

REASSESSMENT OF NORTHERN REPRESENTATIVES OF THE *ANTECHINUS*
STUARTII COMPLEX (MARSUPIALIA: DASYURIDAE): *A. SUBTROPICUS* SP. NOV.
AND *A. ADUSTUS* NEW STATUS

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Antechinus subtropicus sp. nov. is described from the subtropical rainforests of southeastern Queensland and northeastern New South Wales, and *A. adustus* from tropical rainforests in northeastern Queensland is elevated to full specific status from *A. stuartii adustus*. *Antechinus subtropicus* differs from other members of the *A. stuartii* complex (which includes *A. stuartii*, *A. agilis* and *A. adustus*) by its larger size (weight, body length and cranial length), relatively longer and narrower rostrum, extremely large palatal vacuities and large entoconid on M₃. *Antechinus adustus* differs from other members of the *A. stuartii* complex by its darker pelage, short, broad rostrum, very large crowned upper incisors, small alisphenoid tympanic wings and fixed differences at 15% of isozymes screened. These species and current research show that much work is still needed to resolve the taxonomy of the *A. stuartii*-*A. flavipes* species complex, and that a combined morphological and biochemical approach is likely to be most productive. □ *Antechinus subtropicus*, *Antechinus adustus*, *Antechinus stuartii*, rainforests, Queensland, northern New South Wales, morphometrics, dasyurid.

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Continuing uncertainty surrounds the taxonomic status of populations currently allocated to *Antechinus stuartii* and *A. flavipes* (Marsupialia: Dasyuridae) in eastern Australia, with substantial morphological variation existing within and between both taxa (Dickman et al., 1998). A lack of reliable diagnostic characters separating these two taxa has persisted for some three decades following the resurrection of *A. stuartii* from synonymy with *A. flavipes* by Wakefield & Warneke (1967).

Macleay (1841) erected the genus *Antechinus* and described *stuartii* on the basis of the collector's notes of a lost specimen from Sydney, although he later examined a skeleton from the same locality (Macleay, 1842). Wakefield & Warneke (1967) selected a neotype from Waterfall, Royal National Park, near Sydney. Prior to Wakefield & Warneke's revision, *A. stuartii* had been synonymised with *A. flavipes* by most authors from Iredale & Troughton (1934).

Dickman et al. (1988, 1998) discovered that *A. stuartii* as recognised by Wakefield & Warneke (1967) actually consisted of more than one electrophoretically and morphologically distinct species. These species appear to be reproductively isolated in sympatry by synchronisation of

ovulation and mating at different rates of change of photoperiod (McAllan & Dickman, 1986; Dickman et al., 1988). *Antechinus stuartii sensu stricto* was found to occur from Kioloa (35°32'S, 150°23'E) in the south to Barrington Tops (32°03'S, 151°27'E) in the north with the new species, *A. agilis*, occurring in southern New South Wales (NSW) and Victoria (Vic.). No electrophoretic sampling of *Antechinus* had been done in northern NSW until Sumner & Dickman (1998), who suggested further that *A. stuartii* extends into southern Queensland (Qld).

Van Dyck (1982a) found that *A. stuartii* from the subtropical rainforest in southeastern Qld differed greatly in morphology from the type of *A. stuartii* and populations in NSW and Vic. Van Dyck (1997) raised the southeastern Qld populations to subspecies level (*A. stuartii subtropicus*) but even at that time suspected that *subtropicus* likely warranted full specific rank. *Antechinus stuartii subtropicus* and *A. stuartii* showed substantial overlap in their distributions, which alerted us to their possible full species status (Van Dyck, 1997).

The distinct nature of *Antechinus adustus* was first realised by Thomas (1923). Initially, he assigned it to *Phascogale flavipes adusta*, but a

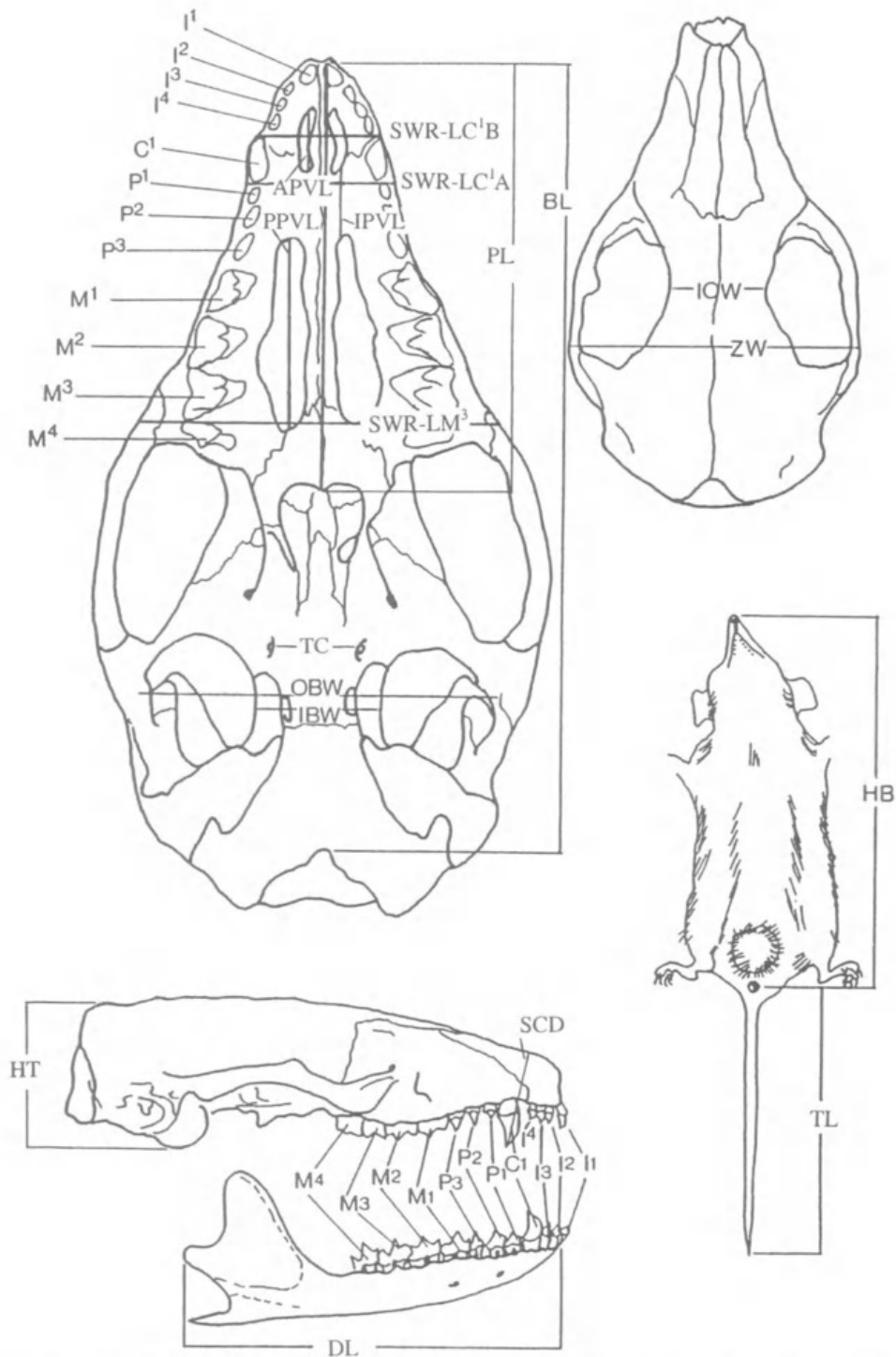


FIG. 1. Measurements taken of skull, dental and external characters of *Antechinus*. Basicranial skull length (BL); length of palate (PL); crown length P^1 to P^3 (P^1-3), crown length P^1 to P^2 (P^1-2); skull width across anterior of C^1-C^1 (SWR-LC¹B); skull width across posterior of C^1-C^1 (SWR-LC¹A); crown length C^1 to M^4 (C^1M^4); inter-palatal vacuity distance (IPVL); skull width level with junction M^3-M^4 (SWR-LM³); minimum separation between transverse canals (TC); interbulla width (IBW); maximum width across bullae (OBW); interorbital constriction (IOW); zygomatic width (ZW); snout- C^1 depth, at right angle to dorsal surface of rostrum (SCD); anterior palatal vacuity length (APVL); posterior palatal vacuity length (PPVL); dentary length, excluding incisors (DL); crown length from M^1 to M^3 (M^1-3); crown length from M^1 to M^4 (M^1-4); skull height (HT); snout-vent length (HB); Tail length, from vent (TV); ear length from the notch to pinna tip (EAR); pes length taken from the heel to distal tip of toe (PES); body weight (WT).

year later, recognising a great similarity between the syntypes of *Phascogale unicolor* and *P. adusta*, assigned his *P. adusta* to Gould's *P. unicolor* (= *A. stuartii stuartii*) (see Thomas, 1924). However, it was another 44 years before *P. adusta* was formally disentangled, along with *A. stuartii*, from synonymy with *A. flavipes* (Wakefield & Warneke, 1967). Since its description until 1967, it was referred to in the literature as a subspecies of *A. flavipes* (e.g., Troughton, 1941 (as *Antechinus*); Tate, 1947; Tate, 1952; Brass 1953; Horner & Taylor, 1959; Marlow, 1961; Walker, 1964). However, Jenkins & Knutson (1983) still considered the *P. adusta* holotype (BMNH 1922.12.8.54) referable to *A. flavipes*. Wakefield & Warneke (1967) concluded that there were insufficient specimens and distribution data to assess the status of the tropical population but noted that 'The population of northeast Qld probably warrants separate subspecific status' (p. 73). Van Dyck (1982a) presented a range of morphological and distributional data supporting the subspecific nature (at the least) of *A. adustus*, but added 'while the subspecific status of *adustus* is justified on the basis of pelage, cranial and dental uniqueness, these factors combined with its geographical isolation should accord it with full specific rank. Its status, however may be revealed more reliably through such channels as reproductive biology and biochemical comparison (Van Dyck 1982a: 749). Results of isozyme electrophoresis have since showed *A. adustus* from Ravenshoe to differ from *A. stuartii* and *A. agilis* from south coastal NSW at 15% of 32 loci scored (Baverstock et al., 1982; Dickman et al., 1998).

In this paper we define a new species, *Antechinus subtropicus*, and raise *A. stuartii adustus* to full species.

METHODS

Listed in Figure 1 are the 21 skull and dental, and 5 external measurements taken, their abbreviations, and the manner in which the measurements were made. Skull and dental dimensions were taken with digital calipers. Age variation was minimised for statistical analysis by using only those skulls which possessed fully erupted permanent P³, and no measurements were taken from sub-adult animals captured in the four months prior to April in any year.

Tooth number follows Luckett (1993), tooth nomenclature follows Archer (1974) and basicranial nomenclature follows Archer (1976).

Colour nomenclature follows Ridgway (1912) and is designated with a capital letter in the text.

Univariate summary statistics and tests, and multivariate statistical analyses were undertaken with Systat 7 (SPSS 1997). Samples were tested for normality with the Kolmogorov-Smirnov Lilliefors test and homogeneity of sample variances was tested with Levene's test. Canonical variates analysis, discriminant function analysis and one-way ANOVA with Tukey's Post Hoc test were used to compare species. Tests were considered significant at the experiment-wide error rate $\alpha < 0.05$ after application of the sequential Bonferroni test (Rice, 1989).

The *A. stuartii* and *A. agilis* used in the analyses were specimens used in Dickman et al. (1998); some were electrophoretically typed, others were from localities mentioned in Dickman et al. (1988). This was to allow for variation within these species as well as minimising the use of undescribed or misidentified taxa. Exact locations are given in Dickman et al. (1998) and are lodged with the Australian Museum.

Institution abbreviations. In the course of this study, many specimens were examined from the Queensland Museum, Brisbane (QM); Australian Museum, Sydney (AM); Museum of Victoria, Melbourne; Australian National Wildlife Collection, Canberra (CSIRO); British Natural History Museum, London (BMNH); and American Museum of Natural History.

SYSTEMATICS

Antechinus subtropicus sp. nov. (Figs 2, 3; Table 1)

ETYMOLOGY. The species name is a reference to the subtropical distribution and habitat of the species.

MATERIAL. HOLOTYPE: QMJ17407, adult male skull, dentaries and puppet skin; 2 July 1969, T.H. Kirkpatrick. **OTHER MATERIAL:** Anstead, Moggill 27°33'S 152°52'E (QM JM9737); Ballandean 28°48'S 151°50'E (J6080); Bellthorpe 26°51'S 152°43' (QM JM9803); Binna Burra 28°12'S 153°11'E (QM J11442); Blackfellow Creek, Gatton 27°45'S 152°13'E (QM JM10269); Border Ranges National Park 28°15'S 153°05'E (QM JM7943-7948, 7965); Ferny Grove 27°24'S 152°56'E (QM JM7813); Jolly's Lookout 27°24'S 152°48'E (QM JM5500); Conondale Range 26°51'S 152°43'E (QM JM2258-2261, 2263-2266) Cunninghams Gap 28°03'S 152°24'E (QM JM256); Eastern Border Ranges National Park 28°27'S 152°50'E (QM JM7941, 7942, 7959-7962); Emu Vale 28°14'S 152°15'E (QM J15888, 9996, 9997); Farm Creek, Mt Colliery 28°17'S 152°09'E (QM J21315); Joyners Ridge 27°16'S 152°52'E (QM JM5504);

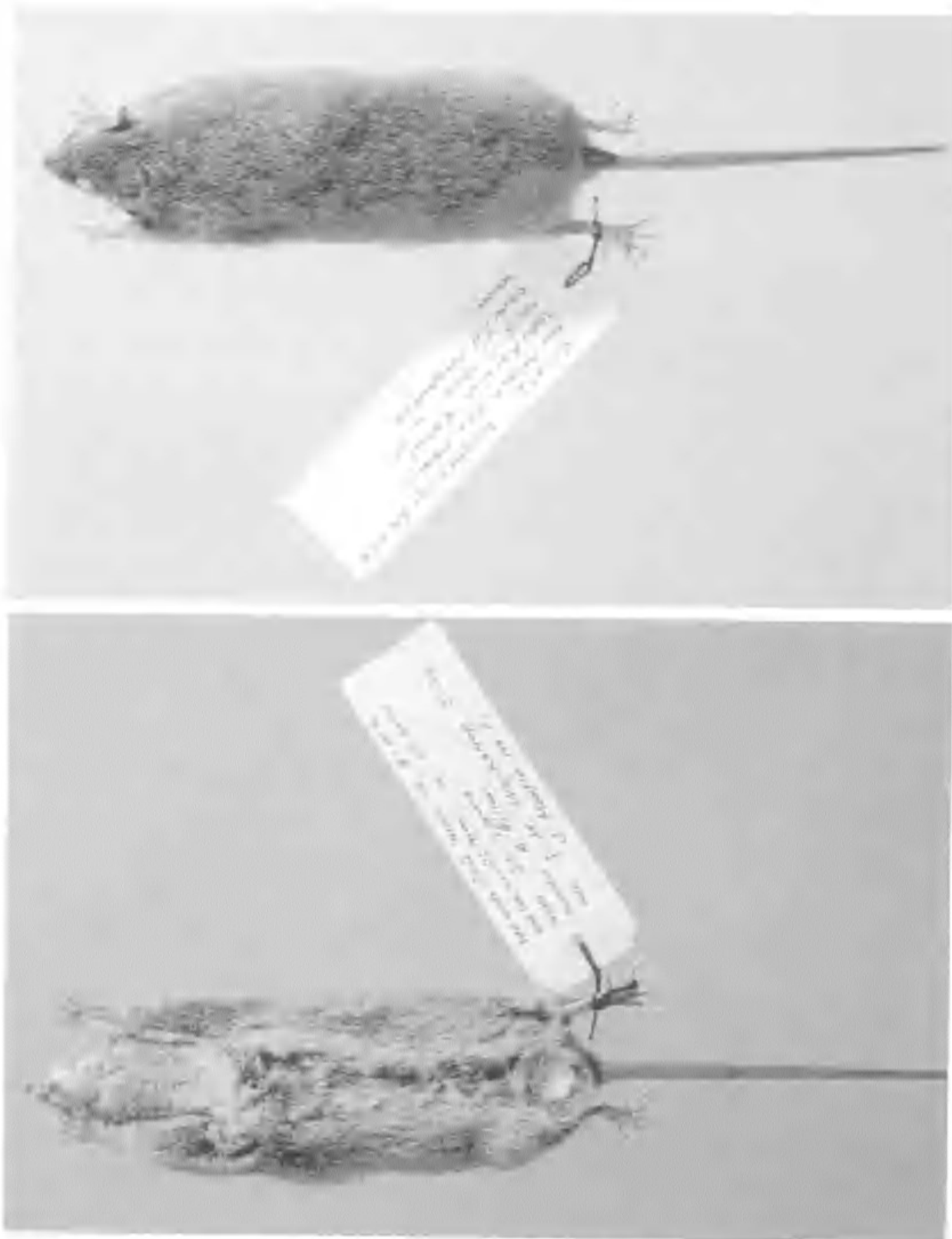


FIG. 2. Study skin of the holotype of *Antechinus subtropicus* (QM J17407). Dorsal view (above) and ventral view (below).

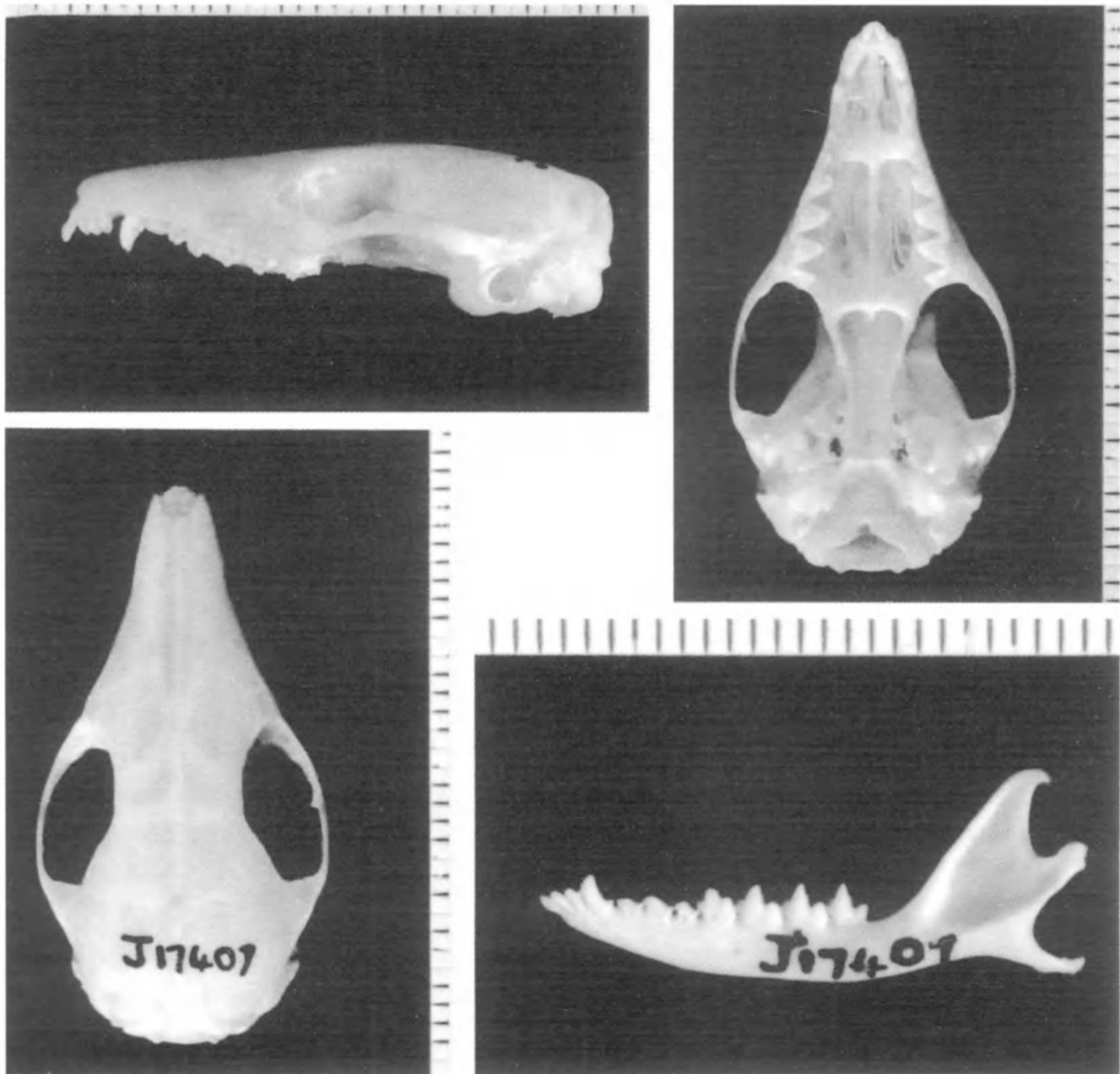


FIG. 3. Skull and left dentary of the holotype of *Antechinus subtropicus*. (QM J17407). Scales in millimetres.

Kondalilla National Park 26°40'S 152°52'E (QM JM1597-1599); Lamington Plateau 28°16'S 153°09'E (QM JM3570); Mapleton 26°38'S 152°52'E (QM JM9944); Mebbin State Forest 28°28'S 153°10'E (CSIRO CM2988, 2991, 3713); Montville 26°41'S 152°54'E (QM JM2770); Morans Falls 28°14'S 153°08'E (QM JM9941); Mt Gannon 28°12'S 153°19'E (QM JM5654, 5655, 6932, 6933); Mt Glorious 27°20'S 152°46'E (QM JM7, 9-15, 19, 22-27, 30, 47, 51, 134, 136-170, 183, 185-188, 205, 206, 569, 570, 1221, 1229, 1421, 1912, 1913, 1920-1936, 2204, 2205, 2290-2292, 2773-2775, 2841, 2850, 2878, 2879, 5653, 5656, 6181-6183, J10471, J10773, J10882, J11098, J11443, J11486, J12669, J13234, J13235, J13244, J13383, J16158, J16458, J16535, J16543, J17410, J17429-J17432, J19864); Mt Nebo 27°24'S 152°47'E (QM JM6184, 5501); Mt Nullum 28°50'S 153°26'E (AM M24904, 24905); Mt Roberts 28°13'S 152°27'E (QM J11618, 11619); Mt

Tamborine 27°56'S 153°12'E (QM J3716); Numinbah Arch, Nerang Valley 28°13'S 153°14'E (QM JM1420); O'Reillys 28°14'S 153°08'E (QM JM7107, 7108); Rozens Lookout, Beechmont 28°08'S 153°12'E (QM JM1418); Rummery Park, Whian Whian State Forest 28°38'S 153°19'E (AM M29961); Sheepstation Creek, Border Ranges National Park 28°24'S 153°01'E (AM M22782-22785, 22789); Sunday Creek 26°44'S 152°30'E (QM JM1601); Uki 28°28'S 153°14'E (QM JM4432); Upper Tallebudgera Creek 28°06'S 153°27'E (QM J20265); Warrie National Park 28°13'S 153°17'E (QM JM1600, 1596); Warwick district 28°13'S 152°02'E (QM J17400-17403, 17406, 17407); Whian Whian State Forest, via Dunoon 28°38'S 153°19'E (QM JM1919, 1419); Woondum State Forest, near Gympie 26°15'S 152°44'E (QM J15870).

TABLE 1. Selected measurements of type specimens (all male) of *Antechinus subtropicus*, *A. adustus*, *A. stuartii*, *A. agilis*, *A. unicolor*, *A. flavipes burrelli* and *A. flavipes* based on measurements taken by Van Dyck, Crowther and Dickman. Abbreviations as in Fig. 1.

Measurement (mm)	<i>A. subtropicus</i> QM J17407	<i>A. adustus</i> BMNH 22.12.18.54	<i>A. stuartii</i> AM M5294	<i>A. agilis</i> AM M33319	<i>A. unicolor</i> BMNH 54.11.19.2	<i>A. flavipes burrelli</i> AM M2593	<i>A. flavipes</i> BMNH 55.12.24.75
BL	27.93	26.2	26.76	25.16		24.4	
PL	15.76	14.8	15.13	13.45		c. 12.2	18.0
p ¹⁻³	3.89	3.29	3.88	3.29	3.46	2.3	3.16
p ¹⁻²	2.82		2.57	2.37		3.3	
SWR-LC ¹ A	4.68	5.45	5.15	4.28	5.51	4.9	5.29
C ¹ M ⁴	11.44		11.00	10.36			
IPVL	2.09		4.44	5.21			
SWR-LM ³	12.04	13.09	12.85	11.28	14.27	12.3	14.1
IBW	4.36	4.68	4.00	4.04	4.34	3.7	
OBW	10.95	10.72	10.87	10.33	11.69		
IOW	7.08	6.65	7.19	6.47	7.21	6.0	6.95
ZW	15.98	16.09	16.73	14.71	17.67	c. 14.3	
SCD	5.26	5.0	5.75	4.46			
APVL	4.16	2.96	2.85	2.30	c. 3.0	2.7	2.99
PPVL	6.82	4.7	5.16	4.15	c. 5.9	5.2	
DL	22.29		21.45	19.80	22.5		
HB	111	107	101	94	127	90	114
TV	91	94	94	79	92	80	85
EAR	16	18	17	15			18
PES	20	21	18	16.5	20		20
WT (g)	36.7			27			

TYPE LOCALITY. Emu Creek 28°13'03"S 152°24'54"E (38km E of Warwick), SE Qld.

DIAGNOSIS. *Antechinus subtropicus* differs from *A. stuartii* in having more highly developed entoconids on M₃; longer posterior and anterior palatal vacuities, and shorter inter-palatal vacuity distance (Fig. 7); relatively narrower rostrum and less expanded lachrymals and jugals (Fig. 9).

Antechinus subtropicus differs from *A. agilis* in larger body size (Fig. 7); dorsal fur brown rather than grey-brown; longer posterior and anterior palatal vacuities with a shorter inter-palatal vacuity distance, both in relative and absolute terms (Fig. 7, Tables 2,4); relatively longer premolar row; significantly more developed entoconids on M₃ and the first interdigital pad is not usually fused with the first inner metatarsal pad.

Antechinus subtropicus differs from *A. adustus* in lighter colour fur; relatively longer, narrower rostrum (Fig. 9); larger alisphenoid tympanic bullae (Fig. 8); relatively longer premolar row; significantly more developed entoconids on M₃;

less pronounced enlargement of I¹⁻⁴; and females have eight nipples instead of six.

Antechinus subtropicus differs from *A. flavipes* in absence of prominent buff fur surrounding the eyes; absence of tannish patch of post-auricular fur, uniform dorsal fur colour compared with a prominent change in antero-posterior fur colour from grizzled greyish shoulders to tannish rump; tail tip generally a uniform colour; relatively narrower rostrum; less expanded lachrymals and jugals; longer premolar row; less massive canines; and significantly more developed entoconids on M₃ (Van Dyck, 1982a).

Antechinus subtropicus differs from *A. bellus* by its darker, more uniform colour; much narrower rostral width; less expanded lachrymals and jugals; a well-developed entoconid and a non-thickened supratragus (Van Dyck, 1997).

Antechinus subtropicus differs from *A. godmani* in having relatively smaller inter-palatal vacuities and a correspondingly greater inter-palatal vacuity distance; a smaller body size; and a non-thickened supratragus (Van Dyck, 1982b).

Antechinus subtopicus differs from *A. leo* by its narrower rostral width at the level of the upper canine; a smaller body size; and having a non-thickened supratragus (Van Dyck, 1980).

Antechinus subtopicus differs from *A. swainsonii* in lighter colouring; having shorter claws; relatively larger ears and eyes; relatively shorter premolars; relatively shorter inter-palatal vacuity distance; a diastema between I^1 and I^2 ; more developed stylar cusp B on M^1 ; having posterior cingula on the upper molars; M_3 talonid wider than the trigonid; and more procumbent upper incisors.

Antechinus subtopicus differs from *A. minimus* in having a relatively longer tail; shorter claws; relatively shorter premolars; having posterior cingula on the upper molars; an upright I^1 ; a diastema between I^1 and I^2 ; the M_3 talonid wider than the trigonid; and no posterior accessory cusp on I^3 .

DESCRIPTION OF HOLOTYPE. *Pelage* (Fig. 2). The fur of the mid-back is up to 12mm long with basal 9mm Slate colour, median 2mm Isabella colour and apical 1mm black. The overall dorsal impression is one of speckled Buffy Brown (a mid biscuit-brown), however, mid-way along the dorsum fur colour warms to become a slightly darker Saccardo's Umber to the base of the tail. Guard hairs, interspersed thinly through the fur, are 13mm on the rump, and reduce to 5mm where they terminate at the crown of the head. Fur on and below the shoulders, thighs, flanks and chin lacks black tips and these areas, and the belly, appear as Chamois (a light fawn).

There is no head-stripe and no impression of a dark head 'patch', nor are there any eye-rings (although animals in the field appear to have a head-stripe). The soft ventral fur (8mm long on the belly) is Mouse Gray on the basal half and Cartridge Buff on the apical half, and is interspersed with colourless medially thickened guard hairs 11mm long. The belly is thus an overall Chamois. Forefeet and hindfeet are thinly covered with Cartridge Buff hairs. The tail is moderately thickly covered with hair and is very weakly bicoloured dorso-ventrally. Hairs average 2.0mm along the tail length but increase to 6.5mm at the tip. Dorsally, the tail hairs are uniform Buffy Brown with Fuscous Black tips, but the distal third is covered with Olive Brown hairs dorsally and Deep Olive Buff ventrally which form a ventral 'crest'. Ventrally, the black

tips are lost completely and the hairs become almost colourless toward the tip.

Vibrissae. There are approximately 22 mystacial vibrissae on each side which are up to 31mm long. The more dorsal mystacial vibrissae are Fuscous Black while those lower are colourless; supra-orbital vibrissae number 2 (left), 1 (right); genals (Fuscous Black and colourless) number 5 (left) and 6 (right); ulna-carpals (colourless) number 4 (left) and 5 (right); submentals (colourless) number 3.

Tail. The tail is shorter than the nose-vent length. It is thin, tapers toward the tip and has a weak ventral crest.

Hindfoot. The interdigital pads are separate and are elongate and striate. Enlarged, unfused, hallucal, post-hallucal and metatarsal pads are present on both feet.

Ears. The ears are rounded with a ventral lobe defined by a shallow notch in the posterior margin. The supratragus is simple and leaf-like with no pronounced thickened posterior-margin or distal-end reflex.

Dentition. (Fig. 3). Upper Incisors. I^1 roots are narrow, crowns are short and high, relatively broad and weakly cingulated buccally. They are procumbent but the crowns are uncurved posteriorly. The roots of LI^1 and RI^1 are separated by a diastema but they contact at the crown tips. For I^{2-4} crown height, $I^2 > I^3 > I^4$. All upper incisors have very weak buccal cingula. The root and crown are clearly differentiated. I^4 carries no anterior cusp and the root of I^4 is narrow.

Upper Canines: C^1 is narrow and caniniform with a distinct boundary between the root and the crown. A weak buccal cingulum and a very weak lingual cingulum are present. There is no anterior cusp, but a minute posterior cingular cusp is present.

Upper Premolars: A very slight diastema occurs between C^1 and P^1 , P^1 and P^2 and P^2 and P^3 . All upper premolars carry strong buccal and lingual cingula. P^1 crown (broken off in RP^1) is shorter than P^2 , which is shorter than P^3 . Small but clearly definable anterior and posterior cusps are present on P^1 , P^2 and P^3 . P^1 and P^2 possess very weak postero-lingual lobes.

Upper Molars: The posterior tip of P^3 is positioned in the parastylar corner of M^1 but lingual to and explanar with stylar cusp A. The anterior cingulum below stylar cusp B is very broad and complete. Stylar cusp B and the paracone are relatively unworn, and a minute protoconule is present at the base of the paracone

apex. The protoconule is accompanied by a small bulge of enamel directly below it on the face of the anterior protocrista. The paracone on M^1 is approximately half the height of the metacone. Styler cusps C and E are not visible. M^1 has a very weak posterior cingulum. Styler cusp D is greatly enlarged and makes a great contribution to endoloph bulk.

In M^2 the broad anterior cingulum, which contacts the metastylar corner of M^1 , tapers quickly as it progresses down and along the base of the paracrista, however it is complete and does not degenerate totally at the base of the paracone apex. A minute protoconule is visible. M^2 lacks styler cusps A and E. Styler cusp D is slightly reduced, broad and there is a very weak posterior cingulum. Styler cusp C is just visible on LM^2 , however it is absent on RM^2 .

In M^3 the anterior cingulum is as in M^2 , and is narrow but complete. Styler cusp D is reduced to a small, sharp peak. Styler cusps C and E are absent. There is a very weak posterior cingulum.

In M^4 the metastylar corner is very poorly developed. The narrow anterior cingulum reduces quickly away from the anterior corner of M^3 and runs to the trigon basin. A posterior cingulum is weakly present. The protocone is reduced but relatively broad. In occlusal view, the angle made between the post-paracrista and the post-protocrista is close to 110° .

Lower Incisors: The crown height of I_1 is taller than I_2 . I_1 and I_2 are oval in antero-lateral view and gouge-like in occlusal view. The crown height of I_2 is larger than in I_3 . I_3 is incisiform in lateral view with an insignificant posterior cusp at the base of the crest, which descends posteriorly from the apex of the primary cusp. The lower canine rests lingually to the posterior cusp. In occlusal view, a small notch separates the posterior cusp from the prominent postero-lingual lobe, and crown enamel of the primary and posterior cusps folds noticeably lingually such that the crest of the two cusps bisects the tooth longitudinally.

Lower Canines: C_1 is caniniform and characterised by upward projection and moderate curvature from root to crown tip. It has weak buccal and lingual cingulation and a weak posterior cusp. Some thegotic wear is evident just anterior to the posterior cusp.

Lower Premolars: There are no diastemata between the premolars, however only P_1 and P_2 contact. Between C_1 - P_1 , and P_2 - P_3 , there is a minute gap between the crowns. All are weakly

cingulated buccally and lingually. In crown height, P_2 is taller than P_1 , which is taller than P_3 . P_1 and P_2 are broad and long. P_3 is narrower and short. All possess posterior cusps. P_1 has weak postero-lingual lobing.

Lower Molars: The M_1 talonid is wider than the trigonid and a very weak anterior cingulum is present. There is no buccal cingulum. The narrow paraconid appears, in occlusal view, as a small inclined spur, the lingual edge of which makes a slight swelling on the endoloph of M_1 . The paracristid is almost horizontal from the paraconid to the paracristid fissure and vertical from the paracristid fissure to the protoconid. The metacristid and hypocristid are roughly oblique to the long axis of the dentary. The short cristid obliqua extends from the hypoconid to the posterior wall of the trigonid intersecting the trigonid at a point just buccal to that point directly below the tip of the protoconid. The hypocristid extends from the hypoconid to the hypoconulid. The entoconid is long but low. From the metaconid posteriorly, the talonid endoloph follows a line more lingual to the axis of the dentary until the base of the hypoconulid.

In M_2 , the trigonid is slightly narrower than the talonid. The anterior cingulum is moderately well-developed originating lingually in a weak parastylid notch into which the hypoconulid of M_1 is tucked. There is a very weak buccal cingulum. A very narrow, weak posterior cingulum extends from the hypoconulid to the posterior base of the hypoconid. The paraconid is well developed and is the smallest trigonid cusp. A very large entoconid, as tall as the protoconid, is present. The cristid obliqua extends from the hypoconulid to the posterior wall of the trigonid intersecting the trigonid at a point directly below the tip of the protoconid but well buccal to the metacristid fissure. The hypocristid (worn in LM_2) extends from the hypoconulid to the tip of the hypoconid. From the base of the metaconid posteriorly, the endoloph follows a line of orientation more lingual than the line of the dentary axis.

In M_3 , the width of the trigonid is equal to that of the talonid. A weak parastylid wraps around the hypoconulid of M_2 and there is a moderately well developed anterior cingulum on M_3 . Buccal and posterior cingula are as in M_2 . The reduced cristid obliqua intersects the trigonid at a point well lingual to the longitudinal vertical mid-line drawn through the tip of the protoconid, but slightly buccal to the metacristid fissure. The

entoconid on M_3 is very well developed and just shorter than the well-developed paraconid. The endoloph on the talonid of M_3 takes a more buccal orientation than that seen in M_2 . The rest of M_3 morphology is as in M_2 .

In M_4 , the trigonid is much wider than the talonid. The anterior cingulum is as in M_2 . The posterior cingulum is absent. Of the three main trigonid cusps, the metaconid is slightly taller than the paraconid but both are dwarfed by the protoconid. The hypoconid of M_4 is small but distinct. Between the hypoconid and the base of the metacristid, the cristid obliqua forms a low crest, which contacts the anterior base of the well-developed entoconid directly below the metacristid fissure. The hypoconulid is reduced to a low crest.

Skull. (Fig. 3). The rostrum is slightly concave due to a depression between the lachrymals at the nasal-frontal sutures. The left and right (damaged) alisphenoid tympanic bullae are widely separated and poorly developed. The foramen pseudovale is large and is not bisected by a bridge of the alisphenoid. The eustachian canal opening is very large. The internal jugular canal foramina are large, the canals are raised and prominent. The posterior lacerate foramina are large and exposed, as are the entocarotid foramina. The large premaxillary vacuity extends from the level of the I^1 root back to the level of the P^1/P^2 diastema. The very large maxillary vacuities extend from the level of the anterior root of P^3 and extend back to the level of the M^3/M^4 interface. Palatine vacuities are not present. There is minimal anterior flaring of the jugals, and the lachrymals are unexpanded, giving the skull a long and narrow appearance when viewed dorsally.

HABITAT AND DISTRIBUTION (Fig. 6). In SE Qld *A. subtropicus* is essentially restricted to subtropical vine-forests, and occurs from sea level (Tallebudgera Creek $28^{\circ}08'S$ $153^{\circ}26'E$) to altitudes of 1000m (Lamington Plateau $28^{\circ}16'S$ $153^{\circ}05'E$). It is abundant in major tracts of vine-forest on or east of the Great Dividing Range south of Gympie $26^{\circ}11'S$ $152^{\circ}40'E$ to NE New South Wales. Structural features of typical complex notophyll vine-forests inhabited by *A. subtropicus* include the abundance of notophylls and microphylls, lianas, vascular epiphytes, plant buttresses, compound entire leaves and trunk-obscuring aroids such as *Pothos* (Webb 1959). The uneven canopy of mixed evergreens and occasional deciduous emergents range in height

from 21-45m. *Antechinus subtropicus* is found rarely in sclerophyll associations, where its presence is limited to humid, dense areas such as fern gullies and vine entanglements along watercourses. It is particularly abundant in the perimeter vegetation of vine forests and favours dense tangled stands of invasive pioneer shrubs such as *Lantana camara*, wild raspberry *Rubus* spp., bleeding heart *Omolanthus* spp., and bracken *Pteridium esculentum*. Braithwaite (1973) studied a population at Mt Glorious ($27^{\circ}20'S$ $152^{\circ}47'E$) and found that *A. subtropicus* avoids both mature forest with sparse ground cover and disturbed areas with cunjevoi (*Alocasia machorhiza*) and young palm growth. He found a greater preference for areas of tangled and fallen lianas, and rotten logs. All areas where *A. subtropicus* occurs experience relatively high average annual rainfall of up to 2000mm (Van Dyck, 1982a).

REPRODUCTION. At Mount Glorious, SE Qld, mating occurs only in the last two weeks of September each year and is followed immediately by the death of all males (Wood, 1970; Braithwaite, 1973). Females of *A. subtropicus* gestate for 25-26 days and all births at Mt Glorious occur in the last two weeks of October. The young remain in the pouch for approximately 5 weeks and are weaned after three months (Wood, 1970). Litter size at Mt Glorious averages 7.5 young (Wood, 1970). In more northerly districts mating occurs slightly earlier than at Mt Glorious (SVD pers. obs.). At the Conondale Range ($26^{\circ}52'S$, $152^{\circ}40'E$), female *A. subtropicus* captured from 21 to 25 October had pouches containing seven or eight 1-1.5cm young. Their ages were therefore approximately 12-20 days (cf. Marlow, 1961); their births having taken place early in October. In New South Wales (near Sydney) *A. stuartii* reproduces nearly six weeks earlier than *A. subtropicus* from SE Qld (Dickman, 1982).

Nipple Number. Nipple numbers appear to be regular in SE Qld. Of 32 female specimens, representing localities over the entire range of *A. subtropicus* in SE Qld, all had pouch areas containing eight nipples. A.B. Rose (pers. comm.) also reported this for animals from the Border Ranges National Park in NE New South Wales. Eight nipples were also found by Cockburn et al. (1983) for SE Qld females.

DECIDUOUS PREMOLAR MORPHOLOGY. The dP^3 may be double- or triple-rooted. When double-rooted the tooth is less molariform, with a

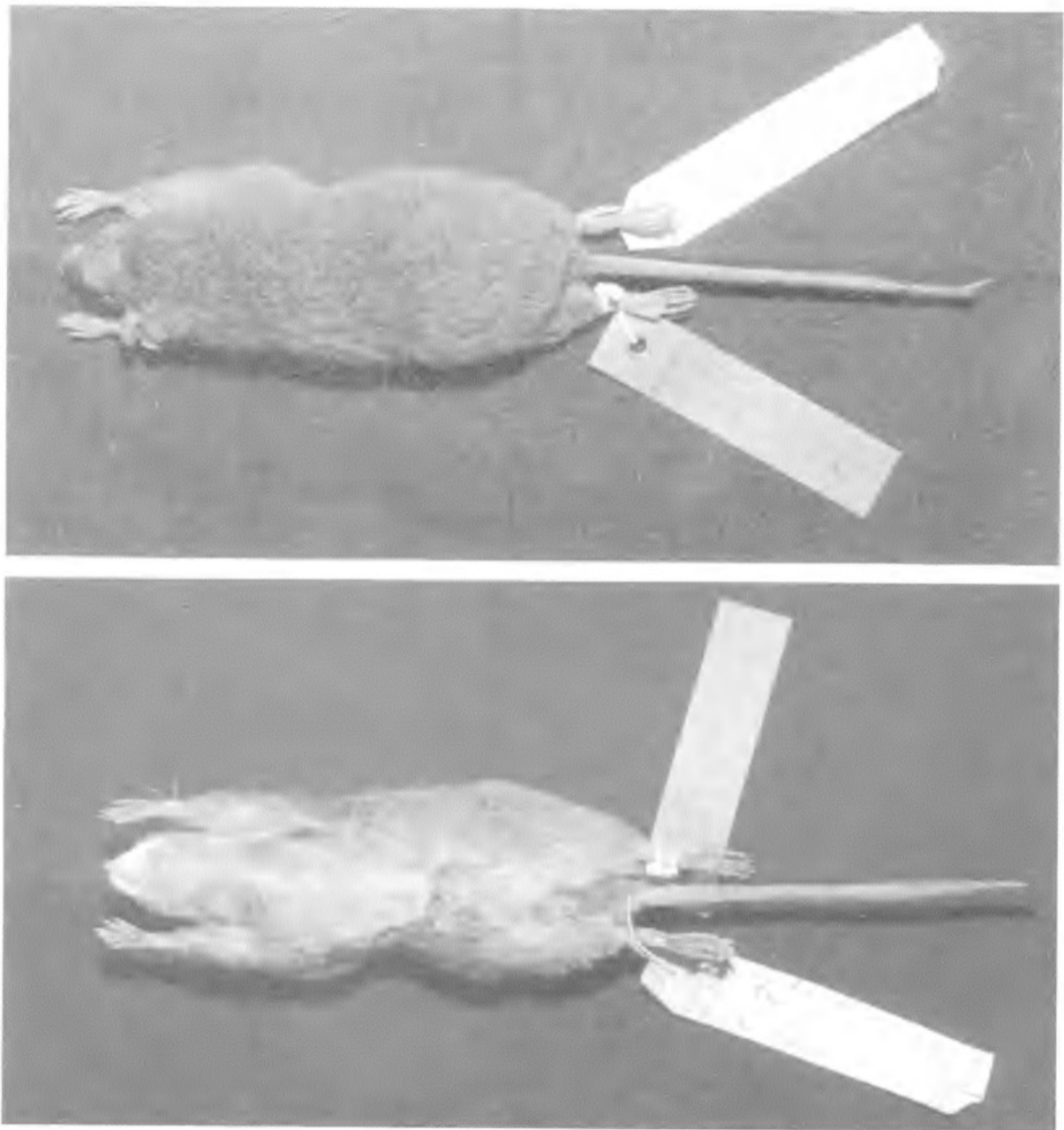


FIG. 4. Study skin of the holotype of *Phascogale flavipes adusta* Thomas, 1923 (now *Antechinus adustus*) (BMNH 1922.12.18.54). Dorsal view (above) and ventral view (below).

poorly developed protocone, well-developed paracone, and a small metacone. When triple-rooted this tooth is more molariform with a well-developed protocone, but with the paracone and metacone coalescing into a single cusp. Buccal cingulation is strong.

The dP_3 may be single or double-rooted. When single-rooted, it is premolariform, exhibiting a single anterior cusp. When double-rooted it is rounded and more molariform with a large

protoconid and possible traces of a metaconid and hypoconid.

***Antechinus adustus* (Thomas, 1923)**
(Figs 4, 5; Table 1)

Phascogale flavipes adusta. Thomas, 1923.

Phascogale unicolor adusta Thomas, 1924.

Antechinus stuartii adustus Wakefield & Warneke, 1967.

MATERIAL. HOLOTYPE: BMNH1922.12.18.54, adult male, skull, dentaries and puppet skin, 1 Jun 1922, T.V. Sherrin. OTHER MATERIAL: Bellenden Ker 17°16'S

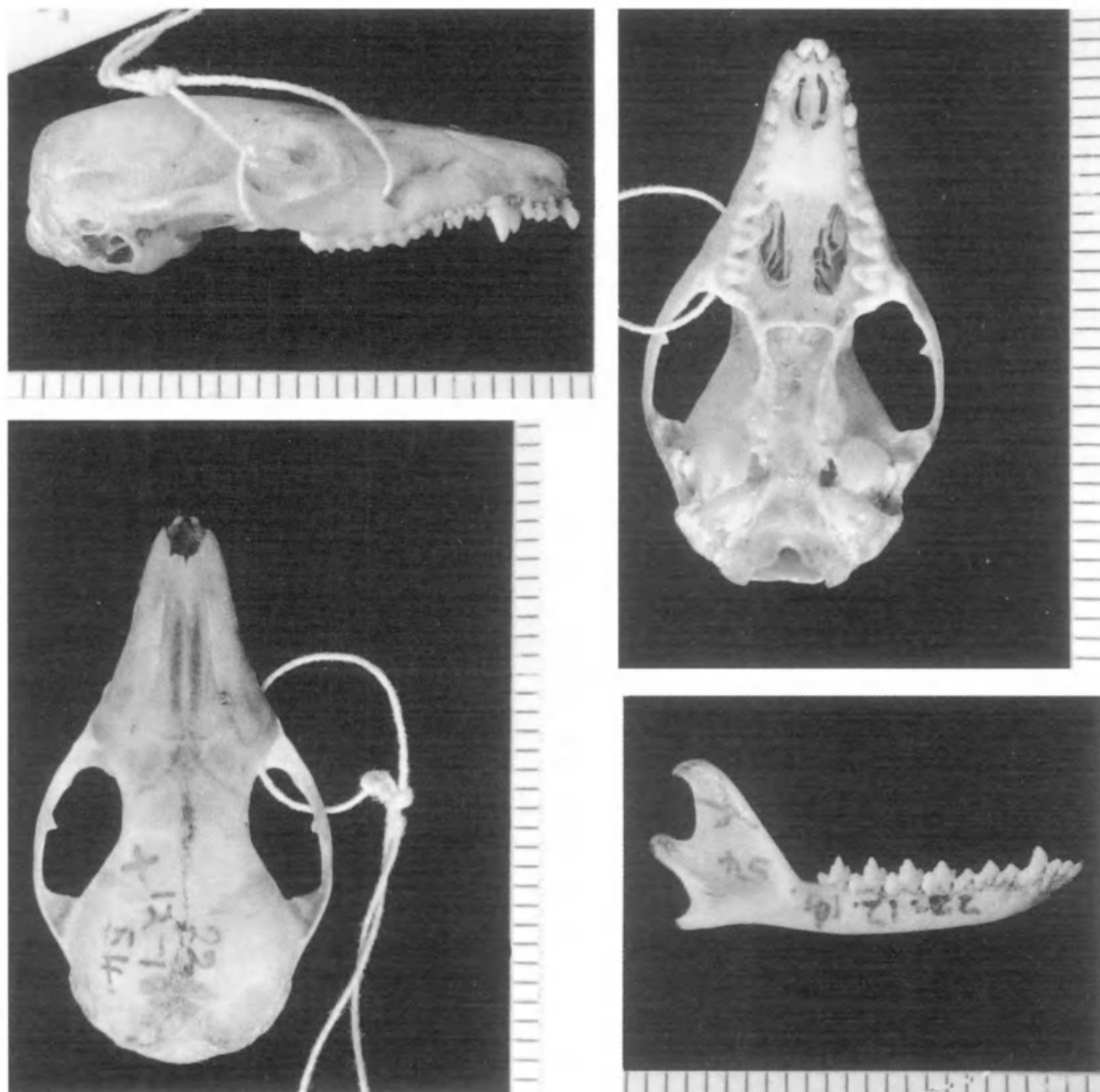


FIG. 5. Skull and right dentary of the holotype of *Phascogale flavipes adusta* Thomas, 1923. (BMNH 1922.12.18.54). Scales in millimetres.

145°55'E (QM J19669); 'Bluewater', 17km S of Rollingstone 19°10'S 146°23'E (QM JM3755, 3756); Charappa Creek, near Ravenshoe 17°38'S 145°35'E (AM M8302, 8317); Ebony Road, Forestry track 20km SE of Ravenshoe 17°44'S 145°33'E (QM JM6715); Ebony Road, 850m 17°44'S 145°32'E (QM JM1785, 1897-1901, 1903-1906, 1910, 1911, 1915, 2751, 3919, 5543); Ebony Road, 780m 17°44'S 145°33'E (QM JM5540-5542); Forestry track 15km SE of Ravenshoe, 840m 17°43'S 145°31'E (QM JM1902); George Creek area 17°49'S 145°32'E (QM JM6898); Koombooloomba Creek 17°51'S 145°35'E (QM JM6889); Macalister Mountains, W of Cardwell, 650m 18°19'S 145°57'E (QM JM6560); Mt Lewis 16°35'S 145°16'E (QM JM3758, 3619); Mt

Lewis 16°36'S 145°15'E (QM JM3757); Mt Lewis Forestry hut, 0.5km S 16°35'S 145°16'E (QM JM6906); Mt Lewis Forestry hut, 1km NW 16°35'S 145°16'E (QM JM6905); Mt Spec, NW of Townsville 18°58'S 146°09'E (QM J10108); Mt Spurgeon 16°26'S 145°12'E (QM JM809, J7143, J7144); Niblet Creek, Kooroomool Saddle Road, 5km ENE of Koombooloomba 17°49'S 145°38'E (QM JM6716, 6717); North Koombooloomba Dam 17°48'S 145°37'E (QM JM6896); Palmerston Range, Forestry road to Maalan, 710m 17°36'S 145°39'E (QM JM1907-1909); Paluma 19°00'S 146°12'E (QM JM2788); Paluma Dam, Forestry track approach, 780m 18°58'S 146°09'E (QM JM1847, 1893-1896 JM1914); Paluma township 19°00'S 146°12'E (QM JM2789); Severin State

Forest 17°11'S 145°40'E (CSIRO CM10561-10563); Windsor Tableland 16°15'S 145°02'E (QM JM2822).

TYPE LOCALITY. Dinner Creek (now Charmillan Creek), Ravenshoe, Qld, 17°42'S 145°31'E, altitude 885m.

DIAGNOSIS. *Antechinus adustus* differs from *A. stuartii* in having a longer, darker pelage; relatively smaller and more widely spaced bullae (Fig. 8) and females have six nipples compared with eight to ten nipples.

Antechinus adustus differs from *A. agilis* in having a longer, darker pelage; a relatively broader rostrum (Fig. 9); relatively smaller bullae (Fig. 8); the first interdigital pad not usually fused with the first inner metatarsal pad; and females having only six nipples.

Antechinus adustus differs from *A. subropicus* in having a smaller body size (Fig. 7, Tables 2, 3); relatively shorter, broader rostrum (Fig. 9); relatively smaller palatal vacuities with a corresponding larger inter palatal vacuity distance (Fig. 7); longer, darker pelage; less developed entoconids on M₃ and females with only six nipples.

Antechinus adustus differs from *A. flavipes* in having a smaller body size; a longer, darker pelage; absence of prominent buff fur surrounding the eyes; absence of tannish patch of post-auricular fur; uniform dorsal fur colour compared with a prominent change in antero-posterior fur colour from grizzled greyish shoulders to tannish rump; tail tip generally a uniform colour, more developed entoconids on M₃; and females with only six nipples.

Antechinus adustus differs from *A. bellus* by its much darker and more uniform colour; smaller body size; well-developed entoconids; much narrower rostral width from the level of the upper canine; through to the level of the upper third molar; and a non-thickened supratragus.

Antechinus adustus differs from *A. godmani* in having a much smaller body size; darker colouration; shorter skull length; relatively shorter, broader rostrum; shorter premolar row; and a non-thickened supratragus (Van Dyck, 1982b).

Antechinus adustus differs from *A. leo* by its narrower rostral width at the level of the upper canine; well-developed entoconids; a smaller body size; darker colour; and non-thickened supratragus (Van Dyck, 1980).

Antechinus adustus differs from *A. swainsonii* in having a narrower inter-orbital width; shorter anterior palatal vacuities; shorter premolar row; a

relatively broader rostrum; smaller body size; shorter claws; more massive I¹; more massive I²⁻⁴; prominent postero-lingual lobes on P¹⁻³; having posterior cingula on the upper molars; an upright I¹; and no posterior accessory cusp on I³.

Antechinus adustus differs from *A. minimus* in having a relatively longer tail; a relatively broader rostrum; a smaller body size; shorter claws; more massive I¹; more massive I²⁻⁴; prominent postero-lingual lobes on P¹⁻³; having posterior cingula on the upper molars; an upright I¹ and no posterior accessory cusp on I³.

DESCRIPTION OF HOLOTYPE. *Pelage* (Fig. 4). Fur of the mid-back (8mm long) with basal 6mm Slate Colour, median 1mm Tawny Olive and apical 1mm Fuscous Black. The back appears overall to be Sepia. Medially thickened guard hairs, interspersed thinly through the fur, are 11mm long on the rump, and reduce to 3mm where they terminate at the crown of the head. Fur on and below the shoulders, thighs, flanks and chin lacks black tips or coarse guard hairs and these areas and belly appear Cinnamon Buff.

The soft ventral fur (7mm long on the belly) is Mouse Gray on the basal 1.5mm and Cinnamon Buff on the apical 5.5mm and is interspersed by Cinnamon Buff guard hairs (8mm long). The belly is thus an overall Cinnamon Buff. Fore and hindfeet are covered with hairs which are coloured Saccardo's Umber. The tail appears weakly bicoloured, this being an illusion due to the denser coverage of hairs ventrally, which are 3.6mm long midway along the tail, and 6.4mm long at the ventral tip. Dorsally, the hairs are 2.7mm long midway down the tail and 2.7mm long at the dorsal tip. All tail hairs are Fuscous Black.

Vibrissae. Approximately 24 mystacial vibrissae occur on each side and are up to 27mm long. The more dorsal vibrissae are coloured Fuscous Black while those lower are colourless; supra-occipital vibrissae (Fuscous Black) number 2 left and 2 right; genals (Fuscous Black and colourless) number 9 left and 9 right; ulna-carpals (colourless) number 4 right and 6 left; submentals (colourless) number 4.

Tail. The tail is shorter than the nose-vent length. It is thin and tapers toward the tip.

Hindfoot. Interdigital pads are separate. The apical pad is enlarged, elongate and striate. Hallucal and post-hallucal pads are separate on both feet. Metatarsal pads or granules are not present in the holotype although a minute calcaneal granule is visible. An auxiliary apical

granule is visible outside left and right third digit apical granules.

Ears. It was not possible to closely examine supratragus morphology in the holotype dry skin. (In other specimens, the supratragus is simple).

Dentition (Fig. 5). Upper incisors: I^1 is massive, broad, very procumbent, strongly curved and taller-crowned than all other upper incisors. It is caniniform with a greatly developed crown. Left and right I^1 touch. I^1 and I^2 are so highly developed that they almost contact, and the diastema traditionally separating I^1 from I^2 in *Antechinus* (other than *A. minimus* and *A. swainsonii*) is minute. In other incisors, $I^3 > I^2 > I^4$, and all have strong buccal cingula. Roots of I^{2-4} are narrow while the crowns are very broad. I^4 carries no anterior cusp but a minute posterior cusp is present.

Upper canines: C^1 is short, stout and caniniform with a distinct boundary between root and crown. It carries a weak buccal and weak lingual cingulum. A minute anterior cingular cusp is present along with a slightly larger posterior cusp.

Upper premolars: There are no diastemata between premolars. All right upper premolars contact. Left P^1 and P^2 crowns are slightly separate. P^1 and P^2 carry strong buccal and lingual cingula. In crown size $P^3 > P^2 > P^1$. There is a small posterior cusp on P^2 and a large posterior cusp on P^3 . P^1 and P^2 bear heavy postero-lingual lobes and in occlusal view appear almost square.

Upper Molars: The posterior tip of P^3 lies in the parastylar corner of M^1 but lingual to and coplanar with stylar cusp A (right dentary) and just below stylar cusp A in the left dentary. The anterior cingulum below stylar cusp B is short, broad and just complete. Stylar cusp B is tall and the paracone is slightly worn. A minute protoconule is present at the base of the paracone apex. The minute protoconule is accompanied by a small bulge of enamel directly below it on the face of the anterior protocrista. The paracone on M^1 is approximately half the height of the metacone. Stylar cusp C is not visible on either LM^1 or RM^1 , and stylar cusp E is not visible. M^1 has a poorly developed posterior cingulum. Stylar cusp D is very large and broad.

In M^2 a broad anterior cingulum which contacts the metastylar corner of M^1 tapers slowly as it progresses down and along the base of paracrista and finally unites with the trigon basin. A small protoconule is visible. M^2 lacks

stylar cusps A, C and E. Stylar cusp D is slightly reduced, but broad, and there is a weak posterior cingulum.

In M^3 the anterior cingulum is as broad as in M^2 , but becomes more indistinct after covering $2/3$ distance between stylar cusp B and the base of the paracone. It does, however, unite with the trigon basin. Stylar cusp D is reduced to a very small, broad peak. Stylar cusp E is absent, as is stylar cusp C.

In M^4 the metastylar corner is poorly developed. The broad, complete anterior cingulum narrows quickly away from the metastylar corner of M^3 , and a posterior cingulum is absent. The protocone is much reduced and narrow. In occlusal view, the angle made between the post-protocrista and the post-paracrista is close to 90° .

Lower Incisors: The gross development of the upper incisors is not reflected in the lowers. The first lower incisor is almost $1\frac{1}{2}$ times the crown height of I_2 . I_1 and I_2 are oval in antero-lateral view and gouge-like in occlusal view. I_2 is subequal in crown height to I_3 . I_3 is incisiform in lateral view but with a conspicuous posterior cusp at the base of the crest, which descends posteriorly from the apex of the primary cusp. The lower canine rests against this posterior cusp. In occlusal view, a small notch separates the posterior cusp from the prominent postero-lingual lobe, and crown enamel of the primary and the posterior cusps fold noticeably lingually, such that the crest of the two cusps bisects the tooth longitudinally.

Lower Canines: C_1 is caniniform, broad and erect, and is characterised by maximum curvature from root to crown tip. It has strong buccal and lingual cingulation and a strong posterior cusp.

Lower Premolars: P_{1-3} are large, rectangularly shaped and all in contact. They are strongly cingulated buccally and lingually. In crown height, P_2 is taller than P_1 , which is taller than P_3 . All possess small posterior cusps; P_1 possesses a very weak anterior cusp. P_1 and P_2 do not have postero-lingual lobes.

Lower Molars: All molars are broad. The M_1 talonid is much wider than the trigonid and the anterior cingulum is present but poorly developed. It terminates at the posterior base of the protoconid. There is no buccal cingulum. The narrow paraconid appears in occlusal view as a small steeply sided spur, the lingual edge of which makes no appreciable swelling on the endoloph of M_1 . The paracristid is almost 45° to

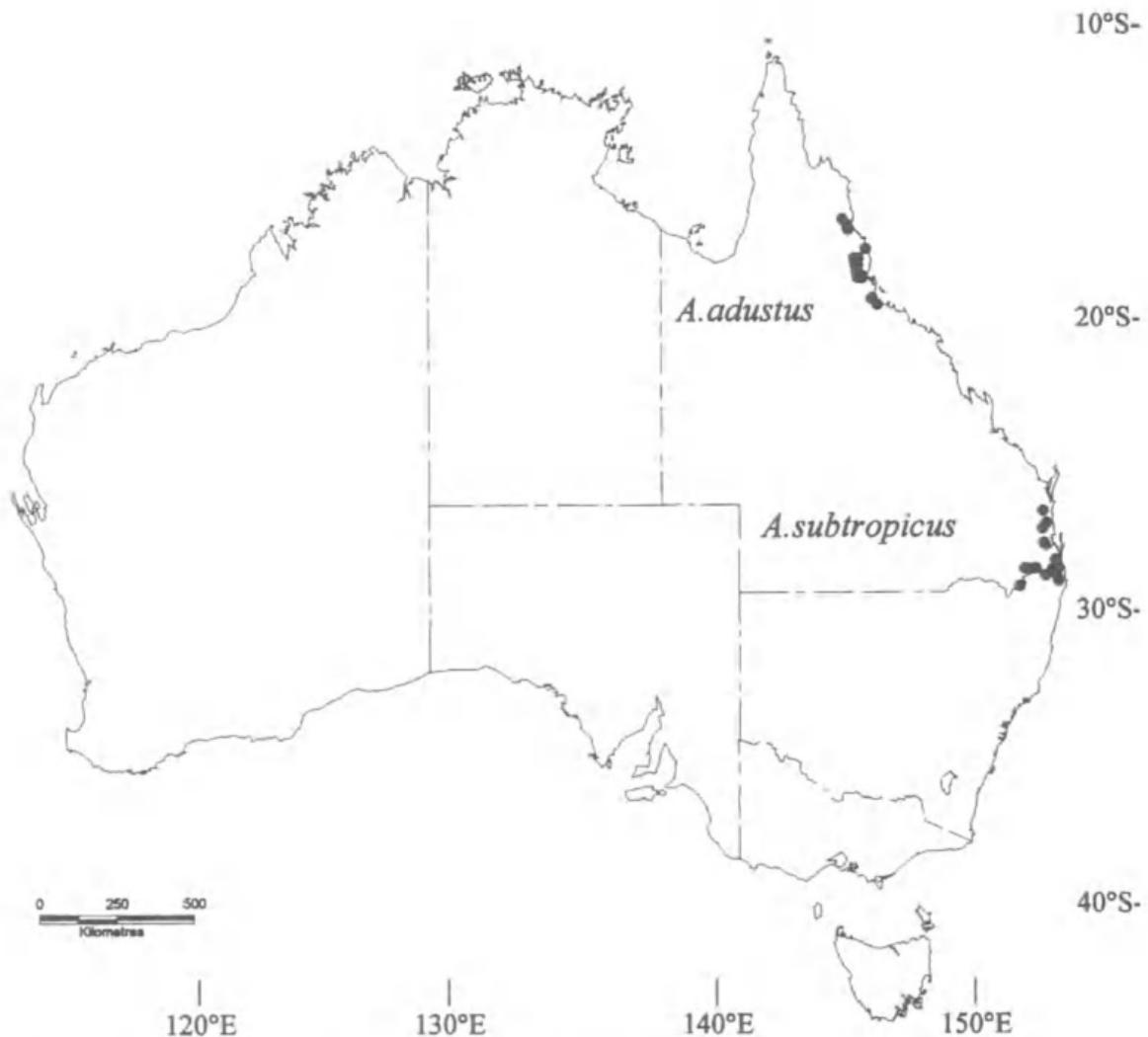


FIG. 6. Distribution of *Antechinus subtropicus* and *A. adustus*.

the horizontal from the paraconid to the paracristid fissure and 45° from the paracristid fissure to the protoconid. The metacristid is roughly oblique to the long axis of the dentary while the hypocristid is oblique. The cristid obliqua is long and extends from the hypoconid to the posterior wall of the trigonid, intersecting the trigonid at a point slightly lingual to that point directly below the tip of the protoconid. The hypocristid terminates midway between the hypoconid and the metastylid. The entoconid is very low. From the base of the metaconid posteriorly, the talonid endoloph follows the line of the dentary until the base of the hypoconulid.

In M_2 , the trigonid is slightly narrower than the talonid. The anterior cingulum is poorly developed, originating lingually in a weak parastylid notch into which the hypoconulid of M_1 is tucked. There is no buccal cingulum. A

strong, broad, posterior cingulum extends from the hypoconulid to the posterior base of the hypoconid. The paraconid is well developed and is the smallest trigonid cusp. A well developed, but narrow entoconid is present. The cristid obliqua extends from the hypoconulid to the posterior wall of the trigonid intersecting the trigonid at a point directly below the tip of the protoconid but well buccal to the metacristid fissure. The hypocristid extends from the hypoconulid to the tip of the hypoconid. From the base of the metaconid posteriorly, the endoloph follows the line of the dentary axis.

In M_3 , the trigonid is as wide as the talonid. A prominent parastylid wraps around the hypoconulid of M_2 and there is a strong anterior cingulum on M_3 . The posterior cingulum is as in M_2 but more poorly developed. The reduced cristid obliqua intersects the trigonid at a point

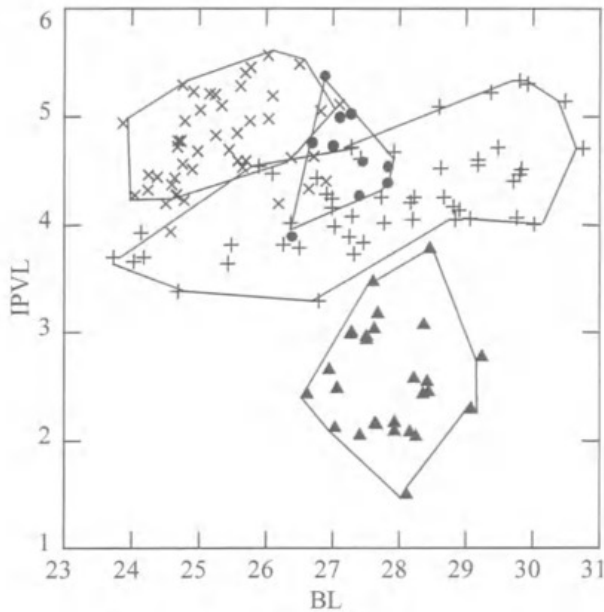


FIG. 7. Bivariate plot of inter-palatal vacuity distance (IPVL) (mm) against basicranial skull length (BL) (mm) for male *Antechinus subtropicus* (▲), *A. adustus* (●), *A. stuartii* (+) and *A. agilis* (×).

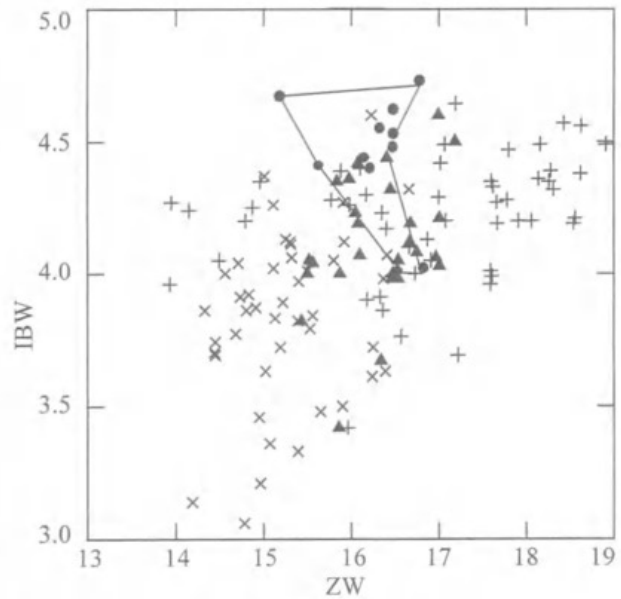


FIG. 8. Bivariate plot of interbulba width (IBW) (mm) against zygomatic width (ZW) (mm) for male *Antechinus subtropicus* (▲), *A. adustus* (●), *A. stuartii* (+) and *A. agilis* (×).

well lingual to the longitudinal vertical mid-line drawn through the tip of the protoconid, but slightly buccal to the metacristid fissure. The entoconid on M_3 is small. The endoloph on the talonid of M_3 follows the line of the dentary axis. The rest of M_3 morphology is as in M_2 .

In M_4 , the trigonid is wider than the talonid. The anterior cingulum is as in M_2 but more poorly developed. The posterior cingulum is absent. Of the three main trigonid cusps, the metaconid is slightly taller than the paraconid but both are dwarfed by the protoconid. The hypoconid of the M_4 talonid is the only cusp. Between the hypoconid and the base of metacristid, the cristid obliqua forms a low, weak crest, which contacts the trigonid wall just lingual to the metacristid fissure. A significant feature of the M_4 morphology is the reduction of talonid crown enamel below the cristid obliqua, which results in the talonid appearing (in occlusal view) as a narrow oblique spur jutting off the trigonid wall.

Skull. (Fig. 5). The rostrum is slightly grooved longitudinally by a depression running along the nasal sutures. There is no concavity at the nasal-frontal sutures. The left and right alisphenoid tympanic bullae are moderately widely separated and only moderately enlarged. The foramen pseudovale is large and not bisected by a bridge of the alisphenoid. The eustachian canal opening is moderately large. The internal jugular canal

foramina are large, the canals are raised and prominent. The posterior lacerate foramina are large and exposed, as are the entocarotid foramina. The premaxillary vacuity extends from the level of the I^2 root back to the level of the posterior edge of the C^1 root. The small maxillary vacuities extend from the level of the posterior root of P^3 back to the level of the metacone root of M^3 . There are no palatine vacuities.

HABITAT AND DISTRIBUTION (Fig. 6). This small species is restricted to dense tropical vine-forests (mostly complex mesophyll on basalt) from Paluma 19°00'S, 146°12'E (60km north of Townsville) to Mount Spurgeon 16°26'S, 145°12'E (near Mossman), a geographically isolated distribution with a north-south range of approximately 300km. It does not inhabit lowland vine-forest and is found only in very wet and cloudy uplands, at altitudes above approximately 800m, in areas that receive highly seasonal rainfall of up to 1500mm annually. This species appears to have similar habitat preferences to *A. subtropicus* and has been trapped most frequently along perimeter vegetation in entanglements of ferns and wild raspberry and around recently fallen and decaying logs. Around Ravenshoe it occurs sympatrically with *A. godmani* and *A. f. rubeculus* (see Van Dyck, 1982a).

TABLE 2. Univariate summary statistics for cranial, dental and external characters of *Antechinus subtypicus*. Abbreviations as in Fig. 1.

Variable	n	Mean	s.d.	Min.	Max.	CV
<i>A. subtypicus</i> males						
BL	28	27.87	0.63	26.62	29.24	2.27
ZW	27	16.31	0.51	15.43	17.19	3.15
IOW	28	7.15	0.20	6.86	5.27	2.84
SWR-LC ¹ B	28	4.74	0.23	4.19	5.83	4.87
SWR-LC ¹ A	28	5.23	0.22	4.89	13.26	4.16
SWR-LM ³	28	12.39	0.51	11.09	13.26	4.15
DL	28	21.88	0.64	20.66	22.97	2.93
C ¹ M ⁴	28	11.13	0.32	10.42	11.74	2.90
APVL	28	3.66	0.64	2.6	4.78	17.40
PPVL	28	6.09	0.44	5.41	7.13	7.23
IPVL	27	2.57	0.51	1.5	3.78	19.90
IBW	28	4.13	0.25	3.42	4.6	6.06
OBW	27	10.88	0.44	9.83	11.78	4.00
PL	28	15.03	0.39	14.22	15.76	2.63
P ¹⁻³	28	3.57	0.24	3.14	4.02	6.60
P ¹⁻²	27	2.46	0.15	2.23	2.82	6.00
M ¹⁻³	27	5.98	0.26	5.43	6.5	4.39
M ₁₋₄	19	7.30	0.29	6.74	7.83	3.97
SCD	28	5.86	0.56	5.01	6.9	9.63
HT	27	9.82	0.46	8.87	10.92	4.65
HB	115	116.59	0.63	102	136	5.80
TV	114	96.54	0.54	84	106	6.00
WT	11	60	5.30	52	67	
<i>A. subtypicus</i> females						
BL	16	26.37	1.19	23.85	24.31	4.52
ZW	16	15.50	0.71	13.66	14.43	4.58
IOW	16	7.12	0.25	6.74	6.74	3.53
SWR-LC ¹ B	16	4.49	0.30	3.86	3.86	6.67
SWR-LC ¹ A	16	5.03	0.33	4.33	4.33	6.60
SWR-LM ³	16	11.78	0.48	10.66	10.66	4.10
DL	16	20.79	0.87	18.9	19.44	4.18
C ¹ M ⁴	16	10.76	0.26	10.11	10.11	2.42
APVL	16	3.39	0.64	2.26	2.26	19.03
PPVL	16	5.68	0.46	5.05	5.05	8.19
IPVL	16	2.64	0.40	1.89	1.89	15.00
IBW	16	4.11	0.37	3.37	3.37	8.90
OBW	16	10.39	0.54	9.2	9.2	5.22
PL	16	13.49	2.59	4.32	4.32	19.17
P ¹⁻³	16	3.33	0.24	2.75	2.75	7.12
P ¹⁻²	16	2.33	0.17	2.03	2.03	7.49
M ¹⁻³	16	5.80	0.26	5.3	5.3	4.56
M ₁₋₄	8	7.21	0.24	6.78	6.84	3.27
SCD	16	5.45	0.54	4.44	4.44	9.90
HT	15	9.30	0.57	8.43	8.6	6.16
HB	32	102.19	1.02	94	112	5.60
TV	32	88.47	0.91	64	100	5.80
WT	6	28	2.44	24	32	

TABLE 3. Univariate summary statistics for cranial, dental and external characters of *Antechinus adustus*. Abbreviations as in Fig. 1.

Variable	n	Mean	s.d.	Min.	Max.	CV
<i>A. adustus</i> males						
BL	10	27.20	0.47	26.4	27.84	1.71
ZW	11	16.28	0.49	15.19	16.83	3.00
IOW	11	7.09	0.22	6.76	7.58	3.15
SWR-LC ¹ B	10	4.87	0.17	4.55	5.08	3.51
SWR-LC ¹ A	11	5.39	0.22	5.02	5.75	4.03
SWR-LM ³	11	12.67	0.48	11.99	13.54	3.79
DL	11	21.06	0.42	20.08	21.7	2.00
C ¹ M ⁴	11	10.65	0.21	10.38	11.06	1.99
APVL	10	2.67	0.19	2.42	2.99	7.02
PPVL	11	4.74	0.56	3.25	5.27	11.91
IPVL	10	4.66	0.42	3.89	5.37	9.04
IBW	11	4.44	0.24	4.01	4.73	5.30
OBW	11	10.94	0.43	10.34	11.67	3.91
PL	10	14.69	0.27	14.13	15	1.86
P ¹⁻³	11	3.34	0.14	3.12	3.58	4.20
P ¹⁻²	11	2.26	0.12	2.06	2.42	5.44
M ¹⁻³	11	5.82	0.07	5.72	5.95	1.27
M ₁₋₄	11	7.11	0.19	6.74	7.34	2.60
SCD	10	5.43	0.30	4.91	5.92	5.54
HT	10	9.39	0.41	8.65	9.93	4.42
HB	9	101.67	8.72	94.00	119.00	7.90
TV	9	98.33	3.77	91.00	103.00	3.80
WT	15	33.4	3.31	30	42	10
<i>A. adustus</i> females						
BL	11	25.84	0.59	25.24	26.94	2.30
ZW	10	15.23	0.44	14.64	16.12	2.91
IOW	11	6.89	0.10	6.74	7.05	1.47
SWR-LC ¹ B	11	4.51	0.26	4.06	4.9	5.84
SWR-LC ¹ A	11	5.12	0.24	4.66	5.43	4.71
SWR-LM ³	11	11.53	0.49	10.68	12.16	4.25
DL	11	19.98	0.48	19.34	20.84	2.38
C ¹ M ⁴	11	10.43	0.24	10.1	10.83	2.31
APVL	11	2.52	0.28	2.17	3.13	11.24
PPVL	10	4.73	0.46	4.14	5.45	9.80
IPVL	11	4.62	0.43	3.93	5.08	9.35
IBW	11	4.41	0.33	3.83	4.95	7.38
OBW	11	10.61	0.42	10.15	11.32	4.00
PL	10	14.19	0.26	13.74	14.61	1.85
P ¹⁻³	11	3.36	0.20	2.95	3.68	6.07
P ¹⁻²	11	2.32	0.15	2.08	2.61	6.66
M ¹⁻³	11	5.72	0.17	5.31	5.96	2.90
M ₁₋₄	11	7.02	0.22	6.66	7.41	3.08
SCD	11	5.13	0.37	4.67	5.74	7.16
HT	11	9.24	0.48	8.33	9.96	5.18
HB	10	93.00	3.05	89.00	100.00	3.30
TV	10	90.10	1.07	89.00	93.00	1.50
WT	15	24.07	3.86	21.00	34.00	16.11

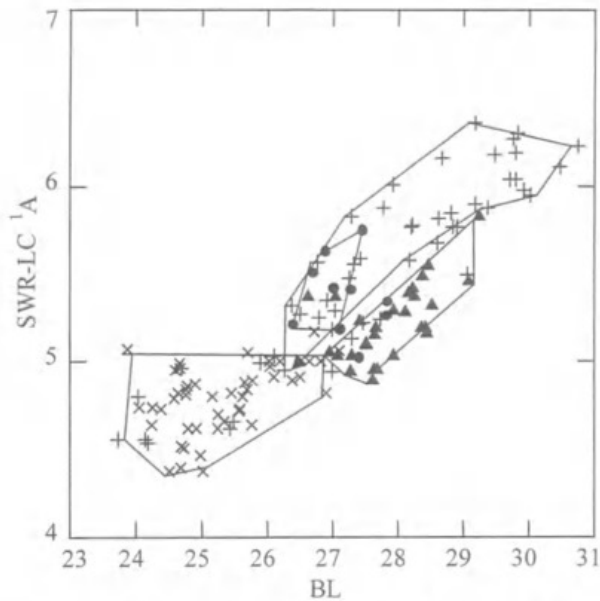


FIG. 9. Bivariate plot of skull width across C^1-C^1 (SWR-LC¹A) (mm) against basicranial skull length (BL) (mm) for male *Antechinus subtropicus* (▲), *A. adustus* (●), *A. stuartii* (+) and *A. agilis* (×).

REPRODUCTION. Van Dyck (1982a) reported that several specimens (e.g., QM JM1907, 1908, 1911) collected near Maalan (17°37'S 145°40'E) on 2 August 1976 had well-developed pouch areas. One of these females (QM JM1908) gave birth to six young on 4 August 1976. From this information, Van Dyck (1982a) suggested that this species probably mates early in July and gives birth early in August. Of thirteen males collected live between 30 June 1976 and 18 July 1976, none survived captivity beyond 29 July 1976 (SVD pers. obs.). Preliminary post-mortem examinations revealed gastric and duodenal haemorrhages, hepatic necrosis, degeneration in proximal tubules of kidneys, and anaemia. Van Dyck (1982a) concluded that male *A. adustus* experience a yearly die-off similar to that described for *A. stuartii* but which probably takes place at the end of July each year. Watt (1997) concluded that mating in *A. adustus* took place from late June to late July. Pouch young were first observed in early August, were carried in the pouch for four to five weeks and suckled until the end of November. All males in the population had died by the first week of August. If *A. adustus* breeds at specific rates of change of photoperiod like those observed in *A. stuartii* and *A. agilis* (McAllan & Dickman, 1986; Dickman et al., 1988), then it is responding to a rate of change as little as 20s day⁻¹.

TABLE 4. F-test values after One-way ANOVA for the four species. See text for results of comparisons after Tukey's *Post Hoc* test. Abbreviations as in Fig. 1.

Variable	Male			Female		
	F	d.f.	P	F	d.f.	P
BL	38.68	3/131	<0.001	22.35	3/95	<0.001
ZW	24.189	3/132	<0.001	10.213	3/93	<0.001
IOW	44.003	3/134	<0.001	19.065	3/96	<0.001
SWR-LC ¹ B	28.547	3/133	<0.001	11.207	3/97	<0.001
SWR-LC ¹ A	31.263	3/133	<0.001	12.964	3/95	<0.001
SWR-LM ³	7.966	3/134	<0.001	4.816	3/94	0.004
DL	33.993	3/133	<0.001	19.278	3/95	<0.001
C ¹ M ⁴	36.404	3/134	<0.001	19.718	3/97	<0.001
APV	51.135	3/131	<0.001	21.696	3/95	<0.001
PPV	95.15	3/133	<0.001	45.906	3/94	<0.001
IPVL	139.056	3/131	<0.001	62.736	3/95	<0.001
IBW	22.048	3/132	<0.001	8.895	3/93	<0.001
OBW	28.352	3/131	<0.001	40.292	3/93	<0.001
PL	27.716	3/132	<0.001	5.472	3/93	0.002
P ¹⁻³	19.411	3/133	<0.001	9.183	3/94	<0.001
P ¹⁻²	16.232	3/132	<0.001	12.832	3/94	<0.001
M ¹⁻³	26.108	3/124	<0.001	19.255	3/92	<0.001
M ₁₋₄	12.467	3/115	<0.001	14.798	3/81	<0.001
SCD	15.87	3/131	<0.001	6.655	3/93	<0.001
HT	19.531	3/130	<0.001	12.448	3/92	<0.001

Nipple Number. Of 10 specimens examined from three collecting localities, all pouches contained six teats. This is consistent with the findings of Cockburn et al. (1983) and Watt (1997).

REMARKS. Several authors (Wakefield & Warneke, 1967; Van Dyck, 1997) synonymised two previously described taxa *Phascogale unicolor* Gould (1854) and *A. flavipes burrelli* (Le Souef & Burrell, 1926) with *A. stuartii*. Thomas (1924) noted the similarity between *A. unicolor* and *A. adustus* and assigned them to the same species. We concur that neither *unicolor* or *flavipes burrelli* are *A. subtropicus* or *A. adustus*. From comparisons of zygomatic breadths, *A. unicolor* appears too large to be *A. adustus* and too broad to be *A. subtropicus* (ZW = 15.67mm). The colour of *A. flavipes burrelli* and *A. unicolor* appears to be too light to be *A. adustus*. No location was given for *A. unicolor* (Gould 1854 said only 'by way of Sydney') but the location for *A. burrelli* is the Guy Fawkes region of New South Wales. No animals showing the characteristics of *A. subtropicus* or *A. adustus* are known at that location.

COMPARISONS WITH OTHER TAXA

A plot of scores for individuals on the three canonical-variate axes based on cranial measurements shows a broad separation of each species for each sex (Fig. 10). The first three canonical-variate axes accounted for all the variation. The classification function generated from linear discriminant-function analysis of the same data enabled allocation of most individuals to correct species for both sexes. One male *A. adustus* was misclassified as *A. stuartii* and one female *A. stuartii* and one female *A. agilis* were misclassified as each other (Table 6).

Antechinus subtropicus separated from all the other taxa on the first canonical-variate axis. Standardised coefficients on the first canonical-variate axis (Table 5) suggests that the characters contributing to species separation are a contrast between BL, C¹M⁴ with ZW, IPVL and SWR-LM³.

Antechinus adustus separated from the other taxa on the third canonical-variate axis. Standardised coefficients on the third canonical-variate axis suggests that the characters contributing to species separation are a contrast between BL, IBW, SWR-LC¹A and SWR-LM³ with ZW, DL and PPVL (Table 5).

COMPARISON BETWEEN *A. SUBTROPICUS* AND *A. ADUSTUS*.

External Characters. Males of *Antechinus subtropicus* are the largest of the *A. stuartii* complex yet described. Braithwaite (1973) recorded the mean weight of *A. subtropicus* caught in September from 1963-1966 as 60g for males (n = 11, range = 52-67) and 28g for females (n = 6, range = 24-32). One male individual collected from Tallebudgera Creek, West Burleigh (J20265) weighed 72g. Collections made by A.B. Rose (pers. comm.) from Border Ranges National Park (NE NSW) in July 1977 had a mean for males of 57g (n = 12, range = 48-68) and a mean for females of 32g (n = 5, range = 22-54).

Antechinus adustus is much smaller than *A. subtropicus*. Males have a mean weight of 33g (n = 15, range = 30-42) and females a mean of 24g (n = 15, range = 21-34). Watt (1997) recorded the average weight of male *A. adustus* from three locations (Mt Spec, Koolmoon Creek and Mt Father Clancy) as 33g (n = 51, range = 23-41) and female *A. adustus* as 28g (n = 63, range = 19-38).

Antechinus subtropicus is much longer than *A. adustus*. The mean male head-body length of *A. subtropicus* from southeastern Qld is 117mm (n =

115, range = 102-136) whereas the mean for *A. adustus* is 98mm (n = 9, range = 91-103) (Van Dyck, 1982a). Braithwaite (1973) recorded an average head-body length of males in September from Mt Glorious as 127mm (n = 8, range = 120-131) and A. B. Rose recorded an average head-body length for males from Border Ranges National Park as 120mm (n = 12, range = 113-130). The mean female head-body length for female *A. subtropicus* from southeastern Qld is 102mm (n = 32, range = 64-100) as opposed to female *A. adustus* which is 90mm (n = 10, range = 89-93) (Van Dyck, 1982a). Braithwaite recorded an average head-body length for first-year females from Mt Glorious as 94mm (n = 6, range = 91-112) and for second-year females as 109mm (n = 5, range = 102-117); and A.B. Rose (pers. comm.) for Border Ranges National Park females as 102mm (n = 5, range = 92-120).

The tails of *A. adustus* are relatively longer than those of *A. subtropicus*. The tails of male *A. adustus* average around 0.89 of the head-body length while the tails of females average around 0.96 of the head-body length (Van Dyck, 1982a). The tails of male *A. subtropicus* average around 0.78 of the head-body length while the tails of females average around 0.87 of the head-body length (Van Dyck, 1982a).

Based on study skins and extensive field observations, fur of *A. adustus* is a much darker brown than that of *A. subtropicus*.

Cranial and Dental Characters. *Antechinus adustus* tends to be much smaller than *A. subtropicus* as reflected by the smaller BL and ZW (Tables 2-4, Figs 7, 8). *Antechinus adustus* has both relatively and absolutely smaller anterior and posterior palatal vacuities and a correspondingly larger inter-palatal vacuity distance (Fig. 7, Tables 2, 4; $P < 0.001$) than *A. subtropicus*. The larger IBW of *A. adustus* reflects its relatively smaller alisphenoid tympanic wings (Fig. 8, Tables 2, 3, 4; $P = 0.003$ for males). The rostrum of *A. adustus* also tends to be relatively wider as indicated by the relatively greater SWR-LC¹A (Fig. 9). Entoconids are well developed on M₃ in both *A. adustus* and *A. subtropicus* but they are much more enlarged in *A. subtropicus* (see Van Dyck 1982a, fig. 21).

The incisors of *A. adustus* are much more specialised than the incisors of *A. subtropicus*. I¹ in particular of *A. adustus* is much more massively crowned and procumbent than I¹ in *A. subtropicus*. I²⁻⁴ are also more massive in *A.*

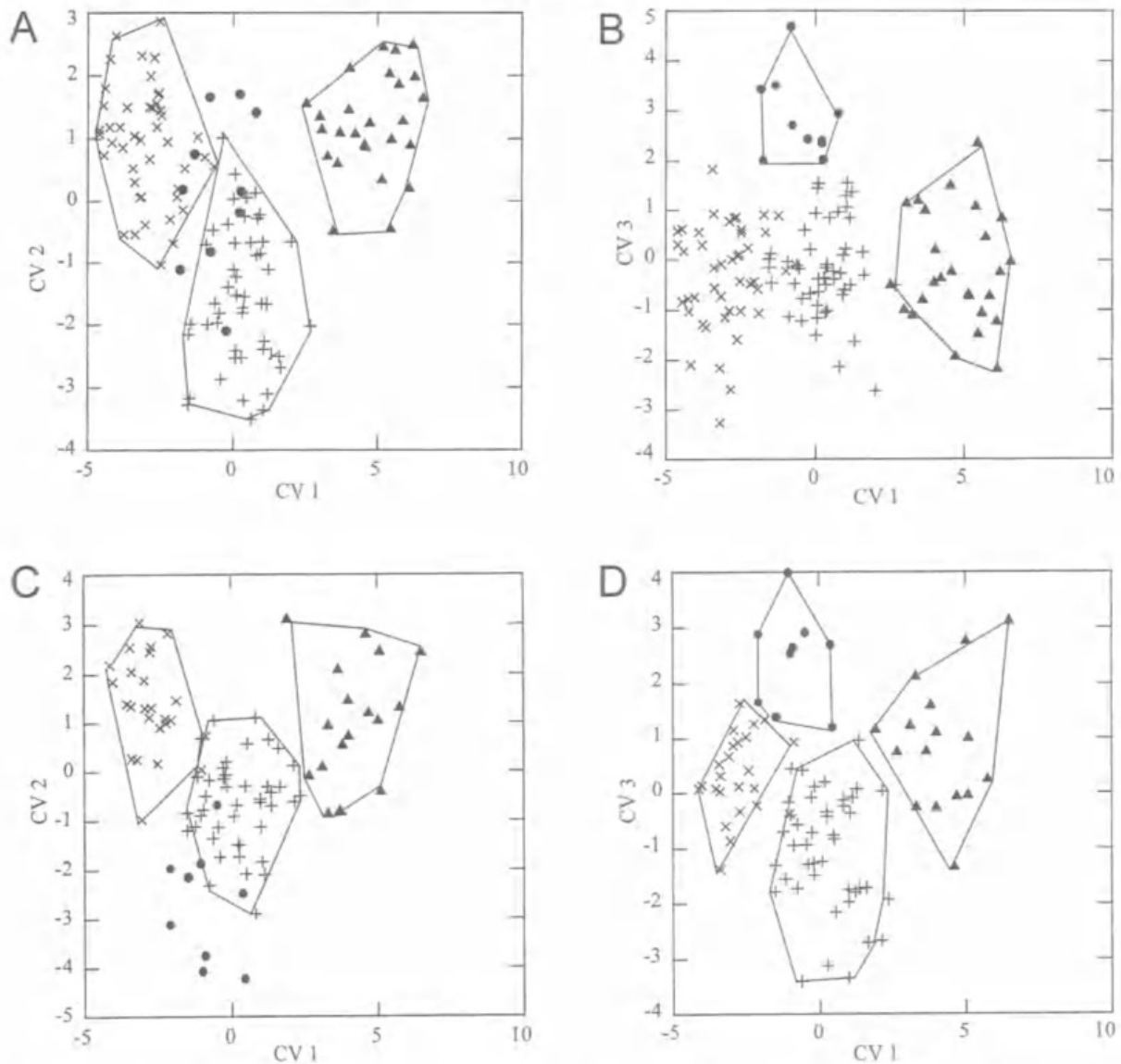


FIG. 10. Plot of canonical-variate (CV) scores for first three CV axes based on 18 cranial and dental measurements for: (A), (B) male *Antechinus* and (C), (D) female *Antechinus*. *Antechinus subtropicus* (▲), *A. adustus* (●), *A. stuartii* (+) and *A. agilis* (×).

adustus than the spatulate incisors of *A. subtropicus*. I^2 and I^3 are also higher crowned in *A. adustus*.

The prominent postero-lingual lobes on P^{1-3} of *A. adustus*, which cause the premolars to appear more rounded, are accentuated in comparison with *A. subtropicus*.

COMPARISONS OF *A. ADUSTUS* AND *A. SUBTROPICUS* WITH *A. STUARTII*.

MATERIAL of *A. stuartii*. Barrington Tops (AM M32936-32949); Jervis Bay (AM M32831-32887); Kioloa (AM M32889, 32891, 32905); Kangaroo Valley (AM M22623); Myall Lakes (AM M3173-3176, 3178,

3179, 3181-3184, 3186, 12591-12593, 12595, 12596); Waterfall (AM M5294).

External Characters. *Antechinus stuartii* is generally smaller than *A. subtropicus*, although the southern-most populations approach *A. subtropicus* in weight. The mean weights of various *A. stuartii* populations are Jervis Bay males 51g ($n = 33$, range = 32-70), Jervis Bay females 26g ($n = 25$, range = 20-33); Ku-ring-gai Chase National Park males 47g ($n = 14$, range = 38-59), Ku-ring-gai Chase National Park females 27g ($n = 14$, range = 22-37); Myall Lakes males 27g ($n = 10$, range = 18-43) and Barrington Tops males 29g ($n = 34$, range = 20-38), Barrington

TABLE 5. Standardised canonical coefficients for each character for canonical-variate analysis of skull and dental measures of *Antechinus*. Abbreviations as in Fig. 1.

Variable	Male			Female		
	1	2	3	1	2	3
BL	0.601	1.637	1.602	0.379	0.072	2.283
ZW	-0.271	-0.330	-0.968	-0.655	1.259	-0.566
IOW	0.356	-0.346	0.206	0.408	-0.21	0.281
SWR-LC ¹ A	0.110	-1.032	0.581	-0.013	-0.738	-0.083
SWR-LM ³	-0.371	0.124	0.147	-0.093	-0.014	0.179
DL	-0.041	-0.629	-1.39	0.209	0.081	-0.897
C ¹ M ⁴	0.405	0.363	0.088	0.574	0.398	-0.669
APVL	0.132	0.023	-0.174	0.188	0.018	-0.139
PPVL	0.058	-0.704	-0.266	-0.09	-0.313	-1.027
IPVL	-0.942	-0.414	0.090	-0.865	-0.605	-0.339
IBW	0.074	-0.250	0.334	0.032	-0.223	0.509
OBW	0.332	0.239	0.643	0.419	-0.873	0.216
P ¹⁻³	-0.287	-0.046	-0.102	-0.422	-0.162	0.023
P ¹⁻²	-0.075	-0.178	-0.536	0.187	-0.289	-0.057
Eigenvalue	7.956	1.549	0.701	5.358	1.714	1.310
Variance (%)	77.95	15.17	6.87	63.92	20.45	15.63

Tops females 21g ($n = 30$, range = 15–28). There appears to be clinal variation within *A. stuartii*, with larger animals in the south and smaller in the north (MSC, pers. obs.).

Antechinus stuartii tends to be smaller in head-body-length than *A. subtropicus*. The mean head-body lengths of various *A. stuartii* populations are Jervis Bay males 117mm ($n = 33$, range = 99–126); Jervis Bay females 98mm ($n = 25$, range = 93–105); Ku-ring-gai Chase National Park males 120mm ($n = 13$, range = 108–140); Ku-ring-gai Chase National Park females 94mm ($n = 15$, range = 85–105); Myall Lakes males 100mm ($n = 8$, range = 85–118), and Barrington Tops males 101mm ($n = 32$, range = 84–120), Barrington Tops females 92mm ($n = 30$, range = 75–108).

The tails of *A. stuartii* appear to be relatively longer than the tails of *A. subtropicus*. The tails of males from Jervis Bay average 0.97, Ku-ring-gai Chase National Park 0.80, Myall Lakes 0.83 and Barrington Tops 0.89 of head-body length. The tails of females from Jervis Bay average 1.00, Ku-ring-gai Chase National Park 0.93 and Barrington Tops 0.87 of head-body length.

Cranial and Dental Characters. The skull length of *A. stuartii* tends to be shorter than in *A. subtropicus* as reflected by the smaller BL. The skull also tends to be more brachycephalic with a

TABLE 6. Classification results from discriminant-function analysis based on 16 cranial and dental measurements for individual *Antechinus*, showing percentage and number (in parentheses) of individuals allocated to groups by species males and females.

Males					
	n	<i>A. subtropicus</i>	<i>A. adustus</i>	<i>A. stuartii</i>	<i>A. agilis</i>
<i>A. subtropicus</i>	26	100 (27)	0	0	0
<i>A. adustus</i>	10	0	100 (10)	0	0
<i>A. stuartii</i>	48	0	2 (1)	98 (48)	0
<i>A. agilis</i>	45	0	0	2 (1)	98 (44)
Females					
	n	<i>A. subtropicus</i>	<i>A. adustus</i>	<i>A. stuartii</i>	<i>A. agilis</i>
<i>A. subtropicus</i>	16	100 (16)	0	0	0
<i>A. adustus</i>	9	0	100 (9)	0	0
<i>A. stuartii</i>	43	0	0	98 (42)	2 (1)
<i>A. agilis</i>	25	0	0	4 (1)	96 (24)

broader rostrum in *A. stuartii* as reflected by the absolutely and relatively greater ZW (Fig. 8, Tables 2, 4; $P = 0.021$ for males) and SWR-LC¹A (Fig. 9, Tables 2, 4; $P = 0.005$ for males). The palatal vacuities in *A. stuartii* also tend to be relatively shorter as reflected by the relatively shorter APVL (Table 2; $P < 0.001$) and PPVL (Table 2, $P = 0.043$ for males) and the corresponding longer IPVL (Tables 2, 4, Fig. 7; $P < 0.001$).

The incisors of *A. adustus* are much more specialised than the incisors of *A. stuartii*. I¹ of *A. adustus* is much more massively crowned and procumbent than I¹ in *A. stuartii*. I²⁻⁴ are also more massive in *A. adustus* than the spatulate incisors of *A. stuartii*. I² and I³ are also higher crowned in *A. adustus*. The prominent postero-lingual lobes on P¹⁻³ of *A. adustus*, which cause the premolars to appear more rounded, are accentuated in comparison with *A. stuartii*. The alisphenoid tympanic bullae tend to be larger in *A. stuartii* compared to *A. adustus* as reflected by the smaller IBW (Tables 3, 4, Fig. 8; $P = 0.037$ for females).

COMPARISONS OF *A. ADUSTUS* AND *A. SUBTROPICUS* WITH *A. AGILIS*.

MATERIAL of *A. agilis*. Bega (AM M33046, 33048, 33050–33068, 33073–33078); Bodalla (AM M32912); Brindabella Ranges (AM M32913–32916, 32918–32920, 32888, 33011, 33015–33017, 33029–33033, 33036–33038, 33157–33159, 33319, 33342, 33343); Gundaroo (AM M33160, 33161); Kioloa (AM M32890, 32892–32911); Mt Canobolas (AM M33344).

External Characters. *Antechinus agilis* is much smaller and lighter than *A. subtropicus*. The mean weights of various *A. agilis* populations are Loch Valley males 30g (n = 29, range = 16-41), Loch Valley females 21g (n = 5, range = 17-26); Mitta Mitta males 26g (n = 21, range = 16-36), Mitta Mitta females 19g (n = 31, range = 14-26) and Brindabella Range males 26g (n = 24, range = 17-35), Brindabella Range females 18g (n = 14, range = 14-26).

Antechinus agilis has a much smaller head-body length than *A. subtropicus*. The mean head-body lengths of various *A. agilis* populations are Loch Valley males 95mm (n = 58, range = 77-107), Loch Valley females 85mm (n = 13, range = 76-93) (Wakefield & Warneke 1967); Mitta Mitta males 104mm (n = 21, range = 85-124), Mitta Mitta females 98mm (n = 29, range = 85-115); Bega males 96mm (n = 13, range = 89-102), Bega females 87mm (n = 15, range = 82-95) and Brindabella Range males 100mm (n = 26, range = 89-110), Brindabella Range females 89mm (n = 13, range = 70-100).

Antechinus agilis generally has a relatively longer tail than *A. subtropicus* but the proportion is similar to that found in *A. adustus*. The tails of males from Loch Valley average 1.03 (Wakefield & Warneke, 1967), Mitta Mitta 0.77, Bega 0.99 and Brindabella Range 0.9 of head-body length. The tails of females from Loch Valley average 1.03 (Wakefield & Warneke, 1967), Mitta Mitta 0.79, Bega 1.00 and Brindabella Range 0.9 of head-body length.

The fur colour of *A. agilis* tends to be a more greyish brown rather than the much darker brown of *A. adustus*. However, Wakefield & Warneke (1967) claim that dark specimens of *A. agilis* from high altitude areas of Victoria (e.g. Mt Macedon, Mt Arnold and Loch Valley) were hard to distinguish on pelage from *A. adustus*.

Cranial and Dental Characters. *Antechinus agilis* tends to be much smaller than *A. subtropicus* as reflected by the absolutely smaller BL (Fig. 7, Tables 2, 4; $P < 0.001$). The skull of *A. agilis* appears to be more brachycephalic than that of *A. subtropicus* as reflected by the relatively greater ZW (Fig. 8). *Antechinus agilis* has both relatively and absolutely smaller anterior and posterior palatal vacuities and a correspondingly larger IPVL (Fig. 7, Tables 2, 4; $P < 0.001$).

The incisors of *A. adustus* are much more specialised than the incisors of *A. agilis*. I^1 in particular of *A. adustus* is much more massively

crowned and procumbent than I^1 in *A. agilis*. I^{2-4} are also more massive in *A. adustus* than the spatulate incisors of *A. agilis*. I^2 and I^3 are also higher crowned in *A. adustus*. *Antechinus agilis* is smaller than *A. adustus* as reflected by the smaller basicranial length (Tables 3, 4; $P < 0.001$). *Antechinus agilis* has a relatively and absolutely narrower rostrum as reflected by the larger SWR-LC¹A (Fig. 9, Tables 3, 4; $P < 0.001$). The alisphenoid tympanic wings of *A. agilis* are relatively larger as reflected by the relatively and absolutely smaller IBW (Tables 3, 4, Fig. 8; $P < 0.001$).

COMPARISONS OF *A. ADUSTUS* AND *A. SUBTROPICUS* WITH *A. FLAVIPES*.

External Characters. *Antechinus flavipes* is much larger and heavier than *A. adustus* (Van Dyck, 1982a; Tables 3, 4).

Antechinus flavipes differs from both *A. subtropicus* and *A. adustus* in the colouration of its pelage. *Antechinus flavipes* is lighter in colour, possesses prominent buff fur surrounding the eyes and tannish patches of post-auricular fur, has dorsal fur with a prominent change in antero-posterior fur colour from grizzled greyish shoulders to a tannish rump and a black tail tip.

Cranial and Dental Characters. Most of the cranial and dental comparisons between *A. subtropicus* and *A. flavipes* are given in Van Dyck (1982a). In summary, *A. flavipes* has: a relatively and absolutely greater zygomatic width (Van Dyck, 1982a fig. 17, table 2); relatively and absolutely shorter anterior and posterior palatal vacuities with corresponding longer inter-palatal vacuity distance (Van Dyck, 1982a, figs 13, 14, 15, table 2); a wider rostrum (Van Dyck, 1982a, fig. 16, table 2); a narrower inter-orbital width (Van Dyck, 1982a, fig. 17, table 2); greater snout-canine depth (Van Dyck, 1982a, fig. 20, table 2); relatively shorter and wider premolars with corresponding shorter premolar row (Van Dyck, 1982a, figs 18, 25, table 2); narrower separation of transverse canal foramina (Van Dyck, 1982a, fig. 19, table 2); and absent to tiny entoconids (as opposed to large entoconids) and narrower talonids on M_3 (Van Dyck, 1982a, fig. 21).

Antechinus flavipes differs from *A. adustus* in larger basicranial length, relatively larger alisphenoid tympanic wings, more massive canines and much smaller entoconids on M_3 .

DISCUSSION

This study, and that by Dickman et al. (1998), shows that a reappraisal of interpopulation variation and taxonomic status of eastern Australian populations currently attributed to *A. stuartii* and *A. flavipes* is required.

Since *A. adustus* is geographically isolated from the rest of the *A. stuartii* complex, it would be difficult to grant it species status on isozymes or morphology alone. It differs from both *A. stuartii* and *A. agilis* at 15% of loci (Baverstock et al., 1982; Dickman et al., 1998), which is higher than the isozyme differentiation of *A. stuartii* and *A. agilis* (see Dickman et al., 1988) and almost as high as the isozyme differentiation of *A. stuartii* from *A. flavipes* (see Baverstock et al., 1982). This work and Van Dyck (1982a) demonstrate the marked morphological distinctiveness between *A. adustus* and the other members of the *A. stuartii* complex, confirming its species status. It is surprising that *A. adustus* is morphologically closer to *A. stuartii* and *A. agilis* than it is to the geographically closest member of the complex, *A. subtropicus*. Watt (1997) found that *A. adustus* is much more similar in ecology to *A. stuartii* and *A. agilis* than it is to *A. subtropicus*, which could explain the morphological similarity.

Sumner & Dickman (1998) found some electrophoretic differences between *A. subtropicus* populations from Mt Glorious and NSW *A. stuartii*. The lack of fixed differences could be caused by examination of an insufficient number of isozymes (*A. stuartii* and *A. agilis* only differ slightly electrophoretically) or the northern NSW sample of *A. stuartii* they examined actually consisted of both *A. stuartii* and *A. subtropicus* which would mask the differences between taxa. Reanalysis of the allozyme work of Sumner & Dickman (1998) is in progress and there are differences in allele frequencies between the species (Crowther & Sumner unpublished). Current work (Crowther, Elphinstone & Baverstock unpubl.) using the control region of mitochondrial DNA also is showing some genetic difference between *A. stuartii* and *A. subtropicus*. Morphological work in progress will indicate whether the species described in this paper correspond with the genetic forms (Crowther unpubl.).

The larger size of *A. subtropicus*, together with its relatively longer, narrower rostrum could be attributed to character release because of a lack of competition from *A. swainsonii* compared to that in *A. agilis* and *A. stuartii*. This has been

suggested by Crowther (1996). Competition has previously been demonstrated between *A. agilis* and *A. swainsonii* (see Dickman, 1986). The large and long rostrum of *A. swainsonii* is absent or very uncommon within the range of *A. subtropicus* (see Van Dyck & Ogilvie, 1977). This could imply that *A. subtropicus* consumes relatively more larger, softer, terrestrial prey than *A. stuartii* or *A. agilis*. The relatively longer tail of *A. agilis* may assist it in climbing trees (Dickman, 1983).

The small size, rounded premolars with shortened premolar row and broad rostrum of *A. adustus* could be the response to competition with the ecological equivalent of *A. swainsonii* in NE Qld, *A. godmani*. *Antechinus adustus* may have to consume more smaller, abrasive and arboreal prey than *A. godmani*. The large, procumbent incisors of *A. adustus* resemble those of the arboreal *Phascogale* and could imply convergence in feeding niche.

In *A. subtropicus*, the premaxillary vacuities extend posteriorly to a position midway between P₁ and P₂. Although Archer (1981) found that a direct correlation existed between the degree of aridity of habitat and length of palatal vacuities in *Sminthopsis* such that those species occupying arid climates have larger vacuities and vice versa; the opposite is true for species of *Antechinus*. In fact, *A. subtropicus* from the vine-forests of SE Qld and NE NSW has a greater proportion of palatal fenestration than most other dasyurids. The size of the palatal vacuities is of great use in diagnosing species of dasyurids, particularly *Antechinus* species (Van Dyck, 1982a; Dickman et al., 1998), and the extremely large palatal vacuities of *A. subtropicus* distinguish it from any other *Antechinus*.

Entoconid size on M₃ was claimed by Van Dyck (1982a) to be a good diagnostic feature separating *A. stuartii* from *A. flavipes*. Dickman et al. (1998) found that this was not the case and that it was often difficult to tell apart *A. stuartii*, *A. agilis* and *A. flavipes* using entoconids alone. The very large entoconids on the M₃ of *A. subtropicus* make it an extremely useful diagnostic character. Archer (1981) could suggest no reason for the difference in entoconid size between *Sminthopsis* species, except that more inland forms tended to have smaller entoconids than coastal forms. He found no clear relationship between the food consumed and the presence or absence of entoconids in dasyurids.

The small alisphenoid tympanic bullae found in *A. adustus* are possibly an adaptation to its dense vine forest habitat. Webster (1961, 1962) and Lay (1972) have produced evidence in rodents and Archer (1981) in *Sminthopsis*, that there is a direct correlation between bulla size and increasing aridity. Webster & Webster (1975) concluded that larger bullae in rodents enhance sensitivity to low frequency sounds such as produced by the attack flight of owls and the strike of snakes. *Antechinus adustus* does not need to forage far from cover and so may not require large bullae. *Antechinus flavipes* inhabits drier, more open country and may thus require larger alisphenoid tympanic bullae.

Extensive examination of specimens from the Queensland Museum shows that *A. subtropicus* is not the only member of the *A. stuartii* complex in southern Qld. Specimens from near Wallangarra 28°55'S 151°55'E (e.g. J7727-7729) and Pyramid Creek, Wyberba 28°50'S 151°57'E (e.g. J8088, J8089) can be currently allocated to *A. stuartii*. The habitat is dry sclerophyll woodland with abundant granite outcrops and bracken gullies as opposed to the subtropical rainforest habitat preferred by *A. subtropicus*. The specimens from these areas have reduced entoconids, smaller palatal vacuities and flaring of the jugals with expansion of the lachrymals which is more typical of *A. stuartii*. The pelage colour and patterning more resemble that of *A. flavipes* than *A. subtropicus*. Further biochemical and morphological work needs to be done on specimens from this area as well as in northern NSW. A complete study of variation within *A. stuartii* and *A. flavipes* has to be completed before any confidence can be placed on the identifications of these specimens. It is even possible that some specimens represent *A. unicolor*, despite synonymisation of this taxon with *A. stuartii* by Wakefield & Warneke (1967).

As stated in Dickman et al. (1998), resolution of species limits among Australian mammals has been neglected during the past four decades, and it is evident from this study, those of Dickman et al. (1988, 1998) and unpublished morphological and molecular by MSC, that *A. stuartii* and possibly *A. flavipes* consist of species-complexes. The results of these studies emphasise the critical importance of a sound taxonomic framework both to mammalian research generally and to conservation management in particular (Parnaby, 1991). An example of the former is geographical differences in nipple number (Cockburn et al., 1983), attributed previously to plasticity within

A. stuartii that now appear to be due in part to interspecific variation. Although '*A. stuartii*' is one of the most intensively studied small mammals in eastern Australia, much of the research in the past two decades will require reassessment in the light of taxonomic revision. At present, '*A. stuartii*' is considered one of the commonest and most widespread species of small mammals in eastern Australia and is not believed to be of conservation significance. This belief will require urgent reassessment and further taxonomic clarification of the group, as it appears that taxa currently included under '*A. stuartii*' comprise several species each with a concomitantly reduced geographic range. We recommend that relevant land-management and conservation agencies acknowledge the importance of studies of combined morphological and biochemical systematics to conservation management.

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