corinnae argenteus*, *Thylagale browni lanatus* and *Phalanger carmelitae coccygis*. Only one endemic mammal species is known from the Huon : *Dendrolagus matschiei*.

Zaglossus bartoni smeenki n. sp.

(Appendix 1, Figs 6-7)

Holotype : AM M96822, adult male skin and skeleton, collected near Marua Point, 20 km SW of Collingwood Bay, PNG, by Mr G. Leach, 12 July 1972.

Etymology : For Dr Chris Smeenk, curator of mammals at the Rijksmuseum of Natural History, Leiden, whose legendary courtesy and hospitality to visiting researchers has been of enormous assistance to both of us at different times.

Diagnosis : The smallest subspecies, invariably possessing five claws on each foot. It is significantly smaller (at 0.05) than all other *Z. bartoni* in all dimensions, except for RBR and IOW in *Z. b. clunius*.

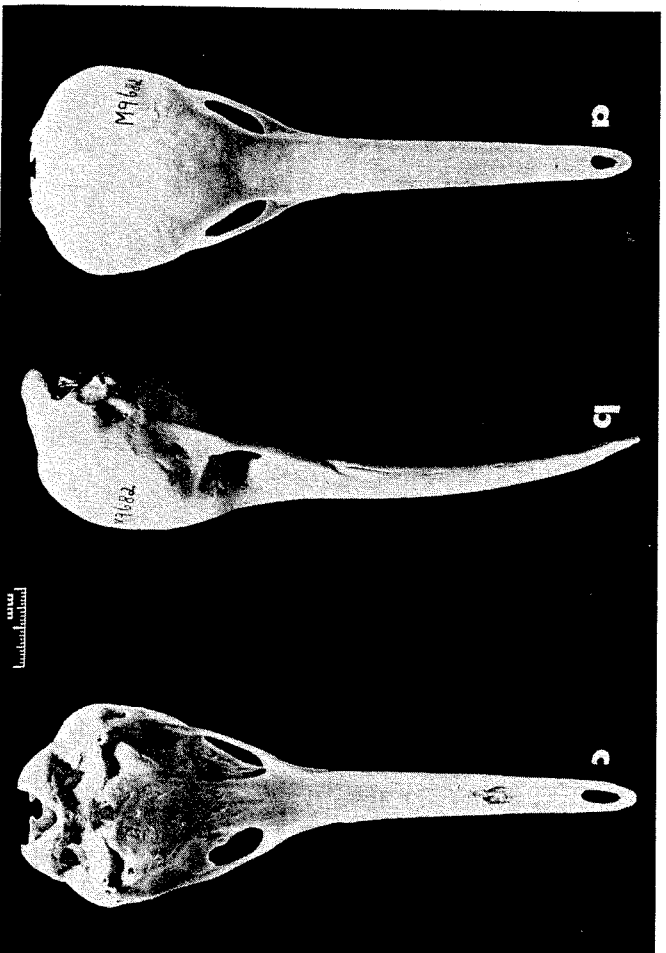


Fig. 6. — Skull of holotype of *Zaglossus bartoni smeenki* n. sp. in A dorsal, B lateral and C ventral views.

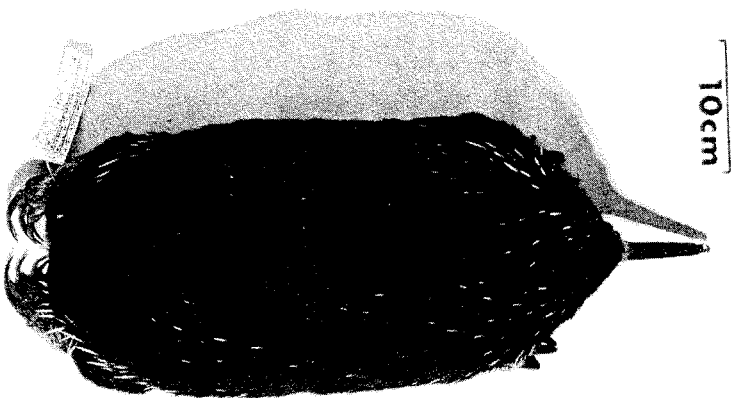


Fig. 7. — Skin of holotype of *Zaglossus bartoni smeenki* n. ssp.

Distribution : Restricted to the mountains of the Nanneau Range, as far west as the Collingwood Bay District in eastern Papua New Guinea (Fig. 1). It has been recorded from 1,540 m elevation on Mt Dayman (AMNH 157072), about 200 m (UP 729) and 1670 metres on Mt Suckling (RMNH 23319). A note on this latter specimen states “Common in open forests (*Araucaria*), grasslands (*Deschampsia*) and riverbanks up to the summits (3676 m). J.F. Veldkamp”.

Specimens seen : 6 adult skulls, two skins.

Description : The fur of the holotype is dark brown in colour, lightening towards the feet and base of the beak to buff. The spines are white, and fur obscures them over most of the back. There are no spines at all on the venter. The tail forms a small, naked nub, the skin of which is, like that of the hands, feet and beak, brown. The skull is small and the rostrum delicate (Fig. 6 and 7).

Discussion : Very little is known of this, the smallest subspecies of *Z. bartoni*. All sexed specimens known are males. It must about or intergrade with *Z. b. bartoni* in the Owen Stanley Ranges between the Efogi area and Collingwood Bay. The ranges are lower in this area than to the east and west. If it proves to overlap rather than intergrade with *Z. b. bartoni*, it will have to be awarded full specific status.

Few other mammals have a distribution similar to *Z. b. smeenki*. *Murexia longicauda*, *Microperoryctes papuensis* and *Peroryctes broadbenti* are all restricted to southern eastern Papua, but all extend slightly further west (at least to the Port Moresby area).

Zaglossus bartoni diamondi n. ssp.

(Appendix 1, Figs 8-9)

Holotype : AM M7955, skin with skull inside. Wissel (Paniai) Lakes area. Coll D.F. McMichael 15 May 1957. Dr McMichael has informed T.F.F. (pers. comm.) that the specimen was captured in the high mountains to the east of the lake, and was alive when he first examined it.

Etyymology : For Professor Jared Diamond of the University of California, who, through his writings and research, has contributed enormously to our understanding of the biology of Melanesia.

Diagnosis : The largest *Zaglossus*, invariably possessing five claws on the forefeet, but variably four or five on the hindfeet. Significantly larger (at 0.05) in all cranial dimensions than *Z. b. smeenki*, and in all but IOW, BIMAST and RH than *Z. b. bartoni*, and all but IOW than *Z. b. clinisus*. The depression between the rostrum and the braincase, usual for other subspecies, is generally lacking in this subspecies. In this it resembles *Z. bruijnii*.

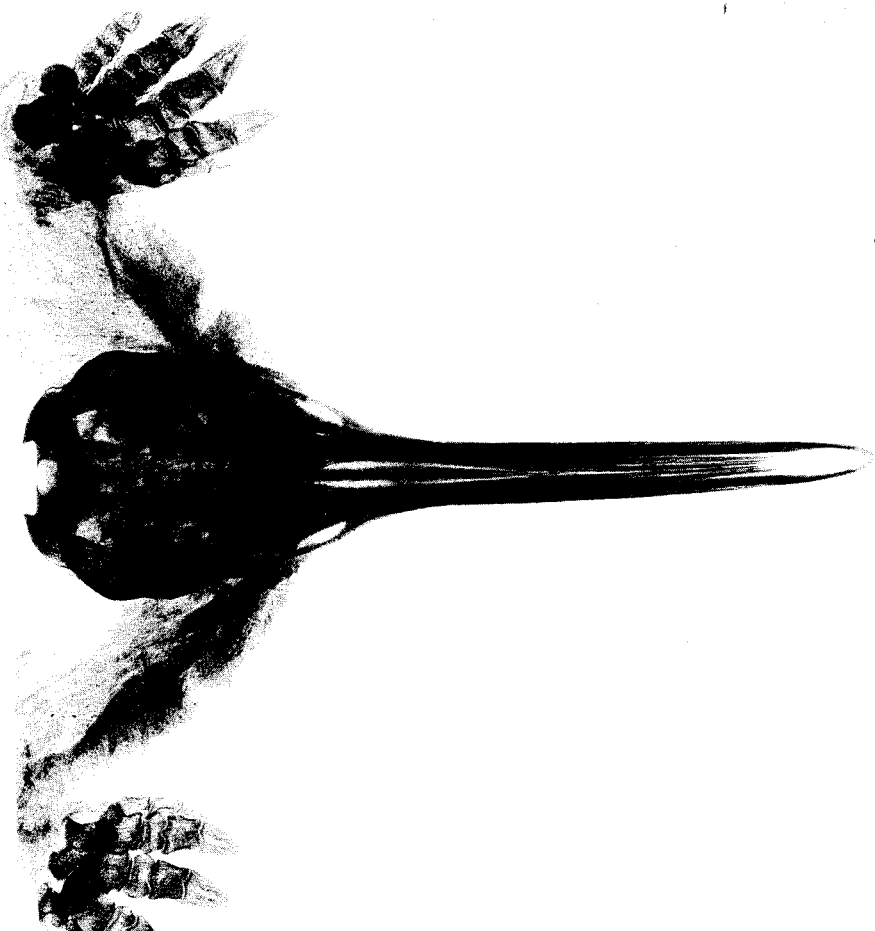


Fig. 8. — X-ray of skull of holotype of *Zaglossus bartoni diamondi* n. ssp., in dorsal view.



Fig. 9. — Skin of holotype of *Zaglossus bartoni diamondi* n. ssp.

Distribution : The mountains of central New Guinea, from the ranges on the western side of the Paniai Lakes, Irian Jaya in the west, to the Kratke Range in the eastern Highlands of Papua New Guinea in the east (sample 4). In the Telefomin area it occurs as low as 1,300 metres elevation on the northern side of the central cordillera (Flannery and Seri 1990), while near Mt Carstensz it has been recorded at 4,150 m (Harrer 1964). It seems to be particularly common in alpine meadows in the Carstensz area.

Specimens seen : 15 adult and 3 juvenile skulls, 4 skins.

Description. The skull is large and the rostrum robust (Fig. 8). The fur of the holotype is dense and extremely dark brown, almost black, on the body. A few spines are visible through the dense fur of the back. The fur lightens to a reddish brown on the extremities of the limbs. The spines are almost entirely white, although some have a minute dark tip. All limbs have five claws, except the left foot, which has four. The venter, which lacks spines, is densely furred, the fur being blackish at the tip and grey at the root. The skin of the paws, tail and beak is blackish brown, as are the claws.

Other individuals differ in colour. AMNH 190859, for example, is a rich mahogany colour, the fur grading to reddish-yellow with some whitish hairs on the limbs and face.

Discussion. *Zaglossus bartoni diamondi* has the widest distribution of any *Zaglossus*. Despite this, it has remained poorly-known and poorly represented in

museum collections. It is the largest known living monotreme. A captive male from the Kubor Range, which was held at Taronga Zoo, reached a maximum weight of 16.5 kilograms. It had been held in captivity for 12 years when weighed.

Its distribution is almost identical to those of several other mammals of the upper montane forest, including *Neophascogale lorentzii* and *Pseudochirulus mayeri*.

Zaglossus attenboroughi n. sp.

(Appendix 1, Figs 10-11)

Holotype : RMNH 17301. Skin, dentary and fragmentary rostral region of skull of an adult, sex not recorded. Collected "Oost-top, Berg Rara, op 1,600 m", Cyclops Mountains, Dutch New Guinea, on July 4th, 1961 by P. van Royen.

Etymology : For Sir David Attenborough, who has contributed greatly to the public appreciation of the New Guinean fauna and flora.

Diagnosis : The smallest member of the genus, with a beak length (measured on the skin, see below) of 70 mm (as opposed to $\bar{x} = 99.1 \pm 13.6$, range 81.0-127.5, $N = 23$ for all other *Zaglossus*), and a dentary length of 107.5 mm ($\bar{x} = 138.1$, range 118.0-157.0, $N = 22$ for all other *Zaglossus* combined). The short beak is also straighter than in other *Zaglossus*. There are 5 claws on each foot. The fur is shorter, denser and finer than in other *Zaglossus* and differs from that of other species in being raw umber dorsally and fawn ventrally.

Distribution : The higher peaks of the Cyclops Mountains near Jayapura, extreme northeastern Irian Jaya (Fig. 1).

Description : The type and only specimen consists of a complete skin and the rostral portions of a badly crushed cranium (Fig. 10). The fleshy part of the beak (mea-



Fig. 10. — X-ray of skull and pes of *Zaglossus attenboroughi* n. sp.



Fig. 11. — Skin of holotype of *Z. attenboroughi* n. sp.

sured along its dorsal edge, from the tip to the margin of the fur) is 70 mm long. The beak is straight, but has been broken and possibly somewhat distorted (Fig. 10). Nonetheless, it is likely that it was straighter (and certainly shorter) in life than in other *Zaglossus*.

In overall size, the specimen conforms closely with *Tachyglossus aculeatus*, being much smaller than other *Zaglossus*. On the basis of comparison with similar-sized *Tachyglossus*, its weight is estimated to have been approximately two to three kilograms.

There are five claws on each foot. There is a small spur (4.4 mm long \times 1.7 mm wide at its base) present on the left ankle. The base is shielded by a fleshy tubercle. A remnant of a similar spur is present on the right foot. These spurs suggest that the specimen is male.

The fur is dense, very fine and short, in all of these characteristics differing from other *Zaglossus* (where the fur is longer, coarser and less dense). It is a distinctive brown colour (close to raw umber) unmatched in any other *Zaglossus*, which vary from reddish brown to black, with an occasional very pale variant. The venter is fawn, again differing from any other member of the genus. The fur of the feet, tail and forehead are yellowish in colour.

There are two hair whorls on the ventral surface on either side of the neck. The short fur covers the spines in the middle of the back, which are extremely sparse, and large portions of the midback entirely lack spines. The spines are narrow (averaging

1.6 mm in diameter at their thickest point) and are all whitish in colour. The thickest spines occur near the rump. Spines are absent from the ventral surface.

Only small fragments of the skull remain, the most important being the dentaries, a crushed rostrum and portions of the orbital and frontal regions. The region of the naso-frontal suture is well preserved, and although portions of the suture are visible through the slightly translucent bone, the suture is entirely closed, indicating that the specimen is adult (Fig. 12). The sutures present on other fragments are all closed. The dentary differs from juveniles in the form of its articulation (which is well-defined and arched sharply above the horizontal ramus), and in its more gradual taper. The articular facet is more rounded than in other *Zaglossus* examined.

Discussion : This species is sample 6 in our analysis. The small size and narrow spines of the holotype made us suspect initially that it might be juvenile. Examination of the cranial fragments and X-ray of the feet soon convinced us, however, that it is adult. Even older subadult *Zaglossus* (such as AM M5993 (*Z. bartoni bartoni*), which has a dentary length of 120, retains open sutures and a juvenile-like dentary structure. Furthermore, juveniles typically have very long fur. This is in contrast to the short, dense fur of the holotype.

The discovery of *Zaglossus attenboroughi* in the higher peaks of the Cyclops Mountains was unexpected. The nearest populations of *Zaglossus* (*Z. b. diamanti* - the largest of all *Zaglossus*) occupy the mid-elevation forests above 1,300 metres in elevation on the northern slopes of the central cordillera, which lies some 200 km to the south. *Zaglossus* is certainly absent from the North Coast Ranges, including the Bewani Mountains (which are no more than 50 km east of the Cyclops Mountains) as extensive survey work (by T.F.F. and others) has failed to reveal its presence there, and echidna-like animals are unknown to local hunters.

The occurrence of *Zaglossus attenboroughi* in the Cyclops Mountains is congruent with a number of endemics which are restricted to one or more peaks in the North

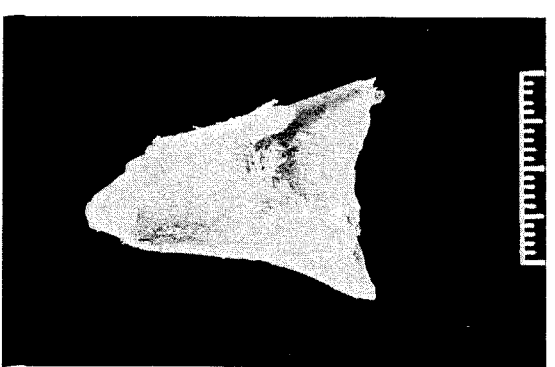


Fig. 12. — Left orbital region (distal end downwards) of *Zaglossus attenboroughi* n. sp.

Coast Ranges. These include *Petaurus abidi*, *Dendrolagus scottae* and *Paraleptomys nigilimus*. There are no other species of mammals, however, which are endemic solely to the Cyclops Mountains. It seems possible that *Z. attenboroughi* was possibly once widespread in the North Coast Ranges, and has found its last refuge in the Cyclops.

DISCUSSION

The degree of geographically-related morphological diversity revealed in this study was unexpected. No comprehensive taxonomic revision of the genus has been attempted previously, but several earlier, partial studies, such as those of Allen (1912) and Van Densen and George (1969), mostly concluded by provisionally placing all *Zaglossus* into a single species.

The morphological diversity detected within the genus here is of particular importance to conservation. *Zaglossus* are endangered throughout much of New Guinea, and attempts are currently being made to breed the only captive individuals at Taronga Zoo (Paul Andrew pers. comm.).

The conservation status of the various species and subspecies of *Zaglossus* is incomplete. *Zaglossus attenboroughi* is known from a single mountain summit, and probably has a total area of habitat of less than 50 km². The region is a declared reserve, but is very close to Jayapura, the capital of Irian Jaya. In 1990 TFF had the opportunity of questioning a hunter, Mr Otto Soangburaeo, who lives on the slopes of the Cyclops Mountains. He hunted the mountains often, but had never seen a *Zaglossus*. He had, however, heard of them from older hunters (Otto was in his 30s), but could not remember their name in his language. He did know, however, that it was an inhabitant of the high, remote peaks only. As the only specimen was collected in 1961, it is possible that this species is already extinct.

The conservation status of *Zaglossus bruijnii* is less grim. Specimens are still being caught on the higher peaks of the Arfaks, and large areas of broken, limestone country on the Fak Fak Peninsula and Vogelkop neck probably provide a refuge for it. In 1981, TFF found *Zaglossus bartoni bartoni* to be common in the grasslands of the Neon Basin on Mt Albert Edward. There is still much suitable habitat at high elevation in the Wharton Range which is not regularly hunted over. *Zaglossus bartoni simeonki* also occurs in large areas which are virtually uninhabited, and may be secure. *Zaglossus bartoni diamondi* has a large distribution, but also has a documented history of decline. It has become extinct on Mt Wilhelm within living memory (G. Hope pers. comm.) and is probably rare or extinct throughout much of the PNG central highlands, where human population density is high. As late as the 1950s it was common in the Telefomin area, being protected there by local custom. As a result of the breakdown of traditional beliefs, it is now all but vanished from the Telefomin area. Clearly, further studies of the conservation status of these vulnerable animals is urgently needed.

It became evident during this study that baby echidnas were entirely absent from world museum collections. The smallest known *Zaglossus* are about 30 cm in length, with a beak length about 72 mm. *Zaglossus* smaller than this are probably hidden by their mothers, and do not emerge from the den, otherwise, surely some specimens would have fallen into the hands of collectors.

ACKNOWLEDGEMENTS

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APPENDIX 1

Cranial measurements for species of *Zaglossus*
 CBL = condylobasal length, BWZ = bizygomatic breadth, IOW = least interorbital width, BIMAST = binas-toid breadth,
 RBR = rostrum breadth*, RH = rostrum height*, PAL = palatal length, B = beak length (to orbital foramen),
 J = length of dentary.

* Measured anterior to the orbits, at the base of the beak where the rostrum tapers to become more parallel-sided.

AMIA = Instituut voor Taxonomie, Amsterdam

AMM = Australian Museum

AMNH = American Museum of Natural History, New York

BMNH = British Museum, Natural History

CM = National History Museum, Canberra

COM = University Museum, Copenhagen

GE = Museo Civico di Storia Naturale "Giacomo Doria", Genoa

MCZ = Museum for Comparative Zoology, Harvard

MMK = Museum of Mankind, London

MZB = Zoology Museum, Bogor

PNGM = Papua New Guinea Museum and Art Gallery

RMNH = Nationaal Natuurhistorisch Museum, Leiden

¹ From Allen (1912)

² Locality "Nordridge N. Guinea"

³ From cast no. A4125, exchanged with Gervais Jarden des Plantes

⁴ Locality "Papua"

⁵ Locality given as Baiyer River District, but probably refers to Baiyer River Sanctuary (ex Taronga Zoo)

⁶ MCZ 12.414 has a spur 7 mm long

⁷ G. Hope says locality probably Mr Albert Edward

⁸ Must be from Arfaks : collector von Rosenberg

⁹ Must be from Arfaks : collector von Rosenberg

Species	Locality	CBL	BWZ	IOW	BIMAST	RBR	RH	PAL	B	J		
<i>Zaglossus bartoni</i> (Peters & Doria, 1876) (Sample 5)	AMA 1	158	-	180	-	-	-	-	-	-		
	MCZ 12.414 ¹	178	-	19	-	55	-	152	-	138.0		
	MCZ 12.415 ¹	172	-	19	-	56	-	145	-	-		
	BMNH 7.9.5.10	-	51.0	21.2	60	58	17.3	160	-	152		
	MZB 400	198	-	19.3	58.1	19.3	-	169	-	-		
	MZB 401	182	-	20.6	58.0	-	-	152.3	-	-		
	MZB 402	-	-	19.6	56.7	-	-	-	-	-		
	MZB 403	198	-	18.2	56.7	-	-	-	-	-		
	loc ?	202	-	21.8	58.9	-	-	174	-	-		
	COM 12 ²	172	-	20.2	58.9	-	-	149.3	-	-		
RMNH cat 3 ³	175	47.3	22.2	56.3	13.0	-	151.6	108.8	-			
GE 1632	-	45.4	19.0	56.3	13.8	-	148.4	-	-			
AM M28184	-	-	18.8	54.9	11.1	-	150.0	108.4	133.3			
AM M28185	165	46.8	20.9	56.5	14.8	10.0	141.6	113.4	-			
AM M28183	-	46.8	20.3	55.1	11.8	-	165.0	123.8	-			
AM M17891f	171	47.1	20.0	60.9	16.1	10.9	165.5	-	131.0			
<i>Zaglossus attenboroughi</i> n. sp. (Sample 6)	RMNH 17301	-	-	-	-	-	12.4	-	-	107.5		
	<i>Zaglossus bartoni bartoni</i> n. subsp. (Sample 1)	RMNH 2319m	161.7	42.5	16.7	51.8	13.5	10.6	141.2	99.5	123.0	
		AMNH 157072m	158	43.7	17.8	52.3	13.6	9.1	138.2	92.2	122.6	
		AMNH 157073	-	43.3	17.3	52.2	14.9	9.8	132.2	92.1	-	
		AM M6882m	154.2	41.2	16.3	52.2	13.9	10.0	133.3	94.2	118.0	
		CM 6055m	155.5	41.7	16.0	52.5	13.8	8.0	135.2	120.6	129.5	
		CM 3709	169.0	41.7	17.8	51.6	14.0	9.8	148.0	-	-	
		<i>Zaglossus bartoni bartoni</i> (Thomas, 1907) (Sample 2)	X	159.680	42.350	16.983	52.080	13.950	9.550	138.017	95.250	122.740
			Min	154.200	41.200	16.000	51.600	13.500	8.000	132.200	92.100	118.000
			Max	169.000	43.700	17.800	52.500	14.900	10.600	148.000	129.500	129.500
N			5	6	6	5	6	6	6	3	5	
Std	5.943		0.991	0.768	0.370	0.501	0.898	5.897	3.114	4.267		
south Chimbu	AM M17292		-	48.3	21.5	-	17.5	12.5	169.3	122.3	-	
	AM M17290		180	46.3	19.7	54.6	15.4	10.7	157.0	113.8	-	
	AM M17291		-	46.0	21.4	54	14.9	10.6	165 ⁴	-	-	
	AM M17273		-	45.7	18.0	57.0	16.0	12.2	167 ⁵	-	-	
	Zaglossus bartoni bartoni (Thomas, 1907) (Sample 2)		X	181.471	46.187	18.841	55.925	15.441	12.339	158.912	111.392	139.243
		Min	160.000	44.200	16.900	51.300	12.400	10.600	138.000	95.300	123.300	
		Max	200.000	48.600	21.500	59.500	17.500	14.400	175.000	148.200	148.200	
		N	14	15	17	16	17	17	17	12	7	
		Std	10.182	1.485	1.473	2.318	1.301	1.106	9.118	7.640	9.379	

APPENDIX 2. - Claw number in *Zaglossus*, including museum specimens examined during this study, as well as those reported in earlier works. Numbers in brackets following references indicate number of specimens examined. For abbreviations see Appendix 1. - = digit damaged.

	CBL	BZW	IOV	BMAST	RBR	RH	PAL	B	J
<i>Zaglossus bartoni</i> <i>clunius</i> Thomas & Rothschild, 1922 (Sample 3)									
AM M12146f	180.6	47.6	19.3	53.6	16.8	11.8	158.4	-	144.5
RM 2 f	183	-	17.5	54	-	-	160	-	-
BMNH 39.4260m	161.2	45.1	18.6	54.7	13.5	-	138.6	100.0	-
BMNH 39.3311m	-	45.3	18.6	53.5	15.2	11.0	143.1	105.9	-
BMNH 28.10322f	168	43.0	21.2	53.7	14.1	10.9	147.9	107.4	-
AMNH 66194m	168	42.6	17.8	51.7	12.8	9.7	146.5	107.9	-
AMNH 195373	-	-	-	-	14.6	11.6	-	122.9	-
AMNH 195369	-	-	19.0	-	14.6	11.0	-	110 ^m	-
AMNH 195370	-	43.2	18.0	50.6	14.3	11.1	153 ^m	110 ^m	-
AMNH 195731	-	46.5	19.3	58.1	14.7	10.8	153.3	113.7	-
AMNH 195732	181.7	44.1	18.3	49.8	14.7	10.2	158.0	117.3	-
RMNH 325	177.6	45.8	16.2	54.1	15.2	11.7	154	110.7	-
<i>Zaglossus bartoni</i> <i>diamondi</i> n. subsp. (Sample 4)									
AMNH 190859	223 ^m	-	-	-	-	-	-	-	-
AM M17274	213 ^m	51.6	20.4	59.7	17.1	11.0	188 ^m	141 ^m	-
PNGM 24763f	178.5	46.0	19.3	52.3	16.6	12.1	156.6	115.1	-
PNGM 24764m	190.0	50.5	20.9	56.6	16.1	11.4	167.0	123.3	-
BBM 22948f	221	-	21.4	58.3	15.5	-	199.6	-	150.3
AMNH 190859f	203	51.0	18.8	58.7	15.9	13.4	181.0	133.5	157.0
AMNH 190860	-	-	-	-	15.5	11.5	-	-	-
AMNH 190861	220 ^m	-	17.0	57.7	16.4	12.5	195 ^m	138 ^m	-
AMNH 110047	231 ^m	-	21.0	52.0	16.7	12.3	-	147.9	-
AM M7998	221 ^m	52.0	19.6	58.9	19.2	13.3	-	-	-
AM M17223	195 ^m	53.5	18.3	63.2	16.0	12.9	170	119 ^m	-
AM M7955f	206 ^m	-	-	58.3 ^m	-	-	-	-	-
AM M32573f	206 ^m	48.3	17.3	52.5	18.0	14.4	157.0	111 ^m	-
MOAK OC3 398	200 ^m	46.0	18.1	54.0	14.6	11.5	165 ^m	125 ^m	-
MOAK OC3 411	-	52.2	22.4	58.3	16.0	12.3	-	-	-
<i>Zaglossus bartoni</i> <i>diamondi</i> n. subsp. (Sample 4)									
M	174.300	44.800	18.633	53.360	14.591	11.045	150.136	113.780	-
Min	161.200	42.600	16.200	49.800	12.800	9.700	138.600	100.000	-
Max	183.000	47.600	21.200	58.100	16.800	11.800	160.000	142.000	-
N	7	9	12	10	11	11	11	10	0
Sid	8.485	1.703	1.257	2.320	1.018	0.659	7.695	11.752	-
<i>Zaglossus bartoni</i> <i>clunius</i> (Sample 3)									
M	205.500	50.122	19.542	57.375	16.431	12.383	175.022	125.762	153.650
Min	178.500	46.000	17.000	52.300	14.600	11.000	156.600	111.200	150.300
Max	231.000	53.500	22.400	63.200	19.200	14.400	195.600	141.000	157.000
N	11	9	12	12	13	12	9	8	2
Sid	15.098	2.731	1.707	3.128	1.174	0.989	15.333	10.823	4.738
<i>Zaglossus bartoni</i> <i>clunius</i> (Sample 3)									
M	178.500	46.000	17.000	52.300	14.600	11.000	156.600	111.200	150.300
Min	178.500	46.000	17.000	52.300	14.600	11.000	156.600	111.200	150.300
Max	231.000	53.500	22.400	63.200	19.200	14.400	195.600	141.000	157.000
N	11	9	12	12	13	12	9	8	2
Sid	15.098	2.731	1.707	3.128	1.174	0.989	15.333	10.823	4.738
<i>Zaglossus bartoni</i> <i>clunius</i> (Sample 3)									
M	205.500	50.122	19.542	57.375	16.431	12.383	175.022	125.762	153.650
Min	178.500	46.000	17.000	52.300	14.600	11.000	156.600	111.200	150.300
Max	231.000	53.500	22.400	63.200	19.200	14.400	195.600	141.000	157.000
N	11	9	12	12	13	12	9	8	2
Sid	15.098	2.731	1.707	3.128	1.174	0.989	15.333	10.823	4.738
<i>Zaglossus bartoni</i> <i>clunius</i> (Sample 3)									
M	205.500	50.122	19.542	57.375	16.431	12.383	175.022	125.762	153.650
Min	178.500	46.000	17.000	52.300	14.600	11.000	156.600	111.200	150.300
Max	231.000	53.500	22.400	63.200	19.200	14.400	195.600	141.000	157.000
N	11	9	12	12	13	12	9	8	2
Sid	15.098	2.731	1.707	3.128	1.174	0.989	15.333	10.823	4.738
<i>Zaglossus bartoni</i> <i>clunius</i> (Sample 3)									
M	205.500	50.122	19.542	57.375	16.431	12.383	175.022	125.762	153.650
Min	178.500	46.000	17.000	52.300	14.600	11.000	156.600	111.200	150.300
Max	231.000	53.500	22.400	63.200	19.200	14.400	195.600	141.000	157.000
N	11	9	12	12	13	12	9	8	2
Sid	15.098	2.731	1.707	3.128	1.174	0.989	15.333	10.823	4.738
<i>Zaglossus bartoni</i> <i>clunius</i> (Sample 3)									
M	205.500	50.122	19.542	57.375	16.431	12.383	175.022	125.762	153.650
Min	178.500	46.000	17.000	52.300	14.600	11.000	156.600	111.200	150.300
Max	231.000	53.500	22.400	63.200	19.200	14.400	195.600	141.000	157.000
N	11	9	12	12	13	12	9	8	2
Sid	15.098	2.731	1.707	3.128	1.174	0.989	15.333	10.823	4.738
<i>Zaglossus bartoni</i> <i>clunius</i> (Sample 3)									
M	205.500	50.122	19.542	57.375	16.431	12.383	175.022	125.762	153.650
Min	178.500	46.000	17.000	52.300	14.600	11.000	156.600	111.200	150.300
Max	231.000	53.500	22.400	63.200	19.200	14.400	195.600	141.000	157.000
N	11	9	12	12	13	12	9	8	2
Sid	15.098	2.731	1.707	3.128	1.174	0.989	15.333	10.823	4.738
<i>Zaglossus bartoni</i> <i>clunius</i> (Sample 3)									
M	205.500	50.122	19.542	57.375	16.431	12.383	175.022	125.762	153.650
Min	178.500	46.000	17.000	52.300	14.600	11.000	156.600	111.200	150.300
Max	231.000	53.500	22.400	63.200	19.200	14.400	195.600	141.000	157.000
N	11	9	12	12	13	12	9	8	2
Sid	15.098	2.731	1.707	3.128	1.174	0.989	15.333	10.823	4.738
<i>Zaglossus bartoni</i> <i>clunius</i> (Sample 3)									
M	205.500	50.122	19.542	57.375	16.431	12.383	175.022	125.762	153.650
Min	178.500	46.000	17.000	52.300	14.600	11.000	156.600	111.200	150.300
Max	231.000	53.500	22.400	63.200	19.200	14.400	195.600	141.000	157.000
N	11	9	12	12	13	12	9	8	2
Sid	15.098	2.731	1.707	3.128	1.174	0.989	15.333	10.823	4.738
<i>Zaglossus bartoni</i> <i>clunius</i> (Sample 3)									
M	205.500	50.122	19.542	57.375	16.431	12.383	175.022	125.762	153.650
Min	178.500	46.000	17.000	52.300	14.600	11.000	156.600	111.200	150.300
Max	231.000	53.500	22.400	63.200	19.200	14.400	195.600	141.000	157.000
N	11	9	12	12	13	12	9	8	2
Sid	15.098	2.731	1.707	3.128	1.174	0.989	15.333	10.823	4.738
<i>Zaglossus bartoni</i> <i>clunius</i> (Sample 3)									
M	205.500	50.122	19.542	57.375	16.431	12.383	175.022	125.762	153.650
Min	178.500	46.000	17.000	52.300	14.600	11.000	156.600	111.200	150.300
Max	231.000	53.500	22.400	63.200	19.200	14.400	195.600	141.000	157.000
N	11	9	12	12	13	12	9	8	2
Sid	15.098	2.731	1.707	3.128	1.174	0.989	15.333	10.823	4.738
<i>Zaglossus bartoni</i> <i>clunius</i> (Sample 3)									
M	205.500	50.122	19.542	57.375	16.431	12.383	175.022	125.762	153.650
Min	178.500	46.000	17.000	52.300	14.600	11.000	156.600	111.200	150.300
Max	231.000	53.500	22.400	63.200	19.200	14.400	195.600	141.000	157.000
N	11	9	12	12	13	12	9	8	2
Sid	15.098	2.731	1.707	3.128	1.174	0.989	15.333	10.823	4.738
<i>Zaglossus bartoni</i> <i>clunius</i> (Sample 3)									
M	205.500	50.122	19.542	57.375	16.431	12.383	175.022	125.762	153.650
Min	178.500	46.000	17.000	52.300	14.600	11.000	156.600	111.200	150.300
Max	231.000	53.500	22.400	63.200	19.200	14.400	195.600	141.000	157.000
N	11	9	12	12	13	12	9	8	2
Sid	15.098	2.731	1.707	3.128	1.174	0.989	15.333	10.823	4.738
<i>Zaglossus bartoni</i> <i>clunius</i> (Sample 3)									
M	205.500	50.122	19.542	57.375	16.431	12.383	175.022	125.762	153.650
Min	178.500	46.000	17.000	52.300	14.600	11.000	156.600	111.200	150.300
Max	231.000	53.500	22.400	63.200	19.200	14.400	195.600	141.000	157.000
N	11	9	12	12	13	12	9	8	2
Sid	15.098	2.731	1.707	3.128	1.174	0.989	15.333	10.823	4.738
<i>Zagloss</i>									

	left, right forefoot		left, right hindfoot	
<u>Zaglossus bartoni diamondi</u> (Sample 4)				
AMNH 190859	12345	12345	12340	12340
Griffiths (1978) (2)	"	"	"	"
" (1)	"	"	12345	12345
AM M 7955	"	"	"	"
<u>Zaglossus attenboroughi</u> (Sample 6)				
RMNH 17301	12345	12345	12345	12345

¹ locality of some specimens uncertain

² locality uncertain