Morphometric analysis of cranial and external characters of *Laephotis* Thomas, 1901 (Mammalia: Chiroptera: Vespertilionidae) from southern Africa

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Morphometric analyses, which included palatal and post-palatal measurements, allow the distinction of *Laephotis botswanae* and *L.* cf. *angolensis* from other *Laephotis* species, and suggest the assignment of specimens from KwaZulu-Natal in South Africa previously identified as *L.* cf. *wintoni* to *L. botswanae.* The distinction between *L. wintoni* and *L. namibensis,* however, was not confirmed and still remains to be clarified. It is suggested that until the species distinction is further clarified by additional characters or other systematic techniques, the current species assignments be retained. Morphometric analyses based on cranial characters, which excluded palatal and post-palatal measurements, show some separation of the *Laephotis* species in the principal component analysis, but not in the cluster analysis. Analyses based on external characters only were not useful for the separation of the *Laephotis* species.

Keywords: *Laephotis,* Species Identification, Cranial and External Measurements, Multivariate Morphometrics.

INTRODUCTION

Although the genus *Laephotis* Thomas, 1901, is poorly known due to the paucity of specimens (Kock and Howell, [1988]; Stanley and Kock, 2004), four species are currently recognized (Koopman, 1993): *L. angolensis* Monard, 1935, *L. botswanae* Setzer, 1971, *L. namibensis* Setzer, 1971, and *L. wintoni* Thomas, 1901. The accurate species identification of individuals of the genus *Laephotis* found in the southwestern (Rautenbach and Nel, 1978) and southeastern (Kearney and Taylor, 1997; Watson, 1990) parts of southern Africa has proved contentious and complicated. The initial identification of a specimen from the Western Cape Province, South Africa as *L. wintoni* (Rautenbach and Nel, 1978) was made on the basis of a multivariate morphometric analysis of nine measurements using mean values calculated for each of the *Laephotis* species from measurements in Hill (1974). This identification was contrary to an assumption of the species' identity as *L. namibensis* based on the closer geographic proximity of the Western Cape locality to localities of *L. namibensis,* whereas the Western Cape locality is much further from localities of the type and other specimens of *L. wintoni.* Rautenbach and Nel (1978) cautioned that their analysis indicated the taxonomic status of species in the genus *Laephotis* was not satisfactorily resolved, and would require further specimens to remedy the problem. Neither Honacki *et al.* (1982) nor Corbet and Hill (1991) followed the contentious identification by Rautenbach and Nel (1978), instead they both referred the specimen from the Western Cape to *L. namibensis.* Later, Koopman (1994) indicated *L. namibensis* was only definitely known from Namibia, and that the Western Cape specimen apparently belonged to *L. wintoni.* However, the species account for *L. wintoni* was withdrawn from the accounts in 'Mammals of the Southern African Subregion' (Skinner and Smithers, 1990:107) as 'further investigation in progress by I.L. Rautenbach and D.A. Schlitter reveal that this specimen is placed more appropriately with *L. namibensis* (I.L. Rautenbach, pers. comm.), with which it is provisionally placed'. Using the same morphometric analysis and measurements as Rautenbach and Nel (1978), subsequent records of *Laephotis* from the Free State, Lesotho (Watson, 1990) and KwaZulu-Natal (Kearney and Taylor, 1997) were also identified as *L. wintoni* and *L.* cf. *wintoni.* Of the currently recognized *Laephotis* species, only *L. wintoni* and *L. botswanae* were assessed in the latest Red Data Book of the Mammals of South Africa (Friedmann and Daly, 2004), since the taxonomic emendation in Skinner and Smithers (1990) recognizing the specimens from the Western Cape as *L. namibensis* was not taken into account.

The measurement suite of nine standard morphometric measurements, one forearm and eight

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cranial and dental measurements, used in previous multivariate analyses to identify specimens of South African *Laephotis* (Rautenbach and Nel, 1978; Watson, 1990; Kearney and Taylor, 1997) did not incorporate Hill's (1974) six palatal and post-palatal measurements. Stanley and Kock (2004) confirmed palatal and post-palatal measurements as characteristic and useful for the separation of at least two of the *Laephotis* species, *L. wintoni* and *L. botswanae.* Hill (1974) identified that in *L. wintoni* the post-palatal measurement of the distance from a line across the rear margins of M^3 to the anterior edge of the mesopterygoid fossa is longer than the distance from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars. In *L. botswanae* and *L. angolensis,* however, the post-palatal measurement of the distance from a line across the rear margins of M^3 to the anterior edge of the mesopterygoid fossa is shorter than the distance from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars (Hill, 1974). The aim of this study was to revisit as many of the specimens of southern African *Laephotis* as possible to assess their identification with reference to palatal and post-palatal measurements (Hill, 1974; Stanley and Kock, 2004) and to include these measurements in a morphometric analysis to evaluate whether they support earlier morphometric identifications.

MATERIAL AND METHODS

Eighteen cranial and mandibular measurements (Table 1, Fig. 1) were taken with digital callipers from 36 specimens of *Laephotis* variously ascribed to the species *botswanae, namibensis,* cf. *wintoni* and *wintoni* (see Appendix I for specimen details). Where appropriate, the same measurement abbreviations used by Stanley and Kock (2004) have been followed. Measurements were made of the same eight cranial and dental lengths included in previous analyses of specimens from South Africa: greatest skull length, from anterior-most point of I^1 to posterior-most point of occipital (Cnr inc); condylocanine length (Cdl); zygomatic width (Zyg); least postorbital breadth (Por); braincase breadth (Bcw); braincase depth, from basioccipital bone to top of braincase (Bcd); greatest breadth across outer edge of upper canines (C–C); width across outer edge of upper third molars (M^3–M^3); maxillary tooth row from anterior surface of canine to posterior surface of upper third molar (C–M^3). An additional four cranial, mandibular and dental measurements were added: skull breadth at mastoids (Mast); length from anterior surface of first upper incisor to posterior surface of upper third molar (I^1–M^3); mandible length (Mand); length from anterior surface of canine to posterior surface of lower third molar (C–M_3). The six palatal measurements described by Hill (1974) included: palatal length from the anterior edge of incisors to anterior edge of mesopterygoid fossa (Palat); length from the rear of pre-palatal emargination to anterior edge of mesopterygoid fossa (Lpp–mesop); length from rear of pre-palatal emargination to line across posterior faces of M^{3-3} (Lpp–M^3); length from line across posterior faces of M^3–M^3 to anterior edge of mesopterygoid fossa (LM^3–mesop); length from anterior edge of mesopterygoid fossa to tip of pterygoid hamulars (Lmesop–ham); length from line across posterior faces of M^{3-3} to tip of pterygoid hamulars (LM^3–ham).

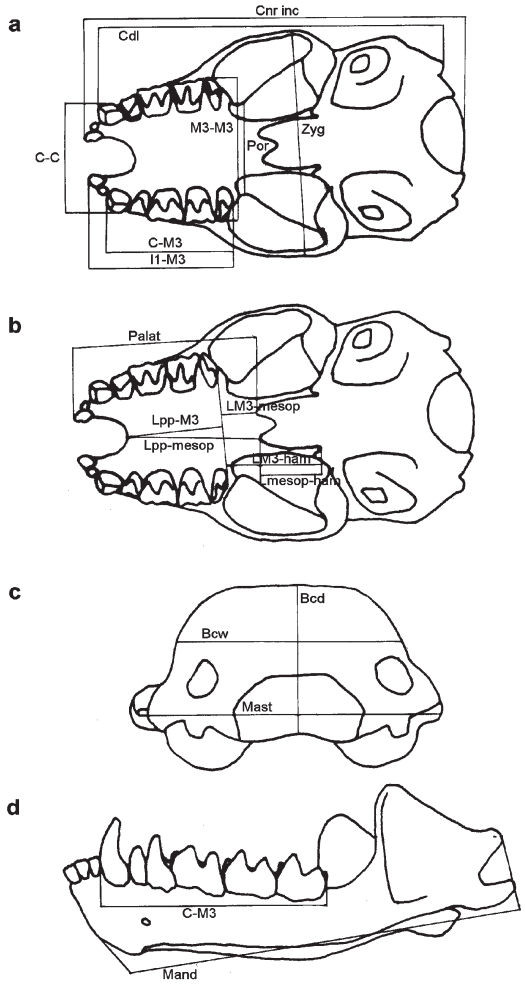

Fig. 1

Diagrams showing the position of measurements on the ventral (**a** and **b**) and posterior (**c**) skull, and lateral mandible (**d**). See material and methods for a description of measurement abbreviations.

Five external measurements (Table 2) were noted

Table 1

Cranial measurements of various *Laephotis* species used in this analysis taken from the literature (L1 = Hill, 1974; L2 = Stanley and Kock, 2004; L3 = Setzer, 1971; L4 = Kock and Howell, [1988]; L5 = Bauer, 1992) or measured (M) by one of the authors (TK). Species identification (Id) records information from the most recent literature and, where unpublished, follows museum records for the specimen: L.cf.a = *L.* cf. *angolensis*; L.b = *L. botswanae*; L.cf.w = *L.* cf. *wintoni*; L.n = *L. namibensis*; L.w = *L. wintoni*. Holotypes are denoted by *, paratypes by +. See text of material and methods for descriptions of measurement abbreviations.

Code	Accession	Source	Id	Cnr inc	Cdl	Zyg	Por	Bcw	Bcd	C–C	M^3–M^3	C–M^3	Mast
ca1	BM57.435	L1	L.cf.a	13.80	13.10	8.10	3.40	6.80	4.50	3.80	5.20	4.30	7.40
ca2	BM57.437	L1	L.cf.a	13.70	12.90	–	3.50	6.80	4.30	3.70	5.00	4.30	7.40
b1	MRAC26.402	L1	L.b	14.50	13.60	–	3.70	7.40	4.60	4.00	5.40	4.50	7.90
b2	MRAC26.403	L1	L.b	14.30	13.50	–	3.70	7.30	4.60	4.00	5.40	4.60	7.60
b3	MRAC26.404	L1	L.b	14.60	13.70	–	3.50	7.10	4.60	4.00	5.40	4.50	7.80
b4	MRAC26.405	L1	L.b	14.30	13.60	–	3.60	7.20	4.70	3.80	5.20	4.50	7.80
b5	BM55.1135	L1	L.b	14.30	13.50	–	3.60	7.10	4.50	4.00	5.50	4.60	7.50
b6	HZM1.2533	L1	L.b	15.00	14.30	8.80	3.70	7.40	4.60	4.30	5.80	4.80	8.40
b7	FMNH84120	L2	L.b	14.90	13.65	8.73	3.70	7.06	4.84	4.37	5.56	4.68	7.63
b8	FMNH83605	L2	L.b	14.52	13.27	8.59	3.65	–	4.75	3.93	5.45	4.52	7.28
b9	FMNH152728	L2	L.b	14.50	13.40	8.50	3.46	7.19	4.84	4.10	5.50	4.58	7.58
b10*	USNM425349*	L3	L.b	14.50	–	8.30	3.40	7.00	4.70	4.40	5.40	4.70	–
b11	NMW19823	L5	L.b	–	–	–	–	–	–	–	–	–	–
b12	TM44544	M	L.b	15.50	14.85	8.75	3.60	7.30	4.91	4.45	5.55	4.90	8.20
b13	TM38153	M	L.b	–	–	8.60	3.65	7.05	5.03	4.20	5.40	4.70	7.90
b14	TM38154	M	L.b	15.05	14.50	8.60	3.60	7.05	4.81	4.20	5.45	4.80	7.80
b15	TM40107	M	L.b	14.90	14.50	8.35	3.60	7.05	–	4.15	5.40	4.75	8.20
b16	TM39946	M	L.b	14.65	13.90	8.00	3.75	7.15	4.58	4.20	5.50	4.70	7.60
b17	TM38123	M	L.b	14.45	13.90	8.25	3.65	6.90	–	4.10	5.50	4.70	7.70
b18	TM38155	M	L.b	14.90	14.25	8.70	3.65	7.30	4.72	4.25	5.55	4.70	8.05
b19	TM39796	M	L.b	14.75	14.35	8.00	3.55	6.95	4.76	4.05	5.30	4.60	7.85
b20	TM34964	M	L.b	14.40	13.80	8.05	3.60	6.85	5.04	4.00	5.20	4.50	7.60
b21	NM29992	M	L.b	14.67	13.81	–	3.75	7.22	4.61	–	5.59	4.66	7.96
b22	NM29592	M	L.b	14.89	14.23	–	3.76	7.26	4.75	4.22	5.37	4.90	7.87
b23	NM30030	M	L.b	14.73	13.47	–	3.57	7.30	4.76	–	5.21	4.55	–
b24	NM58131	M	L.b	14.55	13.43	–	3.63	7.05	4.53	4.10	5.39	4.67	–
b25	NM59330	M	L.b	14.50	13.41	–	3.53	7.13	4.71	4.12	5.38	4.80	7.60
b26	NM63201	M	L.b	14.14	13.12	–	3.64	6.97	4.60	3.92	5.17	4.59	7.64
b27	NM63202	M	L.b	14.60	13.55	–	3.63	6.96	4.57	4.08	5.53	4.94	7.63
cw1	DM6898	M	L.cf.w	15.22	14.27	8.73	3.75	7.43	4.45	4.47	5.65	4.86	8.28
cw2	DM5351	M	L.cf.w	14.99	13.97	8.66	3.72	7.36	4.86	4.35	5.53	4.91	8.14
cw3	DM6899	M	L.cf.w	15.00	13.95	8.46	3.84	7.19	4.76	4.41	5.33	4.82	8.03
n1*	USNM342152*	L3	L.n	16.50	–	9.00	3.20	7.50	4.70	4.00	5.20	4.90	–
n2*	USNM342153+	L3	L.n	16.50	–	–	3.60	7.60	4.90	4.00	5.40	5.00	–
n3	TM37548	M	L.n	16.30	15.40	8.85	3.65	7.95	5.12	4.30	5.50	4.85	8.15
n4	TM37586	M	L.n	16.90	16.20	9.00	3.60	7.70	4.92	4.30	5.45	5.15	8.20
n5	TM37547	M	L.n	16.10	15.40	8.55	3.65	7.95	4.87	4.15	5.10	4.75	7.95
n6	TM33472	M	L.n	16.25	15.25	8.40	3.45	7.40	4.82	3.95	5.20	4.90	7.80
n7	TM37608	M	L.n	16.10	15.25	8.95	3.75	7.80	4.89	4.15	5.20	5.00	8.10
n8	TM37609	M	L.n	16.05	15.45	8.75	3.65	7.65	4.77	4.10	5.30	4.90	8.00
n9	TM28316	M	L.n	16.25	15.65	8.85	3.80	7.60	5.00	4.30	5.55	5.20	8.40
n10	TM38426	M	L.n	17.00	16.70	9.15	3.90	7.95	5.32	4.35	5.55	5.35	8.60
n11	ZM41415	M	L.n	16.66	15.26	9.15	3.85	7.95	5.13	4.46	5.44	5.24	8.68
n12	ZM41417	M	L.n	16.61	15.28	9.00	3.64	7.68	5.05	4.33	5.46	5.18	8.58
w1	NMB6698	M	L.w	15.97	15.31	9.19	4.14	7.96	5.17	4.64	5.72	5.33	8.54
w2	NMB6687	M	L.w	15.90	15.18	9.22	3.95	8.05	5.12	4.45	5.79	5.16	–
w3	NMB6688	M	L.w	–	15.17	9.00	3.97	7.87	–	4.40	5.63	5.22	8.70
w4	NMB6686	M	L.w	15.94	15.12	–	3.94	7.77	5.06	4.61	5.69	5.25	8.59
w5	NMB6697	M	L.w	15.98	15.33	9.03	3.84	7.87	4.94	4.47	–	5.25	8.50
w6	NMB6379	M	L.w	15.58	14.93	8.99	3.92	7.86	4.97	4.39	5.42	5.11	8.26
w7	NMB6378	M	L.w	15.78	15.23	8.76	3.94	7.82	4.98	4.38	5.62	5.18	8.48
w8	BM72.4398	L1	L.w	16.30	15.50	9.40	3.90	7.50	4.70	4.60	5.90	5.20	8.50
w9	BM72.4397	L1	L.w	16.30	15.60	8.90	3.70	7.40	4.80	4.50	5.60	5.20	8.30
w10*	BM1.5.6.5*	L1	L.w	15.80	15.20	–	3.70	7.40	4.80	4.30	5.50	5.00	8.50
w11	BM72.4399	L1	L.w	16.20	15.80	9.10	3.70	7.60	4.80	4.50	5.50	5.00	8.50
w12	SMF66961	L4	L.w	15.80	14.80	9.00	3.90	7.70	–	–	5.90	5.20	8.20
w13	FMNH171300	L2	L.w	16.20	14.92	9.50	3.87	7.61	5.04	4.52	5.87	5.16	8.21

Table 1 (*continued*)

Code	Accession	Source	Id	I^1–M^3	Mand	C–M_3	Palat	Lpp–mesop	Lpp–M^3	LM^3–mesop	Lmesop–ham	LM^3–ham
ca1	BM57.435	L1	L.cf.a	–	8.80	4.80	6.20	4.80	3.60	1.20	2.00	3.20
ca2	BM57.437	L1	L.cf.a	–	8.90	4.70	6.10	4.80	3.50	1.30	1.90	3.20
b1	MRAC26.402	L1	L.b	–	9.40	4.90	6.60	5.20	3.70	1.50	2.00	3.50
b2	MRAC26.403	L1	L.b	–	9.10	4.90	6.60	5.20	3.70	1.50	1.90	3.40
b3	MRAC26.404	L1	L.b	–	9.50	5.00	6.40	5.20	3.80	1.40	1.90	3.30
b4	MRAC26.405	L1	L.b	–	9.20	5.00	6.50	5.30	3.80	1.50	1.90	3.40
b5	BM55.1135	L1	L.b	–	9.20	4.90	6.40	5.20	3.70	1.50	1.90	3.40
b6	HZM1.2533	L1	L.b	–	9.90	5.20	7.10	5.60	4.10	1.50	2.00	3.50
b7	FMNH84120	L2	L.b	–	9.85	5.15	7.29	5.26	3.92	1.34	1.90	3.24
b8	FMNH83605	L2	L.b	–	–	–	6.31	–	–	1.22	2.22	–
b9	FMNH152728	L2	L.b	–	9.45	4.94	6.16	4.90	3.96	0.94	2.24	3.28
b10*	USNM425349*	L3	L.b	–	–	–	–	–	–	–	–	–
b11	NMW19823	L5	L.b	–	–	–	6.60	5.20	3.80	1.50	1.90	3.40
b12	TM44544	M	L.b	5.65	10.35	5.15	7.15	5.63	4.18	1.45	2.18	3.45
b13	TM38153	M	L.b	–	9.95	4.80	6.70	5.47	3.87	1.58	1.68	3.16
b14	TM38154	M	L.b	5.45	10.25	5.20	6.78	5.56	4.17	1.45	2.05	3.15
b15	TM40107	M	L.b	5.50	10.05	5.10	6.73	5.21	4.02	1.40	2.26	3.41
b16	TM39946	M	L.b	5.47	9.99	5.18	6.64	5.19	3.85	1.47	1.89	3.08
b17	TM38123	M	L.b	5.48	10.01	5.16	6.85	5.45	4.18	1.47	1.95	3.07
b18	TM38155	M	L.b	5.45	10.05	5.10	–	–	3.68	–	–	2.64
b19	TM39796	M	L.b	5.35	10.00	4.90	6.97	5.54	4.01	1.65	1.84	3.33
b20	TM34964	M	L.b	5.20	9.70	4.80	–	–	4.02	–	–	3.37
b21	NM29992	M	L.b	5.34	10.00	5.06	6.51	5.10	3.91	1.49	2.14	3.44
b22	NM29592	M	L.b	5.42	10.24	5.17	6.78	5.29	3.84	1.49	2.26	3.62
b23	NM30030	M	L.b	5.20	–	4.78	6.40	4.99	3.79	1.31	–	–
b24	NM58131	M	L.b	5.34	–	4.97	6.43	4.93	3.67	1.45	–	–
b25	NM59330	M	L.b	5.46	–	5.16	–	–	–	–	–	–
b26	NM63201	M	L.b	5.29	–	4.84	–	–	–	–	–	–
b27	NM63202	M	L.b	5.37	9.94	5.03	–	5.03	3.67		2.09	3.60
cw1	DM6898	M	L.cf.w	5.63	10.41	5.26	7.03	5.49	3.99	1.57	2.30	3.70
cw2	DM5351	M	L.cf.w	5.63	10.17	5.20	6.94	5.40	4.31	1.54	2.13	3.29
cw3	DM6899	M	L.cf.w	5.61	10.20	5.06	6.94	5.60	4.25	1.69	2.01	3.53
n1*	USNM342152*	L3	L.n	–	–	–	–	–	–	–	–	–
n2*	USNM342153'	L3	L.n	–	–	–	–	–	–	–	–	–
n3	TM37548	M	L.n	5.70	10.85	5.75	7.93	6.37	4.61	2.30	2.13	4.18
n4	TM37586	M	L.n	5.95	11.50	5.40	8.20	6.74	4.53	2.34	2.00	4.32
n5	TM37547	M	L.n	5.64	11.21	5.10	7.63	6.23	4.42	2.19	–	–
n6	TM33472	M	L.n	5.60	10.35	5.05	7.59	6.39	4.24	1.86	–	–
n7	TM37608	M	L.n	5.77	10.80	5.28	7.81	6.13	4.36	2.16	2.00	3.94
n8	TM37609	M	L.n	5.60	10.65	5.10	7.75	6.11	4.24	2.21	2.01	4.01
n9	TM28316	M	L.n	6.10	11.15	5.40	8.24	6.47	4.62	1.96	–	–
n10	TM38426	M	L.n	6.30	11.50	5.50	8.72	6.78	4.68	2.47	2.61	4.54
n11	ZM41415	M	L.n	6.22	10.95	5.45	8.24	6.39	4.69	2.18	2.50	4.31
n12	ZM41417	M	L.n	6.14	11.13	5.53	7.97	6.39	4.62	2.08	2.49	4.27
w1	NMB6698	M	L.w	6.18	11.56	5.62	8.18	6.68	4.58	2.11	2.22	3.93
w2	NMB6687	M	L.w	6.09	11.46	5.45	8.13	6.74	4.63	2.03	2.25	4.17
w3	NMB6688	M	L.w	6.15	11.29	5.53	8.13	6.90	4.86	2.13	2.47	4.41
w4	NMB6686	M	L.w	6.22	–	5.46	8.23	6.57	4.50	2.04	2.46	4.34
w5	NMB6697	M	L.w	6.11	11.25	5.46	8.16	6.75	4.43	2.10	2.43	4.48
w6	NMB6379	M	L.w	6.04	10.88	5.44	7.90	6.43	4.40	1.97	2.18	4.03
w7	NMB6378	M	L.w	5.99	11.17	5.40	7.91	6.47	4.52	2.15	–	–
w8	BM72.4398	L1	L.w	–	10.70	5.50	8.20	6.40	4.20	2.20	2.00	4.20
w9	BM72.4397	L1	L.w	–	10.80	5.60	8.10	6.80	4.40	2.40	1.80	4.20
w10*	BM1.5.6.5*	L1	L.w	–	10.60	5.50	7.90	6.50	4.40	2.10	1.90	4.00
w11	BM72.4399	L1	L.w	–	–	5.50	8.50	6.80	4.30	2.50	1.90	4.40
w12	SMF66961	L4	L.w	–	10.90	5.40	–	–	–	–	–	–
w13	FMNH171300	L2	L.w	–	10.49	5.55	8.01	6.47	4.20	2.20	1.92	4.07

Table 2

External measurements used in this analysis (Source) taken from the literature (L1 = Hill, 1974; L2 = Stanley and Kock, 2004; L3 = Setzer, 1971; L4 = Kock and Howell, [1988]; L5 = Bauer, 1992), specimen labels (S), measured on dry skins (M) by one of the authors (TK), and calculated (C) (see material and methods for explanation). Species identification (Id) records information from the most recent literature and, where unpublished, follows museum records for the specimen: L.cf.a = *Laephotis* cf. *angolensis*; L.b = *L. botswanae*; L.cf.w = *L.* cf. *wintoni*; L.n = *L. namibensis*; L.w = *L. wintoni*. Holotypes are denoted by '*', paratypes by '+'. See materials and methods for a description of measurement abbreviations.

Code	Accession no.	Source	Id	TL	T	HF	E	FA
ca1	BM57.435	L1	L.cf.a	–	–	–	16.0	35.5
ca2	BM57.437	L1	L.cf.a	–	–	–	15.9	34.3
b1	MRAC26.402	L1	L.b	–	–	–	16.5	37.8
b2	MRAC26.403	L1	L.b	–	–	–	16.3	35.8
b3	MRAC26.404	L1	L.b	–	–	–	16.8	37.0
b4	MRAC26.405	L1	L.b	–	–	–	17.9	36.4
b5	BM55.1135	L1	L.b	–	–	–	–	35.3
b6	HZM1.2533	L1	L.b	–	–	–	–	37.0
b7	FMNH84120	L2	L.b	100.0	45.0	6.0	19.0	37.5
b8	FMNH83605	L2	L.b	96.0	44.0	6.5	19.0	37.0
b9	FMNH152728	L2	L.b	99.0	43.0	6.0	18.0	34.8
b10*	USNM425349*	L3	L.b	96.0	41.0	8.0	21.0	37.3
b11	NMW19823	L5	L.b	–	39.5	7.5	16.0	35.3
b12	TM44544	M	L.b	–	–	–	18.1[C]	37.5
b13	TM38153	M	L.b	–	–	–	18.6[C]	37.6
b14	TM38154	M	L.b	–	–	–	17.1[C]	36.5
b15	TM40107	S	L.b	95.0	40.0	7.0	19.0	35.6
b16	TM39946	M	L.b	–	–	–	18.6[C]	35.5
b17	TM38123	M	L.b	–	–	–	17.1[C]	–
b18	TM38155	M	L.b	–	–	–	18.6[C]	35.5
b19	TM39796	S	L.b	98.0	44.0	–	16.5	35.0
b20	TM34964	M	L.b	94.0	40.0	7.0	17.0	34.2
b21	NM29992	S	L.b	–	–	–	–	35.4
b22	NM29592	S	L.b	94.5	43.5	8.0	20.5	37.0
b23	NM30030	S	L.b	90.2	43.6	–	18.9	36.4
b24	NM58131	S	L.b	92.6	46.0	6.3	17.8	34.2
b25	NM59330	S	L.b	90.0	44.0	8.0	19.0	36.0
b26	NM63201	S	L.b	90.0	40.0	8.0	21.0	33.0
b27	NM63202	S	L.b	100.0	46.0	8.0	20.0	36.0
cw1	DM6898	M	L.cf.w	113.0	45.0	7.8	19.6	38.1
cw2	DM5351	M	L.cf.w	94.0	43.0	7.0	19.0	37.0
cw3	DM6899	M	L.cf.w	109.0	42.5	8.0	20.0	36.9
n1*	USNM342152*	L3	L.n	106.0	47.0	8.0	25.0	38.2
n2*	USNM342153+	L3	L.n	104.0	46.0	8.0	24.0	38.6
n3	TM37548	M	L.n	–	–	–	23.1[C]	38.0
n4	TM37586	M	L.n	–	–	–	23.1[C]	37.2
n5	TM37547	M	L.n	–	–	–	22.6[C]	36.2
n6	TM33472	S	L.n	91.0	38.0	8.0	24.0	39.0
n7	TM37608	M	L.n	–	–	–	22.6[C]	35.9
n8	TM37609	M	L.n	–	–	–	23.1[C]	36.6
n9	TM28316	S	L.n	111.0	46.0	–	22.0	38.9
n10	TM38426	M	L.n	–	–	–	-	39.5
n11	ZM41415	M	L.n	96.0	47.0	8.0	20.0	37.4
n12	ZM41417	M	L.n	103.0	47.0	9.0	25.0	39.0
w1	NMB6698	S	L.w	108.0	47.0	9.0	21.0	40.0
w2	NMB6687	S	L.w	107.0	50.0	9.0	23.0	40.0
w3	NMB6688	S	L.w	106.0	49.0	9.0	21.0	39.0
w4	NMB6686	S	L.w	107.0	47.0	9.0	21.0	40.0
w5	NMB6697	S	L.w	111.0	47.0	9.0	24.0	40.0
w6	NMB6379	S	L.w	102.0	46.0	9.0	23.0	39.0
w7	NMB6378	S	L.w	91.0	38.0	8.5	23.0	40.0
w8	BM72.4398	L1	L.w	–	–	–	21.1	40.2
w9	BM72.4397	L1	L.w	–	–	–	21.4	40.7
w10*	BM1.5.6.5*	L1	L.w	–	–	–	–	37.2
w11	BM72.4399	L1	L.w	–	–	–	21.5	40.2
w12	SMF66961	L4	L.w	–	44.5	6.3	21.2	39.0
w13	FMNH171300	L2	L.w	96.0	42.0	8.0	23.0	39.0

from specimen records, or recorded from dry museum specimens: total length (TL), tail length (T), hind foot length (HF), ear length (E), and forearm length (FA). Ear length was measured from dry skins of 11 specimens that lacked records of external measurements. In order to account for shrinkage due to the dried nature of the specimens, a mean shrinkage value of 3.13 mm was calculated from four specimens by subtracting the measurement of ear length made on the dried specimen from the measurement recorded in the museum records. The calculated shrinkage value was added to measurements made from dried specimens.

Cranial (Table 1) and external (Table 2) measurements for an additional 21 specimens of *Laephotis* were added from the literature (Setzer, 1971; Hill, 1974; Kock and Howell, [1988]; Stanley and Kock, 2004). These specimens were largely records from localities extra-limital to the range of the southern African specimens measured for this analysis. Unfortunately most of the cranial measurements for a new specimen of *L. botswanae* from Tanzania (Bauer, 1992) could not be included as the cranial measurements presented were ambiguous. Palatal measurements and some external measurements from this specimen were, however, included in this analysis. Measurements from the literature included information for the holotype of *L. wintoni* (Hill, 1974) (BM 1.5.6.5), the holotype of *L. botswanae* (Setzer, 1971) (USNM 425349), and the holotype and a paratype of *L. namibensis* (Setzer, 1971) (USNM 342152 and USNM 342153, respectively). Unfortunately, the *L. botswanae* and *L. namibensis* type specimens lacked post-palatal measurements. The species identifications used in the text and tables follow what is most recently published in the literature, and where unpublished, follow the identification in museum records for the specimen. Cranial measurements of two new *L. wintoni* specimens from Ethiopia (Lavrenchenko *et al.,* 2004) were not included as these were given as a mean for the specimens and did not include all the measurements used in this analysis. These specimens were, however, included in the distribution map (Fig. 1) and in calculations of vegetation biome associations.

The statistical package NTSYS-pc, version 2.01h (Rohlf, 1997) was used for principal component analyses (PCA) using correlation matrices based on standardized measurements, and unweighted pair group method using arithmetic averages (UPGMA) cluster analyses based on distance matrices of standardized measurements. PCA and UPGMA analyses were based on five different data suites to allow the analysis of external and cranial measurements together and separately, as well as compensate for specimens with missing variables. The measurements and number of specimens included in each of analyses were as follows:

1. six palatal measurements (Palat, Lpp–mesop, Lpp–M^3, LM^3–mesop, Lmesop–ham, LM^3–ham), introduced by Hill (1974), from 40 specimens;
2. 17 cranial measurements (Cnr inc, Cdl, Por, Bcw, Bcd, Mast, C–C, M^3–M^3, C^1–M^3, Mand, C–M_3, Palat, Lpp–mesop, Lpp–M^3, LM^3–mesop, Lmesop–ham, LM^3–ham) from 31 specimens;
3. two external (E, FA) and 14 cranial measurements (Cnr inc, Por, Bcw, Mast, C–C, M^3–M^3, C^1–M^3, C–M_3, Palat, Lpp–mesop, Lpp–M^3, LM^3–mesop, Lmesop–ham, LM^3–ham) from 31 specimens;
4. one external (FA) and seven cranial measurements (Cnr inc, Por, Bcw, Bcd, C–C, M^3–M^3, C^1–M^3) from 46 specimens – these measurements were chosen specifically to include literature records of type specimens of *L. botswanae, L. namibensis,* and *L. wintoni,* together with as many other specimens as possible;
5. five external measurements (TL, T, HF, E, FA) from 27 specimens.

Only the first, second and third analyses included palatal and post-palatal measurements.

An updated distribution map for the different species was plotted based on museum voucher records. Biomes associated with distributions of each of the species were assessed using Rutherford and Westfall's (1994) biome data for South Africa, Lesotho, Swaziland, Namibia and Botswana (supplied as a GIS shape file data 'SA Biomes (Rutherford)' at the South African National Botanical Institute's website http://www.plantzafrica.com/vegetation/vegmain.htm), and using the ecoregion data of Olsen and Dinerstein (2002) for the rest of Africa (supplied as a GIS shape file data at the World Wildlife Foundation Global 200 Ecoregions website http://worldwildlife.org/science/data/terreco.cfm).

RESULTS

Post-palatal measurements of specimens from Hella-Hella in KwaZulu-Natal that were previously identified as *L.* cf. *wintoni* (Table 1) fall within the ranges described by Hill (1974) for *L. botswanae.* Furthermore, as described by Hill (1974) for *L. botswanae,* the distance from a line across the rear margins of both M3 to the anterior edge of the mesopterygoid fossa is less than the distance from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars in specimens from Hella-Hella in KwaZulu-Natal. Hill's (1974) description of palatal and post-palatal measurements did not include *L. namibensis.* Table 1 shows that in specimens of *L. namibensis* from Namibia, as in *L. wintoni,* the distance from a line across the rear margins of M^3 to the anterior edge of the meso-

pterygoid fossa (LM3–mesop) is longer than the distance from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars. Specimens from the Western Cape and Free State Provinces in South Africa and from Lesotho do not, however, follow the condition noted by Hill (1974) for *L. wintoni* in that the distance from a line across the rear margins of both M^3 to the anterior edge of the mesopterygoid fossa does not exceed the distance from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars. In these specimens measurements from a line across the rear margins of both M^3 to the anterior edge of the mesopterygoid fossa, and from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars (Table 1), are larger than those for *L. botswanae* and *L. angolensis,* being instead more like measurements for *L. wintoni* (Hill, 1974; Stanley and Kock, 2004).

The PCA and UPGMA results of all three analyses that included palatal and post-palatal measurements (Figs 2–4) show a distinction of specimens identified as *L. angolensis* from the other *Laephotis* species, and a clear distinction of specimens identified as *L. botswanae* from specimens identified as *L. wintoni* and *L. namibensis.* As indicated by palatal measurements, specimens from Hella-Hella in KwaZulu-Natal that were previously identified as *L.* cf. *wintoni* are found together with specimens of *L. botswanae* in all three analyses (Figs 2–4). Of the three analyses that included palatal and post-palatal measurements (Figs 2–4), only the PCA, but not the UPGMA, of 17 cranial measurements (Fig. 3a) separates specimens of *L. wintoni* from *L. namibensis* on the second principal component axis. The other PCA and UPGMA results (Figs 2–4) show no clear distinction between specimens identified as *L. wintoni* and *L. namibensis.* Each of the three analyses (Figs 2–4) show slightly different clustering patterns of specimens identified as *L. wintoni* and *L. namibensis.*

Loadings of individual measurements on the first principal component axis (Table 3), of all three principal component analyses that included palatal and post-palatal measurements, indicate the same measurements are most important in distinguishing between species. All loadings on the first principal component axis are positive. The highest positive loading in each case is always palatal length and the least positive loading is always length from anterior edge of mesopterygoid fossa to tip of pterygoid hamulars. Table 4 shows that in palatal length and length from anterior edge of mesopterygoid fossa to tip of pterygoid hamulars the ranges for *L.* cf. *angolensis* and *L. botswanae* overlap, as do those for *L. namibensis* and *L. wintoni,* although there is no overlap in the ranges of *L.* cf. *angolensis* / *L. botswanae* and *L. namibensis* / *L. wintoni.* Other measurements that are important to the separation on the first principal component axis and are common to more than one analysis are: maxillary tooth row from anterior surface of canine to posterior surface of upper third molar; greatest skull length; and length from the rear of pre-palatal emargination to anterior edge of mesopteygoid fossa (Table 3). Table 4 shows that for each of these measurements the ranges for *L.* cf. *angolensis* and *L. botswanae* do not overlap. The ranges for the different species of greatest skull length and length from the rear of pre-palatal emargination to anterior edge of mesopteygoid fossa also separate *L. botswanae* from *L. namibensis* and *L. wintoni,* but do not separate *L. namibensis* from *L. wintoni* (Table 4). For maxillary tooth row length the ranges for the different species separate *L. botswanae* from *L. wintoni* but not *L. namibensis,* while *L. namibensis* and *L. wintoni* overlap (Table 4).

On the second principal component axis, length from a line across posterior faces of M^{3-3} to anterior edge of mesopterygoid fossa is most important in distinguishing between species in two of the three analyses that included palatal and post-palatal measurements (Table 3). Table 4 shows that ranges of measurements of length from a line across posterior faces of M^{3-3} to anterior edge of mesopterygoid fossa in *L.* cf. *angolensis* and *L. botswanae* do not overlap the ranges for *L. namibensis* and *L. wintoni.* Other important measurements on the second principal component, which are also common to more than one analysis, are length from a line across posterior faces of M^{3-3} to tip of pterygoid hamulars and width across outer edge of upper third molars (Table 3). Table 4 shows that ranges of measurements of length from a line across posterior faces of M^{3-3} to tip of pterygoid hamulars in *L.* cf. *angolensis* and *L. botswanae* do not overlap the ranges for *L. namibensis* and *L. wintoni.* In width across the outer edge of upper third molars, the range of measurements for *L.* cf. *angolensis* do not overlap the range of measurements for *L. wintoni,* whereas the ranges for the other species overlap (Table 4).

In all three UPGMA cluster analyses that included palatal and post-palatal measurements, specimens of *L. botswanae* split into three different clusters (Figs 2b–4b). A specimen from Hwange National Park in Zimbabwe (FMNH152728) separated from the rest of the specimens, and the remaining specimens split into two major clusters. What separates the majority of the *L. botswanae* specimens into two clusters is not clear, although geographic locality appears to have some influence since all specimens from the Democratic Republic of Congo cluster together.

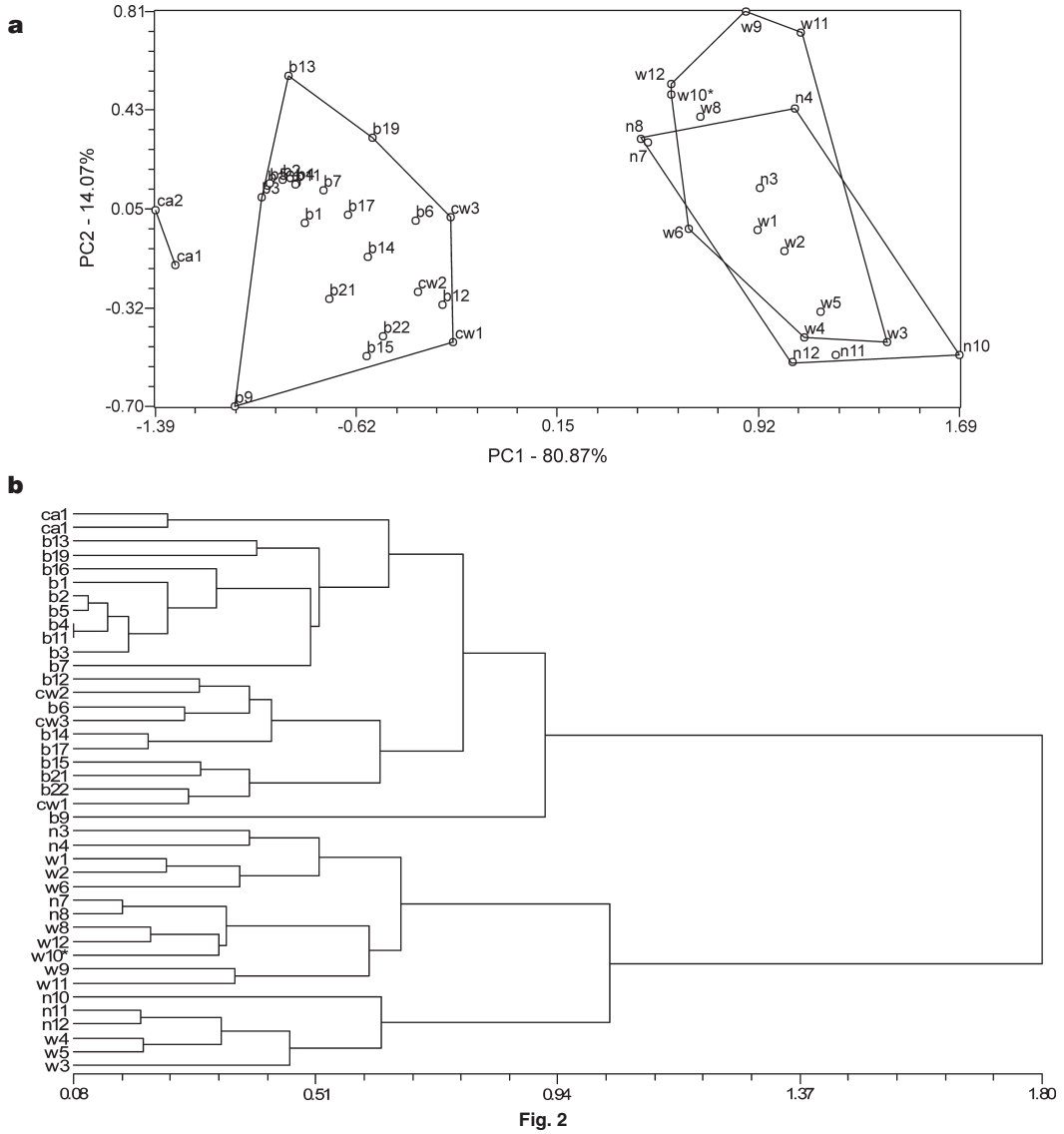

Fig. 2

PCA plot (**a**) showing the first two principal components, and a UPGMA phenogram (**b**) from analysis 1 of six palatal measurements from 41 specimens of *Laephotis*. See Table 1 for identification of specimen codes.

The analysis based on one external and seven cranial measurements (which excluded palatal and post-palatal measurements), included measurements from the literature of type specimens of three *Laephotis* species, *L. botswanae, L. namibensis,* and *L. wintoni* that were not included in the analyses above as they were lacking palatal and post-palatal measurements. Although the PCA of one external and seven cranial measurements (Fig. 5a) is similar to the analyses above in that there is an oblique separation of the specimens along the first and second PC into three groups which distinguishes specimens of *L.* cf. *angolensis* and *L. botswanae* from those of *L. wintoni* and *L. namibensis,* this PCA places the type specimen of *L. wintoni* closer to the group of specimens that includes the type specimen of *L. botswanae.* Maxillary tooth row length is the most important measurement causing separation on the first principal component axis (Table 3). Maxillary tooth row length is also an important measurement in the separation of species along the first principal component axis in the analyses of 17 cranial measurements and two external, and 14 cranial measurements. Other measurements that

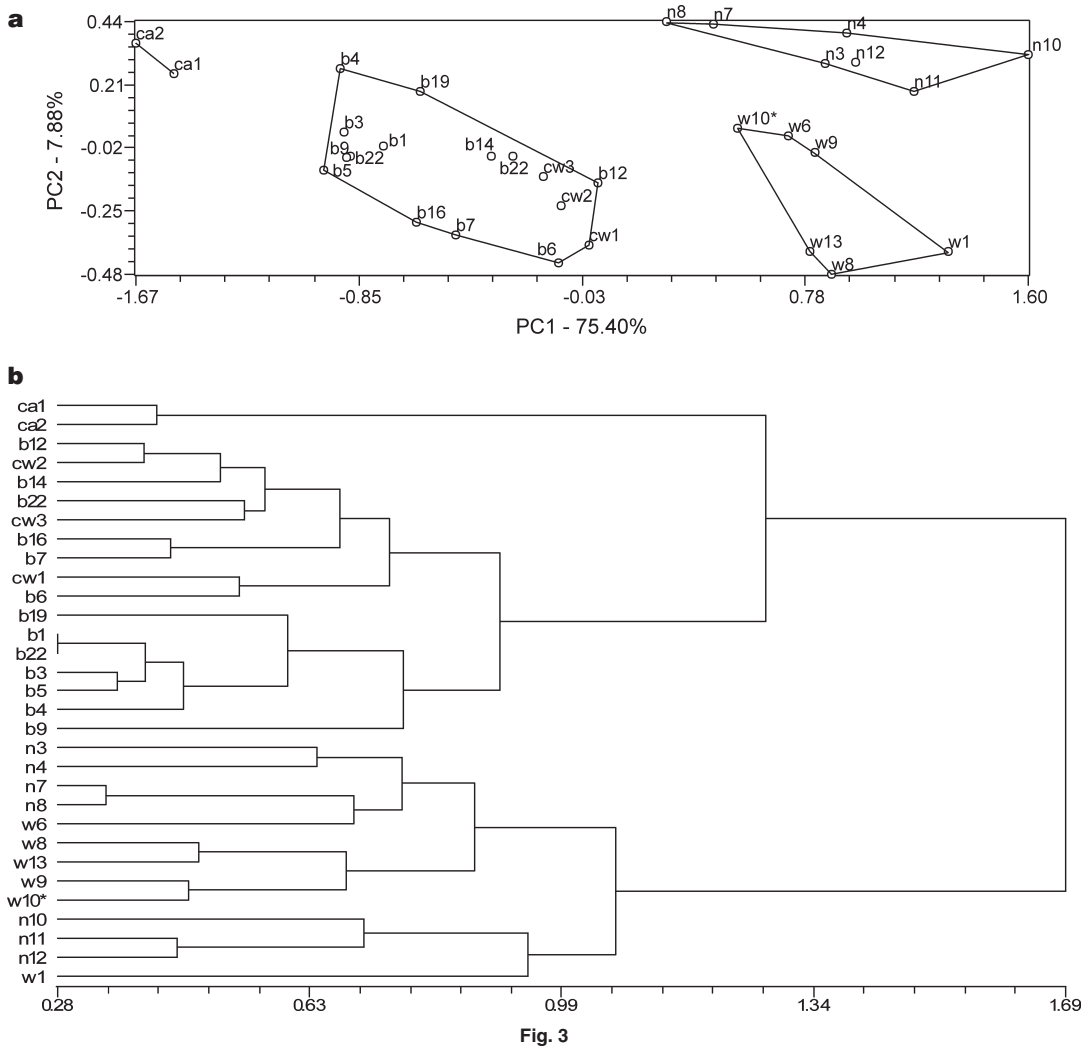

Fig. 3

PCA plot (**a**) showing the first two principal components, and a UPGMA phenogram (**b**) from analysis 2 of 17 cranial measurements from 31 specimens of *Laephotis*. See Table 1 for identification of specimen codes.

were important on the first principal component axis are braincase breadth, greatest breadth across outer edge of upper canines, and forearm length (Table 3). The range of braincase breadth for each of the species (Table 4) shows that the measurement for *L.* cf. *angolensis* does not overlap the range of measurements for the other species, which all have overlapping ranges of braincase breadth. Table 4 also shows that the ranges for greatest breadth across outer edge of upper canines in *L.* cf. *angolensis* and *L. botswanae* overlap, but the range of *L.* cf. *angolensis* is different to that for *L. namibensis* and *L. wintoni,* and the ranges of the other species overlap. Forearm lengths of *L.* cf. *angolensis* are smaller than those for *L. wintoni* (Table 4), whereas the ranges for each of the other species overlap. On the second principal component axis the measurements that are most important are greatest skull length, which loads highest, and width across outer edge of upper third molars, which loads lowest (Table 3). Greatest skull length is also important in separation along the first principal component axis, while width across the outer edge of upper third molars is also important in separation along the second principal component axis in analyses of 17 cranial characters and two external and 14 cranial characters.

The UPGMA cluster analysis (Fig. 5b) identified four major clusters that combine specimens contrary to the current species distinctions. Hence,

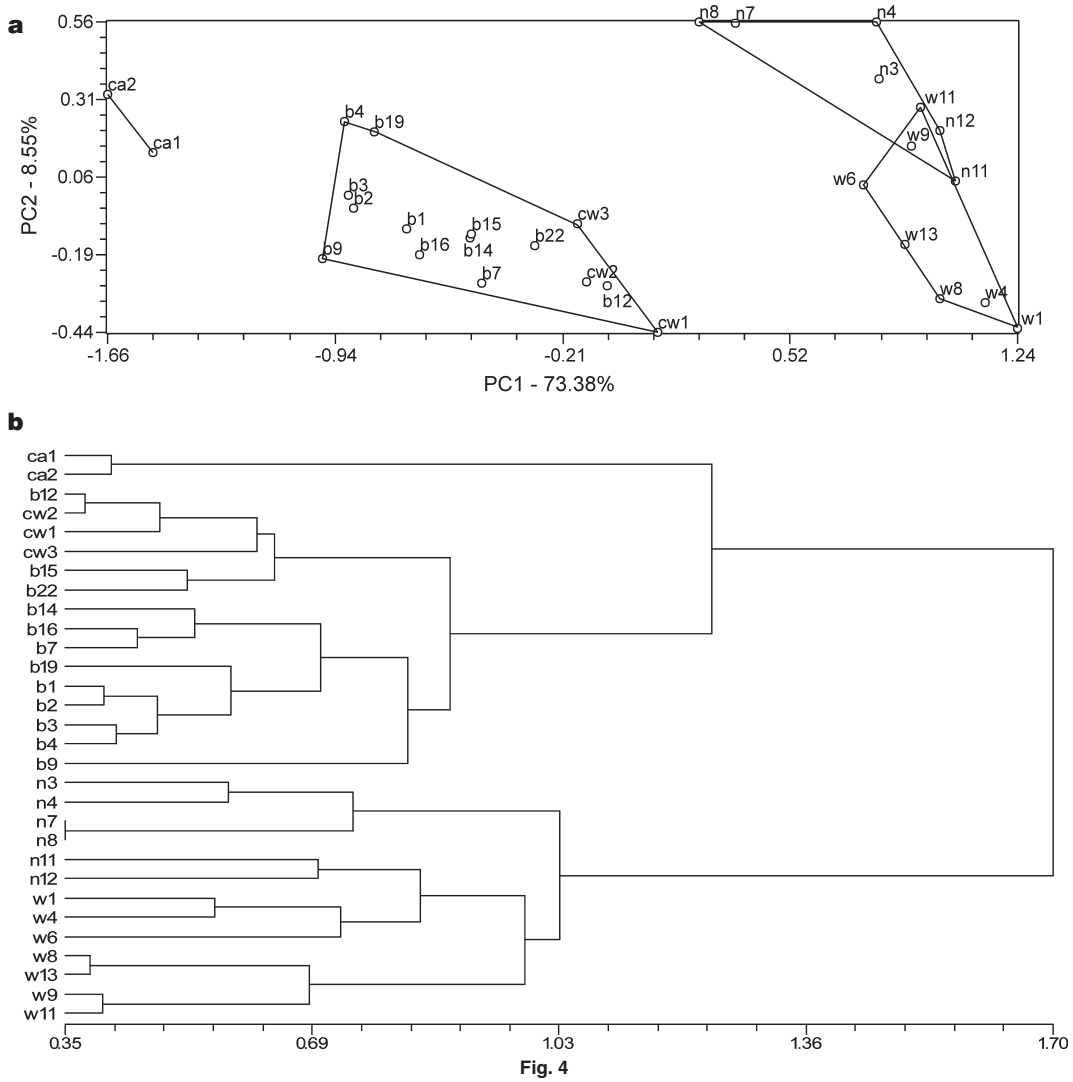

Fig. 4

PCA plot (**a**) showing the first two principal components, and a UPGMA phenogram (**b**) from analysis 3 of two external and14 cranial measurements from 31 specimens of *Laephotis*. See Table 1 for identification of specimen codes.

the first cluster contains specimens of *L.* cf. *angolensis* together with specimens of *L. botswanae.* The second cluster contains specimens of *L. botswanae* (including the holotype), the holotype of *L. wintoni,* and specimens from KwaZulu-Natal in South Africa previously assigned to *L.* cf. *wintoni.* The third cluster contains specimens of *L. namibensis* (including the type specimens). The fourth cluster contains specimens of *L. namibensis* together with specimens from the Western Cape Province in South Africa previously assigned to *L. namibensis* and specimens from the Free State Province in South Africa and Lesotho previously assigned to *L. wintoni.*

The PCA based on five external measurements (Fig. 6a) shows no clear separation of specimens into different species groups, and as in the analysis based on one external and seven cranial measurements the UPGMA analysis based on five external measurements (Fig. 6b) also gives results that are contrary to the current species distinctions. Hind foot length is important on both the first and second principal component axes (Table 3). The ranges of hind foot lengths of the different species overlap between *L. botswanae* and *L. wintoni,* and between *L. namibensis* and *L. wintoni,* whereas those for *L. botswanae* and *L. namibensis* form a continuum (Table 4). The other measurements that load highly on the first principal component axis are

Table 3

Factor matrix showing measurement loadings for the first two principal component axes in the five different analyses. Boldface loadings indicate strong variable participation in the respective axis. See material and methods for a description of measurement abbreviations.

Measurement	1		2		3		4		5	
	PCA 1	PCA 2	PCA 1	PCA 2	PCA 1	PCA 2	PCA 1	PCA 2	PCA 1	PCA 2
Cnr inc			0.965	0.145	0.944	0.211	0.830	**0.465**		
Cdl			0.935	0.197						
Por			0.694	–0.418	0.702	–0.412	0.739	–0.371		
Bcw			0.892	0.126	0.881	0.135	**0.853**	0.337		
Bcd			0.821	0.137			0.786	0.331		
Mast			0.906	–0.100	0.915	–0.107				
C–C			0.804	–0.525	0.855	–0.433	0.852	–0.368		
M^3–M^3			0.524	**–0.760**	0.637	**–0.615**	0.688	**–0.628**		
C–M^3			0.968	–0.113	0.959	–0.110	**0.944**	0.086		
Mand			0.957	0.058						
C–M_3			0.926	–0.124	0.940	–0.033				
Palat	**0.976**	0.126	**0.970**	0.078	**0.962**	0.159				
Lpp–mesop	0.974	0.167	0.956	0.110	0.953	0.210				
Lpp–M^3	0.925	–0.137	0.936	0.140	0.899	0.121				
LM^3–mesop	0.930	**0.315**	0.893	0.245	0.882	**0.386**				
Lmesop–ham	**0.555**	**–0.826**	**0.514**	0.124	**0.395**	–0.307				
LM^3–ham	0.960	0.006	0.906	**0.251**	0.910	0.278				
E					0.848	0.281			0.766	–0.515
FA					0.827	–0.249	0.851	0.005	**0.873**	–0.198
TL									0.747	0.517
T									0.637	**0.665**
HF									**0.835**	**–0.291**

forearm and ear lengths (Table 3). Forearm length also loads highly on the first principal component axis in the analysis of one external and seven cranial measurements (Table 3). The range of ear length for each species (Table 4) shows overlap in the ranges of *L. botswanae, L. namibensis* and *L. wintoni,* while the range of *L.* cf. *angolensis* is smaller than in all the other species. On the second principal component axis tail length loads highest (Table 3). Table 4, however, shows no separation between the different species in their ranges of tail length.

Figure 7 gives an up-dated distribution map of *Laephotis* species based on museum voucher specimens. The locality of a specimen (AMNH 87244) identified as *L.* cf. *angolensis* by Hill and Carter (1941) from '35 km E of Dande', which is also the locality information associated with the specimen in the American Museum of Natural History (T. Pacheco, pers. comm.), has been plotted in subsequent literature at two different localities. Hill (1974), Kock and Howell ([1988]) and Bauer (1992) plotted the locality of AMNH 87244 north of the type locality in the northeastern corner of Angola, whereas Crawford-Cabral (1989) plotted AMNH 87244 occurring west and slightly south of the type locality. The point plotted by Crawford-Cabral (1989) follows the coordinates given in the

Table 4

Ranges of measurement for each species, *Laephotis* cf. *angolensis, L. botswanae* (including specimens previously identified as *L.* cf. *wintoni*), *L. namibensis,* and *L. wintoni,* for cranial and external measurements that were important in distinguishing between species in the different principal component analyses. See materials and methods for a description of measurement abbreviations.

Measurement	*L.* cf. *angolensis*	*L. botswanae*	*L. namibensis*	*L. wintoni*
Palat	6.10–6.20	6.16–7.29	7.59–8.72	7.90–8.50
LM^3–mesop	1.20–1.30	0.94–1.69	1.86–2.47	1.97–2.50
Lmesop–ham	1.90–2.00	1.68–2.30	2.00–2.61	1.80–2.47
Lpp–mesop	4.80	4.90–5.63	6.11–6.78	6.40–6.90
LM^3–ham	3.20	2.64–3.70	3.94–4.54	3.93–4.48
C–M^3	4.30	4.50–4.94	4.75–5.35	5.00–5.33
Cnr inc	13.70–13.80	14.10–15.50	16.05–17.00	15.58–16.30
M^3–M^3	5.00–5.20	5.17–5.80	5.10–5.55	5.42–5.90
BcW	6.80	6.85–7.43	7.40–7.95	7.40–8.05
C–C	3.70–3.80	3.80–4.50	4.00–4.50	4.30–4.60
FA	34.0–36.0	33.0–38.0	36.0–40.0	37.0–41.0
HF	–	6.0–8.0	8.0–9.0	6.3–9.0
T	–	40.0–46.0	38.0–47.0	38.0–50.0
E	15.9–16.0	16.0–21.0	20.0–25.0	21.0–24.0

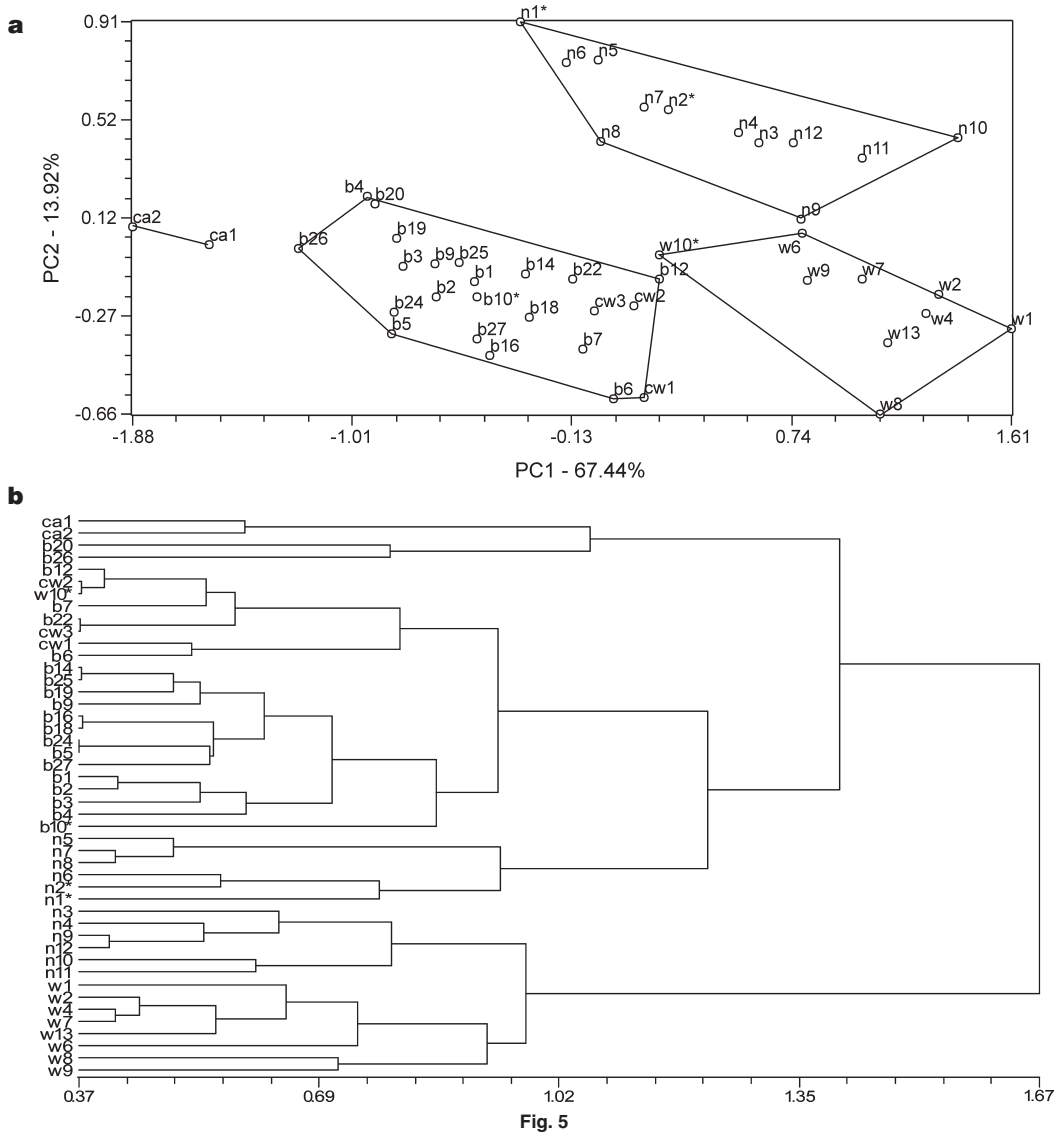

Fig. 5

PCA plot (**a**) showing the first two principal components, and a UPGMA phenogram (**b**) from analysis 4 of one external and seven cranial measurements from 46 specimens of *Laephotis*. See Table 1 for identification of specimen codes.

gazetteer of Hill and Carter (1941) for 'Dande (= Dando) 11°10′S, 17°10′E'. It also coincides with the description in the body of the text of Dande being 'nearly 330 kilometers south-west from the type locality' (Hill and Carter, 1941), as the type locality for *L. angolensis* is on the Tyihumbwé (Chiumbe) River, 15 km west of Dala (Monard, 1935). Following the information in Hill and Carter (1941) the locality would be close to the present day town of Dando (*Encarta World Atlas,* 1995–1997; 10th edition of the *Times Atlas of the World,* 1999). A possible explanation for the locality of AMNH 87244 being plotted in the northeast of Angola (Hill, 1974; Kock and Howell, [1988]; Bauer, 1992) is that Dande became confused with the locality Dundo (D. Kock, pers. comm.). Mammal species, including bats, albeit no *Laephotis,* were collected for the Dundo Museum by A. de Barros Machado from in and around Dundo in the Lunda District of northeastern Angola and recorded by Sanborn (1951) and Hayman (1963). The gazetteer in Hayman (1963) gives the coordinates for Dundo as 7°22′S, 20°50′E.

Table 5 lists the biomes associated with each of the species distributions. Two localities, Mazumbai

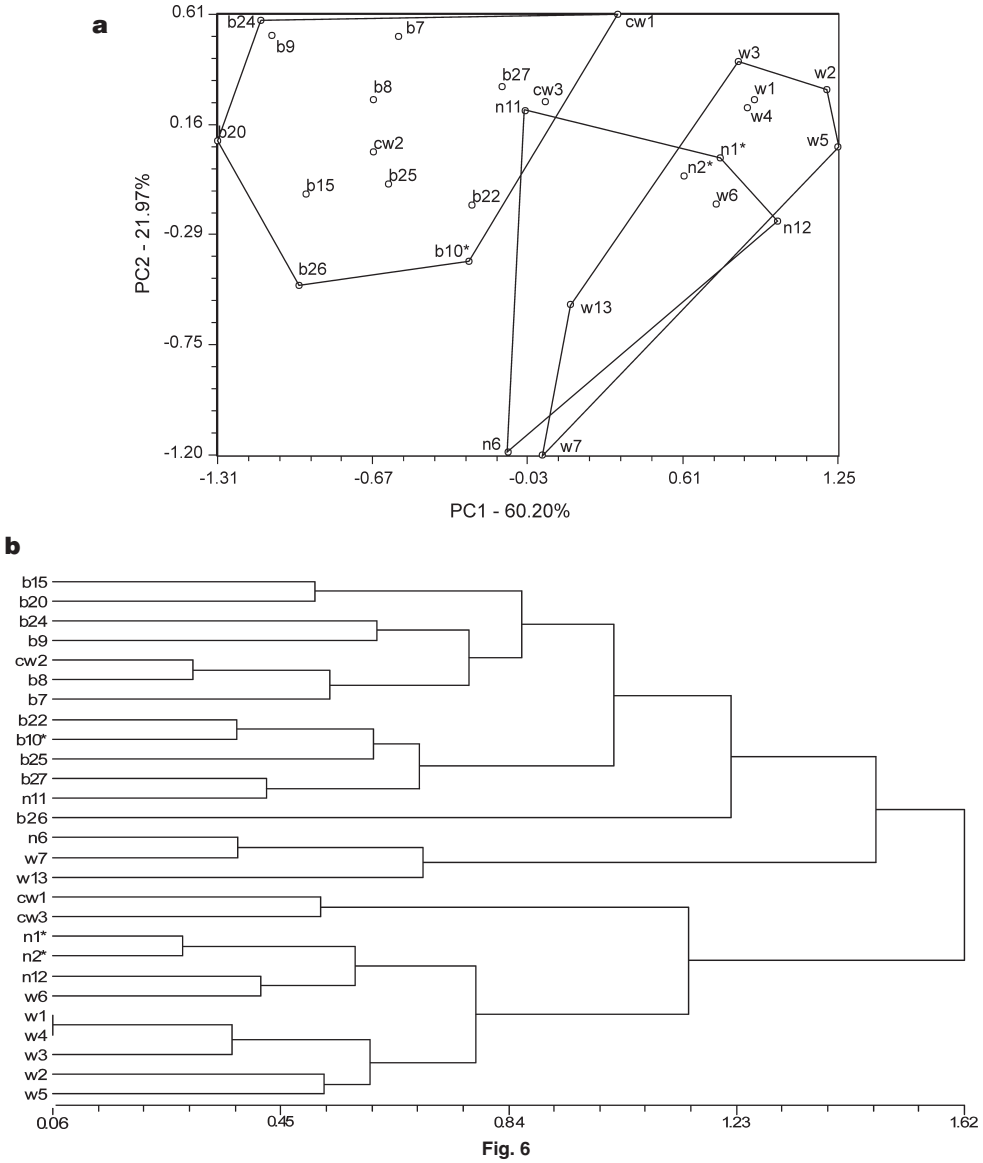

Fig. 6

PCA plot (**a**) showing the first two principal components, and a UPGMA phenogram (**b**) from analysis 5 of five external measurements from 27 specimens of *Laephotis*. See Table 1 for identification of specimen codes.

Forest Reserve and Beletta Forest, were identified by the GIS spatial biome data as savanna and grassland respectively. However, since both were known to be near forests (Kock and Howell, [1988]; Lavrenchenko *et al.,* 2004), the assignments indicated by the spatial data were ignored and these localities were assigned to the forest biome. This highlights the problem associated with the GIS information due to spatial and scale errors, which should be borne in mind while interpreting the results. *Laephotis* cf. *angolensis* is entirely confined to the savanna biome. *Laephotis botswanae* was found in both savanna (75%) and grassland (25%) biomes, the latter being in their distribution in Malawi. As was identified by Kock and Howell ([1988]), 62.5% of the distribution of *L. wintoni* in East Africa (Ethiopia, Kenya and Tanzania) was within the forest biome and 37.5% in the savanna, whereas in South Africa and Lesotho, the distribution of *L.* cf. *wintoni* was only within the grassland biome. Of the different *Laephotis* species, *L. namibensis* was associated with the largest number

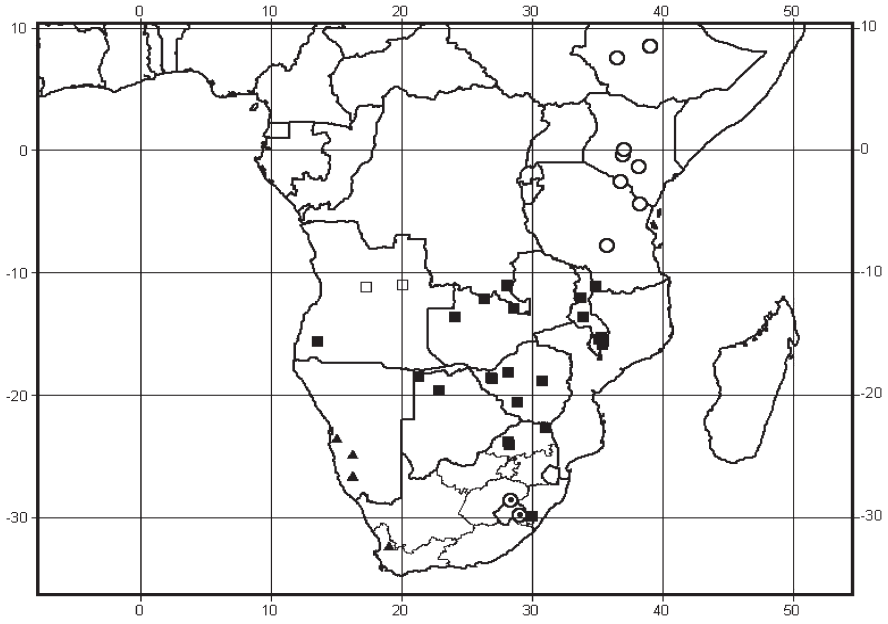

Fig. 7

Distribution of *Laephotis angolensis* (□); *L. botswanae* (■), *L. namibensis* (▲), *L. wintoni* (○), and *L.* cf. *wintoni* (⦿) based on museum specimen records (see Appendix 1 for further information).

of different biomes: desert (60%), fynbos (20%) and savanna (20%). In southern Africa, the genus *Laephotis* was absent from two biomes, namely the succulent Karoo and Nama Karoo.

DISCUSSION

This study confirmed Stanley and Kock's (2004) suggestion that Hill's (1974) post-palatal measurements, previously overlooked in the identification of southern African species of *Laephotis,* are useful for the distinction of *L. botswanae* from *L. wintoni.* However, specimens from the Western Cape and Free State Provinces in South Africa identified as *L. namibensis* and specimens from Lesotho identified as *L. wintoni* do not fit Hill's (1974) descriptions for *L. angolensis, L. botswanae* or *L. wintoni,* of the distance from a line across the rear margins of both M^3 to the anterior edge of the mesopterygoid fossa relative to the distance from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars. The keys to the southern African species of *L. botswanae, L. namibensis,* and *L. wintoni* in Meester *et al.* (1986) and Taylor (2000) emphasize skull and ear lengths for distinguishing between the different species. The skull and ear length measurements of *Laephotis* specimens presented here indicate these keys are in need of revision as the ranges of ear lengths for *L. namibensis* and *L. wintoni* overlap, and the ranges of skull lengths for *L. botswanae, L. namibensis,* and *L. wintoni* are greater than indicated in Meester *et al.* (1986) and Taylor (2000).

These results did not show a clear distinction between *L. namibensis* and *L. wintoni,* instead they suggest *L. namibensis* and *L. wintoni* are different forms of the same species. This supports an earlier

Table 5

Biome associations of the different *Laephotis* species, giving the number of localities each species is currently known from (No. loc), and the number of locations found within each biome.

Species	No. loc	Fynbos	Desert	Savanna	Grassland	Forest
L. angolensis	3	–	–	3	–	–
L. botswanae	28	–	–	21	7 [(1)]	–
L. wintoni	8	–	–	4/(3) [(2)]	1/(0) [(3)]	3/(5) [(2/3)]
L. cf. *wintoni*	2	–	–	–	2	–
L. namibensis	5	1	3	1	–	–

[(1)]All localities are in Malawi (Happold and Happold, 1997); [(2)] the Mazumbai Forest Reserve locality was transferred to the forest biome; [(3)] the Beletta Forest locality was transferred to the forest biome.

suggestion by Peterson (1973: 602) that 'additional specimens from the area of hiatus' between *L. wintoni* and *L. namibensis* 'may prove that they are rather well-marked eastern and western geographic races of the same species', where the paler colour distinction of *L. namibensis* from *L. wintoni* could be a local adaptation to the drier desert regions in which it is found, rather than a character for species distinction. Since *L. wintoni* Thomas, 1901, antedates *L. namibensis* Setzer, 1971, *L. wintoni* would be the valid name for this species. Four measurements (greatest skull length, braincase breadth, length from the rear of pre-palatal emargination to anterior edge of mesopteygoid fossa, length from line across posterior faces of M^{3-3} to tip of pterygoid hamulars) were identified from principal component analyses that separated specimens of *L.* cf. *angolensis* from specimens of *L. botswanae,* and *L. wintoni* / *L. namibensis.* These analyses were, however, based on only two individuals of *L.* cf. *angolensis,* and it may be that with more individuals of both *L. angolensis* and *L. botswanae* the small differences observed between these species may disappear, and as with *L. namibensis* and *L. wintoni* they may be shown to be different forms of the same species. If so, this would support a suggestion previously made by Peterson (1973: 602) that '*L. botswanae* may prove to be a larger, southern race of *L. angolensis*'. Five measurements (greatest skull length, palatal length, length from line across posterior faces of M^{3-3} to anterior edge of mesopterygoid fossa, length from the rear of pre-palatal emargination to anterior edge of mesopteygoid fossa, length from line across posterior faces of M^{3-3} to tip of pterygoid hamulars) were identified from principal component analyses that separated specimens of *L.* cf. *angolensis* and *L. botswanae* from specimens of *L. wintoni* / *L. namibensis.* All measurements that were important in separation of the different species have featured in earlier written descriptions of differences between the different *Laephotis* species (Setzer, 1971; Peterson, 1971, 1973; Hill, 1974).

Further analyses, incorporating other characters and possibly molecular data, are required to clarify the species distinctions between *L. wintoni* and *L. namibensis,* and between *L. angolensis* and *L. botswanae.* This study, being based for the most part on museum specimens comprising dry skins and cleaned skulls, was unable to present detailed information on soft palate and tragus characteristics which have previously been used to characterize different *Laephotis* species (Setzer, 1971; Peterson, 1971, 1973; Hill, 1974; Stanley and Kock, 2004). Baculum morphology, while proving a useful character for species identification of several other vesper species occurring in southern Africa of the genera *Eptesicus, Hypsugo, Neoromicia* and *Pipistrellus,* showed no differences between *L. botswanae* and *L. namibensis* specimens (Kearney *et al.,* 2002). In the interest of nomenclatural stability, pending further studies required to confirm the lack of species distinction between *L. wintoni* and *L. namibensis* identified in this study, it may be premature to reassign all *L. namibensis* to *L. wintoni.* Instead, it is suggested that current species designations should be retained.

The re-assignment of KwaZulu-Natal specimens to *L. botswanae* supported by these results extends the known range of *L. botswanae* 658 km farther south. Although the KwaZulu-Natal, Free State, and Lesotho localities are relatively close to each other (217 km and 91 km from the KwaZulu-Natal to the Free State and Lesotho localities, respectively), the morphometric results clearly identify the specimens from KwaZulu-Natal as *L. botswanae* whereas those from the Free State and Lesotho are part of the *L. wintoni* / *L. namibensis* group. The higher altitude of the localities in the Free State and Lesotho than the locality in KwaZulu-Natal is, however, consistent with earlier descriptions of *L. wintoni* as a montane species found at high altitudes (above 1000 m) in Ethiopia, Kenya and Tanzania (Kock and Howell, [1988]; Stanley and Kock, 2004). An association between the distribution of *L. wintoni* and higher altitudes could explain the disjunct pattern of distribution as well as the differences in biome association seen across the distribution of *L. wintoni.* High altitude localities at higher latitudes (East Africa) are dominated by forests, while at lower latitudes (southern Africa: Malawi and South Africa) high altitude localities fall within the grassland biome. The vegetation association of *L. botswanae* over most of its distribution to the savanna biome, and the association of *L. wintoni* with higher elevations, suggests the identification of the Malawian specimens found in a grassland biome at higher elevations (Happold and Happold, 1997) might be reconfirmed using palatal and post-palatal measurements (Hill, 1974).

CONCLUSION

These results support the re-assignment of specimens from KwaZulu-Natal from *L.* cf. *wintoni* to *L. botswanae.* However, further studies are required to clarify the species distinction between *L. wintoni* and *L. namibensis,* and between *L. angolensis* and *L. botswanae.* Pending this, it is suggested current species designations assigned to specimens should be retained.

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Appendix I

Specimen details of all known voucher specimens of *Laephotis,* incorporating species re-assignments suggested in this analysis.

AMNH, American Museum of Natural History, New York; BMNH, The Natural History Museum, London; DCHC, David C.D. Happold collection; DNSM, Durban Natural Science Museum, Durban; FMNH, Field Museum of Natural History, Chicago; HZM, Harrison Zoological Museum, Sevenoaks; KMMA, Koninklijk Museum voor Midden-Afrika, Tervuren; MHNC, Musée La Chaux-de-Fonds, Neuchâtel; NHMZ, National Museums of Zimbabwe, Bulawayo; NMB, National Museum Bloemfontein, Bloemfontein; NMW, Naturhistorisches Museum, Wien; ROM, Royal Ontario Museum, Toronto; SAMC, Iziko (South African) Museum, Cape Town; SMF, Senckenberg Museum, Frankfurt; TMSA, Transvaal Museum, Pretoria; USNM, United States National Museum, Washington D.C.; ZMMU, Zoological Museum, Moscow University, Moscow.

Laephotis angolensis

ANGOLA: 35 km E Dande (syn. Dando) (11°10′S, 17°10′E): AMNH 87244. 15 km W Dala, Tshiumbe (syn. Tyihumbwe, Tyhumbwe, Chiumbe) river, tributary of Kasai river, (11°02′S 20°04′ E): MHNC (holotype).

Laephotis cf. angolensis

DEMOCRATIC REPUBLIC OF CONGO: 68 km E Lubumbashi (= Elisabethville), Musonge (11°07′S, 28°08′E): BM 57.435. 70 km E of Lumbumbashi (= Elisabethville), Mumene, (11°07′S, 28°08′E): BM 57.437.

Laephotis botswanae

ANGOLA: Huila (15°04′S, 13°32′E): FMNH 83605, FMNH 84120.

BOTSWANA: 50 mi W, 12 mi S of Shakawe (18°33′S, 21°18′E): USNM 425349. Kurunxaraga (syn. Xugana Lagoon) (*c.* 19°40′S, 22°50′E): NHMZ 59310.

DEMOCRATIC REPUBLIC OF CONGO: 70 km E of Lumbumbashi (syn. Elisabethville), Mumene, (11°07′S, 28°08′E): BM 57.436, BM 57.438, KMMA 26.402–26.407, SMF 16868. 68 km E Lubumbashi (= Elisabethville), Musonge (11°07′S, 28°08′E): SMF 16869.

MALAWI: Nkhota-kota Game Reserve, Chipata Camp, 1350 m asl. (13°04′S, 33°56′E): DCHC 2937. Viphya Plateau, Luwawa Dam, 1700 m asl. (12°07′S, 33°44′E): DCHC 2673. 3 km N Namadzi Village, Kapalasa Farm, 1000 m asl. (15°31′S, 35°11′E): DCHC 2972, DCHC 2992. Mt Mulanje, Likabula Mission (15°57′S, 35°24′E): TM 44544. Namadzi, Kapina Estates, Kapino Dam, 1000 m asl. (15°31′S, 35°11′E): DCHC 3040. Thondwe, Mpalanganga Dam, 1100 m asl. (15°27′S, 35°15′E): DCHC 2855. Zomba District, Zomba town, Bone's Garden, 16th Avenue, 800–900 m asl. (15°23′S, 35°19′E): DCHC 2269, DCHC 2456, DCHC 2682. Zomba Plateau, Chagwa Dam, (15°21′S, 35°20′E): DCHC 3012.

SOUTH AFRICA: *Kwazulu-Natal Province:* Hella-Hella, Game Valley Estates (29°54′S, 30°03′E): DNSM 5351, DNSM 6898–6899. *Limpopo Province*: Kruger National Park, 2.5 km NE of Punda Maria, Maditobe Witsand Dam (22°41′S, 31°02′E): TM 38123, TM 38153–38155. Waterberg, 30 km NE Vaalwater, Farm Klipfontein (24°08′S, 28°08′E): TM 39946, TM 40107. Waterberg, 65 km N Vaalwater, Lapalala Wilderness area (23°51′S, 28°09′E): TM 39796.

TANZANIA: Songea District, SE Mbinga, Ugano Plantation, 1 560m asl. (11°06′S, 34°55′E): NMW 19823.

ZAMBIA: Ndola (12°58′S, 28°38′E): HZM 1.2533. NORTH-WEST PROVINCE: Kabompo (syn. Kabompo Boma) (*c.* 13°38′S, 24°08′E): NHMZ 9111. Solwezi Boma (12°10′S, 26°23′E): BM 55.1134–55.1135. Between Livingstone (17°52′S, 25°51′E) & Lochinvar (15°51′S, 27°14′E): NHMZ 2801.

ZIMBABWE: Hwange National Park (syn. Wankie N.P.), 15 mi E Dett, 3000 ft asl. (18°37′S, 26°52′E): FMNH 152728. Eastern Matopos, Lunare Valley (*c.* 20°36′S, 28°52′E): NHMZ 29992. Eastern Matopos, Mtshavezi Valley (*c.* 20°36′S, 28°52′E): NHMZ 29592. 75 km W Gokwe, Sengwa Wildlife area (18°10′S, 28°13′E): NHMZ 30030, NHMZ 63201–63202, TM 34964. Gem Tree Ranch, Sebakwe River (*c.* 18°55′S, 30°50′E): NHMZ 58131. Hostes Nicoll Research Institute (18°10′S, 28°13′E): NHMZ 59330.

Laephotis namibensis

NAMIBIA: *Lüderitz Region*: 3 km W Aus, Farm: Klein Aus 8 (26°39′S, 16°13′E): TM 37547–37548. Tiras Mountains, Helmeringshausen (26°45′S, 16°15′E): TM 33472. Maltahöhe Region: 70 km W Maltahöhe, Farm Zwartmodder 101 (24°54′S, 16°17′E): TM 37586, TM 37608–37609. *Swakopmund Region*: Gobabeb, Namibia Desert Research Station (syn. DERU) (23°33′S, 15°03′E): USNM 342152–342153.

SOUTH AFRICA: *Western Cape Province*: Cederberg, Algeria State Forest campsite (32°21′S, 19°03′E): SAMC 41415, SAMC 41417, TM 28316, TM 38426.

Laephotis wintoni

ETHIOPIA: 38 km SW Jimma, Beletta Forest, 2050 m asl. (07°32′N, 36°33′E): ZMMU S-165956, ZMMU S-165957. Koka, 1700 m asl. (08°27′N, 39°06′E): BM 72.4397–72.4399.

KENYA: Nyeri, 6000 ft (00°24′S, 36°57′E): HZM 2.3020. Kitui (01°22′S, 38°12′E): BM 1.5.6.5. 37 km W of Mt Kenya, Nanyuki (syn. Nanguki) (00°01′N, 37°04′E): ROM 66245. Kajiado District, Namanga, 4200 ft (02°33′S, 36°48′E): ROM 36368.

TANZANIA: 6 km E Iringa, Kibebe Farms (07°47′S, 35°45′E): FMNH 171300. West Usambara Mountains, Mazumbai Forest Reserve (04°25′S, 38°15′E): SMF 66961.

Laephotis* cf. *wintoni

LESOTHO: *Qacha's Nek District:* Sehlabathebe National Park, small dam (29°51′S, 29°06′E): NMB 6686–6688, NMB 6697–6698.

SOUTH AFRICA: *Free State Province*: Clarens, Farm Schaapplaas (*c.* 28°37′S, 28°22′E): NMB 6378–6379.