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A new species of false antechinus (Marsupialia: Dasyuromorphia: Dasyuridae) from the Pilbara region, Western Australia

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Abstract – *Pseudantechinus roryi* sp. nov. from the Pilbara region of Western Australia is described. The new species is close genetically to *P. macdonnellensis* but differs from that species and all other members of the genus in aspects of cranial, dental and external morphology. *Pseudantechinus roryi* is found in regional sympatry with *P. woolleyae*, but is narrowly allopatric with *P. macdonnellensis* of the central Australian uplands. A revised generic diagnosis of *Pseudantechinus* is given and the phylogenetic position of *Pseudantechinus* within the Dasyurinae is discussed.

INTRODUCTION

Knowledge of the taxonomic diversity of the false antechinuses has expanded greatly over the last three decades, with the description of *Pseudantechinus woolleyae* from mid-western and Pilbara regions of Western Australia (Kitchener and Caputi, 1988) and *P. ningbing* from the Kimberley region (Kitchener, 1988), and reinstatement of *P. mimulus* Thomas from the northeastern Northern Territory (Kitchener, 1991). These species were all previously included within or synonymized under *Pseudantechinus macdonnellensis* (Spencer), which has more recently been restricted to the uplands of Central and Western Australia. The species *bilarni* has also been included within *Pseudantechinus* by some workers (Kitchener and Caputi, 1988), while others have grouped *bilarni* with *apicalis* from southwestern Australia under the genus *Parantechinus* Tate (Archer, 1982; Woolley and Begg, 1998).

In this paper we examine patterns of morphological and genetic variation within *Pseudantechinus macdonnellensis*. Our results show that western and central populations of *P. macdonnellensis* are readily distinguished on both craniodental and external criteria, with no evidence of clinal intergradation or obvious interspecific interaction where their ranges abut. Although these two forms display only a low level of genetic differentiation, they are nevertheless diagnosable by their allozyme profiles. We herein describe the western populations as a new species closely related to, but distinct from, *P. macdonnellensis*. Our broader comparative studies support Kitchener and Caputi's (1988) concept of *Pseudantechinus* that includes *P. bilarni* (Johnson) but excludes *Parantechinus apicalis* (Gray). We provide a revised generic diagnosis for the genus *Pseudantechinus*.

MATERIALS AND METHODS

Morphological Study

A total of 75 specimens of *Pseudantechinus* were measured in this study. These included 10 individuals of *P. macdonnellensis* from the general region of the type locality, MacDonnell Ranges in the Northern Territory; 21 individuals referred to *P. macdonnellensis* from nine localities in Western Australia; and 20 individuals referred to the new species from six localities in northwestern and central Western Australia. Samples of *P. woolleyae* (n = 16) and *P. mimulus* (n = 8) were included in the statistical analysis. Multiple specimens of *P. ningbing* and *P. bilarni* and representatives of other dasyurine genera (*Myoictis, Dasycercus, Dasyuroides, Dasyurus, Parantechinus, Dasykaluta*) were examined for purposes of morphological comparison. Table 1 lists all individuals used in the statistical analysis by species and locality.

Tooth numbering follows Luckett (1993). Skull measurements are illustrated in Figure 1. All skull and external measurements are given in mm. The measurements are: GSL, Greatest Skull Length; BL, Braincase Length; BW, Braincase Width; ZW, Zygomatic Width; LIW, Least Interorbital Width; POB, Post Orbital Breadth; TWAW, Tympanic Wing of Alisphenoid Width; TWAL, Tympanic Wing of Alisphenoid Length; EW, Ectotympanic Width; BT, Bulla Total Length (periotic + alisphenoid); BP, Bulla Periotic Length; WOB, Width outside Bullae; WIB, Inter-bullar Width; C^1M^4, Distance from Upper Canine to end of Upper Molar 4; M^1M^4, Upper Molar Row Length; LM^3RM^3, Width across outside of Upper Right and Left Molar 3; MLTD, Distance between Pterygoids; MLPV, Maxillary Vacuity Length; PAL, Length of Palate; DL, Dentary Length; I_1M_4, Distance from First Lower Incisor to

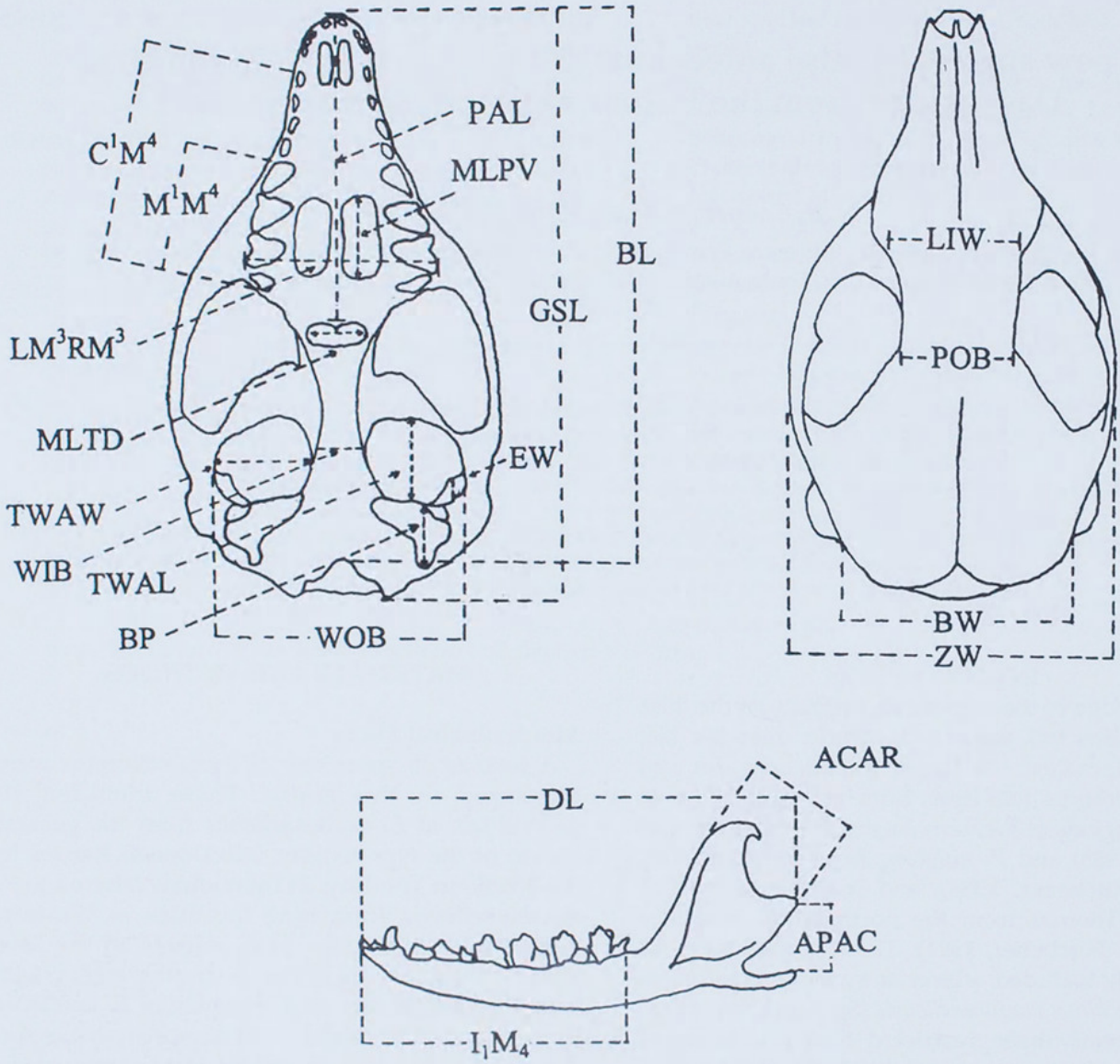


Figure 1 Cranial, tooth and dentary measurements.

Lower Molar 4; APAC, Distance from Angular Process to Articular Condyle; ACAR, Distance from Articular Condyle to anterior margin of Ascending Ramus; SV, Snout-Vent Length; TV, Tail-Vent Length; EAR, Ear Length; TR, Tragus Length; PESL, Pes Length (minus claw); PESW, Width of Pes at base of Hallux.

Skulls were categorized into three age groups (juvenile, adult, mature), according to dental eruption, extent of toothwear, and fusion of cranial sutures. Most individuals fell into the adult class. Sexual maturity was confirmed by examination of external reproductive structures. Sex of the specimen was determined from the body or from information recorded with the skull.

All measurements (Table 2a, b) were recorded with digital calipers and all statistical analysis was carried out using Genstat 5 (Genstat 5 Committee, NAG, 1993).

Genetic Study

Genetic profiles were established by allozyme electrophoresis of liver homogenates on cellulose acetate gels (CellogelÒ), based on procedures described in Richardson *et al.* (1986). Four individuals from two localities in northwestern Australia were compared with seven individuals from seven localities in northern South Australia.

The following enzymes and proteins were scored: aconitate hydratase (ACON, EC 4.2.1.3), acid phosphatase (ACP, EC 3.1.3.2), aminoacylase (ACYC, EC 3.5.1.14), adenosine deaminase (ADA, EC 3.5.4.4), alcohol dehydrogenase (ADH, EC 1.1.1.1), adenylate kinase (AK, EC 2.7.4.3), albumin (ALB, non-enzymatic plasma protein), aldehyde dehydrogenase (ALDH, EC 1.2.1.5), alkaline phosphatase (AP, EC 3.1.3.1), carbonate dehydratase (CA, EC 4.2.1.1), diaphorase (DIA, EC 1.6.99.*), enolase (ENOL, EC 4.2.1.11), esterase (EST, EC 3.1.1.*), fructose-bisphosphatase (FDP, EC 3.1.3.11), fumarate hydratase (FUM, EC 4.2.1.2), guanine deaminase (GDA, EC 3.5.4.3), glutamate dehydrogenase (GDH, EC 1.4.1.3), glucose dehydrogenase (GLDH, EC 1.1.1.47) lactoyl-

Table 1 Locality, latitude, longitude, sex (m=male, f=female and u=unknown) and Registration number (WAM, Western Australian Museum; U=Museum of Northern Territory) of animals measured.

P. mimulus
Northern Territory: Centre Island, 15°41'00"S, 136°46'00"E, 3f, U1460, U1573, U1438; North Is, 15°34'00"S, 136°52'00"E, 2f, U1439, U40712; South West Is, 15°43'00"S, 136°40'00"E, m, U1437, f, U1463; Tambirini, 16°16'48"S, 134°19'12"E, f, U1212

P. roryi sp. nov.
Western Australia.
Clutterbuck Hills, 24°35'00"S, 126°17'00"E, m, WAM M17446; Eginbah Hmsd, 21°00'00"S, 120°00'00"E, f, WAM M4291; Great Sandy Desert, 22°27'00"S, 123°54'00"E, m, WAM M22691; Mundabullangana Hmsd, 20°42'00"S, 118°17'00"E, f, WAM M4483; Woodstock Station, 21°36'30"S, 118°57'30"E, m, WAM M5280, f, WAM M5511; 21°37'00"S, 118°56'00"E, m, WAM M6068, 21°37'00"S, 118°57'00"E, m, WAM M7123; 21°37'00"S, 118°57'00"E, f, WAM M7127, 21°35'00"S, 21°35'00"S, f, WAM M7128, 21°32'25"S, 118°59'30"E, f, WAM M29372, 21°36'42"S, 118°57'20"E, m, WAM M34277, 21°36'34"S, 118°58'28"E, m, WAM M 34282, 21°36'45"S, 118°53'30"E, 2m, WAM M34289, WAM M34290; 21°40'15"S, 119°02'30"E, m, WAM M34296; 21°36'45"S, 118°53'30"E, m, WAM M34304, 3f, WAM M34339, WAM M34340-1; Yardie Well, 22°19'30"S, 113°48'30"E, f, WAM M18139.

P. macdonnellensis
Northern Territory
Billack, 24°11'00"S, 132°26'00"E, m, U1738, Chewings, 23°54'00S, 132°32'24"E, f , U1088, 2m, U1090, U1093; Kathleen, 24°14'24"S, 131°24'00"E, m, U1756; Milton Peak, 23°22'48"S, 133°24'00"E, m, U1113; Windajong, 21°18'00"S, 132°31'48"E, m, 1750, f, U1749; Narwietoom, 23°18'36"S, 132°29'24"E, m, U1110; Tennant Creek, 19°39'00"s, 134°15'00"E, f, U6289; Arapanya Stn, 22°19'00"S, 133°22'00E, f, U1289.
Western Australia.
Blackstone Ridge, 26°00'00"S, 128°11'00"E, 2m, WAM M15369, WAM M15371, f, WAM M15370; Charlies Knob, 25°45'00"S, 126°11'00"E, 2f, WAM M14670-1, 25°03'00"S, 124°59'00"E, f, WAM M14671; Decker Airfield, 25°02'30"S, 124°59'30"E, 2m, WAM M24101-2; Featherstonehaugh Hill, 26°49'00"S, 126°21'00"E, m, WAM M23135; Gibson Desert, 25°03'00"S, 124°59'00"E, f, WAM M29292; Gill Pinnacle, 24°54'00"S, 128°47'00"E, m, WAM M15372; Lightning Rock, 26°00'00"S, 127°40'00"E, 3f, WAM M8927-8, WAM M8930, 3m, WAM M8931-3, 26°04'40"S, 127°45'50"E, f, WAM M8937, m, WAM M8938, 26°00'00"S, 127°40'00"E, m, WAM M8942; Mount Charles, 25°45'00"S, 126°11'00"E, f, WAM M14669; Winduldurra Rockhole, 26°31'15"S, 126°01'30"E, m, WAM M13855.

P. woolleyae
Western Australia.
Barlee Range Nature Reserve, 23°45'00"S, 116°20'00"E, m, WAM M3478, 23°06'21"S, 115°59'52"E, m, WAM M41840, 23°05'45"S, 116°00'35"E, m, WAM M43369; Barton Mine, 21°53'00"S, 120°17'00"E, m, WAM M2554; Harding River, 21°02'10"S, 117°07'30"E, f, WAM M24151; Mardie Hmsd, 21°15'00"S, 116°07'40"E, m, WAM M19676; Marymia, 25°10'00"S, 119°50'00"E, m, WAM M37023; Millstream, 21°35'00"S, 117°04'00"E, f, WAM M29227; Murrum Stn, 28°16'00"S, 117°23'00"E, f, WAM M21153; Pamelia Hill, 23°16'50"S, 119°11'20"E, f, WAM M19496; Poona Hill, 27°36'00"S, 116°17'00"E, m, WAM M24300; Robe River, 21°48'00"S, 116°15'00"E, m, WAM M37021; ; Wanjarri Nature Reserve, 27°21'00"S, 120°36'00"E, f, WAM M23577; Woodstock Stn, 21°36'25"S, 119°02'23"E, m, WAM M34268, 21°32'25"S, 118°59'15"E, f, WAM M34346, 28°28'00"S, 122°50'00"E, m, WAM M34375.

glutathione lyase (GLO, EC 4.4.1.5), aspartate aminotransferase (GOT, EC 2.6.1.1), glycerol-3-phosphate dehydrogenase (GPD, EC 1.1.1.8), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), glutathione peroxidase (GPX, EC 1.11.1.9), 3-hydoxybutyrate dehydrogenase (HBDH, EC 1.1.1.30), isocitrate dehydrogenase (IDH, EC 1.1.1.42), cytosol aminopeptidase (LAP, EC 3.4.11.1), L-lactate dehydrogenase (LDH, EC 1.1.1.27), malate dehydrogenase (MDH, EC 1.1.1.37), 'malic' enzyme (ME, EC 1.1.1.40), mannose-6-phosphate isomerase (MPI, EC 5.3.1.8), dipeptidase (valine-leucine) (PEPA, EC 3.4.13.*), tripeptide aminopeptidase (leucine-glycine-glycine) (PEPB, EC 3.4.11.), proline dipeptidase (phenylalanine-proline) (PEPD, EC 3.4.13.*), phosphoglycerate mutase (PGAM, EC 5.2.4.1), 6-phosphogluconate dehydrogenase (6PGD, EC 1.1.1.44), phosphoglycerate kinase (PGK, EC 2.7.2.3), phosphoglucomutase (PGM, EC 5.4.2.2), pyruvate kinase (PK, EC 2.7.1.40), superoxide dismutase (SOD, EC 1.15.1.1), L-iditol dehydrogenase (SORDH, EC 1.1.1.14), triose-phosphate isomerase (TPI, EC 5.3.1.1). The nomenclature for referring to enzymes, loci and allozymes follows Adams *et al.* (1987). Genetic distances were calculated as either percentage fixed differences (%FD, Richardson *et al.*, 1986) or corrected Nei distance (Nei D, Nei, 1978).

Canonical Variate Analysis (CVA)

Analysis of cranial and external variables was carried out separately, but the same statistical procedure was used for both sets of variables.

Initially, multiple regression was used to investigate variation due to sex, age and species differences for each of the 23 cranial and 6 external characters. These analyses checked for normality and detected statistical outliers which were then re-checked for measurement accuracy. Each variable was regressed on sex, age and species.

Table 2a Measurements in mm for Skull Variables by sex. N, Sample size; $\bar{X}$, mean; Min, minimum; Max, maximum; SD, standard deviation.

Variable	GSL		BL		BW		ZW		LIW		POB		TWAW	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
P. mimulus														
N	1	7	1	7	1	8	1	8	1	8	8	8	1	8
$\bar{X}$	24.75	24.87	23.00	23.21	10.90	11.05	15.00	14.96	5.750	5.472	5.740	5.606	4.220	4.130
Min	24.75	24.28	23.00	22.50	10.90	10.60	15.00	14.36	5.750	5.330	5.740	5.400	4.220	3.600
Max	24.75	25.57	23.00	23.87	10.90	11.32	15.00	15.59	5.750	5.770	5.740	5.770	4.220	4.500
SD	*	0.266	*	0.3532	*	0.0740	*	0.1724	*	0.02014	*	0.01466	*	0.08660
P. roryi sp. nov.														
N	7	7	7	7	9	7	8	7	9	7	9	7	9	8
$\bar{X}$	26.45	25.84	25.14	24.41	11.21	11.02	16.00	15.41	5.674	5.339	5.221	5.021	4.779	4.671
Min	24.92	24.33	23.59	23.59	1039	10.59	15.16	15.01	5.210	5.130	4.910	4.760	4.310	4.390
Max	28.17	27.22	26.39	25.49	12.08	11.47	16.83	15.78	6.020	5.670	5.980	5.210	5.050	4.750
SD	1.2340	0.910	1.0201	0.5340	0.2214	0.0853	0.1609	0.0858	0.05668	0.027150	.135980	0.02868	0.05644	0.01645
P. macdonnellensis														
N	16	8	16	8	17	9	17	9	17	9	17	9	16	9
$\bar{X}$	27.48	26.56	25.66	24.52	11.86	11.62	16.26	15.86	5.988	5.698	5.439	5.338	4.384	4.213
Min	25.67	25.50	23.93	23.27	11.49	10.93	15.04	14.79	5.610	5.050	5.090	4.810	3.970	3.900
Max	28.46	27.67	26.71	25.60	12.31	12.31	17.12	16.92	6.490	6.220	5.830	5.780	4.680	4.580
SD	0.5868	0.723	0.4828	0.9448	0.0458	0.2797	0.3250	0.5672	0.04733	0.18627	0.04257	0.13497	0.04132	0.06403
P. woolleyae														
N	5	5	5	5	4	5	5	5	5	5	5	5	5	5
$\bar{X}$	29.59	28.01	27.32	26.44	12.49	12.59	17.42	16.99	6.504	6.184	6.214	6.602	5.058	4.826
Min	28.13	25.69	26.21	24.62	11.51	12.23	16.51	16.35	6.100	5.670	6.100	5.670	4.740	4.430
Max	30.55	29.41	28.57	27.80	13.52	12.98	18.73	17.58	6.980	6.540	6.290	6.310	5.330	5.130
SD	0.8146	2.143	0.9367	1.6489	0.8442	0.1017	0.6772	0.3179	0.12133	0.10063	0.00583	0.06172	0.08687	0.07083

LM4RM4		MLTD		MLPV		PAL		DL		I1M4		APAC		ACAR	
♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
1	8	1	8	1	8	1	7	1	8	1	8	1	8	1	8
8.790	8.670	2.400	2.663	2.590	2.974	13.47	13.59	18.31	18.11	10.98	10.86	5.740	5.530	4.800	4.701
8.790	8.440	2.400	2.470	2.590	2.550	13.47	12.95	18.31	16.76	10.98	10.34	5.740	4.960	4.800	4.070
8.790	9.040	2.400	2.870	2.590	3.380	13.47	14.12	18.31	19.00	10.98	11.55	5.740	5.770	4.800	.5.030
*	0.04466	*	0.01782	*	0.0642	*	0.1847	*	0.6263	*	0.1977	*	0.07237	*	0.067
9	7	9	7	8	7	7	7	9	7	9	7	9	6	9	7
8.696	8.420	2.553	2.430	3.461	3.324	14.24	13.92	19.68	18.77	11.55	11.29	6.113	6.010	5.704	5.404
8.190	8.010	2.290	2.270	2.890	2.460	13.47	13.49	18.34	18.04	10.79	10.89	5.640	5.880	5.260	5.200
9.120	8.730	2.860	2.670	4.330	4.440	14.94	14.52	21.02	19.30	12.16	11.91	6.520	6.130	6.080	5.680
0.08650	0.06053	0.03172	0.01457	0.2502	0.4833	0.3496	0.1829	0.7112	0.2147	0.2360	0.1066	0.0847	0.00700	0.10458	0.0362
17	9	17	9	17	9	15	8	17	9	17	9	16	9	17	9
8.956	8.831	2.675	2.687	3.997	3.861	14.79	14.18	20.39	19.88	12.26	11.70	6.018	5.887	5.651	5.351
8.520	8.220	2.390	2.480	2.370	3.210	13.75	13.39	18.76	18.73	11.73	10.80	5.650	5.430	4.970	4.830
9.330	9.170	3.010	2.880	4.670	4.460	15.61	14.81	21.70	21.28	12.77	12.24	6.490	6.360	6.190	6.030
0.06050	0.12879	0.02866	0.01830	0.3852	0.2645	0.2014	0.3445	0.6732	0.8314	0.0840	0.2857	0.0472	0.09650	0.11172	0.1990
5	5	5	5	5	5	5	5	5	5	5	5	5	.	5	.
6.594	9.452	3.106	2.934	3.582	3.494	15.64	15.15	21.95	20.91	12.85	12.47	6.208		5.786	
9.250	9.170	3.040	2.730	3.070	2.800	15.10	14.08	21.10	19.40	12.37	11.91	5.600		5.340	
10.020	10.040	3.180	3.090	4.400	4.130	16.00	15.95	22.81	22.22	13.30	13.10	6.930		6.050	
0.08483	0.12392	0.00433	0.01853	0.2443	0.3190	0.1374	0.5701	0.4060	1.1901	0.1445	0.2014	0.2276		0.08478	

The extent of interactions between these factors was investigated for any evidence of interdependence. Two cranial variables, APAC and BW, showed significant interactions ($p = 0.001$, d.f.=2 and 0.005, d.f.=2 respectively) between sex and age. Two other cranial variables showed minor interaction between sex and age (BT; $p = 0.035$, d.f.=2) and species and age (MLPV; $p = 0.030$, d.f.=4) respectively. External measurements were taken on a reduced number of animals that did not permit testing of all potential interactions between species, sex and age. One external variable showed minor interactions between sex and age (TV; $p = 0.023$, d.f.=1). The variables

TWAL		EW		BT		BP		WOB		WIB		C1M4		M1M4	
♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
1	8	1	6	1	8	1	8	1	8	1	8	1	8	1	8
3.560	3.386	1.370	1.448	5.680	5.366	2.550	2.544	11.18	11.22	3.050	3.234	10.20	9.56	6.170	5.990
3.60	3.160	1.370	1.050	5.680	5.200	2.550	2.190	11.18	10.89	3.050	3.020	10.20	9.380	6.170	5.830
3.560	3.630	1.370	1.810	5.680	5.570	2.550	2.750	11.18	11.61	3.050	3.320	10.20	9.78	6.170	6.320
* 0.03203		* 0.05970		* 0.02551		* 0.03291		* 0.04817		* 0.01317		* 0.0301		* 0.20791	
9	7	9	7	9	7	9	7	9	7	9	7	9	7	9	7
4.570	4.377	1.503	1.431	6.797	6.650	2.933	3.103	11.80	11.56	2.600	2.453	9.90	9.68	6.071	5.936
1.120	4.140	1.030	1.270	6.320	6.170	2.540	2.860	11.40	11.27	2.390	2.220	9.56	9.260	5.850	5.680
4.810	4.770	1.930	1.590	7.390	7.350	3.470	3.480	12.48	11.69	3.070	2.790	10.33	10.18	6.290	6.340
0.05280	0.03816	0.10035	0.02278	0.1349	0.15163	0.07565	0.05229	0.1242	0.01920	0.05052	0.04719	0.07192	0.1061	0.02661	0.04313
16	9	16	8	16	9	16	9	17	9	17	9	17	9	17	9
3.919	3.774	1.477	1.470	3.130	5.893	2.761	2.672	11.74	11.51	3.204	3.293	10.45	10.05	6.442	6.270
3.640	3.520	1.180	1.310	5.580	5.630	2.500	2.100	10.81	10.96	2.870	2.990	10.20	9.290	6.200	5.700
4.480	3.980	1.930	1.780	6.630	6.540	3.080	2.980	12.09	11.84	3.420	3.460	10.76	10.62	6.660	6.630
0.04717	0.02275	0.04165	0.03120	0.0830	0.06955	0.01837	0.06594	0.1237	0.10754	0.02748	0.02180	0.03054	0.2240	0.01843	0.13552
5	5	5	5	16	5	5	5	5	5	5	5	5	5	5	5
4.768	4.544	1.500	1.398	6.130	6.842	3.620	3.284	13.08	12.64	3.014	2.964	11.38	11.02	6.788	6.506
4.450	4.150	1.310	1.270	5.580	6.570	3.250	3.080	12.28	11.92	2.610	2.820	11.08	10.690	6.430	6.250
5.010	4.900	1.650	1.500	6.630	7.200	4.050	3.450	13.71	13.05	3.250	3.130	11.55	11.56	7.030	6.920
0.04402	0.10513	0.01590	0.00762	0.0830	0.10467	0.09790	0.02153	0.3717	0.18123	0.06443	0.01613	0.04447	0.1039	0.05012	0.07263

which showed significant interactions were not used in further analyses.

For cranial variables, females were significantly smaller than males in all species; only EW, BP, WIB, MLTD showed no statistically significant sexual dimorphism (Table 3). No external variable showed significant sexual dimorphism. Regression coefficients were used to transform all variables by removing age and sex differences while retaining the inter-specific variation. Male and female values were adjusted to the mean of the two sexes, and juvenile and mature age classes adjusted to the adult mean. The values of these transformed variables were used in all succeeding analyses.

Canonical Variate Analysis (Discriminant Analysis) was used to examine the multivariate relationships between groups. Where a subset of characters was required, they were selected by sequential multivariate analysis of variance, using backward elimination and Wilks' Lambda as the selection criteria.

A CVA using cranial variables and *a priori* grouping by taxon showed a clear separation between each of *P. macdonnellensis*, *P.* sp. nov., and *P. woolleyae*, with less complete separation between *P. macdonnellensis* and *P. mimulus* (Figure 2). Only 1 individual out of 53 was misallocated (a *P. mimulus* classified as *P. macdonnellensis*). This analysis was based on five characters selected by backward elimination, but essentially the same results were obtained using the full set of 19 cranial measures or by forward selection of the five best (which produced four of the same characters as backward selection). The first two CVs accounted for 65% and 30% of the between group variance (Table 4). The pattern of correlation between the five selected characters and the first canonical function show that this is largely a shape discriminator. Canonical Variate Analysis of five external variables (excluding TV because of interaction), with *a priori* grouping by species, gave no clear separation among the same suite of species.

A crucial specimen of *P.* sp. nov. (WAM M17446) from Clutterbuck Hills, very close to the distribution of *P. macdonnellensis*, did not provide a full set of cranial measures. To establish the position of this animal in a CVA, a further analysis was performed using only the available variables. As before, the CVA was *a priori* grouped by species, but this time labelled by location (Figure 3). As expected, the Clutterbuck Hills animal grouped with *P.* sp. nov. and is distant from the cluster of *P. macdonnellensis* on both the first and second axes. The possibility of clinal variation was investigated by plotting the CV1 scores from the previous analysis against longitude (Figure 4). This shows a clear lack of longitudinally-related, clinal structure in the sample of *P. macdonnellensis*, and further illustrates the separation on CV1 between *P.*

Table 2b Measurements in mm for externals. N, Sample size; $\bar{X}$, mean; Min, minimum; Max, maximum; SD, standard deviation.

Variable	SV		TV		EAR		TRAGUS		PESL		PESW	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
P. minulus												
N	0	0	0	0	0	0	0	0	0	0	0	0
$\bar{X}$	*	*	*	*	*	*	*	*	*	*	*	*
Min	*	*	*	*	*	*	*	*	*	*	*	*
Max	*	*	*	*	*	*	*	*	*	*	*	*
SD	*	*	*	*	*	*	*	*	*	*	*	*
P. roryi sp. nov.												
N	8	16	8	16	8	15	7	14	8	16	8	16
$\bar{X}$	85.37	83.38	75.25	73.75	16.23	15.28	3.943	3.793	13.80	13.57	4.200	4.012
Min	83.00	77.00	66.00	66.00	13.70	10.30	3.200	3.200	12.10	12.10	3.700	3.200
Max	90.00	90.00	88.00	88.00	19.00	19.00	4.600	4.600	15.00	15.00	1.600	4.600
SD	7.41	11.58	42.50	30.60	2.516	5.050	0.2862	0.1884	0.9943	0.6236	0.09714	0.1385
P. macdonnellensis												
N	18	30	18	30	18	30	18	30	18	30	18	30
$\bar{X}$	83.00	83.23	79.28	79.03	17.08	16.92	3.772	3.807	13.78	13.70	4.228	4.203
Min	77.00	72.00	72.00	71.00	14.50	12.50	3.100	3.100	12.00	12.00	3.700	3.600
Max	89.00	96.00	85.00	90.00	19.30	21.10	4.500	4.600	14.90	14.90	4.700	4.700
SD	13.88	28.81	18.68	23.69	1.516	3.110	0.1221	0.1324	0.5430	0.4527	0.08095	0.0969
P. woolleyae												
N	5	7	5	7	5	7	5	7	5	7	5	7
$\bar{X}$	85.80	88.86	82.80	82.71	19.02	19.17	3.780	4.200	13.94	14.10	4.200	4.214
Min	79.00	79.00	76.00	75.00	17.80	17.80	3.000	3.000	13.00	13.00	3.900	3.900
Max	92.00	99.00	97.00	97.00	20.50	20.50	5.100	5.500	15.00	15.50	4.500	4.500
SD	29.20	48.81	67.70	63.90	1.352	1069	0.6920	0.9967	0.7880	0.9333	0.08000	0.0748

Table 3 Probabilities from regression of variables, species, sex, age: testing for interactions.

Variable	species	sex	age	species/ sex	species/ age	sex/age	species/ sex/age
GSL	<0.001	0.003	0.826	0.519	0.311	0.309	0.320
BL	<0.001	0.002	0.477	0.596	0.504	0.469	0.775
BW	<0.001	0.051	0.112	0.247	0.343	0.005	0.263
ZW	<0.001	0.009	0.093	0.204	0.092	0.137	0.950
LIW	<0.001	<0.001	0.782	0.985	0.353	0.151	0.775
POB	<0.001	0.054	0.231	0.603	0.637	0.080	0.854
TWAW	<0.001	0.029	0.272	0.712	0.312	0.737	0.572
TWAL	<0.001	0.008	0.109	0.961	0.847	0.082	0.098
EW	0.847	0.538	0.688	0.940	0.728	0.645	0.652
BT	<0.001	0.015	0.635	0.484	0.689	0.035	0.478
BP	<0.001	0.496	0.733	0.037	0.713	0.336	0.007
WOB	<0.001	0.018	0.727	0.734	0.141	0.173	0.562
WIB	<0.001	0.850	0.402	0.091	0.249	0.658	0.358
C^1M^4	<0.001	<0.001	0.087	0.946	0.682	0.239	0.894
M^1M^4	<0.001	0.009	0.043	0.864	0.740	0.182	0.200
LM^3RM^3	<0.001	0.052	0.940	0.726	0.344	0.843	0.276
MLTD	<0.001	0.148	0.825	0.249	0.894	0.622	0.493
MLPV	0.011	0.051	0.956	0.986	0.030	0.412	0.847
PAL	<0.001	0.006	0.8939	0.705	0.606	0.388	0.469
DL	<0.001	0.003	0.826	0.519	0.311	0.309	0.320
I_1M_4	<0.001	0.001	0.509	0.605	0.407	0.1623	0.551
APAC	0.039	0.048	0.748	0.798	0.245	<0.001	0.148
ACAR	0.083	0.008	0.925	0.974	0.233	0.672	0.427
SV	0.699	0.555	0.116	0.151	0.298	0.050	
TV	0.004	0.547	0.527	0.209	0.357	0.023	
EAR	0.006	0.062	0.665	0.136	0.130	0.265	
TRAGUS	0.080	0.360	0.283	0.313	0.528	0.166	
PESL	0.804	0.299	0.689	0.344	0.849	0.729	
PESW	0.216	0.054	0.800	0.316	0.647	0.628	

Table 4 Skulls. Canonical Variate Analysis scores, grouping by species (*P. macdonnellensis, P. mimulus, P. woolleyae, P. roryi* sp. nov.).

variable	SC1	SC2
TWAL	0.6765	0.1352
C1M5	0.2001	0.7781
POB	0.0633	0.5634
WIB	-0.4835	0.5217
NASL	0.1375	0.4179

macdonnellensis and *P.* sp. nov., despite the overlap in their longitudinal ranges.

Finally, to verify the species groupings, Canonical Variate Analysis was carried out with *a priori* grouping by location rather than by species. Using the regression coefficients for all variables, the data for this analysis were transformed by removing age and sex differences while retaining the inter-location variation. The resultant plots were essentially identical to those produced using *a priori* grouping by species. All of the above analyses were also replicated using untransformed data. The results were essentially the same in all cases. A CVA of *P. macdonnellensis* and *P.* sp. nov., with *a priori* grouping by species, produced a complete separation of CV scores. The most significant discriminating variables were GSL, WIB, TWAL, WOB and ACAR. (Table 5).

To assist with quick diagnosis of skulls, various bivariate distributions were examined. The two most informative plots are GSL against C1M4 (Figure 5a), reflecting a difference in relative tooth size between the two taxa, and GSL against WIB (Figure 5b), reflecting the difference in degree of inflation of the auditory bulla.

Results of Allozyme Analysis

A total of 53 putative loci were scorable in the present study. Table 6 presents the allozyme profile at 11 variable loci of seven specimens of *Pseudantechinus macdonnellensis* and four specimens of *Pseudantechinus* sp. nov. The following 42 loci were invariant: *Acon1, Acon2, Acp, Acyc, Ada2, Adh1, Ak1, Ak2, Aldh, Ap1, Ap2, Ca, Dia2, Enol, Est1, Est2, Fdp, Fum, Gda, Gdh, Glo, Got2, Gpd1,Gpd2, Gpi, Gpx, Hbdh, Idh1, Idh2, Lap, Mdh2, PepA, PepD, Pgam, 6Pgd, Pgk, Pgm, Pk1, Pk2, Sod, Sordh,* and *Tpi.*

Table 5 Skulls. Canonical Variate Analysis score, grouping by species (*P. macdonnellensis, P. roryi* sp. nov.).

variable	SC1
GSL	-1.497
WIB	-5.630
TWAL	4.577
WOB	1.217
ACAR	1.735

As is typical for dasyurids, the allozyme data reveal low levels of within-taxon genetic variation. Eighty-five percent of all loci were invariant in at least one taxon and all but one of the variable loci (*Gldh*) displayed only two alleles. The estimates of direct count heterozygosity are Ho = 0.027 ± 0.013 for *P. macdonnellensis* and Ho = 0.047 ± 0.017 for *P.* sp. nov.

Despite the large number of loci screened, only one fixed difference was observed, at the *Me* locus. In addition, the *Mpi* locus was nearly fixed for alternate alleles, with a single heterozygous individual from Nifty Mine in the Great Sandy Desert. No other significant differences in allele frequency were present. Although individuals can be unequivocally diagnosed by their genetic profiles at the two key loci, the overall level of genetic differentiation between the two taxa is low (2% fixed differences; Nei D = 0.033).

The seven individuals of *P. macdonnellensis* showed no clear evidence of genetic differentiation across the range of sampling localities. Similarly, there are no indications of genetic heterogeneity between the two specimens of *P.* sp. nov. from Nifty Mine and the two from Woodstock Station. Although these represent very small samples on which to examine within-taxon genetic divergence, it is important to note that increasing sample sizes does not generally produce a significant increase in either Nei's D or % FD between two sample sets. Of course, sampling of additional localities might always lead to the discovery of new dimensions of genetic variation, a problem shared by all forms of systematic analysis.

Summary of Morphological and Genetic Comparisons

The combined morphological and genetic data indicate that the northwestern *Pseudanthechinus* populations are both distinct and diagnosable from central Australian *P. macdonnellensis*. Despite their ease of morphological separation, the allozyme data demonstrate a close sibling relationship between the two taxa.

The decision to recognise the northwestern population as a distinct species rather than a geographic race of *P. macdonnellensis* has been taken for several reasons. Most important is the observation that both taxa maintain their distinct morphological identities over substantial geographic ranges, and show no indication of clinal intergradation or interspecific interaction in central Western Australia where their ranges approach to within 140 km. Further, the multivariate analysis indicates that the crania of the two taxa differ more in 'shape' than in size, suggesting possible dietary and other ecological differences between them.

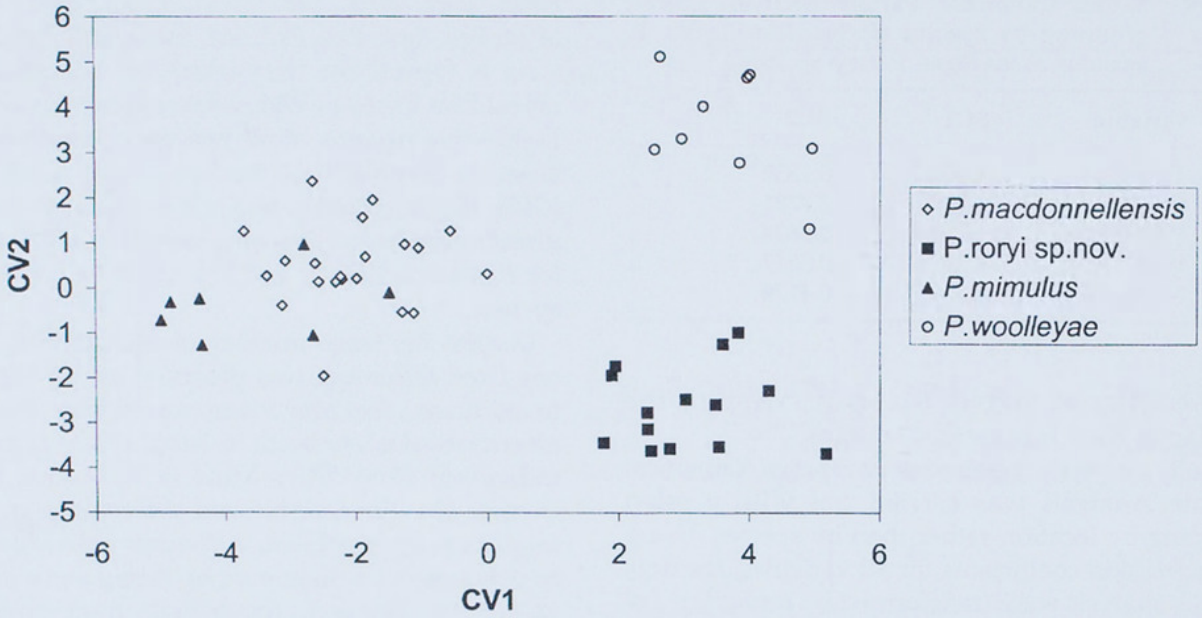


Figure 2 CVA of 5 variables, grouped by species.

Lastly, whilst the allozyme data by themselves are not compelling as to their specific status, they do document a level of genetic divergence consistent with that found for other sibling species of dasyurid (Baverstock *et al.*, 1982).

Further investigation could usefully focus on the issue of mitochondrial DNA lineage segregation between the northwestern population and *P. macdonnellensis*, and on the zone of potential parapatry/sympatry in the area south of the Clutterbuck Hills.

SYSTEMATICS

Pseudantechinus Tate, 1947: 139.

Revised generic diagnosis

Pseudantechinus differs from all other genera of

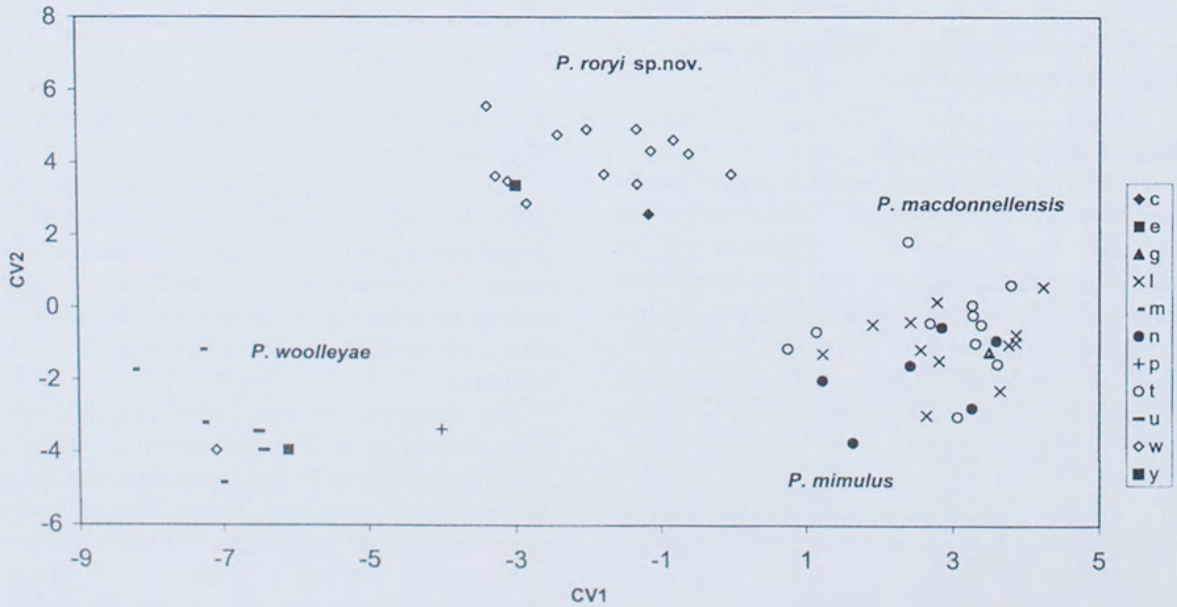


Figure 3 CVA, grouped by species, labelled by location. Alpha character representing location. **c**: Clutterbuck Hills; **e**: Barton Mine, Edginbah Hmsd; **g**: Charlies Knob, Decker airbase, Mount Charles; **l**: Blackstone Ridge, Featherstonehaugh Hill, Gill Pinnacle, Lightning Rock, Winduldurra Rockhole; **m**: Barlee Range, Harding River, Mardie Hmsd, Millstream, Robe River; **n**: Centre Is, North Is, South West Is; **p**: Marymia, Pamelia Hill; **t**: Billack, Chewings, Kathleen, Milton Peak, Narwietoom, Tambirini, Tennant Ck, Windajong; **u** : Murrum Stn, Poona hill; **w**: Mundabullangana Hmsd, Woodstock Hmsd; **y**: Yardie Well.

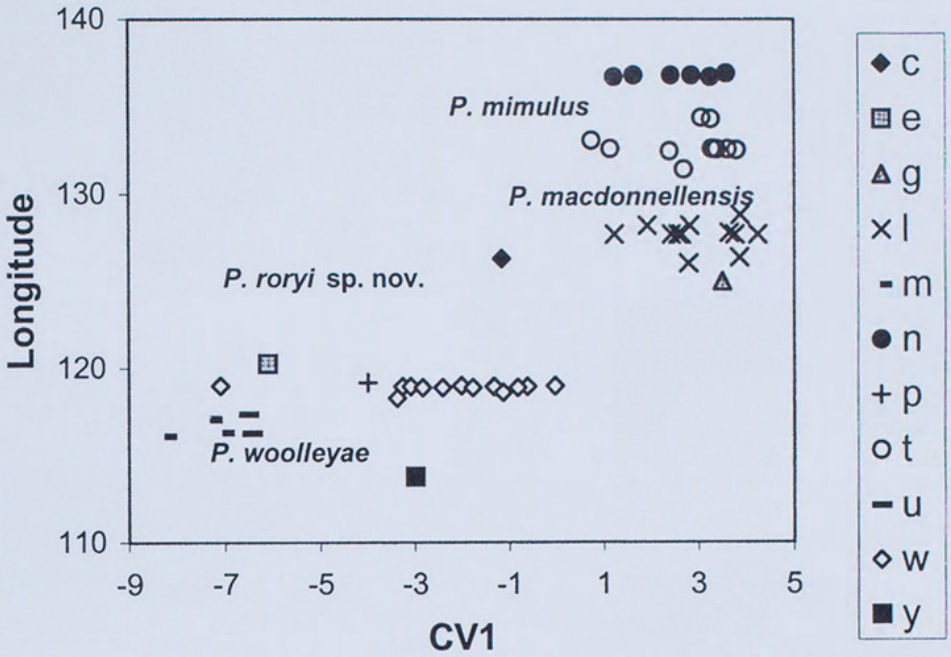
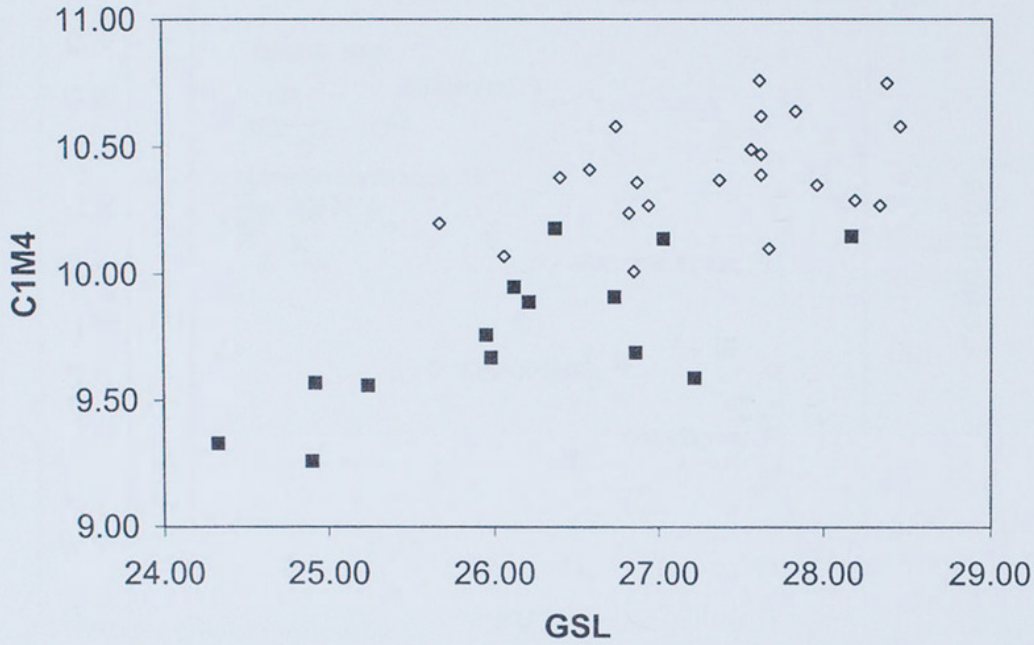


Figure 4 CV1 vs Longitude. CVA grouped by species, labelled by location. See figure 3 for key.

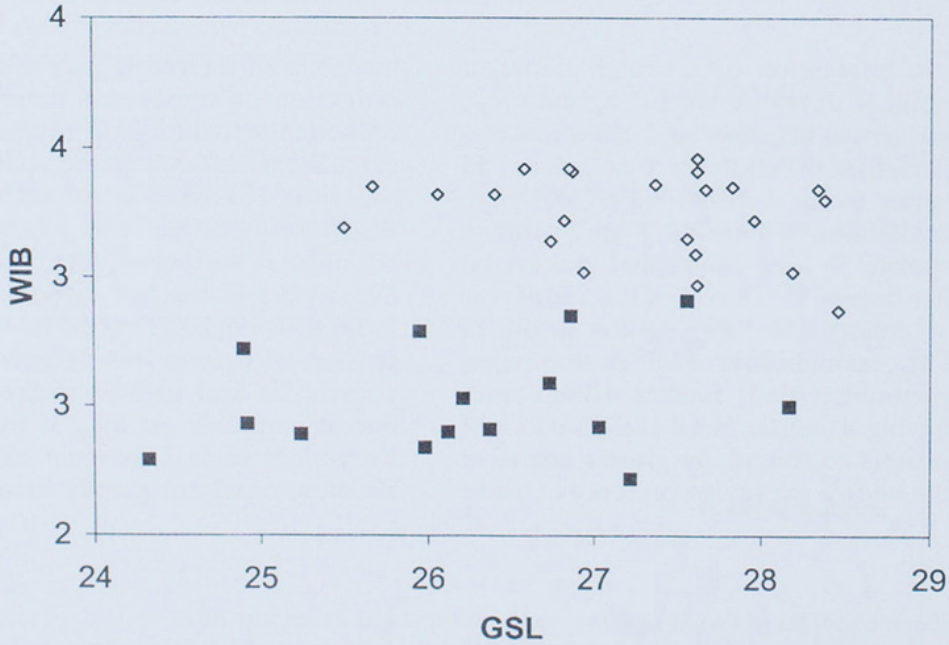
Dasyurinae in possession of a broad, flattened braincase; minimal development of sagittal crest; and reduction in size of upper and lower canines (Figure 6). It further differs from *Parantechinus* in having a shorter facial skeleton (Figure 7); more extensive fenestration of maxillary and palatine portions of palate; lack of postorbital process on frontal; greater degree of inflation of the middle ear cavity; lack of enlargement of P^2; greater degree of reduction of M_{2-3} talonids; loss of M^{2-3} protoconules; and less procumbent I^1. It further differs from *Myoictis* in having a shorter facial skeleton; lack of postorbital process on frontal; far greater degree of inflation of the middle ear cavity; presence of broad maxillary shelf forming floor to orbital fossa; lack of reduction of transverse canal in basisphenoid; reduction in width and interruption of anterior cingula and loss of protoconules on M^{1-4}; greater degree of reduction of M^4 protocone; and greater degree of reduction of M_{1-3} entoconids and of M_{1-4} talonids. It further differs from *Dasycercus* and *Dasyuroides* in the less extreme shortening of the facial skeleton; less extreme fenestration of palatine portion of palate; less extreme reduction of M_1 paraconid; and greater degree of reduction of buccal cingulids on M_{1-4}. It further differs from *Dasykaluta* in less extreme shortening of facial skeleton; nasal not greatly broadened posteriorly;

Table 6 Allozyme profiles of *Pseudantechinus macdonnellensis* and *P. roryi* sp. nov.

Regno	Locality	*Ada1*	*Adh2*	*Alb*	*Dia1*	*Gldh*	*Got1*	*Ldh*	*Mdh1*	*Me*	*Mpi*	*PepB*
Pseudantechinus macdonnellensis.												
SAMAM17093	Ronald Bore	c	b	b	ab	c	b	b	a	a	a	a
SAMAM17401	Illintjitja	c	b	b	b	c	b	b	a	a	a	ab
SAMAM17711	Cooperinna	c	b	b	ab	c	b	b	a	a	a	ab
SAMAM18123	Ungarinna Rockhole	c	b	b	a	cd	b	b	a	a	a	a
SAMAM18313	Pipalyatjara	c	ab	b	a	c	b	b	a	a	a	ab
SAMAM18784	Oolarinna East Bore	c	b	b	a	c	b	b	a	a	a	a
SAMAM19449	Mt Lindsay	c	ab	b	a	c	c	ab	a	a	a	ab
P. roryi sp. nov.												
WAMM34277	Woodstock Stn WA	c	b	ab	b	c	b	b	a	b	b	ab
WAMM34304	Woodstock Stn WA	ac	ab	b	a	cd	b	b	ab	b	b	a
WAMM47244	Nifty Mine WA	c	b	b	a	c	b	b	a	b	ab	b
WAMM45090	Nifty Mine WA	c	b	b	ab	bc	b	b	a	b	b	ab



a



b

Figure 5 a, GSL vs C1M4, raw data. *P. macdonnellensis* (◇) and *P. roryi* sp. nov. (■); b, GSL vs WIB, raw data. *P. macdonnellensis* (◇) and *P. roryi* sp. nov. (■).

retention of small to moderate-sized P^3; and greater degree of reduction of buccal cingulids on M_{1-4}. It further differs from *Dasyurus* (sensu lato) in absence of postorbital process on frontal; greater degree of inflation of the rostral tympanic process of petrosal; retention of small to moderate-sized P^3; lack of enlargement of P^2; reduction in width and interruption of anterior cingula and loss of protoconules on M^{1-4}; and greater degree of reduction of M_{1-3} entoconids. It further differs from *Sarcophilus* in less extreme broadening of temporal fossa and lateral flaring of zygomatic arch; less extreme shortening of the facial skeleton; greater degree of fenestration of the palatal portion of palate; greater degree of inflation of the rostral tympanic process of petrosal; non-transverse orientation of the upper incisor series; retention of small to moderate-sized P^3; less extreme

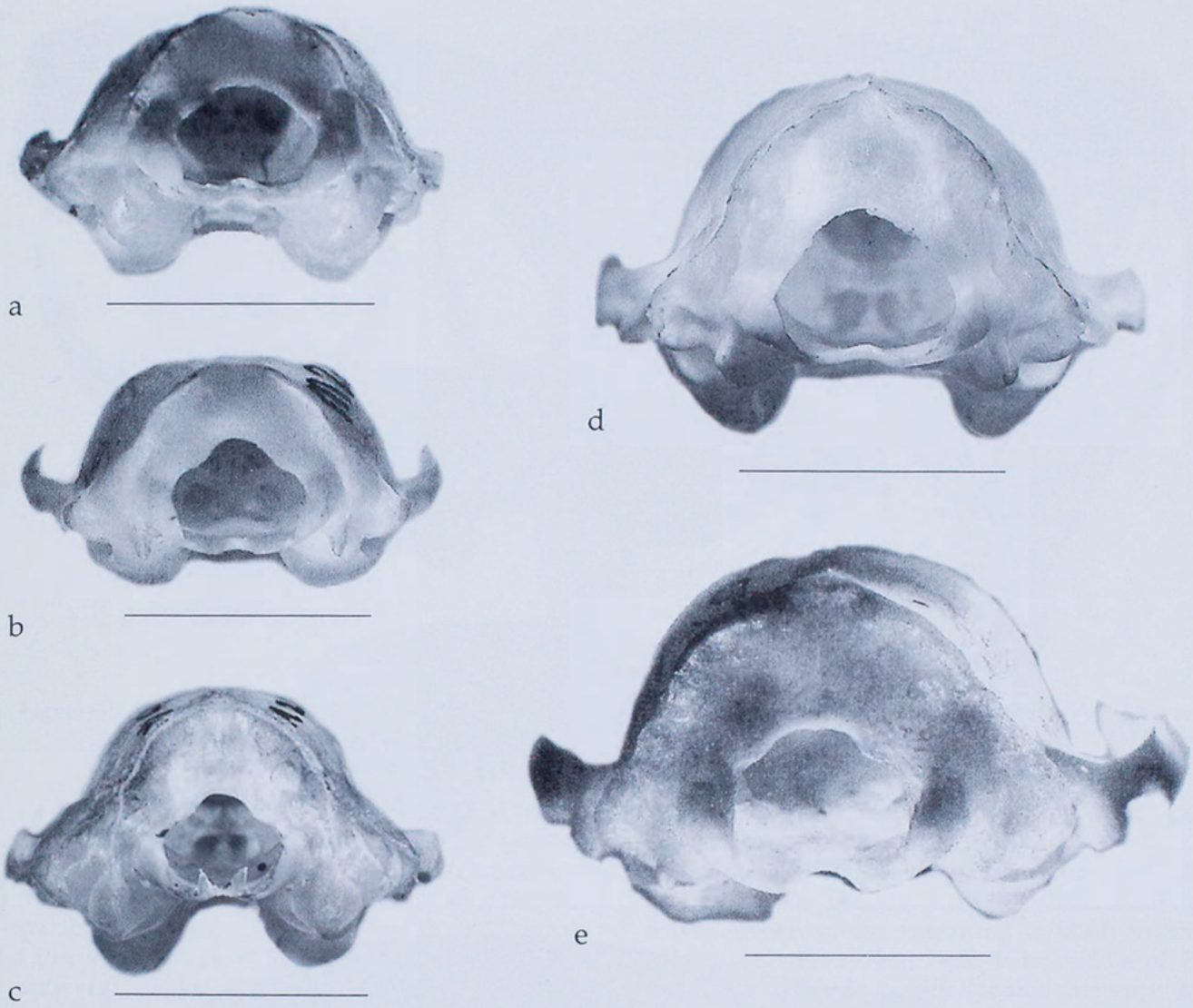


Figure 6 Rear view of skulls of (a) *Pseudantechinus macdonnellensis*, (b) *P. bilarni*, (c) *Dasykaluta rosamondae*, (d) *Parantechinus apicalis* and (e) *Myoictis melas*. All scale lines = 1 cm.

enlargement of metastylar corner of M^{2-4}; less extreme reduction of M_1 paraconid; lack of posterior displacement of M_{1-4} metaconids; and less extreme reduction of M_{1-4} talonids and M^{1-3} protocones.

Pseudantechinus roryi sp. nov.

Material Examined

Holotype

Western Australian Museum catalogue number M34277: adult male; carcass fixed in 4% formalin, preserved in 75% ethanol; skull and dentaries separate. Caught in an Elliott trap by R. A. How *et al.* on 29 July 1990.

Paratypes

See specimens examined.

Type Locality

Woodstock Station, 500 metres north of the homestead, in 21°36′42″S, 118°57′20″E.

Habitat

Low open woodland of *Acacia pyrifolia* (2–3 m tall, 3% canopy cover), *Hakea suberea* (2–3 m tall, <0.5% canopy cover) and *Acacia* sp. (2–3 m tall, <0.5% canopy cover) over *Triodia* spp. (c. 0.5 m tall, 80% canopy cover). Soil a coarse sandy-loam with granite bedrock at 30–40 cm (How *et al.*, 1990).

Diagnosis

Pseudantechinus roryi (Figures 8–10) differs from all other species of *Pseudantechinus* in having the following combination of characters: maxillary palatal vacuity expanded anteriorly either to level

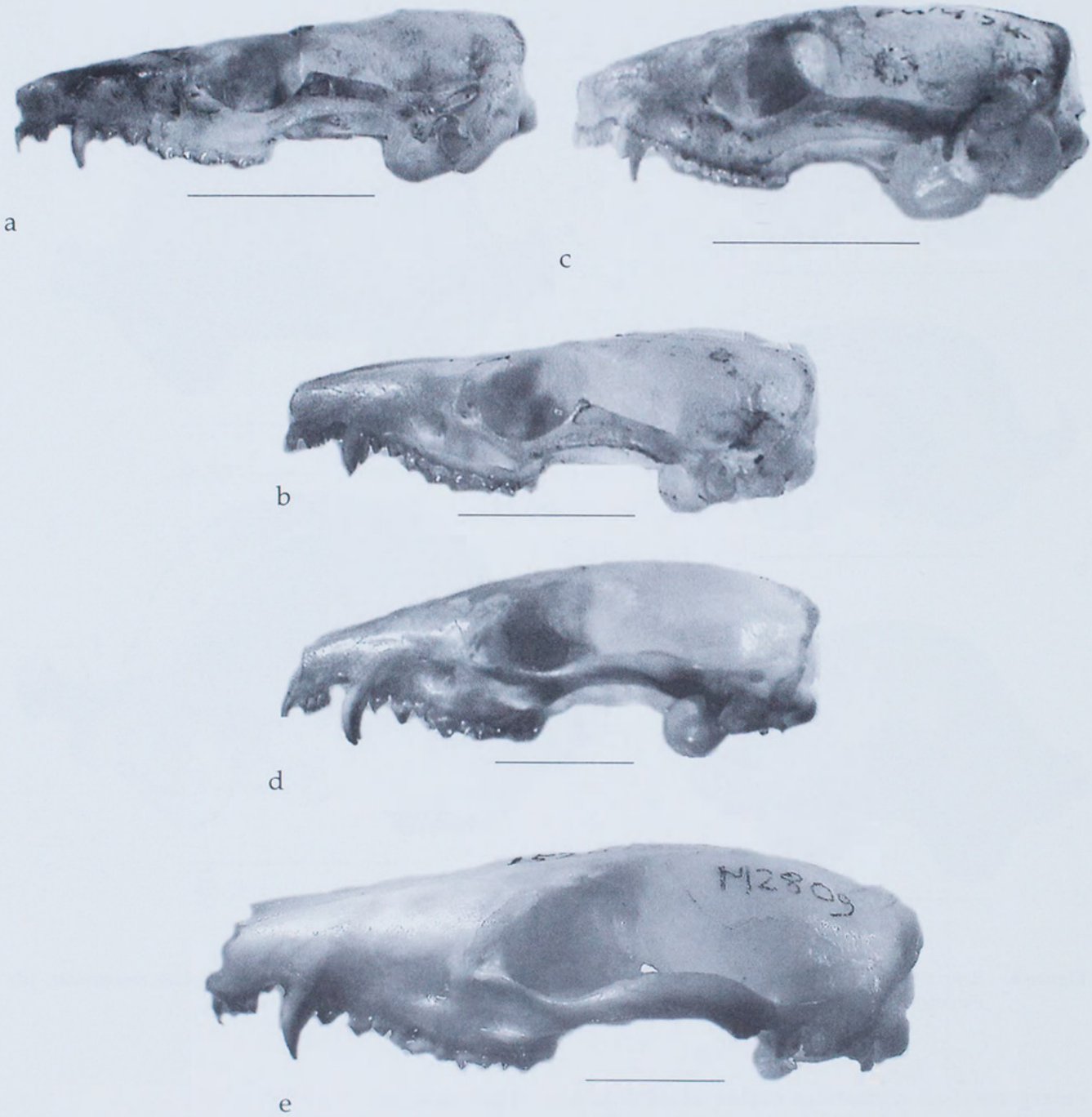


Figure 7 Lateral view of skulls of (a) *Pseudantechinus macdonnellensis*, (b) *P. bilarni*, (c) *Dasykaluta rosamondae*, (d) *Parantechinus apicalis* and (e) *Myoictis melas*. All scale lines = 1 cm.

of metastyle or to protocone on M^1; anterior root of zygomatic arch with shallow muscular fossa; P^3 single-rooted, lower and smaller in crown area than both P^1 and P^2; P^2 slightly taller and larger in crown area than P^1; M^1 with conical paracone, lacking preparacrista and stylar cusp B (StB); M^{1-4} anterobuccal cingula broad but reduced in lateral extent; M^{2-3} with small stylar cusp E (StE); P_3 absent; P_2 subequal in height and crown area to P_1; M_1 paraconid and metaconid both extremely reduced; M_1 lacking entoconid; M_{2-3} with vestigial entoconids; and M_{2-4} with narrow precingulids and poorly developed parastylids; penis with elongate ventral process presumably formed from accessory corpora cavernosa; pouch of female with six teats.

Description

Skull and Dentary

Braincase low but gently rounded; lambdoidal crest distinct but not overhanging occipital surface of skull; temporal ridges low but distinct, converge posteriorly and usually meet in older individuals

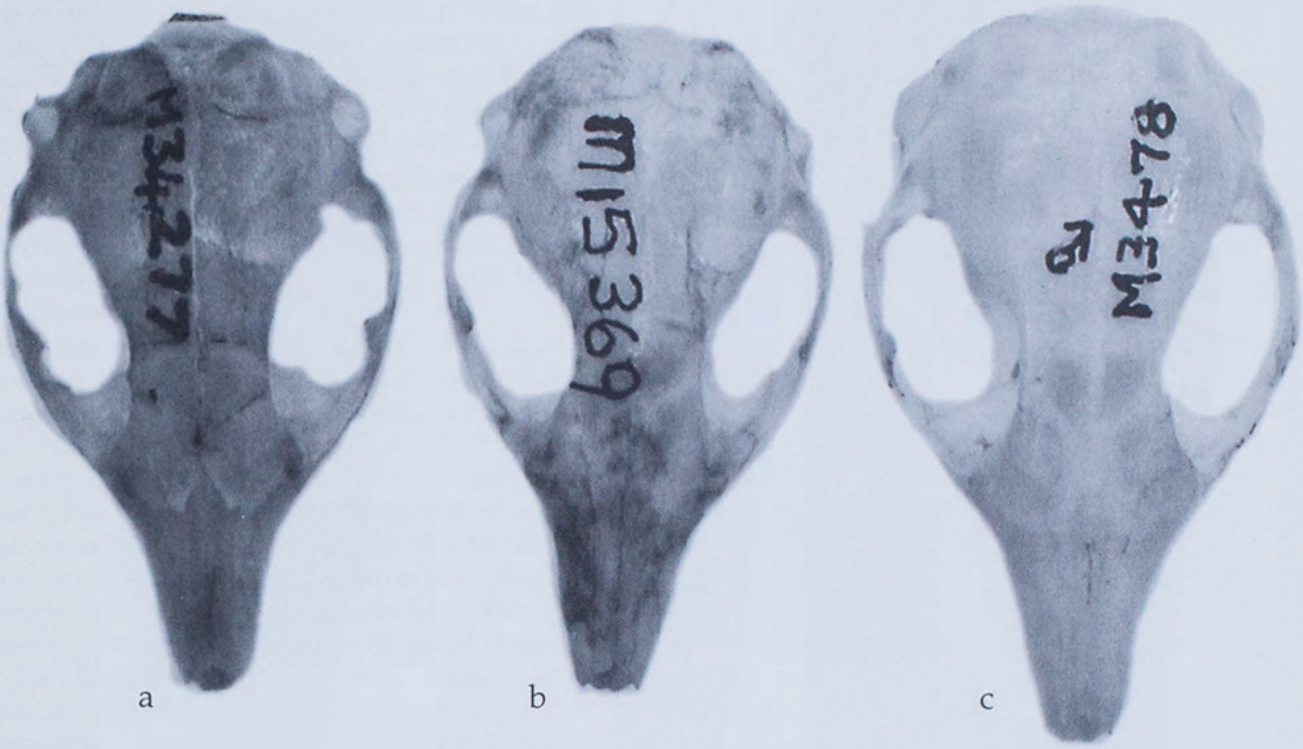


Figure 8 Dorsal view of skulls of (a) *Pseudantechinus roryi* sp. nov., WAM34277, (b) *P. macdonnellensis* WAM15369 and (c) *P. woolleyae* WAM3478.

to form short sagittal crest at rear of skull; squamosal contacts frontal on lateral wall of braincase in 71% of sample, excluded from contact in remaining specimens by narrow alisphenoid-parietal contact (average length 0.62 mm); interorbital region flattened, lateral margins converge slightly to rear; postorbital processes absent; cranium attains maximum width just forward of glenoid fossae.

Rostrum moderately elongate and not markedly inflated; nasals broadest at point of intersection of maxillo-frontal suture, narrowing to front; anterior palatal foramina extend from I^3 to middle of C^1; maxillary palatal vacuity located between M^1

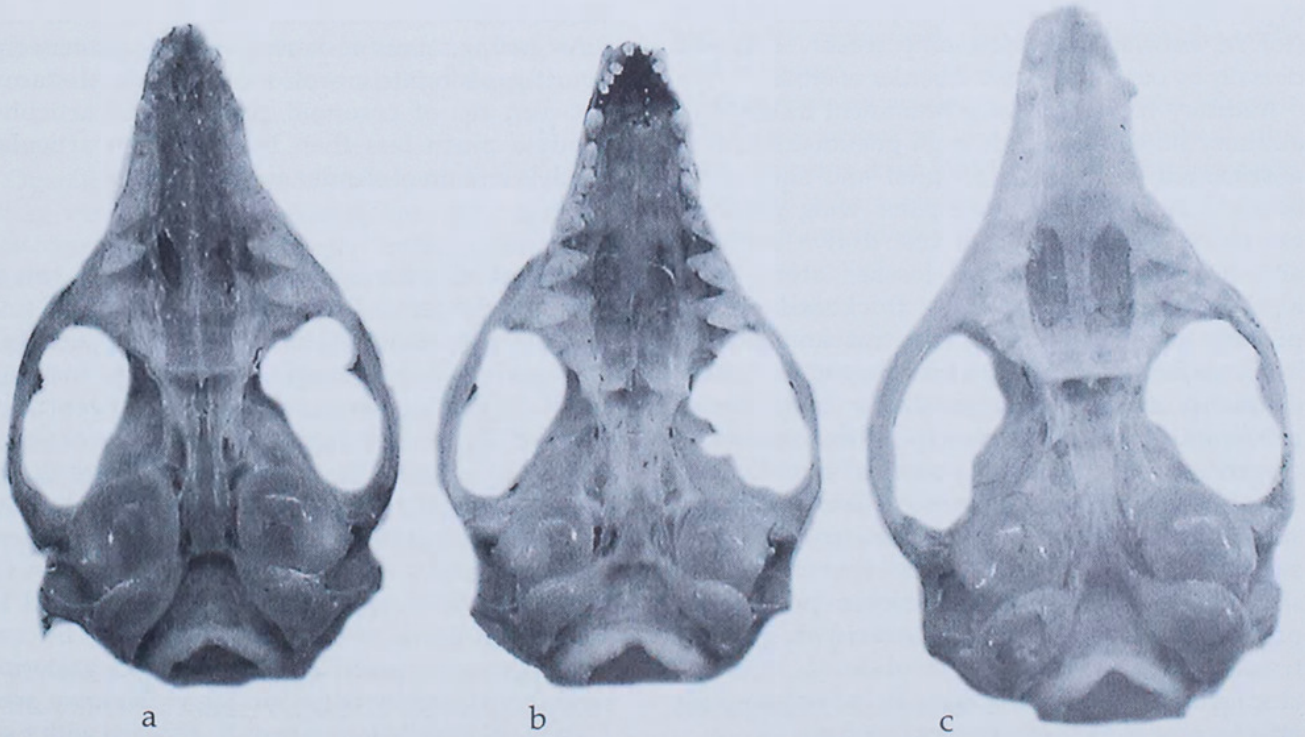


Figure 9 Ventral view of skulls of (a) *Pseudantechinus roryi* sp. nov., (b) *P. macdonnellensis* and (c) *P. woolleyae*.

Figure 10 Lateral view of skulls of (a) *Pseudantechinus roryi* sp. nov., (b) *P. macdonnellensis* and (c) *P. woolleyae*.

metacone and posterior end of M^3; palatine palatal vacuity small, occasionally absent. Anterior root of zygomatic arch with poorly developed muscular fossa (for *M. maxillonasolabialis*), only weakly enclosed dorsally by out-turned ventral border of orbit.

Auditory region showing prominent inflation of auditory bulla, formed through pneumatisation of alisphenoid, periotic, exoccipital and squamosal bones. Alisphenoid hypotympanic wing globular, expanded well forward of line drawn between anterior border of glenoid fossae; lateral edge almost completely enclosing thickened meatal process of ectotympanic. Rostral and caudal hypotympanic wings of petrosal together form a distinct posterior component of the 'bulla'; small paroccipital process of exoccipital encloses small extension of posterior pneumatic chamber; squamosal epitympanic sinus expanded laterally such that braincase width measured across squamosals is only slightly less than maximum skull width across zygomatic arches; postglenoid process of squamosal relatively high but transversely narrow; anterolateral wall of alisphenoid hypotympanic wing lacks bony spur for attachement of glenoid capsular ligament.

Cranial foramina show typical dasyurid arrangement (Archer, 1976b); bilateral transverse canal foramina relatively large and with distinct lateral sulci.

Ascending ramus of dentary inclined posteriorly, bearing elongate coronoid process; distance between tip of coronoid process and articular condyle much less than that between articular condyle and tip of slender angular ramus.

Dentition

I^1 tallest of upper incisors, separated from rest of series by diastema; I^1 crowns project forward and medially but remain separated at tips; I^2, I^3 and I^4 all subequal in crown height and length, forming regular series, crown apices posteroventrally directed; I^4 separated from C^1 by diastema equal in length to combined I^{3-4} crown lengths; C^1 vertically oriented, usually with weak buccal and lingual cingula terminating in distinct anterior and posterior basal cuspules; no diastema between C^1 and P^1 or within upper premolar series; P^1 and P^2 similar in form with well developed buccal cingulum and associated anterior and posterior cuspules; P^2 slightly taller and larger in crown area than P^1; P^2 slightly larger than P^1; P^{1-2} each with two clearly distinct roots; P^3 usually present,

approximately one third crown area of P^1 and with single root; StB very low and indistinct on M^2, preparacrista very short; StD taller than StB on M^2, but equal in height on M^3 ; M^3 ectoloph deeply indented between StB and StD; M^{1-3} with well-developed anterobuccal cingulum, forming complete shelf with preprotocrista on M^1 but interrupted on other molars; M^2 usually lacks StC but with distinct StE. M^4 narrower than M^3 and lacking metacone.

I_1 taller crowned than I_{2-3}, all with distinct posterior heel; C_1 twice the height of P_2 and with complete cingulum and associated anterior and posterior cuspules; P_1 and P_2 two-rooted with the primary cusp positioned above the anterior root; P_1 and P_2 with complete basal cingulum; P_1 usually lacking anterior cingular cuspule; P_2 with distinct anterior and posterior cingular cuspules; P_2 slightly taller and larger in crown area than P_1; P_3 absent; P_2 separated from M_1 by short diastema; M_1 paraconid reduced to small basal cuspule associated with buccal and lingual cingula; M_1 metaconid small to indistinct, positioned low on posterolingual flank of protoconid; M_1 lacking entoconid but with well developed postcingulid; M_2 to M_4 protoconid much taller than metaconid which is slightly taller than paraconid which is taller than hypoconid; M_{2-3} with small but distinct entoconids which produce slight bulge in lingual margin of talonid; M_{2-3} with well-developed postcingulids but precingulids and buccal cingulum poorly developed; M_{2-4} with weak preparacristid spurs; M_{2-3} cristid obliqua terminate well buccal to protocristid notch; M_4 trigonid similar to that of M_{2-3} except narrower and shorter, but talonid greatly reduced, consisting of hypoconid and narrow talonid basin only; M_4 with weak buccal cingulum below cristid obliqua.

Pelage

Overall fur colour is reddish-brown dorsally and white ventrally. Hairs on back and shoulders are dark grey for basal half, topped with bright tan and bearing darker tips. Guard hairs are darker. Hairs on belly and chin are dark grey for basal third, topped with white. Face and cheeks with grizzled appearance. Hairs on face and cheeks pale tan with dark grey for basal third and at tips. Bright orange patch located behind ear. Hairs on upper surfaces of hands and feet white. Scrotum almost black with white hairs. Tail is distinctly bicoloured, hairs on upper surface tan, some with darker tips, usually paler to white below.

Pes

Pattern of pads is similar to the other species of *Pseudantechinus* (see Figure 11): terminal pads smooth; interdigital pads separate and clearly striated; hallucal and posthallucal pads and metatarsal granule clearly striated; plantar surface, including hallux, very granular; plantar surface hairless except for short hairs on medial side of heel.

Figure 11 Plantar pes of *P. roryi* sp. nov.

Reproductive Anatomy

Females consistently have 6 teats in the well-defined pouch.

Males have an accessory penile process which is positioned ventral to, and is only slightly shorter than, the penis itself. The tip of the penis is weakly bifid and lacks a median dorsal lobe of the kind present in *Antechinus* spp.

Distribution

Pseudantechinus roryi is widespread through the northern Pilbara, north of the Hamersley Range and extending into the Great Sandy Desert as far east as Clutterbuck Hills (Figure 12). It also occurs on the Cape Range Peninsula. A population on Barrow Island probably represents *P. roryi*, although the few specimens in the Western Australian Museum are too damaged to be identified with certainty. *Pseudantechinus roryi* is sympatric over the southern and western part of its range with *P. woolleyae*.

Interspecific comparisons

Pseudantechinus roryi can be distinguished from *P. macdonnellensis* of central Australia in being smaller

in most cranial measurements except for those related to bulla size (Table 2a) and in the following aspects of craniodental morphology: middle ear cavity more inflated in *P. roryi*, especially marked in case of posterior component (formed from rostral tympanic process of petrosal) which is more nearly comparable in size to alisphenoid portion; squamosal contacts frontal on lateral wall of braincase in higher population of cases in *P. roryi* (71% vs 56%; average separation in *P. macdonnellensis* is 0.93mm); I^1 and C^1 projecting further forward in *P. roryi* rather than slightly recurved; P^3 less markedly reduced in *P. roryi*; P^1 and P^2 cingula broken anteriorly and posteriorly in *P. roryi* rather than completely encircling crown; M^1 anterior cingulum is usually incomplete in *P. roryi*, with gap between anterobuccal cingulum and preprotocrista, rather than complete; M^2 lacks stylar cusp C in *P. roryi* rather than sometimes present; M^{2-3} usually with low stylar cusp E in *P. roryi* rather than lacking that cusp; C_1 of *P. roryi* with complete basal cingulum linking anterior and posterior cingular cuspules, rather than with incomplete cingulum and only occasionally with anterior and posterior cuspules; P_{1-2} subequal in height and crown area in *P. roryi*, with primary cusps positioned more forward, closer to anterior root, rather than P_2 slightly higher and larger in crown area than P_1 and with more centrally primary cusps; P_{1-2} also relatively narrower in *P. roryi*; P_1 anterior cingular cuspule only occasionally present in *P. roryi* rather than usually present; anterior end of P_2 contacts back of P_1 lingual to midpoint in *P. roryi* rather than centrally; M_1 with anterior portion of trigonid including paraconid reduced in *P. roryi*, resulting in shortening of trigonid relative to talonid; buccal cingulum on M_1 complete in *P. roryi* rather than incomplete; M_{2-3} of *P. roryi* with cristid obliqua straighter and contacting posterior surface of trigonid in a more buccal position, rather than concave buccally and shifted lingually; M_{2-4} of *P. roryi* with relatively broader postcingulids which continuearound base of hypoconid rather than terminating on posterior surface of hypoconid; and

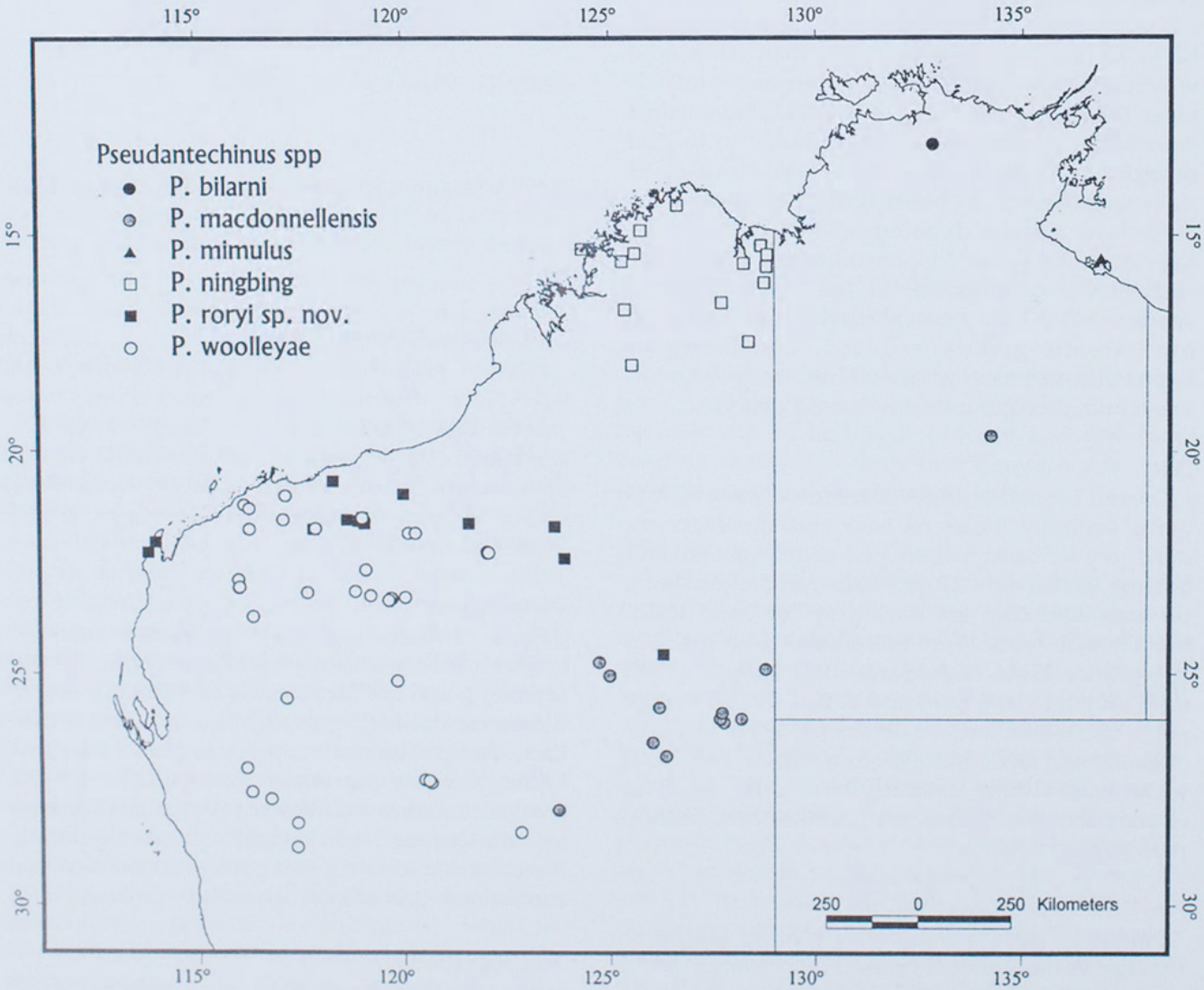


Figure 12 Localities of Pseudantechinus spp measured in this study.

M_{2-3} entoconids less reduced in *P. roryi*, usually larger on M_3 than on M_2, rather than larger on M_2.

Externally, all species of *Pseudantechinus* are very similar in pelage colour and pattern, with the variation within species encompassing that seen between species. The major variation is in the redness of the dorsal hair, the percentage of grey in the basal part of the ventral and dorsal hair, the shade of grey in the dorsal and ventral hair and the degree of differentiation of the dorsal and ventral colour of the tail. All species have a flash of orange behind the ears. External differences are mainly in the ratio of the tail to head + body (snout-vent) length. The pattern of footpads is essentially the same in all species (Figure 11).

Pseudantechinus roryi differs from *P. macdonnellensis* in being smaller in all external measurements except SV; and having smaller external ears. The scrotum of *P. roryi* is wider and longer than that of *P. macdonnellensis* (scrotal width: mean = 13.2, range = 11.6–14.9, n = 8 vs 11.4, 10.3–13.9, 8; scrotal length: mean = 12.1, range = 7.9–13.9, n = 8 vs 10.1, 8.7–13.8, 8. A t-test comparing the scrotal widths and lengths between the two species indicated that scrotal width was significant at 0.001 (T=3.75) but there was no significant difference in length of scrotum. The sample of *P. roryi* was collected between May and August and the *P. macdonnellensis* sample between February and August. Woolley (1991) found that wild-caught *P. macdonnellensis* from Abydos and Woodstock produced young later in the year (births in October) than animals from central Australia (births in August to early September). Three females collected at Woodstock Station in October–November 1990 (How *et al.*, 1990) were all carrying pouch young.

Pseudantechinus roryi differs from the widely sympatric *P. woolleyae* in being smaller in all external measurements and all craniodental measurements except for EW. It also differs in numerous aspects of craniodental morphology: petrosal component of bulla less strongly inflated in *P. roryi*; muscular fossa on anterior root of zygomatic arch slightly better developed in *P. roryi*; P^3 smaller than P^2 in *P. roryi* rather than subequal to P^2; M^1 generally lacking stylar cusps B and C, rather than well-developed as in *P. woolleyae*; P_3 absent, rather than retained as in *P. woolleyae*; and M_{1-3} entoconids and precingulids substantially more reduced in *P. roryi*.

Externally, *Pseudantechinus roryi* differs from *P. woolleyae* in having shorter ears. Female *P. woolleyae* have six teats as in *P. roryi*. Male *P. woolleyae* lack an accessory penile appendage and have a conspicuously smaller scrotum than *P. roryi*.

Pseudantechinus roryi is similar to *P. ningbing* of the Kimberley region in most external and craniodental measurments but differs from this species in the following craniodental features: maxillary palatal vacuity extends further anteriorly in *P. roryi*; nasals broadening posteriorly in *P. roryi*, rather than remaining narrow; petrosal component of auditory bulla more strongly inflated in *P. roryi*; I^4 smaller in crown area than I^3 in *P. roryi*, rather than subequal; P^2 larger than P^1 in crown height and area in *P. roryi*, rather than subequal; M^{2-3} with stylar cusp E more often present in *P. roryi*; P_2 subequal to P_1 in crown height and area in *P. roryi*, rather than larger than P_1; M_1 metaconid in *P. roryi* more reduced in size and height; and M_{2-3} entoconids in *P. roryi* low but distinct, rather than indistinct to absent.

Externally, *Pseudantechinus roryi* differs from *P. ningbing* in having the tail generally shorter than the head + body. Female *P. ningbing* have four teats in the pouch. Male *P. ningbing* have a very small accessory penile appendage and a conspicuously smaller scrotum than *P. roryi*.

Pseudantechinus roryi is larger than *P. mimulus* of the Northern Territory in most craniodental and external measurements and also differs from this species in the following craniodental features: maxillary palatal fenestra extends further anteriorly in *P. roryi*; palatine palatal vacuity larger in *P. roryi*; squamosal and frontal in *P. roryi* commonly in contact on side wall of braincase, rather than excluded by contact of alisphenoid and parietal; petrosal component of auditory bulla more strongly inflated in *P. roryi*; anterior root of zygomatic arch in *P. roryi* with distinct muscular fossa enclosed by dorsal flange, rather than indistinct, poorly enclosed fossa; I^4 in *P. roryi* smaller in crown area than I^3, rather than subequal; P^3 in *P. roryi* less reduced and bearing two roots, rather than tiny and single-rooted; P_2 subequal to P_1 in crown height and area in *P. roryi*, rather than larger than P_1; M_1 metaconid more reduced in size and height in *P. roryi*; M_{2-3} entoconids more reducedand M_{2-4} precingulids narrower and less distinct in *P. roryi*.

Female *P. mimulus* have 6 teats in the pouch. Male *P. mimulus* appear to lack an accessory penile appendage and have a conspicuously smaller scrotum than *P. roryi*

Pseudantechinus roryi is smaller in most craniodental and external measurements than *P. bilarni* and also differs in numerous craniodental features; petrosal component of auditory bulla more inflated in *P. roryi*; muscular fossa on anterior root of zygomatic arch in *P. roryi* poorly developed, rather than well-developed and enclosed by out-turned rim of orbit; maxillary palatal fenestra extends further anteriorly in *P. roryi*; palatine palatal vacuity larger in *P. roryi*; squamosal and frontal commonly in contact on side wall of braincase in *P. roryi*, rather than excluded by contact of alisphenoid and parietal; I^4 smaller than I^3 in *P. roryi*, rather than subequal to I^3; P^3 smallest tooth of premolar series in *P. roryi*, rather than largest tooth

of series; M^1 lacks stylar cusp B in *P. roryi*, rather than retaining distinct stylar cusp B; M^4 protocone less markedly reduced in *P. roryi*; P_3 never present in *P. roryi*, rather than commonly present; M_1 metaconid smaller and lower in *P. roryi* and M_1 entoconid absent, rather than low but distinct; M_{2-3} entoconids low but distinct in *P. roryi*, rather than absent, and M_{2-4} precingulids less distinct.

Externally *Pseudantechinus roryi* differs from *P. bilarni* in having the tail generally shorter than the head + body. Female *P. bilarni* have 6 teats in the pouch. Male *P. bilarni* lack an accessory penile appendage and have a conspicuously smaller scrotum than *P. roryi*.

Etymology

After Rory Cooper, the son of one of the authors. Rory is Gaelic for red and *Pseudantechinus roryi* is generally a brighter reddish-brown dorsally than the other species of *Pseudantechinus*.

DISCUSSION

Recognition of Sibling Species

We have argued that the false antechinus populations previously identified as *Pseudantechinus macdonnellensis* are more appropriately divided into two closely-related but diagnosable species. In our view, true *Pseudantechinus macdonnellensis* is found in the central Australian uplands, extending west to Yamarna Hmsd, and north into the Tanami Desert. Its sibling, the newly described *Pseudantechinus roryi*, inhabits the Pilbara uplands, extending north and east into the Great Sandy and Gibson Deserts. Although the distributions of the two taxa appear to be allopatric, their ranges approach to within 140 km in the Gibson Desert, and further collecting in this little-studied region may yet find them in sympatry.

The two species are diagnosable using the allozyme data, although only weakly so, with a single fixed difference and one other near-fixed difference. Significantly however, the limited genetic sampling within each of the two taxa suggests a high degree of genetic uniformity across very large distances, with very low levels of allelic variation overall. Similar low levels of heterozygosity and genetic uniformity across large distances have been noted in previous electrophoretic studies of dasyurid marsupials (Baverstock *et al.*, 1982, 1983, 1984; Dickman *et al.*, 1988) and appear to be fairly characteristic of the group. Most importantly, a number of other sibling species show low levels of genetic divergence (ie less than 10% fixed differences) amongst dasyurids (Baverstock *et al.*, 1982).

Morphologically, the two taxa are readily distinguished by a range of contrasting craniodental features including the relative degree of inflation of the middle ear cavity, the relative size of the cheekteeth, and details of cranial and dental anatomy. These differences suggest likely ecological differences between the two taxa, although both are primarily confined to upland, rocky habitats or to local outcrops and breakaways within the sedimentary basin deserts. In contrast to these between-species differences, morphometric analysis has shown each of *P. macdonnellensis* and *P. roryi* to be morphologically uniform across their respective ranges, with no evidence of clinal intergradation. This is an important observation that adds further strength to our suggestion that the two populations be distinguished at species level.

In concluding this section, it should be noted that Cooper and Woolley (1983) earlier postulated from electrophoretic evidence that the Tanami Desert population of *P. macdonnellensis* might represent a distinct race to those in Central Australia. Unfortunately, it has not been possible to locate voucher specimens for the Tanami population to examine the craniodental morphology of this population. Nevertheless, it can be noted that the reported genetic differentiation was limited to an allele frequency difference at the transferrin locus, a protein known for its unusually high rate of genetic variability.

Broader Relationships and Classification of the False Antechinuses

The process of describing *P. roryi* has stimulated a re-examination of broader relationships among the false antechinuses and their relatives. The picture which emerges is one of considerable morphological and genetic diversity and complexity. In the remainder of this discussion, we will review the various lines of morphological and molecular evidence that collectively bear on the phylogeny and classification of this problematic group.

Craniodental variation within this group has been discussed by Tate (1947), Ride (1964), Archer (1976a, b, 1982) and Kitchener and Caputi (1988). Tate's (1947) interpretation of craniodental variation among dasyurids was remarkably prescient. He clearly recognized that the affinities of the 'false' antechinuses lay with the larger dasyurines, rather than with the phascogalines, and he also appreciated the significant differences in craniodental morphology between *Pseudantechinus* (for *macdonnellensis* and *mimulus*) and *Parantechinus apicalis*. His diagnosis of *Pseudantechinus* emphasised the reduction of the last premolars; the enlargement of I^4; the flatness of the skull; the narrowness of the nasals; and the inflated character of the auditory bulla. This contrasted with the high cranium of *Parantechinus*; its broader nasals; and its unenlarged I^4. Tate's diagnosis of Dasyurinae mentioned only the "progressive obsolescence of p^4

(= P^3)..(as) .. a prime criterion for membership in the subfamily" (Tate 1947: 136). Tate's phylogenetic tree of the Dasyuridae (1947: figure 1) placed *Pseudantechinus* as the sister lineage to a group consisting of *Myoictis*, *Dasycercus* and *Dasyuroides*, with this group as a whole the sister lineage to *Dasyurus* (sensu lato); *Parantechinus* was placed as the sister genus to *Neophascogale*, with *Phascolosorex* (both New Guinean endemics) as their next closest relative.

Ride (1964) returned all of the 'false' antechinuses to the broadly-conceived genus *Antechinus*, and in so doing, dismantled Tate's phylogenetic vision. Archer (1976b) initially followed Ride's generic concepts. However, following publication of new information on genetics and penile anatomy, Archer (1982) not only reinstated Tate's genera but created a third, *Dasykaluta*, for Ride's *rosamondae*. Archer (1982) also formally resurrected Tate's concept of a dasyurine radiation including *Pseudantechinus*, *Parantechinus*, *Myoictis*, *Dasyurus* (sensu lato) and *Sarcophilus* but excluding *Neophascogale* and *Phascolosorex*, which he placed in a separate subfamily. Kitchener and Caputi (1988) included a variety of skull and tooth characters in their cladistic analysis of the 'false' antechinuses but failed to discuss the implications of the inferred phylogeny for craniodental evolution in this group.

Our own comparative studies of the skull and teeth of dasyurines have confirmed many of the findings of these earlier studies, but have also highlighted a number of new characters of potential significance. As indicated in the generic diagnosis, *Pseudantechinus* differs from all other genera of Dasyurinae in the degree of flattening of the braincase; the minimal development of a sagittal crest; and reduction in size of the upper and lower canines. Dentally, the group is characterised by a series of trends or 'tendencies' (e.g., for reduction of P_3 in advance of P^3; for reduction of P_2; for reduction of the preparacrista and stylar cusp B on M^1; for reduction of stylar cusps C and E and of the anterior cingulum on all upper molars; for reduction of the proto- and meta- conules, with narrowing of the protocone; for reduction of the paraconid and metaconid on M_1; and for reduction of the entoconid and shortening of the talonid on all lower molars. However, for each of these characters, a relatively unspecialised condition is present in one or more species of *Pseudantechinus* (e.g., M^1 stylar B distinct in *P. woolleyae* and *P. bilarni*; P^3 unreduced in *P. bilarni*; M_x entoconids less reduced in *P. woolleyae* and *P. mimulus*), and it would seem inescapable that a great deal of parallel dental evolution has occurred within the group. Interestingly enough, many of these same features are also observed in other dasyurine genera, most notably in *Dasycercus* and *Dasyuroides*, which apart from being larger, are remarkably close to some *Pseudantechinus* spp. in dental morphology.

Among the various other species of *Pseudantechinus*, *P. roryi* most closely resembles *P. macdonnellensis* and *P. ningbing* in craniodental morphology. These species alone show contact between the squamosal and frontal bones on the side wall of the cranium, either as the typical condition (*P. ningbing*) or in a high proportion of cases (*P. macdonnellensis* and *P. roryi*). They also share an extreme reduction of the metaconid on M_1; an unusual narrowing of the precingulids and reduction of the parastylid spur on M_{2-4}; and a lingual restriction but broadening of the anterobuccal cingulum on M^{2-4}. Together with *P. mimulus*, these species also display extreme reduction of both upper and lower third premolars, with complete loss of the lower tooth. All of these characters are judged to be derived or apomorphic in the broader context of the dasyurid radiation (Archer 1976a, b).

Each of *P. woolleyae* and *P. bilarni* appear morphologically more isolated; the former on account of its combination of a relatively unspecialised dentition (P^3 only slightly reduced; M^1 with distinct stylar cusp B; P_3 retained; M_{2-3} with less reduced entoconids) and a greatly enlarged auditory bulla; and the latter with several highly derived dental characteristics (P^3 unreduced but P_3 tiny or absent; M_3 lacking entoconid; M_4 talonid and M^4 protocone extremely reduced) and a distinctive cranial form with an anteriorly flaring zygomatic arch and posteriorly flaring nasals.

As noted by Tate (1947), *Parantechinus apicalis* differs from *Pseudantechinus* spp. in having a high-vaulted braincase, broader nasals, and a small but distinct postorbital process. It also differs in having less extensive fenestration of the maxillary and palatine portions of palate; a lesser degree of inflation of the auditory bulla (especially of the petrosal component); a noticeable enlargement of P^2; a lesser degree of reduction of M_{2-3} talonids and of M^{2-3} protoconules; and a more procumbent I^1. In most of these features, *P. apicalis* is significantly less specialised than *Pseudantechinus*; an exception is the unusual character of P^2 enlargement which is shared with certain *Dasyurus* species (e.g., *D. hallucatus*, *D. geoffroii*). Tate (1947) suggested that *P. apicalis* might be related to *Neophascogale* based on the shared features of a striped appearance and unusually elongate claws. However, these species differ in numerous aspects of craniodental morphology (Archer 1976a, b) that far outweigh the few superficial similarities.

Information on the anatomy of the penis played a major role in the recent resurrection of Tate's concept of the 'false' antechinuses. Woolley and Webb (1977) reported the presence of an accessory penile appendage in various genera of dasyurids

including *Dasyurus*, *Sarcophilus*, *Myoictis* and *Antechinus* (*sensu lato*). Later, Woolley (1982) demonstrated that the penis of all *Pseudantechinus* and *Parantechinus* species features an anterior expansion and elaboration of the corpus cavernosum. In some species this forms a distinct appendage, which is short and indistinct in *P. ningbing*, but elongate and conspicuous in *P. macdonnellensis* and *Parantechinus apicalis*. However, the accessory appendage of *P. apicalis* differs from the other species in internal structure and shows some similarities with the unadorned but internally complex penis of *P. bilarni*. Kitchener and Caputi (1988; data supplied by Woolley) reported that *P. woolleyae* possesses an accessory corpus cavernosum but lacks a distinct appendage. The species of *Dasykaluta*, *Dasycercus* and *Dasyuroides* lack any specialisation of the corpus cavernosum (Woolley, 1982, 1987), as does the species *hallucatus* within *Dasyurus* (P. Woolley, personal communication). As reported in this paper, *P. roryi* has a conspicuous accessory appendage that is at least superficially similar to that of *P. macdonnellensis*, whereas *P. mimulus* lacks any obvious accessory structure; these species have not been examined microscopically (P. Woolley, personal communiaction.).

The phylogenetic significance of this variation in penile anatomy is moot. Archer (1982) used the penile anatomy to support placement of *bilarni* and *apicalis* within *Parantechinus*. In so doing he emphasised Woolley's (1982) characterisation of the accessory corpus cavernosum of these particular taxa as 'trifid' rather than the more typical 'bifid' condition. However, the 'trifid' condition in both taxa would appear to be a consequence of broadening of the accessory corpus cavernosum, resulting in an enclosure of the paired corpus spongiosum veins. In *P. bilarni*, the accessory corpus cavernosum encircles these veins to reform as a single median lobe; this does not occur in *P. apicalis*, which therefore has a distinctive, three pronged corpus cavernosum. Unfortunately, much of the information needed to assess the significance of these penile characters is not yet available, especially as regards the internal structure of the accessory penile appendages in *Dasyurus* spp., *Sarcophilus harrisii* and *Myoictis* spp. However, in view of our conclusions regarding the craniodental evidence, we regard it as potentially significant that within *Pseudantechinus*, a distinct accessory penile appendage has to date been recorded only in *P. roryi*, *P. macdonnellensis* and *P. ningbing* (albeit small).

Various genetic and molecular studies have included at least some of the species under consideration here. Baverstock *et al.* (1982) reported a genetic distance of 41% Fixed Difference (FD) between *P. macdonnellensis* and *P. bilarni*, based on a sample of 32 presumptive loci. Cooper and Woolley (1983) reported a larger genetic distance (59% FD) between *P. macdonnellensis* and *P. bilarni* based on a smaller number of presumptive loci, and distances of 44% FD and 41% FD between each of these species and *P. ningbing*. An unpublished genetic study by M. Adams documented a genetic distance of 38% FD between *P. roryi* and *P. woolleyae* from Woodstock Station and 15% FD between *P. macdonnellensis* and *P. mimulus*. These results also show *P. apicalis* to be at least 30% FD from all other members of the group including *P. bilarni*. These intrageneric distances are comparable to those which separate other genera of Dasyurinae (e.g., *Antechinus* vs *Phascogale*; *Ningaui* vs *Sminthopsis*; Baverstock *et al.*, 1982), and thus provide no support for either the monophyly of *Pseudantechinus* or for the recognition of additional species-groups within this group.

DNA sequence studies by Krajewski *et al.* (1993, 1994, 1997) also point to considerable phylogenetic diversity among the assemblage of smaller dasyurine species. Their most recent analysis of combined Cytochrome *b*, 12S rRNA and Protamine P1 sequence data suggests monophyly of *Pseudantechinus roryi* (as *macdonnellensis*) and *P. woolleyae*, but show wide separation of these taxa from each of *bilarni* and *apicalis*. Of these latter taxa, *bilarni* is placed as a possible sister taxon to a large clade containing *Dasyurus*, *Sarcophilus*, *Phascolosorex* and *Neophascogale*, while *apicalis* is linked to *Dasykaluta rosamondae*, albeit with low bootstrap support. Incomplete sequence data for *P. ningbing* fails to show a special relationship with any of these taxa.

Taken at face value, the DNA sequence data appear to challenge our notion of a monophyletic *Pseudantechinus*. However, it is perhaps prudent at this point to note certain other discrepancies between the results of Krajewski *et al.* (1997) and some well-established notions of dasyurine phylogenetics; for example the basal separation in the Krajewski *et al.* dataset between *Dasycercus* and *Dasyuroides*, which on other genetic and DNA sequence data should probably be regarded as congeneric (Bavestock *et al.*, 1982; Cooper and Adams, unpublished data). One possible explanation of such discrepancies is the presence in the Krajewski *et al.* dataset of one or more pseudogene sequences. Although the issue of pseudogenes (sometimes called nuclear paralogues) has been acknowledged for many years (Zhang and Hewitt, 1996), their ubiquitous nature and their preferential amplification in some tissues but not others has only recently become apparent (Greenwood and Paabo, 1999). Until such time as this possibility has been explored [several procedural methods are available; e.g., Keogh (1998)], we do not regard the published molecular phylogenetic perspective as carrying any special weight.

To attempt to stabilize taxonomic classifications

in the face of this largely contradictory and glaringly incomplete suite of evidence might seem premature. Nevertheless, we feel sufficiently confident to draw a number of conclusions regarding the phylogeny and classification of the smaller dasyurines. The first is that the degree of molecular and morphological diversity within the loose assemblage of false antechinuses more than justifies the current recognition of multiple genera, viz. *Pseudantechinus*, *Parantechinus* and *Dasykaluta*. Secondly, within this group, there seem to be strong morphological grounds (and some molecular genetic support) for recognising a core group within *Pseudantechinus*, comprising *macdonnellensis*, *roryi*, *ningbing* and *mimulus*. Thirdly, we are confident that each of *apicalis* and *rosamondae* are phyletically distant to the core *Pseudantechinus* cluster, and further, that each warrant generic distinction as *Parantechinus* and *Dasykaluta* respectively. This leaves us with two species, *woolleyae* and *bilarni*, both of which share a number of derived craniodental features with the 'core' *Pseudantechinus*, but which appear to be each somewhat removed from the core group. In the case of *woolleyae*, this is mainly due to the retention of many plesiomorphic features, especially in the dentition. In contrast, *bilarni* shows a more complex mosaic of plesiomorphic and autapomorphic features that make it phenetically distinct from all other false antechinuses. Nevertheless, we are quite confident that *bilarni* does not have any special relationship with *Parantechinus apicalis*, as some workers have suggested.

The fundamental taxonomic problem is of course the perennial one of how best to classify cladistic 'radicals', whether basal ones, as in the case of *woolleyae*, or highly autapomorphic ones, as in *bilarni*. Our suggested solution is to include both of these taxa within *Pseudantechinus*, with which they show the greatest overall phenetic similarity. However, in so doing, we admit the possibility that the genus *Pseudantechinus* is rendered paraphyletic with respect to other dasyurine genera including *Dasycercus* and *Dasyuroides*.

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REFERENCES

Adams, M., Baverstock, P.R., Watts, C.H.S., and Reardon, T. (1987). Electrophoretic resolution of species boundaries in Australian Microchiroptera. I. *Eptesicus* (Chiroptera, Vespertilionidae). *Australian Journal of Biological Sciences* **40**: 143–162.

Archer, M. (1976a). The dasyurid dentition and its relationship to that of didelphids, thylacinids, borhyaenids (Marsupicarnivora) and peramelids (Peramelina: Marsupialia). *Australian Journal of Zoology. Supplementary Series* No. 39.

Archer, M. (1976b). The basicranial region of marsupicarnivores (Marsupialia), inter-relationships of carnivorous marsupials , and affinities of the insectivorous marsupial peramelids. *Journal of the Linnean Society of London, Zoology* **59**: 217–322.

Archer, M. (1978). The nature of the molar- premolar boundary in marsupials and a reinterpretation of the homology of marsupial cheekteeth. *Memoirs of the Queensland Museum* **18**: 157–164.

Archer, M. (1981). Results of the Archbold Expeditions No. 104. Systematic revision of the marsupial dasyurid genus *Sminthopsis* Thomas. *Bulletin of the American Museum of Natural History* **168**: 61–224.

Archer, M. (1982). Review of the dasyurid (Marsupialia) fossil record, integration of data bearing on phylogenetic interpretaion of suprageneric classification. *In* M. Archer *Carnivorous Marsupials* Vol. 2 (ed.): 397–443. Royal Zoological Society of New South Wales, Sydney.

Baverstock, P.R., Archer, M., Adams, M. and Richardson, B.J. (1982). Genetic relationships among 32 species of Australian dasyurid marsupials. *In* M. Archer (ed.), *Carnivorous Marsupials* Vol. **2**: 641–650. Royal Zoological Society of New South Wales, Sydney.

Baverstock, P.R., Adams, M., Archer, M., McKenzie, N. and How, R. (1983). An electrophoretic and chromosomal study of the dasyurid marsupial genus *Ningaui* Archer. *Australian Journal of Zoology* **31**: 381-392.

Baverstock, P.R., Adams, M. and Archer, M. (1984). Electrophoretic resolution of species boundaries in the *Sminthopsis murina* complex (Dasyuridae). *Australian Journal of Zoology* **32**: 823-832.

Cooper, D.W. and Woolley, P.A. (1983). Confirmation of a new species of small dasyurid marsupial by electrophoretic analysis of enzymes and proteins. *Australian Journal of Zoology* **31**: 743–751.

Dickman, C.R., King, D., Adams, M. and Baverstock, P.R. (1988). Electrophoretic identification of a new species of *Antechinus* (Marsupialia: Dasyuridae) in south-eastern Australia. *Australian Journal of Zoology* **36**:455-463.

Greenwood, A.D., and Paabo, S. (1999). Nuclear insertion sequences of mitochondrial DNA predominate in hair but not blood of elephants. *Molecular Ecology* **8**: 133–137.

How, R.A., Dell, J. and Cooper, N.K. (1990). Vertebrate Fauna. *In* Ecological survey of Abydos-Woodstock Reserve, Western Australia. *Records of the Western Australian Museum*, Supplement No. **37**: 78–125.

Keogh, J.S. (1998). Molecular phylogeny of elapid snakes and a consideration of their biogeographic history. *Biological Journal of the Linnean Society* **63**: 177–203.

Kitchener, D.J. and Caputi, N. (1988). A new species of false antechinus (Marsupialia: Dasyuridae) from Western Australia, with remarks on the generic classification within the Parantechini. *Records of the Western Australian Museum* **14**: 35–59.

Kitchener, D.J. (1988). A new species of false antechinus (Marsupialia: Dasyuridae) from the Kimberley, Western Australia. *Records of the Western Australian Museum* **14**: 61–71

Kitchener, D.J. (1991). *Pseudantechinus mimulus* (Thomas, 1906) (Marsupialia: Dasyuridae): rediscovery and redescription. *Records of the Western Australian Museum* **15**: 191–202

Krajewski, C., Painter, J., Driskell, A.C., Buckley, L. and Westerman, M. (1993). Molecular systematics of New Guinean dasyurids (Marsupialia: Dasyuridae). *Science in New Guinea* **19**: 157–166.

Krajewski, C., Painter, J., Buckley, Land Westerman, M. (1994). Phylogenetic structure of the marsupial family Dasyuridae based on Cytochrome *b* DNA sequences. *Journal of Mammalian Evolution* **2**: 25–35.

Krajewski, C., Painter, J., Buckley, L., Woolley, P.A. and Westerman, M. (1997). Reconstructing the evolutionary radiation of dasyurine marsupials with Cytochrome *b*, 12S rRNA and Protamine P1 gene trees. *Journal of Mammalian Evolution* **4**: 217–236.

Luckett, W.P. (1993). An ontogenetic assessment of dental homologies in therian mammals. *In* F.S. Szalay, M. J. Novacek and M.C. McKenna (eds), *Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials*: 192–204. Springer-Verlag, New York.

Nei, M. (1978). Estimation of average heterozygosity and genetic distance from a number of individuals. *Genetics* **89**: 583–590.

Richardson, B.J., Baverstock, P.R. and Adams, M. (1986). *Allozyme Electrophoresis. A handbook for animal systematics and population studies.* Academic Press, Sydney.

Ride, W.D.L. (1964). *Antechinus rosamondae*, A new species of dasyurid marsupial from the Pilbara District of Western Australia: with remarks on the classification of *Antechinus*. *Western Australian Naturalist* **9**: 58–65

Tate, G.H.H. (1947). Results of the Archbold Expeditions. No. 56. On the anatomy and classification of the Dasyuridae (Marsupialia). *Bulletin of American Natural History* **88**: 97–156

Woolley, P.A. (1982). Phallic morphology of the Australian species of *Antechinus* (Marsupialia: Dasyuridae): a new taxonomic tool? *In* M. Archer (ed.), *Carnivorous Marsupials*, Vol **2**: 767–781. Royal Zoological Society of New South Wales, Sydney.

Woolley, P.A. (1987). Phallic Morphology of *Dasyuroides byrnei* and *Dasycercus cristicauda* (Marsupialia: Dasyuridae). *Australian Journal of Zoology* **35**: 535–40

Woolley, P.A. (1991). Reproduction in *Pseudantechinus macdonnellensis* (Marsupialia: Dasyuridae): Field and Laboratory Observations. *Wildlife Research* **18**: 13–25

Woolley, P.A. and Begg, R.J. (1998). Northern Dibbler. *In* R. Strahan (ed.), *The Mammals of Australia*: 72–73. Australian Museum/ Reed Books, Chatswood.

Woolley, P.A. and Webb, S.J. (1977). The penis of dasyurid marsupials. *In* B. Stonehouse and D. Gilmore (eds), *The Biology of Marsupials*: 307–323. The MacMillan Press Ltd, London.

Zhang, D.X. and Hewitt, G.M. (1996). Nuclear integrations; Challenges for mitochondrial DNA markers. *Trends in Ecology and Evolution*, **11**: 247-251.

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