

A new species of false antechinus (Marsupialia: Dasyuridae) from Western Australia, with remarks on the generic classification within the Parantechini

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Abstract

Pseudantechinus woolleyae sp. nov., from the Pilbara, Ashburton, Murchison and Little Sandy Desert regions of Western Australia, is described as a new species. It is phenetically closest to *Pseudantechinus macdonnellensis* and phylogenetically closest to *Pseudantechinus macdonnellensis*, *Pseudantechinus bilarni* and *Pseudantechinus 'ningbing'*.

Introduction

Tate (1947) in his taxonomic monograph on Dasyuridae placed *Antechinus apicalis* (Gray, 1842) in the monotypic genus *Parantechinus*. This was because it differed from all other *Antechinus*, except *A. macdonnellensis* (Spencer, 1896), in having an extreme reduction of the posterior premolars to single rooted vestiges. He placed *A. macdonnellensis* and *A. mimulus* (Thomas, 1906) in the genus *Pseudantechinus*, because in addition to the reduction of their upper posterior premolar, they totally lacked the corresponding lower tooth and also had an inflated alisphenoid and mastoid bulla.

Ride (1964), in comments accompanying his description of *Antechinus rosamondae*, considered that the morphology of his new species cast considerable doubt on the validity of the genera *Parantechinus* and *Pseudantechinus*. *Antechinus rosamondae* had no posterior upper or lower premolar and an even more greatly inflated bulla than *A. macdonnellensis*. Rather than erect yet another monotypic genus, Ride argued for the return to the wider concept of *Antechinus*, noting that *A. macdonnellensis* spanned the range of dental characters of *Antechinus* (*sensu lato*) and that bulla inflation or its absence did not divide *Antechinus* into two groups. Ride (1970) returned to the broader concept of *Antechinus*. However in more recent years, workers (see Kirsch 1982) have recognised that *Antechinus sensu* Ride, 1970 is polyphyletic. This polyphyly has been demonstrated by phylogenetic analysis based on cranial and dental characters using the Wagner algorithm (Kirsch and Archer 1982) and isozyme electrophoresis (Baverstock *et al.* 1982).

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The latter authors recognised among the dasyurids they studied, that the *Antechinus* suprageneric group was genetically very heterogeneous; species fell into two broad groups. One group comprised the 'true' *Antechinus* species as well as *Phascogale*. The other comprised the 'false' *Antechinus* (*A. macdonnellensis*, *A. bilarni* Johnson, 1964, and *A. rosamondae* Ride, 1964) on one hand and species of *Dasyuroides* Spencer, 1896; *Dasyercus* Peters, 1875; *Dasyurus* Geoffroy, 1796 and *Sarcophilus* Geoffroy and Cuvier, 1837 on the other. Interestingly Kirsch (1977) had found that *A. rosamondae* was serologically closer to *Dasyurus* than it was to species of 'true' *Antechinus* (e.g. *A. flavipes*). Baverstock *et al.* (1982) considered that within the 'false' *Antechinus*, "recognition of at least one distinct generic rank for the species of this group is warranted" and that "there may be grounds for recognising three separate genera". They showed that *Dasyurus* – *Dasyuroides* rather than *Antechinus* (*sensu stricto*) were the sister group to the 'false' *Antechinus*. They commented further that *A. apicalis* and *A.* 'ningbing' (an as yet undescribed species) may also be referable to the 'false' *Antechinus* group. Cooper and Woolley (1983) investigated the electrophoretic mobilities of enzymes and proteins of eight species of dasyurid marsupials and concluded that the *Antechinus* 'ningbing' is a "probable new species" and that its nearest relative is possibly *Dasyercus cristicauda* Krefft, 1866.

The phallic morphology of 12 species of *Antechinus* was described by Woolley (1982) who reported that *A. macdonnellensis*, *A. bilarni*, *A. apicalis* and *A.* 'ningbing' formed a distinct group from other *Antechinus* species in not having a bifid tip to the penis, having short urethral grooves and no dorsal median lobe. She concluded that these latter five species could be further subdivided on the occurrence and form of accessory structures derived from the corpora cavernosa.

Archer (1982) acknowledged the distinctness of the 'false' *Antechinus* group which he considered comprised the same species listed by Woolley (1982) as lacking a bifid tip to the penis. Archer (1982) investigated the generic status of these five 'false' *Antechinus* species through a cladistic analysis of cranial, dental and tail characters. He determined their phylogenetic association, however, on the basis of the additional contribution of their phallic morphology as elucidated by Woolley (1982). Archer (1982) concluded that the 'false' *Antechinus* should be placed into three genera: *bilarni* and *apicalis* in *Parantechinus* Tate, 1947; *macdonnellensis* and 'ningbing' in *Pseudantechinus* Tate, 1947 and *rosamondae* in *Dasykaluta* – a new genus which he proposed. He further proposed the tribe Parantechini to comprise these three genera.

While examining specimens attributable to *Pseudantechinus macdonnellensis* in the collections of the Western Australian Museum, it became apparent that some of the dental variation referred to by Ride (1964) in this species resulted from the presence of a distinct form (e.g. WAM M2554), which occurred in very close geographic proximity, perhaps even sympatrically, at Woodstock Station, Pilbara District, with *P. macdonnellensis* (*sensu stricto*). This form is herein described as a new species. However, when attempting to allocate this new species

to one of the Parantechini genera of Archer (1982) it was seen to share diagnostic characters of both *Parantechinus* and *Pseudantechinus*. For this reason it was also necessary in this paper to examine again the generic relationships of the species within the Parantechini.

Materials and methods

Measurements

Our description of morphology follows Archer (1981). Tooth number follows Archer (1978). Cranial and external points used for measurements also follow Archer (1981) with the exception of three additional measurements, asterisked below. Nineteen measurements of skull and dental characters, five of external body characters (in mm) and weight (in gms) were recorded from adult specimens listed in Specimens examined and in the Description sections. Abbreviation for these measurements are as follows: MAXL, maximum skull length; BASCRANL, basicranial length; MSKH, maximum skull height; MSKW, width across zygoma; OBUL, outside bullae distance; INBUL, inside bullae distance; BULTOT*, length of tympanic wing of alisphenoid and periotic, from posterior lacerate foramen to anterior edge of alisphenoid wing; BULPER*, length of periotic tympanic wing from lacerate foramen to contact point with alisphenoid tympanic wing, measured in the same line as for BULTOT; C¹-M⁵, M²-M⁵, I₁-M₅, M₂-M₅ crown lengths; RM⁴-LM⁴, width outside crowns; INORB, minimum interorbital width; MAXVAC*, maximum length of maxillary palatal vacuity; NASL, nasal length; DC-I₁ dentary condyle to I₁; ANGCON, tip of angular process to articular condyle; CONRAM, articular condyle to anterior border of ascending ramus; NV, tip of rhinarium to vent length; TV, tail tip to vent length; HF, hind foot length; EAR, ear height from notch; TRAG, supratragus width; WT, weight.

Qualitative bi or multi-state characters codes (C1-C36). These are listed in Table 1.

Pelage and skin

Colour of pelage, when capitalised, follows Ridgway (1912). Specimens were regarded as adult if M⁵ and P³ were fully erupted. Only adults were included in the statistical appraisal.

Morphometric analyses

Means, standard deviations and ranges were computed for skull, dentary, teeth (hereafter referred to as skull characters) and external body measurements and for weight. The latter variable was not employed in systematic analyses because it was absent from many specimen records. Sexual dimorphism was examined using a two factor analysis of variance for measurements of each of the skull, and external characters for the factors species and sex.

Table 1 Codification of characters used in phylogenetic analysis.

Number	Character Code	
C1	P ³ crown size relative to P ²	1- absent, 2- tiny, 3- small, 4- moderate, 5- large
C2	P ₃	1- absent, 2- present
C3	I ² crown length relative to I ⁴	1- smaller, 2- subequal, 3- taller
C4	P ³ root number	1- absent, 2- one, 3- two
C5	StB on M ² size	1- absent/low, 2- moderate, 3- tall
C6	M ⁵ width relative to M ⁴ width	1- narrower, 2- subequal, 3- wider
C7	M ₂ paraconid size	1- absent, 2- small, 3- moderate
C8	M ₂ metaconid size	1- absent, 2- small, 3- moderate
C9	M ₄ entoconid size	1- absent, 2- small, 3- moderate, 4- large
C10	M ⁴ protocone lateral compression	1- uncompressed, 2- slight, 3- moderate
C11	extent of proximal nasal flare	1- none, 2- slight, 3- moderate, 4- very
C12	squamosal/frontal contact	1- not close, 2- not in contact/close, 3- in contact
C13	Palatine vacuities	1- absent, 2- small, 3- moderate, 4- large
C14	alisphenoid tympanic bulla size	1- small, 2- moderate, 3- large, 4- very large
C15	alisphenoid tympanic inflation	1- slight, 2- moderate, 3- inflated
C16	periotic tympanic size	1- small, 2- moderate, 3- large, 4- very large
C17	periotic tympanic bulla inflation	1- slight, 2- moderate, 3- inflated
C18	skull depth	1- flat, 2- moderately deep, 3- deep, 4- very deep
C19	extent of lambdoidal crest	1- absent, 2- slight, 3- moderate, 4- large
C20	post orbital swellings	1- absent, 2- slight, 3- moderate, 4- large
C21	tail incrassation	1- absent, 2- incrassate
C22	tail fur	1- slight, 2- moderate, 3- heavy
C23	tail length relative to snout-vent	1- less, 2- subequal, 3- longer
C24	striation on pes interdigital pads	1- none, 2- moderate, 3- very
C25	metatarsal, hallucal and post hallucal pads	1- all absent, 2- post hallucal absent, 3- all present
C26	ear length	1- small, 2- moderate, 3- long, 4- very long
C27	supratragus	1- uncurled, 2- curled
C28	number of female nipples	1- four; 2- six, 3- eight, 4- ten
C29	penis: levator muscle length	1- short, 2- medium, 3- long
C30	penis: accessory corpora cavernosa	1- absent, 2- present
C31	penis: accessory structure appendage	1- present, 2- absent
C32	penis: location of tendon	1- arises mesially, 2- arises laterally
C33	penis: tip	1- not bifid, 2- bifid
C34	penis: urethral groove	1- short, 2- long
C35	penis: median dorsal lobe	1- absent, 2- present
C36	external hallux	1- absent, 2- present

Principal component analysis, was based on the correlation matrix of the skull characters and the first three principal component scores were examined. Canonical variate (discriminant) analyses, using skull measurements alone, were performed on the recognised species using SPSS^x package.

Phylogenetic analyses were performed using the PAUP programme for constructing phylogenetic trees (Swofford 1984). This analysis was based on the

modal values of the coded characters listed in Table 1 using the MULPARS option. The coded characters were treated as unordered. The tree was rooted using five outgroup species.

Institutional specimens

Institutional origin of specimens are denoted by prefixing their catalogue number as follows: JM, Queensland Museum, Brisbane; NT, Northern Territory Museum; WAM, Western Australian Museum, Perth and FMNH, Field Museum of Natural History, Chicago.

Systematics

Pseudantechinus woolleyae sp. nov.

Table 2, Figures 1 and 2

Holotype

Western Australian Museum catalogue number M14740; adult male; body fixed in 10 per cent formalin, preserved in 75 per cent ethanol — skull and dentaries separate; found dead on ground (believed poisoned) by Mr Jim Daly on 31 July 1976.

Type locality

Near Newlingunn bore, 10 km 117° from Errabiddy Homestead (25°33'00"S, 117°08'00"E).

Paratypes

Listed in Specimens examined.

Diagnosis

Pseudantechinus woolleyae differs from *Pseudantechinus macdonnellensis* in having the skull generally larger. For example: bulla (BULTOT) longer 7.6 (7.1-8.2) v. 6.5 (6.0-7.0), periotic (BULPER) longer 3.8 (3.3-4.3) v. 3.1 (2.7-3.5), distance outside bullae (OBUL) greater 12.9 (12.4-13.4) v. 11.6 (10.8-12.3), skull (MAXL) generally longer 29.9 (28.0-31.2) v. 27.5 (25.9-29.7), C¹-M⁵ longer 11.3 (10.8-11.6) v. 10.2 (9.3-10.7), distance outside upper molars (RM⁴-LM⁴) wider 9.6 (9.1-10.3) v. 8.8 (8.3-9.3); P³ crown area more than three quarters, rather than less than half, that of P²; P³ with two roots rather than one; P₃ normally present; M² styler cusp B moderately large rather than very low or absent; M₄ entoconid moderate to large rather than small or absent; hind foot longer 15.0 (13.5-15.9) v. 13.8 (12.8-15.0) and male without a penile appendage.

It differs from *Pseudantechinus bilarni* in averaging larger in all skull and dental measurements except distance between bullae (INBUL) (Table 1), having bulla larger: the proportion BULTOT/MAXL 0.252 (0.242-0.264) v. 0.209 (0.198-0.219); distance between bullae (INBUL) smaller 2.8 (2.4-3.3) v. 3.5 (3.2-3.9); periotic length (BULPER) larger 3.8 (3.3-4.3) v. 2.7 (2.3-2.9); distance between both dentary angular process and condyle (ANGCON) and condyle and ascending

a

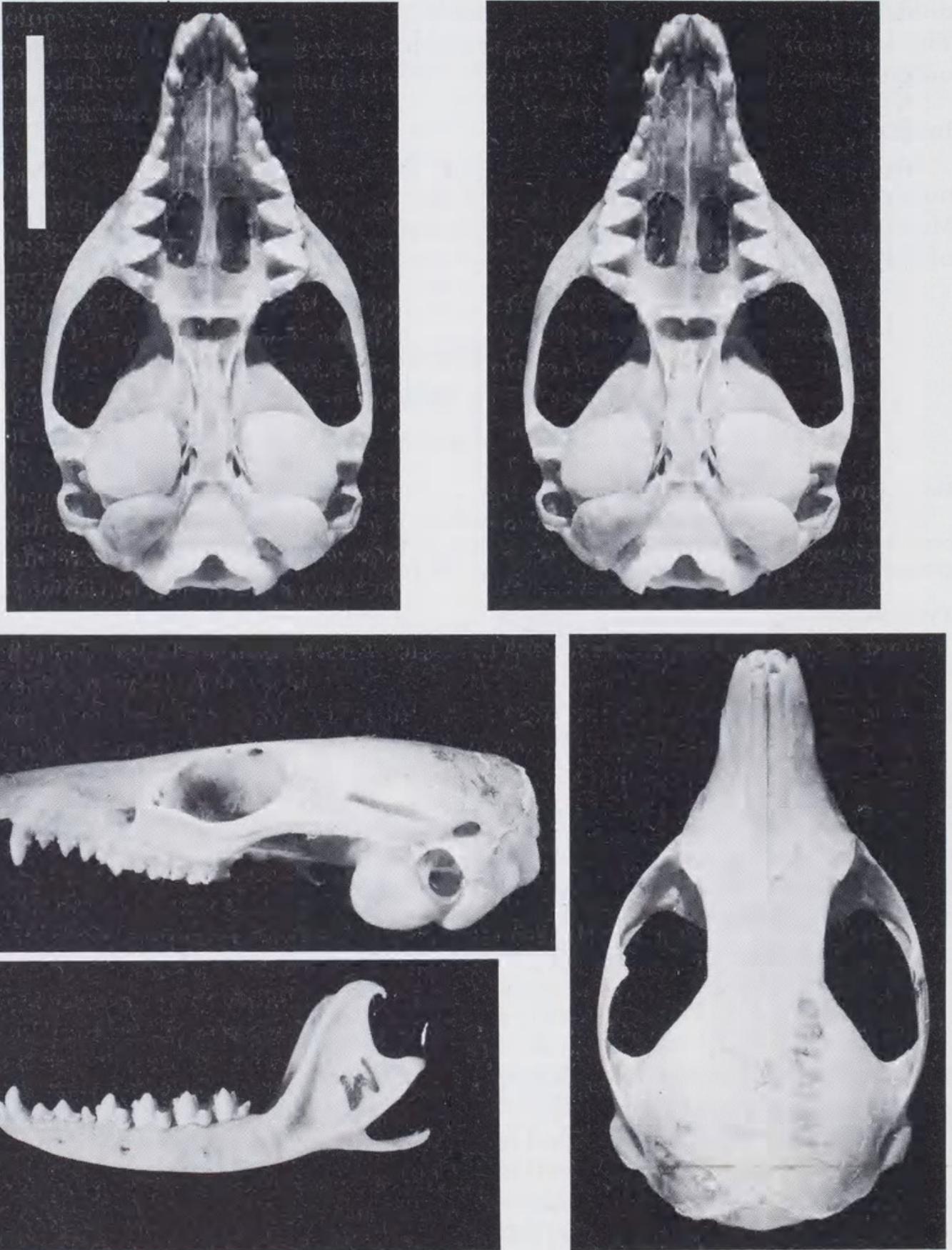
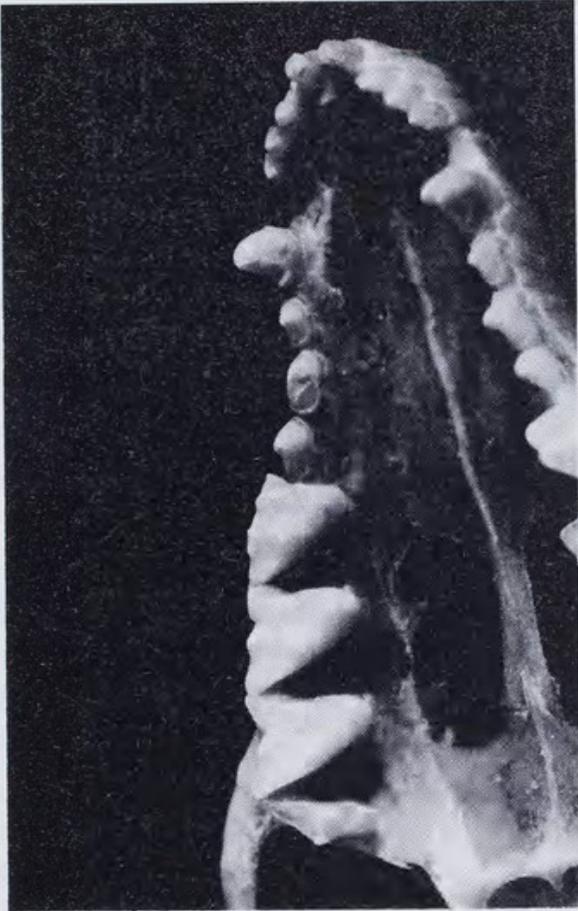
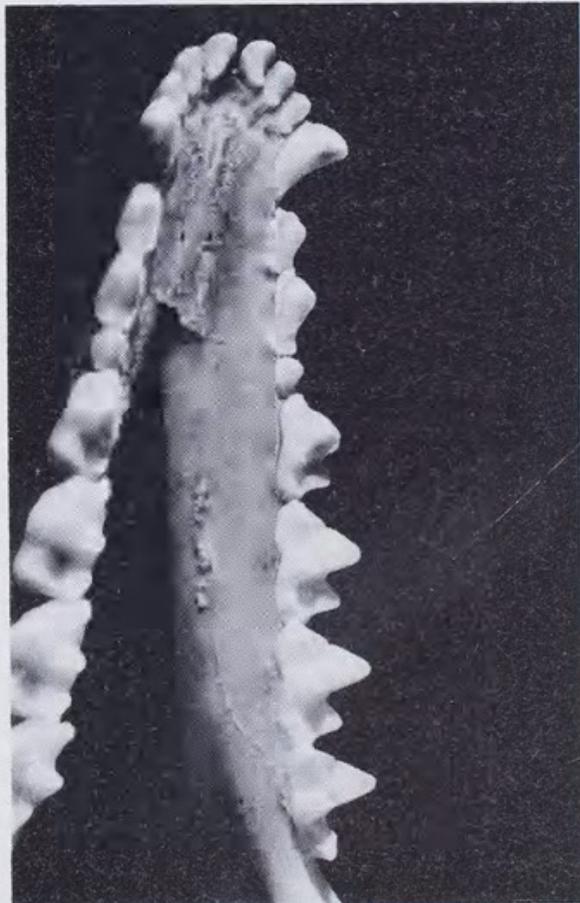
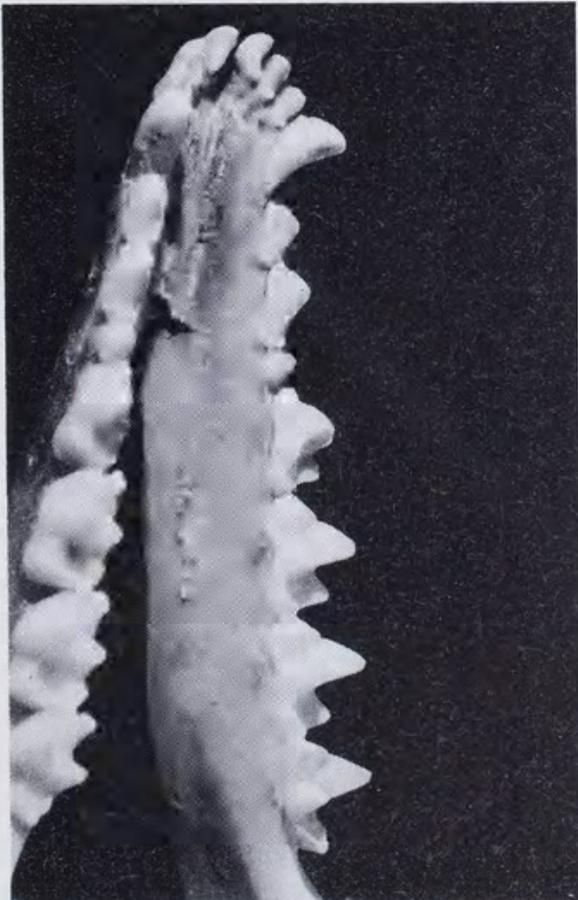


Figure 1 (a) skull and dentary, (b) upper and (c) lower tooth rows of *Pseudantechinus woolleyae* holotype — tooth rows and ventral aspect of skull as stereopairs. Scale lines; tooth rows, 2 mm; skull and dentary, 10 mm.

b



c



ramus (CONRAM) greater 6.1 (5.6-6.5) v. 5.1 (4.0-5.7) and 5.6 (4.6-6.0) v. 4.9 (4.2-5.6), respectively; M^5 width greater or equal to M^4 width; hind foot shorter 15.0 (13.5-15.9) v. 16.6 (14.8-18.4) and tail incrassate.

It differs from the 'ningbing' form of *Pseudantechinus* in being generally larger in all skull and dental measurements (except distance between bullae, INBUL), having bullae larger: BULPER 3.8 (3.3-4.3) v. 3.0 (2.5-3.5), BULTOT 7.6 (7.1-8.2) v. 5.9 (5.5-6.5); periotic more inflated; P^3 crown area more than three-quarters, rather than less than one-half that of P^2 ; P_3 usually present rather than usually absent; squamosal/frontal contact not close; M^2 styler cusp B moderately large rather than very low or absent; M_4 entoconid moderate or large rather than absent; females with six rather than four teats; tail shorter than snout to vent length, heavily incrassate and slightly more heavily furred.

Description

Skull and dentary

Skull moderately large but not especially robust, cranium and lambdoidal crest low and sagittal crest and postorbital swellings absent; nasal length moderate; nasals usually slightly flared proximally, occasionally moderately flared; squamosal and frontal not closely abutted; maxillary palatal vacuities moderate, located between a line drawn from posterior edge of M^4 and M^2 ; premaxillary palatal vacuities do not extend posterior to a line joining C^1 posterior edge; palatine vacuities usually small, occasionally absent or large; alisphenoid tympanic bulla large and inflated, covers ectotympanic wing, in wide contact with periotic tympanic wing; bullae close together. Dentary with distance between tip of angular process and articular condyle subequal to that between articular condyle and tip of ascending ramus.

Dentition

I^1 tallest of upper incisors, separated from I^2 by diastema which approximates I^1 thickness; I^2 ; I^3 and I^4 approximately same height and crown area, occasionally I^2 shorter than I^4 ; I^4 separated from C^1 by substantial diastema; C^1 with slight antero- and posterolingual cingulum with slight to moderate posterior cingular cuspule; C^1 crown height about twice that of P^3 ; usually slight diastema between C^1 and P^1 and between upper premolars; crown height increases from P^1 to P^3 ; upper premolars with antero- and posterobasal cingular cuspules, encircled by moderate cingula except for lingual and buccal aspect where it narrows; crown area of P^3 usually larger or subequal to P^2 , larger than P^1 ; P^3 with two roots; metacone taller than StD on M^2 , taller or subequal on M^3 and M^4 ; StD taller than StB on M^2 and M^3 but subequal on M^4 ; StB shorter than paracone on M^2 and M^3 but subequal on M^4 ; StE shorter than paracone on M^2 and M^3 but subequal on M^4 ; StE on M^2 to M^4 variably present, small; StB on M^2 of variable height, low to tall; preprotocrista terminates at anterior base of M^{2-4} paracone, occasionally forms narrow contact with anterior cingular shelf on M^2 ; preparacrista connects

StB directly to paracone; postprotocrista connects to posterolingual base of metacone; posterior lingual and buccal cingula absent M^2 to M^5 ; on M^2 preparacrista subequal to postparacrista, which is half length of premetacrista, which is slightly less than half length of postmetacrista; on M^3 preparacrista almost twice length of postparacrista, which is half length of premetacrista, which is just less than half length of postmetacrista; on M^4 preparacrista almost three times longer than postparacrista which is half length of premetacrista which is about half length of postmetacrista; on M^5 metacone rudimentary, protocone (usually uncompressed) and paracone very reduced, preparacrista about twice length of postparacrista, occasional slight bulge in ectoloph probably homologous to StD; M^5 width generally subequal to M^4 , occasionally narrower.

I_1 taller crowned than I_2 which is subequal in length to I_3 ; I_1 to I_3 with posterior cingular cuspule; I_3 also with smaller posterobuccal cuspule, such that the notch separating these posterior cuspules loosely accommodates C_1 anterior edge; C_1 tall, twice height of P_2 , slight lingual cingulum and occasional small posterior cingular cuspule; crown area $P_3 < P_1 < P_2$; P_3 present in all specimens except WAM M24151, has low posterior cingular cuspule; P_1 to P_3 have narrow encircling cingulum except for buccal aspect above P_1 and P_2 anterior root; P_3 and M_2 separated by short diastema; on M_2 protoconid much taller than metaconid, which is taller than paraconid (sometimes rudimentary), which is shorter than hypoconid, hypoconulid rudimentary, entoconid varies in height, usually subequal to paraconid; on M_3 and M_4 protoconid taller than subequal metaconid and paraconid, which are much taller than the variable entoconid (rudimentary or large) which is taller than hypoconid, which is taller than hypoconulid; M_5 similar in shape to M_3 and M_4 except that talonid much reduced, particularly hypoconid; crista obliqua contacts metacrista at base of central notch in M_5 but moves progressively closer to protoconid in M_4 to M_2 ; on M_2 paracristid slightly longer than metacristid which is subequal in length to crista obliqua and hypocristid; on M_3 paracristid longer than metacristid and hypocristid, which are much longer than crista obliqua; on M_4 paracristid longer than metacristid, which is longer than hypocristid which is longer than crista obliqua; on M_5 paracristid slightly longer than metacristid, which is much longer than crista obliqua; M_2 to M_4 have anterior and posterior cingula but no lingual or buccal cingula.

Externals

Pelage and skin colour

Described from four 'puppet' skins WAM (M716, M2406, M2554, M7122).

Overall fur colour dorsally Sayal Brown, ventrally Pinkish Buff.

Hairs on shoulder, back and flanks up to 9.5 mm, base of hairs Neutral Gray, distal 3.5 mm Pinkish Cinnamon lightly tipped with Warm Sepia. Hairs on forehead, rostrum and sides of face shorter (up to 3.5 mm), base of hairs Warm Sepia, distal 2 mm Light Pinkish Cinnamon tipped with Warm Sepia. Ears lightly furred with 2 mm long hairs, these Pinkish Cinnamon lightly tipped with Warm Sepia on

both the inner and outer surfaces. Hairs on inner ear surface of the anterobasal helix, central antihelix and general antitragal area are thicker, longer (up to 3 mm), these Warm Sepia at base, distal 2 mm Pinkish Cinnamon. Guard hairs on dorsum numerous up to 11.5 mm long, Warm Sepia. Hairs on ventral surface of body and throat up to 7 mm long, base of hairs Light Neutral Gray, distal 3 mm Pale Pinkish Buff. Hair on chin, sides of mouth, manus and pes up to 2.5 mm long, these Warm Sepia at base, distal 1 mm Pale Pinkish Buff.

Tail moderately well furred. On dorsal surface of tail hairs up to 4 mm long, basal 0.5 mm Warm Sepia, central 1.5 mm Pinkish Cinnamon, distal 2 mm Warm Sepia; this distal region of the hairs appreciably thinner than at the base. On ventral surface hairs up to 3 mm long, Light Pinkish Cinnamon. Hairs at tail tip up to 6 mm long, Warm Sepia, extending slightly beyond tip but not forming obvious tuft. Up to 30 mystacial vibrissae, posteriorly these are up to 35 mm long, Warm Sepia at base through Cinnamon to Pale Pinkish Buff distally. On edge of lips shorter (up to 7 mm long), Pale Pinkish Buff. One or two supraorbital vibrissae up to 20 mm long and six to eight genal vibrissae up to 30 mm long, the colouration as for that of the posterior mystacial vibrissae. Five submental vibrissae, up to 5 mm long and two interramal vibrissae, up to 11 mm long, Pale Pinkish Buff. Up to six ulnar carpal vibrissae, Pale Pinkish Buff, up to 11 cm long. Two to three vibrissae between the anconeal and medial antebrachial regions of the foreleg, Cinnamon at base becoming Pale Pinkish Buff distally, up to 10 mm long.

Skin of pes and manus Pinkish Buff. Skin of ear Mikado Brown.

Pes

Terminal digital pads small, smooth; the three interdigital pads large, elongate, separate from each other; hallucal pads elongate, approximately half size of interdigital pads; metatarsal and post hallucal pads subequal in size to interdigital pads. All pads, except the terminal ones, heavily striate.

Distribution

Pseudantechinus woolleyae is not recorded outside Western Australia (Figure 2). It has been collected from across the Fortescue (Pilbara), west Ashburton, (Ashburton region), western half of Austin (Murchison Region) and a single record from central north Keartland (Little Sandy Desert) botanical Districts of Beard (1980). These Districts are characterised as having an arid climate with summer rain and precipitation ranging from 200-300 mm. The northern districts (Fortescue and Keartland) have a tropical arid climate. The Fortescue District is essentially tree and shrub steppe communities with *Eucalyptus* trees, *Acacia* shrubs and *Triodia* spp. The Keartland District is shrub steppe. The Ashburton District is almost entirely mulga (*Acacia aneura*). The Austin District is predominantly mulga low woodland on plains reduced to scrub on hills and tree steppe of *Eucalyptus* spp. and *Triodia basedowii* on sandplains. Soils and topography vary greatly between these Districts. However the Fortescue district, from which most specimens of *P. woolleyae* have been collected, is a rugged mountainous region

chiefly of hard alkaline red soils on plains and pediments with shallow and skeletal soils on the ranges. The Ashburton and Austin Districts are principally shallow earthy loams overlying red-brown hardpan with shallow stony loams on hills and ranges. The single specimen from Rudall River National Park in the Keartland District was from a small stony hill of brown salty sand with 50 per cent stones.

The sparse habitat notes accompanying specimens of *P. woolleyae* reflect the variety of habitats of the botanical districts described above. Only six specimens have any such information. In addition to its occurrence on small stony hills at Rudall River it has been collected from "gemstone bearing country, granite boulder country and a rocky hillside"; one specimen was from "Buffle grass, *Cenchrus ciliaris*, on small salt-flat plain". Vegetation is listed as "mulga, sparse bloodwood over *Acacia* scrub over spinifex and *Acacia inaequilatera* scrub steppe".

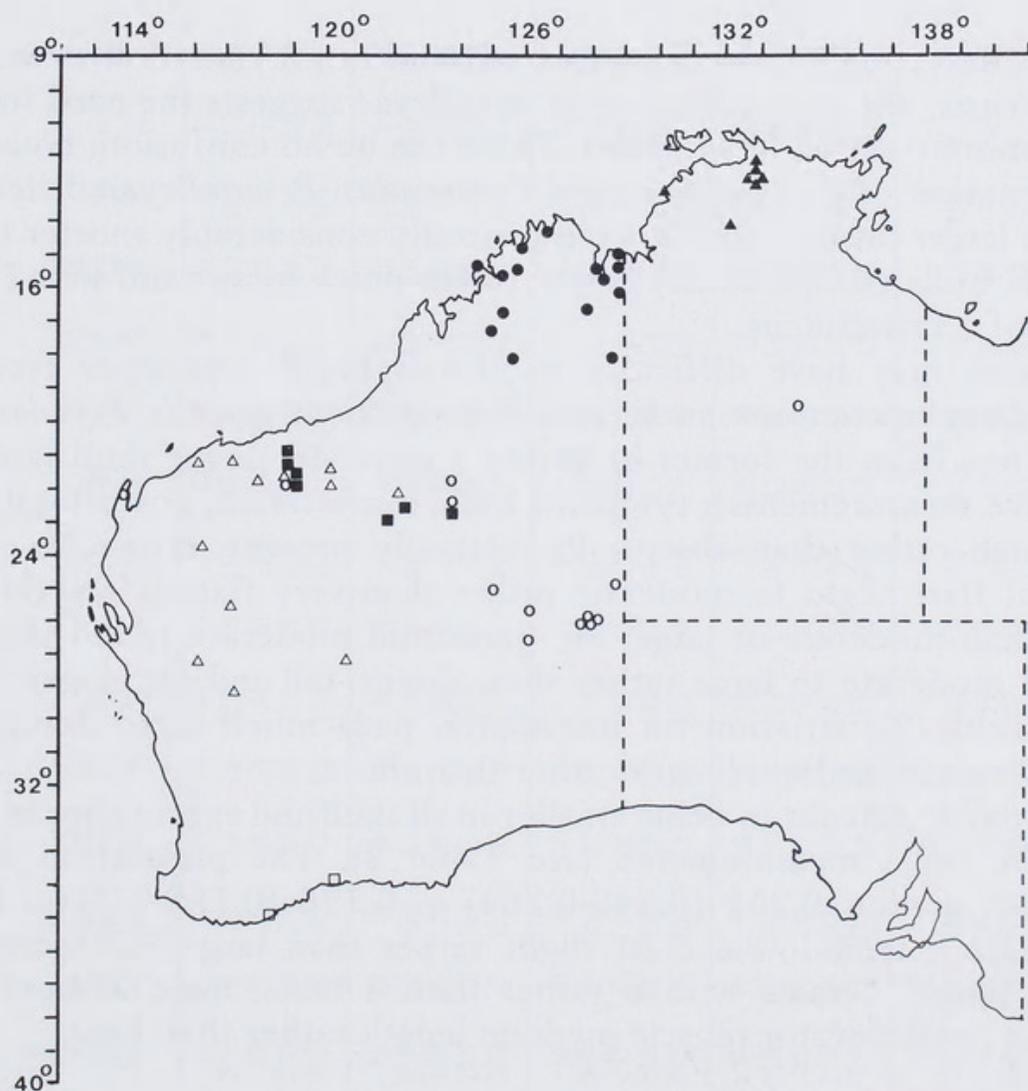


Figure 2 Distribution of specimens of Parantechini sensu Archer (1982) examined. *P. woolleyae* (Δ), *P. macdonnellensis* (\circ), *P. bilarni* (\blacktriangle), *P.* 'ningbing' (\bullet), *P. apicalis* (\square) and *D. rosamondae* (\blacksquare).

Etymology

Named after Dr Pat Woolley, La Trobe University, Victoria, in recognition of her contribution to studies on dasyurids and to the Mammal Department of the Western Australian Museum.

Remarks

The specimens herein considered as *P. macdonnellensis* closely accord to the description of that species in Spencer (1906); they have comparable external and skull measurements and P₃ absent or minute.

Thomas (1906) in his description of *Phascogale mimulus* stated that it was closest to *P. macdonnellensis* but differed from that species in being much smaller in overall size and in having: narrower and more granulated feet; body smaller such that tail nearly equal in length to head and body; nasals shorter and broader, bulla conspicuously smaller, P⁴ (= P³) well developed and two rooted but P₄ (=P₃) absent.

Although Ride (1964) and subsequent authors synonymised *P. mimulus* with *P. macdonnellensis*, the recognition of *P. woolleyae* suggests the need for caution as to the taxonomic status of *mimulus*. There can be no confusion, however, between the distinction of *P. woolleyae* and *P. mimulus*. *P. woolleyae* differs from it in being much larger overall, having a tail generally considerably shorter than head to body length, bulla conspicuously larger, nasals much longer and with P₃ present in all but one of 13 specimens.

Some workers may have difficulty in identifying *P. woolleyae* from partial specimens of *Dasykaluta rosamondae* and *Parantechinus apicalis*. *Pseudantechinus woolleyae* differs from the former in having a generally larger skull (see Table 2 for comparative measurements); tympanic bulla less inflated; postorbital swellings absent; P³ large rather than absent; P₃ normally present; crown length I² < I⁴; proximal nasal flare slight to moderate rather than very flared; lambdoidal crest slight rather than moderate or large; M₂ paraconid moderate rather than absent; M₄ entoconid moderate to large rather than absent; tail and ear longer; hind foot shorter (see Table 2); striation on interdigital pads much more developed and penile levator muscle medium length rather than short.

It differs from *P. apicalis* in being smaller in all skull and external measurements, except for the bulla measurements (see Table 2). The proportion BULTOT/MAXL is much greater 0.252 (0.242-0.264) v. 0.196 (0.188-0.201); P³ larger; skull much flatter; lambdoidal crest slight rather than large; tail incrassate; tail more lightly furred, female with 6 rather than 8 teats, male without a penile appendage and penile levator muscle medium length rather than long.

Table 2 Sample size (N) mean (\bar{X}), standard deviation (SD), minimum (Mn) and maximum (Mx) values for measurements (mm) and weight (gms) for *Pseudantechnus* spp., *Parantechnus apicalis* and *Dasykaluta rosamondae*. Explanation of character codes in Methods.

Characters	MAXL	BASCANL	MSKH	MSKW	BULPER	BULTOT	OBUL	INBUL	C-M ₅	M ₂ -M ₅	RM-LM	INORB	MAXVAC	NASL	DC-L ₁	I-M ₅	M ₂ -M ₅	ANGCON	CONRAM	NV	TV	HF	EAR	TRAG	WEIGHT	
<i>P. woolleyae</i>	N	12	12	11	13	13	13	13	13	13	13	13	12	12	13	13	13	13	12	12	8	8	8	8	8	3
	X	29.9	27.5	7.1	17.2	3.8	7.6	12.9	2.8	11.3	6.7	9.6	5.9	3.9	10.8	21.7	13.4	7.5	6.1	5.6	91.6	82.0	15.0	20.0	4.8	28.6
	SD	.93	.86	.19	.72	.28	.34	.34	.28	.27	.24	.37	.20	.58	.70	.77	.43	.35	.27	.37	6.56	5.56	.84	1.23	.48	12.90
	Mn	28.0	25.6	6.8	15.9	3.3	7.1	12.4	2.4	10.8	6.3	9.1	5.5	2.9	9.0	19.9	12.6	6.9	5.6	4.6	84.3	73.9	13.5	18.5	4.0	18.0
	Mx	31.2	28.7	7.4	18.7	4.3	8.2	13.4	3.3	11.6	7.1	10.3	6.2	4.7	11.4	22.8	13.9	8.0	6.5	6.0	101.0	88.1	15.9	21.7	5.3	43.0
<i>P. macdonnel-</i>	N	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	11	11	11	11	11	12
	X	27.5	25.3	6.7	15.9	3.1	6.5	11.6	2.9	10.2	6.4	8.8	5.2	3.8	10.1	20.1	12.2	7.2	5.4	5.4	84.9	76.3	13.8	17.1	4.1	24.5
	SD	1.07	1.05	.25	.60	.19	.34	.38	.43	.50	.32	.31	.31	.43	.72	.83	.68	.38	.29	.30	3.00	3.88	.61	1.18	.37	4.78
	Mn	25.9	23.4	6.2	14.9	2.7	6.0	10.8	2.1	9.3	5.8	8.3	4.6	2.8	8.6	18.8	10.4	6.5	4.8	4.6	80.1	69.0	12.8	15.2	3.3	17.5
	Mx	29.7	27.0	7.2	17.0	3.5	7.0	12.3	3.4	10.7	6.8	9.3	5.7	4.4	11.4	21.4	12.9	7.6	5.8	5.9	90.5	81.6	15.0	19.5	4.5	33.0
<i>P. bilarni</i>	N	10	10	10	10	10	11	11	11	12	12	11	11	11	12	12	12	12	12	12	10	10	10	10	10	5
	X	28.3	26.0	7.0	16.6	2.7	5.9	11.6	3.5	10.7	6.5	9.1	5.8	2.8	10.6	20.6	12.8	7.2	5.1	4.9	88.3	105.4	16.6	19.4	4.3	26.4
	SD	1.21	1.33	.33	1.16	.18	.31	.53	.22	.41	.31	.55	.25	.45	.71	.98	.59	.23	.45	.43	5.05	6.95	1.03	.96	.26	3.78
	Mn	26.3	24.0	6.4	15.0	2.3	5.5	10.7	3.2	10.0	6.1	8.0	5.4	2.2	9.3	19.1	11.6	6.8	4.0	4.2	80.0	99.0	14.8	18.0	4.0	21.0
	Mx	30.5	28.2	7.4	18.4	2.9	6.3	12.5	3.9	11.4	7.2	9.7	6.2	3.8	11.6	22.4	13.6	7.4	5.7	5.6	96.2	119.6	18.4	20.7	4.9	30.0
<i>P. ningbingi</i>	N	27	28	28	28	28	28	28	28	28	28	28	28	28	28	28	28	28	27	28	17	16	17	15	14	24
	X	27.1	24.9	6.7	15.6	3.0	5.9	11.1	3.1	10.2	6.2	8.7	5.5	3.6	10.2	19.6	12.2	7.0	5.1	4.9	82.3	84.8	14.3	18.0	4.1	20.0
	SD	.78	.82	.23	.54	.23	.25	.37	.26	.32	.24	.27	.29	.45	.47	.63	.39	.30	.30	.26	5.64	6.15	.66	1.09	.34	5.26
	Mn	25.5	23.3	6.3	14.6	2.5	5.5	10.5	2.8	9.0	5.8	8.2	5.0	2.4	9.5	18.5	11.6	6.3	4.5	4.4	72.5	73.8	13.0	16.4	3.4	10.0
	Mx	29.1	27.1	7.1	17.0	3.5	6.5	11.9	3.8	10.9	6.8	9.4	6.2	4.3	11.2	21.5	13.0	7.4	6.0	5.5	93.0	93.7	15.4	20.8	4.6	33.0
<i>P. apicalis</i>	N	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	3	3	3	3	3	3
	X	36.2	32.9	10.4	20.4	3.2	7.1	14.3	5.0	14.0	8.5	12.4	7.0	5.3	12.6	26.9	17.3	9.6	6.3	6.5	124.2	102.7	24.7	17.1	4.1	97.0
	SD	1.37	1.32	.31	.83	.18	.26	.44	.27	.28	.15	.21	.20	.80	.46	1.09	.28	.08	.13	.30	9.26	7.83	.87	.75	.06	18.08
	Mn	34.3	31.2	10.1	19.3	3.0	6.8	13.7	4.7	13.5	8.3	12.1	6.7	4.5	12.2	25.7	16.8	9.5	6.2	6.1	116.1	96.0	24.1	16.2	4.0	80.0
	Mx	37.7	34.1	10.9	21.3	3.4	7.4	14.7	5.4	14.2	8.7	12.6	7.2	6.6	13.2	28.2	17.5	9.7	6.5	6.9	134.3	111.3	25.7	17.5	4.1	116.0
<i>D. rosamondae</i>	N	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	5	5	5	5	5	2
	X	25.6	23.8	7.4	15.9	2.7	6.9	11.7	2.6	9.5	6.2	8.9	5.5	2.6	8.0	19.0	11.6	6.9	5.5	5.4	81.3	58.6	16.4	12.3	3.8	22.5
	SD	.74	.82	.27	.80	.35	.28	.56	.26	.18	.13	.39	.16	.22	.67	.54	.32	.15	.38	.50	6.80	5.28	.34	.60	.22	3.54
	Mn	24.5	23.0	7.1	15.2	2.3	6.3	10.9	2.3	9.2	6.0	8.3	5.3	2.2	7.0	18.2	11.2	6.7	4.9	4.7	74.4	50.9	15.9	11.4	3.5	20.0
	Mx	27.0	25.4	7.9	17.2	3.2	7.2	12.7	3.0	9.8	6.4	9.5	5.8	2.9	8.8	20.1	12.0	7.1	6.1	6.2	90.7	63.8	16.8	13.0	4.1	25.0

Multivariate analysis: results and discussion

Phenetic analysis

Univariate analyses

The means, standard deviations and range of the skull and external characters for the six species are shown in Table 2.

The two factor ANOVA resulted in significant ($p < 0.05$) sexual dimorphism in 16 of the 25 characters examined, with the males larger in each of these characters except for MAXVAC. The nine characters not significantly different were BULPER, BULTOT, INBUL, M^2 - M^5 , M_2 - M_5 , NV, EAR and TRAG. All characters were significantly different between species and only BULPER had a significant interaction between sex and species.

Principal component analysis

This *a priori* analysis was carried out on skull and dental measurements of combined male and female adults. Factors 1, 2 and 3 explain a total of 89.6 per cent of the observed variation (Table 3). Plots of Factors 1 and 2 (Figure 3a) show *P. woolleyae* to be distinct from all but *D. rosamondae*, although it is well separated from that species on Factor 3 (Figure 3b). The *P. macdonnellensis* and *P.* 'ningbing' clusters overlap in both Figures 3a and b. *Parantechinus apicalis* and *D. rosamondae* are quite distinct from the other species.

Table 3 Principal component factor scores produced by varimax rotation based on skull measurements of adult *Pseudantechinus* species (*woolleyae*, *macdonnellensis*, *bilarni* and 'ningbing'), *Parantechinus apicalis* and *Dasykaluta rosamondae*.

Character	Factor 1	Factor 2	Factor 3
MAXL	.978	-.083	.085
BASCRANL	.981	-.044	.062
MSKH	.876	-.095	-.337
MSKW	.937	.065	-.126
BULPER	.426	.627	.503
BULTOT	.535	.791	-.100
OBUL	.911	.308	-.147
INBUL	.781	-.539	-.049
C^1 - M^5	.966	-.155	.101
M^2 - M^5	.924	-.186	-.052
RM^4 - LM^4	.967	-.036	-.120
INORB	.859	-.152	-.245
MAXVAC	.631	.026	.586
NASL	.712	-.304	.496
DC-I ₁	.983	-.050	.049
I ₁ -M ₅	.957	-.202	.039
M ₂ -M ₅	.923	-.181	-.028
ANGCON	.739	.565	-.109
CONRAM	.783	.350	-.186
Variation explained (%)	72.3	11.2	6.1

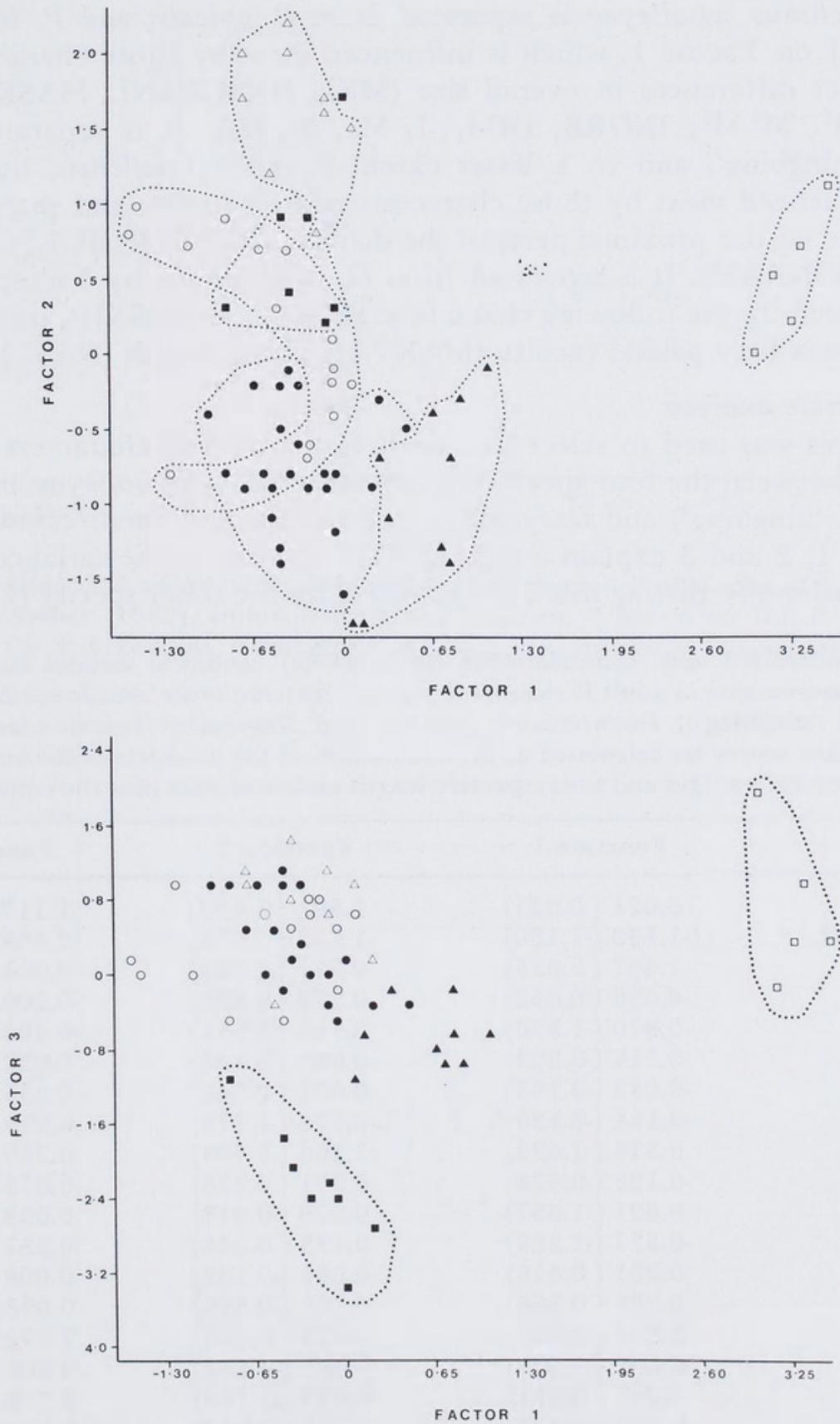


Figure 3 Principal component analysis based on skull characters of species of Parantechini sensu Archer (1982). (a) Factors 1 and 2, (b) Factors 1 and 3. *P. woolleyae* (Δ), *P. macdonnellensis* (\circ), *P. bilarni* (\blacktriangle), *P. 'ningbing'* (\bullet), *P. apicalis* (\square) and *D. rosamondae* (\blacksquare).

Pseudantechinus woolleyae is separated from *P. apicalis* and *P. bilarni* (to a lesser extent) on Factor 1, which is influenced most by those characters (Table 3) that reflect differences in overall size (MXL, BASCRANL, MASKH, MSKW, OBUL, C¹-M⁵, M²-M⁵, INORB, DC-I₁, I₁-M₅, M₂-M₅). It is separated from *P. bilarni*, *P. 'ningbing'*, and to a lesser extent *P. macdonnellensis*, by Factor 2, which is influenced most by those characters related to size and shape of bullae and the shape of the proximal parts of the dentary (BULPER, BULTOT, INBUL, ANGCON, CONRAM). It is separated from *D. rosamondae* by Factor 3 which is most influenced by the following characters: skull height (MSKH), periotic length (BULPER), maxillary palatal vacuity (MAXVAC), nasal length (NASL).

Canonical variate analysis

This analysis was used to select the combination of skull characters which best discriminate between the four species of *Pseudantechinus* (*woolleyae*, *macdonnellensis*, *bilarni*, 'ningbing') and *Dasykaluta rosamondae* and *Parantechinus apicalis*.

Functions 1, 2 and 3 explain a total of 94.2 per cent of the variance (Table 4). Function 1 primarily distinguishes *P. apicalis* from the other species (Figure 4). It

Table 4 Standardised and unstandardised (in brackets) canonical variates based on skull measurements of adult *Pseudantechinus* species (*woolleyae*, *macdonnellensis*, *bilarni*, and 'ningbing'), *Parantechinus apicalis* and *Dasykaluta rosamondae*. Canonical variate scores are calculated as the summation of the products of the unstandardised canonical variates and the respective length measurements plus the constant.

Character	Function 1	Function 2	Function 3
MAXL	0.021 (0.021)	1.801 (1.839)	-1.117 (-1.141)
BASCRANL	-1.130 (-1.130)	-1.978 (-1.978)	-0.469 (-0.469)
MSKH	1.447 (5.655)	-0.757 (-2.960)	-0.004 (0.014)
MSKW	0.038 (0.052)	-0.279 (-0.376)	-0.200 (-0.270)
BULPER	-0.370 (-1.570)	0.719 (3.051)	-0.400 (-1.697)
BULTOT	-0.115 (-0.393)	-0.043 (-0.146)	0.952 (3.244)
OBUL	-0.083 (-0.198)	0.901 (2.148)	0.335 (0.798)
INBUL	-0.154 (-0.530)	-0.574 (-1.973)	-0.219 (-0.754)
C ¹ -M ⁵	0.514 (1.420)	1.266 (3.499)	-0.795 (-2.196)
M ² -M ⁵	-0.122 (-0.474)	0.071 (0.276)	-0.073 (-0.281)
RM ⁴ -LM ⁴	0.621 (1.687)	0.006 (0.015)	0.099 (0.269)
INORB	-0.327 (-1.223)	0.173 (0.646)	0.237 (0.887)
MAXVAC	0.201 (0.415)	-0.091 (-0.188)	0.008 (0.017)
NASL	0.223 (0.366)	-0.195 (-0.320)	-0.008 (-0.014)
DC-I ₁	0.357 (0.451)	0.529 (0.668)	1.072 (1.353)
I ₁ -M ₅	-0.203 (-0.408)	-0.075 (-0.150)	0.065 (0.131)
M ₂ -M ₅	0.283 (0.951)	-0.627 (-2.108)	0.778 (2.616)
ANGCON	-0.124 (-0.377)	-0.310 (-0.942)	0.183 (0.556)
CONRAM	-0.465 (-1.319)	-0.106 (-0.302)	0.159 (0.450)
CONSTANT	(-28.789)	(-29.464)	(-10.323)
Variation explained (%)	60.2	19.9	14.1

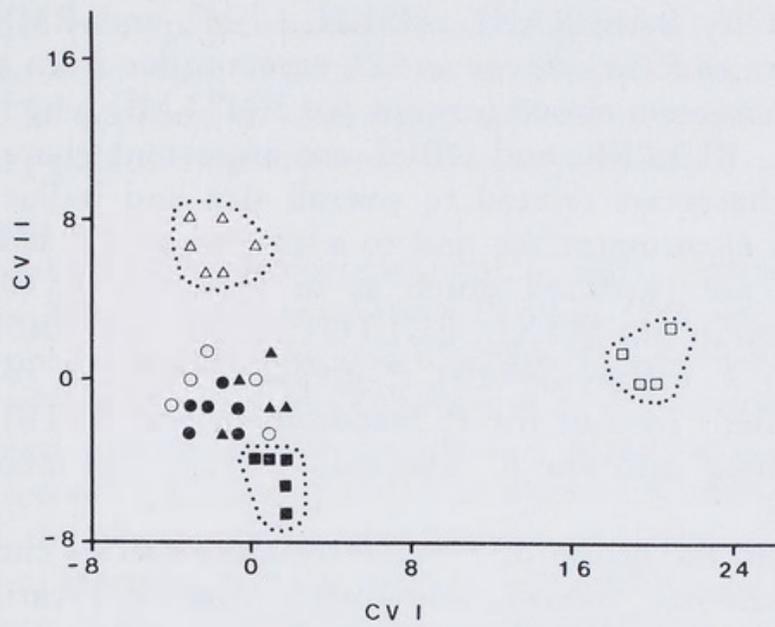


Figure 4 Canonical variate analysis based on skull characters of species of *Parantechini sensu* Archer (1982), with variates 1 and 2 shown. *P. woolleyae* (Δ), *P. macdonnellensis* (\circ), *P. bilarni* (\blacktriangle), *P. 'ningbing'* (\bullet), *P. apicalis* (\square) and *D. rosamondae* (\blacksquare).

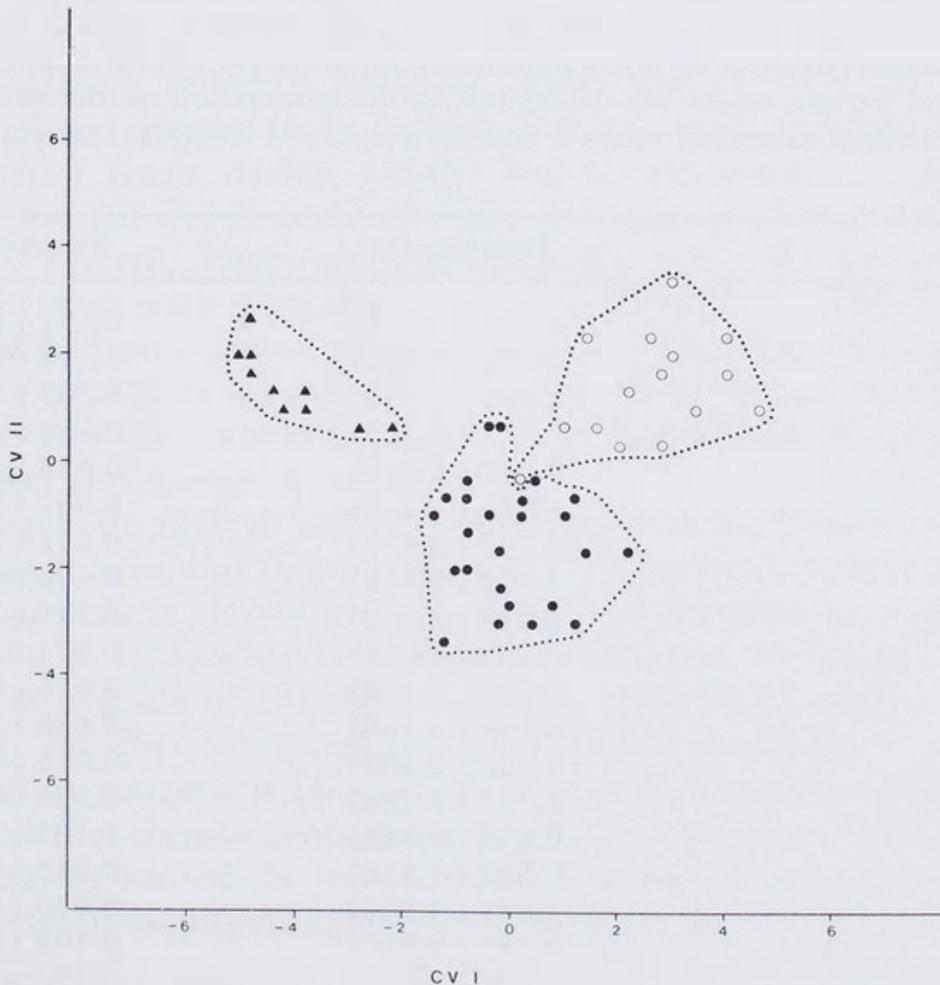


Figure 5 Canonical variate analysis based on skull characters with variates 1 and 2 shown. *P. bilarni* (\blacktriangle), *P. 'ningbing'* (\bullet) and *P. macdonnellensis* (\circ).

is greatly influenced by BASCRANL, MSKH, C¹-M⁵ and RM⁴-LM⁴ (Table 4). Function 2 best separates *P. woolleyae* and *D. rosamondae* from the other species. In addition to the characters above (except for RM⁴-LM⁴) which load heavily on this function, MAXL, BULPER, and OBUL are important characters in this separation. These are characters related to overall size and bullae size and shape. Function 3 separates *D. rosamondae* and to a lesser extent *P. woolleyae* from the other species which are clustered much as in Function 2. Characters loading heavily on this Function are MAXL, BULTOT, C¹-M⁵ and DC-I₁ (Table 4). All *P. woolleyae* (N=11), *P. bilarni* (N=10), *P. apicalis* (N=5), *D. rosamondae* (N=4) were correctly classified. Two of the *P. macdonnellensis* (N=16) were incorrectly classified as *P. 'ningbing'* and one *P. 'ningbing'* (N=25) was incorrectly classified as *P. macdonnellensis*.

In order to examine the group of *Pseudantechinus* species clustering closely in Figure 4 (*macdonnellensis*, *bilarni*, 'ningbing'), canonical variate analysis was carried out on these three species alone (Figure 5).

Factor 1 clearly separates *P. bilarni* from the other two species. This Function is largely influenced by characters (MAXL, MSKW, C¹-M⁵, NASL, M₂-M₅, CON

Table 5 Standardised and unstandardised (in brackets) canonical variates based on skull measurements of adult *Pseudantechinus macdonnellensis*, *P. bilarni* and *P. 'ningbing'*. Canonical variate scores are calculated as the summation of the products of the unstandardised canonical variates and the respective length measurements plus the constant.

Character	Function 1	Function 2
MAXL	-1.192 (-1.225)	0.157 (0.162)
BASCRANL	-0.023 (-0.023)	-1.798 (-1.773)
MSKH	0.063 (0.243)	-0.359 (-1.374)
MSKW	-1.248 (-1.730)	0.799 (1.107)
BULPER	0.127 (0.591)	-0.473 (-2.203)
BULTOT	0.329 (1.117)	0.867 (2.947)
OBUL	0.262 (0.637)	0.521 (1.266)
INBUL	0.215 (0.709)	0.476 (1.568)
C ¹ -M ⁵	-1.039 (-2.592)	-0.517 (-1.291)
M ² -M ⁵	-0.420 (-1.501)	0.921 (3.290)
RM ⁴ -LM ⁴	-0.091 (-0.243)	0.016 (0.043)
INORB	0.099 (0.336)	-0.638 (-2.157)
MAXVAC	0.222 (0.492)	-0.615 (-1.363)
NASL	1.002 (1.724)	-0.396 (-0.681)
DC-I ₁	0.654 (0.836)	1.163 (1.485)
I ₁ -M ₅	-0.822 (-1.516)	0.243 (0.449)
M ₂ -M ₅	1.531 (4.966)	0.040 (0.130)
ANGCON	0.163 (0.469)	0.108 (0.312)
CONRAM	1.332 (4.159)	-0.232 (-0.723)
CONSTANT	(2.712)	(-17.165)
Variation explained (%)	72.3	27.7

RAM) (Table 5) which reflect overall size. Function 2 clearly separates *P.* 'ningbing' from the other two species except for one specimen of *P. macdonnellensis*; characters important to this function were BASCRANL, MSKW, BULTOT, M²-M⁵ and DC-I₁. In addition to characters reflecting overall size those reflecting bullae and maxillary palatal vacuities were also important.

Phylogenetic analysis

This study, employs PAUP and uses only discontinuous (bi or multistate) characters in the analysis. This is because of the difficulty experienced with continuous measurements in producing phylogenies of dasyurid marsupials (Kitchener *et al.* 1983, 1984) and with other groups (Felsenstein 1982, Archie 1985). These difficulties relate, at least in part, to the problem of adjusting continuous characters for size and in representing some important characters as measurements.

Examination of the phylogenetic relationships of the species within the Parantechini was aimed at determining the appropriate genus for *woolleyae*. It was not designed to evaluate wider relationships — although some conclusions regarding these can be drawn.

The PAUP phylogenetic analysis is based on the coded values for the character states of the species presented in Table 6. In the initial analysis *Dasyercus cristicauda*, *Dasyuroides byrnei*, *Dasyurus hallucatus* and *Sarcophilus harrisii* were entered as designated outgroup taxa (Baverstock *et al.* 1982 had shown them to be closely related). However, these species were an ingroup with *P. apicalis* the sister species to *S. harrisii*. Subsequently the relationship between the Parantechini *sensu* Archer (1982) and *D. cristicauda*, *D. byrnei*, *D. hallucatus* and *S. harrisii* were examined using five species of true *Antechinus* (*bellus*, *flavipes*, *leo*, *stuartii*, *swainsonii*) as outgroup taxa. Six equally parsimonious phylogenetic trees were produced each with a length of 135 and a consistency index of 0.504. Two of these trees are shown in Figure 6. The other four equally parsimonious trees have a similar topology to those shown except for reversal of position between the following pairs: *P. macdonnellensis*/*P.* 'ningbing', *P. woolleyae*/*P. bilarni* and *A. swainsonii*/*A. leo*.

Our phylogenetic analysis indicates that *woolleyae* is closest to *macdonnellensis*, 'ningbing' and *bilarni*, but that the relationships between these taxa is not resolved. The species *apicalis* is clearly not closely related to *bilarni* as suggested by Archer (1982). While it is possible to recognise *woolleyae*, 'ningbing', *macdonnellensis* and *bilarni* as a grade of congeneric species, cladistically such a genus would be paraphyletic. Another interpretation of Figure 6 would be to regard all the ingroup species as congeneric (*Dasyurus*). Such a decision would be a radical departure from existing classification and depends completely on the correct rooting of the tree. When we rooted the tree in Figure 6 at a point so as to make the *Pseudantechinus* species monophyletic (midway between *D. byrnei* and the nearest *Pseudantechinus* species), it produced a tree of 151 units length. This was 16 units longer than the Figure 6 tree. Interestingly, Baverstock *et al.* (1982) considered that our ingroup species formed an unresolved trichotomy.

Table 6. Modal values for character code scores of the species used in the phylogenetic analysis (see Table 1 for explanation of character code). Penis characters for *Pseudantechinus woolleyae*, *Dasyurus cristicauda*, *Dasyuroides byrnei*, *Dasyurus hallucatus* and *Sarcophilus harrisi* from P. Woolley (pers. comm.); other species from Woolley (1982).

Character code	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	C15	C16	C17	C18	C19	C20	C21	C22	C23	C24	C25	C26	C27	C28	C29	C30	C31	C32	C33	C34	C35	C36										
<i>P. apicalis</i>	3	2	2	3	3	1	1	3	1	2	3	1	4	1	3	3	1	3	4	2	1	1	2	1	3	1	2	3	2	2	1	1	1	1	1	1	1	1								
<i>P. bilarni</i>	6	2	2	3	2	1	1	2	1	3	2	2	2	2	3	2	2	2	2	1	1	1	3	3	3	2	2	2	2	1	2	1	1	1	1	1	1	1	1	1						
<i>P. macdonnellensis</i>	2	1	2	2	1	1	1	1	2	2	2	2	2	2	3	2	2	2	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1					
<i>D. rosamondae</i>	1	1	3	1	2	2	1	2	1	4	1	1	1	1	3	2	3	3	3	3	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1				
<i>P. woolleyae</i>	6	2	2	3	2	2	2	2	3	1	2	2	2	2	2	4	2	2	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1				
<i>P. 'ningbing'</i>	3	1	2	3	1	2	1	2	1	2	2	2	2	2	3	3	3	3	3	4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1				
<i>D. byrnei</i>	3	1	3	2	1	1	1	1	2	2	2	1	4	3	3	3	3	3	4	1	1	3	1	2	1	1	3	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
<i>D. cristicauda</i>	2	1	2	2	1	2	1	2	1	3	1	4	4	4	3	2	2	2	3	4	3	2	1	1	1	1	3	2	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
<i>D. hallucatus</i>	1	1	2	1	1	2	1	2	4	2	3	1	2	1	3	3	1	2	4	3	1	3	2	3	3	3	2	2	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
<i>S. harrisi</i>	1	1	1	1	1	1	1	1	3	3	2	1	1	1	3	1	1	1	4	4	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
<i>A. stuartii</i>	6	2	3	3	3	1	3	4	4	2	3	1	1	1	1	3	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>A. leo</i>	6	2	3	3	3	2	3	4	4	3	4	1	1	1	1	2	1	2	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>A. flavipes</i>	6	2	3	3	3	2	3	4	4	2	1	2	1	1	3	1	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>A. bellus</i>	6	2	3	3	3	1	2	3	1	2	2	1	1	2	2	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>A. swainsonii</i>	6	2	2	3	3	2	2	4	1	1	3	1	1	1	1	3	1	3	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

† Archer (1974) records that *D. hallucatus* has an accessory penile appendage. P. Woolley (pers. comm.) found this appendage to be absent in the 26 specimens of this species she examined (including one from the same area as the one studied by Archer).

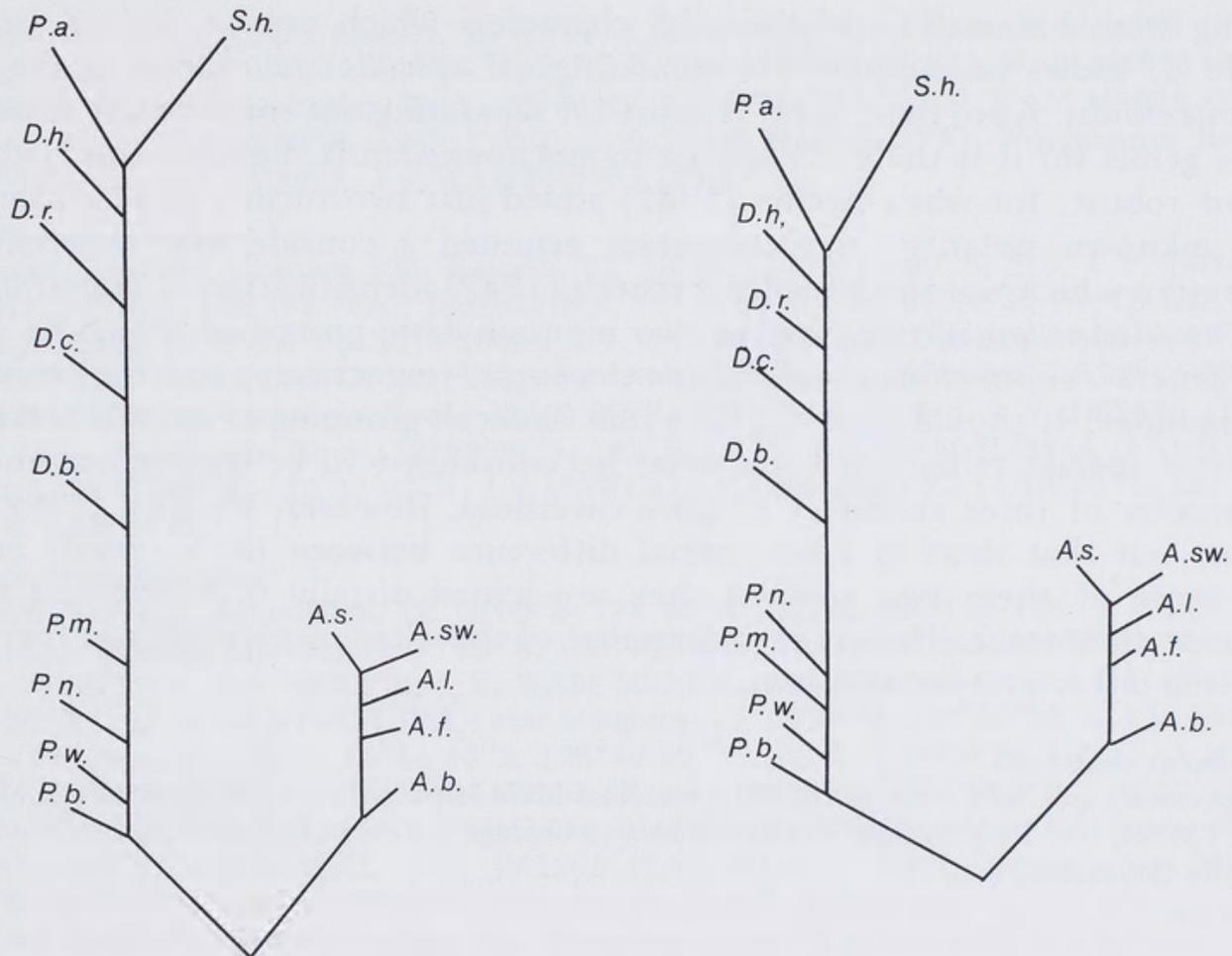


Figure 6 Two equally parsimonious phylogenetic trees, based on the modal coded values in *macdonnellensis*; *P. w.*, *Pseudantechinus woolleyae*; *P. b.*, *Pseudantechinus bilarni*; of *Antechinus* were designated outgroup taxa. Branch lengths are proportional to patristic distances. *P. a.*, *Parantechinus apicalis*; *S. h.*, *Sarcophilus harrisii*; *D. h.*, *Dasyurus hallucatus*; *D. r.*, *Dasykaluta rosamondae*; *D. c.*, *Dasycercus cristicauda*; *D. b.*, *Dasyuroides byrnei*; *P. n.*, *Pseudantechinus* 'ningbing'; *P. m.*, *Pseudantechinus macdonnellensis*; *P. w.*, *Pseudantechinus woolleyae*; *P. b.*, *Pseudantechinus bilarni*; *A. sw.*, *Antechinus swainsonii*; *A. s.*, *Antechinus stuartii*; *A. l.*, *Antechinus leo*; *A. f.*, *Antechinus flavipes*; *A. b.*, *Antechinus bellus*.

We believe that a more comprehensive phylogenetic appraisal, which is beyond the scope of this study, is required before proposing the placement of all our in-group in *Dasyurus*. Such a study would need to investigate other character states and use alternate phylogenetic analyses to evaluate the robustness of our tree; also additional outgroups should be tested (e.g. *Murexia*).

In conclusion, we tentatively place *woolleyae*, *macdonnellensis*, *bilarni* and 'ningbing' in *Pseudantechinus* and *apicalis* in *Parantechinus*.

Archer (1982, Fig. 17) produced a "cladogram of hypothetical phylogenetic relationships" of his Parantechini species *bilarni*, *apicalis*, *rosamondae*, 'ningbing' and *macdonnellensis*. He stated that this 'cladogram' was based on the 15 cranial, dental and external character-states of his Table 2. The most likely cladogram

arising from his analysis of these 15 characters which can be derived from his Table 4, shows no support for separating off *apicalis* and *bilarni* in the genus *Parantechinus*. Also, there is no support for separating out *rosamondae* as a monotypic genus for it is the sister species to *macdonnellensis*. Further, this cladogram is not robust, for when Archer (1982) added just two further phallic characters (of unknown polarity) the cladogram assumed a considerably different configuration which was the basis for Archer's (1982) identification of *bilarni/apicalis* and *macdonnellensis*/'ningbing' as two monophyletic groups on which he settled the genera *Parantechinus* and *Pseudantechinus*, respectively, and *Dasykaluta* for *rosamondae*. It should be noted here that Archer's grouping of *apicalis* and *bilarni* as sister species relies solely on what he considered to be their synapomorphic possession of three accessory corpora cavernosa. However, Woolley (1982: 777) points out that there is a substantial difference between the accessory corpora cavernosa of these two species; they are joined distally in *bilarni* and remain separate in *apicalis*. Thus in our treatment of this character we refer to them only as being either present or absent.

Specimens examined

Specimens prefixed with WAM, Western Australian Museum; with JM, Queensland Museum; with FMNH, Field Museum of Natural History, Chicago, USA; with CAWC, Central Australian Wildlife Collection.

Specimens as (all have skulls); S, skin; P, postcranial skeleton; FA, bodies fixed in 10 per cent formalin and preserved in 75 per cent ethanol. All specimens are adult unless stated otherwise.

Pseudantechinus woolleyae (paratypes)

Western Australia 29 km S of Roebourne, 21°02'10''S, 117°07'30''E, 1 ♀, WAM M24151 (FA); Mardie Station, 21°15'00''S, 116°07'40''E, 1 ♂, WAM M19676 (FA); Woodstock Station, 21°37'00''S, 118°57'00''E, 1 ♀, WAM M7122/001 (S, 4 ♀ pouch young — M7122/022-5*); Mount Florence Hmsd, 21°47'00''S, 117°51'00''E, 1 ♂, WAM M22339 (FA); Nullagine, 21°53'00''S, 120°07'00''E, 1 ♂, WAM M716 (S); Barton Battery, 21°53'00''S, 120°17'00''E, 1 ♀, WAM M2554 (S); Rudall River National Park, 22°20'25''S, 122°02'03''E, 1 ♀, WAM M25772 (FA); Barlee Range, 23°45'00''S, 116°20'00''E, 1 ♂, WAM M3478 (FA); Wooleen Hmsd, 27°05'00''S, 116°10'00''E, 1 ♀, WAM M2406 (S, 5 pouch young — 4 ♂, 1 unknown, M2407-11*); Poona Hill, 27°36'00''S, 116°17'00''E, 1 ♂, WAM M24300 (FA); Kathleen Valley Station, 27°20'00''S, 120°30'00''E, 1 ♀, WAM M8462 (juvenile, FA); Yoweragobbie, 28°16'00''S, 117°23'00''E, 1 ♀, WAM M21153 (FA).

Pseudantechinus macdonnellensis

Northern Territory. Near Tennant Creek, 19°39'00''S, 134°15'00''E, 1 ♀, WAM M6289 (FA).

Western Australia. Woodstock Stn, 21°36'30''S, 118°57'30''E, 1 ♀, WAM M5511 (FA); Woodstock Stn, 21°37'00''S, 118°57'00''E, 1 ♂, WAM M7123 (S); Lake Auld, 21°44'00''S, 123°40'00''E, 1 ♀, WAM M25602 (S, FA); near Yardie Well, 22°19'30''S, 113°48'30''E, 1 ♀, WAM M18139 (FA); Great Sandy Desert, 22°27'00''S, 123°54'00''E, 1 ♂, WAM M22691 (FA); near Gill Pinnacle, 24°54'00''S, 128°47'00''E, 1 ♂, WAM M15372 (FA); Young Range, 25°02'30''S, 124°59'30''E, 1 ♂, WAM M24101 (FA); Young Range, 25°03'00''S, 124°59'30''E, 1 ♂,

* M7122/004 & 005, M2407, M2408 heads removed and sectioned.

WAM M24102 (FA); Mount Charles, 25°45'00''S, 126°11'00''E, 1 ♀, WAM M14669 (FA); Lightning Rock, 26°00'00''S, 127°40'00''E, 2 ♂, 1 ♀, WAM M8931 (S, FA), WAM M8933 (FA); WAM M8927 (S); near Lightning Rock, 26°04'40''S, 127°45'50''E, 1 ♀, WAM M8938 (FA); Blackstone Range, 26°00'00''S, 128°11'00''E, 1 ♂, WAM M15369 (FA); Winduldurra Rock-hole, 26°31'15''S, 126°01'30''E, 1 ♂, WAM M13855 (FA).

Pseudantechinus bilarni

Northern Territory. Cannon Hill, Kakadu, 12°22'00''S, 132°57'00''E, 2 ♂, 1 ♀, JM1440 (FA), JM1194 (FA), JM1193 (FA); Jabiluka Hill, 12°30'00''S, 132°53'30''E, 1 ♀, CAWC1021 (FA); Ja Ja Camp, 12°31'00''S, 132°54'00''E, 1 ♀, CAWC1000 (FA); Djawamba Massif, 12°33'00''S, 132°55'30''E, 1 ♂, CAWC1022 (FA); near Mount Brockman, 12°44'00''S, 132°54'00''E, 1 ♂, JM2316 (FA); Nourlangie Rock, 12°51'00''S, 132°49'00''E, 1 ♂, 1 ♀, JM2320 (FA), JM2319 (FA); Nourlangie Rock, 12°52'00''S, 132°50'00''E, 1 ♂, WAM M23844 (FA); Table Top Range, 13°07'00''S, 130°11'00''E, 1 ♀, CAWC472 (S); Ferguson R., 14°04'00''S, 132°19'00''E, 1 ♂, CAWC475.

Pseudantechinus 'ningbing'

Western Australia. Kalumburu, 14°18'00''S, 126°38'00''E, 2 ♂, WAM M7124 (S, FA), WAM M7126 (FA); Mitchell Plateau, 14°53'25''S, 125°44'35''E, 1 ♂, WAM M21719 (FA); Mitchell Plateau, 14°53'30''S, 125°45'00''E, 1 ♀, WAM M22035 (FA); Mitchell Plateau, 14°53'40''S, 125°45'20''E, 1 ♂, WAM M15787 (FA); near Ningbing, 14°58'10''S, 128°35'30''E, 1 ♀, FMNH 120549 (FA); Ningbing Bore, 15°14'30''S, 128°40'30''E, 1 ♂, 3 ♀, WAM M7130 (FA), WAM M7129 (FA), WAM M7125 (S, P), WAM M7131 (S); near Ningbing, 15°15'00''S, 128°40'00''E, 1 ♂, 4 ♀, JM2315 (FA), JM2325 (FA), JM1480, JM1477, WAM M24505.001 (FA); near Ningbing, 15°17'00''S, 128°40'00''E, 2 ♀, JM1208 (FA), JM1481; South Heywood Is, 15°20'00''S, 124°20'00''E, 1 ♀, WAM M9252 (FA); Prince Regent R. Reserve, 15°26'12''S, 125°36'42''E, 1 ♂, WAM M12334 (FA); 44.5 km N Kununurra, 15°28'00''S, 128°45'00''E, 1 ♂, JM 2314 (FA); Prince Regent R. Reserve, 15°37'32''S, 125°18'04''E, 1 ♀, WAM M12368 (FA); Parry Creek, 15°40'00''S, 128°15'00''E, 1 ♀, WAM M7132 (S, P); Ord R., 16°07'15''S, 128°44'40''E, 1 ♂, WAM M11592 (FA); Elgee Cliffs, 16°35'00''S, 127°43'00''E, 1 ♀, WAM M15933 (S, FA); Beverley Springs, 16°44'40''S, 125°22'30''E, 1 ♀, WAM M15931 (S, FA); Napier Downs, 17°15'00''S, 124°44'00''E, 1 ♀, FMNH119802 (FA); Brooking Springs, 18°01'05''S, 125°31'40''E, 1 ♀, WAM M15932 (FA); near Brooking Springs, 18°01'20''S, 125°32'20''E, 1 ♀, FMNH 119800 (S).

Parantechinus apicalis

Western Australia. Jerdacuttup, 33°53'00''S, 120°14'00''E, 1 ♂, WAM M23495 (mummified); near Mount Many peaks, 34°53'20''S, 118°24'00''E, 2 ♂, 2 ♀, WAM M9669 (FA); WAM M23496 (FA), WAM M9668 (FA), WAM M24378.

Dasykaluta rosamondae

Western Australia. Tabba Tabba, 20°50'00''S, 118°53'00''E, 1 ♀, WAM M8089.001 (FA); Abydos, 21°25'00''S, 118°55'00''E, 2 ♂, WAM M2937 (S), WAM M3416 (S); Woodstock, 21°37'00''S, 118°57'00''E, 1 ♂, WAM M3421 (FA); Tambourah, 21°45'00''S, 119°11'00''E, 1 ♀, WAM M2186 (S); Great Sandy Desert, 22°27'00''S, 123°54'00''E, 1 ♀, WAM M22689 (FA); Great Sandy Desert, 22°33'00''S, 122°23'00''E, 1 ♀, WAM M22688 (FA); Moongoongunyah, 22°51'30''S, 121°49'00''E, 1 ♂, WAM M15413 (FA).

Dasyuroides byrnei

Queensland. Birdsville, 25°54'00''S, 139°21'00''E, 1 ♂, WAM M4541 (S).

No data. 1 ♂, 1 ♀, WAM M8390 (S, P), WAM M18918 (FA).

Dasyercus cristicauda

Northern Territory. 258 km NNW Alice Springs, 22°04'00''S, 132°06'00''E, 1 ♀, WAM M6535 (S).

Queensland. Sandringham, 24°05'00''S, 139°04'00''E, 1 ♂, 1 ♀, WAM M9670 (FA), WAM M9671 (FA).

Western Australia. Kuduarra Well (No. 46) Canning Stock Route, 20°40'00''S, 126°26'00''E, 2 ♂, WAM M1512 (S), WAM M1513 (S); Mallowa Well (No. 32) Canning Stock Route, 22°25'00''S, 124°35'00''E, 1 ♂, WAM M1497 (S).

Dasyurus hallucatus

Northern Territory. Deaf Adder Creek, 12°59'00''S, 132°47'00''E, 1 ♂, WAM M7863 (P).

Western Australia. Anjo Point, 13°57'00''S, 126°34'00''E, 1 ♀, WAM M10355 (FA); Kalumburu, 14°18'00''S, 126°38'00''E, 1 ♀, WAM M7168 (S, P); Wollaston Is, 14°29'30''S, 125°28'40''E, 1 ♂, WAM M9349 (FA); Prince Regent R. Reserve, 15°35'00''S, 125°11'00''E, 1 ♀, WAM M22417 (FA); Dolphin Is, 20°29'00''S, 116°50'00''E, 1 ♂, WAM M11214 (FA).

Sarcophilus harrisii

Tasmania. 2 ♂, 1 ?sex, WAM M17183-5 (S), Swansea, 42°08'00''S, 148°04'00''E, 2 ?sex, WAM M16592-3.

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