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Hiding in plain sight: two new species of diminutive marsupial (Dasyuridae: *Planigale*) from the Pilbara, Australia

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Abstract

Many of Australia's smaller marsupial species have been taxonomically described in just the past 50 years, and the Dasyuridae, a speciose family of carnivores, is known to harbour many cryptic taxa. Evidence from molecular studies is being increasingly utilised to help revise species boundaries and focus taxonomic efforts, and research over the past two decades has identified several undescribed genetic lineages within the dasyurid genus *Planigale*. Here, we describe two new species, *Planigale kendricki* sp. nov. (formerly known as '*Planigale* 1') and *P. tealei* sp. nov. (formerly known as '*Planigale* sp. Mt Tom Price'). The two new species have broadly overlapping distributions in the Pilbara region of Western Australia. The new species are genetically distinct from each other and from all other members of the genus, at both mitochondrial and nuclear loci, and morphologically, in both external and craniodental characters. The new species are found in regional sympatry within the Pilbara but occupy different habitat types at local scales. This work makes a start at resolving the cryptic diversity within *Planigale* at a time when small mammals are continuing to decline throughout Australia.

Key words. Arid species, Diversity, Endemism, Dasyuromorphia, Systematics, Taxonomy

Introduction

Some of the most speciose groups of mammals are insectivores (Burgin *et al.* 2018), and in Australia, approximately one quarter of all terrestrial mammal species belong to the family Dasyuridae — the carnivorous and insectivorous marsupials (AMTC 2021). Among these are the shrew-like *Planigale*, tiny insectivorous marsupials weighing 3–17 grams with species that occur in a wide range of habitats collectively across most of the continent (Baker & Dickman 2018). There are currently five recognised species of *Planigale*, including one from New Guinea, but evidence from molecular studies (Painter *et al.* 1995; Blacket *et al.* 1999; Westerman *et al.* 2016) suggests this is an underrepresentation of the true diversity within the genus. Mammal species in Australia have suffered greatly since European colonisation (Woinarski *et al.* 2015), with 100 species listed as threatened under the Environment Protection and Biodiversity Conservation Act 1999 (DoCCEEW 2022), 38 of which are considered to be extinct. Despite these alarming numbers, mammals continue to decline, including in regions previously thought to be relatively undisturbed, such as northern Australia (Woinarski *et al.* 2011; Cremona *et al.* 2022), so now is a crucial time to better document Australia's extant mammal fauna.

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None of the four Australian *Planigale* species are listed as threatened under federal legislation (DoCCEEW 2022), but the current conservation status does not account for highly diverse lineages found within the two most widespread species (Westerman *et al.* 2016). The Australian species include *Planigale gilesi* Aitken, 1972, *P. maculata* (Gould, 1851), *P. ingrami* (Thomas, 1906) and *P. tenuirostris* Troughton, 1928, collectively distributed throughout northern and eastern Australia (Fig. 1).

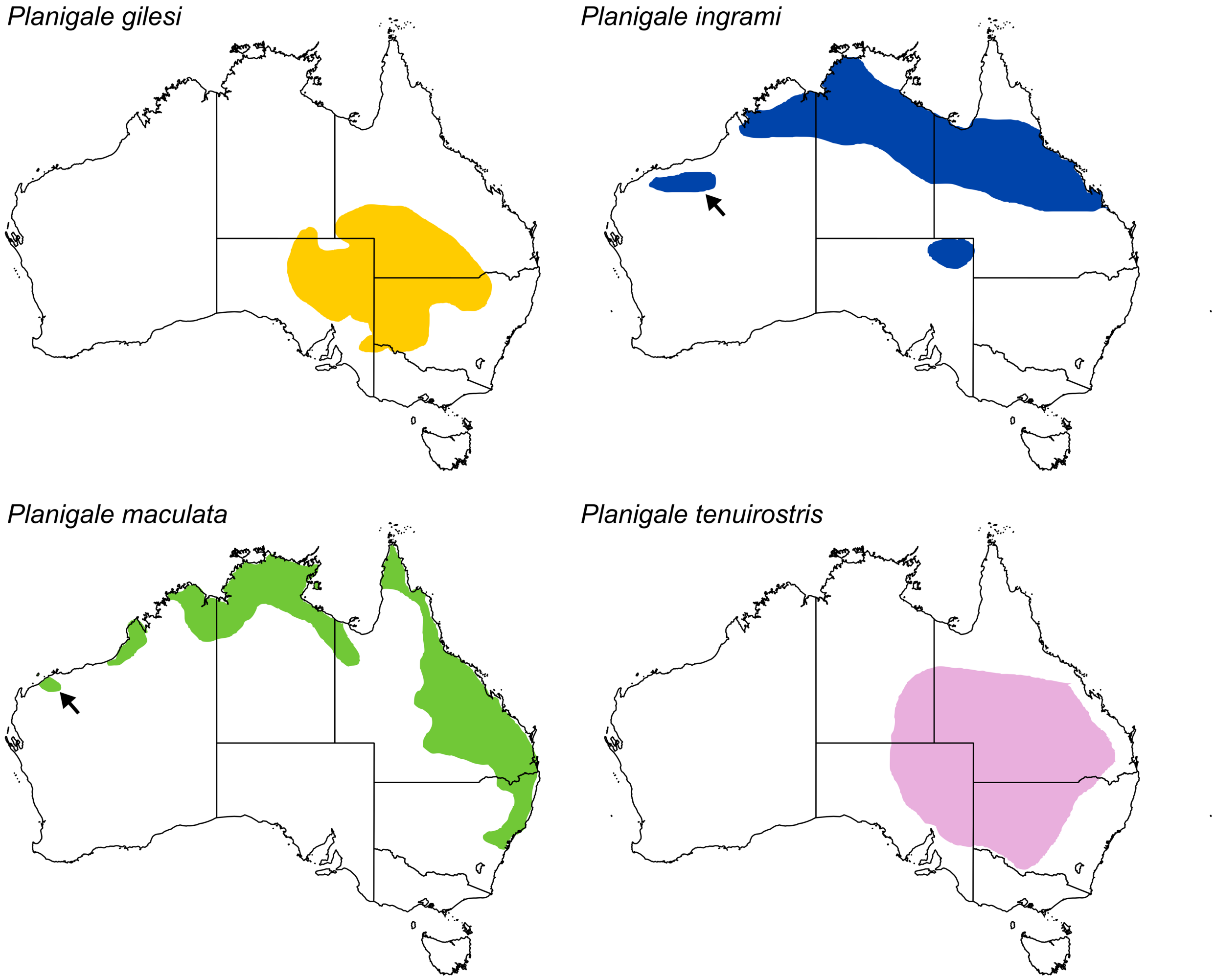

FIGURE 1. The approximate distributions of the four currently recognised species of Australian planigale adapted from Van Dyck & Strahan (2008), with Pilbara distributions added from Menkhorst & Knight (2004) and indicated with arrows.

Archer (1976a) revised the genus *Planigale* and placed the species into three groups based on overall anatomical similarity: (1) the *P. maculata* group, also including *P. novaeguineae* Tate & Archbold, 1941 from New Guinea; (2) the *P. ingrami* group, also including *P. tenuirostris*; and (3) the *P. gilesi* group. In his revision, Archer (1976a) noted various unusual specimens that might represent additional species, including one (WAM M3432) from Tambrey in the Pilbara in north-western Western Australia, at approximately 22° S and 118° E. Subsequent collections revealed the presence of two forms in this region, a small form generally referred to *P. ingrami* and a larger form referred to *P. maculata* (Strahan 1995).

The first molecular study of planigales by Painter *et al.* (1995) examined variation in a mitochondrial gene (cytochrome *b*) and included two individual ‘planigales’ from the Pilbara region in Western Australia. Both of these samples represented unrecognised lineages and were labelled *Planigale* 1 and 2; however, *Planigale* 2 was subsequently determined to belong to another dasyurid genus, *Ningaui* (Krajewski *et al.* 1997b). Blacket *et al.* (2000) used 12S rRNA gene sequences and allozyme electrophoresis to examine genetic variation within a more extensive sample of planigales. Their study demonstrated substantial genetic heterogeneity within *P. maculata* and also highlighted the existence of two possibly unnamed species in the Pilbara; one of these was *Planigale* 1 of Painter *et al.* (1995), the other was a newly identified genetic lineage given the informal label of *Planigale* sp. Mt Tom Price (later also referred to as *Planigale* sp. 2 by Gibson & McKenzie 2009 and Umbrello *et al.* 2020). The genetic relationships within *Planigale* were further examined by Westerman *et al.* (2016) using a combination of four mitochondrial and four nuclear markers, corroborating the presence of the *Planigale* 1 and *Planigale* sp. Mt Tom Price lineages in the Pilbara. While Blacket *et al.* (2000) found from analysis of 12S rRNA sequences that neither of the Pilbara planigales was closely related to any other previously known species, the increased genetic coverage (including four nDNA loci, P1, IRBP, bfib7 and e-globin) of Westerman *et al.* (2016) placed *P.* sp. Mt Tom Price as part of the *P. ingrami* clade and *Planigale* 1 as the sister lineage to *P. tenuirostris*. This suggested the two Pilbara planigale lineages had long, separate evolutionary histories, as their closest relatives occurred outside of the region.

Prior to 1980, only nine specimens of *Planigale* had been collected from the Pilbara. Since then, surveys by government scientists and environmental consultants have yielded more than 600 additional vouchered specimens, many with associated tissue samples, lodged in museum collections. As the two Pilbara lineages can readily be identified through genetic screening (Blacket *et al.* 2000; Westerman *et al.* 2016), the phylogeography of each Pilbara lineage was examined by Umbrello *et al.* (2020) by sequencing mtDNA and nDNA from all genetic samples in the Western Australian Museum collection (n = 275). The resultant sequence data provided information on the identity and distributional extent of the two Pilbara lineages. Here, we add to the published genetic data with additional individuals screened for the key allozyme loci identified by Blacket *et al.* (2000) and compare the mtDNA sequence data from Umbrello *et al.* (2020) with existing published data of *P. maculata* and *P. ingrami*. We also undertake a morphological revision of Pilbara planigales to identify and describe morphological differences between *Planigale* 1 and *Planigale* sp. Mt Tom Price and compare these forms with existing named species, particularly *P. maculata* and *P. ingrami.* This culminates in the description of two highly distinctive, new species of *Planigale*, formally recognising and naming the divergent *Planigale* 1 and *Planigale* sp. Mt Tom Price.

Material and Methods

Allozyme electrophoresis and mitochondrial relationships. The demonstration by Blacket *et al.* (2000) of two undescribed candidate species in the Pilbara prompted a follow-up allozyme study in 2001, involving the 36 additional frozen tissues from that region held by the Western Australian Museum at the time. This allozyme study also included two individuals previously genotyped by Blacket *et al.* (2000), namely one *P. maculata* from the Kimberley and one *Planigale* 1 from the Pilbara. As advocated by Richardson *et al.* (1986), this study allowed us to allocate all companion voucher specimens to their appropriate candidate taxon, thus ensuring that our initial morphological analyses would maximise any attempt to delineate the two taxa.

Liver homogenates from these 38 individuals were profiled for 35 of the most informative allozyme loci employed by Blacket *et al.* (2000) and the resultant allozyme dataset subjected to a Principal Co-ordinates Analysis (PCoA) on a pairwise genetic distance matrix (Rogers R) among individuals. Stepwise PCoA was then used to assess whether additional genetic heterogeneity was evident in deeper PCoA dimensions (rationale in Adams *et al.* 2014). Diagnosability was assessed by calculating the number of fixed allozyme differences between the primary PCoA lineages and taxa. All laboratory protocols and analytic methodologies are contained in Blacket *et al.* (2000).

Additionally, published cytochrome *b* (cytb) sequences of planigale species (Painter *et al.* 1995; Krajewski *et al.* 1997a; Mitchell *et al.* 2014; Westerman *et al.* 2016; Umbrello *et al.* 2020) were downloaded from the Genbank NCBI database and aligned in Geneious Prime (Kearse *et al.* 2012) using the MAFFT alignment builder (Katoh *et al.* 2002). A maximum likelihood phylogenetic tree was then built on the cytb alignment using the RAxML plugin in Geneious (Stamatakis 2006) with 1000 bootstrap replicates and *Sminthopsis macroura* (ABTC21626) used as an outgroup. One *Planigale* 1 sample (M99464) appeared to contain multiple sequence errors and resolved as sister to all other *Planigale* 1 samples, so it was removed from the alignment and the tree analysis run again without it.

Morphological examination. Voucher specimens (Table 1) were examined from the following institutions: Australian National Wildlife Collection, CSIRO (ANWC); South Australian Museum (SAMA); Queensland Museum (QM); Western Australian Museum (WAM). Specimens were selected to include a broad sampling across the species' distributions and include individuals genotyped by Blacket *et al.* (2000) and Umbrello *et al.* (2020) (Fig.

2). We did not include specimens of the New Guinean species *Planigale novaeguineae* in this study as they have previously been shown to be morphologically (Archer 1976a) and genetically (Westerman *et al.* 2016) distinct from the Australian species.

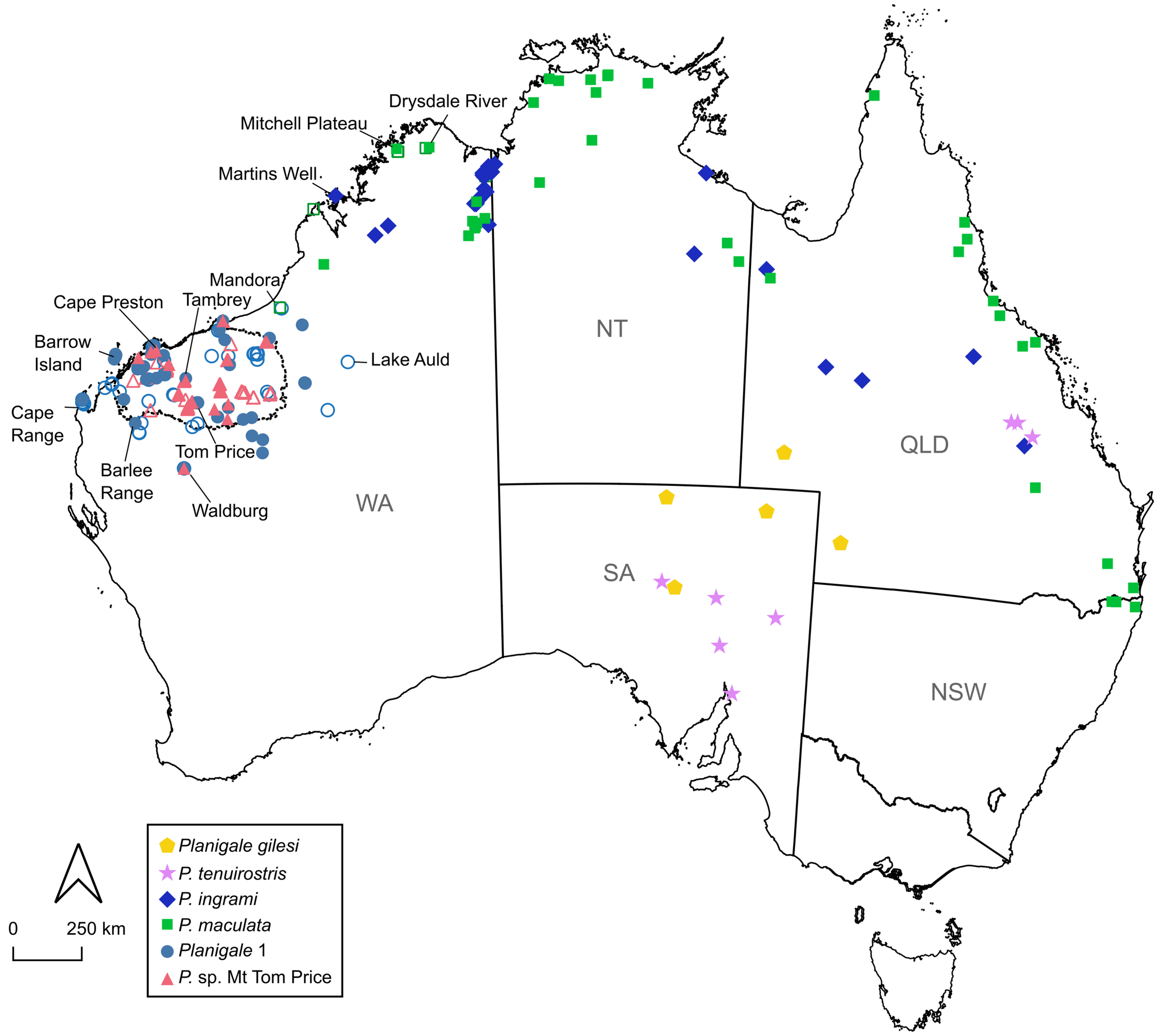

FIGURE 2. Distribution of planigale specimens examined in this study (*Planigale gilesi*, yellow pentagon; *P. tenuirostris*, pink star; *P. ingrami*, blue diamond; *P. maculata*, green square; *Planigale* 1, grey-blue circle; *P.* sp. Mt Tom Price, salmon triangle). Open symbols indicate individuals for which DNA was sequenced during this study or in previous studies. The Pilbara region in Western Australia is denoted by a broken line and key locations mentioned in the text are labelled.

Tooth numbering follows Luckett (1993), and anatomical terminology of teeth and cranial features follows Beck *et al.* (2022). Skull measurements are illustrated in Fig. 3 and taken from Archer (1976a) and Baker *et al.* (2015) with additional measurements on the alisphenoid tympanic process and the pterygoid to capture cranial flattening of this area. The measurements are as follows: ATL, alisphenoid tympanic process length; ATW, alisphenoid tympanic process width; BH, braincase height; BL, basicranial skull length, excluding incisors; BPL, bulla petrosal length; BPW, bulla petrosal width; DL, dentary length, excluding incisors; IBW, minimum width between auditory bullae; IFL, length of incisive foramen; IOW, minimum width of interorbital constriction; LCML, maximum length of lower tooth row from canine to M_4; MFL, length of maxillopalatine fenestra; ML, maxilla length; MW, maximum width across braincase; NL, maximum length of nasals; NW, width of nasals at the nasal/maxilla/frontal junction; PL, length of palate; PML, length of premaxilla, measured as length of sutural contact between nasal bone and premaxilla; PW, width between pterygoids; UCML, maximum length of upper tooth row from canine to M^4; UML, maximum length of upper molar row, M^1–M^4; UPL, crown length of upper premolar row P^1–P^3; ZW, maximum zygomatic width. The following external measurements were taken from preserved (wet) specimens of Pilbara planigales: HV, snout-vent length; TV, tail-vent length; EAR, ear length; PES, pes length (minus claw); HL, head length; HD, head depth and HW, head width (Fig. 3E and F). All skull and external measurements are given in mm.

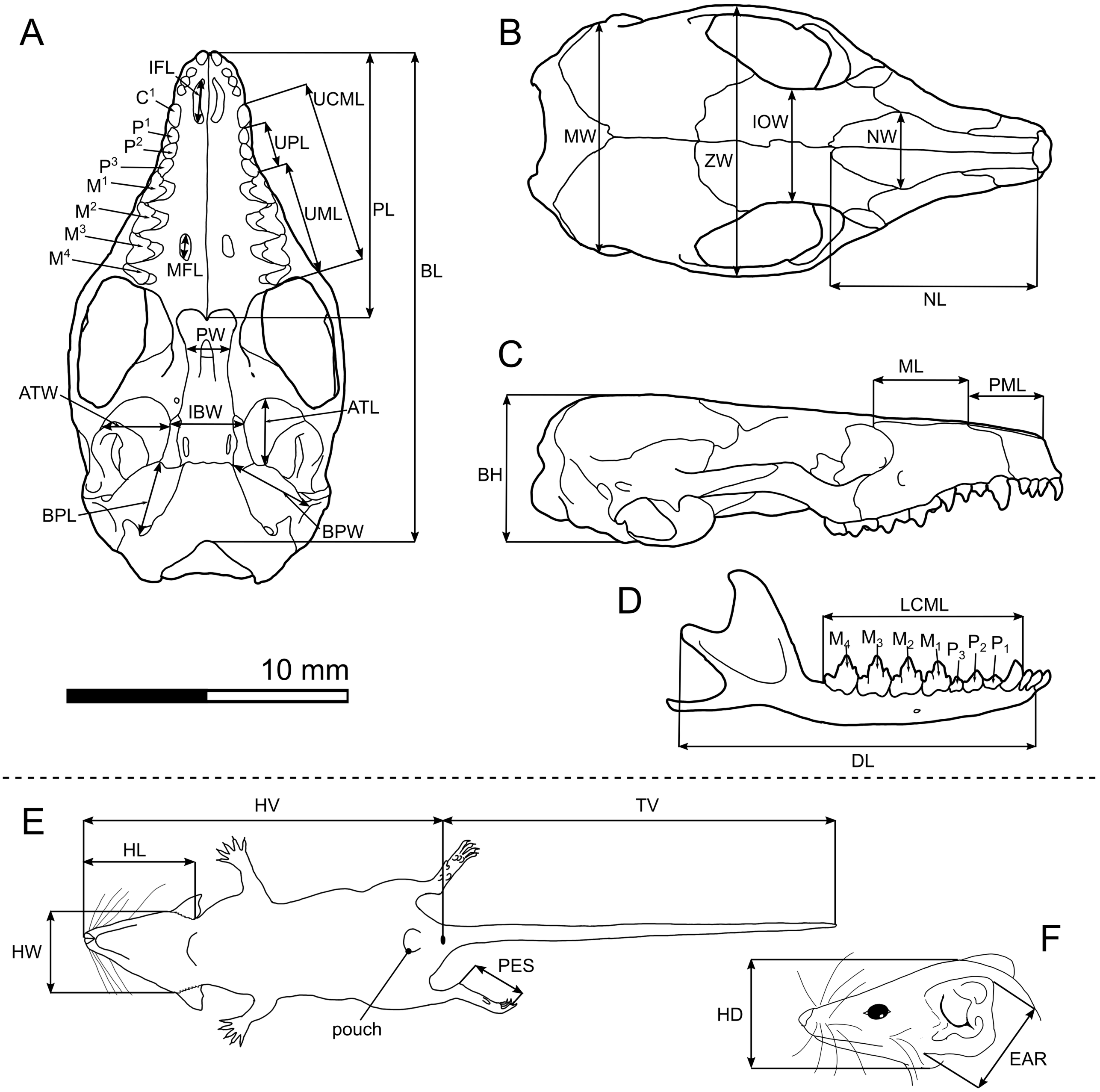

FIGURE 3. Illustration of *Planigale* cranium (A, ventral; B, dorsal; C, lateral views) and dentary, D, (based on *Planigale* sp. 1 WAM M25773) with measurements and teeth labelled, and external measurements, stylised from a female, E and F. Note scale does not apply to illustrations below the dashed line.

Skulls were categorized into two age groups (juvenile or adult), according to dental eruption and wear (M^4 unerupted and presence of deciduous premolar, dP3–juvenile; loss of deciduous premolar and fully emergent and descended adult premolar 3–adult). Most individuals fell into the adult class and juveniles were excluded from the morphometric analyses. Where wet-preserved bodies were present, sexual maturity was confirmed by development of the external reproductive structures (i.e., presence and size of testes or pouch). Sex of the specimen was determined from the body or from information recorded with the skull at the time of museum registration. Specimens from the Pilbara region were classified as either *Planigale* sp. 1 or *Planigale* sp. Mt Tom Price for morphometric analysis based initially on genetic data from the 2001 allozyme study (presented here), mtDNA sequence data in Blacket *et al.* (2000) and Umbrello *et al.* (2020), then based on morphological differences as determined by K. P. Aplin.

All measurements were recorded with digital callipers to 0.01 mm and statistical analyses were carried out using the package 'MorphoTools2' (Šlenker *et al.* 2022) in the computing program R (R Core Team 2013). First, summary statistics were obtained, and variables with greater than 20% missing data were removed, this cut off was chosen to reduce the amount of missing data while maximising the number of measurement variables retained in the dataset, with the only individuals having >10% missing data being *P. gilesi* and *P. tenuirostris* which were not the focal species in this study. Any individuals with more than 20% missing data after this initial step were subsequently removed (these were QMJM8244, 32% missing and WAM M18793, 26% missing). The remaining missing data was imputed using predictive mean matching in the 'MICE' package (Buuren & Groothuis-Oudshoorn 2011) using the default settings except that we increased the number of iterations from five to 50. We accounted for multicollinearity of variables by checking the Spearman rank correlation coefficients, and PL was removed as it was highly correlated (> 90–95%) with five other variables. To visualise the filtered craniodental measurement data, we conducted a Principal Component Analysis (PCA) using the pca.cor function in 'MorphoTools2'. As PCA is sensitive to scaling of variables, as those with the highest variances (e.g., basicranial length) will tend to dominate the first few principal components (Jolliffe 2002), we used the correlation matrix, following previous studies on dasyurids (Aplin *et al.* 2015; Umbrello 2018; Lavery *et al*. 2022). In morphological datasets, a high proportion of the variance explained by PC1 is usually due to size (Jolicoeur 1963; Berner 2011) and accounting for the effect of size has been shown to help distinguish between morphologically cryptic dasyurid species as it allows for a comparison on skull shape (Viacava *et al.* 2023). To account for size effects (specifically caused by isometric scaling) between species, we used log-shape ratios by calculating the geometric mean of all variables, per individual, as a proxy for skull size, dividing each variable by the geometric mean then log-transforming this ratio (Mosimann 1970; Onley *et al.* 2022; Pavón-Vázquez *et al.* 2022; Viacava *et al.* 2023). We then re-ran the PCA on the 'size-corrected' dataset.

Small or uneven sample sizes can be problematic in multivariate discriminant analyses (Williams & Titus 1988), so we excluded *P. gilesi* and *P. tenuirostris* specimens from further analyses. These two species were deemed less important for inclusion due to their disparate distributions from the Pilbara (Fig. 1) and previous morphological (Archer 1976a) and molecular (Blacket *et al.* 2000; Westerman *et al.* 2016) studies reporting these species as clearly distinct from all other planigales. Size differences between the remaining species (*P. ingrami*, *P. maculata* and the two Pilbara forms *Planigale* 1 and *P*. sp. Mt Tom Price) were tested using a Kruskal-Wallis rank sum test on the geometric means. This was followed by a pairwise Wilcoxon rank sum test to check the pairwise differences between groups with p-values adjusted for multiple group testings using the Benjamini & Hochberg (1995) method. Based on these results, we grouped the sexes for some species (*P. ingrami* and *P*. sp. Mt Tom Price) as they were not significantly different in size.

To ensure the size-corrected dataset satisfied the requirements for discriminant analyses (namely that characters cannot be linear combinations of each other, nor highly correlated ($r > 0.95$), and that the number of characters must not exceed the number of samples minus the number of groups; Büyüköztürk & Çokluk-Bökeoðlu 2008) we used a step-wise discriminant analysis, the stepdisc.calc function in 'MorphoTools2', to find the best linear combination of characters for discriminating the groups. A canonical discriminant analysis (CDA) was then run on the selected characters, which were BH, NL, UPL, IOW, ATW, LCML, MW, PML, BPW and ATL, to investigate shape differences between species. The CDA showed little shape differentiation between the sexes in *P. maculata* and *Planigale* 1, so males and females were then pooled within species. A one-way non-parametric multivariate analysis of variance (PERMANOVA) was run to test for shape differences between the four groups, *P. ingrami*, *P. maculata*, *Planigale* 1 and *P*. sp. Mt Tom Price, in the package 'vegan' (Oksanen *et al*. 2022) using a Euclidean dissimilarity matrix and pairwise comparisons were checked in a post hoc test with Bonferroni-corrected p values. Additionally, one-way ANOVAs were run on individual variables to identify if any measurements differed significantly between pairs of species that were not significantly different in the PERMANOVA. Finally, group membership was tested using non-parametric k-nearest neighbours classifications with the optimal number of correct classifications occurring at $k = 10$.

As the external measurements were often taken on different individuals than the cranial measurements, due to skulls being removed, we analysed this dataset separately. Depending on how specimens have been preserved it is not always possible to obtain the full set of measurements on each specimen; for example, the hind-foot is often curled tightly and the ears may be crumpled leading to measurement error. As such, each variable was examined separately through two-way analysis of variance (ANOVA; except for head-width, as this was not normally distributed for *Planigale* sp. Mt Tom Price, even after data transformations were performed) to test for differences between the two

Pilbara forms and for sexual dimorphism within groups. Additionally, female spirit specimens were examined for the type of pouch development (Woolley 1974; Read 1984; Krajewski *et al.* 2000), nipple number and the presence of pouch young. Note, throughout this work we have followed the unified species concept of De Queiroz (2007).

Results

Molecular analyses. The final allozyme dataset comprised the allozyme profiles of 38 *Planigale* individuals at 35 putative loci (raw data in Appendix Table 1). A PCoA on these individuals (Fig. 4) revealed the presence of three primary lineages, corresponding to *Planigale* 1 (n = 32) and *Planigale* sp. Mt. Tom Price (n = 3) from the Pilbara, and *P. maculata* from north-western Western Australia (n = 3). These three lineages were unequivocally diagnosable from one another by fixed differences at 7–10 allozyme loci (Fig. 4), levels of diagnosability that strongly contend for the presence of three candidate species among the individuals sampled (Unmack *et al.* 2022). No additional genetic heterogeneity was evident in deeper PCoA dimensions (analyses not shown) for the two Pilbara lineages, but each of the three *P. maculata* was allocated into either the 'M1' (n = 1 from Mandora and sympatric with *Planigale* 1) or 'M2' genetic lineages (n = 2, Kimberley region) previously found by Blacket *et al.* (2000). While these two Western Australian lineages of *P. maculata* displayed fixed differences at three allozyme loci, their allopatric status and the small sample sizes involved preclude any taxonomic inferences based on genetic data alone.

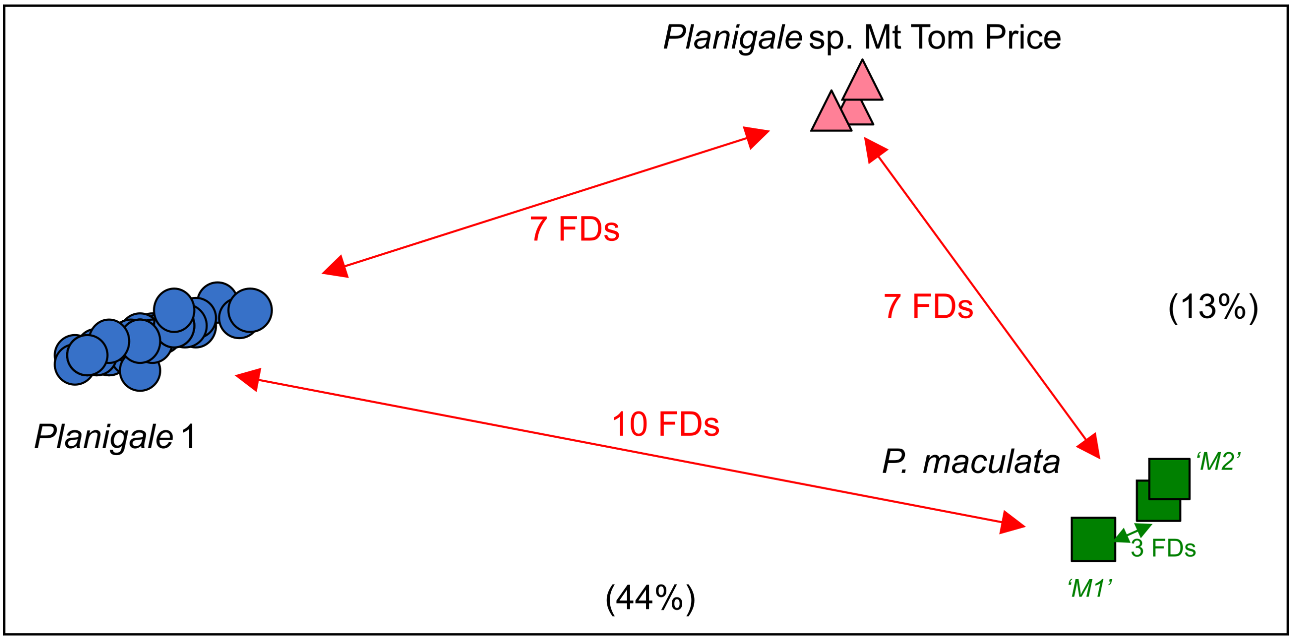

FIGURE 4. Scatterplot of ordination scores in the first two dimensions for the initial Principal Coordinates Analysis (PcoA) on the 38 planigale included in the 2001 allozyme study. The relative contribution of each dimension is given in brackets (axes not scaled accordingly). Individuals are colour-coded by species following Figure 2. The pairwise number of fixed allozyme differences (FDs) between candidate species and between the 'M1' and 'M2' lineages of *P. maculata* are also shown.

In the mitochondrial cytb dataset the samples from the Pilbara were resolved into one of two monophyletic clades by RaxML (Fig. 5). The *Planigale* sp. Mt Tom Price samples formed a distinct, well-supported clade positioned as sister to *P. ingrami*, consistent with the results of Westerman *et al.* (2016), and *Planigale* 1 samples formed a distinct, well-supported clade positioned near *P. maculata* samples from Genbank. There was low support for the placement of higher relationships among planigale species (< 80%) likely due to only one locus being used in the analysis. There was little intraspecific differentiation shown within the two Pilbara lineages, which has been discussed in more detail previously (Umbrello *et al.* 2020).

Morphological analyses. A total of 298 specimens of *Planigale* were examined in this study, which included 171 individuals from the Pilbara region, previously tentatively identified as either *P. maculata*, *P. ingrami, Planigale* 1 and/or *P.* sp. Mt Tom Price. Of these specimens, 29 were genotyped as *Planigale* 1 and two genotyped as *P.* sp. Mt Tom Price in the allozyme data presented here (Table 1; Fig. 4), which adds to the three *Planigale* 1 and one *P.* sp.

Mt Tom Price from Blacket *et al.* (2000) and the 21 *Planigale* 1 and 40 *P.* sp. Mt Tom Price specimens sequenced in Umbrello *et al.* (2020) (see superscripts in Table 1). Additionally, a total of 127 individuals of *P. maculata*, *P. ingrami*, *P. gilesi* and *P. tenuirostris* were examined from throughout Australia (Table 1).

TABLE 1. List of museum specimens examined in this study. Species (*Pg*, *Planigale gilesi*; *Pi*, *P. ingrami*; *P*1, *Planigale* 1; *Pm*, *P. maculata*; *P*MTP, *P.* sp. Mt Tom Price, *Pt*, *P. tenuirostris*), museum registration number (WAM, Western Australian Museum; QM, Queensland Museum; ANWC, Australian National Wildlife Collection; SAMA, South Australian Museum), locality, latitude, longitude, collection date, sex (M, male; F, female), age (A, adult; SA, subadult) and type of specimen examined. Those that were not measured are in italics. Subscripts indicate where DNA has been sequenced by [a]Blacket *et al*. (2000), [b]Umbrello *et al*. (2020), or [c]allozyme loci scored in this study.

Species	Reg. number	Locality	Latitude	Longitude	Date	Sex	Age	specimen as
Pg	SAMA M9533	Glengyle, QLD	-24.7833	139.5833	30/03/1972	M	A	skull
Pg	SAMA M18742	Mungutana Dam, SA	-29.3806	135.6822	05/10/1995	M	A	skull
Pg	SAMA M18998	Witjira NP, SA	-26.4206	135.2808	Aug 1997		A	skull
Pg	SAMA M20623	Newalton Downs, SA	-26.7503	139.0514	Nov 1993	M	A	skull
Pg	SAMA M24039	Innamincka, QLD	-27.6300	141.9200	18/12/2001	M	A	skull
Pi	ANWC M11916	Bing Bong Stn, NT	-18.3333	136.0333	20/05/1976	F	A	skull
Pi	ANWC M11970	Barkly Tableland, NT	-15.6167	136.3500	22/05/1972	M	A	skull
Pi	QM JM10079	Cannington Stn, QLD	-21.8667	140.9000	18/05/1993	M	A	skull; spirit
Pi	QM JM4943	Natal Downs, QLD	-21.0833	146.1500	18/09/1980	M	A	skull; spirit
Pi	QM JM571	Glenorina, QLD	-23.8167	148.3667		M	A	skull; spirit
Pi	QM JM8666	Lawn Hill, QLD	-18.7500	138.5833	14/04/1991	F	A	skull; spirit
Pi	WAM M2846	Ord River, WA	-17.3833	128.8500	~1950	M	A	skull
Pi	*WAM M3191*	Wotjulum, WA	-16.1833	123.6167	~1956	F	A	skull; spirit
Pi	WAM M9662	Kununurra, WA	-15.7166	128.7000	Aug 1972	F	A	skull; spirit
Pi	WAM M11068	Ord River, WA	-16.1763	128.7361	17/01/1972	F	A	skull; spirit
Pi	WAM M11069	Argyle Downs, WA	-16.2805	128.8000	08/01/1972	F	A	skull; spirit
Pi	WAM M11070	Argyle, WA	-16.2805	128.8000	08/01/1972	F	A	skull; spirit
Pi	WAM M11072	Ord River, WA	-15.6500	128.7000		M	A	skull; spirit
Pi	WAM M14434	Kununurra, WA	-15.7750	128.7417	03/12/1975	M	A	skull; spirit
Pi	WAM M16255	Kununurra, WA	-15.7750	128.7417	~1986	M	A	skull; spirit
Pi	WAM M16866	Lisadell, WA	-16.6666	128.3869	28/04/1980	F	A	skull; spirit
Pi	WAM M16976	Mount Percy, WA	-17.5819	124.9017	20/05/1980	M	A	skull; spirit
Pi	WAM M18793	Mount Evelyn, WA	-16.4944	128.5625	11/10/1980	F	A	skull; spirit
Pi	WAM M18794	Mount Evelyn, WA	-16.4944	128.5625	10/10/1980	F	A	skull; spirit
Pi	WAM M18795	Mount Evelyn, WA	-16.5311	128.5417	07/10/1980	M	A	skull; spirit
Pi	WAM M18831	Mount Evelyn, WA	-16.4944	128.5625	15/10/1980	M	A	skull; spirit
Pi	WAM M19287	Lisadell, WA	-16.6722	128.4444	26/02/1981	M	A	skull; spirit
Pi	*WAM M19289*	Lisadell, WA	-16.6722	128.4444	25/02/1981	F	A	skull; spirit
Pi	WAM M19290	Lisadell, WA	-16.6388	128.4500	25/02/1981	M	A	skull; spirit
Pi	WAM M19295	Lisadell, WA	-16.6722	128.4444	27/02/1981	M	A	skull; spirit
Pi	*WAM M23965*	Mount Pitt, WA	-16.6694	128.4444	30/01/1985	M	A	skull; spirit
Pi	*WAM M23966*	Mount Pitt, WA	-16.6694	128.4444	30/01/1985	F	A	skull; spirit
Pi	WAM M29300	Napier, WA	-17.2875	125.3681	03/07/1988	M	A	skull; spirit

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TABLE 1. (Continued)

Species	Reg. number	Locality	Latitude	Longitude	Date	Sex	Age	specimen as
Pi	WAM M47255	Knox creek, WA	-15.6202	129.0050	19/10/1996	M	A	skull; spirit
Pi	WAM M52008	Winton, QLD	-22.2194	142.2422	Mar 1996	F	A	skull
Pi	WAM M52046	Kununurra, WA	-15.4286	128.8989	08/06/1999	F	A	skull; spirit
Pi	WAM M52048	Kununurra, WA	-15.4538	128.9867	08/06/1999	M	A	skull; spirit
Pi	*WAM M52049*	Kununurra, WA	-15.3558	129.1194	09/06/1999	M	A	skull; spirit
Pi	*WAM M52050*	Kununurra, WA	-15.4538	128.9867	10/06/1999	F	SA	skull; spirit
Pi	*WAM M52051*	Kununurra, WA	-15.4538	128.9881	10/06/1999	M	A	skull; spirit
Pi	*WAM M52053*	Kununurra, WA	-15.5891	128.9833	11/06/1999	M	A	skull; spirit
*P*1	*WAM M3432*	Tambrey, WA	-21.8000	117.8000	03/08/1958	M	SA	skull; skin
*P*1	WAM M11019	Barrow Island, WA	-20.7250	115.4000	26/08/1973	M	A	skull; spirit
*P*1	WAM M11020	Barrow Island, WA	-20.7250	115.4000	26/08/1973	M	A	skull; spirit
*P*1	WAM M11330	Barrow Island, WA	-20.7666	115.4000	28/08/1973	F	A	Skull; skin
*P*1	WAM M12190	Karratha, WA	-20.8833	116.6667	Jul 1973	M	A	skull
*P*1	WAM M13865	Mount Virchow, WA	-21.2500	116.3533	12/07/1975	F	SA	skull; spirit
*P*1	WAM M15160	Mount Bruce, WA	-22.6375	118.1333	02/12/1976	M	A	skull; spirit
*P*1	WAM M15161	Mount Bruce, WA	-22.6486	118.1375	28/11/1976	M	A	skull; spirit
*P*1	WAM M18006	Mount Bruce, WA	-22.6402	118.0889	06/05/1978	M	A	skull; spirit
*P*1	WAM M18226	Mount Bruce, WA	-22.6500	118.1375	25/01/1979	F	A	skull
*P*1	WAM M18245	Mount Meharry, WA	-23.1847	118.7917	19/06/1979	M	A	skull; spirit
*P*1	WAM M19669	Mount Burrup, WA	-20.6013	116.7736	28/06/1981	M	A	skull; spirit
*P*1	WAM M19674	Mardie Stn, WA	-21.3083	116.1194	10/07/1980	M	A	skull; spirit
*P*1	WAM M22699	Great Sandy Desert, WA	-20.4000	122.1333	15/05/1979	M	A	skull; spirit
*P*1	WAM M22700	Great Sandy Desert, WA	-20.4000	122.1333	15/05/1979	M	A	skull; spirit
*P*1	WAM M24146	Roebourne, WA	-20.9583	117.1028	09/04/1982	F	SA	skull; spirit
*P*1	WAM M24591	Mardie Stn, WA	-21.2500	116.1278	Jul 1980	M	A	skull; spirit
*P*1	WAM M24920	Millstream, WA	-21.6000	117.0667	1983	F	A	skull; spirit
*P*1	WAM M25601[c]	Lake Auld, WA	-21.7333	123.6667	13/06/1986	M	A	Skull; skin
*P*1	WAM M25773	Yandagooge Creek, WA	-22.3141	122.0553	18/04/1986	F	A	skull; spirit
*P*1	WAM M25775	Yandagooge Creek, WA	-22.3280	122.0842	27/04/1986	F	A	skull
*P*1	WAM M25776	Yandagooge Creek, WA	-22.3400	122.0725	27/04/1986	M	A	skull; spirit
*P*1	WAM M26905[a]	Millstream, WA	-21.5833	117.0667	10/05/1986	M	A	skull
*P*1	WAM M28456	Millstream, WA	-21.5833	117.0667	06/05/1986	M	A	skull; spirit
*P*1	WAM M28922	Mungowarra, WA	-21.3166	116.2500	12/10/1987	F	A	skull; spirit
*P*1	WAM M30851	Barrow Island, WA	-20.7500	115.4167	30/09/1989	M	A	skull; spirit
*P*1	WAM M30852	Barrow Island, WA	-20.8000	115.4000	30/09/1989	M	A	skull; spirit
*P*1	WAM M40541	Shaw River, WA	-20.6666	119.3333	03/08/1992	M	A	skull; spirit
*P*1	WAM M41803[c]	Barlee Range, WA	-23.3891	115.8867	10/06/1994	M	A	skull; spirit

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TABLE 1. (Continued)

Species	Reg. number	Locality	Latitude	Longitude	Date	Sex	Age	specimen as
*P*1	WAM M41804[c]	Barlee Range, WA	-23.4113	115.8942	11/06/1994	F	A	skull; spirit
*P*1	WAM M41812[c]	Barlee Range, WA	-23.3891	115.8867	13/06/1994	M	A	skull; spirit
*P*1	WAM M41839[c]	Barlee Range, WA	-23.0958	116.0097	19/06/1994	F	SA	spirit
*P*1	WAM M43169[a,c]	Nifty Mine, WA	-21.6666	121.5833	Apr 1994	F	SA	skull; spirit
*P*1	WAM M43217	Barlee Range, WA	-23.0797	115.7903	10/08/1993	M	A	skull; spirit
*P*1	WAM M44940 [a]	Yaleen Stn, WA	-21.7000	116.4667	23/09/1997	F	A	skull; spirit
*P*1	WAM M45026[c]	Cape Range, WA	-22.2027	114.0403	05/10/1997	F	A	spirit
*P*1	WAM M45029[c]	Cape Range, WA	-22.1597	113.9897	05/10/1997	M	A	spirit
*P*1	WAM M45030[c]	Cape Range, WA	-22.1505	113.9978	05/10/1997	M	A	skull; spirit
*P*1	WAM M45035[c]	Cape Range, WA	-22.2286	114.0350	07/10/1997	M	A	skull; spirit
*P*1	WAM M45041[c]	Cape Range, WA	-22.1594	113.9886	08/10/1997	M	A	skull; spirit
*P*1	WAM M45053	Cape Range, WA	-22.0716	114.0067	11/10/1997	M	A	skull; spirit
*P*1	WAM M45065[c]	Cape Range, WA	-22.0705	114.0050	12/10/1997	M	A	skull; spirit
*P*1	WAM M46307	Weeli Wolli Spring, WA	-22.9166	119.2167	06/04/1995	M	A	skull; spirit
*P*1	WAM M46716	Newman, WA	-23.3166	120.0333	Aug 1995	M	A	skull; spirit
*P*1	*WAM M47294*	Pannawonica, WA	-21.6833	116.3833	08/10/1996	M		skull
*P*1	WAM M47508	Newman, WA	-23.3500	119.7167	1997	M	A	skull; spirit
*P*1	*WAM M47687*	Tom Price, WA	-22.8069	117.7831	19/05/1997	F	SA	skull; spirit
*P*1	WAM M47725[a,b]	Roebourne, WA	-21.1269	117.0956	08/07/1997	M	A	skull; spirit
*P*1	WAM M47774	Newman, WA	-23.1858	118.8067	15/06/1997	M	A	skull; spirit
*P*1	WAM M48185	Weelarinna, WA	-23.9166	119.9833	18/06/1996	F	A	skull; spirit
*P*1	WAM M48187	Weelarinna, WA	-24.0752	120.3606	17/08/1997	M	A	skull; spirit
*P*1	WAM M48545	Cane River, WA	-22.2491	115.4900	04/05/1999	M	SA	skull; spirit
*P*1	WAM M48901[c]	Port Hedland, WA	-21.1600	118.8100	03/05/2001	M	A	skull; spirit
*P*1	WAM M49025[b]	Onslow, WA	-21.6758	115.1458	12/09/2003	M	A	spirit
*P*1	WAM M49195[b]	Burrup, WA	-20.6169	116.7850	01/11/2001	M	A	skull; spirit
*P*1	WAM M49196[b]	Burrup, WA	-20.6169	116.7850	01/11/2001	M	A	skull; spirit
*P*1	WAM M49197[b]	Burrup, WA	-20.6169	116.7850	01/11/2001	F	A	skull; spirit
*P*1	WAM M49198[b]	Burrup, WA	-20.6169	116.7850	01/11/2001	M	A	skull; spirit
*P*1	WAM M51415[b]	Onslow, WA	-21.7830	114.8697	25/11/1999	M	SA	skull; spirit
*P*1	WAM M51417	Beyondie, WA	-24.5091	120.3067	15/09/1999	M	A	spirit
*P*1	WAM M51423	Barrow Island, WA	-20.8833	115.3333	14/10/1999	M	A	skull; spirit
*P*1	WAM M51581[c]	Mandora, WA	-19.7977	121.4478	18/10/1999	F	A	skull; spirit
*P*1	WAM M51643[c]	Meentheena, WA	-21.2163	120.3406	27/05/2000	M	A	spirit
*P*1	WAM M51668[c]	Meentheena, WA	-21.4200	120.4258	29/05/2000	M	A	skull; spirit
*P*1	WAM M51673[c]	Burrup, WA	-20.6500	116.7500	14/05/2001	M	A	spirit
*P*1	WAM M51684[c]	Mount Minnie, WA	-21.9738	115.3736	27/06/2000	M	A	spirit
*P*1	WAM M51746[c]	Meentheena, WA	-21.2177	120.4556	30/09/2000	M	A	spirit
*P*1	WAM M51749[c]	Meentheena, WA	-21.2300	120.3128	01/10/2000	M	A	skull; spirit

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TABLE 1. (Continued)

Species	Reg. number	Locality	Latitude	Longitude	Date	Sex	Age	specimen as
*P*1	WAM M51792[c]	Meentheena, WA	-21.4200	120.4258	24/05/2001	M	A	skull; spirit
*P*1	WAM M51793[c]	Meentheena, WA	-21.4216	120.4267	24/05/2001	M	A	spirit
*P*1	WAM M51804[c]	Meentheena, WA	-21.2288	120.4258	15/09/2001	F	SA	spirit
*P*1	WAM M51805[c]	Meentheena, WA	-21.2555	120.4553	15/09/2001	M	A	skull; spirit
*P*1	WAM M51807[c]	Meentheena, WA	-21.2177	120.4556	17/09/2001	F	A	skull; spirit
*P*1	WAM M51811[c]	Meentheena, WA	-21.4200	120.4258	18/09/2001	F	A	skull; spirit
*P*1	WAM M52212[c]	Mount Herbert, WA	-21.3561	117.1283	15/09/1999	F	A	skull; spirit
*P*1	WAM M52421[c]	Brockman, WA	-22.3105	117.3167	19/11/1998	M	A	skull; spirit
*P*1	WAM M52422[c]	Brockman, WA	-22.2919	117.2833	19/11/1998	F	A	skull; spirit
*P*1	WAM M52423[c]	Brockman, WA	-22.3105	117.3167	19/11/1998	M	A	skull; spirit
*P*1	WAM M53961[b]	Onslow, WA	-21.7038	115.1289	11/09/2003	M	A	spirit
*P*1	WAM M53962[b]	Onslow, WA	-21.7038	115.1289	11/09/2003	M	A	spirit
*P*1	WAM M56247[b]	Waldburg Stn, WA	-24.7500	117.3667	21/10/2004	M	A	spirit
*P*1	WAM M56658	Mount Elvire, WA	-21.6828	116.7522	06/10/2005	F	A	spirit
*P*1	WAM M56880[b]	Mount Berry, WA	-22.4080	116.3717	12/10/2004	M	A	spirit
*P*1	WAM M57718	Spear Hill, WA	-21.5058	119.4194	04/05/2006	F	SA	spirit
*P*1	WAM M57733[b]	Mount Berry, WA	-22.4080	116.3717	18/05/2005	F	A	spirit
*P*1	WAM M60052[b]	Goldsworthy, WA	-20.3358	119.1375	26/05/2006	F	A	spirit
*P*1	WAM M60072	Goldsworthy, WA	-20.3264	119.1753	28/05/2006	F	SA	spirit
*P*1	WAM M60075	Goldsworthy, WA	-20.0339	119.3339	28/05/2006	M	A	spirit
*P*1	WAM M60563[b]	Dresser, WA	-21.2181	119.4019	06/05/2006	M	A	spirit
*P*1	WAM M61079	Warrawagine, WA	-20.7481	120.9314	04/10/2005	M	A	spirit
*P*1	WAM M61116[b]	Goldsworthy, WA	-20.3358	119.1375	14/10/2005	F	A	spirit
*P*1	WAM M61405[b]	Lake Disappointment, WA	-23.2767	122.8195	05/05/2013	F	A	spirit
*P*1	WAM M61757[b]	Balfour Downs, WA	-22.6111	120.7289	17/05/2006	M	A	spirit
*P*1	WAM M61764[b]	Balfour Downs, WA	-22.5180	120.6780	15/05/2006	F	A	spirit
*P*1	WAM M61778[b]	Balfour Downs, WA	-22.6111	120.7289	13/05/2006	M	A	spirit
*P*1	WAM M61789[b]	Paraburdoo, WA	-23.4189	117.8419	09/10/2005	M	A	spirit
*P*1	WAM M62266	Waldburg Stn, WA	-24.7500	117.3667	~2006	M	A	spirit
*P*1	WAM M64770[b]	Paraburdoo, WA	-23.3353	118.0361	29/05/2006	F	A	spirit
Pm	ANWC M233	Urbenville, NSW	-28.4889	152.4500	28/03/1961	M	A	skull; skin
Pm	ANWC M492	Boomi Creek, NSW	-28.4667	152.6000	01/01/1955	F	A	skull
Pm	*ANWC M7406*	Cannon Hill, NT	-12.4000	132.9500	14/08/1972	F		skull; skin
Pm	*ANWC M7797*	Cannon Hill, NT	-12.3667	132.9667	30/01/1973	F		skull; skin
Pm	*ANWC M7810*	Cannon Hill, NT	-12.3667	132.9667	31/01/1973	M		skull; skin
Pm	*ANWC M7826*	Cannon Hill, NT	-12.3667	132.9667	03/02/1973	M		skull; skin
Pm	*ANWC M7827*	Cannon Hill, NT	-12.3667	132.9667	03/02/1973	M		skull; skin
Pm	ANWC M7828	Cannon Hill, NT	-12.3667	132.9667	03/02/1973	F	A	skull; skin
Pm	*ANWC M7841*	Cannon Hill, NT	-12.3667	132.9667	04/02/1973	M		skull; skin

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TABLE 1. (Continued)

Species	Reg. number	Locality	Latitude	Longitude	Date	Sex	Age	specimen as
Pm	ANWC M7847	Cannon Hill, NT	-12.3667	132.9667	05/02/1973	M	A	skull; skin
Pm	ANWC M7849	Cannon Hill, NT	-12.3667	132.9667	06/02/1973	F	A	skull; skin
Pm	ANWC M6980	Springville Stn, NT	-18.5333	137.6000	24/08/1967	M	A	skull; skin
Pm	ANWC M6994	Nicholson River, NT	-17.9333	137.1667	30/08/1967	M	A	skull; skin
Pm	*ANWC M7850*	Cannon Hill, NT	-12.3667	132.9667	06/02/1973	M		skull; skin
Pm	*ANWC M7852*	Cannon Hill, NT	-12.3667	132.9667	07/02/1973	M		skull; skin
Pm	*ANWC M7853*	Cannon Hill, NT	-12.3667	132.9667	08/02/1973	F		skull
Pm	*ANWC M7940*	Cannon Hill, NT	-12.3667	132.9667	23/07/1973	F		skull; skin
Pm	WAM M8093	Humpty Doo, NT	-12.5666	131.3167	21/03/1959	F	A	skull; skin
Pm	WAM M8095	Humpty Doo, NT	-12.5000	131.0000	08/03/1959	F	A	skull; skin
Pm	*ANWC M8863*	Cannon Hill, NT	-12.3667	132.9667	18/03/1974	F		skull; skin
Pm	*ANWC M8864*	Cannon Hill, NT	-12.3667	132.9667	18/03/1974	M		skull; skin
Pm	*ANWC M8865*	Cannon Hill, NT	-12.3667	132.9667	19/03/1974	F		skull; skin
Pm	*ANWC M8866*	Cannon Hill, NT	-12.3667	132.9667	19/03/1974	M		skull; skin
Pm	*ANWC M8867*	Cannon Hill, NT	-12.3667	132.9667	19/03/1974	M		skull; skin
Pm	*ANWC M8868*	Cannon Hill, NT	-12.3667	132.9667	21/03/1974	M		skull; skin
Pm	ANWC M8869	Cannon Hill, NT	-12.3667	132.9667	21/03/1974	M	A	skull; skin
Pm	ANWC M8870	Cannon Hill, NT	-12.3667	132.9667	21/03/1974	F	A	skull; skin
Pm	ANWC M8871	Cannon Hill, NT	-12.3667	132.9667	21/03/1974	M	A	skull; skin
Pm	*ANWC M8912*	Cannon Hill, NT	-12.3667	132.9667	24/09/1974	M		skull; skin
Pm	ANWC M8924	Kapalga Stn, QLD	-12.5333	132.3833	02/08/1973	M	A	skull; skin
Pm	ANWC M10010	Humpty Doo, NT	-12.6333	134.3000	05/01/1972	M	A	skull; skin
Pm	ANWC M10024	Humpty Doo, NT	-12.5667	131.3167	27/10/1971	M	A	skull
Pm	ANWC M12705	Atherton Tableland, QLD	-17.2167	145.4833	27/05/1982	M	A	skull; skin
Pm	ANWC M12721	Atherton Tableland, QLD	-17.2167	145.4833	17/06/1982	M	A	skull; skin
Pm	ANWC M18163	Daly River, NT	-13.3000	130.4667	01/01/1973	M	A	skull; spirit
Pm	*ANWC M18164*	Daly River, NT	-13.3000	130.4667	01/01/1973	F		spirit
Pm	*ANWC M18165*	Daly River, NT	-13.3000	130.4667	01/01/1973	F		spirit
Pm	*ANWC M24193*	Tweed Valley, NSW	-28.5278	153.3533	28/01/1995	F		spirit
Pm	QM J8244	Herberton, QLD	-17.6667	145.2333		F	A	skull; spirit
Pm	QM J15892	Mount Molloy, QLD	-16.6667	145.3333	15/11/1968	M	A	skull; spirit
Pm	QM J20256	Coorgango Stn, QLD	-20.3667	148.2833	23/06/1970	M	A	skull; spirit
Pm	QM JM823	Woodstock, QLD	-19.6333	146.9167	2/09/1970	M	A	skull; spirit
Pm	QM JM979	Mount Molloy, QLD	-16.6667	145.3333		F	A	skull; spirit
Pm	QM JM2757	Mount Tambourine, QLD	-27.9167	153.1667	24/09/1978	F	A	skull; spirit
Pm	QM JM5651	Weipa, QLD	-12.6833	141.8833	4/12/1981		A	skull; spirit
Pm	QM JM6477	Riversleigh, QLD	-19.0333	138.7333	26/06/1988	M	A	skull; spirit

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TABLE 1. (Continued)

Species	Reg. number	Locality	Latitude	Longitude	Date	Sex	Age	specimen as
Pm	QM JM7084	Glenhaughton Stn, QLD	-25.1333	148.9667		F	A	skull; spirit
Pm	QM JM10764	Crows Nest, QLD	-27.2667	152.0500		F	A	skull; spirit
Pm	QM JM12712	Townsville, QLD	-19.1722	146.6250	5/10/1998	M	A	skull; spirit
Pm	WAM M6203	Bellmore Station, QLD	-20.5500	147.8500	~1958	F	A	skull; spirit
Pm	WAM M9946	Mount Basedow, WA	-12.9666	132.5667	25/05/1969	M	A	skull; spirit
Pm	WAM M14305	Drysdale River, WA	-14.7166	126.9000	19/08/1975	M	A	skull; spirit
Pm	WAM M15356	Mitchell Plateau, WA	-14.7208	125.7861	23/03/1977	F	A	skull; spirit
Pm	WAM M16196	Edgar Range, WA	-18.4444	123.0500	28/09/1980	M	A	skull; spirit
Pm	WAM M16883	Lisadell, WA	-16.6033	128.4594	02/05/1980	F	A	skull; spirit
Pm	WAM M18054	Jasper Gorge, WA	-16.0000	130.6417	26/05/1978	M	A	skull; spirit
Pm	WAM M21617[a]	Mitchell Plateau, WA	-14.8250	125.8250	24/10/1981	M	A	skull; spirit
Pm	WAM M21706[a]	Mitchell Plateau, WA	-14.8208	125.8417	09/01/1982	M	A	skull; spirit
Pm	WAM M21847[a]	Mitchell Plateau, WA	-14.7427	126.7833	28/04/1982	M	A	skull; spirit
Pm	*WAM M21998*[c]	Mitchell Plateau, WA	-14.8250	125.8250	08/09/1982	M	A	skull; spirit
Pm	WAM M22667[a]	Martins Well, WA	-16.5805	122.8292	23/06/1981	M	A	skull; spirit
Pm	WAM M30872	Purnululu, WA	-17.3166	128.4500	17/06/1989	F	A	skull; spirit
Pm	*WAM M30873*	Purnululu, WA	-17.7333	128.1500	16/07/1989	M		skull; spirit
Pm	*WAM M30874*	Purnululu, WA	-17.7333	128.1500	18/07/1989	M	A	skull; spirit
Pm	*WAM M30875*	Purnululu, WA	-17.7333	128.1500	19/07/1989	M		skull; spirit
Pm	WAM M30876	Purnululu, WA	-17.3166	128.4500	16/06/1989	M	A	skull; spirit
Pm	*WAM M30877*	Purnululu, WA	-17.3166	128.4500	17/06/1989	M		skull; spirit
Pm	*WAM M30879*	Purnululu, WA	-17.4333	128.4000	07/07/1989	M		skull; spirit
Pm	WAM M30880	Purnululu, WA	-17.7333	128.1500	17/07/1989	M	A	skull; spirit
Pm	*WAM M30881*	Purnululu, WA	-17.7333	128.1500	18/07/1989	M		skull; spirit
Pm	*WAM M30882*	Purnululu, WA	-17.4333	128.4000	04/07/1989	M		skull; spirit
Pm	*WAM M30883*	Purnululu, WA	-17.1666	128.7333	28/07/1989	M		skull; spirit
Pm	*WAM M30884*	Purnululu, WA	-17.1666	128.7333	29/07/1989	M		skull; spirit
Pm	*WAM M32662*	Purnululu, WA	-17.2500	128.3000	25/11/1989	F	SA	skull; spirit
Pm	WAM M32663	Purnululu, WA	-17.4833	128.3667	06/12/1989	M	A	skull; spirit
Pm	WAM M36964	Cutta Cutta Caves, WA	-14.5833	132.4333	28/04/1990	F	A	skull; spirit
Pm	WAM M43137[a]	Mirima NP, WA	-15.7544	128.7850	1994	F	A	skull; spirit
Pm	*WAM M51586*[c]	Mandora, WA	-19.7683	121.3928	18/10/1999	F		skull; skin
*P*MTP	*WAM M18979*	Marillana Stn, WA	-22.7958	119.2292	19/12/1980	M	SA	skull; spirit
*P*MTP	WAM M19497	Pamela Hill, WA	-23.2791	119.1500	02/04/1981	F	SA	skull; spirit
*P*MTP	WAM M47329[a]	Tom Price, WA	-22.7500	117.7667	06/11/1996	M	A	skull; spirit
*P*MTP	WAM M47683	Tom Price, WA	-22.8069	117.7842	15/05/1997	F	A	skull
*P*MTP	WAM M47684	Tom Price, WA	-22.8086	117.7786	20/05/1997	M	A	skull
*P*MTP	WAM M47832[c]	Tom Price, WA	-22.8072	117.7500	10/11/1997	M	A	spirit

......*Continued on the next page*

TABLE 1. (Continued)

Species	Reg. number	Locality	Latitude	Longitude	Date	Sex	Age	specimen as
*P*MTP	WAM M47841[c]	Tom Price, WA	-22.8072	117.7500	12/11/1997	F	A	skull; spirit
*P*MTP	WAM M47916	Newman, WA	-22.9161	118.7133	27/09/1997	M	A	skull; spirit
*P*MTP	WAM M47923	Millstream, WA	-21.2872	117.2642	02/07/1997	M	A	skull; spirit
*P*MTP	WAM M49546	Tom Price, WA	-22.8108	117.7472	25/03/2001	M	A	skull
*P*MTP	WAM M49549	Tom Price, WA	-22.7952	117.7886	25/03/2001	M	A	skull
*P*MTP	WAM M51820[b]	Munni Munni, WA	-21.1633	116.8375	20/10/2001	M	A	skull; spirit
*P*MTP	WAM M52366	Cape Preston, WA	-20.938	116.2008	20/04/2000	F	A	skull; spirit
*P*MTP	WAM M52753	Mulga Downs, WA	-22.3175	118.9799	04/05/2004	F	SA	spirit
*P*MTP	WAM M53052	Coolawanyah, WA	-21.8647	117.7871	25/11/2003	F	A	spirit
*P*MTP	WAM M53341	Mulga Downs, WA	-22.1068	119.0007	04/05/2004	M	A	spirit
*P*MTP	WAM M54583	Karratha, WA	-20.7716	116.8498	21/11/2003	M	SA	spirit
*P*MTP	WAM M55060	Munjina Roadhouse, WA	-22.3466	119.0100	23/03/2004	F	A	skull; spirit
*P*MTP	WAM M55062	Munjina Roadhouse, WA	-22.2991	119.0228	25/03/2004	F	SA	skull; spirit
*P*MTP	WAM M55113[b]	Roy Hill, WA	-22.4697	119.8683	04/07/2004	M	A	skull; spirit
*P*MTP	WAM M55117[b]	Roy Hill, WA	-22.4200	119.7594	04/07/2004	F	SA	skull; spirit
*P*MTP	WAM M55118[b]	Roy Hill, WA	-22.4200	119.7594	04/07/2004	M	A	skull; spirit
*P*MTP	WAM M55123[b]	Roy Hill, WA	-22.4200	119.7594	05/07/2004	M	A	spirit
*P*MTP	WAM M55126[b]	Roy Hill, WA	-22.6544	120.1719	06/07/2004	M	A	skull; spirit
*P*MTP	WAM M55127[b]	Roy Hill, WA	-22.6544	120.1719	06/07/2004	M	A	skull; spirit
*P*MTP	WAM M55133[b]	Roy Hill, WA	-22.4697	119.8683	06/07/2004	M	A	skull; spirit
*P*MTP	WAM M55135[b]	Roy Hill, WA	-22.6494	120.1594	06/07/2004	M	A	skull; spirit
*P*MTP	WAM M55136[b]	Roy Hill, WA	-22.4388	119.8000	07/07/2004	M	A	skull; spirit
*P*MTP	WAM M56182[b]	Pannawonica, WA	-21.6680	115.9106	10/08/2005	M	A	spirit
*P*MTP	WAM M56250	Waldburg Stn, WA	-24.7500	117.3667	18/10/2004	M	A	skull; spirit
*P*MTP	WAM M56257	Waldburg Stn, WA	-24.7500	117.3667	15/10/2004	M	A	skull; spirit
*P*MTP	WAM M56505[b]	Roy Hill, WA	-22.4697	119.8683	08/07/2004	F	S	skull; spirit
*P*MTP	WAM M56508[b]	Roy Hill, WA	-22.6544	120.1719	08/07/2004	M	A	skull; spirit
*P*MTP	WAM M56513[b]	Roy Hill, WA	-22.4200	119.7594	08/07/2004	M	A	skull; spirit
*P*MTP	WAM M56516[b]	Roy Hill, WA	-22.4388	119.8000	09/07/2004	F	SA	skull; spirit
*P*MTP	WAM M56664[b]	Pannawonica, WA	-21.6219	116.3897	07/10/2005	F	A	spirit
*P*MTP	WAM M56677[b]	Marble Bar, WA	-21.3403	119.3656	12/10/2005	M	A	spirit
*P*MTP	WAM M56679[b]	Marble Bar, WA	-21.3403	119.3656	13/10/2005	F	A	spirit
*P*MTP	WAM M56685[b]	Marble Bar, WA	-21.3403	119.3656	14/10/2005	M	A	spirit
*P*MTP	WAM M56691[b]	Marble Bar, WA	-21.3403	119.3656	16/10/2005	M	A	spirit
*P*MTP	WAM M56865[b]	Mount DeCourcy, WA	-22.7112	116.4004	07/10/2004	M	A	skull; spirit
*P*MTP	WAM M56870[b]	Mount DeCourcy, WA	-22.7112	116.4004	08/10/2004	F	A	skull; spirit
*P*MTP	WAM M57242	Pilbara, WA			~2005	M	A	skull; spirit
*P*MTP	WAM M57261[b]	Karratha, WA	-20.7945	116.8567	06/10/2004	M	A	skull; spirit

......*Continued on the next page*

TABLE 1. (Continued)

Species	Reg. number	Locality	Latitude	Longitude	Date	Sex	Age	specimen as
*P*MTP	WAM M57278[b]	Coolawanyah, WA	-21.8764	117.7413	11/10/2004	M	A	skull; spirit
*P*MTP	WAM M57284[b]	Coolawanyah, WA	-21.8764	117.7413	11/10/2004	M	A	skull; spirit
*P*MTP	WAM M57685[b]	Mulga Downs, WA	-22.3469	119.0104	20/10/2004	F	A	skull; spirit
*P*MTP	WAM M57705	Marble Bar, WA	-21.3403	119.3656	02/05/2006	M	SA	spirit
*P*MTP	WAM M57711	Marble Bar, WA	-21.3403	119.3656	04/05/2006	F	A	spirit
*P*MTP	WAM M57912[b]	Barowanna Hill, WA	-21.3949	117.1708	09/05/2005	M	SA	skull; spirit
*P*MTP	WAM M57914[b]	Mulga Downs, WA	-22.1068	119.0007	05/05/2005	F	SA	skull; spirit
*P*MTP	WAM M60028[b]	Warrawagine, WA	-20.8542	120.8533	21/05/2006	M	A	Spirit
*P*MTP	WAM M60031	Warrawagine, WA	-20.8606	120.8206	21/05/2006	M	SA	Spirit
*P*MTP	WAM M60042[b]	Goldsworthy, WA	-20.0339	119.3339	26/05/2006	F	A	Spirit
*P*MTP	WAM M60074	Goldsworthy, WA	-20.0339	119.3339	28/05/2006	M	A	spirit
*P*MTP	WAM M60558[b]	Balfour Downs, WA	-22.6033	120.7833	13/10/2005	M	A	spirit
*P*MTP	WAM M61037[b]	Coongan River, WA	-20.8250	119.5364	25/09/2005	M	A	spirit
*P*MTP	WAM M61040[b]	Coongan River, WA	-20.8250	119.5364	25/09/2005	M	A	spirit
*P*MTP	WAM M61071	Warrawagine, WA	-20.8606	120.8206	03/10/2005	M	A	spirit
*P*MTP	WAM M61081	Warrawagine, WA	-20.8606	120.8206	04/10/2005	M	A	spirit
*P*MTP	WAM M61086	Warrawagine, WA	-20.8606	120.8206	05/10/2005	M	A	spirit
*P*MTP	WAM M61094	Warrawagine, WA	-20.8636	120.7653	06/10/2005	M	A	spirit
*P*MTP	WAM M61155	Tom Price, WA	-22.6072	117.9356	30/05/2006	F	A	spirit
*P*MTP	WAM M61158	Tom Price, WA	-22.6072	117.9356	30/05/2006	F	SA	spirit
*P*MTP	WAM M61162	Tom Price, WA	-22.3058	117.4797	18/05/2006	F	A	spirit
*P*MTP	WAM M61163	Tom Price, WA	-22.3058	117.4797	18/05/2006	F	A	spirit
*P*MTP	WAM M61659[b]	Tom Price, WA	-22.6072	117.9356	30/05/2006	F	A	spirit
*P*MTP	WAM M61675[b]	Tom Price, WA	-22.6072	117.9356	28/05/2006	M	A	spirit
*P*MTP	WAM M61774[b]	Balfour Downs, WA	-22.5442	120.7992	13/05/2006	F	SA	spirit
*P*MTP	WAM M62896[b]	Millstream NP, WA	-21.4767	117.1490	22/03/2015	M	SA	spirit
*P*MTP	WAM M62897[b]	Millstream NP, WA	-21.4365	117.1585	24/03/2015	F	A	spirit
*P*MTP	WAM M64697[b]	Tom Price, WA	-22.5047	117.7036	21/05/2006	M	SA	spirit
*P*MTP	WAM M64700[b]	Tom Price, WA	-22.3058	117.4797	21/05/2006	M	SA	spirit
*P*MTP	WAM M64756	Tom Price, WA	-22.3058	117.4797	26/05/2006	M	SA	spirit
*P*MTP	WAM M64893	Dampier, WA	-20.8025	116.6653	15/09/2006	M	A	spirit
Pt	QM JM10774	Capella District, QLD	-23.0833	148.0167		F	A	skull; spirit
Pt	QM JM14377	Mt Stuart, QLD	-23.5000	148.6167	1/08/1998		A	skull; spirit
Pt	QM JM14444	Prairie, QLD	-23.1000	147.7833	9/12/2000		A	skull; spirit
Pt	SAMA M8405	Mulga Creek Well, SA	-30.2333	139.6333	16/09/1970		A	skull
Pt	SAMA M11028	Mount Remarkable NP, SA	-32.8083	138.0750	24/10/1982	F	A	skull
Pt	SAMA M18743	Backadinna Hill, SA	-29.1964	135.1814	04/10/1995	M	A	skull
Pt	SAMA M18745	New Years Gift Bore, SA	-29.6731	137.2919	25/03/1996	F	A	skull
Pt	SAMA M26276	Yeltacowie Stn, SA	-31.2400	137.5053	09/09/2007	F	A	skull

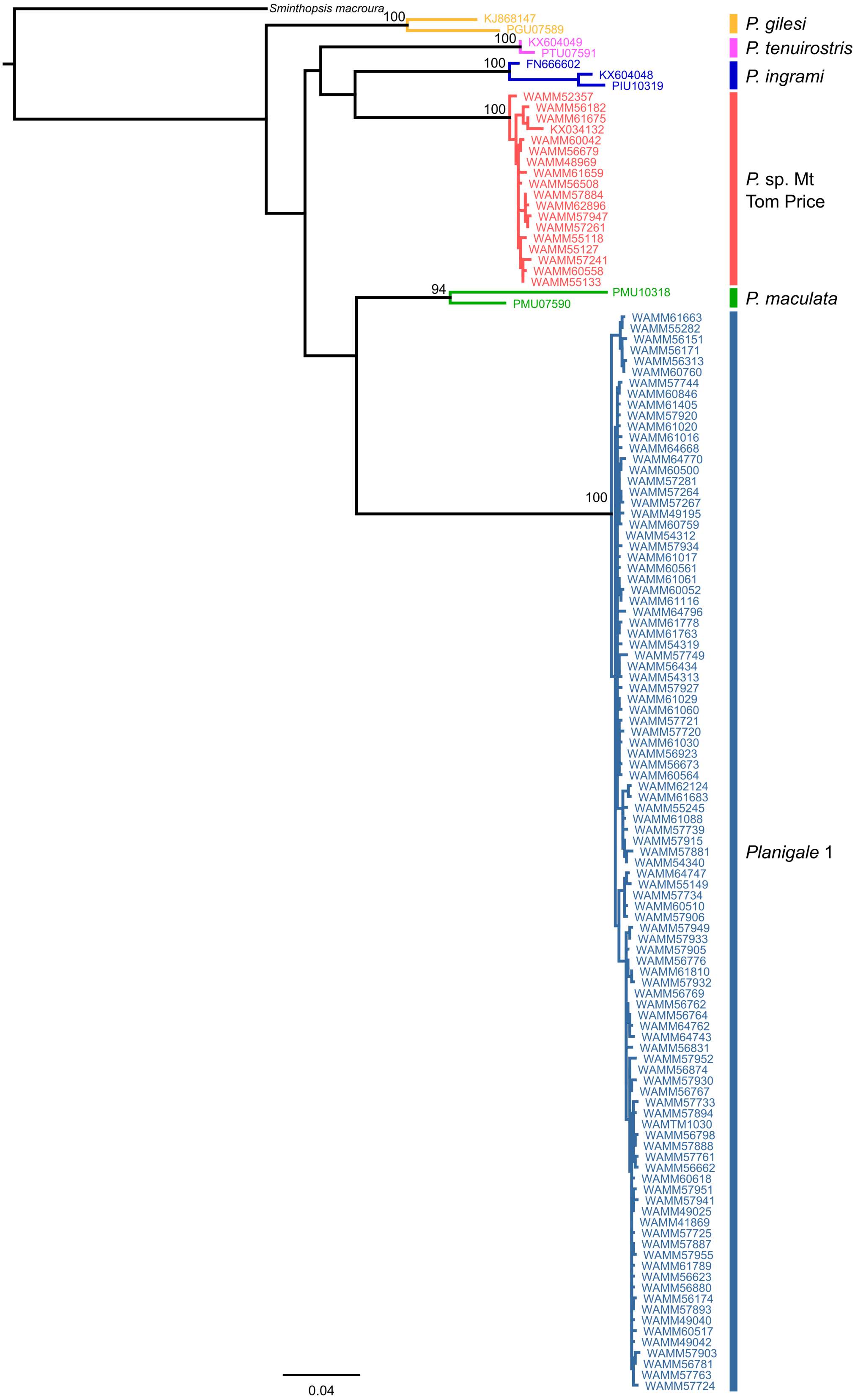

FIGURE 5. Maximum likelihood phylogenetic tree of planigale cytochrome *b* sequence data (n = 128) from previous studies (Painter *et al*. 1995; Krajewski *et al*. 1997a; Mitchell *et al*. 2014; Westerman *et al*. 2016; Umbrello *et al*. 2020) using *Sminthopsis macroura* as an outgroup. Branch support lower than 90% not shown.

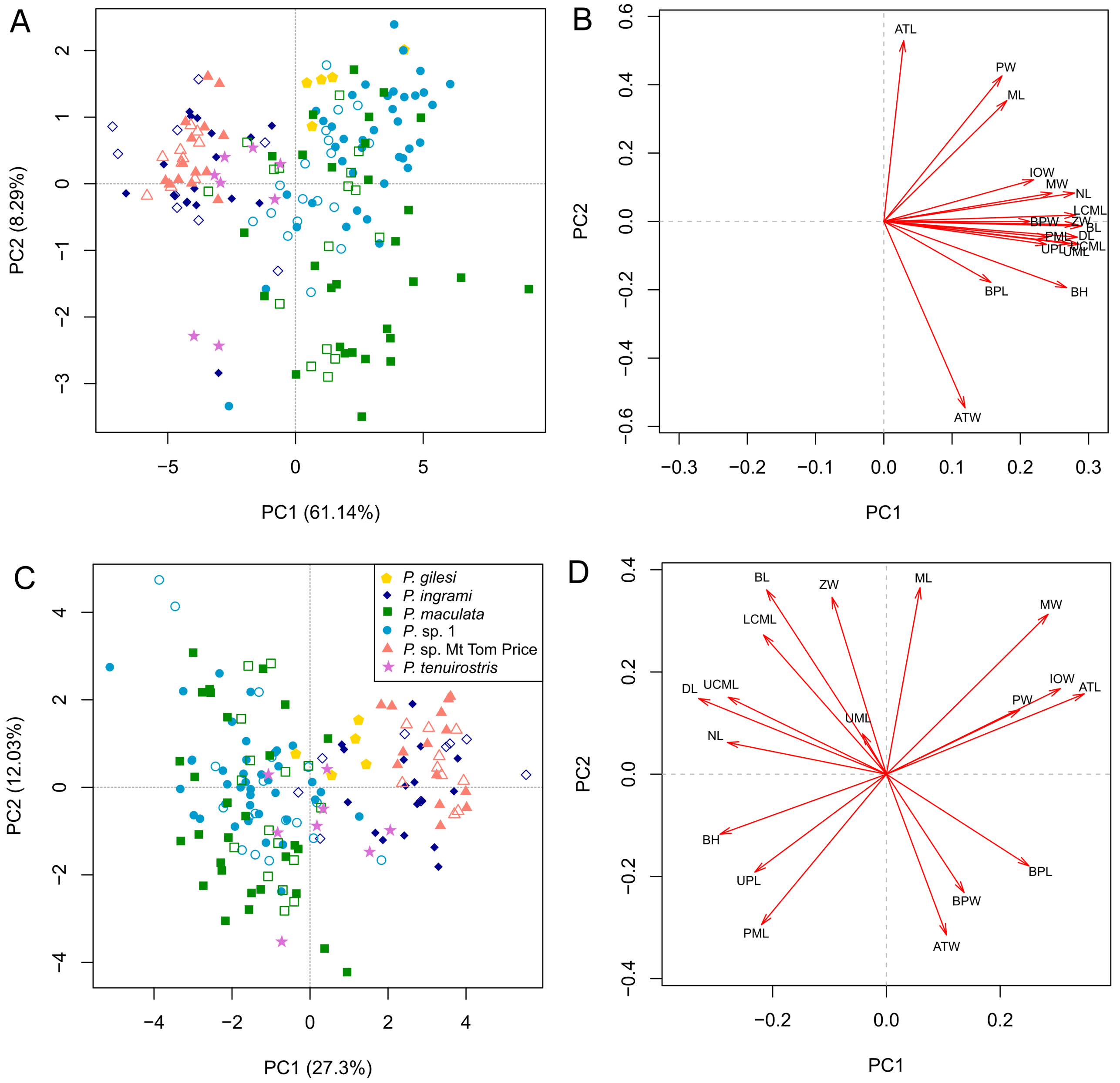

FIGURE 6. PCA on the craniodental measurement data for *Planigale* in this study, males are closed symbols and females open symbols (note sex is not indicated for *Planigale gilesi* and *P. tenuirostris*). A) PCA before skull size has been accounted for, variation explained by PC1 axis can be interpreted as size, and B) character loadings (eigenvectors) showing the contribution of each measurement variable to PC1 and PC2. C) PCA and D) character loadings after skull size has been accounted for, less variation is explained by PC1 and with size continuing to influence PC1. PCA axes are not scaled accordingly. Note both before and after size correction there is no overlap in the distribution of samples of the two Pilbara forms.

The craniodental dataset had an average of 5% missing data and no individual more than 30% data missing. The two characters that were removed due to the missing data threshold of 20% were APF (26% missing) and MLPV (33% missing); both occur on the palate, which had not been cleaned completely in some specimens. The initial PCA on the non-size corrected data had PC1 explaining 61.14% and PC2 explaining 8.29% of the variance in the dataset (Fig. 6A), with large and small animals distributed at either end of PC1. An examination of the contribution of each measurement character to the PC loadings showed that all characters were tending towards the positive of PC1, a clear indication that larger size was contributing the most to the variation of PC1 (Fig. 6B). When the effect of size was removed, the amount of variation explained by the first two PCs was reduced (PC1 = 27.5%; PC2 = 12.03%; Fig. 6C), but the overall placement of individuals in the PC space remained the same and the measurement variables contributed to both PC1 and PC2 more evenly (Fig. 6D).

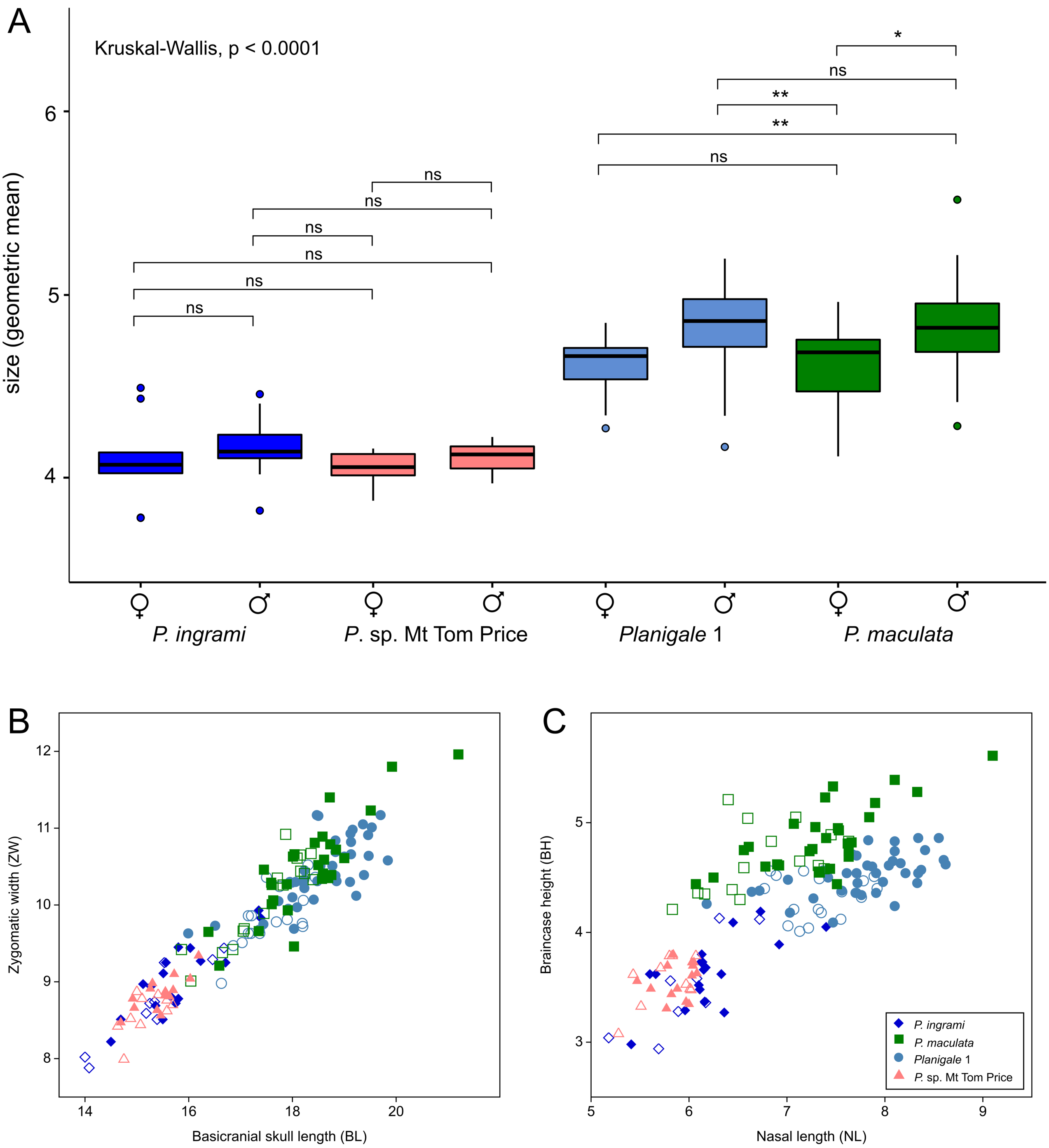

FIGURE 7. A) Comparison of overall skull size (geometric mean) between male and female planigales from four species, *Planigale ingrami*, *P*. Mt Tom Price, *Planigale* 1 and *P. maculata*. All pairwise comparisons had $p < 0.0001$ unless indicated otherwise ($p > 0.05$, ns; $p < 0.05$, *; $p < 0.001$, **). B) and C) comparisons of selected cranial measurements (in mm) for *Planigale ingrami*, *P. maculata*, *Planigale* 1 and *P*. sp. Mt Tom Price, closed symbols are males, open symbols are females. B) overall skull size using basicranial skull length and zygomatic width; C) length of nasals vs. braincase height, which demonstrates separation of the two Pilbara planigale lineages.

The results of the Kruskal-Wallis rank sum test on the geometric mean showed a significant difference between groups (species and sex; $p < 0.001$; Fig. 7A). The pairwise Wilcox test showed no significant difference in size between males and females within the smaller planigales (*P. ingrami* or *P*. sp. Mt Tom Price; $p > 0.05$) but there were significant size differences between the sexes of the larger planigales (*P. maculata* and *Planigale* 1; $p = 0.001–0.05$), with males being larger than females for both species. Between species, there were only significant size differences between the small vs. large species, for example, *P. ingrami* vs. *P. maculata* ($p < 0.0001$; Fig. 7A). The smaller two forms were consistently smaller for all variables than the larger two species (Table 2) and *Planigale* 1 and *P*. sp. Mt Tom Price specimens could be reliably separated using BH (braincase height) and NL (length of nasals) (Fig. 7C).

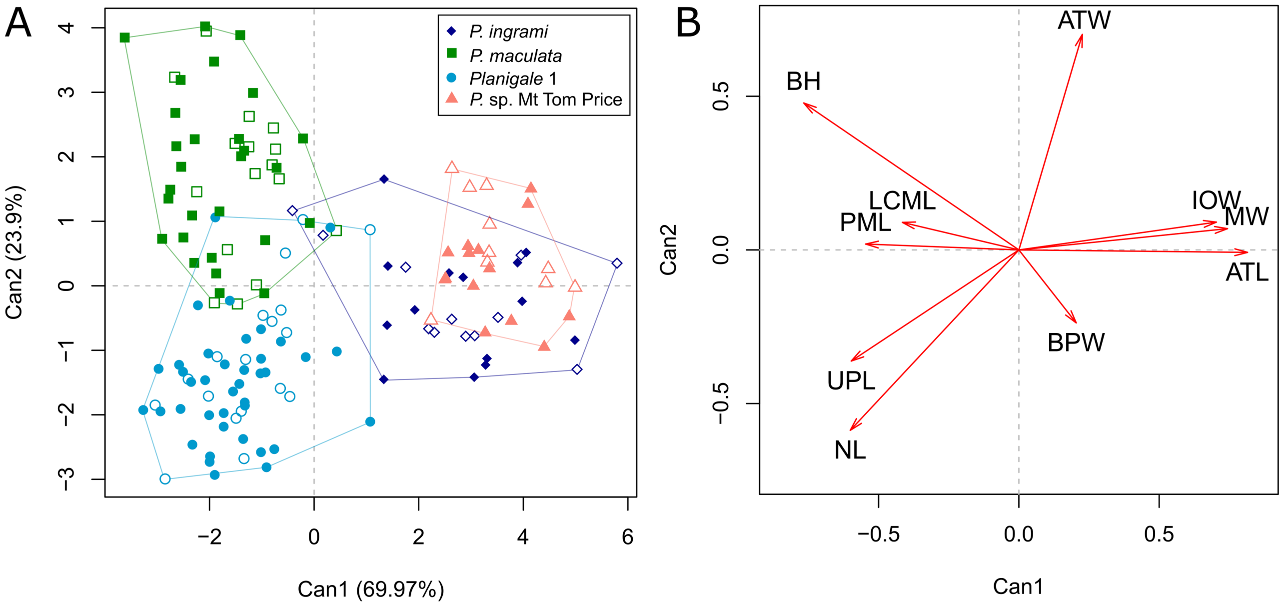

FIGURE 8. A) CDA on the craniodental measurement data where size has been accounted for, for *Planigale* 1, *P. maculata*, *P. ingrami* and *P*. sp. Mt Tom Price, note males and females shown as closed and open symbols, respectively. Character contributions to canonical axes 1 and 2 as total canonical structure coefficients. Axes not scaled accordingly.

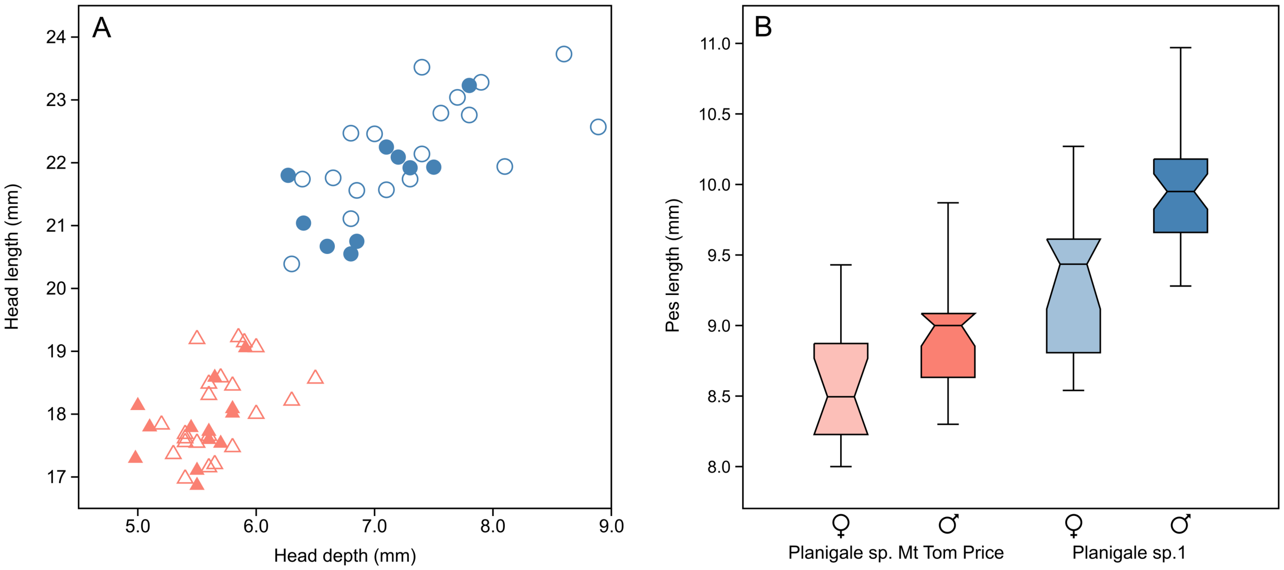

FIGURE 9. A) External head length vs. head depth (mm) of the two forms of Pilbara *Planigale* (salmon *Planigale* sp. Mt Tom Price, blue *Planigale* 1) closed symbols are males and open are females. B) Box plots of pes length (mm) measurements for male and female *Planigale* sp. Mt Tom Price (salmon) and *Planigale* 1 (blue).

The CDA on the size-corrected data, which was used to find differences in skull shape, showed a high percent of variation explained by Canonical axis 1 (70%) which separated the smaller and larger species, with characters such as tooth row lengths and braincase and inter-orbital widths important for distinguishing between them (Fig. 8). Canonical axis 2 accounted for 24% of the variation and separated the two larger species, *Planigale* 1 and *P. maculata*, based on braincase height, nasal length and upper premolar row length. There was little separation between *P. ingrami* and *P*. sp. Mt Tom Price, and there were no clear shape differences between the sexes within *P. maculata* or *Planigale* 1, despite the previous analysis finding they were significantly different in size. As such,

TABLE 2. Summary of cranial measurements (in mm) of Planigale species measured in this study, number of individuals (n), minimum and maximum value (range), mean and standard deviation ($\bar{x} \pm \sigma$). Species: *Pg*, *Planigale gilesi*; *Pi*, *P. ingrami*; *P*1, *Planigale* 1; *Pm*, *P. maculata*; *P*MTP, *P.* sp. Mt Tom Price, *Pt*, *P. tenuirostris*.

Species		MW	ML	PML	NW	NL	IOW	ZW	IFL	BH	BL	BPL	BPW
Pg	*n*	5	5	5	5	5	5	5	5	5	5	5	5
	range	8.01–8.50	3.50–4.02	2.68–3.79	3.00–3.54	6.76–8.07	4.02–4.55	9.72–10.80	1.26–1.57	3.85–4.44	17.11–18.63	3.09–3.22	3.06–3.43
	$\bar{x} \pm \sigma$	8.18 ± 0.20	3.77 ± 0.21	3.11 ± 0.46	3.23 ± 0.24	7.48 ± 0.49	4.30 ± 0.24	10.23 ± 0.40	1.46 ± 0.13	4.17 ± 0.21	17.79 ± 0.57	3.16 ± 0.05	3.28 ± 0.14
Pi	*n*	10	10	10	9	10	10	10	9	10	10	9	9
F	range	6.80–7.59	3.09–3.95	1.69–3.37	2.51–2.91	5.18–6.72	3.75–4.09	7.88–9.44	1.12–1.49	2.94–4.13	14–16.68	2.75–3.09	2.7–3.23
	$\bar{x} \pm \sigma$	7.16 ± 0.24	3.5 ± 0.31	2.12 ± 0.48	2.68 ± 0.12	5.96 ± 0.43	3.89 ± 0.12	8.67 ± 0.54	1.30 ± 0.11	3.49 ± 0.41	15.24 ± 0.89	2.89 ± 0.11	2.90 ± 0.18
Pi	*n*	17	17	17	13	17	17	17	12	17	16	16	17
M	range	6.88–7.72	2.98–4.31	1.69–3.16	2.50–3.15	5.41–7.40	3.54–4.04	8.22–9.93	1.13–1.45	2.98–4.19	14.5–17.39	2.86–3.37	2.82–3.52
	$\bar{x} \pm \sigma$	7.29 ± 0.23	3.44 ± 0.36	2.30 ± 0.35	2.79 ± 0.19	6.22 ± 0.48	3.86 ± 0.15	9.04 ± 0.47	1.29 ± 0.11	3.64 ± 0.31	15.78 ± 0.82	3.02 ± 0.16	3.14 ± 0.18
*P*1	*n*	18	18	18	17	18	18	15	17	18	18	18	18
F	range	7.52–8.16	3.31–4.45	2.38–3.07	2.48–3.48	6.77–7.92	3.63–4.46	8.98–10.52	1.07–1.59	4.01–4.56	16.63–18.44	2.45–3.49	2.75–3.88
	$\bar{x} \pm \sigma$	7.82 ± 0.17	3.81 ± 0.33	2.75 ± 0.24	2.93 ± 0.22	7.33 ± 0.36	4.06 ± 0.21	9.80 ± 0.38	1.42 ± 0.18	4.33 ± 0.19	17.56 ± 0.54	3.11 ± 0.31	3.33 ± 0.25
*P*1	*n*	39	39	39	39	39	39	37	39	39	39	39	39
M	range	7.12–8.55	2.91–5.38	2.19–4.30	2.67–3.64	6.18–8.62	3.55–4.86	9.63–11.17	1.02–2.06	4.09–4.86	15.99–19.84	2.78–3.72	2.58–4.05
	$\bar{x} \pm \sigma$	7.97 ± 0.35	4.1 ± 0.44	3.00 ± 0.45	3.11 ± 0.25	7.79 ± 0.55	4.31 ± 0.25	10.45 ± 0.44	1.57 ± 0.30	4.52 ± 0.19	18.56 ± 0.81	3.23 ± 0.24	3.42 ± 0.28
Pm	*n*	16	17	17	8	17	17	16	7	17	16	16	16
F	range	7.23–8.36	3.13–4.96	2.04–3.66	2.62–3.23	5.83–7.63	3.19–4.49	9.01–10.92	0.92–1.66	4.21–5.21	15.86–18.4	2.38–3.57	2.78–3.72
	$\bar{x} \pm \sigma$	7.71 ± 0.34	3.69 ± 0.56	2.75 ± 0.49	2.91 ± 0.18	6.81 ± 0.53	4.11 ± 0.29	10.09 ± 0.55	1.37 ± 0.26	4.63 ± 0.3	17.48 ± 0.81	3.05 ± 0.24	3.29 ± 0.27
Pm	*n*	29	29	29	11	29	29	29	10	29	29	29	29
M	range	7.24–9.10	2.82–4.37	2.22–3.81	2.74–3.37	6.07–9.10	3.91–5.00	9.10–11.96	1.29–1.55	4.44–5.61	16.28–21.2	2.61–3.95	2.56–3.87
	$\bar{x} \pm \sigma$	7.96 ± 0.43	3.69 ± 0.44	3.08 ± 0.47	3.00 ± 0.23	7.34 ± 0.63	4.3 ± 0.25	10.43 ± 0.67	1.43 ± 0.09	4.86 ± 0.30	18.24 ± 1.02	3.16 ± 0.37	3.27 ± 0.3
*P*MTP	*n*	10	10	10	10	10	10	10	8	9	10	10	10
F	range	7.22–7.64	3.16–3.61	1.72–2.40	2.42–2.94	5.28–6.07	3.86–4.19	8.01–8.89	1.12–1.52	3.09–3.80	14.63–15.69	2.79–3.01	2.68–3.19

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TABLE 2. (Continued)

Species		MW	ML	PML	NW	NL	IOW	ZW	IFL	BH	BL	BPL	BPW
	$\bar{x} \pm \sigma$	7.37 ± 0.14	3.33 ± 0.14	2.13 ± 0.20	2.73 ± 0.14	5.76 ± 0.28	4.00 ± 0.11	8.61 ± 0.26	1.30 ± 0.13	3.54 ± 0.23	15.17 ± 0.37	2.90 ± 0.08	2.87 ± 0.19
*P*MTP	*n*	14	14	14	14	14	14	14	12	13	14	14	14
M	range	7.29–7.68	3.19–3.83	1.56–2.50	2.48–2.87	5.47–6.08	3.80–4.29	8.49–9.36	1.15–1.49	3.32–3.81	14.69–16.19	2.81–3.17	2.54–3.22
	$\bar{x} \pm \sigma$	7.46 ± 0.14	3.5 ± 0.19	2.14 ± 0.27	2.67 ± 0.13	5.88 ± 0.18	4.07 ± 0.13	8.87 ± 0.23	1.33 ± 0.10	3.58 ± 0.16	15.45 ± 0.42	2.98 ± 0.12	2.88 ± 0.2
Pt	*n*	8	8	8	5	8	8	8	5	8	8	8	8
	range	6.47–7.72	3.31–3.70	2.27–2.84	2.64–3.03	6.15–7.25	3.58–4.15	7.97–9.89	1.35–1.54	3.46–4.16	15.59–17.09	2.73–3.71	2.90–3.36
	$\bar{x} \pm \sigma$	7.22 ± 0.38	3.49 ± 0.14	2.58 ± 0.23	2.80 ± 0.14	6.75 ± 0.40	3.81 ± 0.21	9.00 ± 0.58	1.44 ± 0.07	3.88 ± 0.22	16.35 ± 0.53	3.11 ± 0.31	3.11 ± 0.16

Species		ATL	ATW	IBW	PW	MFL	PL	UCML	UPL	UML	DL	LCML
Pg	*n*	4	4	5	5	3	5	5	5	5	5	5
	range	2.46–2.79	2.36–2.65	2.43–2.92	1.89–2.28	1.02–1.28	8.95–9.83	6.45–7.24	1.36–1.59	3.92–4.45	12.97–14.10	6.71–7.69
	$\bar{x} \pm \sigma$	2.66 ± 0.14	2.54 ± 0.13	2.74 ± 0.20	2.03 ± 0.15	1.14 ± 0.13	9.28 ± 0.34	6.67 ± 0.33	1.49 ± 0.09	4.18 ± 0.19	13.29 ± 0.46	7.03 ± 0.40
Pi	*n*	9	9	9	7	5	9	10	10	10	10	10
F	range	2.31–2.56	2.23–3.17	1.98–2.56	1.54–1.95	0.55–1.23	6.90–8.74	5.16–6.52	1.31–1.89	3.21–3.96	9.98–12.82	5.44–6.72
	$\bar{x} \pm \sigma$	2.42 ± 0.08	2.47 ± 0.29	2.25 ± 0.19	1.73 ± 0.15	0.76 ± 0.28	7.77 ± 0.70	5.72 ± 0.44	1.52 ± 0.17	3.57 ± 0.25	11.35 ± 0.99	5.98 ± 0.48
Pi	*n*	16	16	15	17	9	17	17	16	17	16	17
M	range	1.76–2.69	2.21–3.10	1.42–2.70	1.42–1.94	0.42–0.96	6.91–8.95	5.40–6.17	1.31–1.59	3.33–4.10	10.34–13.33	5.56–6.39
	$\bar{x} \pm \sigma$	2.45 ± 0.21	2.50 ± 0.24	2.24 ± 0.32	1.72 ± 0.13	0.64 ± 0.17	7.89 ± 0.51	5.74 ± 0.21	1.47 ± 0.08	3.57 ± 0.19	11.59 ± 0.74	5.97 ± 0.25
*P*1	*n*	18	18	18	18	18	18	18	18	18	18	18
F	range	2.05–2.95	2.17–2.81	1.70–3.08	1.50–2.15	0.59–1.32	8.66–9.86	6.43–7.16	1.43–2.30	3.69–4.22	12.56–14.12	6.35–7.53
	$\bar{x} \pm \sigma$	2.37 ± 0.25	2.42 ± 0.16	2.33 ± 0.31	1.81 ± 0.17	1.06 ± 0.18	9.31 ± 0.29	6.69 ± 0.22	1.9 ± 0.24	4.03 ± 0.14	13.31 ± 0.52	6.96 ± 0.28
*P*1	*n*	39	39	39	39	39	39	39	39	39	39	39
M	range	2.11–2.87	2.21–2.87	1.74–2.99	1.12–2.15	0.59–1.37	8.5–10.85	6.23–7.66	1.59–2.37	3.42–4.48	12.33–15.2	6.12–7.98
	$\bar{x} \pm \sigma$	2.44 ± 0.16	2.49 ± 0.14	2.57 ± 0.29	1.91 ± 0.21	1.17 ± 0.15	9.8 ± 0.50	6.95 ± 0.32	2.02 ± 0.19	4.15 ± 0.22	14.1 ± 0.74	7.23 ± 0.40

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TABLE 2. (Continued)

Species		ATL	ATW	IBW	PW	MFL	PL	UCML	UPL	UML	DL	LCML
Pm	*n*	16	16	15	17	7	17	17	17	17	17	17
F	range	2.10–2.70	2.09–3.46	2.03–2.90	1.71–1.96	0.75–1.34	8.22–9.65	6.06–6.99	1.61–2.10	3.82–4.29	11.77–14.29	6.46–7.36
	$\bar{x} \pm \sigma$	2.36 ± 0.20	2.83 ± 0.51	2.53 ± 0.23	1.83 ± 0.08	1.09 ± 0.21	9.21 ± 0.39	6.65 ± 0.24	1.81 ± 0.14	4.06 ± 0.13	13.38 ± 0.75	6.89 ± 0.28
Pm	*n*	28	28	27	29	10	29	29	29	29	29	29
M	range	2.10–2.89	2.25–3.71	2.25–3.13	1.64–2.16	0.77–1.43	8.77–11.16	6.34–8.05	1.52–2.27	3.79–4.77	11.73–16.10	6.45–8.16
	$\bar{x} \pm \sigma$	2.39 ± 0.20	3.02 ± 0.47	2.61 ± 0.24	1.84 ± 0.13	1.06 ± 0.20	9.71 ± 0.51	6.95 ± 0.41	1.86 ± 0.18	4.20 ± 0.24	13.99 ± 0.97	7.28 ± 0.44
*P*MTP	*n*	10	10	9	9	9	9	10	9	10	10	10
F	range	2.27–2.58	2.24–2.69	1.86–2.43	1.57–1.91	0.42–1.13	7.28–8.10	5.51–5.79	1.38–1.50	3.39–3.59	10.72–11.46	5.58–6.18
	$\bar{x} \pm \sigma$	2.44 ± 0.11	2.41 ± 0.13	2.17 ± 0.18	1.74 ± 0.11	0.64 ± 0.21	7.69 ± 0.26	5.63 ± 0.08	1.44 ± 0.04	3.51 ± 0.06	11.16 ± 0.25	5.91 ± 0.18
*P*MTP	*n*	12	13	11	14	9	14	14	14	14	14	14
M	range	2.28–2.60	2.22–2.57	1.86–2.45	1.56–1.98	0.59–0.93	7.37–8.43	5.51–5.98	1.35–1.64	3.43–3.67	10.31–12.06	5.82–6.47
	$\bar{x} \pm \sigma$	2.46 ± 0.10	2.40 ± 0.09	2.25 ± 0.19	1.71 ± 0.12	0.76 ± 0.10	7.95 ± 0.28	5.73 ± 0.15	1.51 ± 0.07	3.54 ± 0.09	11.24 ± 0.41	6.04 ± 0.19
Pt	*n*	7	7	6	8	3	8	8	8	8	8	8
	range	2.08–2.49	2.20–2.92	2.32–2.54	1.46–2.03	0.58–0.97	8.00–8.98	5.83–6.21	1.60–1.97	3.39–3.84	11.53–13.02	6.00–6.71
	$\bar{x} \pm \sigma$	2.30 ± 0.15	2.45 ± 0.29	2.44 ± 0.08	1.77 ± 0.20	0.79 ± 0.20	8.39 ± 0.32	6.01 ± 0.14	1.76 ± 0.12	3.66 ± 0.14	12.15 ± 0.47	6.32 ± 0.23

the sexes were grouped for further tests as we did not find significant sexual dimorphism for skull shape for any of the four species. The PERMANOVA results showed a significant difference in shape between species (F = 22.84; p < 0.0001), and the pairwise comparisons were significantly different between all pairs (p < 0.001) except *P. ingrami* and *P*. sp. Mt Tom Price (p = 0.19), consistent with the CDA results.

While the PERMANOVA and CDA failed to detect significant differences between *P. ingrami* and *P*. sp. Mt Tom Price specimens, it is noteworthy that the k-nearest neighbour classification assigned *P*. sp. Mt Tom Price (n = 24) into the correct group 100% of the time (Table 3). The next best sorted group was *Planigale* 1 (93%, n = 57), followed by *P. maculata* and lastly *P. ingrami*. The latter two groups are purported to be species complexes, based on molecular sequence data (Blacket *et al.* 2000; Westerman *et al.* 2016), which could explain the lower performance of the analyses as grouping these as separate distinct taxa, as they likely currently contain multiple morphologically diverse forms. One-way ANOVAs on individual variables showed significant differences between the two smaller species, *P. ingrami* and *P*. sp. Mt Tom Price, at three variables, MW (p = 0.005), NL (p = 0.012) and IOW (p < 0.0001).

TABLE 3. Results from the k-nearest neighbour classification analysis showing the number of specimens placed into the original or different 'taxon' and the percent correct assignments per species.

Taxon	as *P. ingrami*	as *Planigale* 1	as *P. maculata*	as *P*. sp. Mt Tom Price	n	% correct
P. ingrami	14	0	3	9	26	53.9
Planigale 1	1	53	3	0	57	93
P. maculata	0	11	33	0	44	75
P. sp. Mt Tom Price	0	0	0	24	24	100
Total	15	64	39	33	151	82.1

TABLE 4. External measurements (in mm) of female (♀♀) and male (♂♂) *Planigale* 1 and *P.* sp. Mt Tom Price specimens measured in this study, number of individuals (*n*), minimum and maximum value (range), mean and standard deviation (x̄ ± σ).

		head-vent	vent-tail	pes	ear	head depth	head width	head length	weight
					***Planigale* 1**				
	n	26	27	16	7	10	10	10	68
♀♀	range	52–69	49–76	8.54–10.27	9.6–12.25	6.27–7.8	9.5–11.0	20.55–23.23	4.1–9.5
	x̄ ± σ	60.2 ± 4.76	64.7 ± 6.24	9.32 ± 0.51	10.70 ± 0.90	6.98 ± 0.49	10.15 ± 0.53	21.62 ± 0.85	6.5 ± 1.29
	n	60	57	43	13	18	18	18	126
♂♂	range	46–74	54–77	9.28–10.97	10.17–12.70	6.30–8.89	9.8–11.9	20.39–23.73	4.5–12.5
	x̄ ± σ	63.5 ± 5.53	66.9 ± 5.06	9.92 ± 0.38	11.04 ± 0.74	7.36 ± 0.72	10.69 ± 0.66	22.25 ± 0.87	7.68 ± 1.66
					***Planigale* sp. Mt Tom Price**				
	n	20	20	14	3	12	12	12	14
♀♀	range	45–60	48–65	7.50–9.43	7.70–9.02	4.98–5.91	8.35–9.20	16.9–19.09	2.9–4.7
	x̄ ± σ	53.0 ± 4.55	56.7 ± 3.29	8.58 ± 0.43	8.03 ± 0.67	5.51 ± 0.30	8.79 ± 0.25	17.85 ± 0.59	3.85 ± 0.48
	n	45	45	24	6	22	22	23	36
♂♂	range	47.5–62.5	52–66	8.30–9.87	7.90–9.01	5.2–6.5	8.30–9.86	16.93–19.26	3.4–6.1
	x̄ ± σ	54.4 ± 3.12	59.0 ± 3.15	8.92 ± 0.38	8.66 ± 0.41	5.68 ± 0.32	8.79 ± 0.38	18.04 ± 0.73	4.6 ± 0.62

In all external measurements, *Planigale* 1 was significantly larger than *Planigale* sp. Mt Tom Price (p < 0.001; Table 4). The two groups were most clearly differentiated on head length with *Planigale* 1 having head lengths greater than 20 mm and *Planigale* sp. Mt Tom Price less than 20 mm (Fig. 9A). There was significant sexual dimorphism in head-vent and pes length for *Planigale* 1, and pes length for *P*. sp. Mt Tom Price (Fig. 9B); all other variables showed no significant size differences between the sexes within the two Pilbara lineages.

Systematics

Order Dasyuromorphia Gill, 1872

Family Dasyuridae Goldfuss, 1820

Genus Planigale Troughton, 1928

Planigale kendricki Aplin, Cooper, Travouillon & Umbrello sp. nov.

(Fig. 10–13, Tables 2, 4)
urn:lsid:zoobank.org:act:DCFFF2D7-37E8-4DB1-BE82-E4DC10ADCF2D
Formerly referred to as '*Planigale* 1' by the following authors: Blacket *et al.* (2000) and Westerman *et al.* (2016), and *Planigale* sp. 1 by Gibson & McKenzie (2009) and Umbrello *et al.* (2020).

FIGURE 10. Photo of *Planigale kendricki* sp. nov. courtesy of R. Teale. Note the rufous, orange-tan colouration of the fur and the orange eye ring.

Holotype. WAM M41812: subadult male with incompletely erupted P_3; Barlee Range Nature Reserve, Western Australia, 23°23'21" S, 115°53'12" E. Collected by P. Kendrick, 13th June 1994. Spirit and skull. Liver tissue, ABTC61747. Specimen located in the Western Australian Museum Mammal collection, Welshpool, Western Australia.

Paratypes. WAM M15160: adult male, Mt Bruce, Western Australia, 22°38’15” S, 118°08’00” E (note: this location is now the Marandoo mine site). Collected by J. Burt, 2nd February 1976. Spirit and skull. WAM M25773, adult female, Karlamilyi National Park, Western Australia, 22°18’51” S, 122°03’19” E. Collected by R. Hart, 18 April 1986. Spirit and skull. WAM M51581: adult female, Mandora, Western Australia, 19°47’52” S, 121°26’52” E. Collected by P. Kendrick, 18th October 1999. Spirit and skull. Liver tissue, ABTC97502; ABTC161754.

Etymology. Named in honour of Dr Peter Kendrick, in recognition of his major contribution to the understanding of the vertebrate fauna of north-western Australia.

Material examined. See Table 1 for a list of all *Planigale kendricki* specimens examined in this study, referred to as *Planigale* 1 in the table.

Diagnosis. *Planigale kendricki* (Fig. 10) is more rufous than all other members of the genus except perhaps some individuals of *P. ingrami*. It is substantially larger than each of *P. ingrami, P. tenuirostris* and *P.* sp. Mt Tom Price, and smaller than *P. novaeguineae* and *P. gilesi*. It is most similar in body size to some populations of *P. maculata* but differs from all populations of this taxon in its brighter dorsal and facial patterning. Craniodentally, it differs from all other *Planigale* species except *P. tenuirostris* in having more elongate nasals that invade deeply between the frontals. It further differs from typical *P. maculata*, and *P. novaeguineae* in having a more depressed cranium, a longer and narrower snout, and larger entoconids on $M_{1–3}$. It further differs from *P. gilesi* in having three upper premolars (reduced to two in *P. gilesi*). It also differs from *P. tenuirostris* in having less reduced $M^{1–4}$ protocones and less reduced entoconids on $M_{1–3}$ (usually absent on $M_{1–2}$ in *P. tenuirostris*).

Description

External morphology. *Planigale kendricki* has a maximum recorded body weight of 12.5 g and snout-vent length of 74 mm for males. Females tend to be slightly smaller than males, with a maximum weight of 9.5 g and snout-vent length 69 mm (see Table 4 for summary of external measurements). The ratio of tail length to snout-vent length was 87–129% (mean 106%) for males and 83–129% (mean 108%) for females. There was no obvious sexual dimorphism in colouration or proportions.

Pelage on the back and upper flanks is dense, moderately thick and very soft, overall orange-tan, ticked with dark brown. The hue is even across the back but paling onto lower flanks. Contour hairs on the mid-back measure c. 4 mm. Hairs are tricoloured: basal two thirds are dull slate, the distal third yellow, frequently with a short, dark brown tip. On the lower flanks, contour hairs have a grey basal half, are yellowish-tan distally and only occasionally with dark tips. Fine guard hairs project 2–3 mm beyond the main pelt over the entire back and flanks but are longer on the rump than elsewhere. Guard hairs on the back are bi-coloured, with the basal half transparent and the distal half dark brown to black. On the flanks, guard hairs are transparent for the entire length. The forearm has three sets of vibrissae (anconeal, antebrachial and carpal); all are pale tan to transparent. The hindlimb has fine, transparent calcaneal vibrissae.

The ventral pelage measures c. 3.5 mm on the abdomen. Hairs are bicoloured, with the basal half dull slate, the distal half cream. The thoracic region is the same colour as the fur of the abdomen but grading forward to pure cream on the throat and chin. The inside of hindlimbs is concolorous with the abdomen but inside of the forelimbs is paler, the hairs are grey basally, off white distally.

The pelage on the head is a more even orange-tan than on the back. Hairs on the snout are only rarely with dark tips, these becoming more conspicuous in the area between the eyes and more abundant on the crown. The upper lip from mouth opening to vibrissal pad with a narrow band of off-white hairs, extending onto lower cheek and back to genal vibrissae. The eye is surrounded by a ring of pale orange fur, weakly set off from the rest of the face. The eyelids are fringed with short, black hairs. The rhinarium is naked, with a deep medial groove and black, granular skin. The mystacial vibrissae are delicate, mostly bicoloured, with a dark basal section and golden tips, although some are all golden in colour; the longest reach to the middle of the pinna when folded back. The genal vibrissae extend past the ears when folded back. The supraorbital vibrissae are short and black with golden tipping. The interramal vibrissae are pale, almost transparent but conspicuous. The vibrissal papillae on the face are unpigmented.

The pinnae are moderately large and rounded with a weak posterior notch. The skin of the pinna is dark grey with the outer surface evenly clothed with fine pale orange hairs and the inner surface more densely furred along the posterior margin. The supratragus is moderately elongate and tall, with the anterior margin curled over the anterior margin of the pinna above the tragus.

The pes, including digits, is densely furred with white hairs mixed with tan near the ankle, grading to pure white on the metatarsal portion and onto the digits. The plantar surface has finely granular skin and seven distinct plantar pads, all consisting of granular mounds capped by apical pads (Fig. 11). The surface of all pads appears smooth but with visible internal striae. The hallucal and post-hallucal pads are connected by a low granular ridge. The small anterior outer metatarsal pad is similarly linked to a larger posterior outer metatarsal pad by a granular ridge. Digits II–IV have strong curved claws. The hallux is without a claw, and the apical pad is level with the centre of first interdigital pad. The under surface of all of the digits is naked with thickened skin folded into transverse rows; the basal 1–2 rows are strongly tuberculate and the others lamellate either variably entire or divided.

FIGURE 11. Pes of typical A) *Planigale kendricki* (WAM M51793), and B) *Planigale* sp. Mt Tom Price (WAM M64697), note relative size difference of pes, shape and placement of apical pads between the species.

The manus is only relatively slightly smaller than the pes. The upper surface of the manus including the digits is clothed with pale tan hairs. The plantar surface has five distinct pads, all constructed as on the pes. All digits are strongly clawed.

The tail is long, narrow, thinly furred, and lacks any sign of incrassation. The skin of the tail contains dark pigment and bears scales that are arranged in regular whorls; these are clearly visible through the sparse fur. Individual tail hairs emerge from beneath the posterior margins of the scales and number 3–4 hairs per scale; the central scale hairs typically are much thicker than the lateral hairs. The hairs on the upper surface and sides of the tail are tan, while those on the under surface are pale tan to cream, giving the tail a weakly to distinctly bicoloured appearance. All tail hairs lack dark tipping and remain fairly constant in number and length along tail, despite the distal reduction in scale size. The distal portion of the tail thus appears hairier and bears a distinct terminal tuft.

The scrotum of adult males has pigmented skin and is clothed in fine cream hairs. The pouch area of females is marked by a patch of hairs with grey bases and cream tipping. In young and sexually regressed individuals up to12 button-like nipples are visible, arranged in two crescentic series on either side of a central patch of wrinkled skin, and often with a low antero-lateral skin fold. In sexually active individuals the nipples are more prominent, the central patch of skin appears more glandular and the folds of skin are better developed, while females with pouch young exhibit well developed nipples; on average only 5–6 (n individuals = 10) are suckled, and the fold of skin expands to mostly cover the pouch young. The pouch of *P. kendricki* is most similar to type 1 and type 2 of other dasyurids as described by Woolley (1974).

Cranium. In lateral view, the cranium is moderately depressed, with an essentially straight dorsal longitudinal profile (Fig. 12E). The braincase is low and broad, without temporal or sagittal cresting. The squamosal is widely separated from the frontal on the side wall of the braincase by the alisphenoid and parietal connecting one another. The occipital surface of the cranium is rounded with the nuchal crests on each side concave and sweeping forward to meet at a point well forward of the posterior surface of the cranium. In dorsal view the interorbital region of the cranium is flat and broad, with parallel sides, lacking any postorbital processes. The interorbital region has a slight central depression. The rostrum is relatively elongate and narrow. The premaxilla has a long posterior process interposed between the nasal and maxilla on the side of the rostrum. The nasals are elongate, very narrow anteriorly and greatly expanded posteriorly such that almost one third of the total length is situated behind the point of maximum nasal width. The posterior nasal margins describe a deep u-shape. The anterior process of the frontal is enlarged and wedged deeply between the nasal and the maxilla on each side (Fig. 12). In lateral view, the lacrimal has an antorbital ridge that is inflated above the lacrimal foramen. The zygomatic arches are relatively robust and of similar thickness behind and in front of the broad frontal process of the jugal. The arches are bowed in lateral profile, widest across orbital fossae, narrowing slightly across temporal fossae. The orbital lamina of the palatine extends high in the medial wall of the orbit. In ventral view, the palate has short maxillopalatine fenestra that are level with the interdental embrasure between $M^{2–3}$. There are no minor palatine foramina. The incisive foramina are bowed, extending from the front of I^2 to midway along the canine alveolus. The posterior margin of the palate has a thickened torus and a strong medial spine. The mesopterygoid fossa is broad, narrowing posteriorly between the delicate pterygoid bones. The foramen rotundum is situated well behind the sphenorbital fissure.

In lateral view, the auditory region of the cranium is dorso-ventrally flattened (Fig. 12E). The alisphenoid tympanic process is relatively small, rounded but tilted anteriorly and in narrow contact posteriorly with the rostral tympanic process of the petrosal. The alisphenoid tympanic process and the ectotympanic appear to be continuous in forming the external wall of the bullae. The ectotympanic has a well-developed meatal process that is broadly exposed posteriorly, and the meatal margin is conspicuously notched anteriorly. The external auditory meatus is broad, weakly enclosed dorsally and ventrally. The rostral tympanic process of the petrosal is quite strongly inflated, and the bone appears spongious. The caudal tympanic process of the petrosal is uninflated but fused to the paracondylar process. The squamosal epitympanic sinus is moderately inflated, being deepest and most fully enclosed posteriorly.

The foramen ovale is capacious and extends from the level of the basioccipital-basisphenoid suture to the transverse level of the glenoid fossae. The carotid foramen is directly medial to the foramen ovale and large and ovate. The transverse canal foramen is usually bilaterally absent, but a small foramen is present unilaterally in WAM M25773 and bilaterally in WAM M15160. The inferior petrosal sinus foramen and jugular foramen are separated by the process of the petrosal, and the jugular foramen is larger in size.

In posterior view, the foramen magnum is relatively broad. The occipital condyles are large and situated entirely behind the mastoid region of the cranium and are visible in dorsal view (Fig. 12C). In ventral view, the hypoglossal foramina are paired and hooded, opening anteriorly.

Dentary. The horizontal ramus is slender and deepest below M_4, tapering gradually to the front with the ventral border describing a gentle curve (Fig. 12F). A single mental foramen is located below the anterior root of M_2. The coronoid process is broad, and the masseteric fossa have well-defined anterior and inferior borders. The angular process is elongate and thin, terminating level with the rear of the mandibular condyle.

Dentition. The I^1 is single rooted, procumbent and the tallest and largest of the incisors; it is canine-like in shape with a weak posterior heel and is separated from $I^{2–4}$ by an obvious diastema. $I^{2–4}$ have a central cusp and small accessory anterior and posterior cusps, and all are single rooted and sub-equal in crown height and length; all possess lingual cingula. I^4 has a lingual heel, which is variably small (as in the holotype) to absent (in WAM M51581). The diastema between I^4 and the canine is equal in length to I^4 (Fig. 12E). The canine is large and heavy and laterally compressed with a slightly recurved tip; a well-developed buccal cingulum links the small anterior cuspule to the larger posterior cuspule. No diastema is present between the canine and P^1 or within the upper premolar series. $P^{1–3}$ form a graded series with $P^3 > P^2 > P^1$ in crown height and length; all upper premolars are double rooted and sub-rounded in occlusal profile, except P^3 which is more elongated and with the crown apex positioned more posteriorly for posterior premolars. All upper premolars have complete buccal and lingual cingula and distinct anterior and posterior cuspules. The main posterior crest of P^3 runs to the base of the posterior cuspule.

FIGURE 12. *Planigale kendricki* holotype (WAM M41812) cranium in ventral (A), dorsal (C), posterior (D) and lateral (E) views, and dentary in occlusal (B) and buccal (F) views. Note deep u-shape of posterior nasal suture in C and extreme dorso-ventral flattening of braincase in D and E.

The upper molars are of typical form for the genus, with reduced paracones, relatively narrow protocones and very thin posterior cingula (Fig. 13). The M[1] has a wide anterior cingulum, which is enclosed buccally by the bladelike stylar cusp A and is narrowly continuous lingually with the preprotocrista. There is no trace of a protoconule, and the paracone is clearly separate from stylar cusp B; the two cusps are linked by a short, transverse preparacrista. The parastylar shelf is enclosed buccally by a stylar crest that is connected anteriorly to stylar cusp B. Stylar cusp D is lower than the metacone but has a low posterior crest that encloses the metastylar shelf; there is no trace of stylar cusp E. The metacone is connected to the metastyle only via the postmetacrista, and no centrocrista is present. The protocone has a descending postprotocrista that ends posterior to the metacone.

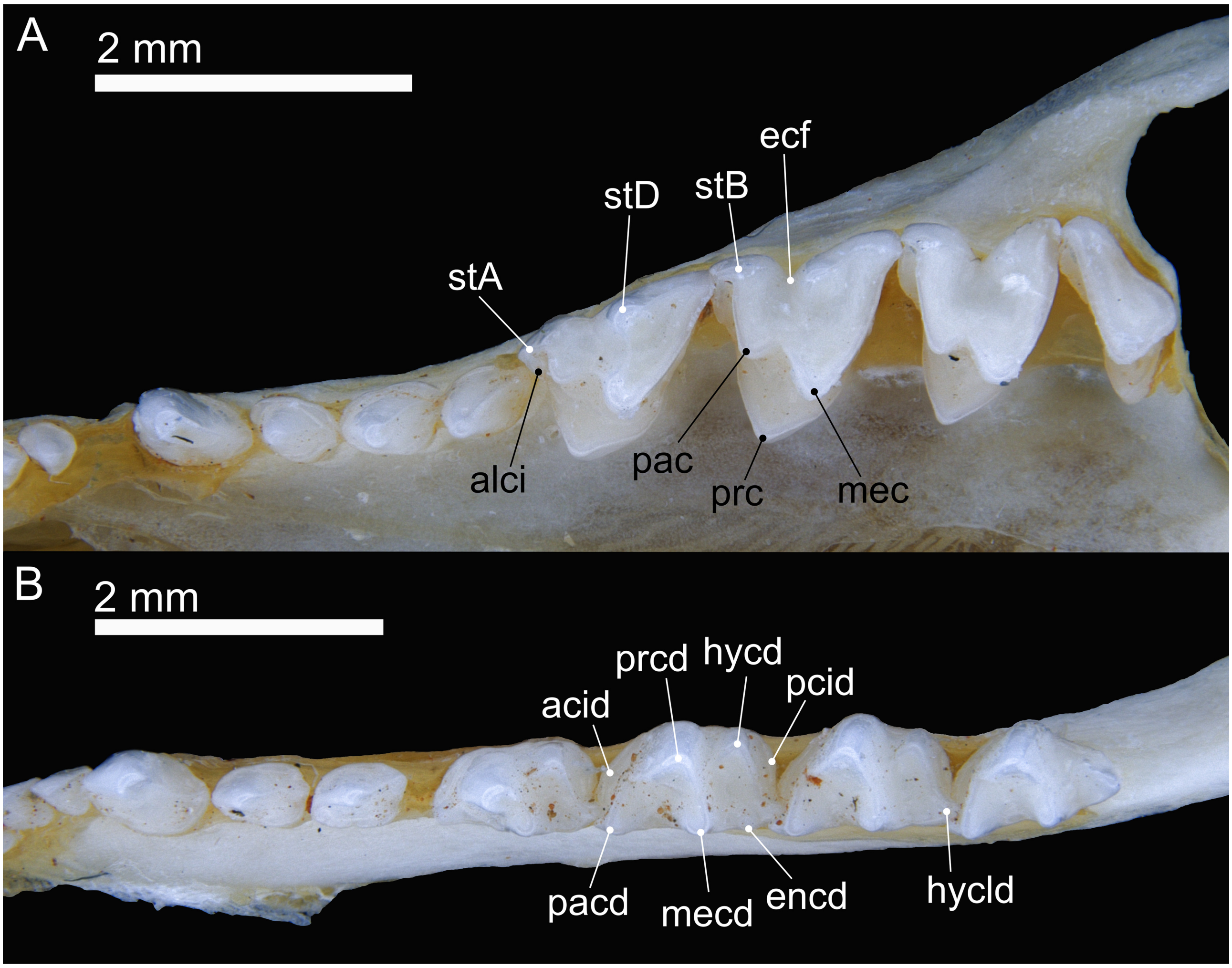

FIGURE 13. Upper and lower dentition of *Planigale kendricki* (WAM M41812, holotype) from canine to M4. A) upper and B) lower dentition in occlusal view. Abbreviations: **acid**, anterior cingulid; **alci**, anterolabial cingulum; **ecf**, ectoflexus; **encd**, entoconid; **hycd**, hypoconid; **hycld**, hypoconulid; **mec**, metacone; **mecd**, metaconid; **pac**, paracone; **pacd**, paraconid; **pcid**, posterior cingulid; **prc**, protocone; **prcd**, protoconid; **stA**, stylar cusp B; **stB**, stylar cusp B; **stD**, stylar cusp D.

M^{2-3} are similar to M^1 except as follows. M^{2-3} have broad anterior cingula that descend buccally on each tooth to meet stylar cusp B; the anterior cingulum is narrowly continuous on each tooth with the preprotocrista; there is no trace of a protoconule; a stylar crest from stylar cusp B is curved ending at the ectoloph, with M^3 being more angular than M^2. Stylar cusp D is reduced in M^3 compared to M^{1-2}, and the posterior crest from stylar cusp D becomes progressively weaker on M^2 and M^3. A postparacrista and premetacrista are present and form a centrocrista. The ectoflexus of M^3 is relatively deep and situated just behind the mid-point of the centrocrista. The parastyla shelf is wider on M^3 and the talon is narrower on M^3. M^4 has a wide anterior cingulum that is broadly connected to the preprotocrista; the protocone is only moderately reduced, and there is no trace of a metacone or stylar cusp D. The width of M^4 is approximately 80% of M^3.

The lower incisors form a graded series, where $I_1>I_2>I_3$ in crown height and length. I_1 projects above the occlusal plane of $I_{2–3}$. $I_{1–3}$ have a posterior heel that descends in size posteriorly. The canine is relatively elongate and broad with a long, cingulated heel on the posterior and lingual side of the tooth. Note that P_3 has not completely erupted in the holotype (although P^3 has erupted) so the description is based on the paratypes as this tooth is more completely erupted. $P_{1–3}$ are low-crowned and broad; all with broad lingual and buccal cingula and low posterior cuspules; $P_2>P_1>P_3$ in length and height. $P_{1–2}$ are always double-rooted, but P_3 usually has a single root and is less commonly double rooted (e.g., bilaterally in WAM M3432 and WAM M41803; right side only in WAM M49224). The lower molars are of typical form for the genus with a short talonid, prominent hypoconulids and well-developed anterior and posterior cingula. M_1 has a well-developed anterior cingulum that terminates just below the paraconid. The trigonid of M_1 has an enlarged protoconid with a notched paracristid and reduced paraconid. The metacristid has a carnassial notch and metaconid only slightly larger than the paraconid. The entoconid is barely discernible and the hypoconid is as tall as the metaconid, the crista obliqua is straight and posterior to the protoconid, and the posthypocrista is straight for most of its length but curves just anterior to the hypoconid; the ectoflexid is present and thin and connects the base of the protoconid and hypoconid.

M_2 is similar to M_1 except as follows. In M_2, the trigonid is wider and the protoconid is taller; the paracristid and metacristid are longer; the paraconid and metaconid are larger; the entoconid is taller with preentocristid present; the talonid is wider and the crista obliqua and posthypocristid are longer; the ectoflexid is small and does not connect the base of the protoconid and hypoconid. M_3 is similar to M_2 except as follows. In M_3, the trigonid is wider; the talonid narrower; and the entoconid is smaller. M_4 is similar to M_3 except as follows. In M_4, the trigonid is narrower; the talonid is extremely reduced with no crista obliqua and the hypoconid is very reduced; the posthypocristid is straight; and the entoconid is absent but the preentocrista is present.

Distribution and sympatry. *Planigale kendricki* is widespread through the Pilbara and surrounding regions in Western Australia, including the Cape Range Peninsula, Ashburton and Gascoyne regions, and isolated records also occur in the Great and Little Sandy Deserts (Fig. 14). Although most records are from upland localities, specimens from Lake Auld in the east, on the border between the Gibson and Great Sandy Deserts, and from Mandora near the southern coastal margin of the Great Sandy Desert, indicate a capacity to exist in lower-lying, predominantly sandy environments.

Throughout most of its range, *P. kendricki* is regionally sympatric with *P.* sp. Mt Tom Price. At Mandora, at the northern limit of its range, it is locally sympatric with *P. maculata* (Fig. 2). Other dasyurids known from comparable habitats in the Pilbara region include *Dasykaluta rosamondae*, *Dasyurus hallucatus*, *Ningaui timealeyi, Pseudantechinus macdonnellenis*, *P. woolleyae*, *Sminthopsis longicaudata, S. macroura*, *S. ooldea* and *S. youngsoni* (Gibson & McKenzie 2009).

Habitat. *Planigale kendricki* occurs on a variety of substrates from sandy plains adjacent to rocky areas, through rocky scree slopes and cobbled creek beds. It was captured at almost half of the survey sites of a widescale biodiversity survey of the Pilbara region and found to prefer rugged substrates with exposed bedrock (Gibson & McKenzie 2009). Tussock grasses of the genus *Triodia* are a constant feature of its environment.

Reproductive biology. Females with poorly developed pouches and up to 12 button nipples have been collected from April to August. Individuals with enlarged nipples and more obvious pouch development and some with pouch young have been collected in September, October and November. Nipples in *Planigale kendricki* are arranged as shown for pouch type 1 of Woolley (1974) with an antero-lateral skin fold more similar to that shown for pouch type 2. Both males and females of *P. kendricki* exhibit the presence of sternal glands (Cooper *et al.* 2005).

Interspecific comparisons. *Planigale kendricki* is similar in size to some populations of *P. maculata.* It is substantially larger than each of *P. ingrami, P. tenuirostris* and *P.* sp. Mt Tom Price., and smaller than *P. novaeguineae*, *P. gilesi* and some populations of *P. maculata*. It will be compared first and in most detail with each of the larger species of *Planigale*.

Planigale maculata as currently delineated is widespread across northern and north-eastern Australia. However, results from genetic studies by Blacket *et al.* (2000) and Westerman *et al.* (2016) suggest that multiple taxa are represented across this range, with several genetically distinct forms present in each of the Top End and Kimberley regions. For the present purposes, we will limit our comparisons to samples of each of the named populations within this group.

Specimens of *P. maculata* from northern New South Wales, near the type locality for this species, are very different in both external and craniodental features from *P. kendricki*. Externally, specimens of *P. maculata* are plain brown finely ticked with black above, grading into pale buff over grey below. The throat is pale tan and there is a pale orange patch of fur below the eye, but overall, the head is less boldly patterned in *P. maculata* than in *P. kendricki*. Patches of all-white fur occur on the flanks and venter in some individuals, including the holotype of *P. maculata* (Gould 1851; Archer 1976a) and ANWC M233. The mystacial vibrissae are shorter in *P. maculata*, compared to *P. kendricki*, barely reaching the base of the ear when lying flat, and the ears are more heavily furred and the supratragus is less prominent in *P. maculata*. The pes of *P. maculata* is broader and has less elongate plantar pads and a shorter hallux, and the tail is short and much hairier than that of *P. kendricki*. The pouch of sexually active females of typical *P. maculata* are well developed with a posteriorly positioned, circular entrance and 5–10 nipples (Archer 1976a). The cranium of typical *P. maculata* (see Archer 1976a: Plate 43) is broader and much less depressed compared to *P. kendricki*, with a shorter, broader and deeper rostrum, wider and posteriorly less expanded nasals, a more rounded and strongly crested neurocranium, and more robust zygomatic arches. The talonid on the M_{1-3} is less reduced in *P. maculata*, the associated posterior cinguli are narrower, and the entoconids of M_{1-3} are even smaller than the reduced structures in *P. kendricki*. The P^3 of *P. maculata* is substantially longer and taller relative to P^{1-2} and the P_2 of *P. maculata* is also larger relative to P_1 and P_3, when compared to *P. kendricki*.

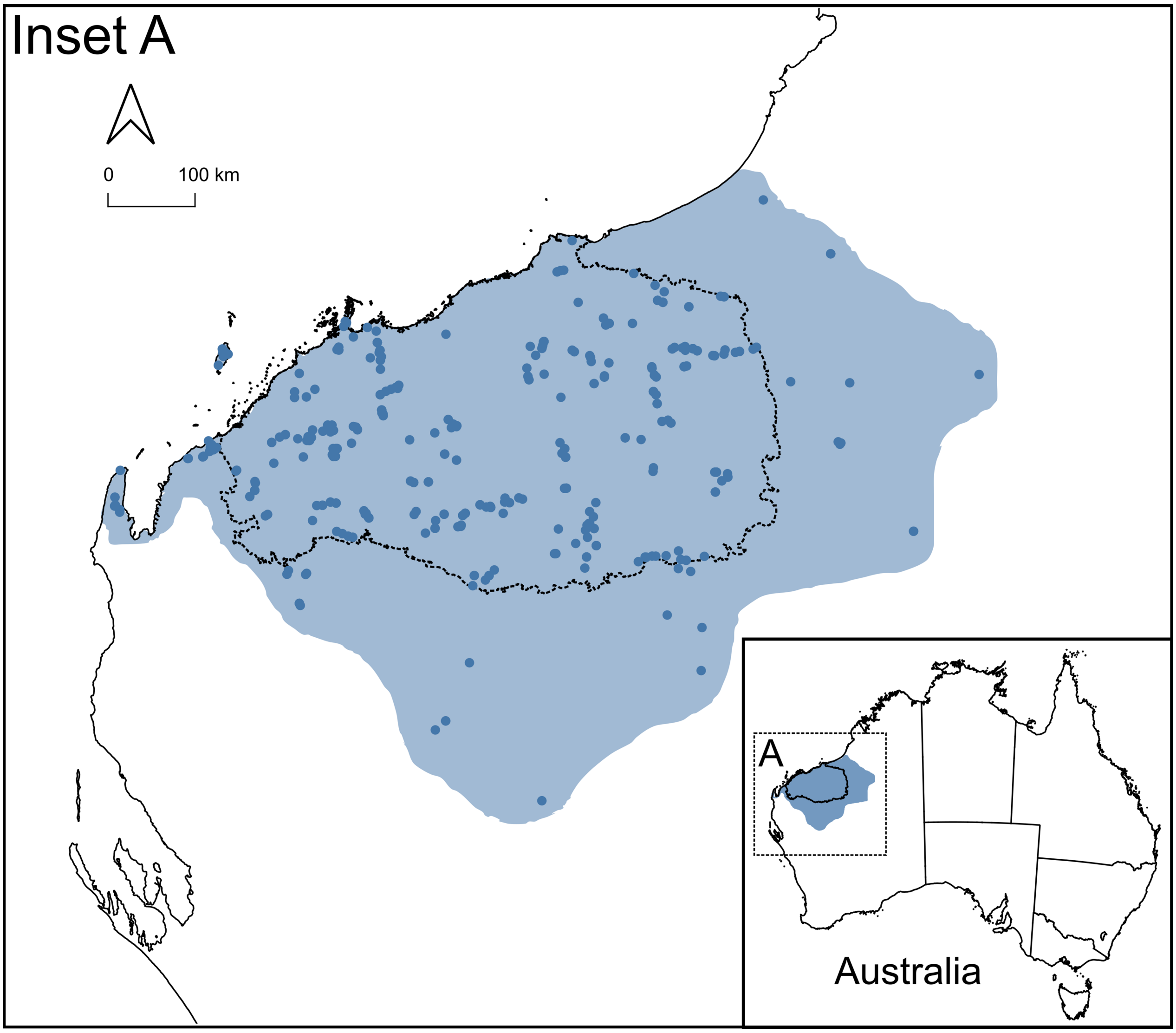

FIGURE 14. Proposed distribution of *Planigale kendricki* inferred from specimens at the Western Australian Museum (blue dots) that were examined during this study. The border of the Pilbara region is shown by the dashed line in inset A.

Planigale novaeguineae is larger and less brightly patterned than *P. kendricki*, and it differs in many of the same features that distinguish the new species from *P. maculata* (e.g., deeper cranium, broader rostrum and less elongate nasals). The I^4 of *P. novaeguineae* is proportionally more elongate than in all other species of *Planigale*, including *P. kendricki*. There is no suggestion of any close relationship between the two taxa.

Planigale gilesi of semi-arid eastern Australia is similar in size or slightly larger than *P. kendricki*. However, *P. gilesi* has a proportionally shorter and much hairier tail, and duller grey-brown pelage with longer projecting guard hairs. The cranium of *P. gilesi* is strongly depressed and resembles that of *P. kendricki* in profile, dorsal outline and the general configuration of the auditory region. However, there are some notable differences that set the two species apart, including the lack of posterior elongation of the nasals in *P. gilesi*, its slightly larger major palatine fenestra, its broader interorbital region and better developed lambdoid and sagittal crests, and most notably, the loss of the last upper and lower premolars, P_3 and P^3 (P_4 and P^4 of Archer, (1976a) who discusses the identity of the remaining teeth). The lower molars of *P. gilesi* and *P. kendricki* share similarly weak development of the entoconids, combined with a relatively unreduced talonid on the M_4; however, *P. gilesi* has the paraconid of M_1 rotated postero-lingually relative to all other species of *Planigale*, and the paracone on M^1 is clearly united with stylar cusp B (well-separated in *P. kendricki*).

The remaining three species of *Planigale* are all smaller than *P. kendricki*, see Results. All have flattened heads, producing a depressed cranial outline similar to that of the larger *P. kendricki* and *P. gilesi*, but in each case, there are differences in detail. The closest similarity in cranial form is observed between *P. kendricki* and *P. tenuirostris* of semi-arid south-eastern Australia. These taxa share a relatively elongate rostrum, producing similar cranial outlines, and a similar slight depression of the interorbital region. In addition, the nasals in both species are elongate, projecting further posteriorly than in any other species of *Planigale*, and the rostral tympanic process of the petrosal is similarly inflated. *Planigale tenuirostris* differs from *P. kendricki* in having a narrower ectotympanic meatal process; single and unshielded hypoglossal foramina; more reduced protocones on M^{1-4}; paracone and stylar cusp B united on M^1; a shorter but higher crowned P^3; a smaller and more crowded P_3; and more reduced entoconids on all lower molars (usually undiscernible on M_{1-2}). Externally, *P. tenuirostris* is much less brightly coloured than *P. kendricki*, being a drab grey-brown above, but the two species share a cream to off-white cheek patch that is unusual in the genus. The ventral pelage of *P. tenuirostris* is off-white on dark grey; the manus and pes are off-white, and the tail is significantly shorter than snout-vent length and much hairier than that of *P. kendricki*.

Comments. We recommend the following common name be used in association with *P. kendricki* sp. nov.: orange-headed Pilbara planigale.

Planigale tealei Aplin, Cooper, Travouillon & Umbrello sp. nov.

(Fig. 11, 15–17, Tables 2, 4)
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Formerly referred to as '*Planigale* sp. Mt Tom Price' by the following authors: Blacket *et al.* (2000) and Westerman *et al.* (2016), and as '*Planigale* sp. 2' by Gibson & McKenzie (2009) and Umbrello *et al.* (2020).

Holotype. WAM M47923 adult male; Millstream, Western Australia, 21°17'14" S, 117°15'51" E. Collected by W. Manson, 2nd July 1997. Spirit and skull. Specimen located in the Western Australian Museum Mammal collection, Welshpool, Western Australia.

Paratypes. WAM M47841, adult female; Tom Price, Western Australia 22°48'26" S, 117°45'00" E. Collected by S. Anstee and N. K. Cooper, 12th November 1997. Spirit and skull. Liver tissue ABTC161752; pouch young from M47841 stored at –80 °C at WAM. WAM M47683, adult female; Tom Price, Western Australia 22°48'25" S, 117°47'03" E. Collected by S. Anstee, 15th May 1997. Spirit and skull, note specimen selected due to intact skull, spirit specimen is in poor condition. WAM M55123, adult male; Roy Hill, Western Australia 22°25'12" S, 119°45'34" E. Collected by R. J. Teale *et al*., 5th July 2004. Spirit specimen with liver and heart tissue stored at –80 °C at WAM.

Etymology. Named in honour of Roy Teale, who has supported the work of the Western Australian Museum over many decades and collected many of the specimens used in this study.

Material examined. Refer to Table 1 for a list of all *P. tealei* specimens examined in this study, labelled as *Planigale* sp. Mt Tom Price in Table 1.

Diagnosis. *Planigale tealei* is considerably smaller in all external and cranial dimensions than each of *P. kendricki*, *P. maculata*, *P. novaeguineae* and *P. gilesi*. It further differs from each of these taxa in having a more depressed cranium and differs from *P. gilesi* in retaining upper and lower third premolars. It is slightly smaller than *P. tenuirostris* and further differs from this species in having a considerably more depressed cranium with a shorter rostrum. It is most similar in size and craniodental morphology to *P. ingrami*, but it differs from this taxon in having a longer snout and proportionally larger pes, and in lacking a distinct eye ring. The cranium differs from that of all named forms of *P. ingrami* in having a broadly rounded rather than square posterior nasal suture, a broader interorbital region, more rounded and elongate alisphenoid tympanic process that makes broad contact with the rostral tympanic process of the petrosal, a less flattened occiput and proportionally larger premolars.

FIGURE 15. Photo of *Planigale tealei* sp. nov. (WAM M62896) photographed by L. Umbrello.

Description

External morphology. *Planigale tealei* has a maximum recorded body weight of 6.1 g and snout-vent length of 62.5 mm for males. Females tend to be slightly smaller than males, with a maximum weight of 4.7 g and snout-vent length of 60 mm (Table 4). The ratio of tail length to snout-vent length was 86–128% (mean 109%) for males and 85–135% (mean 110%) for females. There was no obvious sexual dimorphism in body proportions or colouration. The pelage on the back and upper flanks is dense, thick and very soft with an overall colour of greyish-brown, ticked with black (Fig. 15). The hue is even across the back but pales evenly onto the flanks. The contour hairs on the mid-back measure c. 4–4.5 mm. The hairs are tricoloured with the basal half pale grey and the distal half pale tan, frequently with short dark brown or black tips. On the lower flanks, the contour hairs are pale grey basally, pale yellow distally and less frequently with dark tips. The fine guard hairs project c. 2 mm beyond the main pelt over the entire back and flanks but project up to 4 mm on the rump. The guard hairs on the back are usually bi-coloured (grey basally, dark brown or black distally), but some are burnished with a golden tip. On the flanks, the guard hairs are grey based but transparent for the distal half. The forearm has three sets of vibrissae (anconeal, antebrachial and carpal) and all are pale tan to transparent. The hindlimb has fine, transparent calcaneal vibrissae.

The ventral pelage measures c. 3.0 mm on the abdomen. Ventral hairs are bicoloured, with the basal half pale grey and the distal half cream. The thoracic region is concolorous with the abdomen but grading forward to pale cream on the throat and chin. The fur on the inside of the hindlimbs is concolorous with the abdomen, but on the inside of the forelimbs it is pale cream and concolorous with the throat.

The pelage on the head is shorter than, but concolorous with, that on the dorsum of the body. The upper lip from mouth opening to vibrissal pad has a narrow band of pale cream hairs, extending broadly onto the cheek and back to the genal vibrissae. The eyelids are fringed with short black hairs but there is no distinct eye ring. The rhinarium is naked, with a deep medial groove and black, granular skin. The mystacial vibrissae are quite thick, all black in the upper rows, all transparent in the lower rows; the longest reach to the middle of the pinna when lying flat. The genal vibrissae are tan and extend past the ears. The supraorbital vibrissae are black with tan tipping. The interramal vibrissae are pale, almost transparent but are still conspicuous. The vibrissal papillae on the face are unpigmented.

The pinnae are small and round, and a slight notch on the posterior margin creates a weakly bilobed outline. The skin of the pinna is pale grey with the outer surface clothed with pale orange hairs and the inner surface with pale tan to cream hairs. The supratragus is moderately broad and tall, with a straight external margin, and the tragus is sparsely furred.

The pes, including digits, is densely clothed above with cream hairs, which grade into pale tan fur around the ankle. The plantar surface has finely granular skin and six approximately equal-sized plantar pads, all consisting of granular mounds capped by apical pads (Fig. 11). The surface of all pads appears smooth but with visible internal striae. The hallucal and post-hallucal pads are connected by a low granular ridge. The posterior outer metatarsal pad has an anterior ridge but lacks a discrete apical pad. Digits II–IV have strong curved claws, but the hallux is unclawed, and the apical pad is level with the rear of the first interdigital pad. The under surface of all digits is naked, with thickened skin folded into transverse rows; the basal 1–2 rows are strongly tuberculate, and others lamellate but variably entire or divided. The manus is small relative to the size of the pes, and densely clothed above with cream hairs, including digits. The plantar surface of the manus has five distinct pads, and all digits are strongly clawed.

The tail is similar to *P. kendricki* but is moderately hairy, such that the skin scales are just visible through the tail fur. The hairs on the upper and side surfaces of the tail are tan, while those on the under surface are cream, giving the tail a distinctly bicoloured appearance. Many of the hairs on the upper surface have darker tips, especially towards the distal end of the tail, giving the appearance of a short black terminal tuft.

The scrotum of adult males has pigmented skin and is clothed in fine cream hairs. The pouch area of females is marked by a patch of fine cream hairs. In young and sexually regressed individuals, up to 12 button nipples are visible, arranged in a circle around a central patch of wrinkled skin. In sexually active individuals the nipples are more prominent, and the central patch of skin appears smooth. A small, crescentic fold of skin is developed along the front of the pouch. In no case is there any evidence of full peripheral enclosure of the pouch. The pouch of *P. tealei* is most similar to pouch Type 1 of Woolley (1974). Sternal glands are present in adult male and female *P. tealei* (Cooper *et al.* 2005).

Cranium. The cranium is similar in basic construction to that of other *Planigale* species, including *P. kendricki*. Only points of special similarity or contrast will be noted below.

In lateral view, the cranium is strongly depressed, with a gently curved dorsal longitudinal profile (Fig. 16E). The braincase is extremely low and broad, with the dorsal surface depressed in midline at the rear and flanked by parietal bulges. There is no trace of sagittal cresting. In dorsal view, the interorbital region of the cranium is extremely flat and broad without any central depression; it is narrowest immediately behind the lacrimal bones and then expands to join the contour of the braincase, with little or no postorbital constriction. The rostrum is relatively short and broad. The premaxilla lacks the elongate posterior process of *P. kendricki*, and instead a much shorter sutural contact occurs between the premaxilla and nasal. The nasals are relatively short and unexpanded posteriorly; less than one-fifth of the total length is situated behind the point of maximum width. The posterior margins of the nasals describe a broad u-shape (not as deep as in *P. kendricki*). The anterior process of the frontal is short and broad and only weakly interposed between the nasal and the maxilla on each side (Fig. 16C). In lateral view, the lacrimal has a preorbital ridge, which is more inflated above the lacrimal foramen. The zygomatic arches are relatively gracile and similar in thickness behind and in front of the weakly developed frontal process of the jugal; they are bowed in lateral profile, widest across the temporal fossae and narrowing forward. The orbital, palatal and pterygoid structures are as in *P. kendricki*, except the posterior margin of the bony palate has a thicker torus and weaker medial spine in lateral and ventral views.

The auditory region of the cranium is very similar in configuration to *P. kendricki* but is slightly proportionally less flattened in lateral view (Fig. 16E). The alisphenoid tympanic process is slightly more rounded and in broader contact posteriorly with the rostral tympanic process of the petrosal. The rostral tympanic process of the petrosal is more strongly inflated than *P. kendricki*, and the bone appears non-spongious.

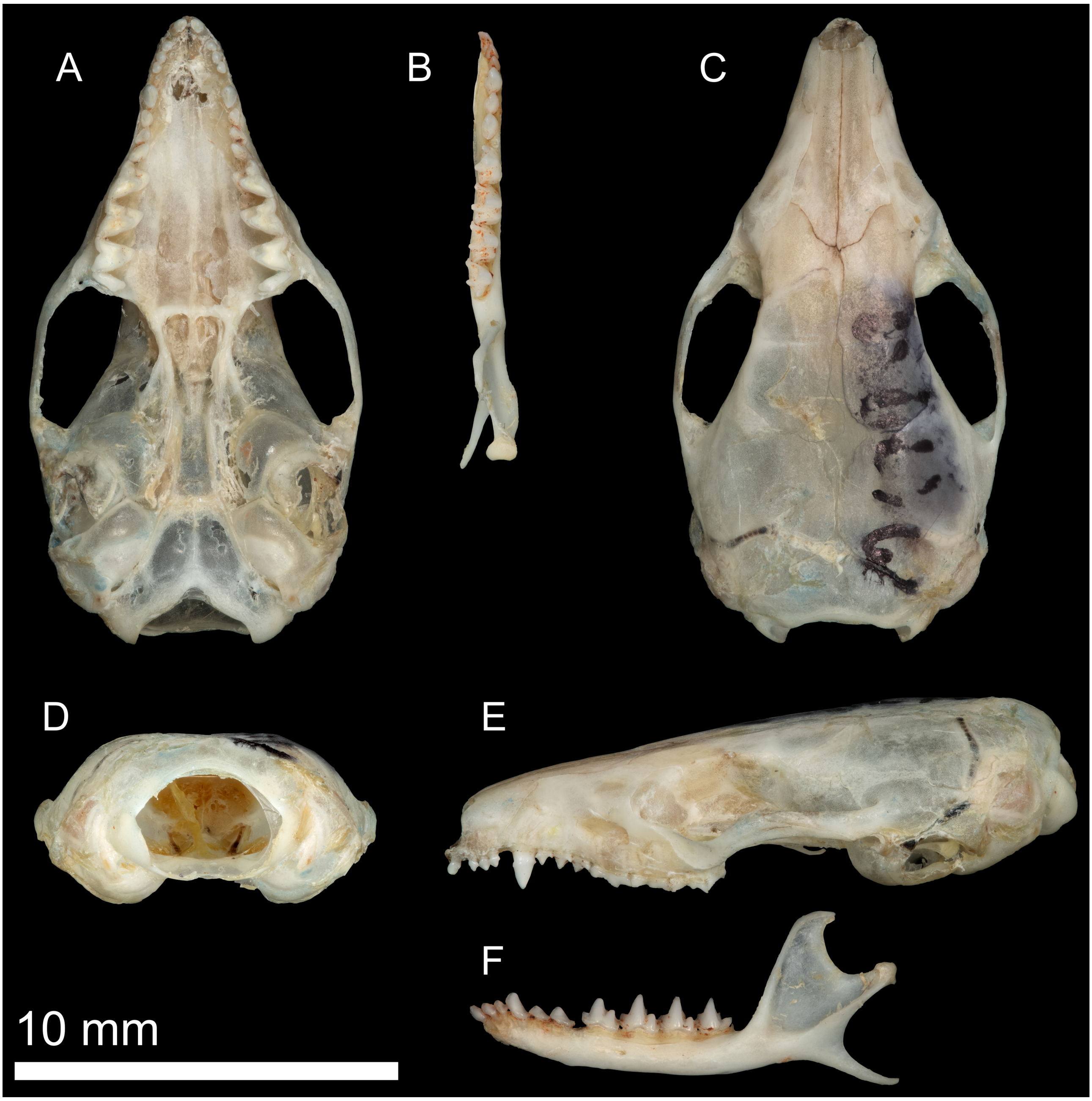

FIGURE 16. Cranium (A, C–E) and dentary (B and F) of the holotype *Planigale tealei* (WAM M47923). Cranium shown in ventral (A), dorsal (C), posterior (D) and lateral (E) views, and dentary pictured in occlusal (B) and buccal (F) views. Note shallower and broader u-shaped posterior suture of nasals, broader interorbital region and overall smaller skull size compared to *P. kendricki*.

In ventral view, the basicranial foramina appears as in *P. kendricki*, except that the transverse canal is bilaterally absent in all specimens of *P. tealei*. In posterior view, the skull is notably flatter than *P. kendricki*, and the foramen magnum is relatively broad and not as deep. The occipital condyles are smaller than in *P. kendricki* in dorsal view (Fig. 16C). The hypoglossal foramina are paired and open ventrally. The paroccipital process is less well developed compared to *P. kendricki*.

Dentary. As in *P. kendricki*, but the horizontal ramus is more even in depth from below the posterior molars to below P_2.

Dentition. In ventral view, the upper incisors are very similar to those of *P. kendricki*, but all teeth are relatively smaller and lower crowned, and I^1 in the holotype is more anteriorly directed than in the paratypes. Upper incisors I^{2-4} all have weakly developed buccal cingula and I^4 has a smaller posterior heel. The canine is lower crowned than in *P. kendricki* with a weak buccal cingulum and tiny anterior and small posterior cuspules (Fig. 17). In lateral view, the canine is more anteriorly directed than in *P. kendricki*. No diastema is present between the canine and P^1 or within the upper premolar series. P^{1-3} are very similar to those of *P. kendricki* but are more crowded, with strong overlap between P^2 and P^3, which are narrower than in *P. kendricki*. P^3 has a stronger posterolingual cingulum and a larger posterior cuspule.

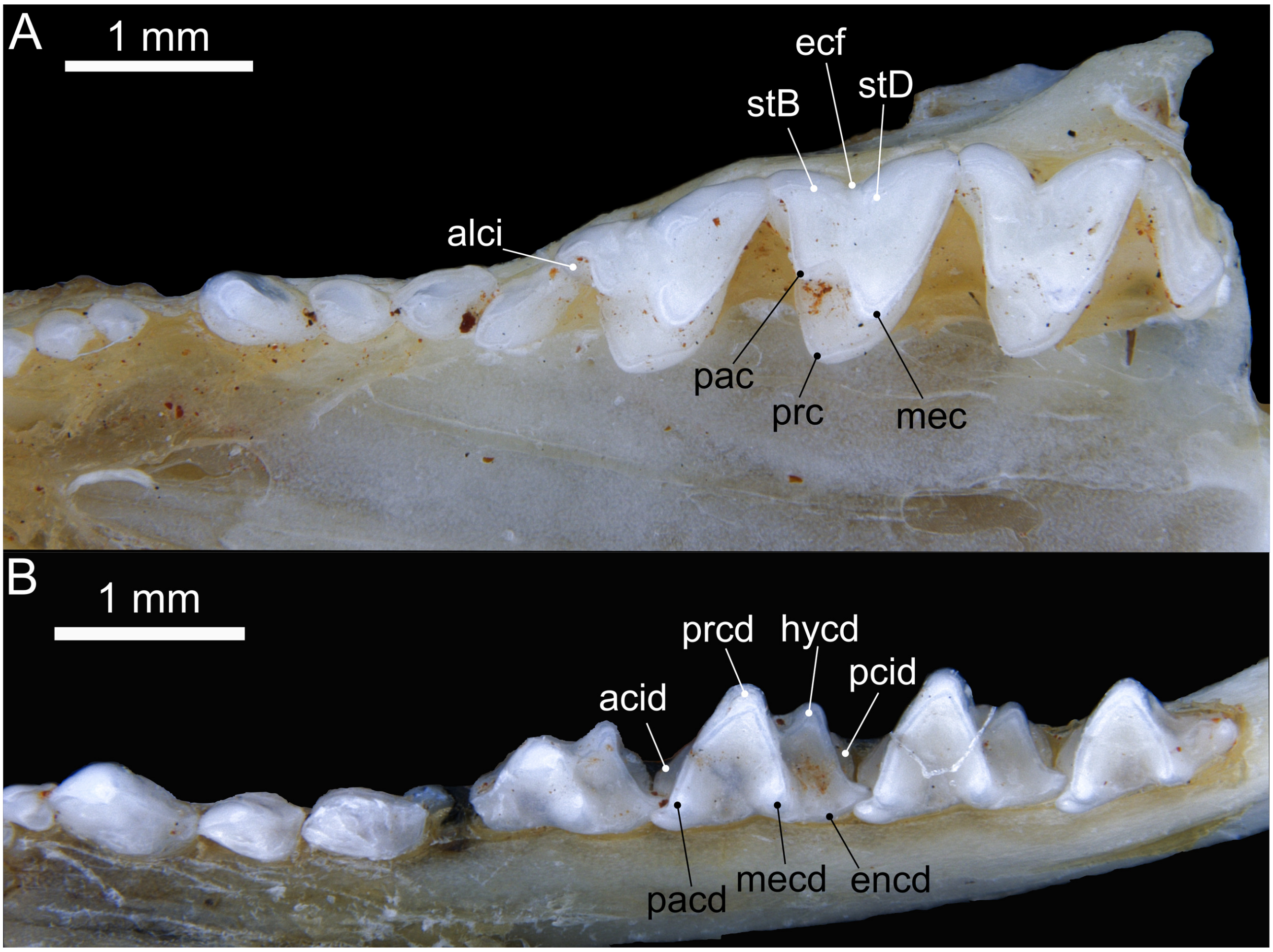

FIGURE 17. Upper and lower dentition of *Planigale tealei* (WAM M47841, paratype) from canine to M4. A) upper and B) lower dentition in occlusal view. Abbreviations: **acid**, anterior cingulid; **alci**, anterolabial cingulum; **ecf**, ectoflexus; **encd**, entoconid; **hycd**, hypoconid; **mec**, metacone; **mecd**, metaconid; **pac**, paracone; **pacd**, paraconid; **pcid**, posterior cingulid; **prc**, protocone; **prcd**, protoconid; **stB**, stylar cusp B; **stD**, stylar cusp D.

The upper molars appear as in *P. kendricki* except for following contrasts. In *P. tealei*, all upper molars are smaller; M^1 has a wider anterior cingulum; stylar cusp B is smaller than in *P. kendricki*; and the postparacrista and premetacrista meet to form a centrocrista. The shelf between the postprotocrista and the metastylar shelf is less wide, and stylar cusp D is higher than the metacone.

M^2 stylar cusp B is higher than the paracone and stylar cusp D is higher than the metacone, the ectoflexus is not as deep and the anterior cingulum is not as wide as in *P. kendricki*; M^3 has a smaller stylar cusp D and less invasive ectoflexus, which is situated opposite the mid-point of the centrocrista, with a slightly broader anterior cingulum than in *P. kendricki*; M^{1-3} have more reduced protocones; M^4 has a more reduced protocone and anterior cingulum.

All the lower teeth are relatively smaller than in *P. kendricki*. The lower incisors and canine are very similar to those of *P. kendricki* except that I_1 is lower crowned and less procumbent, and the canine is narrower. Likewise for the lower premolars, except that P_1 is more reduced relative to P_2 and P_3 is more reduced and crowded between P_2 and M_1. P_3 always has a single root in *P. tealei* and usually lacks a posterior heel, with the crown often rotated to 45°. P_3 is occasionally absent (e.g., bilaterally in WAM M47923 and unilaterally in WAM M55126), but this probably reflects loss rather than congenital absence as WAM M47923 has partially infilled alveolar pits for P_3 on both sides. The lower molars in *P. tealei* are very similar to those of *P. kendricki* but with M_1 having a less bulbous protoconid and a narrower posterior cingulum and more reduced entoconids that are only discernible on unworn M_{2-3}; the posterior cingulum is narrower; M_4 has a more reduced talonid.

Distribution. *Planigale tealei* is apparently almost completely restricted to the Pilbara IBRA, with limited records outside of the Pilbara extending as far south as Waldburg Station and west from Cane River and east to Roy Hill (Fig. 18).

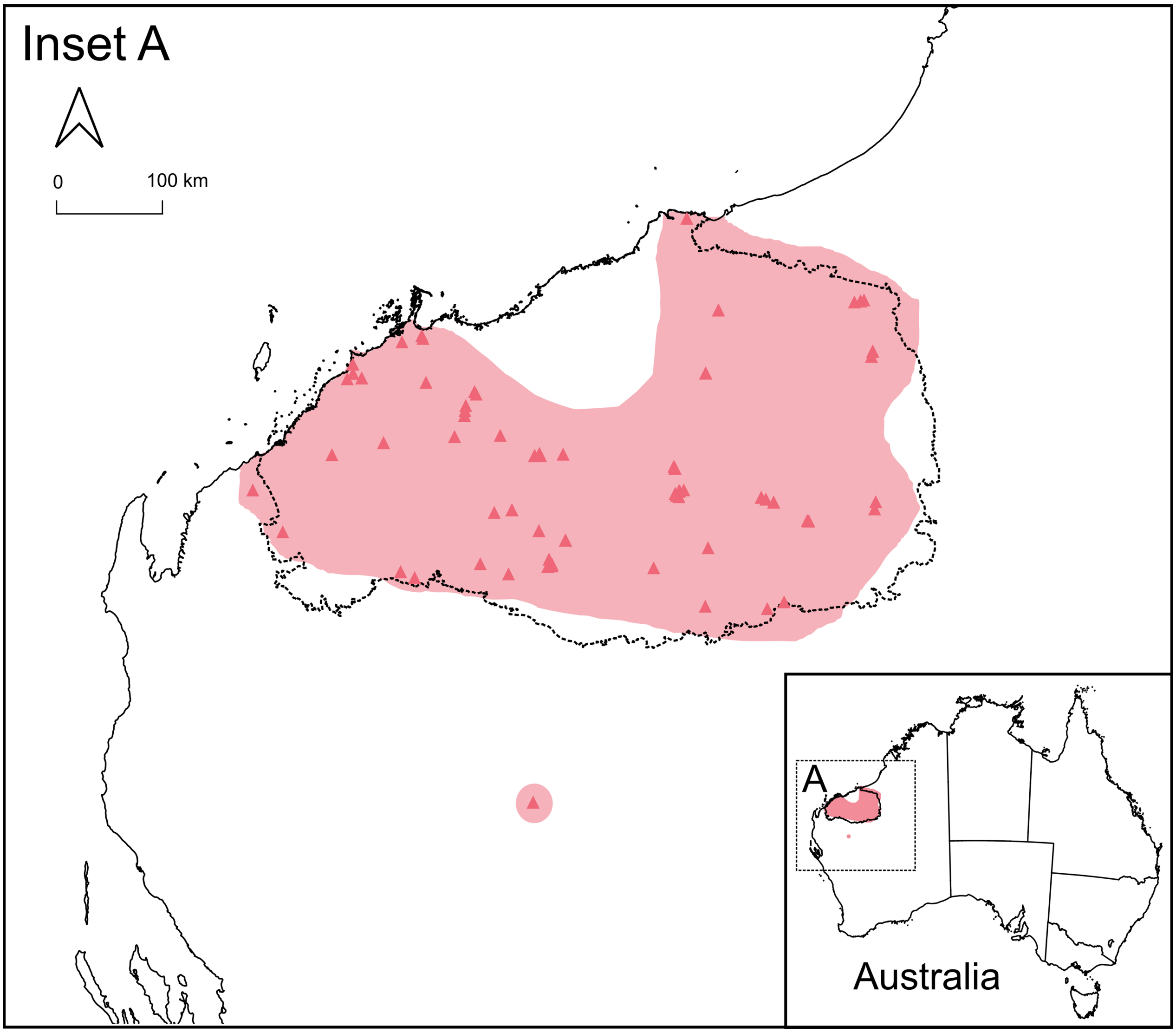

FIGURE 18. Proposed distribution of *Planigale tealei* inferred from specimens (pink triangles) in the Western Australian Museum that were examined during this study, including southern locality of Waldburg Station. The border of the Pilbara is shown by a dotted line in Inset A.

Habitat. Specimens of *Planigale tealei* have almost always been captured on cracking clay substrates, and the species appears to prefer heavy soils with a high clay content. They are less likely to occur in habitats with abundant rocky outcrops (Gibson & McKenzie 2009).

Reproductive biology. Females with up to 12 button nipples and a developing antero-lateral skin fold have been collected from March to July. Specimens collected in October and November have extended nipples and more prominent pouch due to a better developed antero-lateral skin fold. Nipples are arranged as shown for a Type 1 pouch of Woolley (1974), and as the pouch develops the skin fold appears as a Type 2 pouch. Compared to *P. kendricki*, the pouch of *P. tealei* is shallower with a less developed antero-lateral skin fold; the arrangement of the nipples is the same.

Interspecific comparisons. *Planigale tealei* is similar in size to *P. ingrami* and *P. tenuirostris*, and it is considerably smaller than each of *P. kendricki*, *P. maculata*, *P. novaeguineae* and *P. gilesi*. It will be compared below first with the sympatric *P. kendricki* and then with *P. ingrami* and *P. tenuirostris*.

Planigale tealei is smaller than the broadly sympatric *P. kendricki* in all external and craniodental measurements (Tables 2, 4). Fig. 9A of head length versus head depth distinguishes these two sympatric species. Externally, *P. tealei* is less brightly coloured than *P. kendricki* with the dorsal pelage being greyish-brown rather than orange-tan, and without the differentiated head of *P. kendricki*. *Planigale tealei* also has smaller external ears (Table 4) that are more densely furred and less deeply notched, more strongly pigmented tail scales (almost black rather than the cream of *P. kendricki*), a hairier tail, and a manus that is proportionally much smaller relative to the pes (manus only slightly smaller than the pes in *P. kendricki*).

The cranium and teeth of the two species also differ in numerous respects. Compared to *P. kendricki*, most notably *P. tealei* has proportionally smaller incisors, a relatively longer P^3, smaller anterior and posterior cuspules on the upper canine, a closer union of the paracone and stylar cusp A on M^1, more reduced protocones on all molars (especially so on M^4), I_1 is lower crowned relative to $I_{2–3}$, the more reduced P_3 is commonly rotated out of alignment, and there are more reduced entoconids on $M_{1–3}$. *Planigale tealei* has a relatively shorter rostrum with a wedge-shaped premaxilla lacking an elongate posterior process, a relatively wider interorbital region that diverges posteriorly from a point just behind the lacrimals (parallel sided in *P. kendricki*), a more depressed neurocranium with a weaker sagittal crest, much shorter nasals that terminate in a broad u-shaped suture (deeply u-shaped in *P. kendricki*), and a more rounded alisphenoid tympanic process that makes broader contact with the rostral tympanic process of the petrosal compared to *P. kendricki*. The skulls of *Planigale tealei* and *P. kendricki* can be readily diagnosed from the measurements of the length of the nasals and the braincase height (Fig. 7C). A summary of key features to aid in field-based identifications of the two new species from each other is presented in Table 5.

TABLE 5. A quick guide to identifying new Pilbara planigale species for ecologists capturing live animals. Values obtained in the field may differ based on individual researchers and the maturity of the animals.

Feature	*Planigale kendricki*	*Planigale tealei*
Head length	> 20 mm	< 20 mm
Body weight	Mostly > 4 g, avg. ~ 7 g	Mostly < 6 g, avg. ~4 g
Relative size of manus	Slightly smaller than pes	Much smaller than pes
Head colouration	Brighter, orange/tan with orange eye-ring	Darker, brown with reddish tinge
Head shape	Longer with pointy nose	Shorter and more wedge-shaped
Overall size	Small, slightly smaller than a house mouse (length and weight)	Tiny, much smaller than a house mouse (length and weight)
Habitat substrate	Variety - rocky, sandy, some heavier soils	Exclusively cracking clays

Planigale ingrami is widely distributed across semi-arid Australia (Archer 1976a; Van Dyck & Strahan 2008). *Planigale tealei* was compared with various regional samples of *P. ingrami* and is clearly distinguishable from all named forms. *Planigale ingrami* specimens from localities in the Kimberley region (Fig. 2) were compared directly with the holotype of *P. i. subtilissima* (A582482), which was loaned by the Stockholm Museum and examined by K. Aplin and N. Cooper. Compared with *P. tealei*, *P. i. subtilissima* has a more grizzled, grey-brown dorsal pelage, a slightly longer tail that is less densely furred and has paler tail scales, smaller claws on the manus and pes and a larger and more distinctly bilobed ear, with a more elongate and taller supratragus. The venter of *P. i. subtilissima* is paler than that of *P. tealei*, with essentially cream hairs. The pouch of *P. i. subtilissima*, as reported by Woolley (1974) usually contains 9–10 nipples in accessory anterior pockets enclosed by a well-developed anterior skin fold, making it more complex than that of *P. tealei*, which has a poorly-developed anterior-lateral skin fold with up to 12 nipples that remain partially exposed.

The teeth and cranium of *P. tealei* differ from *P. i. subtilissima* in various ways. In *P. tealei*: the cranium is more depressed especially at rear above occipital region (*P. i. subtilissima* has a weakly domed occiput), the rostrum is slightly longer and narrower, the nasals are shorter and their combined posterior margin is broadly u-shaped (squared off in *P. i. subtilissima*), the alisphenoid tympanic process is more inflated and in longer contact with the rostral tympanic process of the petrosal, the rostral tympanic process of the petrosal is more inflated, and the paraoccipital process is less prominent. The auditory region in *P. i. subtilissima* appears flattened overall, and the alisphenoid tympanic process is slightly inclined forward. In *P. tealei*: $I^{2–4}$ are more elongate, $P^{1–2}$ is less reduced relative to P^3,

$M^{1–3}$ have a narrower anterior cingulum, M^4 has a larger protocone, P_3 is more reduced and commonly rotated out of alignment, $P_{1–3}$ have weaker cingula, $M_{1–3}$ have less reduced entoconids, and M_4 has a less reduced talonid.

Planigale tealei differs even more conspicuously from *P. tenuirostris*. The latter is more grizzled grey-brown dorsally, has a less depressed cranium with a much longer rostrum, and has longer nasals that extend further back onto the interorbital surface. Additionally, *P. tenuirostris* has a much taller P^3 and indistinct to absent entoconids on $M_{1–3}$.

Comments. We recommend the following common name be used in association with *P. tealei* sp. nov.: cracking-clay Pilbara planigale.

Discussion

Identity and distribution of Pilbara Planigales

The large number of *Planigale* specimens vouchered from north-western Western Australia in recent decades provides a firm basis for taxonomic clarification of these enigmatic dasyurids. Our study corroborates earlier work (Painter *et al.* 1995; Strahan 1995; Blacket *et al.* 2000; Gibson & McKenzie 2009; Westerman *et al.* 2016; Umbrello *et al.* 2020;) that two distinct species of *Planigale* are present in the Pilbara and reveals broadly overlapping distributions with numerous instances of local sympatry: *P. kendricki* (formerly known as '*Planigale* 1' from Blacket *et al.* (2000) and Westerman *et al.* (2016)) and *P. tealei* (formerly known as '*Planigale* sp. Mt Tom Price' from Blacket *et al.* (2000) and Westerman *et al.* (2016)).

Each of the two species found in the Pilbara was formerly associated with more widely distributed species. A specimen of *P. kendricki* from Tambrey formed the basis of Ride's (1970) inclusion of the Pilbara uplands in the geographic range of *P. maculata*. Archer (1976a) recognised the distinctiveness of this specimen but referred another specimen of *P. kendricki* (WAM M11020) from Barrow Island to *P. maculata sinualis*. Specimens of *P. tealei* were not available at the time of Archer's review. The first specimen of *P. tealei* was collected on Marillana Station in December 1980 and, along with subsequent specimens, was tentatively identified as *P. ingrami* due to their extremely small size. The taxonomic distinctiveness of both of these Pilbara taxa was previously highlighted by the mitochondrial and nuclear fragment genetic studies of Painter *et al.* (1995), Blacket *et al.* (2000) and Westerman *et al.* (2016), and their conclusions are strongly corroborated by our additional molecular data. Our morphometric analyses, while clearly discriminating the new species at both k-nearest neighbour classifications and ANOVAs on some individual characters, were not able to separate these two tiny planigale species as easily as the molecular data, suggesting they are very similar in size and that perhaps the linear measurements we used did not capture enough detail at that minute size. Developments in 3D geometric morphometric analysis are proving useful for discriminating between species of morphologically similar *Antechinus* (Viacava *et al.* 2022, 2023) and may prove useful for the smaller planigale species as well.

Each of *P. kendricki* and *P. tealei* are well-differentiated species that vary in numerous aspects of external and craniodental morphology, both from each other and from all other previously described species of *Planigale*. Of the two new species, *P. kendricki* appears to have the wider distribution, including isolated populations on Barrow Island and the Cape Range peninsula, both adjacent to the Pilbara region of Western Australia. *Planigale kendricki* is also captured more frequently than *P. tealei* and appears to occupy a wider range of habitats, including areas of essentially sandy terrain as well as rocky substrates (Gibson & McKenzie 2009). In contrast, *P. tealei* appears to be more closely restricted to the Pilbara region and tends to be associated with one particular habitat type—cracking clays on heavy soils. Both species may be abundant in appropriate habitats. No other *Planigale* species is found in the Pilbara, and as noted above, the Barrow Island population included within *P. maculata* by Archer (1976a) is herein referred to *P. kendricki*.

Interspecific relationships of the Pilbara Planigales

For *P. kendricki*, the greatest genetic (see Westerman *et al*. 2016) and indeed phenetic similarity is with *P. tenuirostris*, the latter owing primarily to the relatively long snout of both species, although this condition is widespread among species of *Sminthopsis* and many other genera of dasyurids, and most likely represents a retained ancestral condition (Archer 1976a; b). The unusual presence of a two-rooted P_3 tooth in some individuals of *P. kendricki* might either represent a retained ancestral condition or an atavism; in either case, it is interesting to note that the P_3 of *P. kendricki* is no larger than in many other populations and species within *Planigale* (Archer 1976a).

Planigale tealei is most similar in overall craniodental configuration to *P. ingrami*. These species share an extreme level of cranial depression that has produced a broad and low neurocranium, a broad interorbital region, a relatively broad rostrum and a sloping occiput. They are also the two smallest members of the genus and are both commonly associated with cracking clay habitat, which planigales are known to shelter in from environmental extremes by crawling into deep, narrow fissures (Read 1987). Although sharing of this ecological trait and morphological adaptation might suggest a phyletic link between *P. tealei* and *P. ingrami*, some details of cranial morphology suggest that the adaptation has evolved independently in each lineage. In particular, the mode of cranial flattening appears to be slightly different in each case. In *P. tealei*, extreme cranial flattening is achieved by lowering and forward inclination of the occiput, which produces a unique midline depression of the parietal bones; in contrast, *P. ingrami* has a more typical, domed neurocranium but shows a distinctive flattening of the auditory region, resulting in a characteristic forward inclination of the alisphenoid tympanic process. Using 3D geometric morphometric approaches, which are able to capture subtle shape, as well as size, differences between individuals may be a suitable method for examination of cranial shape differences between these two taxa.

Diversity among Pilbara mammals

The Pilbara has long been recognised as a biodiversity hotspot in arid Australia, harbouring a suite of endemic flora and fauna that have diversified in a multitude of habitats within the rugged terrain, reliant on seasonal cyclonic rainfall (Pepper *et al.* 2013). Among vertebrates, 180 species of reptile and frog occur in the Pilbara, and 36 (20%) of these are endemic to the region, with a further 12 species with distributions centred on the Pilbara and only limited records in surrounding bioregions (Doughty *et al.* 2011; with updated numbers provided pers. comm. P. Doughty, Western Australian Museum data). Similarly, within the avifauna, numerous subspecific taxa are recognized as endemic to the Pilbara region (Johnstone *et al.* 2013).

The diversity and rate of endemism in Pilbara mammals is comparatively lower than other faunal groups. Our two newly described planigales join two other near-endemic dasyurids, *Dasykaluta rosamondae* and *Ningaui timealeyi*, which are among the 12 dasyurid species known to occur in the Pilbara, with *D. rosamondae* being endemic at the generic level (Archer 1982; Krajewski & Westerman 2003). Many arid-inhabiting dasyurids have large distributions (Baker & Dickman 2018), and genetic data can elucidate whether the Pilbara has played a role in driving local adaptation, diversity and population structure. The largest dasyurid in northern Australia, *Dasyurus hallucatus*, has a disjunct population in the Pilbara that is genetically (Hohnen *et al.* 2016; von Takach *et al.* 2022) and potentially morphologically (Umbrello 2018) distinct. Other dasyurid species widely distributed across the arid zone that also occur in the Pilbara are *Antechinomys laniger*, *Dasycercus blythi*, *Pseudantechinus macdonnellensis*, *P. woolleyae*, *Sminthopsis longicaudata* (although Westerman *et al.* (2023) places this in *Antechinomys*), *S. macroura*, *S. ooldea* and *S. youngsoni* (Gibson & McKenzie 2009). Of these species, *S. ooldea* exhibits strong genetic structure associated with the Pilbara craton, while others show weak to little genetic structure across the geological boundary (Umbrello *et al.* 2020).

Among other groups of ground-dwelling mammals, only two other endemics (a murid rodent, *Pseudomys chapmani* and a rock-wallaby, *Petrogale rothschildi*) are recognised among the 48 or so mammal species recorded from the Pilbara region (Van Dyck & Strahan 2008). It is likely that further research into the taxonomic and genetic distinctiveness of other Pilbara mammal species, particularly those with disjunct and isolated populations, may result in other endemic forms being recognised.

Conclusion

It has long been recognised that *Planigale* likely contains cryptic species, and here we taxonomically resolved two known genetic lineages from the Pilbara region in Western Australia. Numerous small dasyurid species have been described fairly recently (in the past 50 years), including species of *Sminthopsis* (Van Dyck *et al.* 1994), *Ningaui*

(Archer 1975) and *Antechinus* (Baker *et al.* 2015). As more collections occur in remote and difficult to access regions, results from molecular analyses should continue to reveal cryptic diversity. Defining this diversity and assessing the distributions of newly described species is one of the first steps needed to inform and implement appropriate conservation measures. Further work on *Planigale* using comprehensive molecular and morphological data from across Australia will be required to finally resolve the *P. maculata* and *P. ingrami* species complexes, and this is underway.

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Appendix

Appendix Table 1. Allozyme profiles at 35 loci for the 38 *Planigale* screened in 2001. The two animals asterisked were also screened by Blacket *et al*. (2001). Taxon abbreviations: Pm = *P. maculata*, Pt = *P. tealei*, Pk = *P. kendricki*. Locus abbreviations, allozyme designations, and the "M1" and "M2" nomenclature for *P. maculata* all follow Blacket *et al*. (2002).

Taxon	WAM Regno	***Acon1***	***Acon2***	***Acyc***	***Ada***	***Adh1***	***Alb***	***Ca***	***Enol***	***Est1***	***Est2***	***Est3***	***Fum***	***Gdh***	***Glo***	***Got1***	***Got2***	***Gpd1***	***Gpd2***	***Gpi***	***Idh1***	***Idh2***	***Ldh1***	***Ldh2***	***Mdh2***	***Me1***	***Me2***	***Mpi***	***PepA***	***PepB***	***PepD***	***6Pgd***	***Pgm***	***Sod***	***Sordh***	***Tpi***
Pm M1	51586	a	b	c	e	a	a	a	a	b	a	b	a	b	b	b	a	a	a	a	a	a	b	a	a	a	a	a	a	b	b	a	b	a	a	a
Pm M2	21998	a	b	a	d	a	a	a	a	b	a	c	a	b	b	b	a	a	a	a	a	a	a	a	a	a	a	a	b	b	b	a	b	a	a	a
Pm M2	43137*	a	b	a	d	a	a	a	a	b	a	b	a	b	b	b	a	a	a	a	a	a	a	a	a	a	a	a	a	b	b	a	b	a	a	a
Pt	47832	a	a	a	a	b	a	b	a	b	a	b	a	b	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	b	b	a	b	a	a	a
Pt	47841	a	a	a	a	b	a	b	a	b	a	b	a	b	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	a	b	a	b	a	a	a
Pt	51472	a	a	ac	a	b	a	b	a	b	a	b	a	b	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	b	b	a	b	a	a	a
Pk	25601	a	a	bd	c	a	a	b	a	a	a	c	a	bc	a	b	a	a	ab	b	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	41803	a	a	d	bc	a	a	b	a	a	a	c	a	b	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	b	a	a	ab	a	b	a
Pk	41804	a	a	d	c	a	a	b	a	a	a	c	a	c	a	b	a	a	ab	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	41812	a	a	bd	c	a	a	b	a	a	a	a	a	b	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	b	a	a	bc	a	b	a
Pk	41839	a	a	bd	c	a	a	b	a	a	a	c	a	bc	a	b	a	a	ab	ab	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	43169*	a	a	bd	bc	a	a	b	a	a	a	c	a	b	a	b	a	a	a	ab	a	b	a	a	a	a	b	a	a	b	ab	a	b	a	b	a
Pk	45026	a	a	b	c	a	a	b	a	a	a	c	a	c	a	b	a	a	ab	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	45029	a	a	b	c	a	a	b	a	a	a	c	a	b	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	45030	a	a	b	c	a	a	b	a	a	a	c	a	bc	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	45035	a	a	bd	c	a	a	b	a	a	a	c	a	c	a	b	a	a	ab	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	45041	a	a	b	c	a	a	b	a	a	a	c	a	c	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	45065	a	a	ad	c	a	a	b	a	a	a	c	a	bc	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	48799	a	a	d	c	a	a	b	a	a	a	c	a	ab	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	48901	a	a	d	bc	a	a	b	a	a	a	c	a	c	a	b	a	a	a	ab	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	51581	a	a	bd	c	a	a	b	a	a	ab	c	a	b	a	ab	a	a	b	b	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	51643	a	a	bd	c	a	a	b	a	a	a	c	a	bc	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	51668	a	a	d	c	a	a	b	a	a	ab	c	a	c	a	b	a	a	a	b	a	b	a	a	a	a	b	a	a	b	ab	a	b	a	b	a
Pk	51673	a	a	bd	b	a	a	b	a	a	a	c	a	bc	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	51684	a	a	bd	bc	a	a	b	a	a	a	c	a	b	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	bc	a
Pk	51697	a	a	d	c	a	a	b	a	a	a	c	a	b	a	b	a	a	a	ab	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	51746	a	a	d	c	a	a	b	a	a	a	c	a	bc	a	b	a	a	ab	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	51749	a	a	d	c	a	a	b	a	a	a	c	a	bc	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	51792	a	a	d	c	a	a	b	a	a	a	c	a	bc	a	ab	a	a	ab	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	51793	a	a	d	c	a	a	b	a	a	a	c	a	b	a	b	a	a	a	ab	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a

......*Continued on the next page*

APPENDIX (Continued)

Taxon	WAM Regno	*Acon1*	*Acon2*	*Acyc*	*Ada*	*Adh1*	*Alb*	*Ca*	*Enol*	*Est1*	*Est2*	*Est3*	*Fum*	*Gdh*	*Glo*	*Got1*	*Got2*	*Gpd1*	*Gpd2*	*Gpi*	*Idh1*	*Idh2*	*Ldh1*	*Ldh2*	*Mdh2*	*Me1*	*Me2*	*Mpi*	*PepA*	*PepB*	*PepD*	*6Pgd*	*Pgm*	*Sod*	*Sordh*	*Tpi*
Pk	51803	a	a	d	bc	a	a	b	a	a	a	-	a	c	a	b	a	a	ab	ab	a	-	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	51805	a	a	bd	bc	a	a	b	a	a	a	c	a	b	a	b	a	a	ab	ab	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	51807	a	a	bd	c	a	a	b	a	a	ab	c	a	b	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	51811	a	a	bd	c	a	a	b	a	a	a	c	a	b	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	52212	a	a	d	c	a	a	b	a	a	a	c	a	b	a	b	a	a	ab	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	52421	a	a	d	c	a	a	b	a	a	a	c	a	b	a	b	a	a	-	ab	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	52422	a	a	bd	c	a	a	b	a	a	a	-	a	bc	a	b	a	a	a	a	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a
Pk	52423	a	a	d	c	a	a	b	a	a	a	c	a	c	a	b	a	a	a	ab	a	b	a	a	a	a	b	a	a	b	a	a	b	a	b	a