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A systematic revision of Australian Emballonuridae (Mammalia: Chiroptera).

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Abstract

Numerical and classical taxonomic approaches based on the morphology of the skull, teeth and external characters, including the morphology of the baculum and glans penis, have been applied to clarify the specific and generic status of the Australian Emballonuridae.

We now recognise the following eight Australian emballonurid species: *Saccolaimus flaviventris, S. mixtus, S. saccolaimus; Taphozous australis, T. georgianus, T. hilli, T. kapalgensis* and *T. troughtoni*.

The genera *Saccolaimus* and *Taphozous* in Australia are separated on cranial, dental and external morphology. A parallel study by us (unpublished data) on generic relationships within the family Emballonuridae, based on phylogenetic analysis of qualitative cranial data, supports the recognition of *Saccolaimus* and *Taphozous* as distinct genera.

Introduction

Emballonurids are widely distributed in the tropical and subtropical regions of the world from the Pacific islands through the Indo-Australian region to Africa and the New and Old Worlds (Hill and Smith 1984). The family is a diverse group comprising about 13 genera and about 50 species (Hill and Smith 1984, Corbet and Hill 1986).

Although there have been several systematic and evolutionary studies of emballonurids (Miller 1907, Thomas 1922, Sanborn 1937, Simpson 1945, Koopman and Cockrum 1967, Barghoorn 1977, Honacki *et al.* 1982, Hill and Smith 1984, Koopman 1984a, Robbins and Sarich 1988) the last major revision of the Australian Emballonuridae was by Troughton (1925). Subsequent to this, some new forms have been described (Sody 1931, Tate 1952, McKean and Friend 1979, Kitchener 1980). Although two genera and seven species are currently recognised in Australia, some named forms have been the cause of considerable taxonomic confusion over the last 50 years, at both generic and specific levels.

Both *Taphozous* E. Geoffroy, 1818 and *Saccolaimus* Temminck, 1838 are generally currently recognised in Australia (Mahoney and Walton 1988), although some modern authorities do not recognise these genera as distinct (Hill and Smith 1984). In Australia, *Taphozous australis* Gould, 1854 and *Saccolaimus flaviventris* (Peters, 1867) were the first species to be ascribed to their respective genera. Since then, 13 more forms have been described from Australia. However, seven species are recognised by most modern

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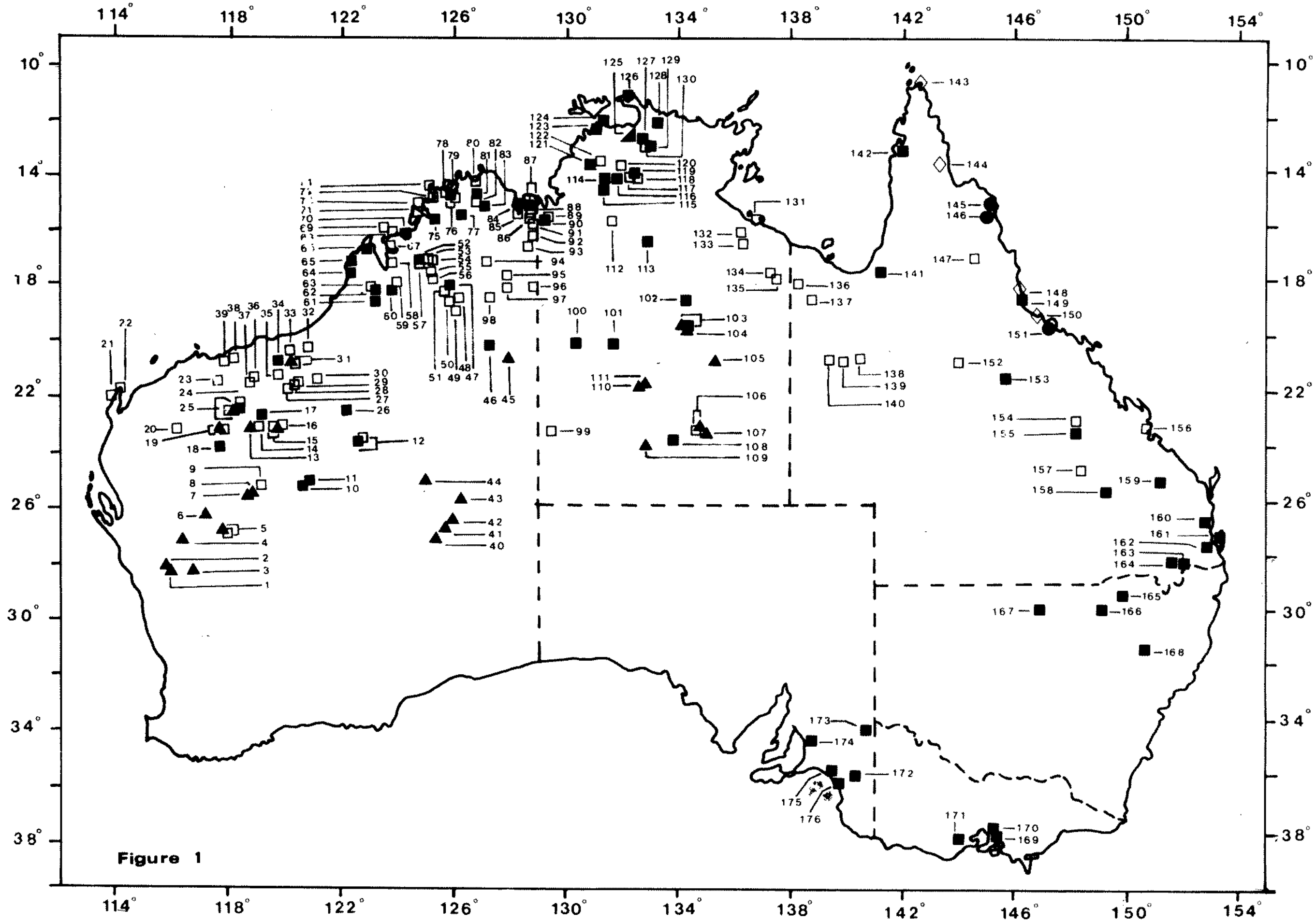

Figure 1 Collecting localities of Australian specimens examined. Species symbols are as follows: *Saccolaimus flaviventris* (■), *S. saccolaimus* (●), *Taphozous australis* (◇), *T. georgianus* (□), *T. hilli* (▲), *T. kapalgensis* (◢).

authorities in Australia (e.g. Strahan 1983, Mahoney and Walton 1988). The seven species and their synonyms, in brackets, are as follows: *Taphozous australis* Gould, 1854 (*T. fumosus* De Vis, 1905), *T. georgianus* Thomas, 1915 (*T. australis* Collet, 1887; *T. australis georgianus* Thomas, 1915; and *T. troughtoni* Tate, 1952), *T. kapalgensis* McKean and Friend, 1979, *T. hilli* Kitchener, 1980, *Saccolaimus saccolaimus* Temminck, 1838 (*S. crassus* Blyth, 1844; *S. pulcher* Elliot, 1844; *S. affinis* Dobson, 1875; *S. nudicluniatus* De Vis,1905; and *S. flavimaculatus* Sody, 1931), *S. flaviventris* (Peters, 1867) (*S. hargravei* Ramsay, 1876; *S. affinis* var. *insignis* Leche, 1884 and *T. australis* Gould, 1854); and *S. mixtus* Troughton, 1925. An historic account of the current generic and specific taxonomic confusion is extensively treated in Chimimba (1987) and the nomenclatural history by Mahoney and Walton (1988).

This paper is an appraisal of the taxonomy of Australian emballonurids at both the generic and specific levels. We have utilised a wider range of morphological taxonomic techniques (numerical and classical) than has previously been applied to these taxa, and include most described Australian forms. Asian taxa that are morphologically similar to some Australian species are also included in this study.

Materials and Methods

Specimens Examined

This study was based on specimens fixed in 10% formaldehyde and preserved in 70% ethanol, including study skins and skulls. Collection localities of Australian specimens examined are indicated in Figure 1. Specimens examined are listed in Appendix I. The collecting localities provide a good representation of the geographic distributions of the named Australian forms. Asian forms included in our study are: *Saccolaimus saccolaimus* from India, Java, Solomon Islands and Borneo; *S. nudicluniatus* from the Solomon Islands and *T. longimanus* from Bali and India. Only specimens judged to be adult were used. Individuals were considered adult if they lacked any swelling of the metacarpal and phalangeal epiphyses, and or had the sutures of the basicranial region closed.

Institutional Sources of Specimens

Specimens examined were from the following institutions: (to denote the institutional origin of specimens, their catalogue numbers are prefixed by the following abbreviations (see Appendix I)).

AM : Australian Museum, Sydney.
AMNH : American Museum of Natural History, New York.
B : Zoology Department, University of Queensland, Brisbane.
C : Museum of Victoria, Melbourne.
CAM : Central Australian Wildlife Collections, Darwin.
CM : Australian National Wildlife Collections, Canberra.
FMNH : Field Museum of Natural History, Chicago.
JM : Queensland Museum, Brisbane.
NTM : Northern Territory Museum, Darwin.
SAM : South Australian Museum, Adelaide.
WAM : Western Australian Museum, Perth.

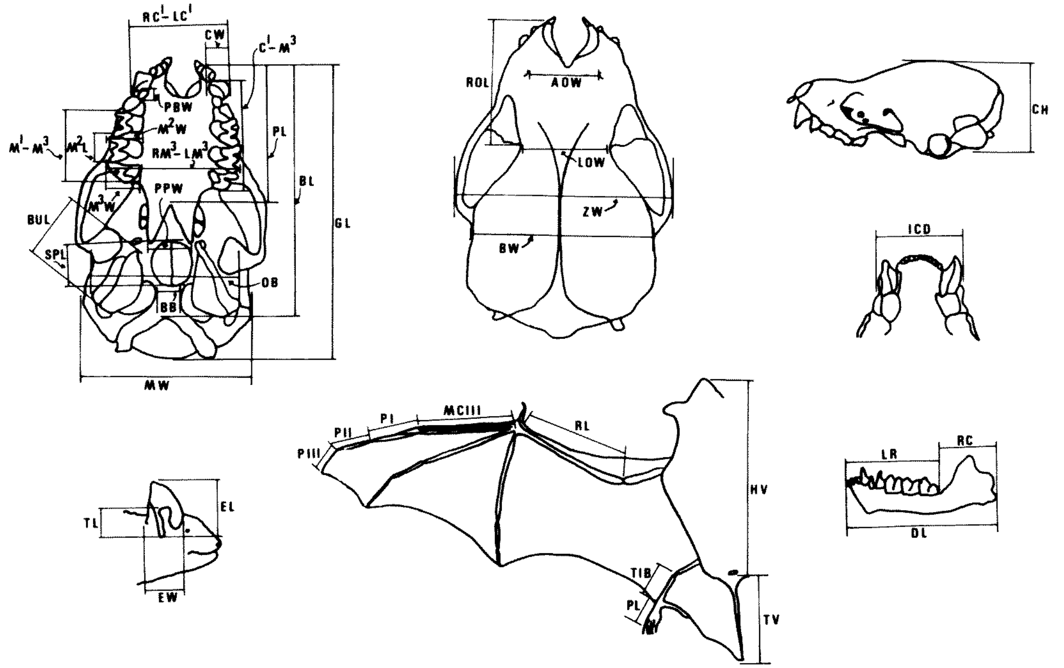

Figure 2 Abbreviations and the recording points of cranial, mandibular and external body measurements referred to in text. GL: greatest skull length; AOW: anteorbital width, between infraorbital foramina; LOW: least interorbital width; ZW: zygomatic width; ROL: rostrum length, from LOW to anterior edge of premaxilla; MW: mastoid width, between mastoid processes; BW: braincase width, at centre of zygomatic-squamosal contact; CH: cranial height, lower arm of calipers placed level with pre — and basisphenoid, upper arm in contact with apex of skull; PL: palatal length; PPW: postpalatal width; BL: basicranial length, between anterior edge of foramen magnum and anterior edge of premaxilla; BUL: bulla length, excluding eustachian part; BB: width of basisphenoid, between cochlea; OB: distance outside bullae, caliper points in contact with anterodorsal edge of tympanic ring; CW: canine width, maximum diameter at base; RC^1-LC^1: inter upper canine distance, at base of cusp; C^1-M^3: upper maxillary tooth row crown length, anterior edge of C^1 to posterior edge of M^3; M^1-M^3: upper molar crown length, anterior edge of M^1 parastyle to posterior edge of M^3; M^{2}L: upper second molar crown length, anterior edge of parastyle to posterior edge of metastyle; M^{2}W: upper second molar crown width, lingual base of protocone to buccal face of paracone, at right angle to occlusal surface; M^{3}W: upper third molar crown width, as for M^{2}W; RM^3-LM^3: inter-upper third molar distance, across buccal face of paracone of RM^3 and LM^3; LR: lower tooth row, posterior edge of M^3 to anterior edge of dentary; RC: angular ramus to dentary condyle, caliper blade along anterior face of ramus and measuring to posterior edge of articular condyle; DL: dentary length, from condyle to anterior tip of dentary; SPL: sphenoid pit length; PBW: P^1 basal width; ICD: inter-lower canine distance, at base of cusp; HV: body length, from tip of rhinarium to anus; TV: tail length, from tip to anus; EL: ear length, apex to basal notch; EW: ear width across basal lobes; TL: tragus length, apex to basal notch; RL: radius length; MCIII: metacarpal III length; PI: digit III/phalanx I length; PII: digit III/phalanx II length; TIB: tibia length; and PL: pes length.

Morphology and Terminology

Terminology of tooth structure follows Slaughter (1970); skull and dentary terminology follows Kitchener and Caputi (1985) while that used for external morphology follows Hill and Smith (1984).

Characters

Twenty-eight quantitative skull and dentary characters (hereafter referred to as skull characters) and 11 external characters were recorded with Mitutuyo dial calipers and taken to the nearest 0.1 mm. The positions and abbreviations of these skull and external measurements are shown in Figure 2.

Measurements of Holotypes and Unique Specimens

Our measurements of holotypes and unique specimens are listed in Appendix II, measurements throughout are in mm.

Glans Penis, Baculum and Pelage

Alizarin S method for gross staining of calcium was used for the preparation of the bacula for examination (McGee-Russel 1958) and for assessing their positions within the glans penis. Descriptions of pelage and skin colour followed Ridgway's (1912) colour standards and nomenclature and were described from 'cabinet' skins.

Statistical Analyses

All statistical analyses were performed at the Western Australian Regional Computing Centre (W.A.R.C.C.) on a Cyber 845.

Sexual Dimorphism

Prior to any analysis the nature and extent of sexual dimorphism was first examined using a one-way analysis of variance (Zar 1974) generated by SPSS subprogramme ONEWAY (Nie *et al.* 1975). Only *Taphozous georgianus*, *T. hilli* and *Saccolaimus flaviventris* had adequate specimens to examine sexual dimorphism.

Delineation of Species by Shape in Relation to Size

To minimise the effects of size, size regression on a selected size variable was used. Through the SPSS subprogramme SCATTERGRAM (Nie *et al.* 1975), the original characters were logarithmically transformed in order to make their interrelationships linear. Intraspecific allometric regression equations based on the greatest skull length (GL) as an overall measure of size were then used to transform each coordinate to the value it would be expected to assume if that coordinate were of a size equivalent to the mean of all taxa (Thorpe 1976).

An *a priori* Recognition of Taxa

Principal Components Analysis (PCA) (Blackith and Reyment 1971, Wiley 1981, Pielou 1984) using quantitative size-free characters was used to assess the distinctiveness of all specimens examined. This analysis was conducted using the SPSS subprogramme FACTOR (Nie *et al.* 1975). Since the primary interest was to obtain scores and loadings of characters, R-mode factoring was adopted. Rotation of factors in general, simplifies the factor structure; consequently, Varimax rotation, which provides factors that are most easily interpretable in terms of the original variables (Nie *et al.* 1975) was further adopted. In addition, the number of factors extracted in factor analysis is highly dependent on the minimum eigenvalue (Nie *et al.* 1975) and is also a function of the correlation among variables (Sokal and Rohlf 1981). Only factors with an eigenvalue ≥ 1 were examined as this corresponds to a single variable in the original data.

In addition to PCA, a classical taxonomic approach was used to examine the morphological distinctiveness of taxa.

An *a posteriori* Recognition of Taxa

The groups obtained from PCA and the classical taxonomic approach were subjected to a stepwise Canonical Variates Analysis (CVA) performed through the SPSS subprogramme DISCRIMINANT (Nie *et al.* 1975; Hull and Nie 1981). This maximises differences between groups, assists recognition of characters important in separating groups, and the classification of individuals to groups. Because the computation of a covariance matrix in CVA is sample-dependent, groups represented by less than three individuals were not included in the "analysis phase", they were however included during the "classification phase".

Groupings of Morphological Data for Statistical Analyses

Some of the specimens had incomplete data sets because only skulls or externals were available. While PCA adjusts for missing variables in the computation of factor scores, CVA deletes a case from the analysis if it has a missing value (Nie *et al.* 1975). For these reasons, both PCA and CVA were performed using three groupings of data: (1) skull characters only; (2) skull, wing and tibia length (TIB); and (3) skull and external characters combined (obtainable only from alcohol preserved specimens).

The latter analysis resulted in the loss of many cases. We excluded postpalatal width (PPW), rostrum length (ROL), and upper second molar crown length (M^2L from the CVA because these measurement were missing from many specimens.

Cluster Analysis

To investigate how species cluster phenetically, cluster analysis was performed through SPSS X subroutine CLUSTER. The transformed mean character values were used to obtain a squared Euclidian distance between species (Mahalanobis 1936; Rao 1948). The squared Euclidian distance was used to calculate a similarity matrix. The similarity matrix was then subjected to a hierarchical cluster analysis using the Unweighted Pair Group Mathematical Averaging method (UPGMA) (Sneath and Sokal 1973; Wiley 1981). Some species (as indicated in Figure 1) were represented by many populations; species rather than local populations were therefore treated as OTU's.

Systematics

The means, ranges and standard deviations (in mm) of characters of the Australian emballonurids are presented in Table 1a for skull, dentary and teeth and Table 1b for external characters. In species in which the glans penis and bacula were examined, the baculum was always located at the very tip of the head mound of the glans penis as indicated in Figure 3a.

Table 1 (a) Skull, dentary, teeth and (b) external measurements, in mm, for adult *Taphozous georgianus*, *T. troughtoni*, *T. hilli*, *T. kapalgensis*, *T. australis*, *Saccolaimus saccolaimus*, *S. flaviventris* and *S. mixtus* from Australian localities. N = Sample size, x = mean, SD = standard deviation, Mn = minimum, Mx = maximum (for code to characters see Figure 2).

Skull, Dentary and Teeth Characters

		GL	AOW	LOW	ZW	ROL	MW	BW	CH	PL	PPW	BL	BUL	BB	OB
	N	259	258	260	253	262	251	255	253	257	210	252	253	253	240
	x	21.4	6.3	6.3	13.2	9.2	10.8	10.5	7.4	8.8	3.6	18.8	4.9	2.1	10.0
T. georgianus	SD	0.48	0.22	0.29	0.34	0.27	0.26	0.28	0.29	0.26	0.27	0.40	0.17	0.15	0.29
	Mn	20.0	5.8	5.6	12.1	8.6	10.1	9.8	5.7	8.1	2.8	17.7	4.3	1.7	9.2
	Mx	23.1	7.0	7.3	14.4	11.5	11.7	11.6	8.4	9.5	4.4	19.9	5.3	2.6	11.0
	N	4	4	4	4	4	4	4	4	4	4	4	4	4	4
	x	24.1	6.9	6.9	14.8	10.3	12.1	11.8	8.5	9.3	4.5	21.1	5.6	2.4	11.4
T. troughtoni	SD	0.13	0.14	0.40	0.10	0.10	0.13	0.10	0.13	0.25	0.26	0.19	0.10	0.21	0.13
	Mn	24.0	6.8	6.4	14.7	10.2	11.9	11.7	8.4	9.8	4.2	20.8	5.4	2.2	11.2
	Mx	24.3	7.1	7.3	14.9	10.4	12.2	11.9	8.7	10.3	4.7	21.2	5.6	2.6	11.5
	N	75	74	74	74	75	75	75	75	75	59	73	75	75	75
	x	20.0	6.0	6.2	12.8	8.0	10.4	10.5	7.4	7.3	3.6	16.8	5.1	2.0	9.9
T. hilli	SD	0.35	0.19	0.28	0.22	0.22	0.19	0.22	0.18	0.20	0.23	0.32	0.13	0.18	0.18
	Mn	19.1	5.6	4.7	12.3	7.1	9.9	9.9	7.0	6.8	3.2	16.0	4.9	1.5	9.5
	Mx	21.1	6.8	6.7	13.4	8.4	11.0	11.0	7.8	7.8	4.4	17.6	5.5	2.8	10.3
	N	9	9	9	9	9	9	9	9	9	5	9	9	9	8
	x	21.6	6.2	6.3	13.1	9.0	11.1	10.9	7.8	8.7	3.7	18.6	5.1	2.2	10.6
T. australis	SD	0.20	0.13	0.17	0.12	0.11	0.17	0.14	0.22	0.17	0.24	0.21	0.12	0.14	0.09
	Mn	21.4	6.0	6.1	12.9	8.8	10.8	10.6	7.4	8.5	3.5	18.5	4.9	2.0	10.5
	Mx	22.0	6.4	6.7	13.3	9.2	11.4	11.1	8.1	9.1	4.1	18.9	5.3	2.4	10.7
	N	3	3	3	3	3	3	3	3	3	2	3	3	3	3
	x	20.3	5.8	6.4	12.9	8.6	11.1	10.8	7.7	7.9	4.3	18.1	5.0	2.4	9.5
T. kapalgensis	SD	0.35	0.07	0.19	0.26	0.15	0.13	0.15	0.13	0.27	0.28	0.25	0.21	0.10	0.41
	Mn	20.0	5.8	6.2	12.6	8.4	11.0	10.6	7.6	7.6	4.1	17.9	4.8	2.3	9.1
	Mx	20.7	5.9	6.6	13.1	8.7	11.2	10.9	7.8	8.1	4.5	18.4	5.2	2.5	9.9
	N	106	107	104	104	109	106	106	107	107	69	103	106	105	101
	x	25.2	8.4	9.1	16.6	10.7	14.1	12.8	8.7	10.9	4.1	22.1	5.3	2.9	12.2
S. flaviventris	SD	0.73	0.44	0.50	0.60	0.37	0.53	0.43	0.40	0.51	0.41	0.68	0.27	0.29	0.42
	Mn	23.8	7.1	8.1	14.8	9.7	12.7	11.8	7.8	9.6	3.2	20.0	4.7	2.2	10.9
	Mx	27.0	9.7	10.3	17.9	11.6	15.7	14.3	9.7	12.3	5.6	23.6	6.0	3.8	13.3
	N	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	x	24.4	7.3	8.3	16.5	10.0	14.2	13.1	9.6	9.9	4.0	20.6	5.1	3.5	12.7
S. saccolaimus	SD	1.3	0.39	0.62	0.96	0.34	0.50	0.55	0.60	0.47	0.40	0.81	0.16	0.35	0.46
	Mn	22.4	6.6	7.4	14.6	9.3	13.4	12.0	8.7	9.2	3.7	19.0	4.9	2.9	11.9
	Mx	25.9	7.8	9.0	17.3	10.6	15.1	13.8	10.1	10.6	4.6	21.8	5.8	4.0	13.4
	N	2	2	2	—	2	2	2	2	2	—	2	2	2	2
	x	21.8	6.6	7.8	—	8.8	12.1	11.6	8.1	8.7	—	18.8	4.8	3.3	11.3
S. mixtus	SD	0.14	0.28	0.23	—	0.22	0.01	0.06	0.18	0.21	—	0.13	0.11	0.13	0.42
	Mn	21.7	6.6	7.6	—	8.6	12.1	11.6	8.0	8.5	—	18.7	4.8	3.2	11.0
	Mx	21.9	6.6	7.9	—	8.9	12.1	11.6	8.3	8.8	—	18.9	4.9	3.4	11.6

Table 1a cont.

Skull, Dentary and Teeth Characters cont.															
		CW	RC^1-LC^1	C^1-M^3	M^1-M^3	M^2L	M^2W	M^3W	RM^3-LM^3	LR	RC	DL	SPL	PBW	ICD
	N	262	258	262	262	261	261	262	253	261	259	260	255	258	259
	X	2.0	4.1	9.7	5.2	2.1	2.5	2.2	9.4	11.7	5.0	18.1	4.2	0.60	3.0
T. georgianus	SD	0.10	0.15	0.26	0.18	0.11	0.12	0.13	0.26	0.33	0.34	0.42	0.20	0.07	0.13
	Mn	1.5	3.4	8.8	4.2	1.7	2.0	1.8	8.6	10.4	4.5	16.7	3.5	0.40	2.6
	Mx	2.3	4.5	10.5	5.7	2.5	2.9	2.6	10.3	14.5	6.0	19.3	4.7	0.80	3.3
	N	4	4	4	4	4	4	4	4	4	4	4	4	4	4
	x	2.3	4.6	10.9	5.9	2.3	2.7	2.4	10.4	13.1	5.6	20.6	4.5	0.65	3.3
T. troughtoni	SD	0.06	0.13	0.10	0.06	0.08	0.06	0.05	0.24	0.05	0.13	0.17	0.25	0.06	0.10
	Mn	2.2	4.5	10.8	5.8	2.2	2.6	2.3	10.2	13.0	5.5	20.3	4.2	0.60	3.2
	Mx	2.3	4.8	11.0	5.9	2.4	2.7	2.4	10.7	13.1	5.8	20.7	4.8	0.70	3.4
	N	75	73	75	75	75	75	75	75	75	75	75	74	74	74
	x	1.7	3.5	8.6	4.7	1.9	2.3	2.0	9.1	10.6	4.4	15.9	4.1	0.46	2.8
T. hilli	SD	0.06	0.61	0.53	0.11	0.09	0.09	0.12	0.22	0.17	0.19	0.44	0.17	0.07	0.13
	Mn	1.5	3.1	7.6	4.5	1.5	2.0	1.7	8.4	10.2	4.1	15.2	3.7	0.30	2.5
	Mx	1.8	4.8	9.8	5.0	2.1	2.4	2.3	9.7	11.0	5.0	18.8	4.4	0.70	3.1
	N	9	9	9	9	9	9	9	9	9	9	9	9	9	8
	x	2.1	4.0	9.6	5.1	2.0	2.4	2.1	9.3	11.5	5.0	17.6	3.4	0.58	3.2
T. australis	SD	0.08	0.08	0.13	0.07	0.13	0.11	0.07	0.11	0.09	0.19	0.21	0.15	0.07	0.06
	MN	2.0	3.9	9.4	5.0	1.8	2.2	2.0	9.2	11.4	4.8	17.4	3.2	0.50	3.1
	Mx	2.2	4.1	9.8	5.2	2.2	2.6	2.2	9.5	11.6	5.4	17.9	3.6	0.70	3.3
	N	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	x	2.0	4.2	9.3	5.0	2.0	2.4	2.1	9.0	11.2	5.2	17.3	3.8	0.63	3.0
T. kapalgensis	SD	0.06	0.22	0.12	0.07	0.07	0.10	0.06	0.20	0.16	0.06	0.26	0.10	0.06	0.21
	Mn	2.0	4.0	9.2	5.0	1.9	2.3	2.1	8.8	11.0	5.1	17.1	3.7	0.60	2.8
	Mx	2.1	4.4	9.4	5.1	2.0	2.5	2.2	9.2	11.3	5.2	17.6	3.9	0.70	3.2
	N	109	107	109	109	109	109	109	105	108	108	107	106	107	104
	x	2.2	6.4	11.5	6.3	2.6	3.0	2.4	11.5	14.1	6.1	21.5	2.9	1.5	4.1
S. flaviventris	SD	0.11	0.27	0.39	0.25	0.16	0.20	0.17	0.43	0.42	0.30	0.57	0.28	0.12	0.21
	Mn	1.9	5.9	10.0	5.5	2.2	2.5	2.0	10.5	13.0	5.6	20.1	2.2	1.0	3.6
	Mx	2.4	7.1	12.4	6.8	2.9	3.5	2.8	12.7	15.0	6.8	22.7	3.5	1.8	4.7
	N	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	x	2.2	5.7	11.2	6.0	2.5	3.1	2.3	11.2	13.4	6.0	20.6	3.6	1.4	4.0
S. saccolaimus	SD	0.12	0.34	0.30	0.21	0.08	0.23	0.11	0.31	0.65	0.27	0.61	0.44	0.12	0.18
	Mn	2.1	5.0	10.7	5.7	2.3	2.7	2.2	10.7	11.8	5.6	19.5	3.0	1.2	3.7
	Mx	2.5	6.2	11.7	6.4	3.5	2.5	2.5	11.7	14.1	6.3	21.4	4.1	1.5	4.3
	N	2	2	2	2	2	2	2	2	2	1	2	2	2	2
	x	1.8	4.6	9.9	5.5	2.2	2.4	2.1	10.1	11.9	5.7	18.6	4.0	0.95	3.1
S. mixtus	SD	0.07	0.22	0.18	0.04	0.09	0.04	0	0.15	0.36	0	0.18	0.04	0.07	0.23
	Mn	1.7	4.5	9.8	5.4	2.1	2.4	2.1	10.0	11.7	5.7	18.4	4.0	0.90	2.9
	Mx	1.8	4.8	10.0	5.5	2.2	2.4	2.1	10.2	12.2	5.7	18.7	4.0	1.0	3.2

Table 1b

		External Characters										
		HV	TV	EL	EW	TL	RL	MCIII	PI	PII	TIB	PES
T. georgianus	N	303	296	302	302	303	295	302	302	297	299	303
	x	72.8	30.0	20.5	14.7	6.9	68.1	61.4	20.6	24.5	27.2	12.4
	SD	3.5	2.9	1.4	1.4	0.69	2.1	2.1	0.96	1.1	1.1	0.72
	Mn	61.6	22.9	16.5	11.8	4.9	61.1	52.7	17.7	19.8	24.2	9.8
	Mx	80.0	39.4	24.1	25.6	8.9	73.4	65.9	23.7	29.1	30.8	14.7
T. troughtoni	N	4	4	4	4	4	4	4	4	4	4	4
	x	83.4	33.7	25.4	17.9	8.4	74.6	69.2	23.5	26.8	31.2	14.8
	SD	3.3	2.5	2.1	1.8	0.76	1.3	0.82	1.1	1.2	0.64	0.80
	Mn	79.4	31.5	22.4	16.2	7.7	72.7	68.1	22.2	25.4	30.6	13.8
	Mx	86.3	36.9	27.1	19.9	9.4	75.6	70.2	24.6	28.4	31.8	15.5
T. hilli	N	102	101	102	102	102	102	102	102	102	102	102
	x	72.6	30.3	21.1	15.4	6.7	67.7	59.9	19.6	23.4	26.8	13.0
	SD	3.1	2.3	1.3	0.94	0.70	1.6	1.5	0.69	0.95	0.88	0.66
	Mn	64.7	23.9	18.5	13.6	5.0	60.4	56.0	17.0	20.7	25.0	10.7
	Mx	81.1	37.7	23.7	18.2	8.6	71.7	64.2	21.6	26.8	31.3	14.3
T. australis	N	13	13	13	13	13	13	13	13	13	13	13
	x	70.0	28.5	22.3	16.2	7.4	65.4	59.2	19.8	22.6	25.7	12.1
	SD	3.7	1.7	1.1	0.96	0.74	1.1	1.1	0.57	0.78	0.75	0.55
	Mn	61.0	25.1	20.2	14.7	5.9	63.5	57.2	18.7	20.8	24.5	11.1
	Mx	74.8	30.6	24.0	17.5	9.0	67.6	60.9	20.9	23.7	27.1	13.0
T. kapalgensis	N	2	2	2	2	3	3	3	3	3	3	2
	x	71.5	22.8	17.0	13.4	6.1	59.3	59.2	21.3	22.1	23.3	12.2
	SD	3.7	0	0.75	0.26	0.67	0.38	1.3	0.28	0.71	0.39	0.26
	Mn	68.8	22.8	16.5	13.2	5.6	58.9	57.8	21.1	21.4	23.0	12.1
	Mx	74.1	22.8	17.6	13.6	6.6	59.7	60.2	21.6	22.8	23.7	12.4
S. flaviventris	N	101	100	104	105	104	106	106	106	105	106	106
	x	81.8	27.0	19.6	14.3	8.1	75.0	77.6	33.4	31.7	30.3	14.1
	SD	3.5	2.8	1.3	1.1	0.84	2.8	2.7	1.5	1.9	1.3	1.3
	Mn	72.3	21.3	16.5	11.1	5.8	65.7	72.6	28.9	27.7	26.7	11.1
	Mx	91.9	33.3	23.0	17.1	9.9	82.1	84.2	36.5	35.9	32.9	16.5
S. saccolaimus	N	3	3	3	3	3	3	3	3	3	3	3
	x	85.7	32.5	18.7	15.6	6.5	74.1	71.6	28.0	28.0	28.6	17.1
	SD	7.7	1.7	1.8	0.55	1.1	3.1	3.3	1.9	1.5	1.6	2.5
	Mn	76.9	30.9	16.6	15.1	5.6	69.2	65.7	25.6	25.6	27.0	14.3
	Mx	90.7	34.2	19.9	16.2	7.7	78.6	75.9	30.2	29.8	30.5	19.1
S. mixtus	N	2	1	1	1	1	2	2	2	2	2	2
	x	74.3	22.6	18.3	14.5	7.6	63.6	62.2	23.5	23.7	24.2	13.1
	SD	2.6	0	0	0	0	0.75	0.88	1.3	0	0.69	1.3
	Mn	72.5	22.6	18.3	14.5	7.6	63.1	61.6	22.6	23.7	23.7	12.2
	Mx	76.2	22.6	18.3	14.5	7.6	64.2	62.8	24.4	23.6	24.7	14.1

Saccolaimus Temminck, 1838

Saccolaimus Temminck, C.J. (1838). Over de geslachten *Taphozous, Emballonura, Urocryptus* en *Diclidurus*. Tijdschr. Natuur. Ges. Physiol. 5: 1-34 pl. 1.

Type species

Taphozous saccolaimus Temminck, 1838 by absolute tautonymy.

Taphonycteris Dobson, G.E. (1876). A monograph of the genus *Taphozous* Geoff. Proc. Zool. Soc. Lond. 1875: 546-556 (548,555) (originally proposed as subgenus of *Taphozous* Geoffroy, 1813).

Referred Australian species

Saccolaimus saccolaimus (Temminck, 1838)
Saccolaimus flaviventris (Peters, 1867)
Saccolaimus mixtus Troughton, 1925

Diagnosis (mean values)

The following diagnosis refers only to Australian emballonurids.

Saccolaimus differs from *Taphozous* in being considerably longer in all measurements; skull heavily rather than lightly ossified; sagittal crest pronounced rather than absent or weak; band separating the anterior lacerate foramen and sphenorbital sinus wide rather than narrow; premaxilla almost abuts rather than overlaps nasals; postorbital ridge strong, joining the sagittal crest near or well posterior to postorbital ridges rather than weak and joining at postorbital ridge; bullae complete rather than incomplete, with less rather than greater than 50 percent of the cochlea exposed; frontal region of skull relatively broad rather than narrow; lower outline of dentary strongly convex rather than concave beneath premolars; anterior premolar relatively large rather than small, almost one-third rather than one-fifth of height and crown area of posterior premolar; sphenoid pit generally shorter rather than longer relative to greatest skull length; base of sphenoid pit v-shaped rather than flat; posteroventral face of basisphenoid in contact with both bulla and cochlea rather than with cochlea only; paraoccipital process same length or slightly longer, rather than shorter than occipital condyles; braincase broader with parietal generally posterolaterally flattened such that braincase wider rather than narrower relative to greatest skull length; first upper molar parastylar area reduced rather than well developed; inner margin of ear not papillate. Length of baculum and glans penis of *S. flaviventris* and *S. saccolaimus* (the two species of *Saccolaimus* available for examination), were longer than in *Taphozous* spp.: baculum (1.0-1.1 v. 0.3-0.4); glans penis (4.2-6.5 v. 2.1-3.3).

Distribution

Saccolaimus occurs in the Indo-Malayan region and Australia and one species *(S. peli)* occurs in West, Central, East and parts of southern Africa (Liberia to Zaire to W. Kenya, Gabon and N.E. Angola) (Honacki *et al.* 1982).

Saccolaimus flaviventris (Peters, 1867)

Figures 3b, 4a, 5; Table 1.

Taphozous flaviventris Peters, W. (1987). On *Taphozous flaviventris*, Gould, a new species of bat from Australia. Proc. Zool. Soc. London 1866: 430.

Taphozous australis flaviventris Dobson, G.E. (1876). A monograph of the genus *Taphozous*, Geoff. Proc. Zool. Soc. Lond. 1875: 546-548.

Taphozous hargravei Ramsay, E.P. (1876). Description of a supposed new species of bat, from Stanwell, near Bulli, N.S.W. Proc. Linn. Soc. N.S.W. 1: 81-82.

Taphozous affinis insignis Leche, W. (1884). On some species of Chiroptera from Australia. Proc. Zool. Soc. Lond. 1884: 49-54.

Holotype

AM 137 (from register compiled by Secretary, Palmer, about 1877) female skin (wet) and skull, from Northern Territory.

Relevant taxonomic decisions

Troughton, E. le G. (1925). A revision of the genera *Taphozous* and *Saccolaimus* (Chiroptera) in Australia and New Guinea, including a new species, and a note on two Malayan forms. *Rec. Aust. Mus.* 14: 313-341 pls 47-48.

Diagnosis (mean values)

Differs from *S. mixtus* in that skull, dentary, teeth and external body measurements larger: mastoid width (14.1 v. 12.1), distance outside bullae (12.2 v. 11.3), canine width (2.2 v. 1.8), inter-upper canine distance (6.4 v. 4.6), upper maxillary tooth row crown length (11.5 v. 9.9), digit III/phalanx I length (33.4 v. 23.5); sphenoid pit deep rather than shallow, posterior margined by an overlapping edge rather than open, median septum as high as the floor of mesopterygoid fossa rather than to a level slightly below that of fossa; males with a secondary gular sac present rather than absent; radial-metacarpal pouch present rather than absent; frontal depression less deeply excavated.

Although of similar skull and body proportions, *S. flaviventris* differs from *S. saccolaimus* in having a relatively smaller sphenoid pit (2.9 v. 3.6), longer digit III/phalanx I length (33.4 v. 28.0) and inter-upper canine distance (6.4 v. 5.7); frontal region of skull relatively broad rather than narrow; posterior floor of mesopterygoid fossa deeply grooved rather than smooth; sphenoid pit deep rather than shallow, median septum as high as floor of mesopterygoid fossa rather than well below level of fossa; zygomata thin and of uniform size rather than large and constricted posteriorly. Glans penis longer (5.6 v. 4.2) and of uniform width rather than club shaped, ventral proximal end smooth rather than with an elevated skin. Baculum narrow distally rather than bifurcated, proximally club-shaped rather than spatulate.

Description (means and ranges)

Skull and Dentary (Figure 5)

Skull large: greatest skull length 25.2 (23.8-27.0); zygomatic width 16.6 (14.8-17.9), mastoid width 14.1 (12.7-15.7), distance outside bullae 12.2 (10.9-13.3), canine width 2.2 (1.9-2.4), inter-upper canine distance 6.4 (5.9-7.1), upper maxillary tooth row crown length 11.5 (10.0-12.4); sagittal crest well developed, reaches occiput; lamboidal crest well developed; zygomata of uniform size; sphenoid pit deep with a median septum rising as high as floor of mesopterygoid fossa; sphenoid pit margined posteriorly by an overlapping edge; mesopterygoid fossa deeply grooved; lower outline of mandible markedly convex beneath premolars to almost straight posteriorly; upper anterior premolar large, equal to or almost half size of posterior premolar, cusps long and sharp.

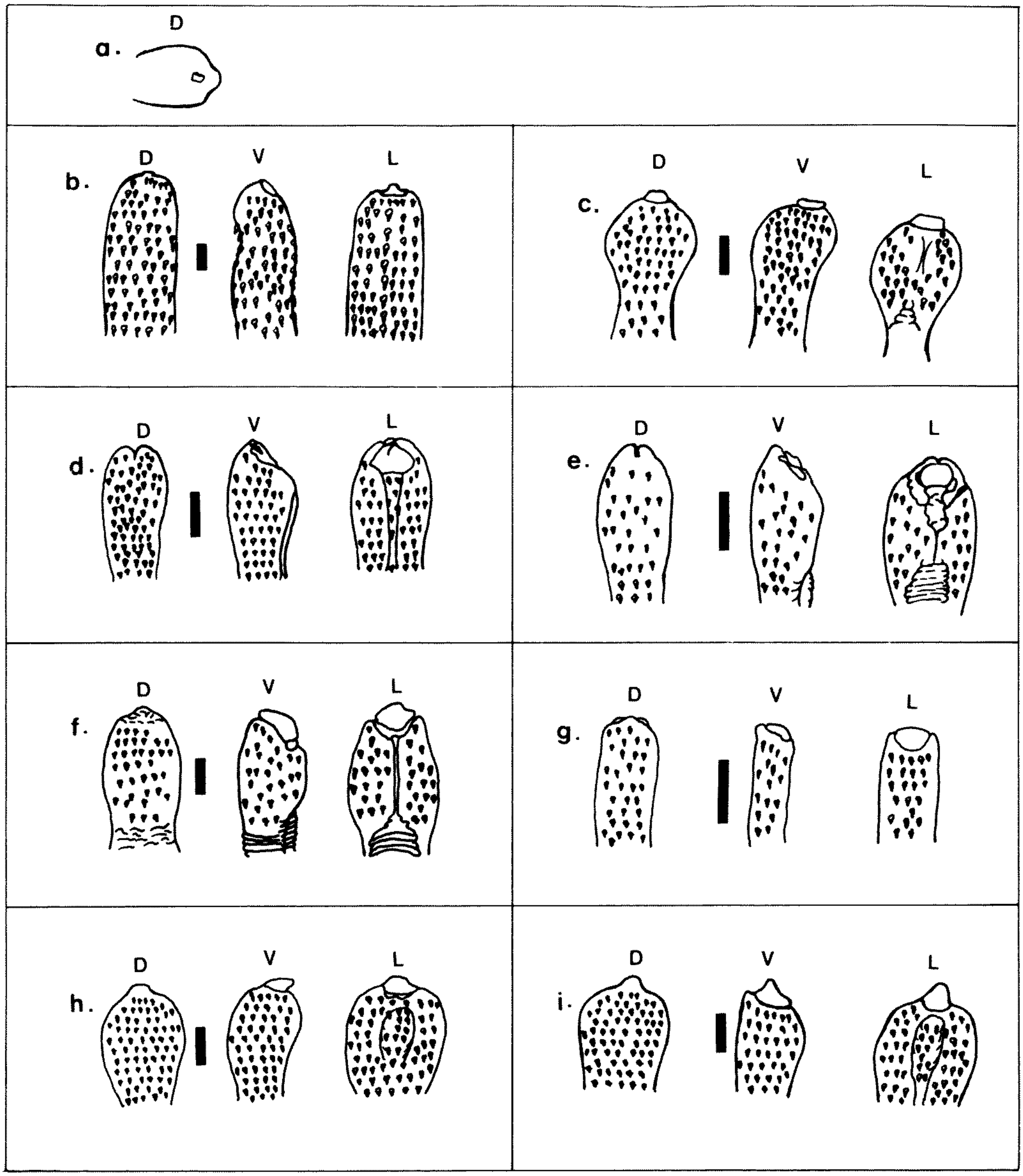

Figure 3 The positioning of the baculum within the glans penis (a) and the ventral (V), dorsal (D) and lateral (L) views of the glans penis of *Saccolaimus flaviventris* (b), *S. saccolaimus* (c), *Taphozous australis* (d), *T. georgianus* (e), *T. troughtoni* (f), *T. hilli* (g), *T. kapalgensis* (h) and *T. longimanus* (i). Scale lines are 1.0 mm.

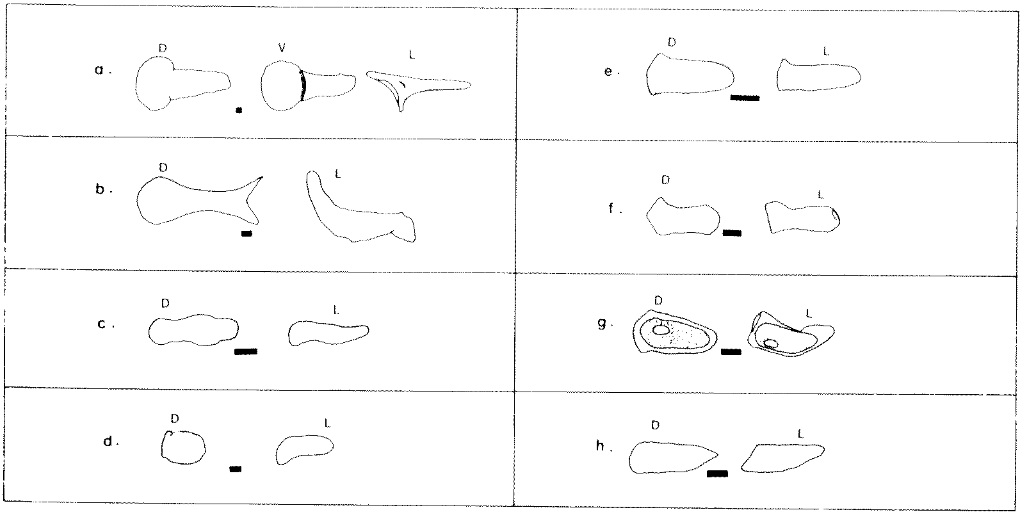

Figure 4 Dorsal (D), lateral (L) and some ventral (V) views of bacula of *Saccolaimus flaviventris* (a), *S. saccolaimus* (b), *Taphozous australis* (c), *T. georgianus* (d), *T. troughtoni* (e), *T. hilli* (f), *T. kapalgensis* (g) and *T. longimanus* (h). Scale lines are 1.0 mm.

External Morphology

Size generally large: radius length 75.0 (65.7-82.1); radial-metacarpal pouch absent in both sexes; large gular sac, with a secondary sac posterior to main sac in males but almost absent in females; outer edge of ear halfway between corner of mouth and posterior base of tragus; inner edge of tragus evenly concave, rounded but somewhat even above with a deep notch just below the top of outer edge.

Pelage and Skin Colour

Dorsal pelage predominantly Black; head well furred to between eyes with Cheatura Black, snout sparsely haired to its tip with this colour; outside ear almost naked except for sparse Brownish Olive hairs at base; similar coloured hairs sparsely but evenly cover inside of ear; shoulder thickly furred with Cream Buff; fur of back extends a short distance onto wing membrane to a line drawn between upper third of humerus and femur, the long fur barely extends onto interfemoral but ends in a lightly haired straight line; ventrally wing membranes lightly haired. The ventral body Cream Buff, with fur extending to sides just behind ear; fur on ventral surface of neck region Colonial Buff; ventral surface of propatagium and plagiopatagium thinly covered with Cream Buff along edge of humerus and radius to radial-metacarpal joint and along edge of body and uropatagium, especially around anal region. Skin of plagiopatagium and propatagium Deep Colonial Buff proximally and Brownish Olive dorsally; skin of dactylopatagium Brownish Olive; skin of ear Black, skin of rhinarium, tragus, inside of ear close to entrance and side of face Brownish Olive.

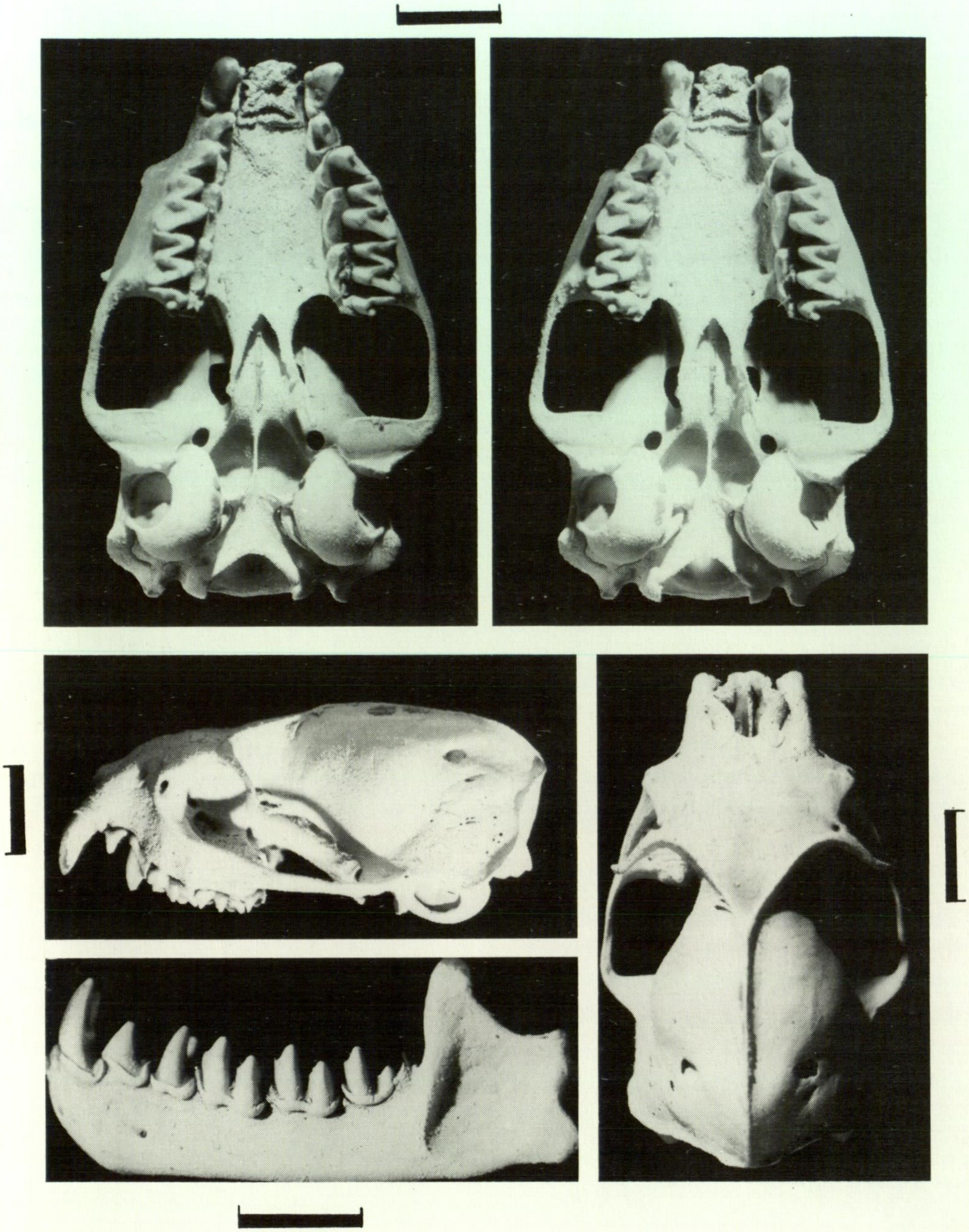

Figure 5 Skull and dentary of *Saccolaimus flaviventris* (CAM M602). Ventral view of skull is presented as stereopairs. Scale lines are 5.0 mm.

Glans Penis

Length 5.6 (5.1-6.5) (N = 6); dorsally of uniform width 2.1 (2.0-2.2); laterally reduced in size on distal one-third; thick short spines present, with thickness decreasing distally; thicker spines located on ventral side with thickest on mid-ventral line; urethral opening subcircular with a relatively short head mound from ventral distal edge (Figure 3b).

Baculum

Relatively long 1.3 (1.0-1.5) (N = 6); narrower distally, proximally club-shaped, inflated laterally (Figure 4).

Distribution

Hall and Richards (1979) and Richards (1983a) state that *S. flaviventris* is widespread over Australia except Tasmania, occurring both in the tropics and well to the south of the tropic of Capricorn (Parker 1973). Specimens examined confirm that in Victoria, *S. flaviventris* extends to the cool temperate climate (38°S) despite the emballonurids' preference for tropical and subtropical regions (Koopman 1984b; Hill and Smith 1984; Taylor 1984) (Figures 1 and 6e).

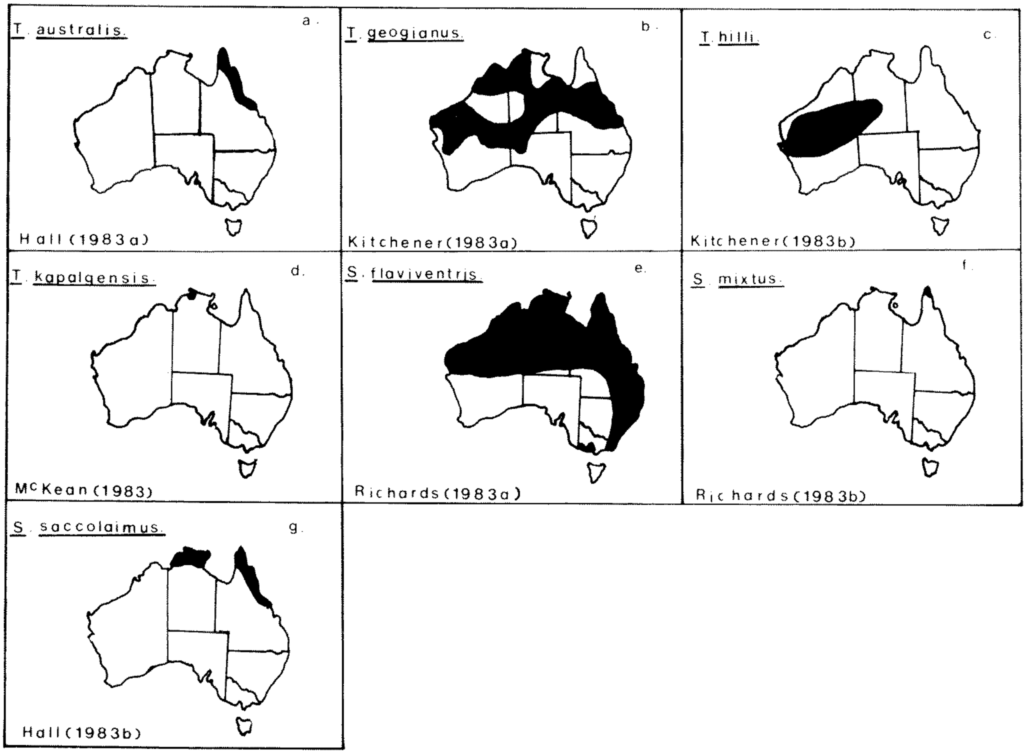

Figure 6 Geographic distribution of *Saccolaimus* and *Taphozous* species in Australia.

Natural History

Saccolaimus flaviventris is relatively rare in collections although it is reported from a wide range of habitats (Richards 1983a). It roosts in tree hollows. It tends to be solitary when roosting but does form small groups of two to six individuals in late winter and spring (Hall and Richards 1979).

It is insectivorous and predatory (Vestjens and Hall 1977), usually foraging above the canopy, but foraging height varies with cover. Its apparent rarity is probably due to its flying so high and fast that it is seldom collected (Richards 1983a).

Aitken (1975) and Richards (1983a) speculate that *S. flaviventris* may be migratory in southern Australia because there are reports of exhausted individuals of these species in open situations. A stepwise multiple regression analysis showed no significant correlations between subcutaneous and mesentric fat categories of individuals between seasons or from individuals from more southern localities (unpublished data).

Pregnancies are always restricted to the right uterine horn. A single young is born between December and mid-March. Subadults are only collected in January and February. There is no indication of an old corpus luteum in either the left or right ovary of the only pregnant female examined that was collected in February, suggesting that it did not breed a second time in one season. However, this requires confirmation. In males, there is no significant difference throughout the year in reproductive parameters, nor is there a significant correlation between male reproductive parameters and depth of the throat pouch (Chimimba and Kitchener 1987).

Specimens Examined

Listed in Appendix I.

***Saccolaimus saccolaimus* (Temminck, 1838)**

Figures 3c, 4b, 7; Table 1.

Taphozous saccolaimus Temminck, C.J. (1838). Over de geslachten *Taphozous, Emballonura, Urocryptus* en *Diclidurus*. Tijdschr. Natuur. Ges. Physiol. 5: 1-34 pl. 1.

Taphozous crassus Blyth, E. (1844). *Taphozous crassus*. J. Asiat. Soc. Bengal 13: 491.

Taphozous pulcher Elliott, D.G. (1844). *Taphozous pulcher*. J. Asiat. Soc. Bengal 13: 492.

Taphozous affinis Dobson, G.E. (1875). Description of a new species of *Taphozous* from Labuan. Ann. Mag. nat. Hist. 16(4): 232.

Taphozous nudicluniatus De Vis, C.W. (1905). Bats. Ann. Qld. Mus. 6: 36-40.

Taphozous granti Thomas, O. (1911). Two new Eastern Bats. Ann. Mag. nat. Hist. 8(8): 378-379.

Saccolaimus flavimaculatus Sody, H.J.V. (1931). Six new mammals from Sumatra, Java, Bali and Borneo. Natuurw. Tijdschr. Ned. — Ind. 91: 349-360.

Relevant taxonomic decisions

Dobson, G.E. (1876). Monograph of the Asiatic Chiroptera and a catalogue of the species of bats in the collection of the Indian Museum, Calcutta. *Trustees of the Indian Museum*. 228 pp; Tate, G.H.H. (1941). Notes on Oriental *Taphozous* and allies. *Am.*

Mus. Novit. 1141: 1-5; Troughton, E. le G. (1925). A revision of the genera *Taphozous* and *Saccolaimus* (Chiroptera) in Australia and New Guinea, including a new species, a note on two Malayan forms. *Rec. Aust. Mus.* 14: 313-341 pls 47-48; and Goodwin, R.E. (1979). The bats of Timor: systematics and ecology. *Bull. Am. Mus. nat. Hist. 163: 73-122.*

Lectotype

Rijksmuseum (NH), Leiden, RMNH 33630, male skin, skull not extracted, from Djawa (= Java), Indonesia, designated by Tate, G.H.H. (1941). Results of the Archbold Expeditions No. 37. Notes on Oriental *Taphozous* and allies. Am. Mus. Novit. 1141: 1-5.

Lectotype is *Taphozous saccolaimus* specimen 'a' of Jentink, F.A. (1888). Museum d'Histoire Naturelle des Pays-Bas. Tome XII. Catalogue systematique des mammiferes (rongeurs, insectivores, cheiroptères, édentés et marsupiax). Leiden: E.J. Brill, 280 pp.

Diagnosis (mean values)

Saccolaimus saccolaimus differs from *S. mixtus* by its larger overall size: mastoid width (14.2 v. 12.1), distance outside bullae (13.3 v. 12.7), canine width (2.2 v. 1.8), inter-upper canine distance (5.7 v. 4.6), upper maxillary tooth row crown length (11.2 v. 9.9), digit III phalanx I length (28.0 v. 23.5); sphenoid pit shorter (3.6 v. 4.0); radial-metacarpal pouch absent rather than present; tragus more circular and bulbous above, hind margin convex rather than concave; frontal depression of skull shallower rather than deeply excavated; posterior floor of mesopterygoid fossa smooth rather than deeply grooved; sagittal crest prominently reaching occiput rather than just reaching occiput; sphenoid pit deep rather than shallow, with a rather low median septum.

Saccolaimus saccolaimus differs from *S. flaviventris* as outlined in the earlier diagnoses of *S. flaviventris*.

Description (mean and range)

Skull and Dentary (Figure 7)

Skull larger: greatest skull length 24.4 (22.4-25.9); zygomatic width 16.5 (14.6-17.3), mastoid width 14.2 (13.4-15.1), distance outside bullae 12.7 (11.9-13.4), canine width 2.2 (1.9-2.4), inter-upper canine distance 6.4 (5.9-7.1), upper maxillary tooth row crown length 11.5 (10.0-12.4); frontal depression not so deeply excavated; posterior floor of mesoptergoid fossa smooth; sphenoid pits deep and divided by comparatively low median septum that is not as high as floor of mesopterygoid fossa; lower outline of mandible convex beneath premolars.

External Morphology

Large size: radius length 74.1 (69.2-78.6); radial-metacarpal pouch absent in both sexes; outer base of ear originating much closer to tragus than corner of mouth; gular pouch present in males, and well defined by an almost naked area encircled posteriorly by rudimentary pouch edges in females; tragus bulbous above and circular in upper outline.

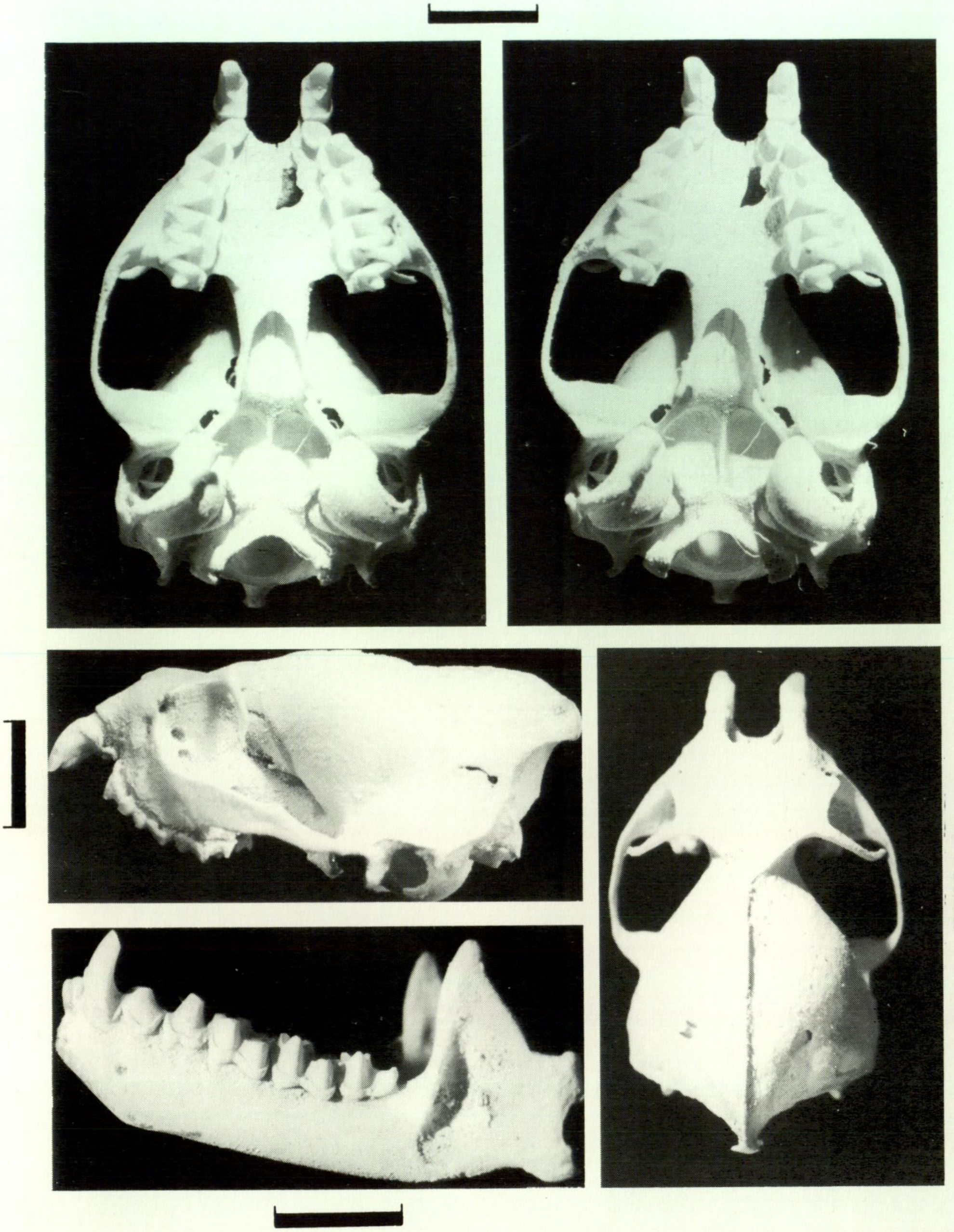

Figure 7 Skull and dentary of *Saccolaimus saccolaimus* (WAM M23324). Ventral view of skull is presented as stereopairs. Scale lines are 5.0 mm.

Pelage and Skin Colour

Dorsal pelage predominantly Clove Brown, scattered with white spots, mottled with irregular patches of white hairs at base. Similar pelage as above sparsely covers face in front of eyes, and as a vertical band of hair behind eyes and external basal third of ear conch; rest of ear naked; tragus and inside of ear evenly but sparsely haired; ventral body surface Bister, scattered with white hairs and fur extends onto wing in area between humerus and femur; posteriorly, ventral surface fur does not extend past femora but ends near tail base; shoulder and proximal third of humerus covered with light longish hairs to a line between upper half of humerus and femur; interfemoral membrane sparsely furred with Clove Brown hairs on dorsal surface, ventrally, fur shorter and thin; chin sparsely haired to level with outer ear base; antebrachial membrane sparsely furred; a post-radial band of Light Buff hairs present, forming a thickish patch in radial-metacarpal angle. Skin of uropatagium, plagiopatagium, propatagium and chin Olive Brown; skin of face, lips, tragus, ear and dactylopatagium Clove Brown.

Glans Penis

Length 4.2 (N = 1): club shaped, both dorsally and laterally, spines present; prominent midventral swelling, terminates into an elevated convoluted skin proximally; tip at urethral opening with approximately rectangular mound, visible from all sides (Figure 3c).

Baculum

Relatively long: 1.1 (N = 1), distally spatulate and proximally club shaped; laterally, rather sinusoidal-shaped (Figure 4b).

Distribution

From India to Sri Lanka through S.E. Asia to Sumatra, Borneo, Java and Timor; Papua New Guinea and Solomon Islands (Honacki *et al.* 1982; Koopman 1984b). In Australia, the species is restricted to northern and northeastern coastal areas from Townsville to Cooktown but is also found in the Alligator River region and Arnhem Land in the Northern Territory (Hall 1983b) (Figure 6g). McKean *et al.* (1980) speculate that *S. saccolaimus* might be expected to occur in tropical Western Australia.

Natural History

Saccolaimus saccolaimus is uncommon in collections. It is mainly insectivorous and predatory, roosts in hollow trees, closed forests, caves and a variety of man-made structures (Hall 1983b). In Australia, Compton and Johnson (1983) observed a colony of *S. saccolaimus* roosting in hollows in Poplar Gum near Townsville, Queensland, although they did not comment on the numbers or group structure. Although gregarious, the species does not form tight clusters (Hall 1983b).

Medway (1977) observed that the Asian *S. saccolaimus* in India have a single young. Females with unweaned juveniles and others in advanced pregnancy were observed in September. There is no study of reproduction of the Australian *S. saccolaimus*, apart from the limited observations by Hall (1983b) who observed that females bear one young and lactate during the tropical wet season. Additionally, Compton and Johnson (1983) noted that *S. saccolaimus* females collected in mid-December in Queensland had advanced pregnancies or attached young.

Specimens Examined

Listed in Appendix I.

Saccolaimus mixtus Troughton, 1925

Figure 8; Table 1

Saccolaimus mixtus Troughton, E. le G. (1925). A revision of the genera *Taphozous* and *Saccolaimus* (Chiroptera) in Australia and New Guinea, including a new species, and a note on two Malayan forms. Rec. Aust. Mus. 14: 313-341 pls 47-48.

Holotype

AM A3257 male, skin (wet), skull not extracted, from Port Moresby, Papua New Guinea.

Diagnosis (mean values)

Saccolaimus mixtus differs from *S. flaviventris* and *S. saccolaimus* in being smaller in addition to other characteristics as outlined in the diagnoses of *S. flaviventris* and *S. saccolaimus*.

Description (means and ranges)

Skull and Dentary (Figure 8).

Skull medium sized: greatest skull length 21.8 (21.7-21.9); mastoid width 12.1, distance outside bullae 11.3 (11.0-11.6), canine width 1.8 (1.7-1.8), inter-upper canine distance 4.6 (4.5-4.8), upper maxillary tooth row crown length 9.9 (9.8-10.0), sphenoid pit length 4.0; frontal depression of skull deep; interorbital region broad, with edges markedly concave; sagittal crest just reaches occiput; a deep groove present on posterior floor of mesopterygoid fossa; sphenoid pit rather shallow, with median septum barely reaching floor of mesopterygoid fossa; dentary lower outline beneath premolars broadly convex, or straight, convexity reaches its maximum beneath posterior premolar.

External Morphology

Medium size: radius length 63.6 (63.1-64.2); radial-metacarpal pouch present; gular sac present in males (females not examined); tragus slightly thickened, rounded, with sac lower inner margin concave, sloping gradually upwards to form obliquely rounded top.

Pelage and Skin Colour

Dorsal pelage Prout's Brown, darkest on head and shoulders, neck region speckled with Buff Brown; ventral surface unicoloured with light shade of greyish Buff Brown; dark brown thick tuft of hair from an area posterior to eye which continues in a sparser band to inside of ear; upper outer two-thirds of ear naked; face anterior to eye thinly furred; dorsally, fur does not extend far onto wing membrane, only to between upper quarter of femur and upper half of humerus; fur does not extend to interfemoral membrane beyond a line level with the anal opening, the rest of the membrane, however, sparsely furred; ventrally, light hairs cover wing membrane to a line along radius, terminating in a thick patch at radial-metacarpal joint; wing membrane and ear conch dark brown and lighter coloured between the digits: ear conch dark brown.

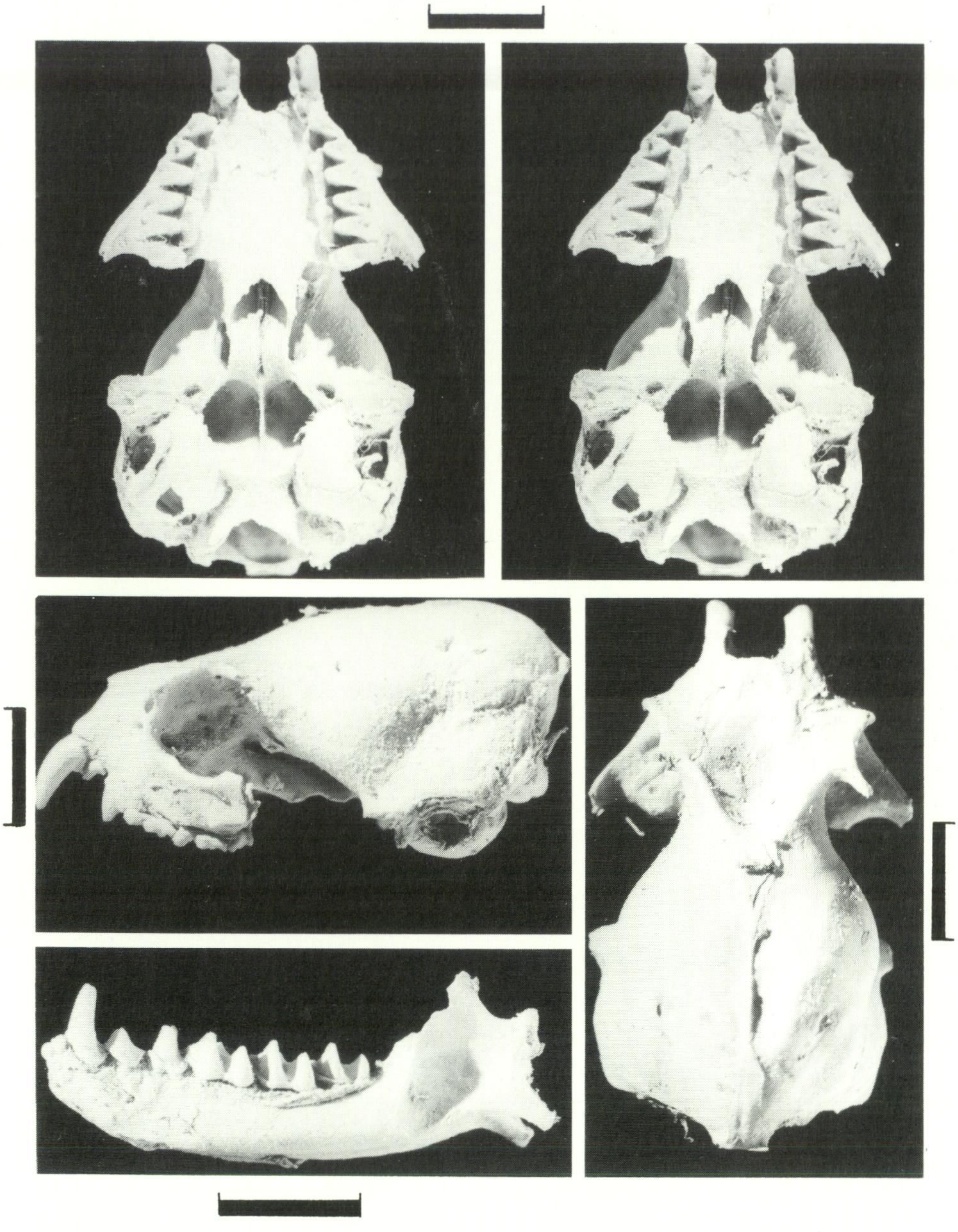

Figure 8 Skull and dentary of *Saccolaimus mixtus* (AM M3258, paratype). Ventral view of skull is presented as stereopairs. Scale lines are 5.0 mm.

Glans Penis

Not available for examination.

Baculum

Not available for examination.

Distribution

Saccolaimus mixtus is chiefly a south east Papua New Guinea species (Honacki *et al.* 1982; Koopman 1984b). In Queensland, three specimens have been collected from Brown's Creek, Pascoe River, in the northern part of Cape York Peninsula and another seven from Weipa (Figure 6f).

Natural History

Saccolaimus mixtus is rare in collections. In western Papua New Guinea it roosts in limestone caves (Richards 1983b). It is insectivorous and predatory, it forages above the canopy in tall open forests. No information is available on its reproduction.

Specimens Examined

Listed in Appendix I.

Taphozous Geoffroy, 1813

Taphozous Geoffroy (Saint-Hilaire), É. (1813). Description des mammifères qui se trouvent en Égypte, pp 99-144. In: *Description de l'Egypte, ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armee Francaise* (Ed. E.F. Jomard), Histoire Naturelle, Paris: L'Imprimerie Impériale Tom. 2 Deuxéme livr. (Vol. IX) (113-114, 126-128).

Type Species

Taphozous perforatus Geoffroy, 1813 by subsequent designation, see Miller, G.S. (1907). The families and genera of bats. Bull. U.S. Natl. Mus. 57: i-xvii, 1-282, pls 1-14.

Referred Australian species

Taphozous australis Gould, 1854
Taphozous georgianus Thomas, 1915
Taphozous troughtoni Tate, 1952
Taphozous kapalgensis McKean and Friend, 1979
Taphozous hilli Kitchener, 1980

Diagnosis (mean values)

The following diagnosis refers only to Australian emballonurids.

Differs from *Saccolaimus* in being considerably smaller in all measurements. Skull moderately rather than heavily ossified; sagittal crest either absent or weak rather than well developed, barely reaches occiput, often terminates with a rounded crest that prominently reaches occiput; anterior lacerate foramen and sphenorbital sinus separated by a thin rather than a wide band; premaxilla almost overlap rather than abut nasals; postorbital ridges weak rather than strong, joining sagittal crest at rather than near or well posterior to postorbital ridges; bulla incomplete rather than complete with greater rather than less than 50 percent of cochlear region exposed; frontal region relatively narrow rather than wide; lower outline of mandible markedly concave rather than convex beneath premolars; anterior premolar relatively small, almost one-fifth rather than one-third height and crown area of posterior premolar; sphenoid pit generally larger, with a flat base rather than small with a v-shaped base; posteroventral face of basisphenoid in contact with cochlea only, rather than with both cochlea and bulla; paraoccipital process shorter than rather than almost level or longer than occipital condyle; braincase relatively robust and narrower relative to greatest skull length; first upper molar parastylar area well developed rather than reduced; inner margin of ear papillate. Baculum and glans penis relatively smaller than in *Saccolaimus* (see diagnosis of *Saccolaimus* for comparative measurements).

Distribution

Distributed in the Ethiopian, Palaearctic, Indo-Malayan and Australian Regions (Koopman 1970, Tate 1941).

Taphozous australis Gould, 1854

Figures 3d, 4c, 9, Table 1

Taphozous australis Gould, J. (1854). The mammals of Australia. Pt. 6, London (1 unnumbered page of text, 14th pl of Pt. 6 (= Vol. 3 pl. 32)

Taphozous fumosus De Vis, C.W. (1905). Bats. Ann. Qld. Mus. 6: 36-40.

Relevant taxonomic decision

Troughton, E. le G. (1925). A revision of the genus *Taphozous* and *Saccolaimus* (Chiroptera) in Australia and New Guinea, including a new species, and a note on two Malayan forms. Rec. Aust. Mus. 14: 313-341 pls 47-48.

Syntypes

BMNH 55.11.7.10, skin and skull and BMNH 55.11.7.11, skin and skull, from maritime caves in sandstone cliffs, Albany Island, Queensland.

Diagnosis (mean values)

Differs from *T. georgianus* in having shorter sphenoid pit (3.8 v. 4.2) and digit III phalanx I length (19.8 v. 20.6); larger mastoid width (11.1 v. 10.8); wider distance outside bullae (10.6 v. 10.0); gular sac present in males and represented by a rudimentary edge in females rather than absent; intertemporal constriction wide rather than narrow; width of braincase at zygomatic arch (BW) wide rather than narrow, e.g. BW: greatest skull length ratio: 0.5 v. 0.49; cranium more inflated; sphenoid pit anteriorly broadly rounded rather than pear shaped, anterior edge terminating approximately 1 mm from the large vacuities outside nasal cavities rather than reaching forward to hind level of these vacuities; sagittal crest weak, not reaching occiput. Glans penis larger (3.1 v. 2.1), with more spines per unit area, head with two mounds one large and the other secondary, rather than a single complex mound; mid ventral ridge uniform, not terminating in an elevated skin. Baculum larger (0.4 v. 0.3), laterally expanded at mid length and sinusoidal in lateral profile rather than small and stump like.

Differs from *T. hilli* in having slightly larger skull, dentary, teeth and external characters: zygomatic width (13.1 v. 12.8), mastoid width (11.1 v. 10.4), distance outside bullae (10.6 v. 9.9), canine width (2.1 v. 1.7), inter-upper canine distance (4.0 v. 3.5), upper maxillary tooth row crown length (9.6 v. 8.6); sphenoid pit smaller (3.4 v. 4.1); frontal depression of skull more deeply excavated; anterior rim of mesopterygoid fossa v-shaped rather than rounded; basisphenoid pit rounded rather than angular; canines large rather than slender; inter-temporal constriction broader; sphenoid pit terminates anteriorly almost 1 mm from large vacuities outside nasal cavity rather than level with these vacuities. Glans penis long (3.1 v. 2.1), constricted proximally rather than a more uniform rod shape; head with two mounds rather than with a single one. Baculum narrower (0.1 v. 0.3), and sinusoidal in lateral profile, not expanded proximally.

Differs from *T. kapalgensis* in averaging slightly larger: zygomatic width (13.1 v. 12.9), distance outside bullae (10.6 v. 9.5), upper maxillary tooth row crown length (9.6 v. 9.3); sphenoid pit shorter (3.4 v. 3.8); intertemporal constriction broader; sphenoid pit broadly rounded anteriorly, edge terminating about 1 mm from vacuities rather than reaching forward to hind level of these vacuities; frontal depression more deeply excavated; zygomatic arch without anterior spike; lambdoidal and sagittal crests weak rather than well developed. Glans penis slightly shorter (3.1 v. 3.3), head with two mounds rather than a single sharply pointed mound. Baculum lateral and dorsal width slightly smaller (0.2 v. 0.3, 0.1 v. 0.2 respectively), dorsally expanded in lateral profile at distal one-third rather than approximate bullet shaped, not differentially ossified.

Differs from *T. troughtoni* in having smaller skull, dentary, teeth and external characters: zygomatic width (12.9 v. 14.8), mastoid width (11.1 v. 12.1), distance outside bullae (9.5 v 11.4), canine width (2.1 v. 2.3), inter-upper canine distance (4.0 v. 4.6), upper maxillary tooth row crown length (9.6 v. 10.9), sphenoid pit length (3.4 v. 4.5), digit III/phalanx I length (19.8 v. 23.5); males with gular pouch, females with rudimentary edge of pouch rather than absent; postorbital process much shorter; mesopterygoid fossa anterior rim less v-shaped rather than sharply v-shaped; sagittal and lambdoidal crests not sharply edged, weaker. Glans penis head with two mounds rather than one; proximal ventral skin at tip not elevated midventrally. Baculum longer (0.4 v. 0.3), dorsal profile swollen mid length rather than bullet shaped, lateral profile sinusoidal rather than bullet shaped.

Description (means and ranges)

Skull and Dentary (Figure 9)

Generally medium sized in most characters: greatest skull length 21.6 (21.4-22.0); zygomatic width 13.1 (12.9-13.3), mastoid width 11.1 (10.8-11.4), distance outside bullae 10.6 (10.5-10.7), canine width 2.1 (2.0-2.2), inter-upper canine distance 4.0 (3.9-4.1), upper maxillary tooth row crown length 9.6 (9.4-9.8), sphenoid pit length 3.4 (3.2-3.6), inter-temporal constriction broad; sphenoid pit short; frontal depression deeply excavated; interorbital region flattened; sphenoid pit deep, median septum rising as high as floor of mesopterygoid fossa; cranium moderately inflated; sphenoid pit rounded anteriorly, anterior edge terminating approximately 1 mm from large vacuities outside nasal cavities; sagittal crest weak, not reaching occiput.

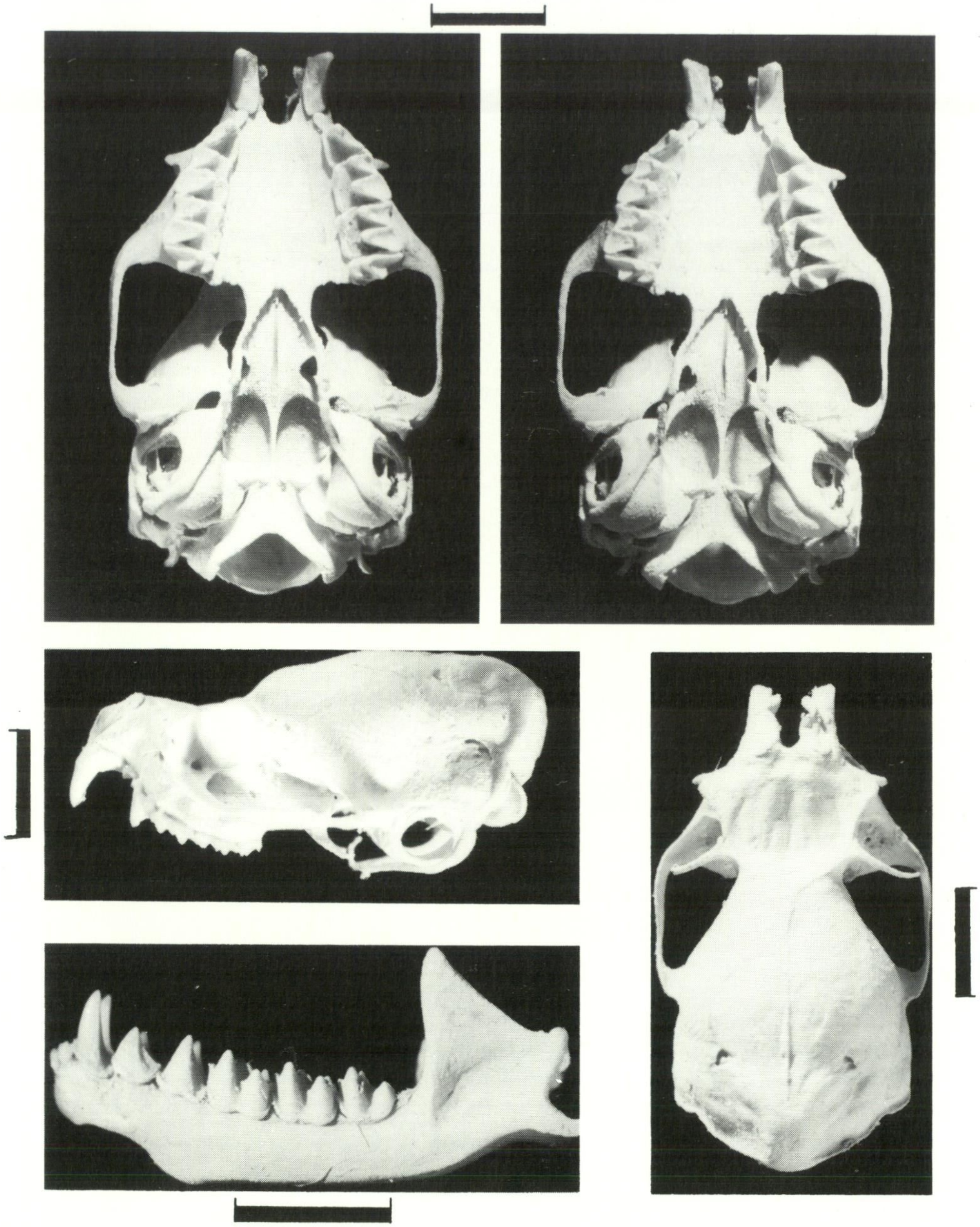

Figure 9 Skull and dentary of *Taphozous australis* (AM M4419). Ventral view of skull is presented as stereopairs. Scale lines are 5.0 mm.

External Morphology

Medium sized: radius length 65.4 (63.5-67.6); males with gular sac, represented by a rudimentary edge only in females; radial-metacarpal pouch present.

Pelage and Skin Colour

Dorsal pelage predominantly Bister with Pale Olive Buff guard hairs; ventral hairs Snuff Brown; sides of proximal half of abdomen heavily furred with Tawny Olive fur; forehead (except area of frontal depression) and chin sparsely haired with Buffy Brown; ear with inner margin speckled with Buffy Brown hair externally, fur extending to lower quarter of external base, remainder either naked or very faintly haired with Buffy Brown hair; sparse Avellaneous fur extends to wing membranes above and below to a line drawn between the proximal one-third of humerus and femur; interfemoral membrane furred dorsally with Tawny Olive to a line where tail perforates membrane, and ventrally not beyond anus and femora; plagiopatagium sparsely furred with Tawny Olive fur posteriorly, antebrachial membrane naked on both surfaces except area close to shoulders; skin of plagiopatagium, rhinarium, lips, face, tragus and ears Saccardo's Umber; basal half of chin almost bare; dactylopatagium Sepia.

Glans Penis

Length 3.1 (3.0-3.1) (N = 3); surface with high density of spines; spines of uniform size; head of glans penis with two mounds, one large, the other secondary (Figure 3d).

Baculum

Length 0.4 (0.3-0.5) (N = 3); dorsal profile swollen mid length; lateral profile sinusoidal (Figure 4c).

Distribution

Except for one old record from southeastern Papua New Guinea which Koopman (1984b) and Honacki *et al.* (1982) speculate is probably accidental or erroneous, the species is restricted to Australia and the Torres Strait Islands, N.E. coastal Queensland and Cape York Peninsula (Figure 6a).

Natural History

Taphozous australis is uncommon in collections. Roosting sites include caves, rock ledges and boulders. Individuals usually roost separately, but clusters of two to five bats may form in winter. The species is usually solitary or forms small social aggregations. It is insectivorous and predatory and leaves roosting sites just after dark to hunt for insects. Feeding is at the daytime roosting sites or at nearby feeding stations (Hall 1983a).

Knowledge on reproduction in *T. australis* is scanty although Hall (1983a) observed that groups of breeding females have been found in September and speculates that most births probably occur in October or November. In males, the testes are abdominal in September but scrotal in April.

There is a build up of body fat in autumn. However, it is not known whether this species undergoes hibernation. Hall (1983a) observed that individuals captured in mid August were inactive for about 10 minutes after being disturbed.

Specimens Examined

Listed in Appendix I.

Taphozous georgianus Thomas, 1915
Figures 3e, 4d, 10; Table 1

Taphozous australis georgianus Thomas, O. (1915). Scientific results from the mammal survey No. XI K. Notes on *Taphozous* and *Saccolaimus*. J. Bombay nat. Hist. Soc. 24: 57-63.

Holotype

BMNH 44.2.27.59 female skin (wet) and skull from King George Sound, Western Australia.

Relevant taxonomic decisions

Troughton, E. le G. (1925). A revision of the genus *Taphozous* and *Saccolaimus* (Chiroptera) in Australia and New Guinea, including a new species, and a note on two Malayan forms. *Rec. Aust. Mus.* 14: 313-341 pls 47-48; and McKean, J.L. and Price, W.J. (1967). Notes on some Chiroptera from Queensland, Australia. *Mammalia* 31: 101-119.

Diagnosis (Mean values)

Differs from *T. australis* as described in the diagnosis of *T. australis*.

Differs from *T. hilli* in that skull, dentary, teeth and external characters average slightly larger: zygomatic width (13.2 v. 12.8), mastoid width (10.8 v. 10.4), canine width (2.0 v. 1.7), inter-upper canine distance (4.1 v. 3.5), upper maxillary tooth row crown length (9.7 v. 8.6), digit III / phalanx I length (20.6 v. 19.6); gular sac absent in both sexes rather than present in males and represented by a rudimentary area in females; frontal depression deeply excavated rather than shallow; mesopterygoid groove anterior rim v-shaped rather than rounded; basiphenoid pit rounded rather than angular; canines larger and wider rather than slender and short. Glans penis longer (2.8 v. 2.1), head complex and larger rather than a simple mound, proximal end with ventral elevated convoluted edge rather than simple. Baculum smaller (0.3 v. 0.4), a tiny almost oval stump in dorsal profile rather than an irregular shape.

Differs from *T. troughtoni* by averaging smaller in most skull, dentary and external characters: zygomatic width (13.2 v. 14.8), mastoid width (10.8 v. 12.1), distance outside bullae (10.0 v. 11.4), canine width (2.0 v. 2.3), inter-upper canine distance (4.1 v. 4.6), upper maxillary tooth row crown length (9.7 v. 10.9), sphenoid pit length (4.2 v. 4.5), digit III / phalanx I length (20.6 v. 23.5); postorbital process short rather than extremely long; mesopterygoid fossa anterior rim not sharply v-shaped; sagittal and lambdoidal crests weaker rather than sharply edged; glans penis shorter (2.3 v. 3.0), head with mound complex rather than simple, midventral line wider rather than narrower. Baculum tiny, almost oval in dorsal profile rather than bullet shaped.

Differs from *T. kapalgensis* in having smaller mastoid width (10.8 v. 11.1), but larger: zygomatic width (13.2 v. 12.9); distance outside bullae (10.0 v. 9.5); upper maxillary tooth row crown length (9.7 v. 9.3), sphenoid pit length (4.2 v. 3.8), digit III / phalanx I length (20.6 v. 21.3); relatively wider interorbital and palatal regions; gular pouch absent in both males and females rather than present in males and represented by a rudimentary edge in females; frontal depression of skull deeply excavated rather than shallow; sphenoid pit edge more circular; upper canines short, more robust and slightly projecting outwards rather than not projecting outwards; inflection of concavity at anterior end of dentary sharp rather than slight; zygomatic spike absent rather than present. Glans penis shorter (2.8 v. 3.3), less inflated laterally; proximal end with elevated convoluted edge rather than without convolution; head with complex rather than simple, elevated and sharply pointed mound. Baculum smaller (0.3 v. 0.4), tiny almost oval stump in dorsal profile, uniformly ossified rather than bullet shaped in dorsal profile and differentially ossified.

Description (means and ranges)

Skull and Dentary (Figure 10)

Generally medium sized: greatest skull length 21.4 (20.0-23.1); zygomatic width 13.2 (12.1-14.4); mastoid width 10.8 (10.1-11.7); distance outside bullae 10.0 (9.2-11.0); canine width 2.0 (1.5-2.3); inter-upper canine distance 4.1 (3.4-4.5), upper maxillary tooth row crown length 9.7 (8.8-10.5), sphenoid pit length 4.2 (3.5-4.7); intertemporal constriction narrow; sphenoid pit pear-shaped, anterior ends narrowed, terminating level with posterior edge of large vacuities outside nasal cavities; sagittal crest weak but reaching occiput.

External Morphology

Medium sized: radius length 68.1 (61.1-73.4); gular sac absent in both sexes; tragus outer margin concave on upper half; radial-metacarpal pouch present.

Pelage and Skin Colour

Dorsum clearly bicoloured: anterior half (with a bare chin) Olive Brown speckled with Buff Brown guard hairs, posterior half Mummy Brown; ventral surface Brownish Olive speckled with Deep Neutral Gray — this pelage also covers anal region; uropatagium ventral surface sparsely haired with Drab along humerus, radius and to radial-metacarpal pouch; skin of plagiopatagium, ears, rhinarium, uropatagium, dactylopatagium and lips Sepia; skin of forehead bare, Sepia.

Glans Penis

Length 2.8 (2.7-2.9) (N = 6); head mound complex with numerous skin folds; midventral line elevated and terminating proximally into a convoluted elevated skin; spines present except at dorsal tip (Figure 3e).

Baculum

A small almost oval stump in dorsal profile 0.3 (0.2-0.35) (N = 6), with ventrolateral proximal protuberance (Figure 4d).

Distribution

Extensive distribution across northern Australia and extends some distance south of the Tropic of Capricorn in Western Australia. There are no published records of this species from near its alleged type locality in Western Australia (contrast Figures 1 and 6b).

Natural History

Taphozous georgianus is very common in tropical and subtropical regions of Australia. Roosting sites include caves, rock fissures and abandoned mines. Because it

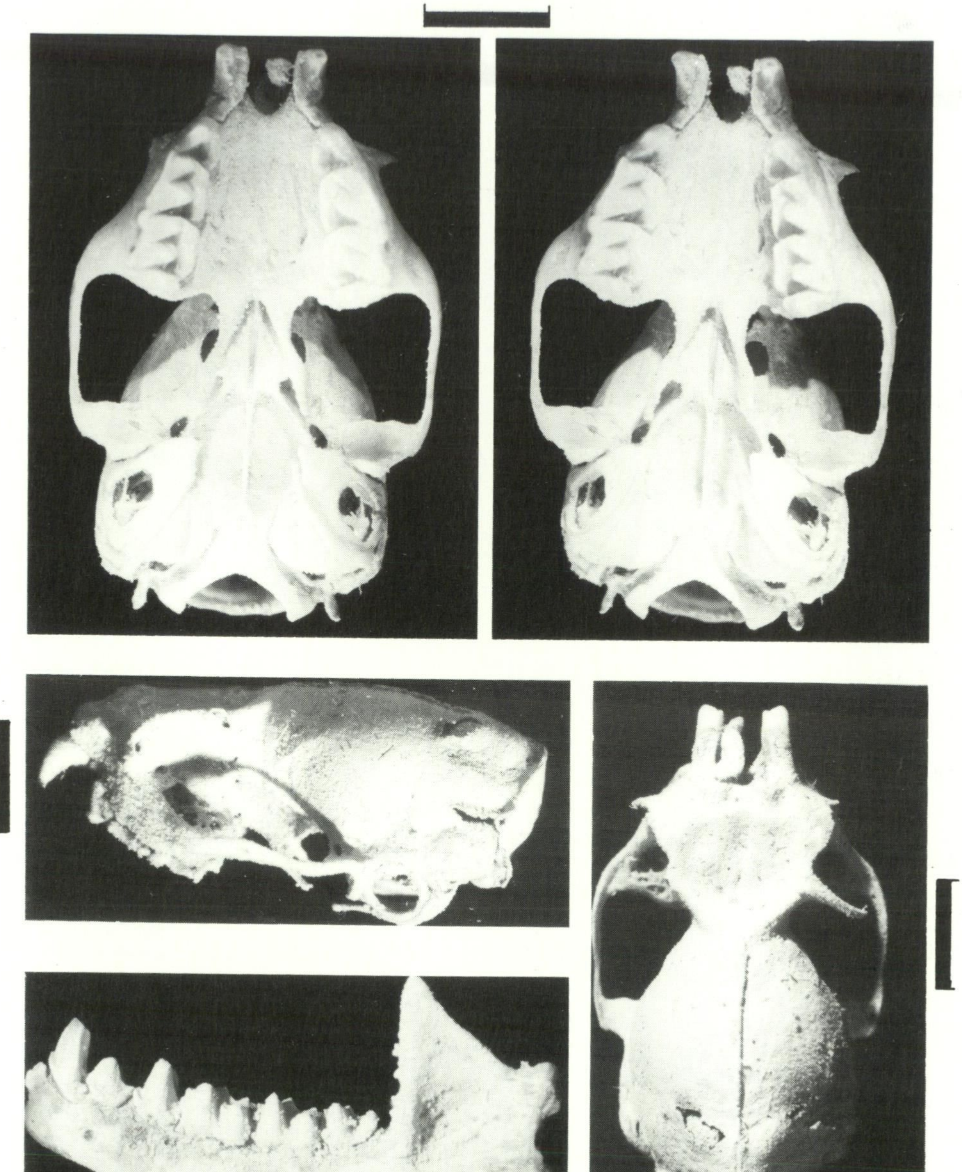

Figure 10 Skull and dentary of *Taphozous georgianus* (WAM M23032). Ventral view of skull is presented as stereopairs. Scale lines are 5.0 mm.

occupies man-made structures soon after they have been vacated its distribution may have expanded in recent times. Populations of this species appear to be locally mobile and they are known to vacate a cave for a considerable part of the year (Kitchener 1983a). Although up to 17 individuals have been collected from one cave the species is usually solitary or forms small aggregations (Kitchener 1983a). However, in two abandoned horizontal asbestos mines in the Hamersley Range and in a vertical mine at Cobra Station (both areas located in the Pilbara region of Western Australia) more than 50 individuals were observed by the senior author in a single mine. Also roosting in the same cave were individuals of *Eptesicus* (= *Pipistrellus*) *finlaysoni*, (see Hill and Harrison, 1987; Volleth and Tidemann 1989). The greatest numbers were found at the end or in the darker portions of the cave. The bats were mainly located roosting in the roof in a horizontal mine or in cracks in a vertical mine. Roosting individuals had a characteristic crab-like posture.

It is insectivorous with an apparent preference for Coleoptera. The bat is frequently seen foraging at intermediate heights above a wide variety of vegetation types and over pools and creeks (Kitchener 1983a).

Kitchener (1973) found that females give birth to young between October and February with only the right ovary functional and foetus only occur in the right uterine horn. In males spermatogenesis proceeds throughout the year but the position of the testes varies seasonally, being scrotal in summer and more abdominal in autumn, winter and spring. Although Kitchener (1973, 1976) concluded that *T. georgianus* is monoestrous, there is the possibility that it may give birth to young a second time during this long breeding season. This fact may not be detected in museum specimens if corpora lutea persists for only a short period following parturition (Chimimba and Kitchener 1987). More importantly, the study by Kitchener (1973) included specimens of *T. hilli* (described subsequently) and will need to be re-examined.

Specimens Examined

Listed in Appendix I.

Taphozous troughtoni Tate, 1952

Figures 3f, 4e, 11; Table 1.

Taphozous troughtoni Tate, G.H.H. (1952). Results of the Archbold Expedition. No. 66. Mammals of Cape York Peninsula, with notes on the occurrence of rain forest in Queensland. Bull. Am. Mus. nat. Hist. 98: 563-616.

Holotype

AMNH 162708 female, skin and skull, from Rifle Creek, 10 miles East of Mt Isa, N.W. Queensland.

Diagnosis (mean values)

Differs from *T. australis* and *T. georgianus* as described in the diagnoses of the two species.

Differs from *T. hilli* in that skull, teeth, dentary and external characters average larger: zygomatic width (14.8 v. 12.8), mastoid width (12.1 v. 10.4), distance outside bullae (11.4 v. 9.9), canine width (2.3 v. 1.7), inter-upper canine distance (4.6 v. 3.5), upper maxillary tooth row crown length (10.9 v. 8.6), sphenoid pit length (4.5 v. 4.1), digit III phalanx I length (23.5 v. 19.6); gular sac absent in both sexes rather than present in males and rudimentary in females; more steeply excavated frontal depression; mesopterygoid fossa posterior rim sharply v-shaped rather than rounded; postorbital processes relatively long rather than shorter; lambdoidal crest much more sharply edged, flattening at its apex to a more rounded crest. Glans penis larger (3.0 v. 2.1), head with mound elevated and pointed rather than simple; swollen midventrally with a proximal skin elevated and convoluted rather than a more uniform proximal outline. Baculum smaller (0.3 v. 0.4), bullet shaped rather than with more irregular outline.

Differs from *T. kapalgensis* generally by its larger size: zygomatic width (14.8 v. 12.9), mastoid width (12.1 v. 11.1), distance outside bullae (11.4 v. 9.5), canine width (2.3 v. 2.0), inter-upper canine distance (4.6 v. 4.2), upper maxillary tooth row crown length (10.9 v. 9.3), sphenoid pit length (4.5 v. 3.8), digit III phalanx I length (23.5 v. 21.3); both sexes without a gular sac rather than present in males and rudimentary in females; postorbital processes extremely long rather than short; mesopterygoid fossa anterior rim more sharply v-shaped; sagittal and lambdoidal crest sharply edged rather than weak; zygomata without spike. Glans penis shorter (3.0 v. 3.3), spines slightly larger rather than minute and almost reduced to wart-like structures; head mound large with a small secondary mound rather than a single small, pointed mound; midventrally elevated, with a proximal elevated convoluted skin rather than elevated distally only. Baculum smaller (0.3 v. 0.4), uniformly rather than differentially ossified, bullet shaped rather than irregular outline with marked dorsoventral constriction.

Description (means and ranges)

Skull and Dentary (Figure 11)

Large *Taphozous*: greatest skull length 24.1 (24.0-24.3); zygomatic width 14.8 (14.7-14.9), mastoid width 12.1 (11.9-12.2), distance outside bullae 11.4 (11.2-11.5), canine width 2.3 (2.2-2.3), inter-upper canine distance 4.6 (4.5-4.8), upper maxillary tooth row crown length 10.9 (10.8-11.0), sphenoid pit length 4.5 (4.2-4.8); extremely long postorbital processes; sagittal and lambdoidal crests sharply edged; mesopterygoid fossa anterior rim sharply v-shaped.

External Morphology

Large: radius length 74.6 (72.7-75.6); gular sac absent in both males and females; radial-metacarpal pouch present.

Pelage and Skin Colour

Predominant pelage colour on dorsal surface Olive Brown, guard hairs, however, Pale Mouse Gray; ventral surface hairs Olive Brown from chin to shoulders, posteriorly, Saccardo's Umber with guard hairs Pale Mouse Gray; uropatagium, close to abdomen from shoulder to femur and including anal region heavily furred with Saccardo's Umber; lower surface of plagiopatagium along radius and humerus to radial-metacarpal pouch sparsely furred with Mouse Gray; skin of rhinarium, plagiopatagium, uropatagium, lips, face, tragus and dactylopatagium Fuscous; area of frontal depression not furred, Fuscous.

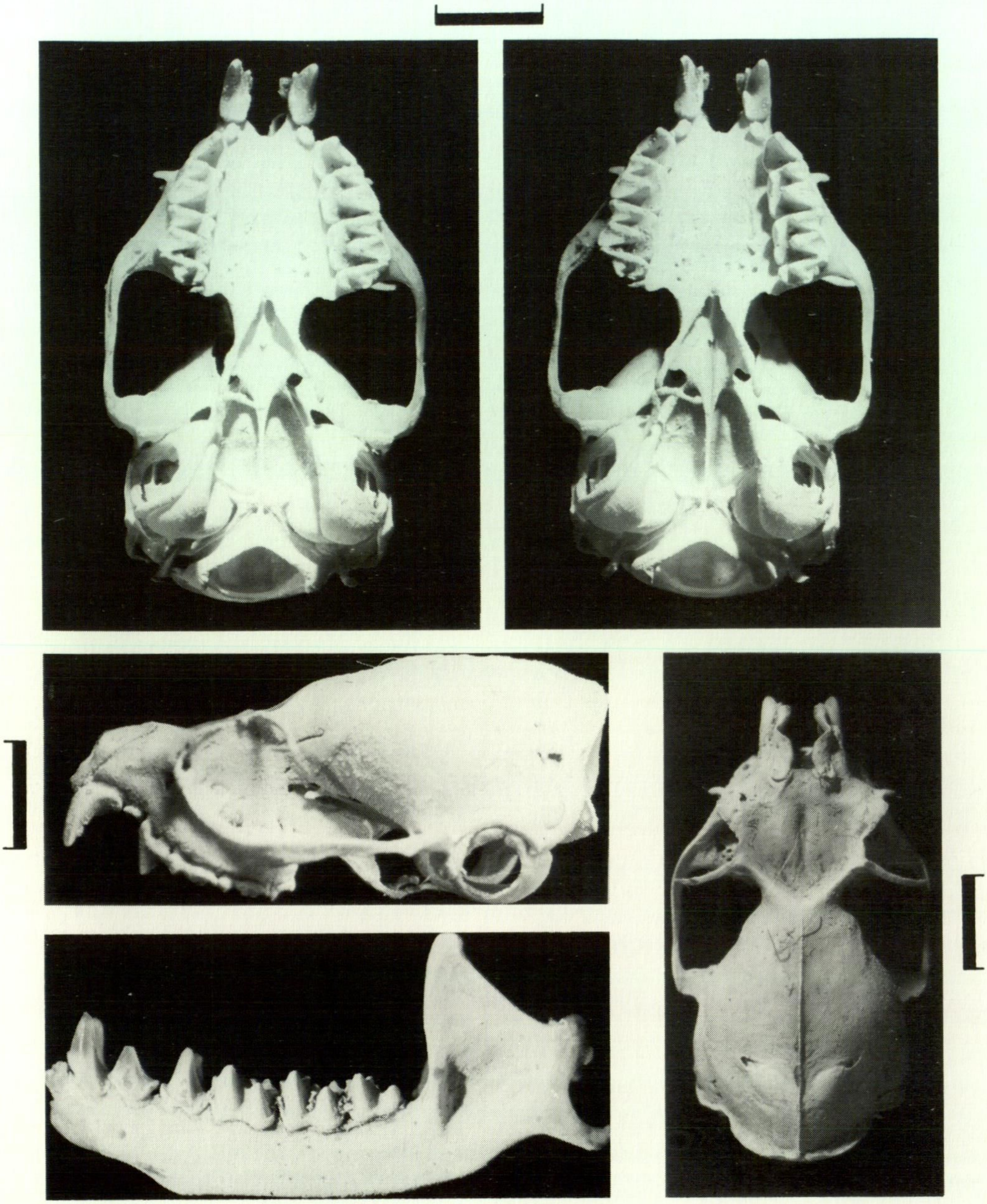

Figure 11 Skull and dentary of *Taphozous troughtoni* (CM M13213). Ventral view of skull is presented as stereopairs. Scale lines are 5.0 mm.

Glans Penis

Length 3.0 (N = 1), head with two mounds, one large, the other secondary, mid-ventrally elevated, terminating proximally with an elevated convoluted skin (Figure 3f).

Baculum

Length 0.3 (N = 1), simple, bullet shape (Figure 4e).

Distribution

Taphozous troughtoni has only been recorded from the Mt Isa area, N.W. Queensland.

Natural History

The species is very rare in collections and nothing is recorded of its natural history.

Taphozous hilli Kitchener, 1980

Figures 3g, 4f, 12, Table 1

Taphozous hilli Kitchener, D.J. (1980). *Taphozous hilli* sp. nov. (Chiroptera: Emballonuridae), a new Sheath-tailed bat from Western Australia and Northern Territory. Rec. West. Aust. Mus. 8: 161-169.

Holotype

WAM M 18260, adult female skin (wet) and skull extracted from Marandoo Mine site, 4.8 km 180° from Mt Bruce (22°30'03"S, 118°08'30"E), Hamersley Range National Park (No. A 30082), Western Australia.

Diagnosis (mean values)

Differs from *T. australis*, *T. georgianus* and *T. troughtoni* as described in the earlier diagnoses of these species.

Differs from *T. kapalgensis* in having slightly smaller skull, tooth, dentary and external characters: mastoid width (10.4 v. 11.1), canine width (1.7 v. 2.0), inter-upper canine distance (3.5 v. 4.2), upper maxillary tooth row crown length (8.6 v. 9.3), digit III/phalanx I length (19.6 v. 21.3); distance outside bullae and sphenoid pit length longer (9.9 v. 9.5, 4.1 v. 3.8 respectively); palatal and interorbital regions wider; zygomatic arch more slender, constricted posteriorly rather than with spike. Glans penis smaller (2.1 v. 3.3), uniform rod shape rather than expanded distally with ventral keel, ventrally, head mound not elevated and pointed, spines larger not reduced to wart-like structures. Baculum dorsally more irregularly shaped, less inflected dorsoventrally, evenly ossified.

Description (means and ranges)

Skull and Dentary (Figure 12)

Skull small: greatest skull length 20.0 (19.1-21.1); zygomatic width 12.8 (12.3-13.4), mastoid width 10.4 (9.9-11.0), distance outside bullae 9.9 (9.5-10.3), canine width 1.7 (1.5-1.8), inter-upper canine distance 3.5 (3.1-4.5), upper maxillary tooth row crown length 8.6 (7.6-9.8), sphenoid pit length 4.1 (3.7-4.4); frontal depression less steeply excavated, shallower; mastoid region less inflated laterally resulting in a more robust cranium; sagittal crest low or absent; lambdoidal crest poorly developed at apex resulting in a more rounded crest; postorbital width broad; rostrum narrow anteriorly; mesopterygoid groove present, posteriorly constricted; mesopterygoid fossa anterior rim round; sphenoid pit angular, long; inner anterior rim of orbit flattened; zygomatic arch

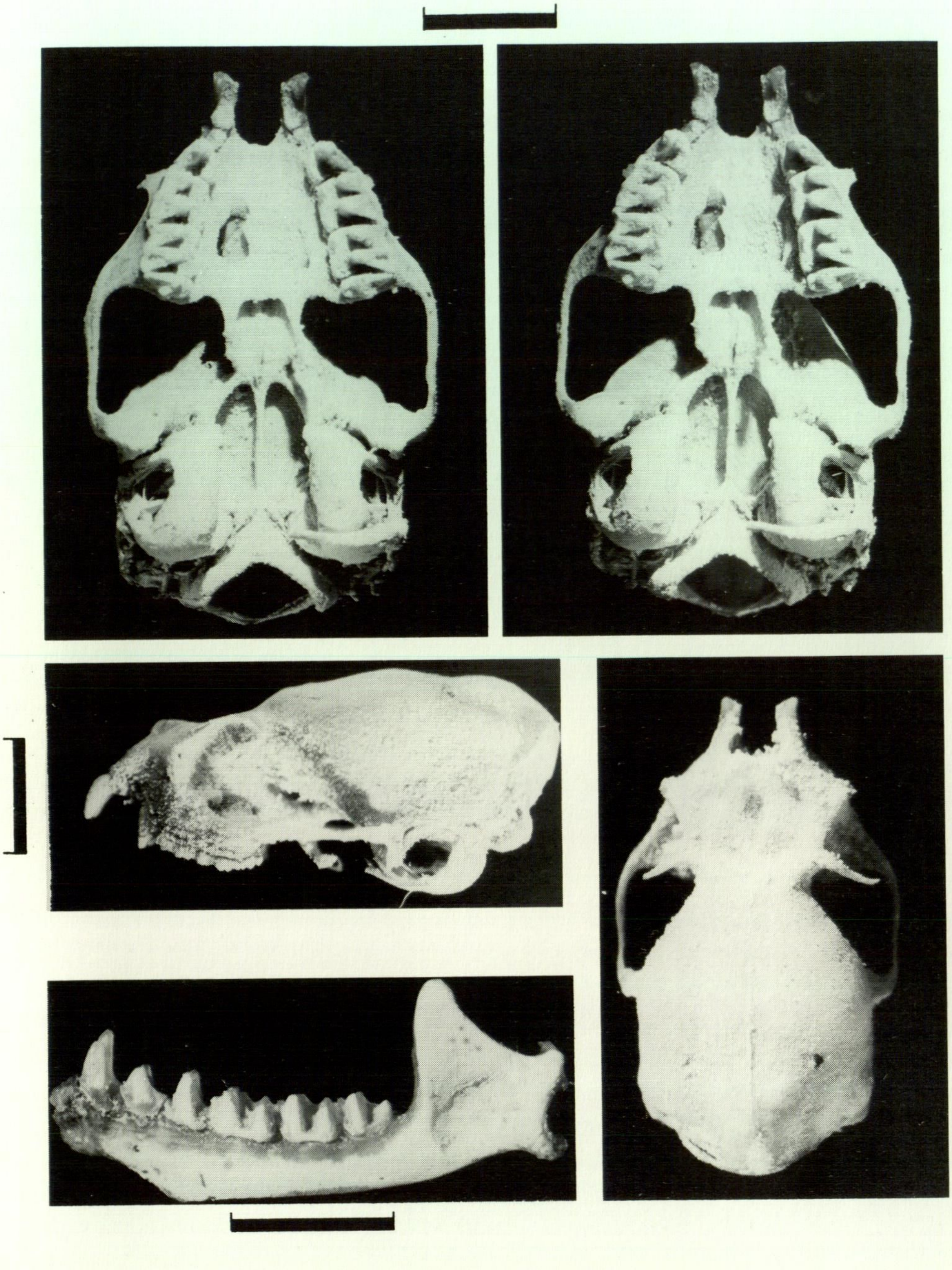

Figure 12 Skull and dentary of *Taphozous hilli* (WAM M18260, holotype). Ventral view of skull is presented as stereopairs. Scale lines are 5.0 mm.

slender, constricted posteriorly; canines short, slender, small anterobasal cusp about a third length of the tooth; anterior upper premolar weak; posterior premolar with small anterobasal cusp and reduced cingulum.

External Morphology

Small size: radius length 67.7 (60.4-71.7); gular pouch present in males and represented by a rudimentary edge in females; radial-metacarpal pouch present.

Pelage and Skin Colour

Dorsal pelage on head to sternal region Mummy Brown, rump Bister these colours from tips of hairs, basal two-thirds of which Buckthorn Brown; Raw Umber hairs cover area where tail passes dorsally through sheath; ventral pelage from head to chest Sepia tipped with Olive Brown, posteriorly Snuff Brown tipped with Saccardo's Umber; uropatagium furred lightly in anal region only; propatagium sparsely covered with Clay colour hairs; plagiopatagium lightly furred with Deep Olive hairs along edges of upper arm and forearm; patch of dense Buffy Brown hairs at entrance of radial-metacarpal pouch; few Buffy Brown hairs cover ventral side of radial-metacarpal pouch; skin of plagiopatagium, lips, face, tragus and ears Olive Brown; skin of dactylopatagium Olive Brown, skin of rhinarium Bister; the first third of chin bare but posterior two-thirds sparsely covered with Olive Brown hairs; fur on forehead not as dense as rest of dorsum, dominant pelage Isabella from guard hairs.

Glans Penis

Length 2.1 (2.0-2.2) (N = 6), rod shaped, surface with minute spines pointing proximally; head of glans penis with small mound visible laterally and ventrally but barely visible dorsally (Figure 3g).

Baculum

Small 0.4 (0.3-0.5) (N = 6), shape irregular, laterally flat at the proximal end, ventral and dorsal surfaces slightly concave (Figure 4f).

Distribution

Widely distributed in the semi-arid Pilbara, Murchison regions and Gibson Deserts of Western Australia as far east as Tennant Creek in the Northern Territory (Figure 6c).

Natural History

This insectivorous bat is probably common. Extensive mining operations in Western Australia have probably led to the extension of its range and may continue to do so since this species appears to utilise adits and mines soon after they have been abandoned by man. *Taphozous hilli* and *T. georgianus* have been observed roosting together. As the two species are of almost similar size, it would be interesting to know how they partition available resources. Differences in the masticatory apparatus (see morphometric analyses results) suggest that they may eat different prey. Although it remains to be demonstrated that the neck-gland plays a role in social behaviour (Kitchener 1983b), the depth of the pouch surrounding the neck gland in males of *T. hilli* is correlated with seasonal enlargement of the seminiferous tubules and accessory male glands (Kitchener 1976). A single young is born between early summer and mid-autumn. After parturition, the female reproductive organs become relatively quiescent until early winter. Males appear to be in active reproductive conditions throughout the year.

Specimens Examined

Listed in Appendix I.

Taphozous kapalgensis McKean and Friend, 1979

Figures 3h, 4g, 13; Table 1

Taphozous kapalgensis McKean, J.L. and Friend, G.R. (1979). *Taphozous kapalgensis*, a new species of Sheath-tailed bat from Northern Territory, Australia. Vict. Nat. 96: 239-241.

Holotype

CM 4800, male, skin and skull, from 'Kapalga', at the edge of a western flood plain of the South Aligator River near Rookery Point (12°32'S, 132°23'E), Northern Territory.

Diagnosis (mean values)

Taphozous kapalgensis differs from *T. australis, T. georgianus, T. troughtoni* and *T. hilli* as described in the earlier diagnoses of these species.

Description (means and ranges)

Skull and Dentary (Figure 13)

Medium size: greatest skull length 20.3 (20.0-20.7); zygomatic width 12.9 (12.6-13.1), mastoid width 11.1 (11.0-11.2), distance outside bullae 9.5 (9.1-9.9), canine width 2.0 (2.0-2.1), inter-upper canine distance 4.2 (4.0-4.4), upper maxillary tooth row crown length 9.3 (9.2-9.4), sphenoid pit length 3.8 (3.7-3.9); palatal and interorbital regions relatively narrow; sphenoid pit circular in outline; upper canines long, slender, not projecting outwards; inflection at anterior end of dentary only slight and not sharp or abrupt as in the other *Taphozous* species; zygomata constricted posteriorly, anterior spike present.

External Morphology

Medium size: radius length 59.3 (58.9-59.7); gular sac developed in males and represented by a rudamentary edge in females; radial-metacarpal pouch present.

Pelage and Skin Colour

Dorsal pelage predominantly Isabella Brown tipped on forehead with Buffy Brown; pelage fine, rather long on hind neck; chin hairs Isabella; rest of the ventral surface Buckthorn Brown, although guard hairs Light Ochraceous-Buff, lateral edges of posterior two-thirds of ventral region Light Ochraceous-Buff; along radius and towards radial-metacarpal pouch plagiopatagium sparsely haired with Light Ochraceous, close to pouch Light Ochraceous to Salmon; skin of plagiopatagium and uropatagium Dresden Brown, dactylopatagium Buckthorn Brown; uropatagium sparsely furred with Dresden Brown on anal region only; upper surface of uropatagium with sparse Isabella Brown fur along edges of body and over interfemoral membrane to point where tail protrudes; a band of Dresden Brown hairs extends over ventral surface of patagium between humerus and femur; ventral surface of patagium furred with Dresden Brown along outer edge of radius; tragus and ears Isabella; rhinarium Tawny-Olive.

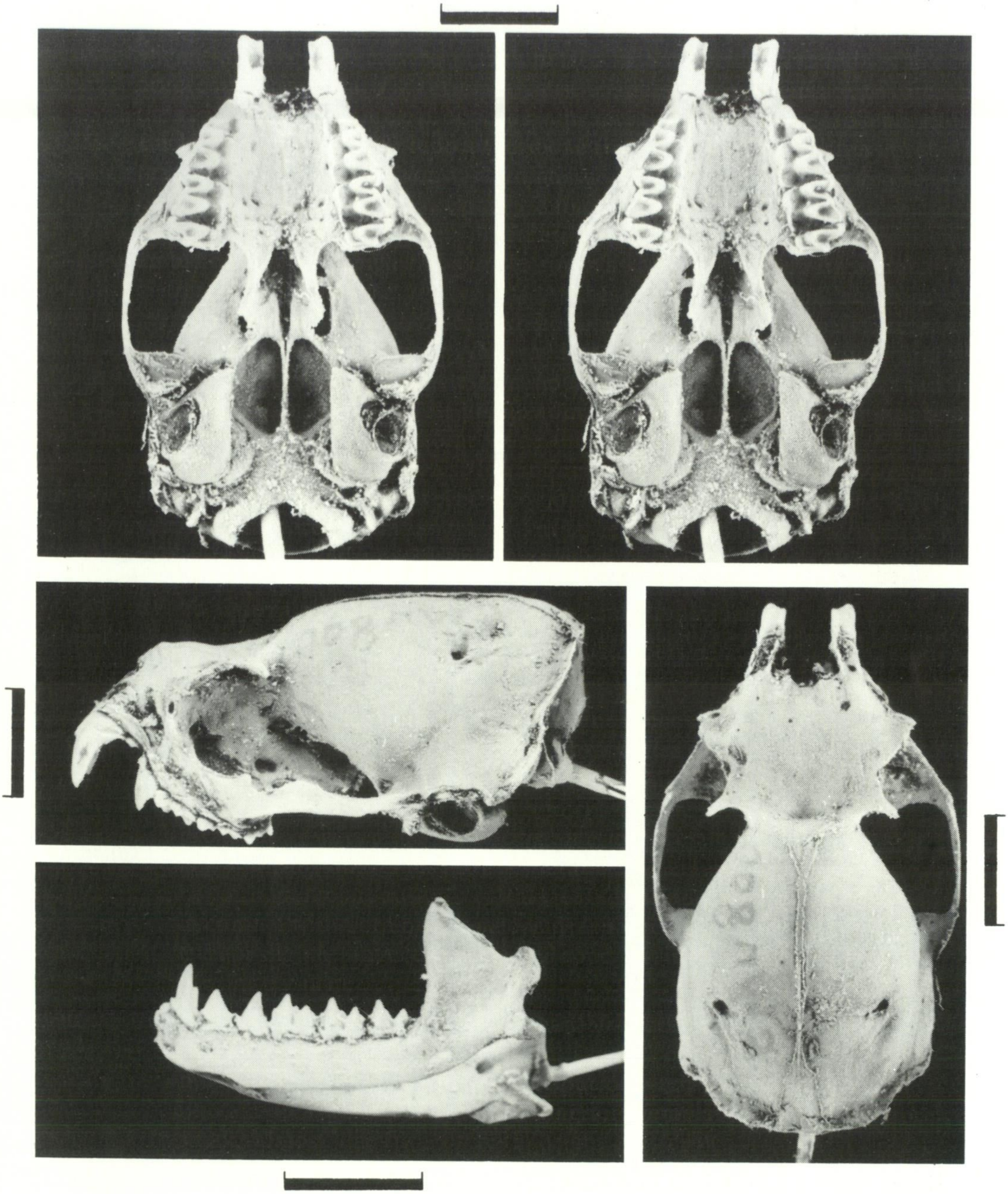

Figure 13 Skull and dentary of *Taphozous kapalgensis* (CM M4800, holotype). Ventral view of skull is presented as stereopairs. Scale lines are 5.0 mm.

Glans Penis

Length 3.3 (N = 1), head swollen, terminating in mound, with ventral keel, spines minute, almost reduced to wart-like structures (Figure 3h).

Baculum

Length 0.4 (N = 1), irregular outline, particularly in lateral profile, constricted at about distal third of length, differentially ossified (Figure 4g).

Distribution

Known only from northern Arnhem Land, Northern Territory (McKean 1983). McKean (1983) however, speculates that it may occur at the top end of the Northern Territory as there have been reports from the local residents of a similar bat in the Rose and Roper Rivers regions (Figure 6d).

Natural History

Rare. Its habitat includes open woodland and closed forest. It roosts in trees. It is insectivorous and has been observed to feed above tree canopy but comes lower when feeding over water (McKean 1983). Nothing else is known of its biology.

Taxonomic Remarks

Comparisons of the baculum and glans penis of *T. kapalgensis* with that of *T. longimanus* (Figures 3h, 3i and 4g and 4h respectively) show some basic differences. While the shape of the glans penis are generally similar the spines are low wart-like structures in *T. kapalgensis* whereas in *T. longimanus*, they are slightly larger. The head mounds are pointed in both species but are more sharply pointed in *T. longimanus*. The midventral keel in *T. kapalgensis* is confined to the distal end, it occupies the entire length of the glans penis in *T. longimanus*. The baculum is of similar length in both species but in *T. longimanus* it is more simple in outline, uniformly ossified and distally constricted; the baculum of *T. kapalgensis* is irregularly shaped and differentially ossified. These basic differences combined with the observed separation using both principal component analysis and canonical variate analyses (see subsequent section) on skull, dentary and external characters support the view that *T. kapalgensis* and *T. longimanus* are not conspecific.

Specimens Examined

Listed in Appendix I.

Morphometric Analyses: Results

Sexual dimorphism

A one-way analysis of variance within *T. georgianus*, *T. hilli* and *S. flaviventris* revealed no sexual dimorphism over all 39 characters examined. Overall, character F-ratios ranged from 0.01 to 1.36 in *T. georgianus*, 0.09 to 2.32 in *T. hilli* and 0.01 to 3.41 in *S. flaviventris*. This finding justified the pooling of males and females in the subsequent analyses.

Principal Components Analyses

Similar results were obtained when PCA's were performed using the following groupings of data: skull characters only; skull, wing and tibia length (TIB); and skull plus all external characters combined. The latter analyses, however, resulted in loss of many cases. Consequently, results presented are based on skull characters alone.

Only two factor axes from PCA's of all groupings of data had eigenvalues greater than 1. The two factor axes based on skull characters explained 87.7% of the variation. The first axis accounts for 81.9% of the variance with an eigenvalue of 20.5. The patterns of these two factor axes are shown in Figure 14. The currently recognised genera in Australia, *Taphozous* and *Saccolaimus* are not clearly separated in factor space. The results indicate that the two genera cannot be discriminated on a single axis, but they do not show any overlap. Discrete clusters are readily distinguishable for the currently recognised species in Australia: *T. hilli, T. kapalgensis* and *S. mixtus*. *Taphozous*

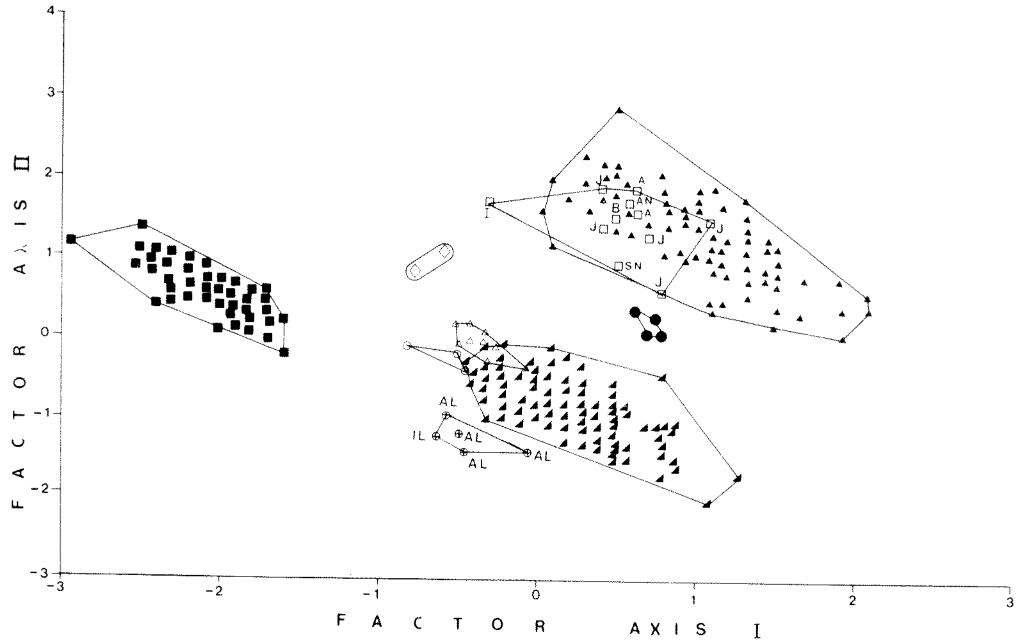

Figure 14 Scores of the first two factor axes of Australian and some Asian emballonurids examined. Data are size-free skull characters, excluding postpalatal width (PPW), with males and females combined. Species symbols are as follows: *Saccolaimus flaviventris* (▲), *S. mixtus* (◇), *S. saccolaimus* (□), *Taphozous australis* (△), *T. georgianus* (◢), *T. hilli* (■), *T. kapalgensis* (○), *T. longimanus* (●) and *T. troughtoni* (●). The locality codes for *S. saccolaimus* individuals are as follows: A = *S. saccolaimus* from Australia, AN = *S. 'nudicluniatus'* from Australia, SN = *S. 'nudicluniatus'* from the Solomon Islands, B = *S. saccolaimus* from Borneo, I = *S. saccolaimus* from India, J = *S. saccolaimus* from Java. The locality codes for *T. longimanus* individuals are as follows: AL = *T. longimanus* from Bali, IL = *T. longimanus* from India. Most points for *S. flaviventris, T. georgianus* and *T. hilli* represent multiple specimens.

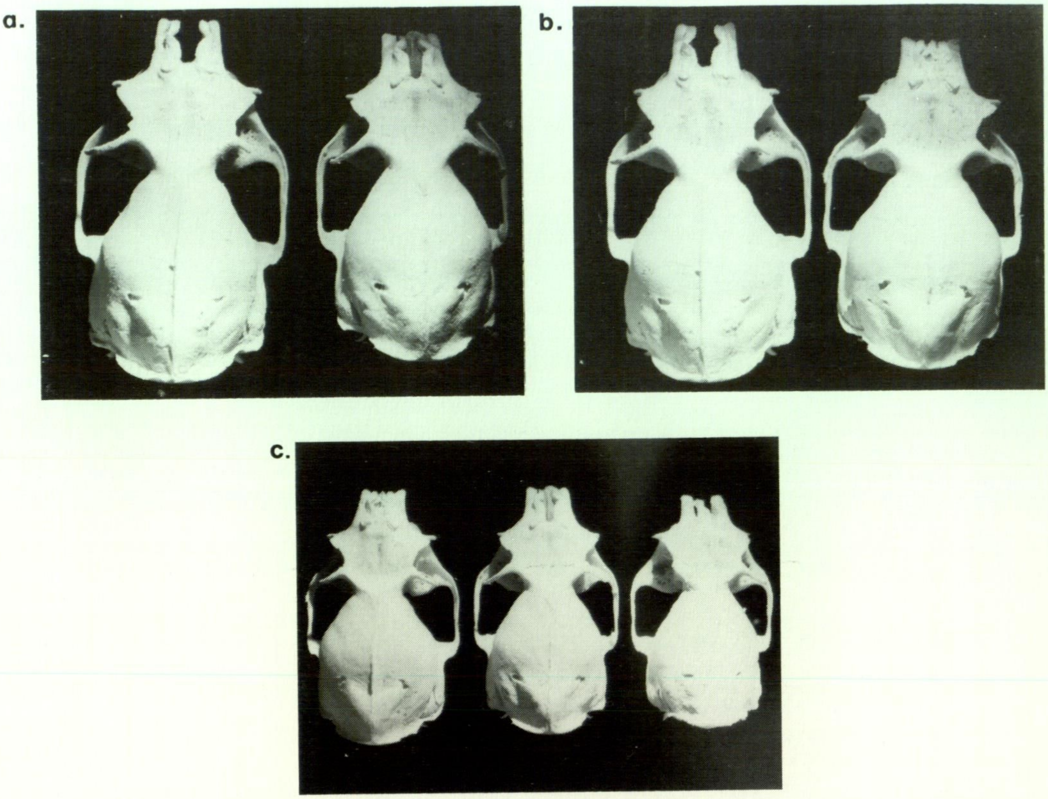

Figure 15 Dorsal view of specimens of *Taphozous georgianus* and *T. troughtoni* collected in sympatry and allopatry to illustrate the differences in dimensions of the two taxa.

(a) Sympatric specimens of *T. troughtoni* (CM M13213) (left) and *T. georgianus* (CM M13216 (right).

(b) Specimens of *T. troughtoni* (CM M13213) from Mount Isa, Queensland (left) and *T. georgianus* from Rockhampton, Queensland (JM M9976) (right).

(c) Specimens of *T. georgianus* from Rockhampton (JM M9976) Queensland, Locality 156 (left), Mount Isa (CM M13213), Queensland, locality 140 (centre) and Derby (WAM M23032) Western Australia, locality 58 in Figure 1 (right).

australis overlaps with *T. georgianus* by five individuals. Similarly, with the exception of the single specimen from India (I), all other individuals of *S. saccolaimus* lie within the *S. flaviventris* cluster. There are no association trends between individuals of *S. saccolaimus* from India (I), Java (J), Borneo (B) and Australia (A); neither are there any trends between individuals designated *S. nudicluniatus* from Australia (AN) or the Solomon Islands (SN) and individuals of *S. saccolaimus* regardless of their collecting locality. All individuals plot randomly in factor space with respect to geographic origin so that phenotypic separation is not evident between the Australian and the Asian *S.*

saccolaimus or between *S. saccolaimus* and *S. nudicluniatus*. Individuals of *T. longimanus* included in the analysis to ascertain the status of *T. kapalgensis* show the two species as distinct on the second factor axis. Within *T. longimanus* there are no trends between Indian (IL) and Balinese (AL) *T. longimanus* to suggest a high variability of the species over its range that might question the status of *T. kapalgensis*.

This analysis also separates the frequently synonymised *T. georgianus* and *T. troughtoni* on the second factor axis. Locality 140 in Queensland (Mount Isa) (Figure 1) is a good example where individuals of both *T. georgianus* and *T. troughtoni* examined occur in broad sympatry. Also available were specimens of *T. georgianus* from nearby allopatric localities 138 (Cloncurry) and 139 (Ballara). Comparative measurements presented in Appendix II and dimensions shown in Figure 15 show that individuals of *T.*

Table 2. Standardised factor scores of each character for the two factors generated from principal components analysis of *Taphozous georgianus*, *T. troughtoni*, *T. hilli*, *T. australis*, *T. kapalgensis*, *T. longimanus*, *Saccolaimus flaviventris*, *S. saccolaimus* and *S. mixtus* using skull characters, with males and females combined (for code to characters see figure 2).

CHARACTER		FACTOR AXES	
		1	2
1	Anteorbital width (AOW)	0.649	0.691
2	Least inter-orbital width (LOW)	0.559	0.778
3	Zygomatic width (ZW)	0.662	0.777
4	Rostrum length (ROL)	0.878	0.416
5	Mastoid width (MW)	0.617	0.772
6	Braincase width (BW)	0.536	0.819
7	Cranial height (CH)	0.487	0.757
8	Palatal length (PL)	0.862	0.449
9	Postpalatal width (PPW)	0.296	0.537
10	Basicranial length (BL)	0.843	0.492
11	Bulla length (BUL)	-0.046	0.760
12	Width of basisphenoid (BB)	0.504	0.707
13	Distance outside bullae (OB)	0.559	0.794
14	Canine width (CW)	0.901	0.116
15	Inter-upper canine distance (RC^1-LC^1)	0.643	0.712
16	Upper maxillary tooth row crown length (C^1-M^3)	0.832	0.453
17	Upper molar crown length (M^1-M^3)	0.801	0.540
18	Upper 2nd molar crown length (M^2L)	0.720	0.567
19	Upper 2nd molar crown width (M^2W)	0.724	0.546
20	Upper 3rd molar crown width (M^3W)	0.780	0.234
21	Inter-upper 3rd molar distance (RM^3-LM^3)	0.621	0.744
22	Lower tooth row length (LR)	0.822	0.539
23	Angular ramus to dentary condyle (RC)	0.754	0.541
24	Dentary length (DL)	0.844	0.499
25	Sphenoid pit length (SPL)	-0.440	-0.727
26	P^1 basal width (PBW)	0.689	0.660
27	Inter-lower canine distance (ICD)	0.662	0.699

Table 3. Standardised factor scores of each character for the two factors generated from principal components analysis of *Taphozous georgianus, T. troughtoni, T. hilli, T. australis, T. kapalgensis, T. longimanus, Saccolaimus flaviventris, S. saccolaimus* and *S. mixtus* using skull and external body characters, with males and females combined (for code to characters see figure 2).

		FACTOR AXES	
CHARACTER		1	2
1	Anteorbital width (AOW)	0.635	0.651
2	Least inter-orbital width (LOW)	0.560	0.727
3	Zygomatic width (ZW)	0.688	0.676
4	Rostrum length (ROL)	0.854	0.397
5	Mastoid width (MW)	0.613	0.732
6	Braincase width (BW)	0.557	0.777
7	Cranial height (CH)	0.505	0.734
8	Palatal length (PL)	0.824	0.440
9	Postpalatal width (PPW)	0.429	0.441
10	Basicranial length (BL)	0.826	0.470
11	Bulla length (BUL)	0.109	0.747
12	Width of basisphenoid (BB)	0.483	0.665
13	Distance outside bullae (OB)	0.581	0.765
14	Canine width (CW)	0.709	0.060
15	Inter-upper canine distance (RC^1-LC^1)	0.672	0.604
16	Upper maxillary tooth row crown length (C^1-M^3)	0.816	0.454
17	Upper molar crown length (M^1-M^3)	0.777	0.513
18	Upper 2nd molar crown length (M^2L)	0.698	0.535
19	Upper 2nd molar crown width (M^2W)	0.694	0.535
20	Upper 3rd molar crown width (M^3W)	0.768	0.190
21	Inter-upper 3rd molar distance (RM^3-LM^3)	0.636	0.691
22	Lower tooth row length (LR)	0.799	0.512
23	Angular ramus to dentary condyle (RC)	0.738	0.509
24	Dentary length (DL)	0.822	0.482
25	Sphenoid pit length (SPL)	-0.385	-0.685
26	P^1 basal width (PBW)	0.627	0.666
27	Inter-lower canine distance (ICD)	0.650	0.661
28	Body length (HV)	0.517	0.584
29	Tail length (TV)	-0.155	-0.145
30	Ear length (EL)	-0.011	-0.073
31	Ear width (EW)	-0.149	0.162
32	Tragus length (TL)	0.450	0.383
33	Radius length (RL)	0.629	0.608
34	Metacarpal III length (MCIII)	0.682	0.670
35	Digit III/phalanx I length (PI)	0.652	0.677
36	Digit III/phalanx II length (PII)	0.663	0.621
37	Tibia length (TIB)	0.642	0.550
38	Pes length (PES)	0.184	0.740

georgianus are smaller regardless of whether they are from sympatric or close allopatric localities (138, 139 and 140) or from more eastern allopatric localities (i.e. localities 147, 152, 154, 156 and 157).

Standardised factor scores for the two factor axes are shown in Table 2. The most important characters are standardised values of the rostrum length (ROL), palatal length (PL), basicranial length (BL), canine width (CW), upper maxillary tooth row crown length (C^1-M^3), upper molar crown length (M^1-M^3), upper second molar crown length (M^2L), upper second molar crown width (M^2W), upper third molar crown width (M^3W), lower tooth row length (LR), angular ramus to dentary condyle length (RC) and dentary length (DL). ROL, PL and BL relate to the lengthwise antero and midventral shape of the basicranium; CW, C^1-M^3, M^1-M^3, M^2L, M^2W and M^3W relate to the shape of the masticatory apparatus; LR, RC, and DL relate to the lengthwise shape of the dentary. Important characters on the second factor axis are the standardised values of the least interorbital width (LOW), zygomatic width (ZW), mastoid width (MW), braincase width (BW), cranial height (CH), bulla length (BUL), width of the basisphenoid (BB), distance outside bullae (OB), inter-upper canine distance (RC^1-LC^1), inter-upper third molar distance (RM^3-LM^3), sphenoid pit length (SPL) and inter-lower canine distance (ICD). All characters with high loadings on the second factor axis generally relate to width of skull and shape of aspects of the basicranium. Specifically, MW, BW and CH define the anteroventral shape of the skull. BUL, BB, OB and SPL define the shape of the posteroventral part of the basicranium.

Analysis based on a combination of skull and all external characters basically reveals the importance of the same skull characters as in Table 2 on both factor axis 1 (81.7% variance, eigenvalue = 22.9) and factor axis 2 (4.8% variance, eigenvalue = 1.3). However, of the external characters, only the pes length (PL) seems to be important and only on the second factor axis (Table 3).

Canonical Variates Analyses

The groups specified for canonical variates analyses included *T. hilli*, *T. troughtoni*, *T. kapalgensis* and *T. longimanus*, which were distinct in the PCA's. Although there were obvious overlaps between *T. georgianus* and *T. australis* and between *S. saccolaimus* and *S. flaviventris*, these four taxa were also treated as separate groups in the canonical variates analyses. This was because a conventional taxonomic examination of individuals revealed them to be morphologically distinct despite similar skull and body proportions. Unlike *T. georgianus*, *T. australis* males have a gular pouch, while this area is represented by a naked area in females. Furthermore, the sphenoid pit extends further into the pterygoid area in *T. georgianus*. Similarly, unlike *S. flaviventris*, *S. saccolaimus* has a smooth posterior floor of the mesopterygoid fossa which lacks a deep groove. In addition, the sphenoid pit is shallower in *S. saccolaimus*, with the median septum not as high as the floor of the mesopterygoid fossa. Since *S. mixtus* was only represented by two specimens, it was not included in the "analysis phase"; it was however, included during the "classification phase" of the CVA.

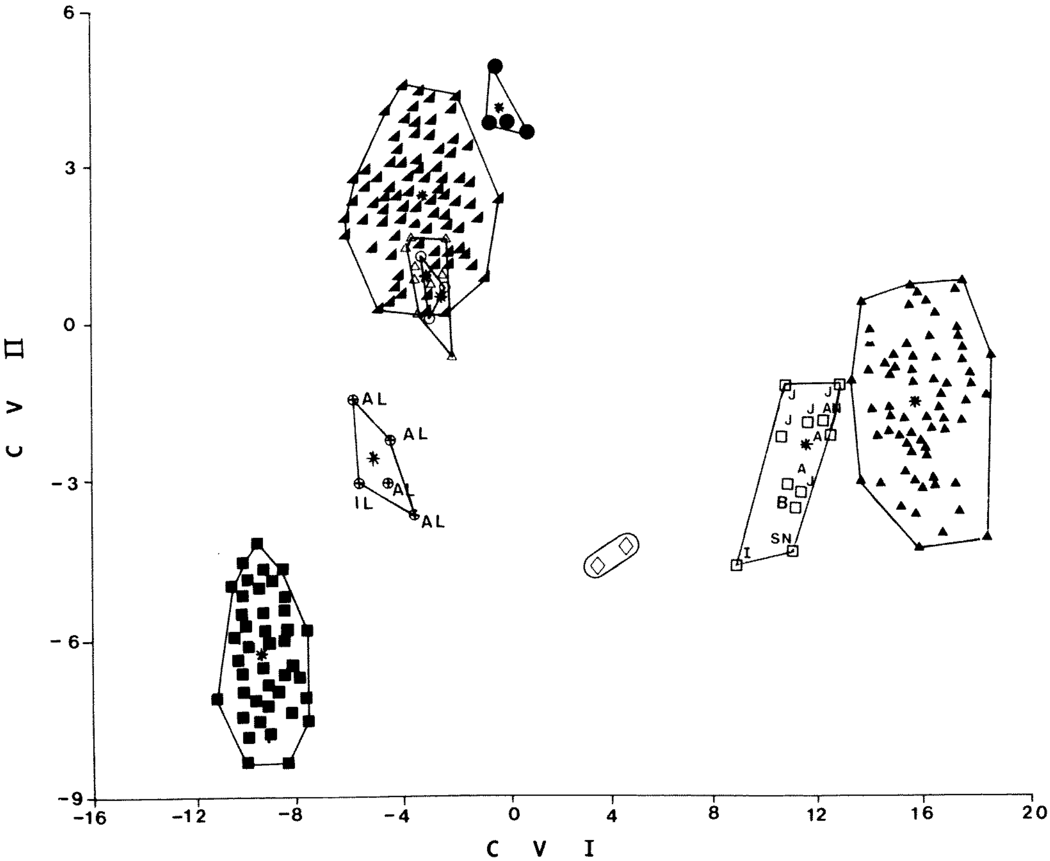

Figure 16 Scores of the first and second canonical variates axes for Australian emballonurids examined, together with *Saccolaimus saccolaimus* and *Taphozous longimanus* from Asia. Data are size-free skull characters, excluding postpalatal width (PPW), with males and females combined. Species symbols are: *S. flaviventris* (▲), *S. mixtus* (◊), *S. saccolaimus* (□), *T. australis* (△), *T. georgianus* (◢), *T. hilli* (■), *T. kapalgensis* (O), *T. longimanus* (●) and *T. troughtoni* (●).

Codes for *S. saccolaimus* and *T. longimanus* individuals are as for figure 14. The distribution of specimens about the group centroid (*) are shown. Most points in *S. flaviventris*, *T. georgianus* and *T. hilli* represent multiple specimens.

Similarly to PCA, results obtained from the CVA based on the three groupings of data were similar. For simplicity, results presented are based on skull characters alone. The first five CV axes account for 99.8% of the total variation: CV1, 81.9%; CV2, 12.1%; CV3-5, 5.8%. A plot of individual scores with minimum convex polygons of the first two CV axes is shown in Figure 16. By using Mahalanobis' distance between clusters of individuals belonging to the two genera currently recognised in Australia, both axes show no absolutely clear separation between members of *Taphozous* and *Saccolaimus* although two divergent lines of variation are evident; there is, for example, no overlap between members of these genera on the first CV axis (*S. mixtus* and *T. troughtoni* are close). This first axis, generally represents overall size and is a reflection of the fact that the *Saccolaimus* studied are generally larger overall than *Taphozous*. *Taphozous hilli, S. mixtus, S. flaviventris* and *S. saccolaimus* form discrete clusters; these are maximally separated on the first CV axis. In addition, *T. troughtoni* forms a distinct cluster and is separated from the above on the second CV axis. The first CV axis maximises the separation between the frequently synonymised *T. troughtoni* and *T. georgianus*. *Taphozous kapalgensis* lies within the *T. australis* cluster, which in turn lies within the *T. georgianus* cluster, except for one individual. However, *T. australis* is separated from

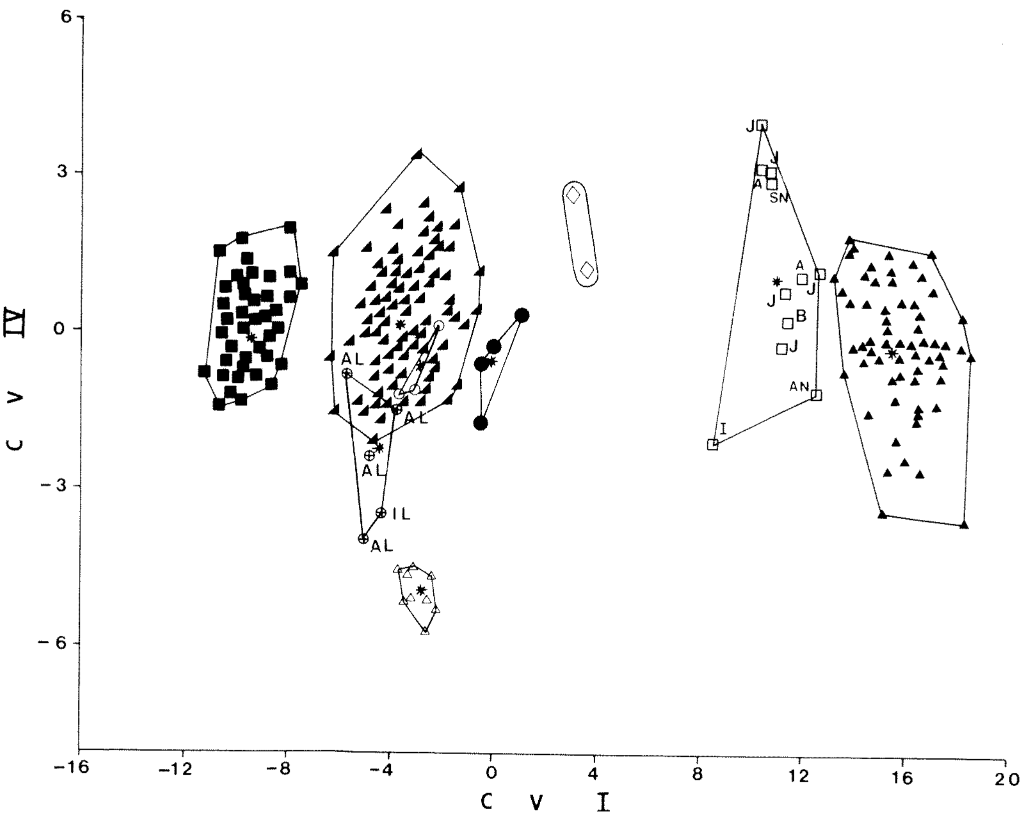

Figure 17 Scores of the first and fourth canonical variates axes for Australian emballonurids, together with Asian *Saccolaimus saccolaimus* and *Taphozous longimanus*. Data are skull characters, excluding postpalatal width (PPW), rostrum length (ROL) and upper second molar crown length (M^2L), with males and females combined. For symbols of species and codes for some individuals, see Figure 14. Most points in *S. flaviventris, T. georgianus* and *T. hilli* represent multiple specimens. The group centroids are indicated by (*).

both *T. kapalgensis* and *T. georgianus*, on the fourth axis (Figure 17), whereas *T. kapalgensis* is separated from both on the fifth CV axis (Figure 18). In CV space, the latter figures indicate the intermediate position of *S. mixtus* between members of the currently recognised genera.

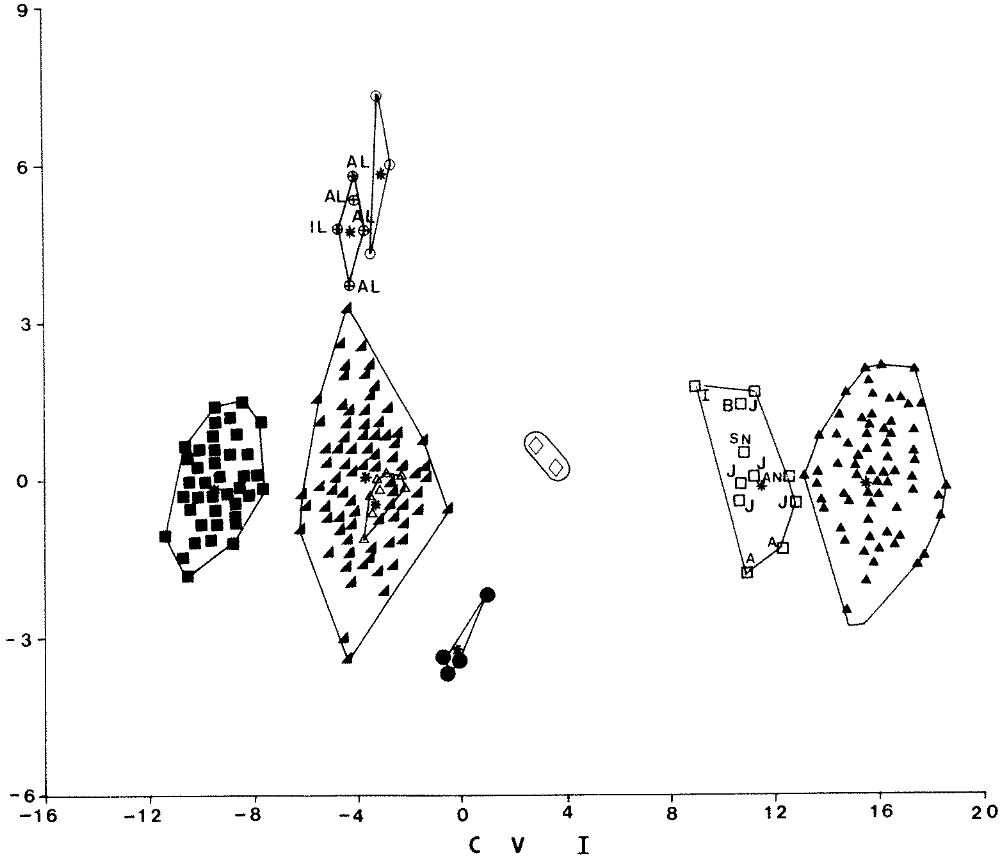

Figure 18 Scores of the first and fifth canonical variates axes for Australian emballonurids, together with Asian *Saccolaimus saccolaimus* and *Taphozous longimanus*. Data are skull characters, excluding postpalatal width (PPW), rostrum length (ROL) and upper second molar crown length (M^2L), with males and females combined. For symbols of species and codes for some individuals, see Figure 14. Most points in *S. flaviventris*, *T. georgianus* and *T. hilli* represent multiple specimens. The group centroids are indicated by (*).

All CV axes examined (Figures 16, 17 and 18) consistently separate *T. kapalgensis* from *T. longimanus* regardless of whether individuals of *T. longimanus* were collected from India (IL) or Bali (AL). Similarly, in *S. saccolaimus*, there are no geographic trends among individuals from India (I), Australia (A), Java (J) and Borneo (B). Neither are there any apparent geographic trends between individuals previously designated *S.*

nudicluniatus from Australia (AN), Solomon Islands (SN), and all other individuals of *S. saccolaimus* regardless of their origin. Overall, 90.3% of specimens were correctly classified to the seven species we recognise.

Table 4. Standardised canonical variates axis coefficients of characters, obtained from the stepwise canonical variates analysis of *Taphozous georgianus, T. troughtoni, T. hilli, T. australis, T. kapalgensis, T. longimanus, Saccolaimus flaviventris, S. saccolaimus* and *S. mixtus* using skull measurements, excluding postpalatal width (PPW), rostrum length (ROL), and upper second molar crown length (M^2L), with sexes combined (for code to characters see figure 2).

	CHARACTER	Variate I	Variate II	Variate III	Variate IV	Variate V
1	Anteorbital width (AOW)	0.137	-0.187	-0.298	-0.027	-0.258
2	Least inter-orbital width (LOW)	0.125	-0.327	-0.235	0.013	0.142
3	Zygomatic width (ZW)	0.112	-0.170	-0.145	0.565	-0.019
4	Mastoid width (MW)	0.415	0.204	0.260	0.302	0.526
5	Braincase width (BW)	-0.028	-0.324	0.174	-0.189	0.200
6	Cranial height (CH)	-0.143	0.001	0.457	-0.218	-0.111
7	Palatal length (PL)	0.112	0.333	-0.022	-0.330	-0.342
8	Basicranial length (BL)	-0.060	0.448	-0.304	-0.098	0.039
9	Bulla length (BUL)	-0.369	-0.318	-0.276	-0.383	0.036
10	Width of basisphenoid (BB)	0.128	0.077	0.316	0.005	0.221
11	Distance outside bullae (OB)	-0.166	-0.147	0.371	-0.368	-0.973
12	Canine width (CW)	-0.205	0.660	0.373	-0.476	0.199
13	Inter-upper canine distance (RC^1-LC^1)	0.626	0.283	-0.091	0.135	0.490
14	Upper maxillary tooth row crown length (C^1-M^3)	0.653	0.355	0.051	0.075	0.445
15	Upper molar crown length (M^1-M^3)	0.104	-0.315	0.033	0.113	-0.140
16	Upper 2nd molar crown width (M^2W)	0.023	0.051	0.808	0.483	0.024
17	Upper 3rd molar crown width (M^3W)	-0.056	0.120	0.022	-0.109	0.104
18	Inter-upper 3rd molar distance (RM^3-LM^3)	-0.129	-0.166	-0.128	-0.001	-0.302
19	Lower tooth row length (LR)	-0.035	-0.243	-0.034	0.301	-0.279
20	Angular ramus to dentary condyle (RC)	0.203	0.107	0.116	0.043	0.216
21	Dentary length (DL)	0.002	0.462	-0.192	0.024	-0.281
22	Sphenoid pit length (SPL)	-0.471	0.151	0.306	0.687	-0.120
23	P^1 basal width (PBW)	0.395	-0.247	0.004	0.178	0.182
24	Inter-lower canine distance (ICD)	0.081	0.001	0.123	0.288	0.003

Characters with high loadings in the first CV axis (Table 4) relate to the standardised values of the inter-upper canine distance (RC^1-LC^1) and the upper maxillary tooth row crown length (C^1-M^3). Both these characters relate to the shape of the anteroventral basicranium. The canine width (CW) is the most important character on the second CV axis (12.1% variance). Important on the fourth CV axis, which is instrumental in maximising the separation between *T. georgianus* and *T. australis* (Figure 17) are the zygomatic width (ZW) and the sphenoid pit length (SPL). The mastoid width (MW) and the distance outside bullae (OB) are important on the fifth CV axis (0.4% variance), which is important in distinguishing *T. kapalgensis* and *T. georgianus* (Figure 18). The mastoid width (MW) and the distance outside bullae (OB) relate to the posteroventral shape of the basicranium. An examination of the important CV axes of the analysis that was performed using a combination of skull and all external characters (Table 5) shows a

Table 5. Standardised canonical variates axis coefficients of characters, obtained from the stepwise canonical variates analysis of *Taphozous georgianus, T. troughtoni, T. hilli, T. australis, T. kapalgensis, T. longimanus, Saccolaimus flaviventris, S. saccolaimus* and S. mixtus using skull and all external measurements combined, excluding postpalatal width (PPW), rostrum length (ROL), and upper second molar crown length (M^2L), with sexes combined (for code to characters see figure 2).

	CHARACTER	Variate I	Variate II	Variate III	Variate IV	Variate V
1	Anteorbital width (AOW)	0.098	0.006	-0.201	0.102	0.361
2	Least inter-orbital width (LOW)	0.169	-0.318	-0.189	-0.017	-0.066
3	Zygomatic width (ZW)	0.044	-0.022	-0.311	0.396	-0.147
4	Mastoid width (MW)	0.363	-0.045	-0.118	0.004	-0.285
5	Braincase width (BW)	0.054	-0.330	0.301	-0.088	0.212
6	Cranial height (CH)	-0.041	0.052	-0.406	-0.249	-0.130
7	Palatal length (PL)	0.133	0.321	0.187	-0.119	0.239
8	Basicranial length (BL)	-0.178	0.628	-0.294	-0.141	-0.205
9	Bulla length (BUL)	0.286	-0.416	-0.154	-0.314	0.088
10	Width of basisphenoid (BB)	0.002	0.073	0.382	-0.014	-0.172
11	Distance outside bullae (OB)	-0.190	-0.129	0.435	-0.236	0.707
12	Canine width (CW)	0.324	0.608	0.190	-0.480	-0.119
13	Inter-upper canine distance (RC^1-LC^1)	0.342	0.193	0.009	0.149	-0.145
14	Upper maxillary tooth row crown length (C^1-M^3)	0.471	0.254	0.325	-0.032	-0.301
15	Upper molar crown length (M^1-M^3)	0.206	-0.227	0.095	0.195	0.043
16	Upper 2nd molar crown width (M^2W)	-0.079	0.088	0.145	0.386	-0.264
17	Upper 3rd molar crown width (M^3W)	-0.071	0.106	-0.102	-0.224	0.041
18	Inter upper 3rd molar distance (RM^3-LM^3)	-0.113	-0.206	0.024	0.049	0.161
19	Lower tooth row length (LR)	-0.021	-0.257	-0.027	0.135	0.164
20	Angular ramus to dentary condyle (RC)	0.198	0.081	0.008	-0.013	-0.132
21	Dentary length (DL)	0.010	0.518	0.099	0.053	0.153
22	Sphenoid pit length (SPL)	-0.484	0.013	0.067	0.518	-0.267
23	P^1 basal width (PBW)	0.450	-0.263	-0.104	0.028	-0.010
24	Inter lower canine distance (ICD)	0.173	0.019	-0.022	0.314	-0.070
25	Body length (HV)	0.043	-0.103	0.172	0.263	-0.090
26	Tail length (TV)	-0.060	0.088	0.038	0.066	0.005
27	Ear length (EL)	-0.147	0.055	0.087	-0.150	0.391
28	Ear width (EW)	-0.040	0.031	-0.089	-0.107	0.142
29	Tragus length (TL)	0.123	0.064	-0.170	-0.092	0.238
30	Radius length (RL)	-0.280	-0.003	0.065	0.121	0.166
31	Metacarpal III length (MCIII)	0.081	-0.312	-0.027	-0.092	-0.058
32	Digit III/phalanx I length (PI)	0.693	-0.155	-0.286	-0.077	-0.225
33	Digit III/phalanx II length (PII)	-0.145	0.206	-0.187	0.166	0.169
34	Tibia length (TIB)	-0.159	0.131	0.022	0.400	0.380
35	Pes length (PES)	-0.005	-0.129	0.374	0.203	0.274

similarity in skull character loadings. However, of the external characters, only the digit III/phalanx I length (PI) is important, on the first CV axis.

Cluster Analysis

There was a marked congruence when the three combinations of data were analysed separately. Analysis based on skull characters alone is presented. This is because alcohol preserved specimens were not available for *S. mixtus* and most specimens of *S. saccolaimus* to allow computation of mean values. The results of the UPGMA clustering of the eight species of *Taphozous* and *Saccolaimus* delineated are shown in Figure 19. The currently recognised genera are not separate in this phenogram because *S. mixtus* clusters with *T. troughtoni. Taphozous georgianus, T. australis* and *T. kapalgensis* form a distinct group with very little morphological differentiation between them. These three species are more similar to *T. troughtoni* and *S. mixtus* than the distinctive *T. hilli. Saccolaimus saccolaimus* and *S. flaviventris* are phenetically similar to each other and are very distinct from the other species.

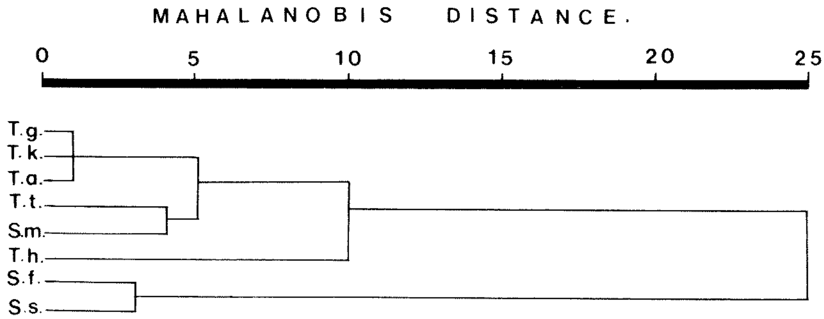

Figure 19 Phenetic relationships of Australian emballonurid species derived by UPGMA cluster analysis. Data are size-free skull characters with males and females combined. Species codes are as follows: *Saccolaimus flaviventris* (S.f), *S. mixtus* (S.m), *S. saccolaimus* (S.s.), *Taphozous australis* (T.a), *T. georgianus* (T.g), *T. hilli* (T.h), *T. kapalgensis* (T.k), and *T. troughtoni* (T.t).

Discussion

There is no strong phenetic separation between *Saccolaimus* and *Taphozous*, although the two genera can be discriminated on the first CV axis. However, the classical taxonomic approach and phylogenetic studies of generic relationships within the Emballonuridae using morphology (Chimimba 1987), and protein electrophoresis and immunology (Robbins and Sarich 1988) separate these genera. The following Australian species are considered valid: *S. flaviventris; S. mixtus; S. saccolaimus; Taphozous australis, T. georgianus, T. hilli, T. kapalgensis* and *T. troughtoni.*

Earlier workers considered that the large *T. troughtoni* was part of a size cline in *T. georgianus* which increases in size from west to east (McKean and Price 1967, Koopman 1984b). However, several points in the present study argue against this synonymy. Firstly, the individuals of *T. troughtoni* examined were collected from Ballara and

Mount Isa in Queensland (Localities 139 and 140 respectively in Figure 1), the latter being the type locality of *T. troughtoni* (Tate 1952). There is also a specimen of *T. georgianus* from Mount Isa (CM 13216) and another from Cloncurry (JM 6550, Locality 138 in Figure 1), an area very close to Mount Isa, suggesting that the two taxa are not geographically separated. Our data show that individuals of *T. georgianus* are smaller than those of *T. troughtoni* in both sympatry and allopatry. In addition, specimens of *T. georgianus* collected further to the east of Mount Isa, Ballara and Cloncurry are also smaller than specimens of *T. troughtoni*. This suggests that while *T. georgianus* may show an eastward increase in size, *T. troughtoni* does not form part of this size cline. Secondly, despite these size differences, the analyses were performed after corrections for size were made, and yet the morphological differences between the two taxa are still apparent. Thirdly, although phenetic relationships based on cluster analyses show that *T. troughtoni* has affinities with *T. georgianus, T. australis* and *T. kapalgensis,* the phenogram confirms a fairly high degree of morphological dissimilarity between *T. troughtoni* and *T. georgianus* (together with *T. kapalgensis* and *T. australis*).

Jones and Genoways (1970) have noted the presence of many sibling species in microchiropteran bats. This fact is stressed by Baverstock (1989) who stated that "many zoologists seem unaware of the high incidence of "cryptic" species". Studies on Australian bats using molecular techniques (Adams *et al.* 1987a, b, 1988), and morphological approaches using multivariate statistics (Carpenter *et al.* 1978; McKean *et al.* 1978; Campbell and Kitchener 1980; Tidemann *et al.* 1981; Kitchener and Caputi 1985; Kitchener *et al.* 1986, 1987) support this view. A most important aspect of the studies cited above is the high degree of concordance between results based on the morphological data and those of parallel studies based on electrophoretic data, although in several instances electrophoretic data indicated the presence of species that could be identified only with great difficulty, or not at all, using morphology. Consequently it is suggested that there is need to further examine the Australian emballonurids using electrophoretic data.

Examination of bacula and glans penis in this study are mostly based on small samples. While these support the Australian species recognised by us, examination of a more extensive sample is required. This is necessary to distinguish different growth stages or stages in ossification of the glans penis and bacula respectively such as observed in Australo-Papuan *Pipistrellus* and *Falsistrellus* by Kitchener *et al.* (1986).

Generally, there was some difficulty separating *T. australis, T. georgianus* and *T. kapalgensis* using PCA. Following the suggestion by Gould and Woodruff (1978) and Gould (1984) of the biological importance of minor axes of PCA (which may also be true for CVA), the minor axes indicate that the three species are morphologically distinct. This distinctiveness is also supported by the traditional taxonomic approach. Cluster analysis also shows that *T. australis, T. georgianus* and *T. kapalgensis* are phenetically very close.

Our results leave little doubt that *T. kapalgensis* and *T. hilli* are not conspecific as suggested by Koopman (1984b). Further, *T. kapalgensis* is distinct from the most similar oriental species, *T. longimanus* (which does not appear to be highly variable over its range as suggested by Dobson, 1878).

We show that *S. nudicluniatus* is conspecific with *S. saccolaimus,* which is in agreement with Goodwin (1979). Although we examined few specimens of *S. saccolaimus* there appeared little variation over its range from India to the Solomon Islands, which is consistent with the observations of McKean *et al.* (1980).

Taphozous troughtoni and *S. mixtus* have closest phenetic affinities with the species cluster, *T. australis, T. georgianus* and *T. kapalgensis.* In the original description of *T. troughtoni,* Tate (1952) recognised the similarity of *T. troughtoni* with *T. georgianus* and *T. australis* but not with *S. mixtus* indicating that the development of the bulla greatly influenced Tate. Within species currently referred to *Taphozous* in Australia, *T. hilli* is the most distinct morphologically. *Saccolaimus flaviventris* and *S. saccolaimus* are phenetically similar to each other, and are the most distinct morphologically of all Australian emballonurids.

Characters determined by CVA to be particularly important in separating Australian emballonurids relate to the inter-upper canine distance, upper maxillary tooth row crown length, canine width, zygomatic width, sphenoid pit length, mastoid width, distance outside bullae, digit III/phalanx I length and pes length. Some of these characters have been used previously to diagnose these species. The most important of these relate to the sphenoid pit length, the bulla length, canine width and pes length. Kitchener (1980) found that the canine was one of the most important diagnostic characters between *T. hilli* and *T. georgianus.* Importantly, these two species were separated on an axis in which the canine width was the only character with a high loading. The *a priori* determination of pes length as an important character accords with Monticelli (1889) who observed that feet were an important distinguishing character between members of *Taphozous* and *Saccolaimus.* In general, Hollister (1913), Thomas (1922) and Troughton (1925) placed much emphasis on the structure of the bulla and the sphenoid pits to distinguish between members of *Taphozous* and *Saccolaimus.* Troughton (1925) attached much importance to the structure of the sphenoid pits to distinguish *T. georgianus* and *T. australis.* In this study, the minor axis instrumental in maximising the separation between *T. georgianus* and *T. australis* involves the sphenoid pit length as one of the important characters. The structure of the sphenoid pit and the bullae have also been used extensively to separate Old World members of *Taphozous* and *Saccolaimus* (Barghoorn 1977); New World members of the subfamily Emballonurinae (Sanborn 1937) and within members of the genus *Emballonura* in the Indo-Australasian region (Tate and Archbold 1939).

Other characters determined as important in distinguishing taxa in this study mostly relate to teeth, the dentary and the width of the skull. These characters can be viewed from a functional standpoint. It is possible that effects of resource partitioning by different species contribute to the importance of the teeth and the dentary. Freeman (1981) relates characteristics of the dentary to possible functional differences in molossid bats. She suggested that thickening of the dentary and increase in the area of insertion of the temporalis muscle at the coronoid process may be related to diet. Similarly, the wideness of the skull may be a result of feeding on different size and texture of food by different species, which in turn may cause changes in the magnitude of forces acting on the skull and the mandible produced by the forces of mastication. Hildebrand (1974) and Buckland-Wright (1978) report that bone thickens where more stress occurs and that mammalian skull bones constantly undergo change by absorption and remodelling of bone tissue that may be functionally influenced.

There are no significant differences between males and females within the emballonurids in which the sample size was adequate for examination: *Taphozous georgianus, T. hilli* and *S. flaviventris.* All these species are predominantly cave dwelling. Without suggesting a biological explanation, Carpenter *et al.* (1978) reported that in Australian *Eptesicus* (×*Pipistrellus,* see Hill and Harrison 1987; Volleth and Tidemann 1989), sexual dimorphism is less pronounced in cave dwelling species than it is in the forest dwelling ones. In most phyllostomatids (Baker *et al.* 1972; Power and Tamsitt 1973; McLellan 1984) and some vespertilionids (Findley and Traut 1970; Myers 1978), males are larger than females. Exceptions are the phyllostomatid *Ametrida centurio* (Peterson 1965) and some vespertilionids (Myers 1978, Campbell and Kitchener 1980) where females are larger than males. The larger females have been associated with a need to compensate for the extra flight load during pregnancy (Ralls 1976).

Key to Genera and Species of Australian Emballonuridae

The Key is to be used in conjunction with pertinent diagnoses, descriptions and measurements in Table 1.

1a Bulla complete, with less than 50 percent of cochlea exposed; skull heavily ossified; saggital crest pronounced and reaching occiput; upper anterior premolar proportionately larger, almost one-third of both height and crown area of posterior premolar; a wide band separating anterior lacerate foramen and sphenorbital sinus; lower outline of dentary convex beneath premolar; posteroventral face of basisphenoid region in contact with both bulla and cochlea; paraoccipital process level or slightly longer than occipital condyles; inner margin of ear not papillate .... Australian *Saccolaimus* 2

1b Bulla incomplete, with greater than 50 percent of cochlea exposed; skull not heavily ossified; saggital crest absent or much weaker, barely reaching occiput or often terminating into a more rounded crest; upper anterior premolar relatively small, almost one-fifth of both height and crown area of posterior premolar; anterior lacerate foramen and sphenorbital sinus separated by a thin band; lower outline of dentary markedly concave beneath premolars; posteroventral face of basisphenoid in contact with cochlea only;

paraoccipital process shorter than occipital condyles; parastylar area well developed; inner margin of ear papillate .... Australian *Taphozous* 4

2a Radial-metacarpal pouch present, size smaller: greatest skull length averages 21.8 (21.7-21.9), radius length averages 63.6 (63.1-64.2); forehead more excavated.................. *Saccolaimus mixtus*

2b Radial-metacarpal pouch absent, size larger: greatest skull length ranges between 22.4-27.0, radius length ranges between 65.7-82.1; forehead less excavated. 3

3a Mesopterygoid fossa deeply grooved; sphenoid pit posteriorly margined by an overlapping edge; sagittal crest reaches occiput but not so prominently .... *Saccolaimus flaviventris*

3b Mesopterygoid fossa smooth; sphenoid pit posteriorly more open; sagittal crest prominently reaching occiput...... *Saccolaimus saccolaimus*

4a Gular sac present in males and represented by a rudimentary edge in females 5

4b Gular sac absent in both sexes 7

5a Anterior rim of mesopteryoid fossa rounded; canines shorter and slender with small anterobasal cusp about one-third length of tooth; posterior premolar with a small anterobasal cusp; angular basisphenoid pit; less steeply excavated frontal depression.. *Taphozous hilli*

5b Anterior rim of mesopterygoid fossa v-shaped; canines relatively longer and less slender and lacking a small anterobasal cusp; posterior premolar lacking small anterobasal cusp; rather pear-shaped basisphenoid pit; frontal depression deeply excavated 6

6a Sphenoid pit do not reach level of large vacuities outside nasal cavities but ending about 1 mm from them; zygomata without spike .... *Taphozous australis*

6b Sphenoid pits reaching to level of nasal cavities; zygomata with spike .... *Taphozous kapalgensis*

7a Anterior rim of mesopterygoid fossa less v-shaped; postorbital processes relatively shorter; sagittal and lambdoidal crests relatively weak; size generally smaller, greatest skull length averaging 21.4 (20.0-23.1).......... *Taphozous georgianus*

7b Anterior rim of mesopterygoid fossa sharply v-shaped; postorbital process extremely long; sagittal and lambdoidal crests sharply edged; size larger, greatest skull length averaging 24.1 (24.0-24.3) .... *Taphozous troughtoni*

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Appendix I Australian emballonurid specimens examined. Collecting locality numbers are those indicated in Figure 1.

Taphozous australis

Locality 143

Possession Island 10°44′, 142°24′, 13 males, 1 female, AM (M4412-17, M4419-22, M4424-25). Locality 144 Coen, 13° 57′, 143°12′, 1 male, JM (M9495). *Locality* 150 Townsville, 10°16′, 146°49′, 1 male, CM (M2176).

Taphozous georgianus

Locality 5

Wilgie Mia, 26°56′, 117°42′, 1 male, CM (M2122). *Locality 9* Three Rivers Homestead, 25°08′, 119°09′, 1 female, WAM (M15235). *Locality 12* Durba Spring, 23°45′20″, 122°31′00, 4 males, 6 females, WAM (M14384-87, M14390-95). *Locality 14* Opthalmia Range, 23°16′50″, 119°11′20″, 1 male, 1 female, WAM (M19503-04). *Locality 15* Opthalmia Range, 23°18′00″, 119°35′20″, 2 females, WAM (M18039-40). *Locality 16* Mt Newman, 23°19′, 119°45′, 1 male, WAM (M6718.003). *Locality 19* Paraburdoo Minesite, 23°13′30″, 117°37′00, 1 male, 1 female, WAM (M14935-36). *Locality 20* Ullawarra Station, 23°24′, 116°10′, 4 males, 6 females, WAM (M4324-30, M4332-34). *Locality 21* Yardie Creek Homestead, 22°02′45″, 114°01′30″, 1 male, 3 females, WAM (M18146-49). *Locality 22* Yardie Homestead, 21°52′, 114°03′, 1 male, WAM (M7476). *Locality 23* Tambrey Homestead, 21°35′00″, 117°33′40″, 1 male, 3 females, WAM (M4319, M4321.001-.002, M4342). *Locality 24* Yampire Gorge (includes Wittenoom Gorge), 22°25′, 119°27′, 4 males, 4 females, WAM (M4318.002-.003, M18288, M18290-92, M19616-17). *Locality 25* Hamersley Range National Park (includes Mt Bruce), 22°36′00″, 118°08′30″, 1 male, 4 females, WAM (M14594-95, M18256-57, M18655). *Locality 27* Hopetoun Mine, 21°55′00″, 120°12′30″, 3 males, WAM (M11050, M11052, M11054). *Locality 28* Nullagine, 21°53′, 120°07′, 1 male, 6 females, WAM (M10536, M11040-45). *Locality 29* Mosquito Creek, 21°44′00″, 120°28′30″, 2 males, 2 females, WAM (M11034-35, M11037-38). *Locality 30* Oakover River, 21°31′, 121°10′, 1 female, WAM (M24328). *Locality 31* Bamboo, 20°55′45″, 120°13′15″, 7 males, 5 females, WAM (M3251-52, M3254-58, M3262, M3276-77), CM (M2151). *Locality 32* Callawa Homestead, 20°22′05″, 120°49′20″, 3 females, WAM (M10560, M16762-63). *Locality 33* Shay Gap, 20°31′, 120°08′, 3 males, 7 females, WAM (M16764-M16772, M16778). *Locality 35* Marble Bar, 21°20′, 119°42′, 1 male, WAM (M3261). *Locality 36* Pullcunah Hill, 21°32′30″, 118°59′00″, 2 females, WAM (M9606-M9607). *Locality 37* Woodstock, 21°37′, 118°57′, 1 male, 1 female, WAM (M7465-66). *Locality 38* Peawah Camp Well, 20°44′, 118°01′, 1 male, WAM M7470. *Locality* 39 Whim Creek, 20°50′, 117°50′, 2 males, 1 female, WAM (M7458-60). *Locality 48* Bugle Gap, Lawford Range, 18°39′45″, 126°03′05″, 3 males, 1 female, WAM (M5709, M5712-13, M5718). *Locality 49* Wattle Spring Creek, 19°14′, 126°03′, 1 female, WAM M24367. *Locality 50* Outcamp Hill, 18°33′30″, 125°55′00″, 5 males, 3 females, WAM (M5706-08, M5710-11, M5713, M5715). *Locality 51* Sadlier Range, 18°18′, 125°35′, 1 male, 1 female, WAM (M5720-21). *Locality 53* Napier Range, including Winjina Gorge, 17°25′35″, 124°25′05″, 8 males, 7 females, WAM (M7472, M18325-29, M18331-32), CM (M1512, 1515-20). *Locality 54* Inglis Gap, includes Lennard River Gorge, 17°07′, 125°11′, 1 male, 2 females, WAM (M7468-69, M18541). *Locality 55* Tunnel Creek, 17°37′, 125°09′, 2 males, 2 females, WAM (M7462-64, M24044). *Locality 56* Leopold Downs Homestead, 17°54′45″, 125°17′12″, 3 females, WAM (M24033-35). *Locality 57* Napier Downs Homestead, 17°14′, 124°38′, 1 male, WAM (M8135). *Locality 58* Derby, 17°18′, 123°38′, 1 male, 2 females, WAM (M7050, M24031-32). *Locality 59* Mt Anderson, 18°01′, 123°56′, 5 males, 2 females, WAM (M5534-37, M18457, M18464-65). *Locality 63* Edgar Range, 18°25′, 123°05′, 4 females, WAM (M15046-47, M14132, M17461). *Locality 68* Koolan Island, 16°08′00″, 123°46′30″, 1 female, WAM M4897. *Locality 69* Cockatoo Island, 16°05′20″, 123°36′00″, 1 female, WAM (M4898). *Locality 71* Augustus Island, 15°22′30″, 124°35′20″, 1 male, 1 female, WAM (M9280-81). *Locality 72* Bat Island, 15°06′10″, 124°54′30″, 3 males, 1 female, WAM (M10460-63). *Locality 73* Boongarie Island, 15°06′00″, 125°12′40″, 5 males, WAM (M10454, M10456-59). *Locality 74* Bigge Island, 14°30′40″, 125°07′47″, 2 males, 1 female, WAM (M15414-16). *Locality 76* Mitchell Plateau, 14°49′30″, 125°50′40″, 1 male, WAM M15702. *Locality 78* Mitchell Plateau, 14°53′40″, 125°45′20, 1 female, WAM M15686. *Locality 79* Mitchell Plateau, 14°36′30″, 125°52′00″, 3 males, 2 females, WAM (M15689-90, M15692, M15697, M15699). *Locality 80* Kalumburu

Mission, 14°17'30", 126°38'40", 2 males, 2 females, WAM (M4080-82, M7457). *Locality 82* Drysdale River National Park, 15°01', 126°49', 1 female, WAM M14096. *Locality 85* Parry Creek, 15°30', 128°13', 1 female, WAM M7471. *Locality 86* Kununnura, 15°46'30", 128°44'00", 1 female, WAM B231. *Locality 87* Ningbing Bore, 15°14'00", 128°40'30", 1 female, WAM M7467. *Locality 88* Cave Springs, includes Mount Cecil, 15°32', 128°50', 4 males, 4 females, WAM (M7053/002, M7053/004, M7053/006-007, M7059/001-003, M19665). *Locality 89* Keep River National Park, 15°45', 128°04', 1 male, 1 female, CM (M524-525). *Locality 91* Argyle Downs (includes Aboriginal Cave) 16°04'15", 128°46'35", 1 male, 4 females, WAM (M9608, M9614, M11459, M11465). *Locality 92* Ord River Area, 16°23', 128°43', 3 males, 5 females, WAM (M9605, M9612, M11498-99, M11500-02, M11613). *Locality 93* Lissadell Homestead (New), 16°39'57", 128°31'03", 2 males, 5 females, WAM (M16899, M16992-97). *Locality 94* Bull Hole Bore, 17°19'55", 127°05'15", 6 females, WAM (M18458-63). *Locality 95* Old Halls Creek, 17°55'00", 127°49'30", 1 female, WAM M7474. *Locality 96* Mount Bradley, 18°22'00", 128°47'30", 2 males, WAM (M6995/001-002). *Locality 97* Halls Creek, 18°21', 127°49', 3 males, 5 females, WAM (M18315-22). *Locality 98* Halls Creek, 18°34', 127°15', 1 female, WAM M24366. *Locality 99* Kintore Cave, Near Katherine, 23°18', 129°24', 5 males, 4 females, C (5003-04, 5051-55, 5057-58). *Locality 106* 8 km east of Arltunga, 23°28', 134°43', 2 males, 3 females, CM (M4428-4430, M4435, M4437). *Locality 112* Delamere Station, 15°44', 131°32', 3 females, SAM (M6655, M7053-54). *Locality 117* Katherine, 14°29', 132°12', 3 males, 2 females, WAM (M6256-58, M6263-64). *Locality 118* Katherine Gorge National Park, 14°19', 132°28', 1 male, 2 females, CM (M636, M649-50). *Locality 120* Pine Creek, 13°49', 131°50', 2 males, 1 female AM M9491, CM (M3984, M10027). *Locality 122* Green Ant Creek, 13°36', 131°12', 1 male, CM M4141. *Locality 131* Portsite Centre Island, Sir Edward Pellew Group, 15°33', 136°47', 2 males, 1 female, CM (M2554-55, M13193). *Locality 132* Caranbirini Waterhole, 16°16', 136°05', 2 females, CM (M11821, M11924). *Locality 133* Amelia Spring, 16°36', 136°11', 1 female, CM M11785. *Locality 134* Nicholson River, 17°46', 137°05', 1 female, NTM M5982. *Locality 135* China Well, 17°50', 137°25', 2 males, CM (M6922-23). *Locality 136* Accident Creek, 18°04', 138°12', 2 males, 2 females, SAM (M6806-07, M6809-10). *Locality 137* Riversleigh, 18°45', 138°35', 5 males, 1 female, WAM B (298-303). *Locality 138* Cloncurry, 20°42', 140°30', 1 male, JM M6550. *Locality 140* Native Bee Mine, Mount Isa, 20°44', 139°29', 1 female, CM M13216. *Locality 147* Chillagoe, 17°09', 144°31', 4 males, 3 females, CM (M2058, M2346, M13190-91, M13194, M13197-98). *Locality 152* Mount Etna, 20°58', 148°01', 2 females, AM (M8117-18). *Locality 154* Capella, 25°05', 148°01', 1 male, 2 females, JM (M13855-57). *Locality 156* Rockhampton, 23°22', 150°32', 2 males, 3 females, AM (M6024-25), CM M13212, JM (M9975-76). *Locality 157* Rewan Station, South West Rolleston, 24°58', 148°22', 1 female, JM M15816.

Taphozous hilli

Locality 1

Tallering Homestead, 28°15', 115°51', 6 males, 6 females, WAM (M10673-78, M10680-85). *Locality 2* Tallering Peak, 28°06', 115°38', 6 males, 6 females, WAM (M11030, M12712, M12714-19, M12459-60). *Locality 3* Yalgoo, 28°18'45", 116°38'00", 6 males, 6 females, WAM (M10115-20, M10125-30). *Locality 4* Murgoo Homestead, 27°28'40", 116°22'10", 3 males, 3 females, WAM (M9653, M10239-40, M10244-45). *Locality 5* Wilgie Mia, 26°56', 117°42', 6 males, 5 females, WAM (M3803-08, M4639, M5964, M8187, M10148-49). *Locality 6* Gnumartina Bat Cave, 26°22'30", 117°08'10", 1 female, WAM M4303. *Locality 7* Peak Hill Gold Mine, 25°36'00", 118°43'30", 3 females, WAM (M12211-13). *Locality 8* Peak Hill, 25°36', 118°49', 1 male, 2 females, WAM (M10716-18). *Locality 13* Mount Meharry, 23°12'00", 118°49'30", 1 male, 6 females, WAM (M16751, M16815, M16817, M16818/001, M16819-20, M18252). *Locality 15* Opthalmia Range, 23°10', 118°50', 1 female, WAM M18041. *Locality 19* Paraburdoo Minesite, 23°13'30", 117°37'00", 1 male, WAM M14937. *Locality 25* Hamersley Range National Park (including Mt Bruce), 22°39'03", 118°08'30", 2 males, 3 females, WAM (M18260 (holotype), M18261, M18264-65). *Locality 31* Bamboo, 20°55'00", 120°13'15", 2 females, WAM (M3273, M7056). *Locality 40* Muggan Rock Holes, 27°01', 125°20', 1 male, 2 females, WAM (M5241/001-002), CAM M408. *Locality 41* Manunda Rock Hole, 26°50'50", 125°39'30", 1 male, WAM M4626. *Locality 42* Gahnda Rock Hole, 26°36', 125°52', 1 male, 3 females, WAM (M5242/001-003, M13372). *Locality 43* Mount Charles, 25°45', 126°11', 1 female, WAM M14640. *Locality 44* Charles' Knob, 25°03', 124°59', 2 females, WAM (M14641-42). *Locality 45* Great Sandy

Desert, 20°50′, 127°59′, 2 males, 2 females, WAM (M22843-44, M22846, M22849). *Locality 103* Tennant Creek, 19°39′, 134°00′, 6 males, 4 females, CM M845, WAM B (128-29), NTM (M357-59), WAM (M5844-47). *Locality 104* Peko Mine, 19°41′, 134°17′, 2 males, 4 females, WAM (M6283-88). *Locality 105* Hatches Creek, 20°56′, 135°12′, 3 females, NTM (M4274-76). *Locality 106* 8 km east of Arltunga, 23°28′, 134°43′, 3 females, CM (M5836, M5838, M13218). *Locality 107* Arltunga Gold Mine, 23°30′, 134°50′, 1 female, CAM M175. *Locality 109* Hermannsburg Station, 29°59′, 132°46′, 1 male, NTM M5331. *Locality 110* Tennant Creek, 19°39′, 134°11′, 1 female, CM M4167. *Locality 111* 10 km south-east Mount Leichard, 21°51′, 132°37′, 1 female, CAM M408.

Taphozous kapalgensis

Locality 125

Kapalga, South Alligator River, 12°36′, 132°25′, 2 males, 1 female, CM (M4806 (paratype), 4823), WAM M18580.

Taphozous troughtoni

Locality 139

Ballara, 20°57′, 139°58′, 1 male, CM M4145. *Locality 140* Native Bee Mine, Mount Isa, 20°44′, 139°29′, 3 females, CM (M13213, M13215, M13217).

Saccolaimus flaviventris

Locality 10

Karri Karri Pool, 25°29′, 120°37′, 1 male, WAM M14400. *Locality 11* Mount Salvado, 25°17′, 120°42′, 1 female, WAM M14639. *Locality 12* Durba Spring, 23°45′20″, 122°31′00″, 3 males, 1 female, WAM (M14396-99). *Locality 17* Marillana Homestead, 22°46′00″, 119°13′08″, 2 males, WAM (M18398, M19406). *Locality 18* Pingandy Creek, 23°58′, 117°40′, 1 female, WAM M6622. *Locality 25* Hamersley Range National Park, 22°38′46″, 118°08′03″, 1 female, WAM M18650. *Locality 26* Great Sandy Desert, 22°32′50″, 122°24′20″, 1 male, WAM M22868. *Locality 34* Coongan River, 20°55′, 119°47′, 1 female, WAM M22870. *Locality 46* Great Sandy Desert, 20°17′, 127°26′, 1 female, WAM M22870. *Locality 47* Fossil Downs, 18°08′30″, 125°36′45″, 1 male, WAM M5732. *Locality 52* Barker Gorge, 17°15′20″, 124°43′45″, 1 male, WAM M18500. *Locality 60* Edgar Range, 18°27′45″, 123°40′30″, 2 females, WAM (M15127-28). *Locality 61* Edgar Range, 18°49′20″, 123°17′50″, 2 males, 3 females, WAM (M15037-39, M22265, M22869). *Locality 62* Edgar Range (Hatches Bore) 18°22′45″, 123°03′25″, 7 males, 3 females, WAM (M15040-45, M15131, M17459). *Locality 64* Waterbank Homestead, 17°44′20″, 122°14′52″, 4 males, 2 females, WAM (M24019-21, M24057, M24065, M24071). *Locality 65* Point Coulomb, 17°21′20″, 122°09′20″, 3 males, 1 female, WAM (M8432, M22531, M22535, M22662). *Locality 66* Cocky Well, 16°43′50″, 122°48′30″, 1 female, WAM M22534. *Locality 70* Wotjulum Mission, 16°11′, 123°37′, 1 male, WAM M3001. *Locality 75* Prince Regent River Reserve, 15°48′11″, 125°20′26″, 2 males, 1 female, WAM (M12252-54). *Locality 76* Mitchell Plateau, 14°49′10″, 125°50′20″, 3 males, 7 females, WAM (M21791, M21828-33, M21852-53, M21875). *Locality 77* Drysdale River Crossing, 15°40′30″, 126°23′45″, 1 female, WAM M14359. *Locality 81* Drysdale River National Park, 14°43′, 126°54′, 2 males, WAM (M14022-23). *Locality 83* Drysdale River National Park, 15°09′, 127°06′, 3 females, WAM (M14019-21). *Locality 84* Wyndham, 15°28′, 128°06′, 1 female, AM M6768. *Locality 90* Keep River National Park, 15°58′, 129°02′ 1 female, CAM M602. *Locality 100* Tanami Desert, 20°09′, 130°15′, 1 female, NTM M2779. *Locality 101* Tanami Desert, 20°13′, 131°47′, 1 male, CAM M8. *Locality 102* Banka Banka Station, 18°48′, 134°02′, 1 female, CM M2472. *Locality 103* Tennant Creek, 19°39′, 134°02′, 1 male, SAM M498. *Locality 108* Temple Bar Creek, Alice Springs, 23°45′, 133°44′, 1 female, CM M2426. *Locality 113* Murrayi, 16°50′, 132°48′, 2 females, CAM M57-58. *Locality 114* Dorisvale, 14°10′, 131°00′, 1 female, CM M6660. *Locality 115* Daly River, 14°48′, 131°24′, 1 female, CAM M36. *Locality 116* Daly River, 14°22′, 131°33′, 1 female, CAM M30. *Locality 119* Katherine Gorge, 14°06′, 132°18′, 5 females, CAM (M610-612). *Locality 121* Twin Peaks, 13°45′, 130°43′, 1 male, 1 female, WAM (M8424-25). *Locality 123* 35 km south of Darwin, 12°27′, 130°50′, 1 male, B 190. *Locality 124* Point Charles, 12°23′, 130°37′, 1 male, C 928. *Locality 126* Smith Point, Coburg Peninsula, 11°16′, 132°09′, 3 males, CM (M1896, M1900-01). *Locality 127* Nourlangie Rock, 12°43′, 132°33′, 1 male, CM M4671. *Locality 128* Oenpelli, 12°19′, 133°03′, 1 female, B 190. *Locality 129* Deaf Adder Creek, 13°06′, 132°56′, 1 male, CAM 4702. *Locality 130* Deaf Adder Gorge, 13°03′, 132°52′, 1 female, AM M10352. *Locality 141* Norman River, Normanton, 17°40′, 141°04′, 1 female, JM 2037. *Locality 142* Gulf of Carpentaria, 13°01′, 141°44′, 1 male, C 1482. *Locality 149* Ingham, 18°39′, 146°10′, 1 male, CM M1580. *Locality 153* Thirlstone, Torres Creek, 21°37′, 145°35′, 1 male, the other sex unknown, JM (M8816-17). *Locality 155* Glengalon, south-east of Emerald, 23°31′, 148°10′, 1 female, JM M15531. *Locality 158* Yebna Station 80 km west of Taroomm, 25°41′, 149°11′, 1 female, JM M15813. *Locality 159* Eidsvold, 25°22′, 151°07′, 1 male, JM 3082. *Locality 160* Landsborough, 26°48′, 152°48′, 1 female, JM M10948. *Locality 161* Cowan Cowan, Morton Island, 27°11′, 153°04′, 1 male, JM 4069. *Locality 162* Mount Crosby, 27°32′, 152°48′, 1 male, JM 9797. *Locality 163* Greymere, 28°14′, 151°45′, 2 females, JM (13308-09). *Locality 164* Durikai, 28°12′, 151°37′, 1 male, 1 female, JM (M13337, M13849). *Locality 165* Moree, 29°28′, 149°51′, 1 male, 1 female, AM (M918, M3228). *Locality 166* Mungindi, 28°59′, 149°00′, 2 males, 1 female, AM (M5521, M7920, M7922). *Locality 167* Brewarrina, 29°58′, 146°52′, 1 male, AM M8190. *Locality 168* Killara, Sydney, 31°28′, 150°36′, 1 female, AM M7384. *Locality 169* Frankston, 38°09′, 145°08′, 1 male, C 5130. *Locality 170* St Albans, 37°45′, 144°48′, 1 male, C 5132. *Locality 171* Winchelsea, 38°15′, 143°59′, 1 female, C 5131. *Locality 172* Coombe, 35°58′, 140°13′, 1 male, SAM M5206. *Locality 173* Berri, 34°17′, 140°36′, 1 male, SAM M7698. *Locality 174* Railway Siding, 34°56′, 138°36′, 1 male, SAM M5659. *Locality 175* Meningie, 35°41′, 139°20′, 1 male, SAM M3155. *Locality 176* Salt Creek, 36°08′, 139°39′, 1 female, SAM M7698.

Saccolaimus mixtus
(non-Australian)

Port Moresby, Papua New Guinea, 1 male, Two specimens sex unknown, AM (M3256 (paratype), M3257 (holotype), M3258 (paratype)).

Saccolaimus saccolaimus
Locality 145

Upper Endeavor River, 15°20′, 145°11′, 1 female, C 310. *Locality 146* Cooktown, 15°59′, 145°08′, 1 female, JM M19028. *Locality 151* Jerona Fauna Sanctuary, 19°34′, 147°13′, 1 male, WAM M23334. *Locality 152* Mosman, 1 female, JM M19028 (*S. 'nudicluniatus'*).

Non Australian Specimens Examined

Saccolaimus saccolaimus

Borneo, 1 male, WAM (M26085); India, 1 female, AMNH (27420); Java, 5 males, 1 female, AMNH (101602-06); Solomon Islands, 1 male, FMNH 54806 (*S. 'nudicluniatus'*).

Taphozous longimanus

Bali, 3 males, 1 female, WAM (M16182-85), Madras, India, 1 male, C 2210.

Appendix II Measurements, in mm for holotypes and unique specimens of some Australian emballonurids examined. Body measurements are from alcohol preserved specimens. For code to characters see Figure 2.

Species / Catalogue No./ Character	*Saccolaimus mixus* AM M3258 (paratype)	*Taphozous hilli* M18260 WAM (holotype)	*Taphozous kapalgensis* CM M4806 (paratype)	*Taphozous troughtoni* CM M13213	*Taphozous georgianus* Derby W.A. WAM M24032	*Taphozous georgianus* Mount Isa Qld CM M13216	*Taphozous georgianus* Rockhampton Qld JM M9976
Sex	?	Female	Male	Female	Female	Female	Female
GL	21.7	20.0	20.7	24.3	21.0	22.0	22.6
AOW	6.6	6.0	5.9	6.8	6.1	6.5	6.5
LOW	7.9	6.2	6.4	7.1	6.1	6.6	6.3
ZW	—	13.0	13.0	14.7	13.1	13.3	14.2
ROL	8.6	8.2	8.7	10.2	8.6	9.2	9.6
MW	12.1	10.5	11.2	12.1	10.5	11.0	11.7
BW	11.6	10.6	10.9	11.7	10.0	10.7	10.5
CH	8.0	7.4	7.6	8.4	7.1	7.5	8.1
PL	8.8	7.1	8.0	9.8	8.6	8.8	8.9
PPW	—	3.4	—	4.7	3.7	3.8	4.1
BL	18.7	16.3	18.4	21.2	18.6	19.1	19.6
BUL	4.9	5.1	5.2	5.6	5.0	5.0	5.1
BB	3.4	2.2	2.3	2.6	2.1	2.0	2.3
OB	11.6	10.2	9.1	11.5	10.0	10.4	10.6
CW	1.8	1.7	2.0	2.2	1.9	2.0	2.1
RC^1-LC^1	4.8	3.5	4.0	4.5	4.0	4.1	4.3
C^1-M^3	10.0	8.8	9.3	11.0	8.8	10.0	10.3
M^1-M^3	5.4	4.8	5.0	5.8	4.9	5.3	5.6
M^2L	2.2	1.9	2.0	2.2	1.9	2.0	2.2
M^2W	2.4	2.4	2.3	2.6	2.5	2.4	2.6
M^3W	2.1	2.0	2.1	2.4	2.1	2.2	2.2
RM^3-LM^3	10.2	8.4	9.1	10.7	9.1	9.2	9.9
LR	12.2	10.7	11.0	13.1	11.4	12.0	12.3
RC	5.7	4.6	5.2	5.8	5.1	5.0	5.4
DL	18.7	16.1	17.1	20.7	17.6	18.8	19.1
SPL	4.0	4.3	3.7	4.6	4.5	3.9	4.0
PBW	1.0	0.3	0.6	0.6	0.5	0.6	0.7
ICD	3.2	2.9	2.9	3.3	2.8	3.0	3.2
HV	—	75.1	68.8	81.8	72.0	74.7	—
TV	—	30.7	22.8	36.9	26.7	32.3	—
EL	—	22.6	17.6	26.6	20.1	19.2	—
EW	—	14.9	13.2	19.0	15.0	14.8	—
TL	—	6.1	5.6	9.4	7.1	7.1	—
RL	—	68.9	59.2	75.6	65.2	69.6	—
MCIII	—	61.7	60.2	69.1	57.2	64.4	—
PI	—	20.4	21.1	24.6	19.2	20.9	—
PII	—	25.7	21.4	27.1	23.5	26.0	—
TIB	—	26.8	23.1	31.7	26.7	27.0	—
PES	—	12.9	12.4	14.7	12.1	12.6	—

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