



Genetic and morphological reassessment of the genus *Isoodon* (Marsupialia: Peramelemorphia) and description of new species and subspecies

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Abstract

Since European colonisation of Australia, bandicoots in the genus *Isoodon* have been heavily affected by the introduction of feral predators and changes to the landscape, resulting in the contraction of their distribution and loss of genetic diversity. Their taxonomy has also been a challenge: 11 species were originally described, with revisions in the 1990s leading to recognition of only three species, but recent studies utilising molecular and morphological analyses led to documentation of two additional species. As a result, five species are currently recognised. To further resolve the taxonomy of this genus, we have opted for a total evidence approach, using both morphological and molecular techniques, including sampling specimens from their historical and extant distributions. All available type specimens were also examined and sampled for DNA analyses. Molecular data were generated from 1000s of nuclear gene loci using exon capture as part of the Oz Mammal Genomics initiative. Our results support two additional species (*I. microtis*, *I. moresbyensis* new stat.) being raised (recognising seven species in the genus), a major range extension for *I. fusciventer* and range reduction for the endangered *I. obesulus obesulus*, and several previously unnamed new subspecies (*I. auratus bundilarrri*, *I. a. marchinbarensis*, *I. fusciventer dawensis*, *I. f. halae*, *I. f. insulanus*, *I. f. terrenus*, *I. macrourus capensis*). This new taxonomic framework has

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important implications for the conservation management of *Isoodon* species, with current translocation plans to mix populations, as most species are currently listed as endangered or vulnerable.

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Introduction

Australia has suffered the highest mammal extinction rate of any continent in the past 200 years, losing 42 mammal species since European colonisation (Woinarski et al. 2015, 2019; Burbidge, 2024 updated for *Dasycercus* (Newman-Martin et al. 2023)). Nearly 20% of these extinct mammals come from the order Peramelemorphia (bandicoots and bilbies). Peramelemorphians are small to medium-sized, terrestrial and omnivorous marsupials (except species of *Chaeropus* which are predominantly herbivorous), which typically dig for their food with large claws and strong forearms (Gordon and Hulbert, 1989; Warburton and Travouillon, 2016). The order has four modern families, the Thylacomyidae (bilbies), the extinct Chaeropodidae (pig-footed bandicoots), the Peroryctidae (New Guinean bandicoots), and the Peramelidae (Australian bandicoots). There are currently 23 extant species found across New Guinea and Australia, with another eight recently extinct species, all from Australia (Warburton and Travouillon, 2016; AMTC, 2024). The introduction of foxes and cats, land clearing for agriculture, and changes to traditional fire practices are all linked to the extinction of these species (Travouillon and Phillips, 2018; Travouillon et al. 2019; Woinarski et al. 2015, 2019).

In Australia, the extant peramelemorphians are listed as Least Concern under the IUCN Red List, except for the Golden Bandicoot *Isoodon auratus* (Ramsay 1887), Shark Bay Bandicoot *Perameles bougainville* Quoy and Gaimard, 1824, Eastern Barred Bandicoot *Perameles gunnii* Gray, 1838 and Greater Bilby *Macrotis lagotis* (Reid, 1837), which are listed as Vulnerable (IUCN, 2024). Under the Australian Environment Protection and Biodiversity Conservation (EPBC) Act, the subspecies *Isoodon obesulus obesulus* (Shaw, 1797) is listed as endangered and *I. auratus* and *I. obesulus nauticus* Thomas, 1922 are listed as vulnerable. These endangered and vulnerable species and subspecies are the subject of many conservation programs, using offshore islands and fenced areas to protect them from introduced predators, giving them a chance to survive (Parrott et al., 2017; Legge et al., 2018). The IUCN Red List was last updated for Australian mammals in 2016, before the recent taxonomic changes within Peramelemorphia. As a result, several species are currently not evaluated including the Quenda *Isoodon fusciventer* (Gray 1841; Travouillon and Phillips, 2018), the Cape York Brown Bandicoot *I. peninsulæ* Thomas, 1922 (Westerman et al., 2012), and the Northern Long-nosed Bandicoot *Perameles pallescens* Thomas, 1923 (Travouillon, 2016). The Shark Bay Bandi-

coot (previously known as Western Barred Bandicoot) *Perameles bougainville* also needs to be re-evaluated as several extinct species were split from this species, including the Marl *Perameles myosuros* Wagner, 1841, the Nullarbor Barred Bandicoot *Perameles papillon* Travouillon and Phillips, 2018, South-eastern Striped Bandicoot *Perameles notina* Thomas, 1922, and Liverpool Plains Striped Bandicoot *Perameles fasciata* Gray, 1841 (Travouillon and Phillips, 2018).

The taxonomic history of the genus *Isoodon* is quite complex (Jackson and Groves, 2015). The Southern Brown Bandicoot was the first bandicoot to be described, as *Didelphis obesula* Shaw, 1797. No type was designated at the time, until Dixon (1981) designated a neotype from Ku-Ring-Gai Chase National Park in Sydney, New South Wales. It was transferred to the genus *Isoodon* by Desmarest (1817), moved into the genus *Perameles* by Waterhouse (1838) and moved back to the genus *Isoodon* by Iredale and Troughton (1934), along with all the taxa mentioned hereafter. The Quenda was the next taxon to be named, as *Perameles fusciventer* Gray 1841, from King George Sound, Western Australia. It was synonymised within *I. obesulus* by Waterhouse (1846) but then designated as a subspecies of *obesulus* by Iredale and Troughton (1934). The Northern Brown Bandicoot was named *Perameles macrourus* by Gould (1842) from Port Essington, Northern Territory. The Tasmanian Southern Brown Bandicoot *Perameles affinis* was named by Gray (1843) as a nomen nudum but was only recognised as a valid taxon (from Kangaroo Point near Hobart, Tasmania) when Waterhouse (1846) published the name as a junior synonym of *obesulus*. It was re-established as a subspecies of *obesulus* by Iredale and Troughton (1934). Ramsay (1877) named two new taxa, *Perameles moresbyensis* from Port Moresby in Papua New Guinea and *Perameles macroura* var. *torosus* from the Endeavour River near Cooktown in north Queensland. Their status changed multiple times to full species, synonyms of *macrourus* or subspecies of *macrourus* (see Jackson and Groves, 2015). The Golden Bandicoot was named *Perameles auratus* by Ramsay (1887) from Derby in Western Australia. It was synonymised with *I. macrourus* by Thomas (1888) but re-established by Thomas (1904). It was then recognised as a subspecies of *I. obesulus* by Tate (1948) before being re-elevated to species rank by Troughton (1967). The Barrow Island Golden Bandicoot, named by Thomas (1901) as *Perameles barrowensis*, was synonymised by Ride (1970) within *I. auratus*, then re-elevated to species by Lyne and Mort (1981) but finally recognised as a sub-

species of *I. auratus* by Strahan (1983). Thomas (1922) described two taxa, *Isoodon nauticus* from Franklin Island in South Australia and *I. peninsulae* from Utingu, Cape York, Queensland. They were both lowered to subspecies of *obesulus* by Tate (1948) but recognised at various statuses by others (see Jackson and Groves, 2015). The final taxon named in the genus was *Isoodon arnhemensis* Lyne and Mort 1981, from Melville Bay, Cape Arnhem, Northern Territory. It was recognised as a subspecies of *auratus* by Strahan (1995) and subsequent authors.

Before molecular data were available for the genus *Isoodon*, the general consensus was that there were three species in the genus as follows (Gordon and Hulbert, 1989): *Isoodon macrourus* with three subspecies (*I. m. macrourus*, *I. m. moresbyensis* and *I. m. torosus*), *Isoodon auratus* with three subspecies (*I. a. auratus*, *I. a. barrowensis* and *I. a. arnhemensis*) and *Isoodon obesulus* with five subspecies (*I. o. obesulus*, *I. o. affinis*, *I. o. fusciventer*, *I. o. nauticus* and *I. o. peninsulae*). Molecular data have since challenged this classification system. An allozyme study by Close et al. (1990) using 23 loci, which included most but not all recognised taxa, recognised two lineages for *I. macrourus*, corresponding to *I. m. macrourus* and *I. m. torosus* (*I. m. moresbyensis* was not sampled). Two lineages were also found for the remaining taxa, one including *I. a. barrowensis*, *I. o. affinis* and *I. o. obesulus* from southeastern Australia, and the other containing *I. o. fusciventer* from Western Australia and *I. o. nauticus* and *I. o. obesulus* from South Australia. The validity of *I. auratus* was challenged as a result. Other studies at the time, including DNA hybridisation studies (Kirsch et al. 1990, 1997) and an albumin study (Baverstock et al. 1990) included very limited sampling of *Isoodon*, which did not help resolve taxonomic questions. The 12S rRNA sequences of Westerman and Krajewski (2000) found similar results to Close et al. (1990), and included *I. m. moresbyensis*, supporting the three subspecies within *I. macrourus*. In contrast, they found little support for *I. o. affinis* and *I. a. barrowensis* as distinct subspecies, though sampling was limited for these taxa, and *I. a. auratus* and *I. a. arnhemensis* were not tested. The dual approach of Pope et al. (2001), which included mitochondrial DNA (mtDNA) control region sequences and discriminant function analysis of skull measurements and included all taxa within *Isoodon* (except *I. m. moresbyensis*), found little evidence for the subspecies of *I. macrourus*, and found that *I. o. peninsulae* was the only divergent lineage in the *I. obesulus*/*I. auratus* clade. Similar results were found by Zenger et al. (2005) using mtDNA and microsatellite data. The combined use of nuclear and mtDNA sequences by Westerman et al. (2012) supported *I. auratus* as a valid species. It also cemented *I. peninsulae* as a distinct and valid species and questioned whether *I. o. fusciventer* should also be recognised as a distinct species. A total evidence analysis by Travouillon and Phillips (2018) produced similar results to Westerman et al. (2012) and officially

raised *I. fusciventer* as a distinct species. A subsequent study by Cooper et al. (2018) that also used nuclear and mtDNA sequences and much larger sample sizes for *Isoodon* populations compared to previous phylogenetic studies found support for retaining *I. o. affinis* as a valid subspecies and also found that the bandicoot populations from Mount Lofty ranges, Kangaroo Island, Franklin and St Francis Islands may warrant a separate taxonomic status from *I. o. obesulus*. The genetic uniqueness of the South Australian populations was also supported in another study using mtDNA and microsatellite data (Thavornkanlapacha et al. 2021) and a population genomics study by Black et al. (2024). Population genetic analyses by Rick et al. (2023), has also found four distinct genetic populations within the Golden Bandicoot, *Isoodon auratus*.

As it stands, there are now five recognised species of *Isoodon* in Australia, widely distributed across the continent but most have suffered significant reductions in their distributions since European arrival (Figure 1). Previous studies have highlighted the complexity of the taxonomic history within the genus (Jackson and Groves, 2015), and several populations, including those in South Australia (Cooper et al. 2018) still require further investigation. The aim of this study is to expand on previous studies and investigate the taxonomy of the genus *Isoodon* using a total evidence approach, including both genetics and morphology, to identify if additional taxa require description or if current taxa are required to be synonymised. We aimed to sample the entire distribution of the genus, using both contemporary tissues and old museum skins to obtain robust molecular data using an exon capture approach developed as part of the OzMammals Genomics Initiative, (Eldridge et al. 2020) and skull measurements and cranio-dental characters to evaluate morphological differences.

Methods

Molecular data

Material examined

The complete list of material used and its metadata is available as a supplementary file (DOI: 10.5061/dryad.8gtht772x).

Sequencing

Contemporary tissue samples (n = 83) were extracted using a salting out procedure or via the Gentra extraction methodology following the manufacturers' protocols. Historical samples (n = 75) were extracted using the DNeasy Blood and Tissue Kit (Qiagen), with modifications based on Joseph et al. (2016). Dried skin samples were rehydrated overnight in 300µl PBS (pH 7.4, Thermo Fisher), before transfer to lysis buffer. Samples were digested for 2-6 hours at 56°C with shaking at 800 rpm, in a lysis buffer mix containing 320µl buffer ATL, 40µl proteinase K, and 40µl 1M DTT (Thermo Fisher). Following lysis, 400µl buffer AL and 3.25 µg carrier RNA (Sigma

Aldrich) were added before incubation at room temperature for 30 minutes. 400µl of ethanol was added to each sample preparation and immediately mixed. Samples were then transferred to DNeasy spin columns in 650µl aliquots, with each centrifuged for 1 minute at 8000 rpm and the supernatant was discarded. Ethanol wash steps followed the manufacturer's protocol. DNA was eluted in 200µl of buffer AE containing 0.05% Tween 20 (Sigma). DNA extraction success was evaluated with the Qubit High Sensitivity DNA kit (Thermo Fisher). To mitigate contamination risks, DNA from historical museum specimens was extracted in a dedicated, physically separated, Trace DNA facility at the Australian National University's Ecogenomics and Bioinformatics Laboratory. Extraction negative controls were included to monitor for contamination.

An exon capture target enrichment library was prepared for each sample using the Meyer and Kircher (2010) protocol, with modifications based on Bi et al. (2013) and Roycroft et al. (2022). We used a set of custom marsupial exon capture probes targeting 1.28Mb of genomic DNA from 2167 exons (SeqCap EZ Developer Library; Roche NimbleGen) as outlined in Bragg et al. (2017). Pooled exon capture libraries were sequenced on Illumina platform sequencers at 200 cycle paired end runs at the ACRF Biomolecular Resource Facility, Australian National University.

Bioinformatic processing

Raw sequencing data were processed using *Exon Capture Pipeline for Phylogenetics* (ECPP, github.com/Victaphanta/ECPP), following the settings described in Roycroft et al. (2020). Historical specimens were processed with the same pipeline, using the modified mapping approach described in Roycroft et al. (2022). Each targeted locus was aligned independently using MAFFT (Kato and Standley, 2013) and alignment ends were trimmed using BMGE (Criscuolo and Gribaldo 2010). This approach also ensured all loci were composed of full codon triplets (beginning on the first and ending on the third codon positions). We excluded loci captured for < 80% of samples, and those which exhibited average heterozygosity > 3% (representing putative paralogous loci) in three or more independent taxa. Where two or fewer taxa exhibited heterozygosity > 3%, only those taxa were removed from the corresponding alignment. This resulted in a filtered set of 2,050 exons, spanning 1.14Mb of genomic DNA.

Population analyses using SNP data

We initially explored relationships among *Isoodon* taxa using population analyses of SNP data via Principal Components Analyses (PCA). From the filtered exon capture alignment described above, two randomly selected SNP datasets were generated from the *Isoodon* in-group samples, excluding genetically divergent *Perameles* and *I. macrourus*, by selecting one SNP from each locus (total of 1,568 SNP). *Isoodon macrourus* was excluded from

the population analyses due to its clear genetic distinction based on previous (Cooper et al. 2018, Pope et al. 2001, Westerman and Krajewski 2000, Westerman et al. 2012) and the current molecular phylogenetic analyses, to explore patterns of population structure within *Isoodon*.

Analyses were conducted in R version 4.5.2 within the RStudio IDE (2026.06.0 build 242) using the *dartR* package (Gruber et al. 2018, Mijangos et al. 2022). Each SNP dataset, along with the relevant sample metadata, was imported and combined into a *dartR* object and analysed separately. For each SNP dataset, samples were grouped by species and subspecies inferred from morphological analyses in the current manuscript; *I. peninsulæ* (n=3), *I. fusciventer fusciventer* (n=23), *I. fusciventer terrenus* (n=11), *I. fusciventer nauticus* (n=2), *I. fusciventer halae* (n=2), *I. fusciventer insulanus* (n=1), *I. fusciventer dawsoni* (n=1), *I. obesulus obesulus* (n=12), *I. obesulus affinis* (n=11), *I. auratus barrowensis* (n=7), *I. auratus bundilarrri* (n=4), *I. auratus auratus* (n=1), *I. auratus arnhemensis* (n=1). Loci that contained missing data for all members in a species were removed from the analysis, remaining missing values were imputed using the nearest neighbour option and the final dataset filtered for any monomorphic loci. Principal Components Analysis (PCA) was used to examine the data for underlying genetic structure.

Molecular and Total evidence phylogenies

Molecular dating challenges

Estimating the timescale of *Isoodon* evolution with the exon capture sequences presents two challenges beyond those typically encountered for dating marsupials at taxonomically deeper levels. The first is the absence of taxonomically or temporally well-defined calibrations among *Isoodon*. The second is that samples with less complete sequences (e.g. more gaps and ambiguity codes) tend to result in branch length overestimation relative to their more complete sister taxa. This is unlikely to affect topology reconstruction and may result in only trivial dating differences between species. However, small branch length errors are effectively amplified within very shallow populations, which if comprising much of the taxon set, can distort the rate distribution model and mislead divergence estimation across the tree.

We addressed the absence of *Isoodon* fossil calibrations by starting with a total evidence dating analysis in MrBayes (Ronquist et al. 2012) that covers the broad diversity of bandicoots and bilbies, using a combined nuclear and mtDNA sequence matrix updated from Phillips et al. (2022) and taxonomically matching morphological data from the present study. Calibration is provided by prior age distributions for six nodes and time stamping from nine Eocene to Pliocene fossils included among the morphological dataset. The resulting total evidence dating posterior age distributions for

the divergences of *Isoodon-Perameles*, for the crown age of *Isoodon*, and for the divergence of *I. fusciventer* – *I. auratus* were subsequently employed as prior distributions for MCMCTree (Ranala and Yang 2007) divergence time estimation with the exon capture DNA dataset (see below).

Total evidence phylogeny

The total evidence matrix combined a DNA alignment updated from Phillips et al. (2022) and morphological data compiled for this study for 30 extant (or recently extinct) taxa and nine Eocene – Pliocene fossil taxa. The original DNA alignment included five nuclear protein-coding genes (*ApoB*, *BRCA1*, *IRBP*, *RAG1*, *vWF*) and three mitochondrial genes (12S rRNA, 16S rRNA, *Cytb*). This study adds the mitochondrial *ND2* gene, and to match the morphological data, we added all available sequences among the above-listed genes for four additional peramelemorphians, *Isoodon fusciventer*, *Perameles pallescens*, *Rhynchomeles prattorum*, and *Macrotis leucura*, and two additional (chimeric) dasyurids, *Planigale maculata/tenuirostris* and *Dasyurus maculatus/geoffroyi*. Accession numbers for the updated DNA matrix are provided in Supplementary Table 1.

After manual alignment in Se-AL 2.0a (Rambaut, 1996), where sites with ambiguous homology were excluded, the 10,352bp DNA matrix was combined with the 161 morphological characters. We estimated the timescale of bandicoot evolution in MrBayes 3.2.7, after Phillips et al. (2022), with the dataset partitioned into the three codon positions for the nuclear protein coding genes, two (1st+2nd and 3rd) codon positions for the mitochondrial protein coding genes, and separate stem and loop partitions for the concatenated 12/16S rRNA coding sequences. The morphological data were treated as an additional partition. These eight partitions were allowed to evolve at different rates but with proportional branch lengths (ratepr=variable). Following Travouillon and Phillips (2018) and Phillips et al. (2022) the mtDNA protein coding 3rd positions were RY-coded to ameliorate the influence of rapid transition substitutions on phylogenetic signal erosion and base compositional non-stationarity. Substitution models were inferred with ModelFinder within IQTREE 2.1.3 (Nguyen et al., 2015) and employed as such in MrBayes (or as the next most general model available): GTR+I+G for mtDNA protein coding 1st and 2nd positions, and for the mtDNA rRNA stems and loops; GTR+G for the nuclear protein coding 1st and 2nd positions; HKY+G for the nuclear protein coding 3rd positions; F81+I+G for the RY-coded mtDNA protein coding 3rd positions; and Mkv+G for the morphological characters.

Calibration for the total evidence dating is described in Supplementary Table 2, with nine fossils providing tip dates and six node calibrations further informing rate variation across the tree under the independent gamma rates (IGR) model with the default prior setting, $\text{igrvpr}=\exp(10)\text{prior}$. A lognormal prior setting for

$\text{clockratepr}=\text{lognorm}(-6.0,0.6)$ was informed by initial analyses with broad, normally distributed clockrate priors and the molecular and morphological relaxed clock models were unlinked. The fossilized birth-death model was employed with the following priors: $\text{speciationpr} = \exp(1)$, $\text{extinctionpr} = \text{beta}(1,1)$, $\text{fossilizationpr} = \text{beta}(1,1)$. Taxon sampling did not specifically target deep-level or clustered diversity, so the default (random) sampling strategy was used with sampling probability 0.35, which is roughly the geometric mean of the included bandicoot and dasyurid extant sampling proportions. Two independent sets of three MCMC chains were run for 15,000,000 generations, with trees sampled every 2,500 generations, and the default 25% burnin. Estimated samples sizes were >500 for the prior, likelihood, tree height and all substitution parameters. Convergence was indicated by average standard deviation of split frequencies of 0.0059. The resulting tree is shown as Supplementary Figure 4.

Exon capture DNA phylogeny and timetree for *Isoodon*

To reduce the disproportionate influence of base ambiguity and non-homology on branch length estimation among shallow clades and the potential downstream (direct and rate modelling) influence on temporal inference, we performed further visual inspection and manual editing on the exon capture sequence alignment, described above in ‘Bioinformatic processing’, using Se-AL v2.0a11 (Rambaut, 1996). This provided a reduced 946 exon (519,636 bp) data matrix for the 92 *Isoodon* and six *Perameles* outgroup taxa. The alignment homology concerns with the longer auto-alignment primarily pertained to the older *Perameles* samples and their impact on rooting *Isoodon*. Hence, the 519,636 bp dataset was employed for inferring the exon capture phylogeny. However, it was appropriate to use the more inclusive exon set for obtaining the SNP dataset, for which *Perameles* was not included.

Maximum likelihood phylogenetic inference was performed in IQ-TREE 2.13 (Nguyen et al., 2015) with models for each partition (GTR+I+G4) selected by ModelFinder within IQ-TREE. Branch lengths were estimated independently (-sp option). Ultrafast bootstrap approximation (2000 replicates, with -bnni option) was employed for assessing confidence in the resulting topologies.

We also reconstructed the *Isoodon* species tree using a summary-coalescent approach; we first used maximum likelihood under the HKY+G model in IQ-TREE to infer gene trees for each of the 946 individual exons that make up the (520 kb) manual alignment. The species tree was then inferred from these gene trees in ASTRAL 5.5.10 (Zhang et al., 2018). The OMG exons are slowly evolving and mostly short, and the phylogenetic depth of this study is shallow. Under these low signal conditions inferred gene trees tend to have low fidelity to underlying incomplete lineage sorting, and coalescent methods can perform poorly compared with concate-

nation methods (e.g. Chou et al., 2015; Xi et al., 2015). We therefore ran a second analysis in ASTRAL with only the gene trees inferred from the 102 exons with alignment lengths of at least 1000 bp. The resulting trees are shown as Supplementary Figure 3 and Figure 3.

The *Isoodon* timetree was estimated in MCMCTree (Ranala and Yang, 2007), within PAML (Yang, 2007) from the 519,636 bp exon capture DNA sequence alignment and with the IQ-TREE maximum likelihood phylogeny employed as the guide tree for the 92 *Isoodon* specimens and six outgroup *Perameles* specimens. Node calibration was implemented using the posterior divergence estimates obtained in the total evidence dating for the *Isoodon-Perameles*, crown *Isoodon*, and *I. fusciventer* – *I. auratus* divergences (each now modelled as skew-normal prior distributions). All calibrations used in MCMCTree are described in Supplementary Table 3.

MCMCTree was run with the independent rates model. The average root to tip evolutionary rate from the IQ-TREE maximum likelihood tree (assuming the median of 5.01 Ma for the *Perameles-Isoodon* root age prior) was 0.00159 substitutions Ma⁻¹. This was used to inform the rate prior, *rgene_gamma* for the MCMCTree analyses (1 629), noting that $1/0.00159 = 629$, and with the time unit being 1 Ma. *Sigma2_gamma* was set to (1 5.01), given the median of 5.01 Ma for the root height prior. For each of the MCMCTree runs the MCMC chain was sampled every 100th generation from among the 500,000 generations, excluding a burn-in covering an additional 25,000 generations. The resulting tree is shown as Supplementary Figure 4.

A further combined evidence (exon capture DNA and morphology) timetree was inferred in MrBayes to incorporate taxa that were unable to be sampled for the DNA data. Nineteen *Isoodon* specimens representing all species and subspecies were included, along with three *Perameles* specimens, for the 161 morphological characters. The 519,636 bp exon capture DNA data was able to be matched to all but three of these specimens; the exceptions being *I. microtis*, *I. a. marchinbarensis*, and *I. m. capensis*. The latter two subspecies were constrained to fall with *I. auratus* and *I. macrourus*, respectively, in the Bayesian combined evidence analysis, so as to avoid missing data artefacts. Both placements were confirmed in preliminary Bayesian inference (MrBayes) reconstructions based solely on the morphological data.

The combined dataset was partitioned into the three codon positions for the exon capture DNA sequences, and a separate morphological data partition. These four partitions were allowed to evolve at different rates but with proportional branch lengths (*ratepr=variable*). Substitution models were inferred with ModelFinder within IQTREE 2.1.3 (Nguyen et al., 2015): GTR+I+G for the DNA partitions and Mkv+G for the morphological characters. Temporal calibration was provided by posterior distributions from the total evidence dating that included fossils. These were translated here as truncated normal

priors, with truncation of the lower bounds at 4 standard deviations from the mean. As such, the prior (minimum, mean, standard deviation) for the *Perameles-Isoodon* divergence and for crown *Isoodon* were (3.12, 6.18, 0.80) and (0.85, 1.78, 0.50) million years, respectively.

The combined evidence timetree was run in MrBayes under the independent gamma rates (IGR) model with the default prior setting, *igrvarpr=exp(10)*prior, and a lognormal prior setting for *clockratepr=lognorm* (-6.41,0.6), informed by average root to tip distances from the preliminary (undated) combined evidence maximum likelihood phylogeny performed in IQ-TREE. In MrBayes, two independent sets of three MCMC chains were run for 15,000,000 generations, with trees sampled every 2,500 generations, and the default 25% burnin. Estimated samples sizes were >250 for the prior, likelihood, tree height and all substitution parameters. Convergence was indicated by average standard deviation of split frequencies of <0.01.

Morphometrics

Material

Over 800 specimens were examined in this study, including all known types of *Isoodon* from museums in Australia and overseas, including Western Australian Museum (prefix WAM, M; Perth, Australia), Queensland Museum (prefix QM, JM or J or F; Brisbane, Australia), Australian Museum (prefix AM, M, P or S; Sydney, Australia), MacLay Museum (prefix MAMU M; Sydney, Australia), Australian National Wildlife Collection (prefix ANWC, CM; Canberra, Australia), South Australian Museum (prefix SAM or SAMA, M, P, CG, THI, CBN; Adelaide, Australia), Flinders University Mammal Collection (prefix FUM M; Adelaide, Australia), Museum Victoria (prefix NVM, C; Melbourne, Australia), Museum and Art Gallery of Northern Territory (prefix MAGNT/NTM, U; Darwin and Alice Springs, Australia), Tasmanian Museum and Art Gallery (prefix TMAG A; Hobart, Australia), Queen Victoria Museum and Art Gallery (prefix QVMAG A; Launceston, Australia), Natural History Museum (prefix NHMUK; London, United Kingdom), Musée Nationale d'Histoire Naturelle (prefix MNHN, ZM MO; Paris, France), Museo di Storia Naturale (prefix MSN, CE; Genoa, Italy), Zoologische Staatssammlung Munchen (prefix ZSM; Munich, Germany), Smithsonian Natural History Museum (prefix SMIN; Washington DC, United States of America) and American Natural History Museum (prefix AMNH; New York, United States of America). The complete list of specimens and measurements are provided as a supplementary file.

Morphometrics analysis

Following the method of Travouillon (2016), Travouillon and Phillips (2018) and Travouillon et al. (2019), 35 cranial measurements were taken on all skulls examined using digital callipers. Measurements were log transformed before being analysed in a Principal Component

Analysis (PCA) and a Linear Discriminant Analysis (LDA) in the software PAST, version 4.13 (Hammer et al. 2001). The same analyses were repeated after removing size from distances, using the allometry vs. standard method in PAST. These analyses were performed at the species level, following the species level identified in the molecular phylogeny (except for *I. microtis* sp. nov.), and also at the subspecies level (shown in the supplementary section, Figure 6) identified through traditional comparison methods. A one-way PERMANOVA was also performed at both the species (see results section) and subspecies level (see Supplementary Tables 4-6), in PAST.

Isoodon fusciventer pes

Pes length was also collected on specimens of *Isoodon fusciventer* and compared to pes data collected by DBCA staff on the south coast of Western Australia at various national parks and reserves. Pes length was found to be a good way to separate *I. f. fusciventer* from *I. f. halae*, with little to no overlap between males and females of each subspecies. The results are presented in the Supplementary Figure 7.

Subspecies investigation

As the subspecies level was much shallower than the species level in the molecular tree, we split up the maximum likelihood tree by species and compared the topology of the tree with Linear Discriminant Analysis (LDA) results at the species level on the cranial dataset. This allowed removal of the overlap between species that had made it difficult to interpret the subspecies level and to directly compare the genetic and morphological results.

Systematics

Note that for the sake of being concise, avoiding repetition and reducing the size of the manuscript, only the new species and subspecies are described here, but with references to how they differ from the already named species and subspecies. As a result, descriptions of the skins, skulls and teeth are kept to those that are essential. Decisions on the taxonomic level, species or subspecies, were made to be consistent between the molecular and morphological datasets, with a total evidence/integrative mindset (Padiol et al. 2010). Species were designated by having well supported monophyly, >95% bootstrap support (BS) in the molecular tree, and strong morphological differentiation. Subspecies were established on shallower clades with evidence of unique morphology.

Results

Population analyses using SNP data.

Analyses of both SNP datasets produced essentially equivalent results, and we therefore only present the results for one of the datasets, with the other provided in the supplementary information (Supplementary Fig-

ure 1). Three major genetic groups are recovered in the PCA, *I. obesulus*, *I. fusciventer* and *I. auratus* + *I. peninsulae* separated along PCA axis 1, which explains 39.8% of the variation (Figure 2A). Axis 2 separates *I. obesulus* and *I. fusciventer* from *I. auratus* + *I. peninsulae*, explained by 11.5% of the variation (Figure 2A). Axis 3, explaining 4.8% of the variation, separates *I. auratus* from *I. peninsulae*, as well as the *I. fusciventer* subspecies from Western Australia from the South Australian subspecies (Figure 2B and 2C, Supplementary Figure 1). Within *I. fusciventer*, apart from the separation of the South Australian and Western Australian taxa, sample size is low for most of the subspecies (*I. f. dawensis*, *I. f. halae*, *I. f. nauticus* and *I. f. insulanus*), making it difficult to determine genetic support with very small sample sizes. *I. o. obesulus* and *I. o. affinis* form discrete clusters that are slightly separated on axis 1 and 2 (Figure 2A-C). The *I. auratus* cluster also shows evidence of genetic differentiation between samples from Barrow Island (*I. a. barrowensis*) and the rest of the *I. auratus* samples on axis 2 and 3 (Figure 2A-C). *I. a. auratus* separates from *I. bundi-larri* and *I. a. arnhemensis* on axis 3 (Figure 2C).

Molecular phylogeny.

The maximum likelihood tree inferred on the 519,636bp concatenated exon-capture alignment supports the presence of seven major clades for *Isoodon* (Figure 3). *Isoodon macrourus* + *I. moresbyensis* are recovered as the sister clade to the rest of *Isoodon*. *Isoodon moresbyensis* is recovered as the sister taxon to *I. macrourus* with high bootstrap support (100%). Specimens from the Mount Lofty Ranges, Kangaroo Island, Franklin islands and St. Francis Island formed a strongly supported (Bootstrap (BS) = 100%) monophyletic group that grouped closely with *Isoodon fusciventer* from WA. This *I. fusciventer* group is sister to a clade containing *I. auratus*, *I. peninsulae* and *I. obesulus*. In the latter clade, *I. peninsulae* is the sister taxon to *I. obesulus*. All the named clades were resolved with high support (BS = 94 to 100%).

The summary-coalescent species tree inferred in ASTRAL (Supplementary Figures 2 and 3) from the 102 gene trees for long exons (1000 bp) recovered the same higher-level groupings among *Isoodon* that were recovered with the concatenated exon-capture alignment. Monophyly of each species, including the grouping of *I. fusciventer* (WA) with *I. fusciventer* (SA) was supported with 100% local posterior probability (LPP), except for *Isoodon auratus* (LPP = 76%). The support for *Isoodon auratus* monophyly increased (LPP = 93%) upon including the gene trees inferred for the shorter exons (giving 946 exons, 520 kb). However, with the short exons included the placement of *I. auratus* shifted from being sister to the clade that includes *I. obesulus* and *I. peninsulae*, to being sister to *I. fusciventer*. Both affinities for *I. auratus* in these ASTRAL analyses are weakly supported (LPP < 65%).

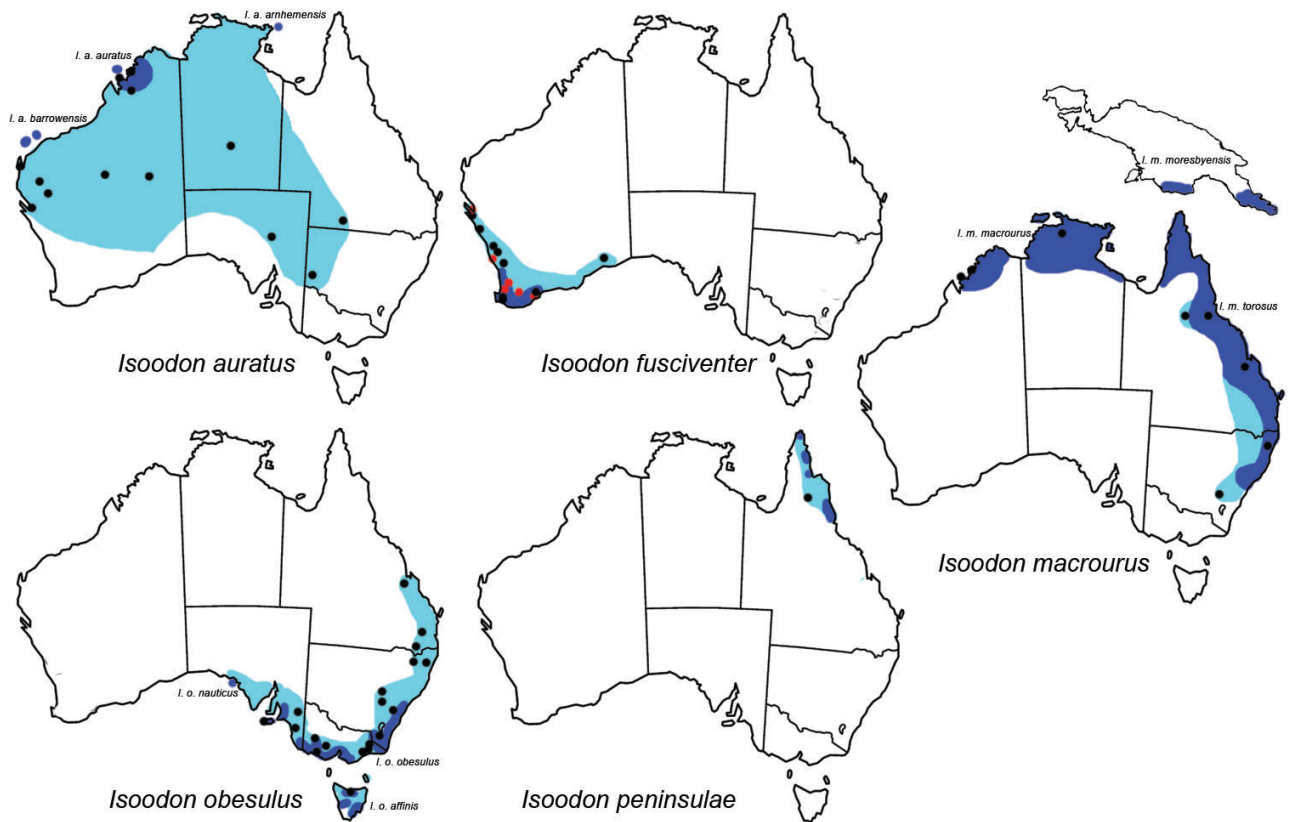


Figure 1. Current distribution of species of *Isoodon*. Dark blue = current distribution; light blue = historical distribution at European arrival in Australia; black dots = subfossil sites; red dots = translocation sites.

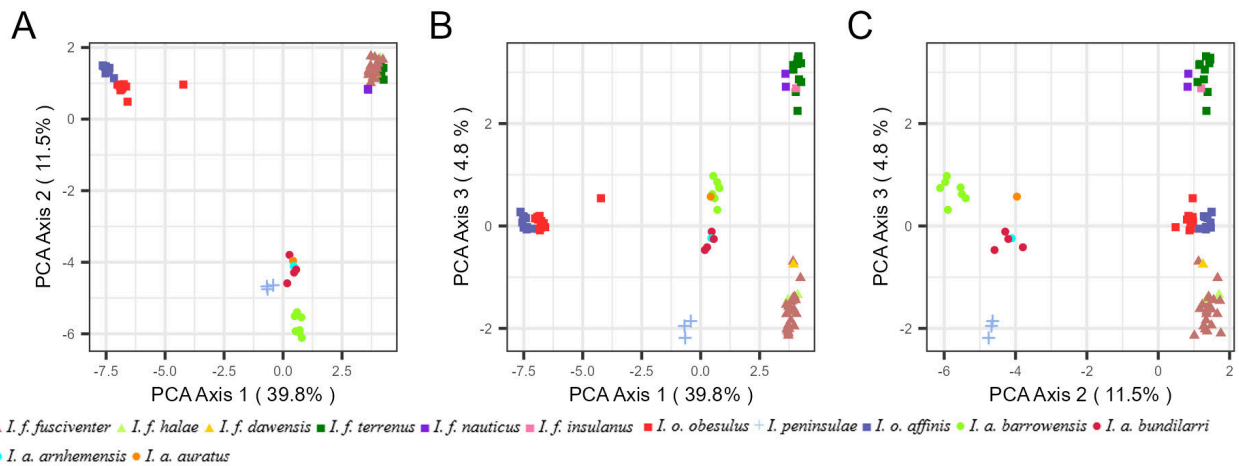


Figure 2. PCA analyses generated from the first randomly selected SNP dataset. A) using axis 1 and 2; B) using axis 1 and 3; C) using axis 2 and 3.

Combined total evidence phylogeny.

The combined total evidence phylogeny shows a similar topology to the maximum likelihood tree, but with the addition of the three taxa not represented in the genetic dataset (Figure 4). *Isoodon macrourus capensis* is recovered as the sister taxon to *I. macrourus macrourus*, but with low statistical support (Bayesian posterior probability, BPP = 51%). *I. auratus marchinbarensis* is recovered as the sister taxon to *I. a. barrowensis* with strong support (BPP = 97%). *I. microtis* is recovered as the sister

taxon to *I. obesulus* with low support (BPP = 49%). The rest of the groupings in the tree are strongly supported.

Morphometrics. The species level cranial morphometric results are shown in Figure 5. In the PCA (Figure 5A), *I. macrourus* and *I. moresbyensis* overlap but are separated from other taxa. All other taxa overlap significantly. *Isoodon obesulus* and *I. fusciventer* overlap the most with each other, but little with *I. auratus*, and not at all with *I. microtis*. When allometry is removed (Figure 5B), all species of *Isoodon* overlap, even *I. macrourus* and

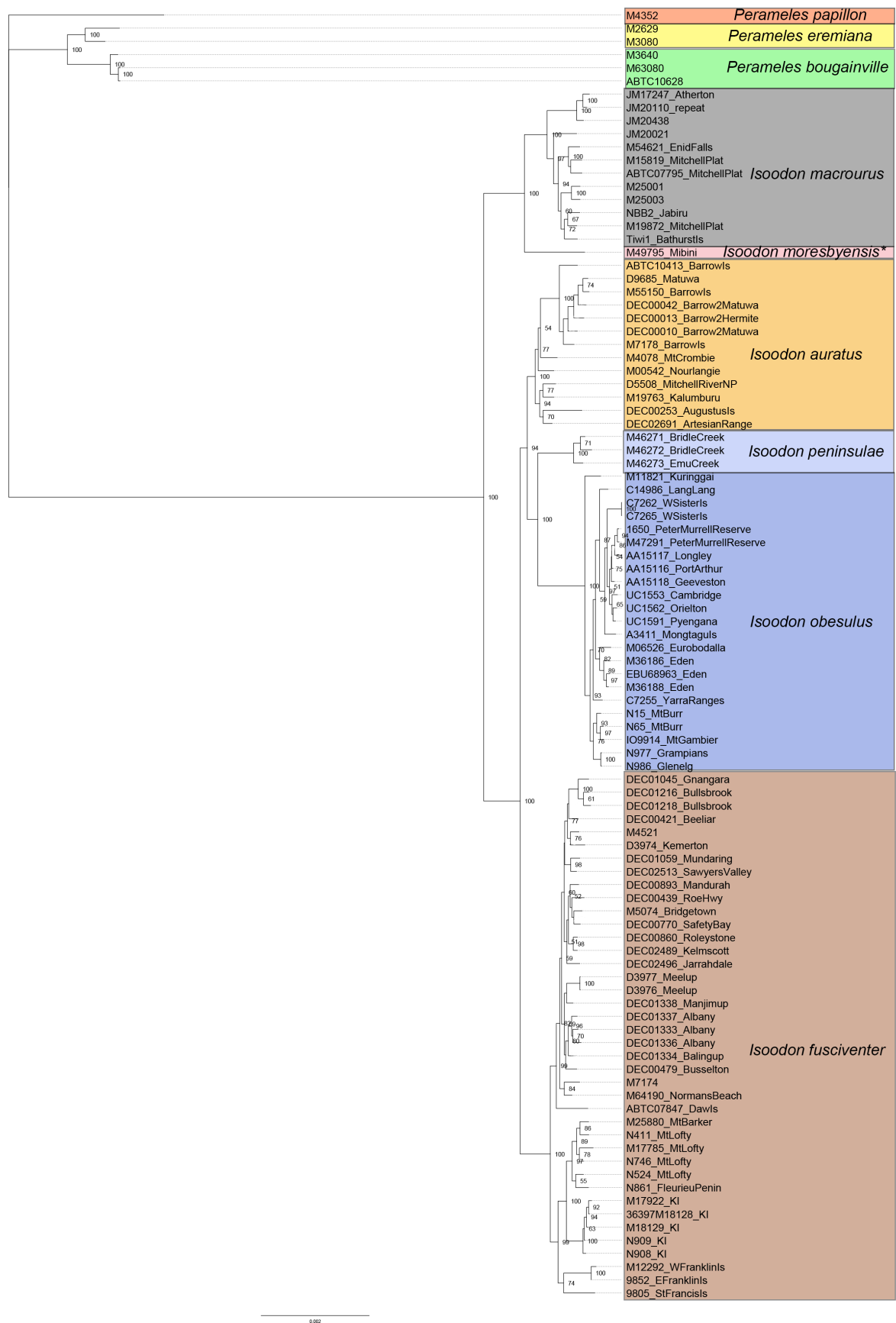


Figure 3. Maximum likelihood phylogeny for *Isodon*, inferred in IQ-TREE on the exon-capture DNA data (519,636 bp), with codon positions modelled separately. Ultrafast bootstrap support values are shown at the nodes. Specimen numbers and locations are indicated as tip names within each designated species.

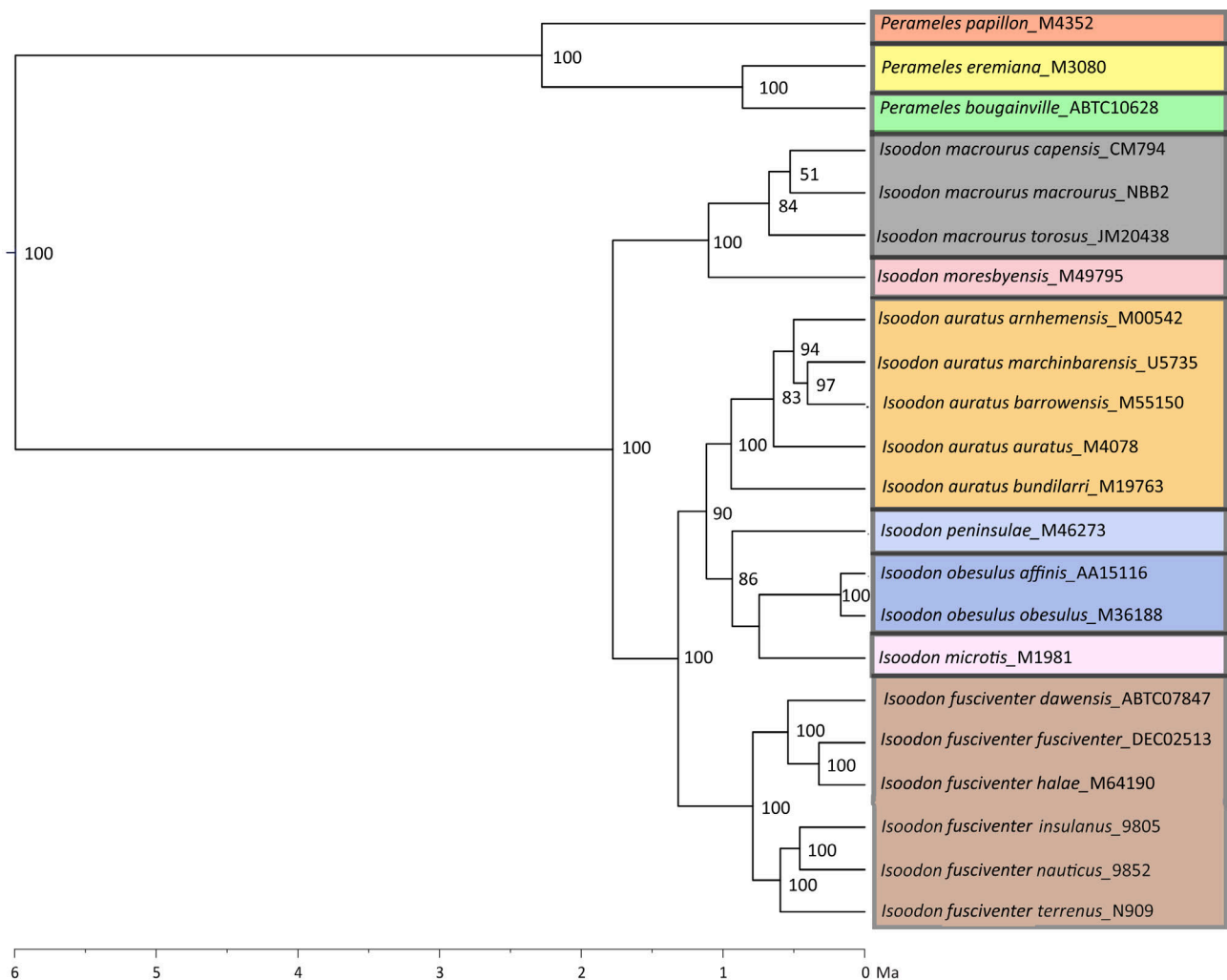


Figure 4. Bayesian inference total evidence timetree for *Isoodon*, inferred in MrBayes on the combined exon-capture DNA data and the discrete morphological dataset. Node values are Bayesian posterior probabilities expressed as a percentage. Specimen numbers are given alongside species (and subspecies) names.

I. moresbyensis, suggesting that size is as important as shape in separating taxa in *Isoodon*. In the LDA (Figure 5C), the overlap between species follows a pattern similar to that of the PCA, but is less extensive. *Isoodon macrourus* is well separated, only with a slight overlap with *I. moresbyensis*. *Isoodon obesulus* overlaps partially with *I. fusciventer*. *Isoodon microtis* is separated from all other taxa. When allometry is removed (Figure 5D), the results are similar to the PCA but the taxa are a little more spread out, with clear regions of non-overlap for *I. macrourus*, *I. auratus*, *I. fusciventer* and *I. obesulus*.

The confusion matrix for the discriminant analysis (Table 1) recovers fairly high levels of correct classification, between 89.2% and 100%. *I. moresbyensis*, *I. peninsulae* and *I. microtis* were all correctly classified (100%), while *I. auratus*, *I. fusciventer*, *I. macrourus* and *I. obesulus* had a few misclassifications (varying between 89.2% and 98.6%).

The one-way PERMANOVA found that the species were significantly different from one another, with a p-value of 0.0001 (Table 2). The pairwise comparison (Table 3)

supports this result, with all pairs found to be significantly different from one another.

***Isoodon fusciventer* pes.** The results are shown in Supplementary Figure 7. Males of *Isoodon fusciventer fusciventer* and *I. f. halae* do not overlap, and neither do females. Only males of *Isoodon fusciventer halae* overlapped in pes measurements with females of *I. f. fusciventer*. All specimens of *I. fusciventer* caught in Two Peoples Bay, Fitzgerald River National Park, Waychinicup (which included Normans Beach where the holotype of *I. f. halae* was caught), Cape Arid National Park and Cape Le Grand were matching the pes measurements of *I. f. halae*, suggesting only that subspecies occurred in these areas. Porongorups had larger specimens, matching *I. f. fusciventer*. Albany had mostly specimens matching *I. f. halae*, except for a few outliers that matched *I. f. fusciventer*. Based on museum specimens, both subspecies were recovered in Albany but it is unclear where exactly in Albany they came from.

Subspecies investigation. The subspecies level investigation results are shown in Figures 6 and 7. In the *I. macrourus/moresbyensis* group (Figure 6A, B), *I. mores-*

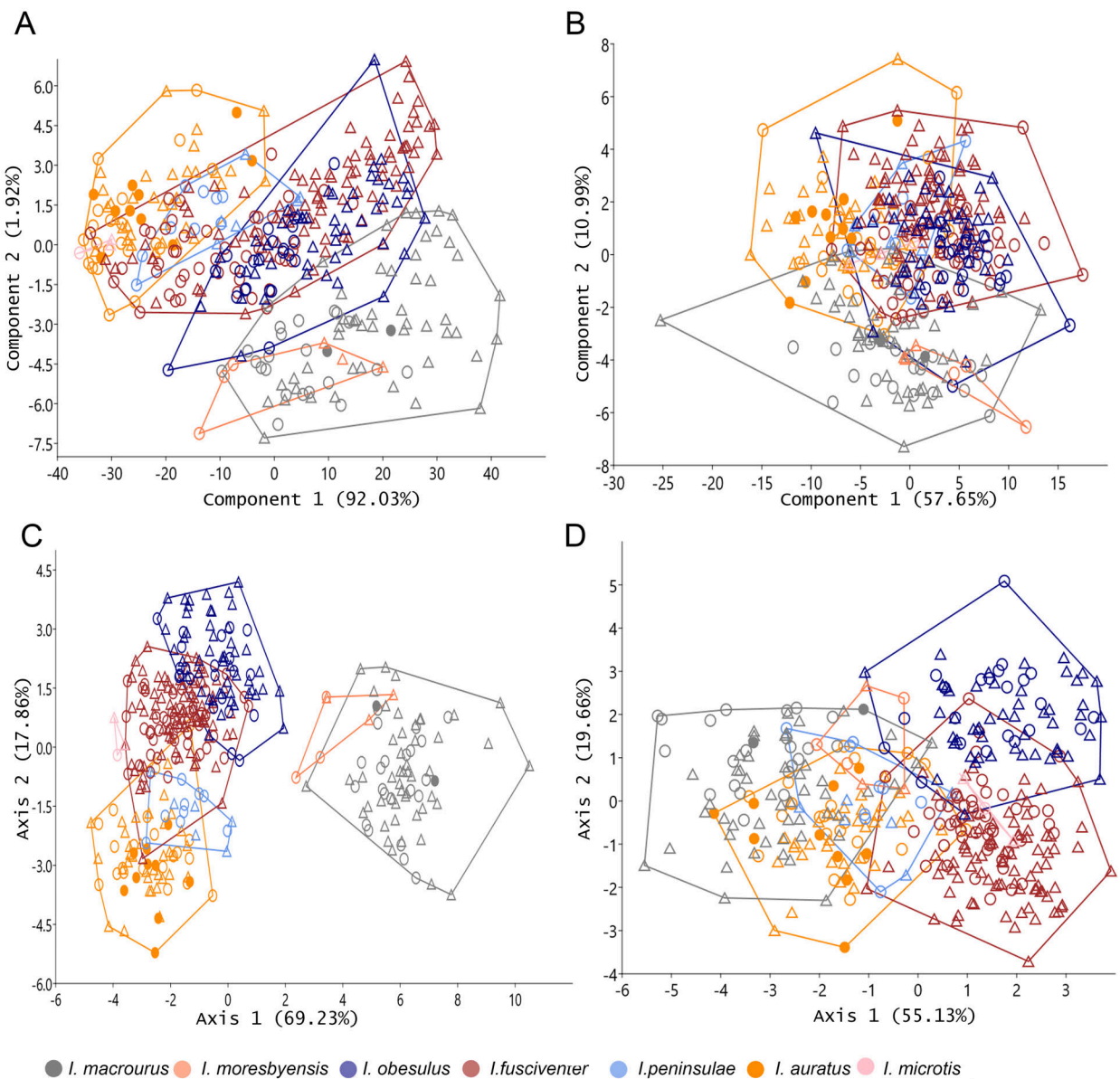


Figure 5. Species-level cranial morphometric analysis. A) PCA of normalised data, B) PCA of allometry-removed data, C) LDA of normalised data, D) LDA of allometry-removed data. Triangles = males; open circles = females; filled circles = unknown.

Table 1. Results of the discriminant analysis (species level) confusion matrix showing the number of specimens in their given groups (rows) and predicted groups (columns), and the percent correctly assigned for each taxon.

Taxon	<i>auratus</i>	<i>peninsulae</i>	<i>fusciventer</i>	<i>obesulus</i>	<i>microtis</i>	<i>macrourus</i>	<i>moresbyensis</i>	n	% correct
<i>auratus</i>	58	5	2	0	0	0	0	65	89.2
<i>peninsulae</i>	0	15	0	0	0	0	0	15	100
<i>fusciventer</i>	2	1	127	4	0	0	0	134	94.77
<i>obesulus</i>	0	0	2	70	0	0	0	72	97.2
<i>microtis</i>	0	0	0	0	3	0	0	3	100
<i>macrourus</i>	0	0	0	0	0	72	1	73	98.6
<i>moresbyensis</i>	0	0	0	0	0	0	6	6	100
Total	60	21	131	74	3	72	7	368	97.11

byensis was recovered as a distinct clade and does not overlap with any *I. macrourus* individuals in analyses of cranial data. *Isodon m. capensis* is not represented in

the molecular data but forms a distinct group in the analyses of cranial data. There is clear separation of *I. m. torosus* and *I. m. macrourus* in both the molecular and

Table 2. Results of the one-way PERMANOVA (species level).

Permutation N:	9999
Total sum of squares:	1.37E+05
Within-group sum of squares:	5.84E+04
F:	69.6
p (same):	0.0001

Table 3. Results of the pairwise comparison of the one-way PERMANOVA (species level) showing p-values for similarity between pairs.

<i>auratus</i>	<i>peninsulae</i>	<i>fusciventer</i>	<i>obesulus</i>	<i>microtis</i>	<i>macrourus</i>	<i>moresbyensis</i>
	0.0002	0.0001	0.0001	0.0335	0.0001	0.0001
		0.0035	0.0001	0.0012	0.0001	0.0069
			0.0089	0.0001	0.0001	0.3458
				0.0001	0.0001	0.1422
					0.0001	0.0249
						0.0071

cranial data. The only exception is the specimen from Moa Island (JM20021) in grey blue, which is the sister lineage to the rest of *I. m. macrourus*, and clustered with *I. m. torosus* in the cranial data.

In the *Isoodon auratus* group (Figure 6C, D), *I. a. bundilarri* is distinct from the rest of *I. auratus* in the molecular tree, but it overlaps with a couple of larger specimens of *I. a. auratus* with cranial data. Both *I. a. barrowensis* and *I. a. arnhemensis* show distinctiveness in both the molecular and cranial data. *I. a. marchinbarensis* is only represented in the cranial data and does not overlap with any other taxa.

In the *Isoodon obesulus/peninsulae* group (Figure 6E, F), *I. peninsulae* is distinct in both datasets. In the molecular tree, *I. o. obesulus* is paraphyletic (incorporating *I. o. affinis*). This is mainly driven by two specimens, the Neotype of *I. o. obesulus* (M11821 from Kuring-gai) recovered as sister to all *I. obesulus* and C14986 from Lang Lang recovered as sister to *I. o. affinis*. M11821 sits in the middle of the cranial data and does not seem to be morphologically distinct from other *I. o. obesulus*. C14986 does not overlap with *I. o. affinis* in the cranial dataset. The only two *I. o. obesulus* specimens overlapping with *I. o. affinis* are from Eden. All island specimens seem to fall within *I. o. affinis* in both datasets.

In the *Isoodon fusciventer* (WA) group (Figure 7A, B), *I. f. dawensis* forms a sister lineage to all other WA *I. fusciventer* taxa (99%), and is very distinct in the cranial dataset. *Isoodon f. halae* and *I. f. fusciventer* form separate lineages in the molecular tree, that is moderately supported (82%). Both taxa form distinct groups based on the analyses of cranial data.

In the *Isoodon fusciventer* (SA)/*microtis* group (Figure 7C, D), *I. f. nauticus* and *I. f. insulanus* form distinct clades and are very distinct in the cranial dataset. *I. microtis* is not represented in the molecular tree but is distinct in the cranial dataset. Two clades are visible within *I. f. terrenus*, one for the mainland and one for Kangaroo Island. They do not differ in the cranial dataset.

Discussion

In this study, we have undertaken the most comprehensive molecular and morphological study of the genus *Isoodon*. Using exon-capture data from the Oz Mammals Genomics Initiative (Eldridge et al., 2020) and craniodental morphology, a phylogeny of the species and subspecies of *Isoodon* was generated and population analyses of SNPs were conducted. Our molecular phylogenetic tree recovered seven distinct clades that we have attributed to *I. macrourus*, *I. moresbyensis*, *I. obesulus*, *I. fusciventer*, *I. peninsulae* and *I. auratus*. Three of these clades, *I. macrourus*, *I. obesulus* and *I. auratus*, are non-contentious and have been recognised previously (Gordon and Hulbert, 1989). Several molecular studies have previously recovered *I. auratus* nested within *I. obesulus* and raised doubts in its validity (Close et al., 1990; Pope et al., 2001; Zenger et al., 2005). Our results do not support this assessment, but instead support the splitting of *I. obesulus*, by elevating some of its subspecies to full species, which follows more recent molecular studies. Westerman et al. (2012) elevated *I. peninsulae* to full species based on nuclear and mitochondrial data. Travouillon and Phillips (2018) similarly elevated *I. fusciventer* based on a total evidence analysis. Li et al. (2014), Cooper et al. (2020) and Thavornkanlapacha et al. (2021) highlighted the genetic uniqueness of the South Australian population in the Mt. Lofty Ranges,

Kangaroo Island and Nuyts Archipelago. Our data support their findings but found that instead of being a subspecies of *I. obesulus*, the different populations in this region of South Australia represent a separate subspecies of *I. fusciventer*.

Within the species *Isoodon fusciventer* in South Australia, we have found additional subspecies from the Mt. Lofty Ranges/Kangaroo Island and from St Francis Island. Earlier studies such as Close et al. (1990) and Westerman and Krajewski (2000) had recovered the Mt. Lofty Ranges/Kangaroo Island population (*I. f. terrenus*) and the Franklin Island population (*I. f. nauticus*) in paraphyly with either *I. fusciventer* (for the former) or *I. peninsulae* (for the latter). More recent studies such as Li et al. (2014), Cooper et al. (2020) and Thavornkanlapacha et al. (2021) found similar results to our present study, where these populations were found to be monophyletic as the sister group to the Western Australian *I. fusciventer*. Our results do suggest that there is genetic differentiation between the Mt. Lofty Ranges and the Kangaroo Island population, each forming distinct clades in our phylogenetic analyses. However, we found no morphological difference between them. The morphological and molecular data both suggested that the Mt. Lofty Ranges/Kangaroo Island populations were distinct enough from the Franklin Island populations to warrant being considered a distinct subspecies *I. f. terrenus*. Similarly, the St Francis Island population (*I. f. insulanus*) was also unique both morphologically and molecularly, to support it representing a new subspecies. In Cooper et al. (2020), this population grouped with *I. obesulus* based on mtDNA analyses and did not form a clade with *I. fusciventer*. This may be due to incomplete lineage sorting or past introgression of mtDNA haplotypes. Alternatively, the mtDNA sequences may reflect a more ancient origin for this population that has been cut-off from other populations of *I. fusciventer* over multiple ice ages. Further analyses of these island populations using additional samples and genomic analyses will be required to definitively test these hypotheses.

Our results recovered some distinction between the Western Australian and South Australian members of *Isoodon fusciventer*. Despite some morphological overlap between them, equivalent to the overlap between *I. fusciventer* and *I. obesulus*, we identified cranial and dental characters separating the WA and SA subspecies. While they are genetically very close, our results suggest the WA and SA *I. fusciventer* separated around 800,000 years ago. This genetic distinction was also found by Close et al. (1990), Cooper et al. (2020) and Thavornkanlapacha et al. (2021). The latter two studies found *I. fusciventer* to be paraphyletic, with some samples clustering with *I. auratus*. These were mainly driven by samples from Daw Island and from the southwest coast which we have identified here as two new subspecies, *I. fusciventer dawensis* and *I. f. halae*. The Daw Island subspecies has been disconnected from the mainland

since the last ice age, and when it was connected, there was likely some gene flow with the South Australia subspecies of *I. fusciventer*, shown by its mtDNA affinities with that subspecies (Cooper et al., 2020). The two other subspecies, *I. f. fusciventer* and *I. f. halae*, are more similar to one another in the molecular results but quite distinct in the morphological results. This result was also found by Cooper (1998), who identified distinct size differences between populations of *I. fusciventer*. One population *I. f. fusciventer* mainly occupies forested habitats in the southwest of Western Australia, while the other *I. f. halae* was found in the woodlands, most of which have been cleared in the wheatbelt, leaving only the coastal woodland population. While the two subspecies generally look the same, *I. f. halae* is smaller, and can be easily separated from *I. f. fusciventer* on pes measurements. Selection pressure from the habitat type has most likely differentiated these two subspecies, a conclusion which was also found through breeding experiments between individuals from Perth and Albany (Hale, 2000). Additionally, Cooper (2000) examined fossil specimens from caves in the southwest of WA and found a sudden change in size which was interpreted as rapid size evolution. We have examined the specimens and the small specimens match *I. f. halae*, while the large specimens match *I. f. fusciventer*. Instead of rapid size evolution, it is more likely that climate change in the Margaret River area shifted the distributions of the two subspecies. This pattern of replacement of taxa is also supported by changes in the distribution of rodent fauna, with more arid adapted rodent species found in the same strata as *I. f. halae*, and more mesic species found with *I. f. fusciventer* (A. Baynes, pers. comm.). Future translocations of *I. fusciventer* should take into account the possible ecological differences of the two subspecies when deciding which subspecies to re-introduce into an area.

The Cape York Brown Bandicoot, *Isoodon peninsulae*, was for a long time considered a subspecies of *I. obesulus*. Close et al. (1990), Pope et al. (2001) and Zenger et al. (2005) recovered it as sister to all *Isoodon* except *I. macrourus*. In Westerman and Krajewski (2000) it was recovered as the sister taxon to the Mt. Lofty Ranges/Kangaroo Island population, while it was recovered as sister to *I. auratus* in Westerman et al. (2012). Cooper et al. (2020) recovered it as sister to all *Isoodon* except for *I. macrourus* and *I. obesulus*. The inconsistent placement of this species perhaps reflects a complex history of gene flow between populations and periods of isolation, or incomplete lineage sorting. Alternatively, it may reflect the low statistical power of the comparatively short DNA sequences employed in those studies. Our results found a closer affinity between *I. peninsulae* with *I. obesulus* (Figures 2 and 4) but also with *I. auratus* (Figures 3 and 5) suggesting that gene flow did occur in the past with both taxa, but more recent isolation has cemented it as a distinct species.

Our results only support two subspecies within *Isoodon obesulus*, which was also found by previous studies (Westerman and Krajewski, 2000; Westerman et al. 2012, Cooper et al., 2020 and Thavornkanlapacha et al., 2021). *I. o. obesulus* is found on the mainland from Sydney following the coast, all the way to the south-east of South Australia, south of the Murray River, and *I. o. affinis* is found in Tasmania and on islands in Bass Strait. *Isoodon obesulus* used to occur further north of Sydney but has gone locally extinct since European arrival. Fossil data suggest it used to occur as far north as Rockhampton in Queensland and co-occurred in the area with *Isoodon peninsulae* in the past (Louys et al., 2023). However, we re-examined the material from that site, and specimen of *I. peninsulae* were misidentified and are all indeed *I. obesulus*. We recovered *I. o. obesulus*, in paraphyly with *I. o. affinis*, the latter subspecies from Tasmania forming a monophyletic group in molecular phylogenies, and we found some structure between the different populations in each State. A similar result was also found by Cooper et al. (2020), Thavornkanlapacha et al. (2021) and Black et al. (2024).

These analyses support the population isolation and subspecies status of *I. o. affinis*, but also highlight the presence of additional genetically distinct populations within *I. o. obesulus* on the mainland. Further research is needed to establish if the genetic divergence of these mainland populations reflects their isolation as a result of recent range contraction (local extinctions), or if there is evidence for historically isolated populations that could be potentially separate subspecies or Evolutionarily Significant Units.

The only species that we could not get reliable sequences from was *Isoodon microtis*. This species is only represented by three skulls and some subfossil material from Eyre Peninsula. The skull from the South Australian Museum was previously identified as *I. auratus*, but the size of the bullae did not match any specimen of *I. auratus*. The two specimens from Museum Victoria were identified as *Isoodon* sp. and were sent there from the South Australian Museum. Our attempt to recover DNA from these skulls failed. As a result, we had to rely solely on morphology to establish it as a distinct taxon. In the total evidence analysis, it was recovered as the sister taxon to *I. obesulus*, despite being co-located with *I. fusciventer terrenus* on the Eyre Peninsula. We only know that the species was present thanks to subfossil specimens that match the morphology of the three skulls. It is unique in having the smallest bullae relative to size for any species of *Isoodon*. It is much smaller in size than *I. fusciventer*, with which it may have been able to co-exist due to niche partitioning. It is unclear when this species went extinct as none of the specimens have collection dates recorded, though they had to be collected before 1920 when the last specimen was donated to the South Australian Museum. In the late 1800s, land clearing for agriculture was prominent on Eyre Peninsula, and was likely a major contribution

to the extinction of this species. If the species was still present by the time foxes were introduced, it is very likely that foxes would have played a role in its extinction.

The other subspecies that we have raised to full species is *Isoodon moresbyensis*. The exon-capture data shows a deep divergence separating it from the *I. macrourus* lineage. Molecular data for *I. moresbyensis* has previously only been included for 12S rRNA, by Westerman and Krajewski (2000), who couldn't split it from *I. macrourus*. In contrast, the distinctiveness of the New Guinean taxon indicated by our exon capture data is corroborated by the morphological data, with *I. moresbyensis* having a distinct skull morphology and much smaller. Within the *I. macrourus* clade, we have identified three subspecies, two previously reported *I. m. macrourus* from the Northern Territory and the Kimberley and *I. m. torosus* from south of the Endeavour River in Queensland to Sydney in NSW. The third subspecies was previously reported to us by Greg Gordon, who had attempted to breed Cape York specimens (north of the Endeavour River) with specimens near Brisbane, but failed to produce any offspring. The Cape York specimens have a unique morphology (i.e. skull shape, see Figure 6) and lack the enlarged M4 typical of *I. macrourus*. We were not able to source genetic samples from this population, and therefore it was not covered in our molecular analysis. This will be important to do in a future study to demonstrate if it is genetically distinct from other subspecies and help to elucidate the biogeographic history of this species. The sample from Moa Island in the Torres Strait (JM20021 in Figures 2 and 6) was recovered as sister to *I. m. macrourus* with the molecular data, but morphologically it was closer to *I. m. torosus*, even though it is geographically situated between *I. moresbyensis* and *I. m. capensis*. This particular sample therefore suggests that the biogeographic history of the species is more complicated than previously thought.

While several studies have sampled *Isoodon auratus* in the past to elucidate its taxonomic position with respect to other species in the genus, early research produced confusing results that prompted researchers to suggest that it was not distinct from *I. obesulus* (Close et al., 1990; Pope et al., 2001; Zenger et al., 2005). Sequencing of larger datasets didn't support this assessment and instead supported splitting *I. obesulus* further (Westerman et al. 2012; Travouillon and Phillips, 2018; Cooper et al., 2020; Thavornkanlapacha et al., 2021). At the subspecies level, most studies had assumed that the three living populations in the Kimberley, Barrow Island and Marchinbar Island were the three described subspecies, *I. a. auratus*, *I. a. barrowensis* and *I. a. arnhemensis*. However, we found that this was not the case, with only *I. a. barrowensis* correctly assigned. Lyne and Mort (1981) had described *I. a. arnhemensis* only from Arnhem Land, and did not include Marchinbar Island, as that population was not known at the time. In their study, they suggested that the Kimberley population was unique and could warrant being a distinct taxon (distinct from *I. a.*

auratus), but due to low sample size, they decided not to name it. Our results here support their finding, that the Kimberley population (*I. a. bundilarri*) is distinct in both morphology and genetics from *I. a. auratus*. We also found that the Marchinbar population was significantly distinct from *I. a. arnhemensis* and warranted its own subspecies status. DNA samples from Marchinbar Island individuals were of poor quality and not able to be used in our analysis. Previous studies showed that it is genetically distinct from the Barrow Island and Kimberley populations and warrants conservation (Rick et al., 2023). We recommend that future work should focus on further vouchers and genetic sampling of the Marchinbar population as current data are limited to a few specimens (N=2) and samples available suggest a requirement for conservation and translocation management of this population.

Within the genus *Isoodon*, only one species is considered extinct, *I. microtis*. It is the smallest species, and it has a unique morphology. It would be difficult to find an ecological analogue to replace it, but *I. f. terrenus*, which co-occurred on Eyre Peninsula (see Figure 27) could be re-introduced to the area to help restore the local environment. At the subspecies level, *I. auratus* has two extinct subspecies, *I. a. auratus* and *I. a. arnhemensis*. There have been several translocations of *I. a. barrowensis* into the former range of *I. a. auratus* which have been successful (Ottewell et al. 2014). Morphologically, *I. a. bundilarri* is closest to both subspecies and would be a suitable replacement in the arid zone and in Arnhem Land, and it would help to increase genetic diversity on the mainland (Rick et al., 2023). Other subspecies that have lost considerable amounts of their former ranges include *I. f. halae*, *I. f. terrenus* and *I. o. obesulus*. One of them, *I. o. obesulus*, is already listed as endangered in NSW at the federal level and given the reduction in the distribution of this taxon with our proposed taxonomic changes, its conservation status needs urgent reassessment. The other two subspecies are new to science and warrant listing and protection.

The results of our total evidence analysis suggest that the common ancestor of all *Isoodon* evolved around 2 million years ago, in the early Pleistocene. This is similar to what was found by Westerman et al. (2012), who estimated the divergence between all species in the genus around 2.4 million years ago. Travouillon and Phillips (2018) estimated the diversification of *Isoodon* at around 3.1 million years ago, but with an age range of 1.8–4.8, within which both Westerman et al. (2012) and our results fit. There is no evidence of *Isoodon* in the Pliocene fossil record, suggesting that either the genus had not evolved yet or that its fossil record has yet to be found (Travouillon et al., 2017). It is more likely that the genus evolved in the early Pleistocene and that speciation occurred relatively quickly, potentially in response to the changes in climate throughout the Pleistocene.

Taxonomy

Isoodon auratus (Ramsay, 1887)

urn:lsid:zoobank.org:act:30FA6F78-958E-4D4D-A23F-08E46375E6DE

Emended species diagnosis. *Isoodon auratus* differs from all other species of *Isoodon* in being usually more golden in colour and smaller in overall size (except for *I. microtis* new sp.). *Isoodon auratus* differs from *I. microtis*, *I. fusciventer* (except *I. f. fusciventer* and *I. f. halae*) and *I. macrourus* in having cristid obliqua of m1 terminating lingual to the protocone. *Isoodon auratus* differs from *I. macrourus*, *I. moresbyensis*, *I. peninsulae*, *I. f. fusciventer* and *I. f. terrenus* in having a moderately expanded submasseteric crest. *Isoodon auratus* differs from *I. microtis* and *I. macrourus* in having a small anterior cingulum on M2. *Isoodon auratus* differs from *I. microtis*, *I. obesulus* and *I. peninsulae* in having the alisphenoid tympanic process terminating anterior to the transverse foramen. *Isoodon auratus* differs from all other species except *I. f. fusciventer*, *I. f. halae*, *I. f. dawensis* and *I. macrourus* in having a posterobucally orientated preparacrista on M1. *Isoodon auratus* differs from *I. fusciventer* (except *I. f. fusciventer* and *I. f. dawensis*) and *I. macrourus* in having the postprotocrista of M4 end level with the most posterior end of the postparacrista. *Isoodon auratus* differs from *I. microtis*, *I. macrourus*, *I. f. nauticus*, *I. f. insulanus* and *I. f. fusciventer* in having a well-developed lingual shelf on P3, not extending to the buccal side. *Isoodon auratus* differs from *I. macrourus* and *I. f. fusciventer* in having a styler crest connected to the metastyle on M1. *Isoodon auratus* differs from *I. f. fusciventer* and *I. f. dawensis* in having a canine-like I5, anterior cingulum of M1 not connected to talon, StA on M1 is small. *Isoodon auratus* differs from *I. macrourus* and *I. moresbyensis* in having a pair of accessory fenestrae, I3 larger than I2 or I4, small metacone on M4, StC/D absent on M4 (except *I. a. marchinbarensis*), preentocristid absent on m4. *Isoodon auratus* differs from *I. peninsulae* in having no StE on M3. *Isoodon auratus* differs from *I. microtis* in having small posterior palatal fenestrae, larger bullae, the paraconid-metaconid distance shorter than the metaconid-protoconid distance on m1. *Isoodon auratus* (except *I. a. marchinbarensis*) differs from *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus* in having a large entoconid on m4.

Common name. Golden Bandicoot

Isoodon auratus auratus (Ramsay, 1887)

Figure 8

urn:lsid:zoobank.org:act:30FA6F78-958E-4D4D-A23F-08E46375E6DE

Perameles auratus Ramsay, 1887: 551.

Holotype. MAMU M468, adult male, skin and skull.

Type locality. Derby, Western Australia, Australia.

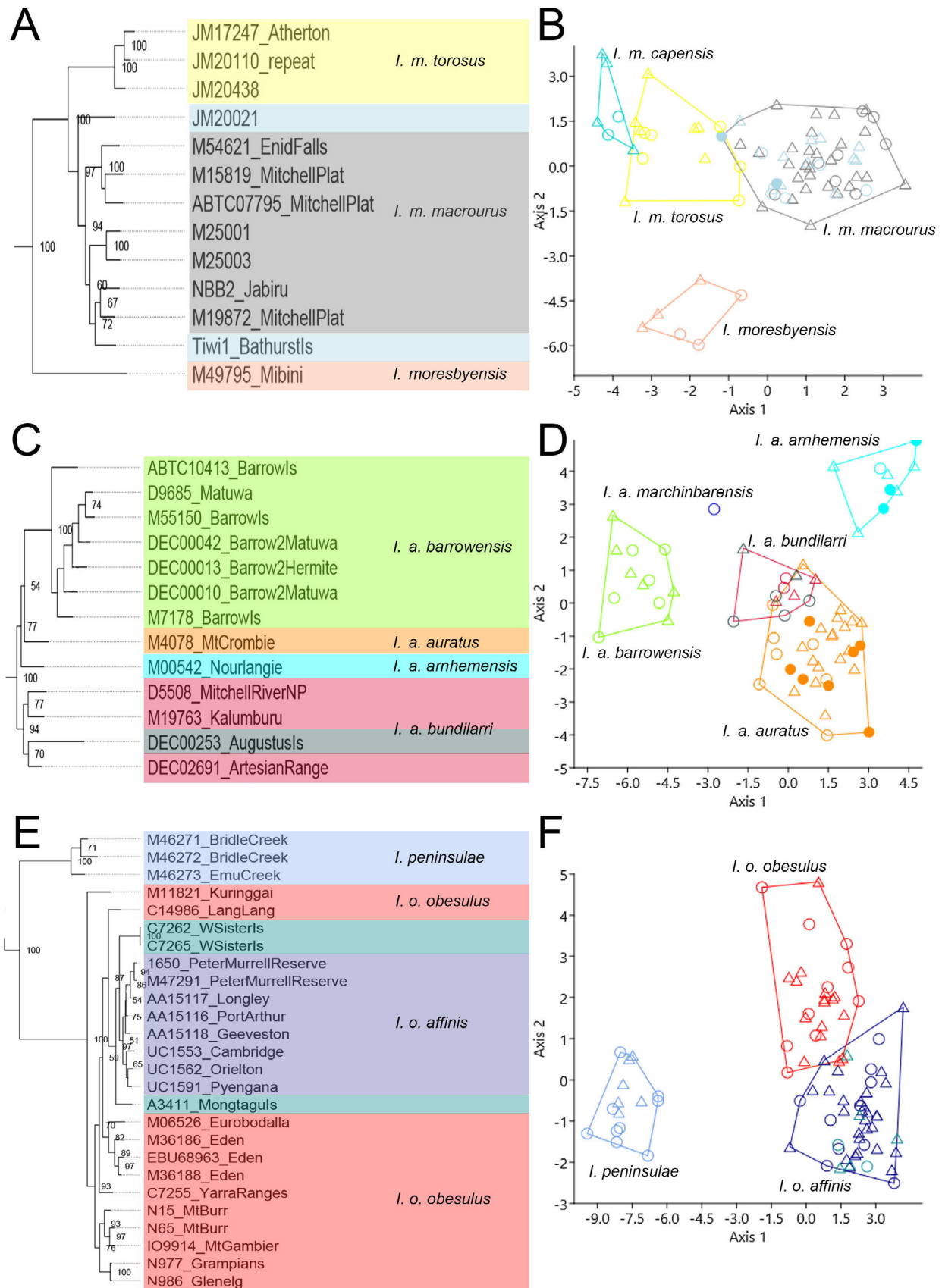


Figure 6. Subspecies-level comparison of the Maximum Likelihood tree of the exon-capture data (A, C, E) and cranial morphometric analysis LDA of normalised data (B, D, F) for *Isoodon macrourus* and *I. moresbyensis* (A, B), *I. auratus* (C, D) and *I. obesulus* and *I. peninsulae* (E, F). Triangles = males; open circles = females; filled circles = unknown.

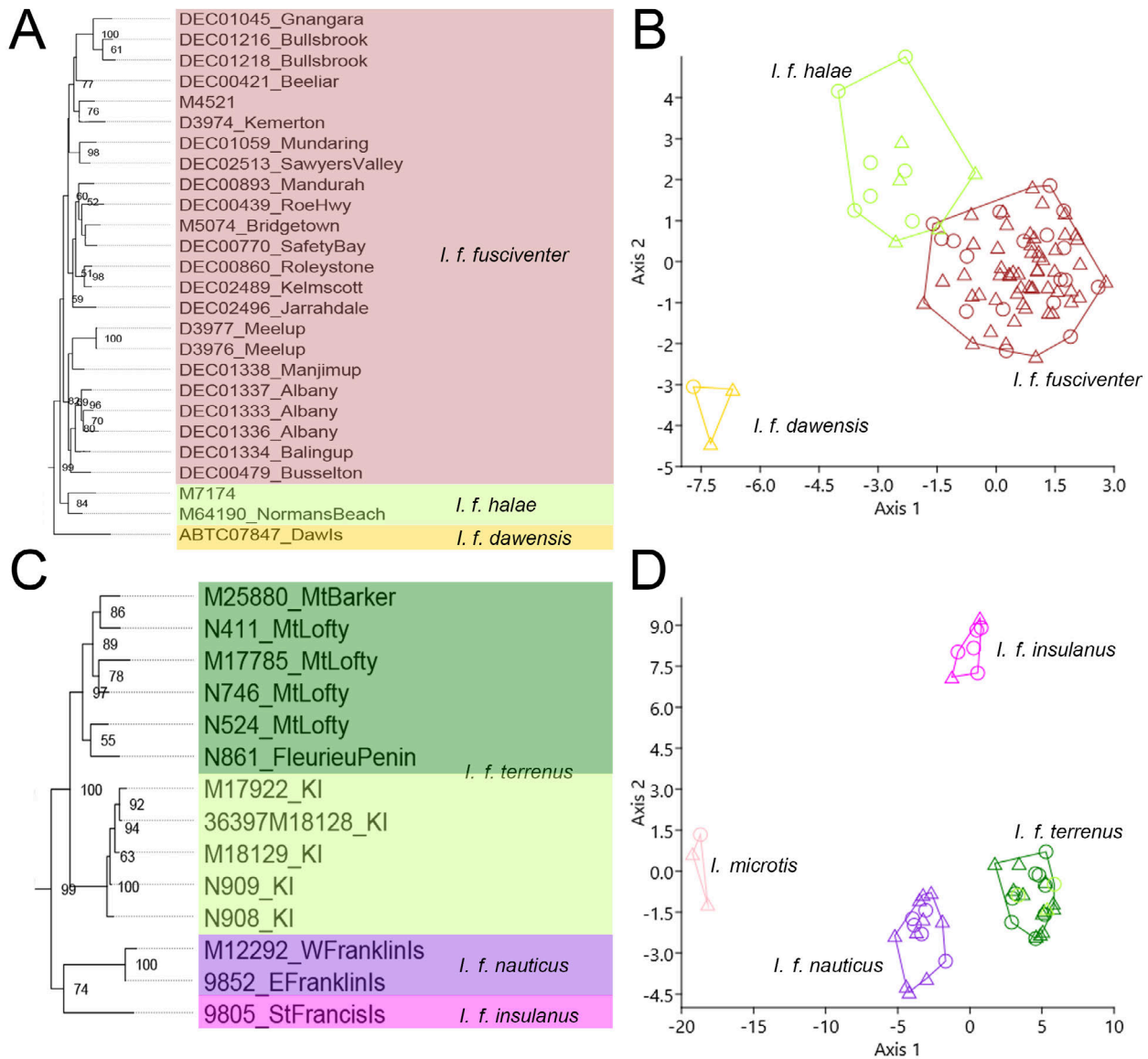


Figure 7. Subspecies-level comparison of the maximum likelihood tree of the exon-capture data (A, C) and cranial morphometric analysis LDA of normalised data (B, D) for *Isodon fusciventer* (WA) (A, B), *I. microtis* and *I. fusciventer* (SA) (C, D).

Emended subspecies diagnosis. *Isodon a. auratus* differs from all subspecies of *I. auratus* in having the largest bullae relative to skull size; no connection of the paracristid to the protoconid on m1. *Isodon a. auratus* differs from all subspecies of *I. auratus* except *I. a. barrowensis* in lacking a cusp within the hypoflexid of m1-3; having the paraconid of m1 directly anterior to the metaconid. *Isodon a. auratus* differs from *I. a. barrowensis* and *I. a. marchinbarensis* in having a thicker dividing septum between the maxillopalatine fenestrae; posthypocristid of m4 oblique to the tooth row. *Isodon a. auratus* differs from all subspecies of *I. auratus* except *I. a. marchinbarensis* in having a small StB on M4. *Isodon a. auratus* differs from *I. a. barrowensis* in having lateral walls present near the presphenoid-basisphenoid suture; P2 subequal in length to P3; p1 is shorter than p2 or p3, with a short diastema between p1 and p2. *Isodon a. auratus* differs from *I. a. arnhemensis* in having P1 shorter than P2; inflated central cusps on P1 and

P2; M1 preparacrista posterobuccally orientated (buccally orientated in *I. a. arnhemensis*); StB and StC fused as a single cusp on M1; a large anterior cingulum connected to the talon on M3; a wide posterior cingulum on M3; postprotocrista of M3 ending near the metastyle; accessory cusps present on c1; having the posthypocristid of m1 and m2 oblique to the tooth row; cristid obliqua of m4 terminates lingual to the midpoint of the tooth width. *Isodon a. auratus* differs from *I. a. bundilarri* in having an infraorbital canal longer than half the molar row; cristid obliqua of m4 terminates lingual to the midpoint of the tooth width. *Isodon a. auratus* differs from *I. a. marchinbarensis* in having accessory cusps absent on C1; inflated central cusps on P1 and P2; a small anterior cingulum on M1; large StA on M1; StB of M2 conical and uncrested; a wide posterior cingulum on M3; postprotocrista of M3 ending near the metastyle; postprotocrista ending level with the most posterior end of the postparacrista on M4; no StC/D on M4; cristid obliqua



Figure 8. Holotype of *Isoodon auratus*, MAMU M468. Study skin in dorsal (A), lateral (B) and ventral views (C). Skull and dentary in dorsal (D), ventral (E) and lateral views (F). Scale bar = 2cm.

terminates lingual to the protoconid at its midpoint on m3; posthypocristid connects to hypoconulid on m3; a larger talonid on m4; a large entoconid on m4.

Remarks. Previously included the Kimberley population. This subspecies is likely to be extinct as it has not been recorded for many years.

Distribution. Arid zone of Australia, from western Queensland and New South Wales, to northern parts of South Australia, southern two thirds of Northern Territory and northern two thirds of Western Australia, except Kimberley region.

Isodon auratus arnhemensis Lyne and Mort, 1981

Figure 9

urn:lsid:zoobank.org:act:8CB3B144-0C39-4ADB-9226-22E2E03693EE

Isodon arnhemensis Lyne and Mort, 1981: 107, 128.

Holotype. AMS M6609, adult, sex unknown, skin and skull.

Type locality. Melville Bay, Cape Arnhem, Northern Territory, Australia.

Paratype. AMS M6606, male, skin and skull; AMS M6610, sex unknown, skin and skull.

Emended subspecies diagnosis. *Isodon a. arnhemensis* differs from all subspecies of *I. auratus* in having the largest body and skull size; no accessory cusps on C1 or c1; P1 as long as P2; M1 preparacrista buccally orientated (posterobuccally orientated in all other subspecies); StB and StC identifiable with StB larger than StC on M1; a small anterior cingulum connected to the talon on M3; postprotocrista of M3 ending posteriorly to the midpoint of the postmetacrista; having the posthypocristid of m1 and m2 perpendicular to the tooth row. *Isodon a. arnhemensis* differs from all subspecies of *I. auratus* except *I. a. bundilarrri* in having cristid obliqua of m4 terminates lingual to the protoconid about midpoint to the tooth width. *Isodon a. arnhemensis* differs from *I. a. auratus* and *I. a. barrowensis* in having a cusp within the hypoflexid of m1-3; having the paraconid of m1 anterolabial to the metaconid. *Isodon a. arnhemensis* differs from *I. a. auratus* and *I. a. marchinbarensis* in having a large StB on M4. *Isodon a. arnhemensis* differs from *I. a. barrowensis* and *I. a. marchinbarensis* new sub in having a thicker dividing septum between the maxillopalatine fenestrae; posthypocristid of m4 oblique to the tooth row. *Isodon a. arnhemensis* differs from *I. a. auratus* in having the paracristid connected to the protoconid on m1. *Isodon a. arnhemensis* differs from *I. a. barrowensis* in having lateral walls present near the presphenoid-basisphenoid suture; P2 subequal in length to P3; a buccal shelf present on P3; p1 is shorter than p2 or p3, with a short diastema between p1 and p2. *Isodon a. arnhemensis* differs from *I. a. bundilarrri* in having an infraorbital canal longer than half the molar row; a buccal shelf present on P3. *Isodon a. arnhemensis* differs from all subspecies of *I. auratus* except *I. a. marchinbarensis* in having the central cusps on P1 and P2 not inflated; a narrow posterior cingulum on M3; a larger talonid on m4. *Isodon a. arnhemensis* differs from *I. a. marchinbarensis* in having a small anterior cingulum on M1; large StA on M1; anterior cingulum of M2 not connected to the talon; StB of M2 conical and uncrested; postprotocrista ending level with the most posterior

end of the postparacrista on M4; no StC/D on M4; cristid obliqua terminates lingual to the protoconid at its midpoint on m3; hypoconulid of m3 is present; a large entoconid on m4.

Remarks. Previously included Marchinbar Island. This subspecies is likely to be extinct.

Distribution. Top end (Northern Territory), Australia.

Isodon auratus barrowensis (Thomas, 1901)

Figure 10

urn:lsid:zoobank.org:act:C0BED48D-D2F3-4949-BAA0-F55E4458FE44

Perameles barrowensis Thomas, 1901: 396

Holotype. NHMUK 1901.5.2.6, adult male, skin and skull.

Type locality. Barrow Island, Western Australia.

Emended subspecies diagnosis. *Isodon a. barrowensis* differs from all subspecies of *I. auratus* in having lateral walls absent near the presphenoid-basisphenoid suture; P2 longer than P3; p1 is as long as p2 or p3, with no diastema between p1 and p2. *Isodon a. barrowensis* differs from all subspecies of *I. auratus* except *I. a. auratus* in lacking a cusp within the hypoflexid of m1-3; having the paraconid of m1 directly anterior to the metaconid. *Isodon a. barrowensis* differs from all subspecies except *I. a. marchinbarensis* new sub in having a very thin dividing septum between the maxillopalatine fenestrae; posthypocristid of m4 perpendicular to the tooth row. *Isodon a. barrowensis* differs from *I. a. auratus* and *I. a. marchinbarensis* in having a large StB on M4. *Isodon a. barrowensis* differs from *I. a. auratus* in having the paracristid connected to the protoconid on m1. *Isodon a. barrowensis* differs from *I. a. arnhemensis* in having P1 shorter than P2; inflated central cusps on P1 and P2; a buccal shelf absent on P3; M1 preparacrista posterobuccally orientated (buccally orientated in *I. a. arnhemensis*); StB and StC fused as a single cusp on M1; a large anterior cingulum connected to the talon on M3; a wide posterior cingulum on M3; postprotocrista of M3 ending near the metastyle; accessory cusps sometimes present on c1; having the posthypocristid of m1 and m2 oblique to the tooth row; cristid obliqua of m4 terminates lingual to the midpoint of the tooth width. *Isodon a. barrowensis* differs from *I. a. bundilarrri* in having an infraorbital canal longer than half the molar row; cristid obliqua of m4 terminates lingual to the midpoint of the tooth width. *Isodon a. barrowensis* differs from *I. a. marchinbarensis* in having accessory cusps absent on C1; inflated central cusps on P1 and P2; a buccal shelf absent on P3; a small anterior cingulum on M1; large StA on M1; anterior cingulum of M2 not connected to the talon; StB of M2 conical and uncrested; a wide posterior cingulum on M3; postprotocrista of M3 ending near the metastyle; postprotocrista ending level with the most posterior end of the postparacrista on M4; no StC/D on

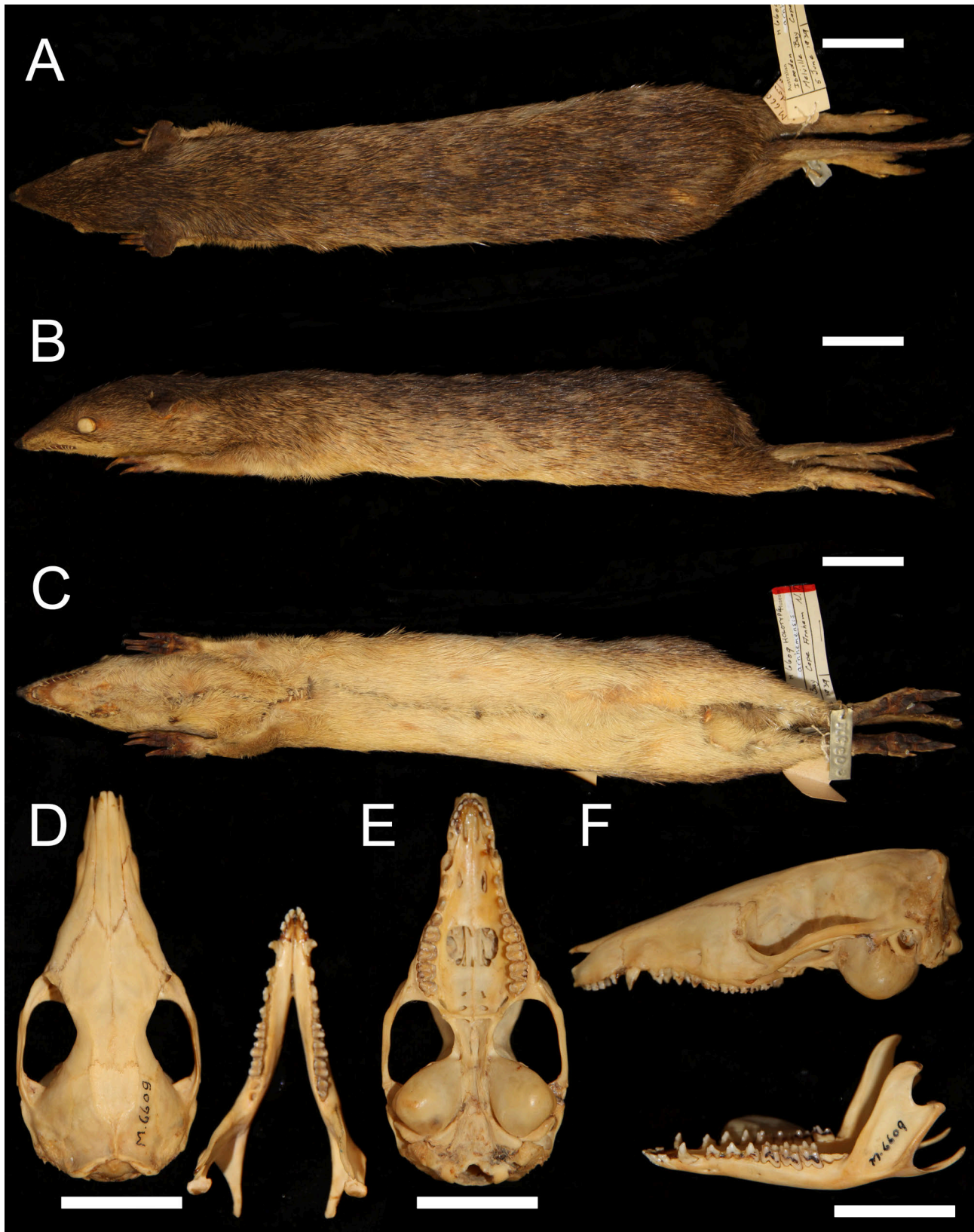


Figure 9. Holotype of *Isoodon auratus arnhemensis*, AMS M6609. Study skin in dorsal (A), lateral (B) and ventral views (C). Skull and dentary in dorsal (D), ventral (E) and lateral views (F). Scale bar = 3cm (skin); 2cm (skull).

M4; cristid obliqua terminates lingual to the protoconid at its midpoint on m3; hypoconulid of m3 is present; a larger talonid on m4; a large entoconid on m4.

Distribution. Barrow Island, Western Australia, Australia.

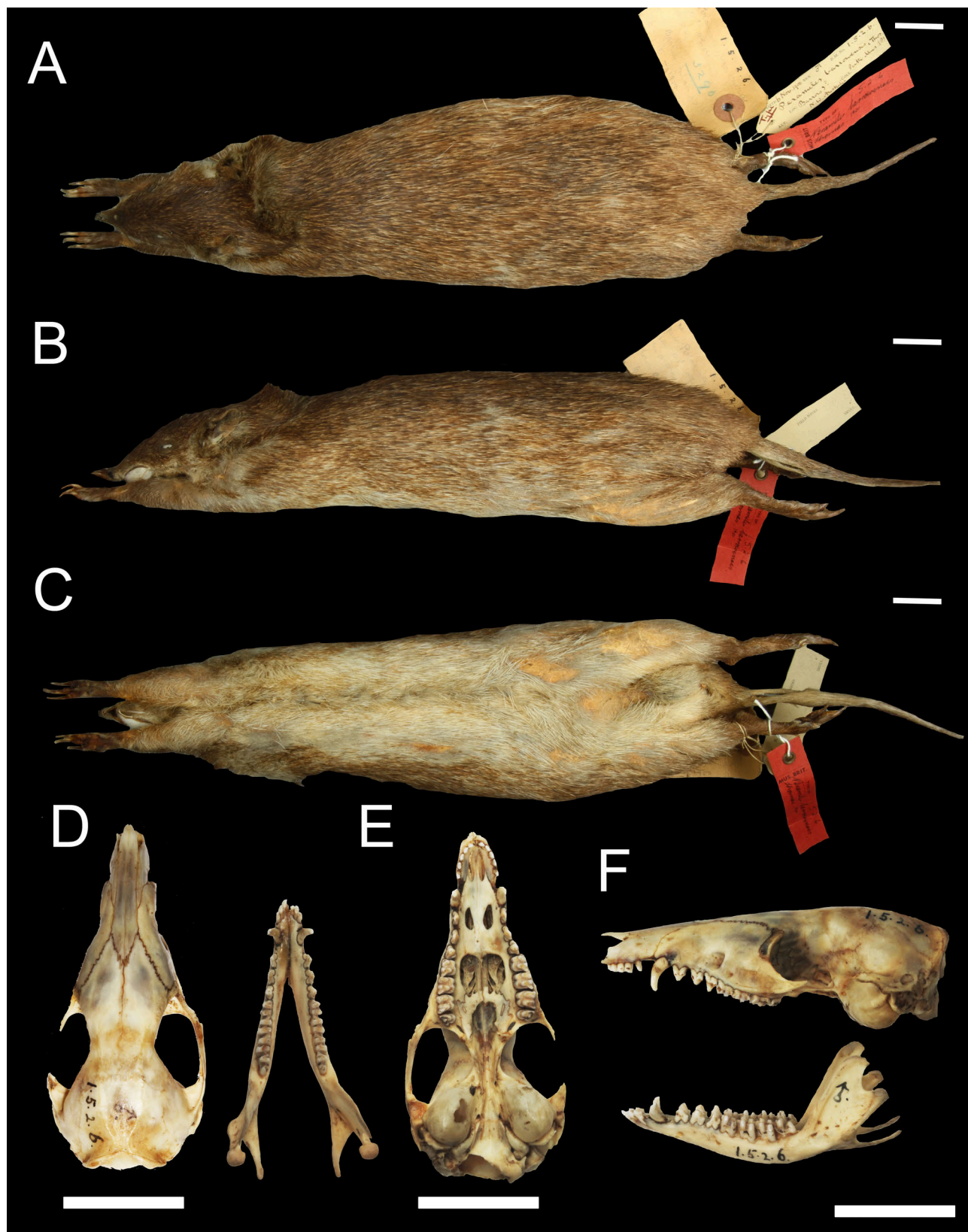


Figure 10. Holotype of *Isoodon auratus barrowensis*, NHMUK 1901.5.2.6. Study skin in dorsal (A), lateral (B) and ventral views (C). Skull and dentary in dorsal (D), ventral (E) and lateral views (F). Scale bar = 3cm.

***Isoodon auratus bundilarri* new subsp.**

Figure 11

urn:lsid:zoobank.org:act:D3F57722-CB31-4FC7-9167-A5593E17F343

Holotype. WAM M65293, subadult male, skin and skull.

Type locality. Mitchell Falls camping ground, Northwest of helicopter bush pad, Mitchell Plateau, Western Australia, Australia.

Paratype. WAM M54835, adult male, alcohol specimen with skull extracted, from Prince Regent Reserve, WA; WAM M12372, adult female, alcohol specimen with skull extracted, from Prince Regent Reserve, WA.

Etymology. Uunguu name for a Golden Bandicoot from Wunambal Gaambera Country, in the north-west Kimberley, Australia. Note the first 'i' in *bundilarri* should be pronounced like the vowel sound in New Zealander's pronunciation of 'fish'.

Subspecies diagnosis. *Isoodon a. bundilarri* differs from all subspecies of *I. auratus* in having a short infraorbital canal equal to half the molar row. *Isoodon a. bundilarri* differs from all subspecies of *I. auratus* except *I. a. arnhemensis* in having cristid obliqua of m4 terminates lingual to the protoconid about midpoint to the tooth width. *Isoodon a. bundilarri* differs from *I. a. auratus* and *I. a. barrowensis* in having a cusp within the hypoflexid of m1-3; having the paraconid of m1 anterolabial to the metaconid. *Isoodon a. bundilarri* differs from *I. a. auratus* and *I. a. marchinbarensis* in having a large StB on M4. *Isoodon a. bundilarri* differs from *I. a. auratus* in having the paracristid connected to the protoconid on m1. *Isoodon a. bundilarri* differs from *I. a. barrowensis* and *I. a. marchinbarensis* new sub in having a thicker dividing septum between the maxillopalatine fenestrae. *Isoodon a. bundilarri* differs from *I. a. barrowensis* in having lateral walls present near the presphenoid-basisphenoid suture; P2 subequal in length to P3; p1 is shorter than p2 or p3, with a short diastema between p1 and p2. *Isoodon a. bundilarri* differs from *I. a. arnhemensis* in having P1 shorter than P2; inflated central cusps on P1 and P2; a buccal shelf absent on P3; M1 preparacrista posterobuccally orientated (buccally orientated in *I. a. arnhemensis*); StB and StC fused as a single cusp on M1; a large anterior cingulum connected to the talon on M3; a wide posterior cingulum on M3; postprotocrista of M3 ending near the metastyle; having the posthypocristid of m1 and m2 oblique to the tooth row. *Isoodon a. bundilarri* differs from *I. a. marchinbarensis* in having inflated central cusps on P1 and P2; a buccal shelf absent on P3; a small anterior cingulum on M1; large StA on M1; StB of M2 conical and uncrested; a wide posterior cingulum on M3; postprotocrista of M3 ending near the metastyle; postprotocrista ending level with the most posterior end of the postparacrista on M4; no StC/D on M4; cristid obliqua terminates lingual to the protoconid at its midpoint on m3; hypoconulid of m3 is present; a larger talonid on m4; a large entoconid on m4.

Description. The fur on the dorsal side of the skin is golden in colour, grizzled with black. The golden colour is similar to that of *I. a. auratus*, but is more grizzled in black overall not as reddish gold in colour as *I. a. auratus*. Easily distinguished from the much browner *I. a. barrowensis* (the holotype seems to be faded as much more recent specimens from Matuwa are much darker brown in colour), and lighter in colour than *I. a. arnhemensis* and *I. a. marchinbarensis*. The ventral fur is white as in all other subspecies, though specimens in

collection often have cream colour due to preservation and age of the specimens as both Ramsey (1887) and Thomas (1901) report white fur for the belly of *I. a. auratus* and *I. a. barrowensis*, respectively, yet their holotypes have now cream coloured bellies. Tail short as in all bandicoots and is dark brown above and greyish below. Ears are rounded and dark as in all *Isoodon*. Forefeet and hind feet are golden on the dorsal side and white on the ventral side. The overall size of the subspecies (head body = 180-250mm) is second to *I. a. arnhemensis* (head body = 250-300mm), only slightly larger than *I. a. auratus* (head body = 180-250mm; note that northern specimens usually don't exceed 230mm but southern specimens from Victoria and South Australia do reach 250mm) and *I. a. barrowensis* (head body = 160-230mm), and much larger than *I. a. marchinbarensis* (head body = 155-210mm).

The skull is the second largest in the species (length = 50-62mm), second to *I. a. arnhemensis* (length = 55-64mm), followed by *I. a. auratus* (length = 49-61mm), *I. a. barrowensis* (length = 48-57mm) and *I. a. marchinbarensis* (length = 49mm). On the dorsal side of the skull, the snout is long and thin is almost half the total skull length. Compared to other subspecies, it only differs to *I. a. auratus* which has a shorter snout but wider skull proportionally. A short sagittal crest is present in adult males, which is also present in *I. a. arnhemensis*, but not present in all other subspecies, except in some specimens of *I. a. auratus*. In lateral view, the bullae are large and prominent, second in size to *I. a. auratus* proportionally, followed in decreasing order by *I. a. arnhemensis*, *I. a. barrowensis* and *I. a. marchinbarensis*. The infraorbital canal is short, equal in length to half the molar row. In ventral view, the septum diving the maxillopalatine fenestrae is thinning centrally but is thicker than in *I. a. barrowensis* and *I. a. marchinbarensis*. Lateral walls are present bordering the lateral sides of the presphenoid-basisphenoid suture.

Accessory cusps on C1 are present in some specimens and absent in others. P1 is shorter than P2, as in all subspecies of *I. auratus*, except *I. a. arnhemensis*. The central cusp of P1 and P2 is inflated as in *I. a. auratus* and *I. a. barrowensis*. P2 is subequal in length to P3 as in all subspecies except *I. a. barrowensis*. There is no buccal shelf in P3, as in *I. a. barrowensis*. On the M1, a small anterior cingulum is present as in all subspecies of *I. auratus* except *I. a. marchinbarensis*. StA is large. StB and StC are fused as a single cusp. The preparacrista is posterobuccally orientated to connect to a posteriorly located StB, as in all subspecies of *I. auratus* except *I. a. arnhemensis*. On the M2, the anterior cingulum connects to the talon in some specimens only. StB is conical and no crest is present. On the M3, a large anterior cingulum is present and connected to talon as in all subspecies of *I. auratus* except *I. a. arnhemensis*. The posterior cingulum is wide as in all subspecies of *I. auratus* except *I. a. arnhemensis* and *I. a. marchinbarensis*. The postprotocrista ends near the metastyle. On the M4, StB is large. The post-

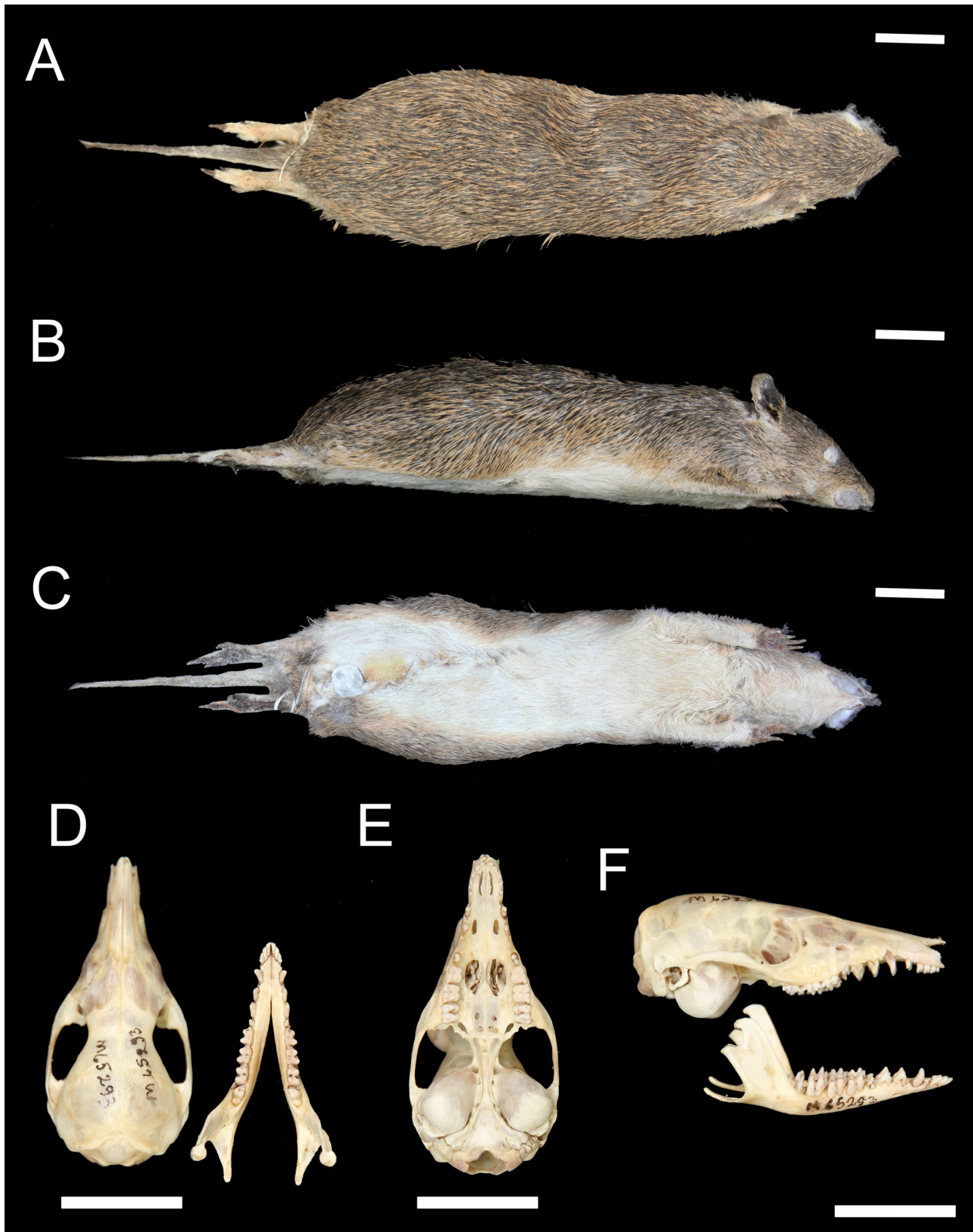


Figure 11. Holotype of *Isoodon auratus bundillari* subsp. nov., WAM M65293. Study skin in dorsal (A), lateral (B) and ventral views (C). Skull and dentary in dorsal (D), ventral (E) and lateral views (F). Scale bar = 3cm (skin); 2cm (skull).

protocrista ends level with the most posterior end of the postparacrista. There are no StC/D present.

Accessory cusps on c1 are present in some specimens and absent in others. The p1 is shorter than p2 or p3,

with a short diastema between p1 and p2. The p2 is longer than p3 in length. An anterior cusp is sometimes present on the p3. A cusp is present on m1-3 within the hypoflexid. The paraconid of the m1 is anterolabial to the metaconid as in all subspecies of *I. auratus*, except *I.*

a. auratus and *I. a. barrowensis*. The paracristid connects the paraconid to the protoconid. The posthypocristid of m1 and m2 is oblique to the tooth row. On the m3, cristid obliqua terminates lingual to the protoconid at its midpoint. The posthypocristid connects to the hypoconulid in some specimens, and to the entoconid in others. Talonid of m4 is small as in all *I. auratus* but much larger than that of *I. a. marchinbarensis*. The cristid obliqua of m4 terminates lingual to the protoconid, about midpoint to the tooth width. The posthypocristid of m4 is oblique to the tooth row in some specimens, and perpendicular in others. The entoconid is large. The hypoconulid is usually absent, but present as a small cusp in some specimens.

Remarks. Previously part of *I. a. auratus*, but shown here to be a distinct subspecies.

Distribution. Kimberley region (Western Australia).

Isoodon auratus marchinbarensis new subsp.

Figure 12

urn:lsid:zoobank.org:act:F788CEDE-4515-4E7B-951B-0FB51E73526A

Holotype. MAGNT U5735, adult female, alcohol specimen with skull extracted.

Type locality. Marchinbar Island, Northern Territory, Australia.

Paratype. MAGNT U5736, juvenile female, alcohol specimen.

Etymology. Named after the type locality.

Subspecies diagnosis. *Isoodon a. marchinbarensis* differs from all subspecies of *I. auratus* in having the smallest body, skull and bullae size; accessory cusps present on both C1 and c1; lacking an anterior cingulum on M1; small StA on M1; StB of M2 oval and crested; postprotocrista of M3 ending on the posterior flank of the metacone; postprotocrista ending posterior to the most posterior end of the postparacrista on M4; StC/D present on M4; cristid obliqua terminates lingual to the midpoint of the tooth width on m3; hypoconulid of m3 is absent; a smaller talonid on m4; a small entoconid on m4. *Isoodon a. marchinbarensis* differs from *I. a. auratus* and *I. a. barrowensis* in having a cusp within the hypoflexid of m1-3; having the paraconid of m1 anterolabial to the metaconid. *Isoodon a. marchinbarensis* differs from all subspecies of *I. auratus* except *I. a. auratus* in having a small StB on M4. *Isoodon a. marchinbarensis* differs from all subspecies except *I. a. barrowensis* in having a very thin dividing septum between the maxillopalatine fenestrae; posthypocristid of m4 perpendicular to the tooth row. *Isoodon a. marchinbarensis* differs from *I. a. auratus* in having the paracristid connected to the protoconid on m1. *Isoodon a. marchinbarensis* differs from *I. a. barrowensis* in having lateral walls present near the presphenoid-basisphenoid suture; P2 subequal in length to P3; a buccal shelf present on P3; anterior cingulum of M2 connected to the talon; p1 is shorter than

p2 or p3, with a short diastema between p1 and p2. *Isoodon a. marchinbarensis* differs from all subspecies of *I. auratus* except *I. a. arnhemensis* in having the central cusps on P1 and P2 not inflated; a narrow posterior cingulum on M3. *Isoodon a. marchinbarensis* differs from *I. a. auratus* in having posthypocristid connects to entoconid on m3. *Isoodon a. marchinbarensis* differs from *I. a. arnhemensis* in having P1 shorter than P2; M1 preparacrista posterobuccally orientated (buccally orientated in *I. a. arnhemensis*); StB and StC fused as a single cusp on M1; anterior cingulum of M2 connected to the talon; a large anterior cingulum connected to the talon on M3; having the posthypocristid of m1 and m2 oblique to the tooth row; cristid obliqua of m4 terminates lingual to the midpoint of the tooth width. *Isoodon a. marchinbarensis* differs from *I. a. bundilarri* in having an infraorbital canal longer than half the molar row; a buccal shelf present on P3; cristid obliqua of m4 terminates lingual to the midpoint of the tooth width.

Description. The fur on the dorsal side of the skin is golden brown in colour, grizzled with black. The golden colour is similar *I. a. arnhemensis*, more grizzled in black than other subspecies. The ventral fur is white though appears cream in the wet specimens. Tail short as in all bandicoots and is dark brown above and greyish below. Ears are light brown and rounded. Forefeet and hind feet are light brown on the dorsal side and white on the ventral side. The overall size of the subspecies is the smallest with head body = 155-210mm.

In lateral view, the infraorbital canal is long, longer than half the molar row. The bullae are large and prominent, but they are the smallest out of all subspecies of *I. auratus*. In ventral view, only one accessory fenestra is present, the one on the right only. The septa diving the maxillopalatine fenestrae is very thin, as in *I. a. barrowensis*, thinner than in other subspecies. The maxillopalatine fenestrae are smallest of all subspecies of *I. auratus*. Lateral walls are present bordering the lateral sides of the presphenoid-basisphenoid suture.

Accessory cusps on C1 are present. P1 is shorter than P2, as in all subspecies of *I. auratus*, except *I. a. arnhemensis*. The central cusp of P1 and P2 is not inflated as in *I. a. arnhemensis*. P2 is subequal in length to P3 as in all subspecies except *I. a. barrowensis*. A buccal shelf is present on the P3 as in *I. a. arnhemensis*. The M1 is lacking an anterior cingulum unlike all subspecies of *I. auratus* which have a small one. StA is small. StB and StC are fused as a single cusp. The preparacrista is posterobuccally orientated to connect to a posteriorly located StB, as in all subspecies of *I. auratus* except *I. a. arnhemensis*. On the M2, the anterior cingulum connects to the talon. StB is oval in shape and has a crest present. On the M3, a large anterior cingulum is present and connected to talon as in all subspecies of *I. auratus* except *I. a. arnhemensis*. The posterior cingulum is narrow as in *I. a. arnhemensis*. The postprotocrista ends on the posterior flank of the metacone. On M4, StB is small. The post-

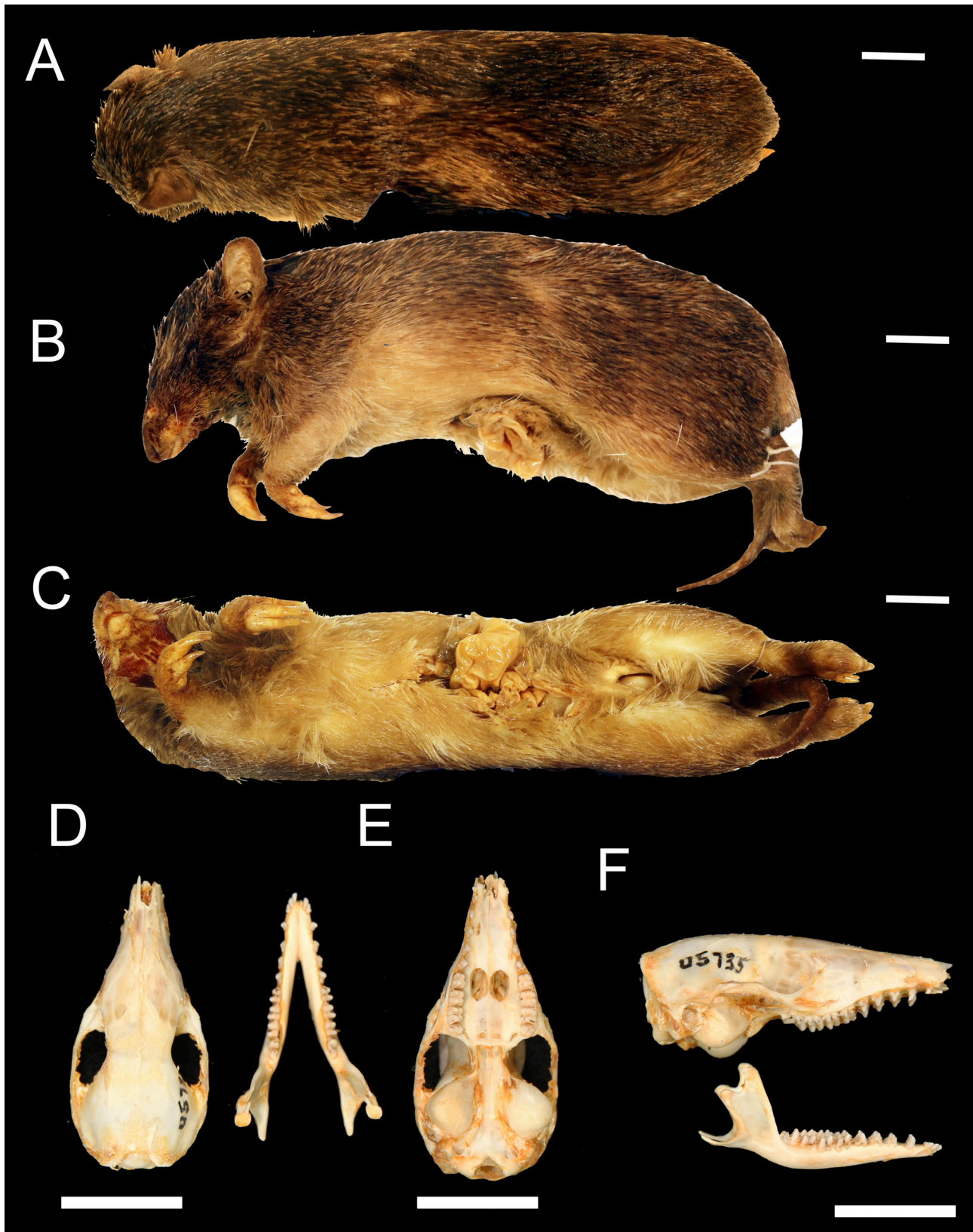


Figure 12. Holotype of *Isoodon auratus marchinbarensis* new subsp., MAGNT U5735. Alcohol preserved body in dorsal (A), lateral (B) and ventral views (C). Skull and dentary in dorsal (D), ventral (E) and lateral views (F). Scale bar = 2cm.

protocrista ends posterior to the most posterior end of the postparacrista. StC/D is present.

Accessory cusps on c1 are present. The p1 is shorter than p2 or p3, with a short diastema between p1 and

p2. The p2 and p3 are subequal in length. An anterior cusp is absent on the p3. A cusp is present on m1-3 within the hypoflexid. The paraconid of the m1 is anterolabial to the metaconid as in *I. a. arnhemensis* and *I. a. bundilarri*. The paracristid connects the paraconid to

the protoconid. The posthypocristid of m1 and m2 is oblique to the tooth row. On the m3, cristid obliqua terminates lingual to the midpoint of the tooth width on m3. The posthypocristid of m3 connects to entoconid as the hypoconulid is absent. The talonid of m4 is smaller in size than in any subspecies of *I. auratus*. The cristid obliqua of m4 terminates lingual to the midpoint of the tooth width. The posthypocristid of m4 is perpendicular to the tooth row. The entoconid is small unlike all other subspecies of *I. auratus*.

Remarks. Previously part of *I. a. arnhemensis* but shown here to be a distinct subspecies. Only two specimens exist in museum collections, both at MAGNT and both wet specimens only, which makes it hard to compare to dry types.

Distribution. Marchinbar Island.

Isoodon fusciventer (Gray, 1841)

urn:lsid:zoobank.org:act:A62724C3-ED62-42CA-A72F-1B3FB6CFF538

Perameles fusciventer Gray, 1841:407.

Common name. Quenda

Remarks. *Isoodon fusciventer* was first described as a species but later on considered to be a subspecies of *Isoodon obesulus*. From a total evidence analysis (combination of genetics and morphology), Travouillon and Phillips (2018) provided evidence that it was a unique species distantly related to *I. obesulus*. Adelaide Hills, Kangaroo Island and Nuyts Archipelago populations previously part of *Isoodon obesulus* but moved to *I. fusciventer* here as a result of the genetic results showing no close affinities with *I. obesulus* and forming a clade within *Isoodon fusciventer* from Western Australia.

Emended species diagnosis. *Isoodon fusciventer* (except *I. f. insulanus*, *I. f. nauticus*, *I. f. terrenus*) differs from all species of *Isoodon* in having a large StA on M1 (except *I. o. affinis*) a premolar-like I5 (except *I. f. halae*), anterior cingulum of M1 connected to talon. *Isoodon fusciventer* differs from *I. microtis*, *I. auratus* and *I. peninsulae* in being larger in size, and smaller in size to *I. macrourus*. *Isoodon fusciventer* (except *I. f. fusciventer* and *I. f. terrenus*) differs from *I. macrourus*, *I. moresbyensis* and *I. peninsulae* in having a moderately expanded submasseteric crest. *Isoodon fusciventer* differs from *I. microtis* and *I. peninsulae* in having a small or large anterior cingulum on M2 connected to the talon. *Isoodon fusciventer* differs from *I. microtis*, *I. obesulus* and *I. peninsulae* in having the alisphenoid tympanic process terminating anterior to the transverse foramen. *Isoodon fusciventer* differs from *I. microtis* and *I. obesulus* in having the posthypocristid oblique to the tooth row on m1. *Isoodon fusciventer* differs from *I. macrourus* and *I. moresbyensis* in having a pair of accessory fenestrae, I3 larger than I2 or I4, small metacone on M4 (except in some *I. f. fusciventer*), preentocristid absent on m4. *Isoodon fusciventer* differs from *I. microtis* in having small posterior palatal fenestrae, larger bullae, the paraconid-

metaconid distance shorter than the metaconid-protoconid distance on m1.

Isoodon fusciventer fusciventer (Gray, 1841)

Figure 13

urn:lsid:zoobank.org:act:A62724C3-ED62-42CA-A72F-1B3FB6CFF538

Perameles fusciventer Gray, 1841: 407.

Holotype. NHMUK 1841.1176, adult, sex unknown (most likely female based on canine morphology), skin and skull

Type locality. King George Sound, Western Australia.

Emended subspecies diagnosis. *Isoodon fusciventer fusciventer* differs from all other subspecies in having a well-developed lingual shelf on P3 that extends on the buccal side, no styler crest connected to StD on M1, postprotocrista of M4 ends level or posterior to the most posterior end of the postparacrista, p2 shorter or equal to p3, paraconid is anterior to metaconid on m1. *Isoodon f. fusciventer* differs from *I. f. halae*, *I. f. dawensis*, *I. f. nauticus* and *I. f. insulanus* in being larger, with longer feet, having deep and wide expansion of the submasseteric crest. *Isoodon f. fusciventer* differs from *I. f. halae* and *I. f. dawensis* in having P1 as long as P2, posthypocristid is perpendicular to the tooth row on m3. *Isoodon f. fusciventer* differs from *I. f. halae*, *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus* in having a premolar-like I5, cristid obliqua terminates lingual to protocone on m1. *Isoodon f. fusciventer* differs from *I. f. dawensis*, *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus* in having StC/D on M4 present. *Isoodon f. fusciventer* differs from *I. f. nauticus* and *I. f. insulanus* in having P2 and P3 subequal in length, a large anterior cingulum connected to talon on M1, large StB on M4. *Isoodon f. fusciventer* differs from *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus* in having a preparacrista posterobuccally orientated on M1, large StA on M1, nasals terminate just anterior to the orbit, p1 is shorter than either p2 or p3, large entoconid on m4. *Isoodon f. fusciventer* differs from *I. f. dawensis*, *I. f. nauticus* and *I. f. insulanus* in having the supraoccipital taller than it is wide, sagittal crest present in males. *Isoodon f. fusciventer* differs from *I. f. insulanus* and *I. f. terrenus* in having a short diastema between p1 and p2. *Isoodon f. fusciventer* differs from *I. f. halae*, *I. f. nauticus* and *I. f. insulanus* in having a large StE on M1 and M2. *Isoodon f. fusciventer* differs from *I. f. halae*, *I. f. dawensis* and *I. f. terrenus* in having a large hypoconulid on m3. *Isoodon f. fusciventer* differs from *I. f. halae* in having a posthypocristid of m4 oblique to the tooth row. *Isoodon f. fusciventer* differs from *I. f. dawensis* in having lateral walls of presphenoid/basisphenoid suture are present, small anterior cingulum on M2, postparacrista of M4 curves as a small centrocrista, cristid obliqua terminates lingual to the protocone about midpoint to the tooth width on m4, hypoconulid small or absent on m4. *Isoodon f. fusciventer* differs from *I. f. nauticus* in having a large anterior cingulum on M4. *Isoodon f. fusciventer* dif-

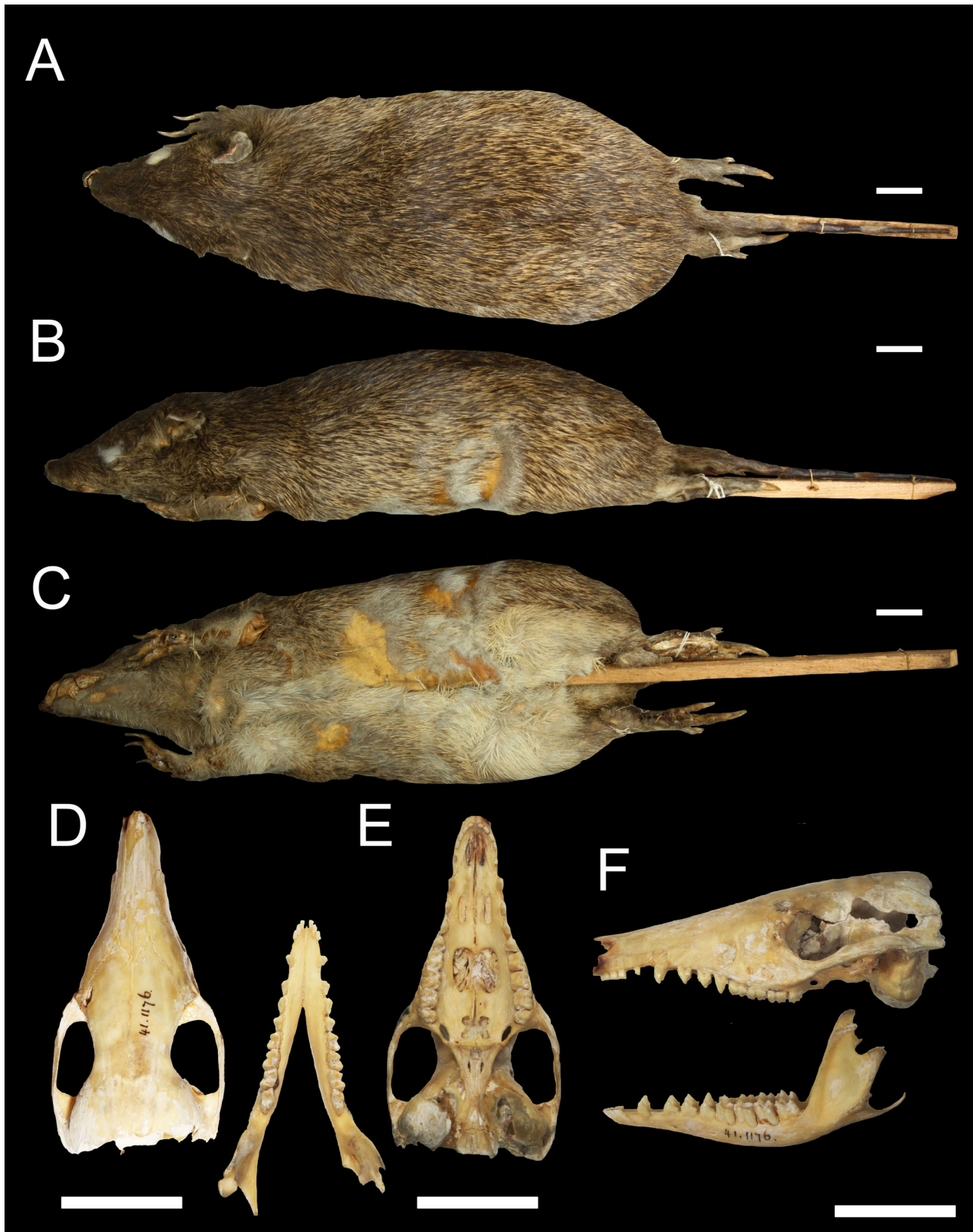


Figure 13. Holotype of *Isoodon fusciventer*, NHMUK 1841.1176. Study skin in dorsal (A), lateral (B) and ventral views (C). Skull and dentary in dorsal (D), ventral (E) and lateral views (F). Scale bar = 2cm.

fers from *I. f. insulanus* in having a styler crest present on M2.

Distribution. Forested areas of south-west Western Australia.

Remarks. No subspecies previously recognised.

***Isoodon fusciventer halae* new subsp.**

Figure 14

urn:lsid:zoobank.org:act:3E916357-3570-4C9F-956A-E26036F5BB43

Holotype. WAM M64190, adult male, skin and skeleton.**Type locality.** Normans Beach Nature Reserve, Western Australia.**Paratype.** WAM M63972, adult female, skin and skeleton, Cape Arid, WA; M4521, adult male, skin and skull, from Lake Grace, WA; M6016, adult female, skin and skull, from Wyalkatchem, WA.**Etymology.** Named in honour of Marie Hale (nee Cooper), for her research on the Quenda, and being the first to identify this new taxon.

Subspecies diagnosis. *Isoodon fusciventer halae* differs from all other subspecies in having the posthypocristid of m4 perpendicular to the tooth row. *Isoodon f. halae* differs from *I. f. fusciventer* and *I. f. dawensis* in having a canine-like I5, postprotocrista of M4 ends anterior to the most posterior end of the postparacrista, cristid obliqua terminates buccal to protocone on m1. *Isoodon f. halae* differs from *I. f. fusciventer*, *I. f. nauticus* and *I. f. insulanus* in having a well-developed lingual shelf that does not extend to the buccal side on P3. *Isoodon f. halae* differs from *I. f. fusciventer*, *I. f. nauticus*, *I. f. terrenus* and *I. f. insulanus* in having P1 shorter than P2, posthypocristid is oblique to the tooth row on m3. *Isoodon f. halae* differs from *I. f. fusciventer*, *I. f. dawensis*, *I. f. terrenus* and *I. f. insulanus* in having a small StE on M1 and M2. *Isoodon f. halae* differs from *I. f. fusciventer* and *I. f. terrenus* in being smaller, with shorter feet, having moderate expansion of the submasseteric crest. *Isoodon f. halae* differs from *I. f. fusciventer* in having styler crest present and connected to StD on M1, paraconid is anterolabial to metaconid on m1. *Isoodon f. halae* differs from *I. f. dawensis*, *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus* in having StC/D on M4 is present. *Isoodon f. halae* differs from *I. f. fusciventer*, *I. f. terrenus* and *I. f. insulanus* in having p2 longer than p3. *Isoodon f. halae* differs from *I. f. dawensis*, *I. f. nauticus* and *I. f. insulanus* in having the supraoccipital taller than it is wide, sagittal crest present in males. *Isoodon f. halae* differs from *I. f. nauticus* and *I. f. insulanus* in having P2 and P3 subequal in length, a large anterior cingulum connected to talon on M1, large StB on M4. *Isoodon f. halae* differs from *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus* in having a preparacrista posterobuccally orientated on M1, large StA on M1, StE present on M3, nasals terminate just anterior to the orbit, p1 is shorter than either p2 or p3, large entoconid on m4. *Isoodon f. halae* differs from *I. f. insulanus* and *I. f. terrenus* in having a short diastema between p1 and p2. *Isoodon f. halae* differs from *I. f. fusciventer*, *I. f. nauticus* and *I. f. insulanus* in having a large hypoconulid on m3. *Isoodon f. halae* differs from *I. f. dawensis* and *I. f. terrenus* in having no buccal shelf of P3. *Isoodon f. halae* differs from *I. f. dawensis* in having a

pair of accessory fenestrae present, lateral walls of pre-sphenoid/basisphenoid suture are present, small anterior cingulum on M2, postparacrista of M4 curves as a small centrocrista, cristid obliqua terminates lingual to the protocone about midpoint to the tooth width on m4, hypoconulid absent on m4. *Isoodon f. halae* differs from *I. f. nauticus* in having a large anterior cingulum on M4, a median buccal cusp present in the hypoflexid of m1-3. *Isoodon f. halae* differs from *I. f. terrenus* in having a small or no anterior cusp on p3. *Isoodon f. halae* differs from *I. f. insulanus* in having a styler crest present on M2.

Description. The fur on the dorsal side of the skin is dark brown in colour, grizzled with light brown. The ventral fur is cream to off-white. Tail is short about a quarter of the body length and is dark brown above and greyish below. Ears are rounded, dark brown on the outside, and bicoloured on the inside. The colour is golden near the edge of the ears, and dark brown on the inside. Forefeet and hind feet are light brown with patches of dark brown on the dorsal side and cream on the ventral side. The holotype is the largest specimen of this subspecies collected and has very worn teeth. It's hindfeet are 58mm in length, this ranges 60-50mm for other similar aged males in the subspecies. This is a useful way to distinguish this subspecies from *I. f. fusciventer*, which has a range of 75-67mm for similar aged males. For females, the hindfeet of adult females (worn teeth) ranges from 54-42mm, compared to *I. f. fusciventer*, which has a range of 63-55mm. The overall size of the subspecies (ranging from 355-220mm for head-body) is smaller than *I. f. fusciventer* (ranging from 445-235mm for head-body), but bigger than *I. f. dawensis*.

In dorsal view, a short sagittal crest is present in males, but smaller than in *I. f. fusciventer*. The snout length (tip of snout to orbit) is equidistant to the cranium length (orbit to back of skull), which make the snout length significantly shorter than *I. f. fusciventer*, which has a snout length longer than cranium length. In lateral view, the infraorbital canal is long, longer than half the molar row in some specimens (mostly males), and short in others (mostly females) as in *I. f. fusciventer*. The bullae are large and prominent, similar in size for males of *I. f. fusciventer* but smaller in size in females. In ventral view, accessory fenestrae are present but small. The septa dividing the maxillopalatine fenestrae is very thin, and the maxillopalatine fenestrae are smaller in females compared to *I. f. fusciventer*. The bullae are more rounded in shape in females, compared to *I. f. fusciventer*. In the dentary, there are three mental foramina on the left side in males, two on the right side. They are positioned under the p1, p3 and m1 respectively. In females and in *I. f. fusciventer*, there are only 2 mental foramina, positioned under the p1 and m1. The submasseteric crest is moderately expanded, smaller than in *I. f. fusciventer*.

The I5 is pointed and canine-like in shape. Accessory cusps on C1 are absent. P1 is shorter than P2 (P1 is

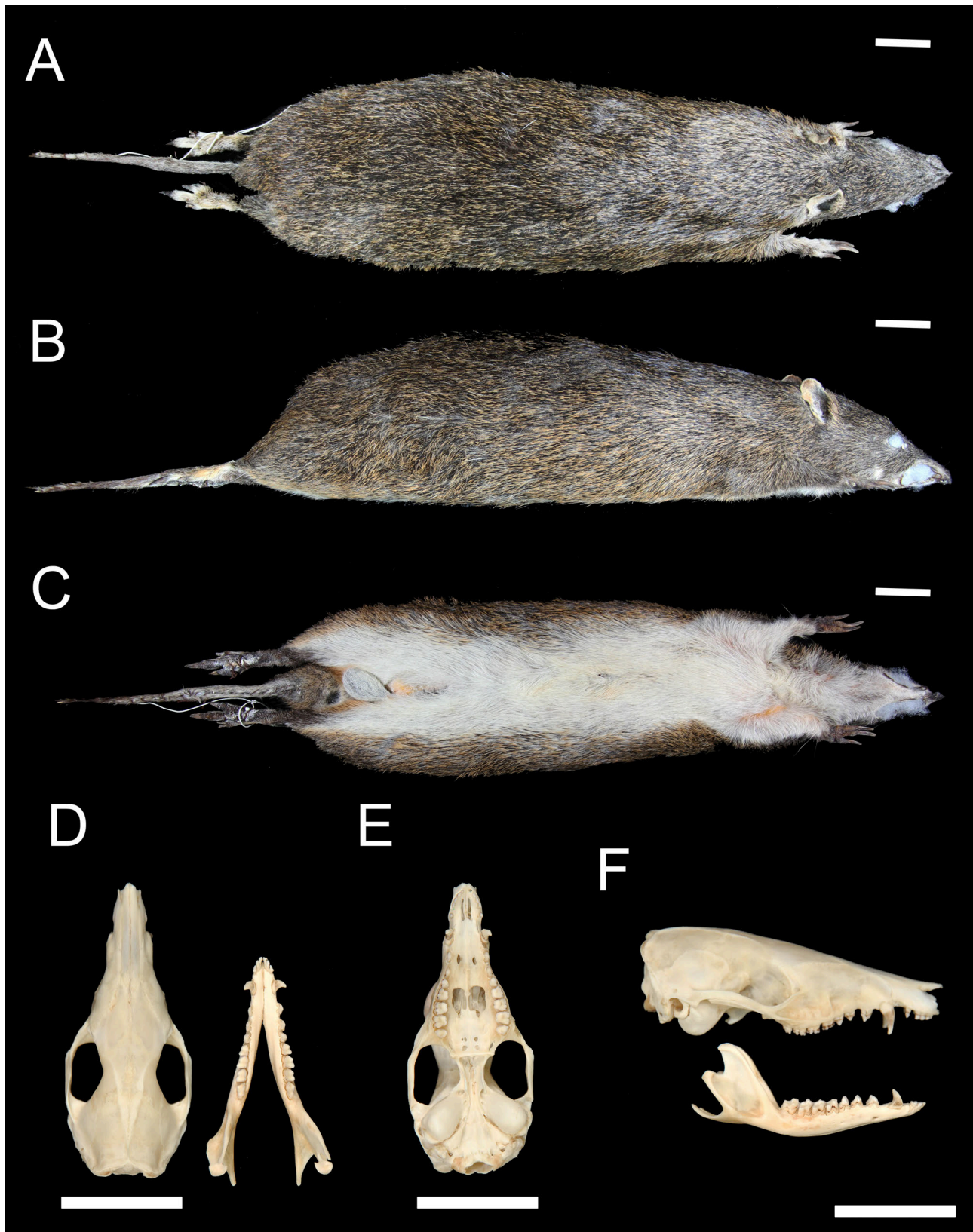


Figure 14. Holotype of *Isoodon fusciventer hae* new subsp., WAM M64190. Study skin in dorsal (A), lateral (B) and ventral views (C). Skull and dentary in dorsal (D), ventral (E) and lateral views (F). Scale bar = 3cm.

as long as P2 in *I. f. fusciventer*). The central cusp of P1 and P2 is inflated as in *I. f. fusciventer*. P2 is subequal in length to P3. The P3 has a well-developed lingual shelf but does not extend buccally as it does in *I. f. fusciventer*. No buccal shelf present on P3. The StD of M1 is coni-

cal but it is not connected to the stylar crest (stylar crest is absent in *I. f. fusciventer*). StE is small on M1 and M2. On the M2, the anterior cingulum is small and connects to the talon as in *I. f. fusciventer*. On the M3, there is no stylar crest between StD and the metastyle, except for a

remnant of StE (sometimes present in *I. f. fusciventer*. On M4, the postparacrista is curved as in *I. f. fusciventer*. The postprotocrista ends anterior to the most posterior end of the postparacrista. The metacone is small and StC/D is present.

Accessory cusps on c1 are present in females but absent in males. The p1 is shorter than p2 or p3, with a short diastema between p1 and p2. The p2 is longer than p3 unlike *I. f. fusciventer* where p2 is shorter or subequal to p3. An anterior cusp is absent on the p3. A cusp is present on m1-3 within the hypoflexid. No anterior cingulid on m1 (sometimes present in *I. f. fusciventer*). The paraconid of the m1 is anterolabial to the metaconid unlike *I. f. fusciventer* (anterior to metaconid). Cristid obliqua of m1 terminates buccal to the protoconid. The posthypocristid of m3 is oblique to the tooth row (perpendicular in *I. f. fusciventer*). The hypoconulid of m3 is large. The cristid obliqua of m4 terminates lingual to the protocone about midpoint of the tooth width as in *I. f. fusciventer*. The posthypocristid of m4 is perpendicular to the tooth row. The hypoconulid of m4 is absent.

Remarks. Recognised as a distinct taxon in Marie Hale's PhD Thesis, but not formally described.

Distribution. Woodland areas of south-west Western Australia.

Isoodon fusciventer dawensis new subsp.

Figure 15

urn:lsid:zoobank.org:act:4318AD99-FC69-4907-9A3B-6E0BCFECA844

Holotype. WAM M3230, adult male, skin and skull.

Type locality. Daw Island, Recherche Archipelago, Western Australia, Australia.

Paratype. WAM M3229, adult female, skull only; WAM M4011, adult male, alcohol specimen and skeleton; WAM M25556, adult male, alcohol specimen.

Etymology. Named after the type locality.

Subspecies diagnosis. *Isoodon fusciventer dawensis* differs from all other subspecies in having a large anterior cingulum on M2, postparacrista of M4 is straight, postprotocrista of M4 ends posterior to the most posterior end of the postparacrista, cristid obliqua terminates lingual to the midpoint of the tooth width on m4, large hypoconulid on m4, lateral walls of presphenoid/basisphenoid suture are absent. *Isoodon f. dawensis* differs from *I. f. fusciventer* and *I. f. halae* in having the StC/D on M4 is absent. *Isoodon f. dawensis* differs from *I. f. fusciventer*, *I. f. halae* and *I. f. terrenus* in having the supraoccipital as tall as it is wide, no sagittal crest in males. *Isoodon f. dawensis* differs from *I. f. fusciventer*, *I. f. nauticus* and *I. f. insulanus* in having a well-developed lingual shelf that does not extend to the buccal side on P3. *Isoodon f. dawensis* differs from *I. f. fusciventer*, *I. f. nauticus*, *I. f. terrenus* and *I. f. insulanus* in having P1 shorter than P2, posthypocristid is oblique to the tooth row on m3. *Isoodon f. dawensis* differs from *I. f. fusciventer*,

I. f. terrenus and *I. f. insulanus* in having p2 longer than p3. *Isoodon f. dawensis* differs from *I. f. fusciventer*, *I. f. nauticus* and *I. f. insulanus* in having a large hypoconulid on m3. *Isoodon f. dawensis* differs from *I. f. fusciventer* and *I. f. terrenus* in being smaller, with shorter feet, having moderate expansion of the submaseteric crest. *Isoodon f. dawensis* differs from *I. f. fusciventer* in having stylar crest present and connected to StD on M1, paraconid is anterolabial to metaconid on m1. *Isoodon f. dawensis* differs from *I. f. halae*, *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus* in having a premolar-like I5, cristid obliqua terminates lingual to protocone on m1. *Isoodon f. dawensis* differs from *I. f. nauticus* and *I. f. insulanus* in having P2 and P3 subequal in length, a large anterior cingulum connected to talon on M1, large StB on M4. *Isoodon f. dawensis* differs from *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus* in having a preparacrista posterobuccally orientated on M1, large StA on M1, StE present on M3, nasals terminate just anterior to the orbit, p1 is shorter than either p2 or p3, large entoconid on m4. *Isoodon f. dawensis* differs from *I. f. halae*, *I. f. nauticus*, *I. f. terrenus* and *I. f. insulanus* in having no accessory fenestrae present. *Isoodon f. dawensis* differs from *I. f. insulanus* and *I. f. terrenus* in having a short diastema between p1 and p2. *Isoodon f. dawensis* differs from *I. f. halae*, *I. f. nauticus* and *I. f. insulanus* in having buccal shelf of P3 present, a large StE on M1 and M2. *Isoodon f. dawensis* differs from *I. f. halae* in having posthypocristid of m4 oblique to the tooth row. *Isoodon f. dawensis* differs from *I. f. nauticus* in having a large anterior cingulum on M4, median buccal cusp present in the hypoflexid of m1-3. *Isoodon f. dawensis* differs from *I. f. terrenus* in having a small or no anterior cusp on p3. *Isoodon f. dawensis* differs from *I. f. insulanus* in having a stylar crest present on M2.

Description. The holotype is the only dry skin in existence in museums. The rest are all alcohol specimens or skulls and skeletons. As a result, the description of the skin is based only on the holotype. The fur on the dorsal side of the skin is lighter brown than the mainland subspecies. The ventral fur is cream. The tail is damaged and likely missing at least a third of its length. It is dark brown above and greyish below. Ears are dark brown on the outside, and tri-coloured on the inside, going from white to gold to dark brown. Forefeet and hind feet are light brown to cream all around, with unusually long foreclaws. The overall size of the subspecies is the smallest with head body = 212mm.

Overall, the skull of males is significantly smaller than that of *I. f. fusciventer* and *I. f. halae*, about 2/3 of their length, but females are only 20% smaller than *I. f. fusciventer*, and only just smaller than female *I. f. halae*. In dorsal view, no sagittal crest is present, unlike males of *I. f. fusciventer* and *I. f. halae*. The snout length (tip of snout to orbit) is equidistant to the cranium length (orbit to back of skull) as in *I. f. halae*, shorter than *I. f. fusciventer*. In lateral view, the infraorbital canal is short. The bullae are smaller and less prominent than in *I. f. halae*.

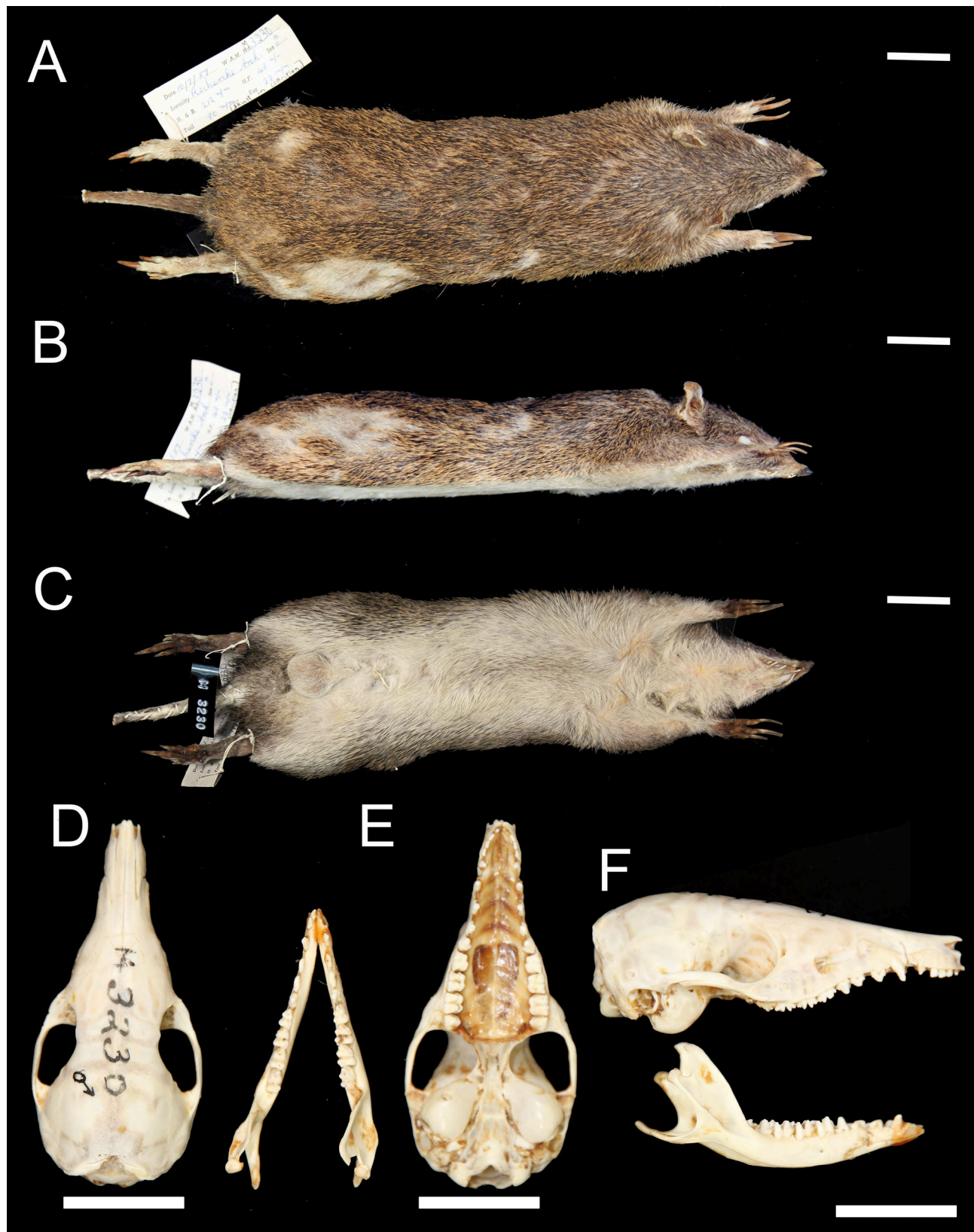


Figure 15. Holotype of *Isoodon fusciventer dawensis* new subsp., WAM M3230. Study skin in dorsal (A), lateral (B) and ventral views (C). Skull and dentary in dorsal (D), ventral (E) and lateral views (F). Scale bar = 3cm (skin); 2cm (skull).

In ventral view, accessory fenestrae are absent, as in *I. macrourus*. The septa dividing the maxillopalatine fenestrae is very thin, and the maxillopalatine fenestrae are similar in size to *I. f. halae*. The lateral walls of presphenoid/basisphenoid suture are absent (present in *I. f. fus-*

civenter and *I. f. halae*). The supraoccipital is as tall as it is wide, while it is taller in *I. f. fusciventer* and *I. f. halae*. In the dentary, there are 2 mental foramina, one under the p1 and one under m1, as in *I. f. fusciventer*. The sub-

masseteric crest is moderately expanded, smaller than in *I. f. fusciventer*.

The I5 is premolar-like in shape as in *I. f. fusciventer*. Accessory cusps on C1 are absent. P1 is shorter than P2, similar to *I. f. halae*. The central cusp of P1 and P2 is inflated. P2 is subequal in length to P3. The P3 has a well-developed lingual shelf as in *I. f. halae*. A small buccal shelf is present on P3. The StD of M1 is conical but it is not connected to the styler crest as in *I. f. halae*. StE is distinct on M1 and M2. On the M2, the anterior cingulum is wide and connects to the talon. On the M3, there is no styler crest between StD and the metastyle, except for a remnant of StE as in *I. f. halae*. On M4, the postparacrista is straight. The postprotocrista ends posterior to the most posterior end of the postparacrista. The metacone is small and StC/D is absent.

Accessory cusps on c1 are present in both males and females. The p1 is shorter than p2 or p3, with a short diastema between p1 and p2. The p2 is longer than p3 as in *I. f. halae*. An anterior cusp is absent on the p3. A cusp is present on m1-3 within the hypoflexid. No anterior cingulid on m1. The paraconid of the m1 is anterolabial to the metaconid as in *I. f. halae*. Cristid obliqua of m1 terminates lingual to the protoconid. The posthypocristid of m3 is oblique to the tooth row as in *I. f. halae*. The hypoconulid of m3 is large. The cristid obliqua of m4 terminates lingual to the midpoint of the tooth width. The posthypocristid of m4 is oblique to the tooth row as in *I. f. fusciventer*. The hypoconulid of m4 is present and large.

Remarks. Previously not recognised as a distinct subspecies.

Distribution. Daw Island, Western Australia.

Isoodon fusciventer nauticus (Thomas, 1922)

Figure 16

urn:lsid:zoobank.org:act:92AA7347-70B3-4E9C-A7B5-477D7C8F2DFE

Isoodon nauticus Thomas, 1922: 678

Holotype. NHMUK 1922.4.15.6, adult male, skin and skull

Type locality. Franklin Island, Nyuts Archipelago, South Australia.

Emended subspecies diagnosis. *Isoodon fusciventer nauticus* differs from all other subspecies in having P2 longer than P3, small anterior cingulum on M4. *Isoodon f. nauticus* differs from *I. f. terrenus* and *I. f. insulanus* in having a short diastema between p1 and p2. *Isoodon f. nauticus* differs from *I. f. dawensis* and *I. f. terrenus* in having no buccal shelf of P3. *Isoodon f. nauticus* differs from *I. f. fusciventer* and *I. f. terrenus* in being smaller, with shorter feet, having moderate expansion of the submasseteric crest. *Isoodon f. nauticus* differs from *I. f. terrenus* in having no anterior cusp on p3. *Isoodon f. nauticus* differs from *I. f. fusciventer*, *I. f. dawensis*, *I. f. terrenus* and *I. f. insulanus* in having a small StE on M1 and

M2. *Isoodon f. nauticus* differs from *I. f. terrenus*, *I. f. fusciventer*, *I. f. halae* and *I. f. dawensis* in having a small anterior cingulum not connected to talon on M1, small StB on M4. *Isoodon f. nauticus* differs from *I. f. terrenus*, *I. f. insulanus*, *I. f. halae* and *I. f. dawensis* in having no median buccal cusp present in the hypoflexid of m1-3. *Isoodon f. nauticus* differs from *I. f. fusciventer*, *I. f. terrenus* and *I. f. insulanus* in having p2 longer than p3. *Isoodon f. nauticus* differs from *I. f. fusciventer*, *I. f. halae* and *I. f. terrenus* in having the supraoccipital as tall as it is wide, no sagittal crest in males. *Isoodon f. nauticus* differs from *I. f. halae*, *I. f. dawensis* and *I. f. terrenus* in having a hypoconulid that is small on m3. *Isoodon f. nauticus* differs from *I. f. fusciventer* and *I. f. dawensis* in having a canine-like I5, postprotocrista of M4 ends anterior to the most posterior end of the postparacrista, cristid obliqua terminates buccal to protocone on m1. *Isoodon f. nauticus* differs from *I. f. fusciventer*, *I. f. halae* and *I. f. dawensis* in having a weakly developed lingual shelf on P3, a preparacrista buccally orientated on M1, small StA on M1, StE absent on M3, nasals terminate well anterior to the orbit, p1 is as long as p2 or p3, small entoconid on m4. *Isoodon f. nauticus* differs from *I. f. halae* and *I. f. dawensis* in having P1 as long as P2, posthypocristid is perpendicular to the tooth row on m3. *Isoodon f. nauticus* differs from *I. f. fusciventer* and *I. f. halae* in having StC/D on M4 absent. *Isoodon f. nauticus* differs from *I. f. fusciventer* in having a styler crest present and connected to StD on M1, paraconid is anterolabial to metaconid on m1. *Isoodon f. nauticus* differs from *I. f. dawensis* in having a pair of accessory fenestrae present, small anterior cingulum on M2, postparacrista of M4 curves as a small centrocrista, cristid obliqua terminates lingual to the protocone about midpoint to the tooth width on m4, hypoconulid small or absent on m4, lateral walls of presphenoid/basisphenoid suture are present. *Isoodon f. nauticus* differs from *I. f. insulanus* in having a styler crest present on M2. *Isoodon f. nauticus* differs from *I. f. halae* in having the posthypocristid of m4 oblique to the tooth row.

Remarks. Previously a subspecies of *I. obesulus*.

Distribution. Franklin Island, South Australia.

Isoodon fusciventer insulanus new subsp.

Figure 17

urn:lsid:zoobank.org:act:98BB8375-BD5F-40DD-AF67-ACF9925AAF31

Holotype. SAMA M8646, adult male, skull only.

Type locality. St Francis Island, Nyuts Archipelago, South Australia.

Paratype. SAMA M8647, adult female, skull only, from St Francis Island, SAMA M8547, adult male, alcohol specimen, from St Francis Island, SAMA M8548, adult female, alcohol specimen, from St Francis Island.

Etymology. From Latin meaning islander, in reference to being only found on St Francis Island.

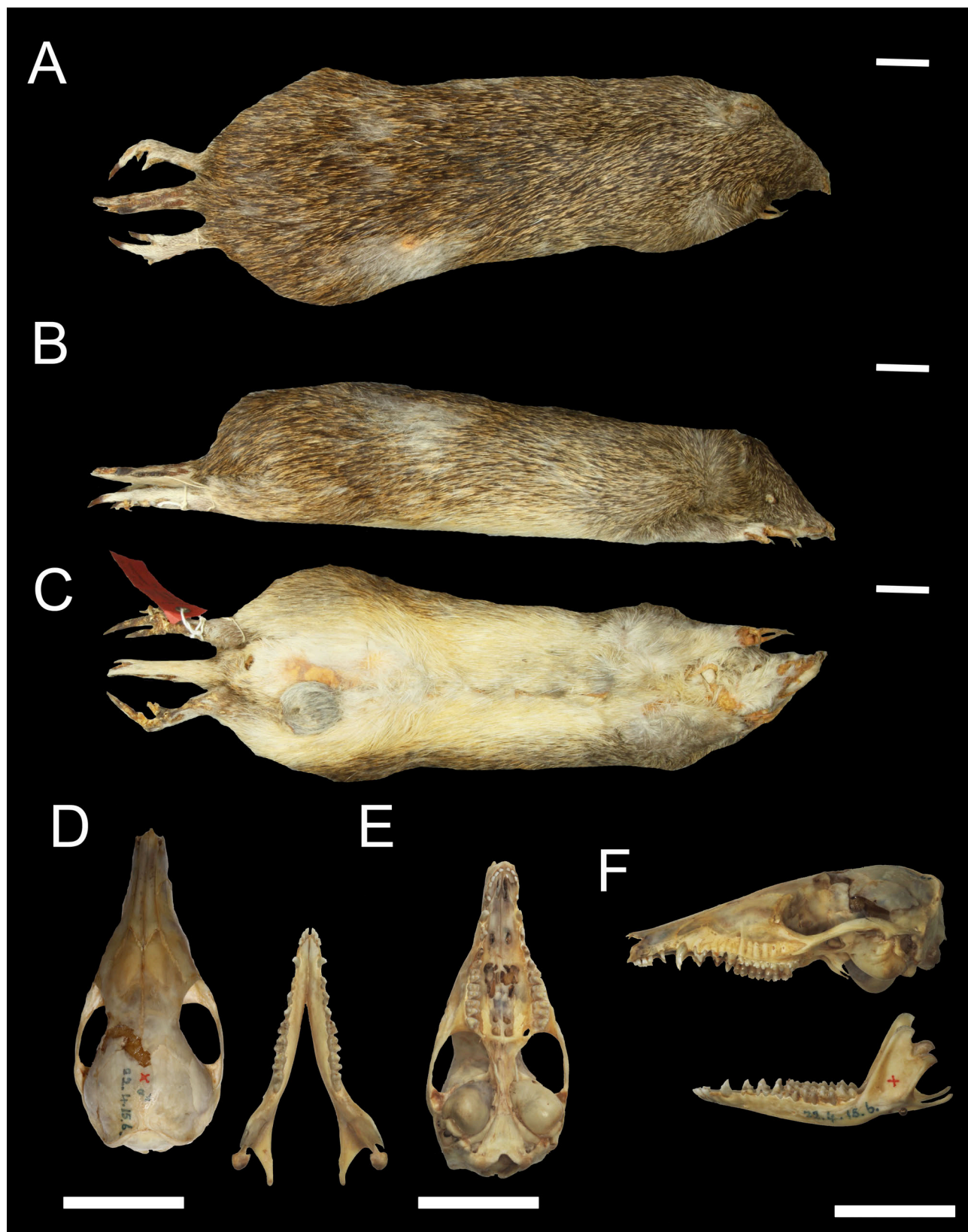


Figure 16. Holotype of *Isoodon fusciventer nauticus* new stat., NHMUK 1922.4.15.6. Study skin in dorsal (A), lateral (B) and ventral views (C). Skull and dentary in dorsal (D), ventral (E) and lateral views (F). Scale bar = 2cm.

Subspecies diagnosis. *Isoodon fusciventer insulanus* differs from all other subspecies in having P2 shorter than P3, no StE on M1 and M2, no styler crest present on M2. *Isoodon f. insulanus* differs from *I. f. fusciventer* and *I. f. terrenus* in being smaller, with shorter feet, having mod-

erate expansion of the submasseteric crest. *Isoodon f. insulanus* differs from *I. f. terrenus* in having, no anterior cusp on p3. *Isoodon f. insulanus* differs from *I. f. dawensis* and *I. f. terrenus* in having no buccal shelf of P3. *Isoodon f. insulanus* differs from *I. f. fusciventer*, *I. f. halae*, *I. f.*



Figure 17. Holotype of *Isoodon fusciventer insulanus* new subsp., SAMA M8646. Skull and dentary in dorsal (A), ventral (B) and lateral views (C). Scale bar = 2cm.

dawensis and *I. f. nauticus* in having no diastema between p1 and p2, p2 subequal in length to p3. *Isoodon f. insulanus* differs from *I. f. terrenus*, *I. f. fusciventer*, *I. f. halae* and *I. f. dawensis* in having a small anterior cingulum not connected to talon on M1, small StB on M4. *Isoodon f. insulanus* differs from *I. f. fusciventer* and *I. f. dawensis* in having a canine-like I5, postprotocrista of M4 ends anterior to the most posterior end of the postparacrista, cristid obliqua terminates buccal to protocone on m1. *Isoodon f. insulanus* differs from *I. f. fusciventer*, *I. f. halae* and *I. f. terrenus* in having the supraoccipital as tall as it is wide, no sagittal crest in males. *Isoodon f. insulanus* differs from *I. f. fusciventer*, *I. f. halae* and *I. f. dawensis* in having a weakly developed lingual shelf on P3, p1 is as long as p2 or p3. *Isoodon f. insulanus* differs from *I. f. fusciventer*, *I. f. halae* and *I. f. dawensis* in having a preparacrista buccally orientated on M1, small StA on M1, StE absent on M3, nasals terminate well anterior to the orbit, small entoconid on m4. *Isoodon f. insulanus* differs from *I. f. halae* and *I. f. dawensis* in having P1 as long as P2, posthypocristid is perpendicular to the tooth row on m3. *Isoodon f. insulanus* differs from *I. f. fusciventer* and *I. f. halae* in having StC/D on M4 absent. *Isoodon f. insulanus* differs from *I. f. halae*, *I. f. dawensis* and *I. f. terrenus* in having a large hypoconulid that is small on m3. *Isoodon f. insulanus* differs from *I. f. fusciventer* in having a styler crest present and connected to StD on M1, paraconid is anterolabial to metaconid on m1. *Isoodon f. insulanus* differs from *I. f. nauticus* in having a large anterior cingulum on M4, median buccal cusp present in the hypoflexid of m1-3. *Isoodon f. insulanus* differs from *I. f. dawensis* in having a pair of accessory fenestrae present, small anterior cingulum on M2, postparacrista of M4 curves as a small centrocrista, cristid obliqua terminates lingual to the protocone about midpoint to the tooth width on

m4, hypoconulid small or absent on m4, lateral walls of presphenoid/basisphenoid suture are present. *Isoodon f. insulanus* differs from *I. f. halae* in having the posthypocristid of m4 oblique to the tooth row.

Description. Two of the paratypes are alcohol specimens which are the only representation of the skin of this subspecies. Both are in poor condition with patches of fur missing, open gut, tail broken or missing and fixed in a position which made it too difficult to photograph. These are not illustrated as a result. The fur on the dorsal side of the skin is golden brown in colour, grizzled with black. The ventral fur is cream. A short portion of the tail is preserved in SAMA M8586, and is golden brown above, and cream below. Ears are rounded. They are dark brown on the outside, and golden and dark brown on the inside. Forefeet and hind feet are golden on the dorsal side and cream on the ventral side.

The skull is similar in size to that of *I. f. nauticus*, but about 20% shorter and less wide than *I. f. terrenus*. In dorsal view, no sagittal crest is present. The snout length (tip of snout to orbit) is equidistant to the cranium length (orbit to back of skull). In lateral view, the infraorbital canal is short. The bullae are smaller than those of either *I. f. nauticus* or *I. f. terrenus*. In ventral view, accessory fenestrae are large, larger than those of *I. f. nauticus* or *I. f. terrenus*. The maxillopalatine fenestrae are the same size as those of *I. f. terrenus* despite having a smaller skull. The dividing septa are thicker than those of *I. f. terrenus*. The bullae are more rounded in shape than *I. f. terrenus*, smaller in size than *I. f. nauticus* and similar in both males and females. The paraoccipital process is short and does not extend above the petrosal. The supraoccipital is as tall as it is wide. In the dentary, the posterior mental foramen is below the pos-

terior root of m1, as in *I. f. nauticus*. The submassesteric crest is moderately expanded.

Accessory cusps on C1 are absent. P1 is as long as P2 with their central cusps inflated. P2 is shorter in length than P3. The P3 has a weakly developed lingual shelf similar to *I. f. nauticus*, much smaller than in *I. f. terrenus*. No buccal shelf present on P3. The anterior cingulum of M1 is small and does not connect to the talon as in *I. f. nauticus*. The StD of M1 is conical but there is no stylar crest between StD and the metastyle. StE is absent on M1 and M2. On M4, the anterior cingulum is large and wide as in *I. f. terrenus*. The StB is small as in *I. f. nauticus*. The metacone is small as in *I. f. nauticus*.

Accessory cusps on c1 are present in females but absent in males. There is no diastema between p1 and p2 as in *I. f. terrenus*. The p2 is subequal in length to p3 as in *I. f. terrenus*. An anterior cusp is absent on the p3 as in *I. f. nauticus*. A cusp is present on m1-3 within the hypoflexid similar to *I. f. terrenus*. The posthypocristid on m3 is perpendicular to the tooth row as in *I. f. nauticus*. The hypoconulid of m3 is small as in *I. f. nauticus*. The hypoconulid of m4 is absent as in *I. f. nauticus*.

Remarks. Previously part of *I. o. nauticus*.

Distribution. St Francis Island, South Australia.

Isoodon fusciventer terrenus new subsp.

Figure 18

urn:lsid:zoobank.org:act:3DD0F410-B8FE-46FA-8DF4-8744BC4C0335

Holotype. SAMA M25880, adult male, skin and skull.

Type locality. 10.8km West South West of Mount Barker, South Australia, Australia.

Paratype. SAMA M8640, adult female, skin and skull, from Carey's Gully, South Australia.

Etymology. From Latin meaning earthly, in reference that it is on the mainland instead of an island.

Subspecies diagnosis. *Isoodon fusciventer terrenus* differs from all other subspecies in having a large anterior cusp on p3. *Isoodon f. terrenus* differs from *I. f. halae*, *I. f. dawensis*, *I. f. nauticus* and *I. f. insulanus* in being larger, with longer feet, having larger expansion of the submassesteric crest. *Isoodon f. terrenus* differs from *I. f. nauticus* and *I. f. insulanus* in having P2 and P3 subequal in length, large anterior cingulum connected to talon on M1, large StB on M4. *Isoodon f. terrenus* differs from *I. f. halae*, *I. f. nauticus* and *I. f. insulanus* in having a large StE on M1 and M2, a well-developed shelf on P3. *Isoodon f. terrenus* differs from *I. f. fusciventer*, *I. f. halae*, *I. f. dawensis* and *I. f. nauticus* in having no diastema between p1 and p2, p2 subequal in length to p3. *Isoodon f. terrenus* differs from *I. f. dawensis*, *I. f. nauticus* and *I. f. insulanus* in having the supraoccipital taller than it is wide, small sagittal crest present in some males. *Isoodon f. terrenus* differs from *I. f. fusciventer* and *I. f. dawensis* in having a canine-like I5, postprotocrista of M4 ends anterior to the most posteri-

or end of the postparacrista, cristid obliqua terminates buccal to protocone on m1. *Isoodon f. terrenus* differs from *I. f. fusciventer* and *I. f. halae* in having StC/D on M4 absent. *Isoodon f. terrenus* differs from *I. f. fusciventer*, *I. f. nauticus* and *I. f. insulanus* in having a well-developed lingual shelf that does not extend to the buccal side on P3. *Isoodon f. terrenus* differs from *I. f. fusciventer*, *I. f. halae* and *I. f. dawensis* in having a preparacrista buccally orientated on M1, small StA on M1, StE absent on M3, nasals terminate well anterior to the orbit, p1 is as long as p2 or p3, small entoconid on m4. *Isoodon f. terrenus* differs from *I. f. halae* and *I. f. dawensis* in having P1 as long as P2, posthypocristid is perpendicular to the tooth row on m3. *Isoodon f. terrenus* differs from *I. f. fusciventer*, *I. f. nauticus* and *I. f. insulanus* in having a large hypoconulid on m3. *Isoodon f. terrenus* differs from *I. f. fusciventer* in having a stylar crest present and connected to StD on M1, paraconid is anterolabial to metaconid on m1. *Isoodon f. terrenus* differs from *I. f. dawensis* in having a pair of accessory fenestrae present, small anterior cingulum on M2, postparacrista of M4 curves as a small centrocrista, cristid obliqua terminates lingual to the protocone about midpoint to the tooth width on m4, hypoconulid small or absent on m4, lateral walls of presphenoid/basisphenoid suture are present. *Isoodon f. terrenus* differs from *I. f. nauticus* in having a large anterior cingulum on M4, median buccal cusp present in the hypoflexid of m1-3. *Isoodon f. terrenus* differs from *I. f. insulanus* in having a stylar crest present on M2. *Isoodon f. terrenus* differs from *I. f. halae* in having the posthypocristid of m4 oblique to the tooth row.

Description. The fur on the dorsal side of the skin is golden brown in colour, grizzled with black. The ventral fur is cream in colour. Tail is short about a third of the body in length and is dark brown above and cream below. Ears are rounded with dark brown on the outside, and golden and dark brown on the inside. Forefeet and hind feet are grey-brown on the dorsal side and golden-cream on the ventral side.

In dorsal view, the holotype lacks a sagittal crest, but instead has two crests converging at the back of the cranium. Sagittal crests are rare in this subspecies, with most specimens having the same morphology as the holotype, minus the small foramen that seems to be an unusual trait in the holotype. The snout length (tip of snout to orbit) is equidistant to the cranium length (orbit to back of skull). In lateral view, the infraorbital canal is shorter than half the molar row. The bullae are large but end level with the molar row (they extend below the molar row in *I. f. nauticus*). In ventral view, accessory fenestrae are present and large. The maxillopalatine fenestrae are large, extending from the P3 to the M2, with a thin dividing septum. Four small palatal fenestrae are present. The bullae are more elongated in males compared to females. The paraoccipital process is tall, extending well above the petrosal. The supraoccipital is taller than it is wide. In the dentary, the posterior mental foramen is below the anterior root of m1 (below the

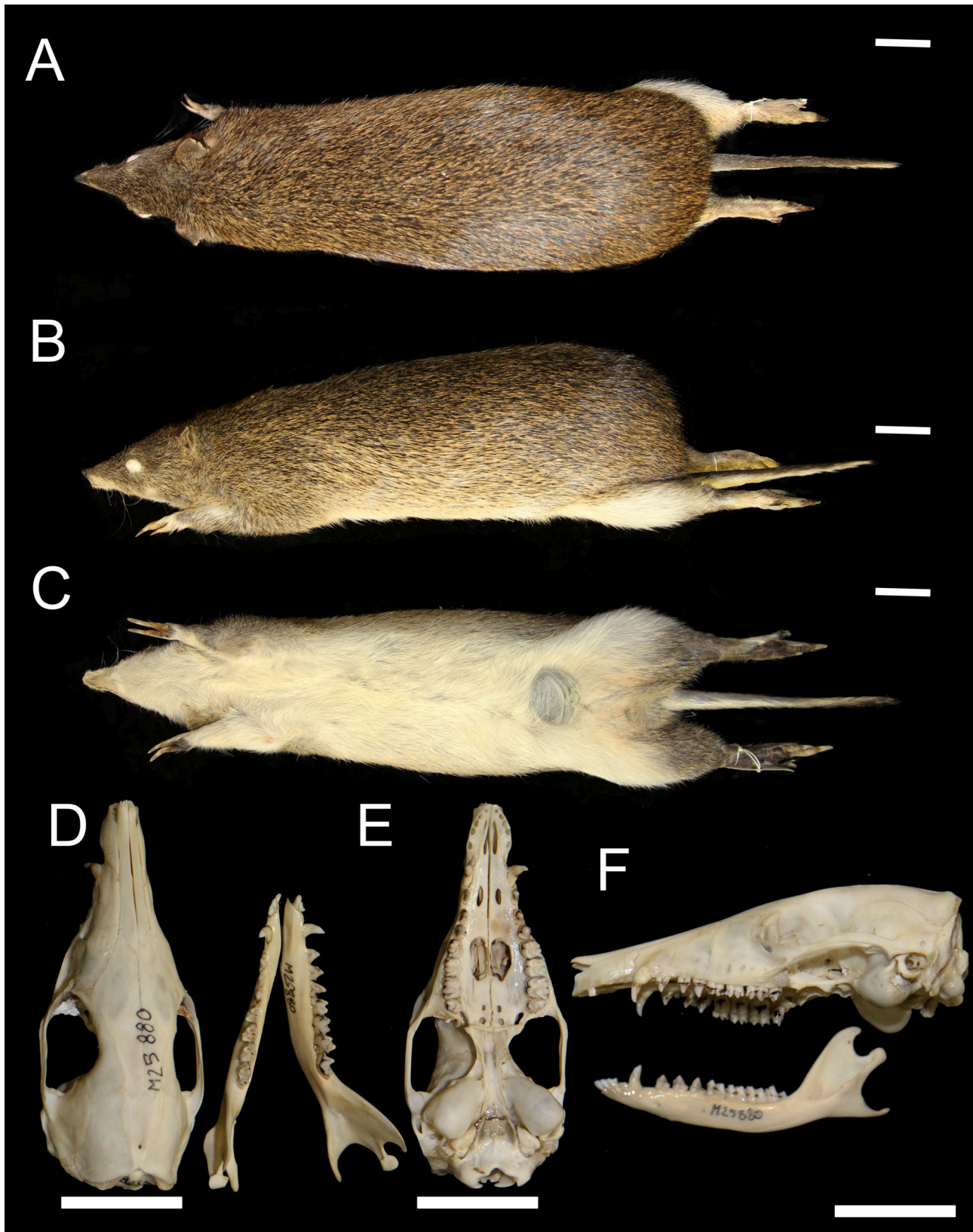


Figure 18. Holotype of *Isoodon fusciventer terranus* new subsp., SAMA M25880. Study skin in dorsal (A), lateral (B) and ventral views (C). Skull and dentary in dorsal (D), ventral (E) and lateral views (F). Scale bar = 3cm (skin); 2cm (skull).

posterior root of m1 in *I. f. nauticus*). The submasseteric crest is moderately to deeply expanded.

Accessory cusps on C1 are absent. P1 is as long as P2 with their central cusps inflated. P2 is subequal in length

to P3 (P2 is longer than P3 in *I. f. nauticus*). The P3 has a well-developed lingual shelf compared to *I. f. nauticus*. A buccal shelf is present on P3 (absent in *I. f. nauticus*). The anterior cingulum of M1 is large and connects to the talon (small and not connected to talon in *I. f. nauticus*).

The StD of M1 is conical but it is not connected to the stylar crest as it is in *I. f. nauticus*. StE is large on M1 and M2 (small in *I. f. nauticus*). On M4, the anterior cingulum is large and wide (small and thin in *I. f. nauticus*). The StB is large (small in *I. f. nauticus*). The metacone varies in size from small to large.

Accessory cusps on c1 are present in females but absent in males. There is no diastema between p1 and p2, unlike *I. f. nauticus* which has a short one. The p2 is subequal in length to p3 (p2 is longer than p3 in *I. f. nauticus*). An anterior cusp is present on the p3 (absent in *I. f. nauticus*). A cusp is present on m1-3 within the hypoflexid, which is absent in *I. f. nauticus*. The posthypocristid on m3 is perpendicular to the tooth row in some specimens, and oblique in others. The hypoconulid of m3 is large (small in *I. f. nauticus*). The hypoconulid of m4 is present in some specimens as a small cusp, absent in others.

Remarks. Previously part of *I. obesulus*.

Distribution. Historically, mainland South Australia, from northern side of Murray River to coastal Eyre Peninsula (including York Peninsula, and Flinders Island) but now restricted to Mount Lofty Ranges, Fleurieu Peninsula and Kangaroo Island.

Isoodon macrourus (Gould, 1842)

urn:lsid:zoobank.org:act:F3736692-2239-40E0-B718-74150184B96E

Perameles macrourus Gould, 1842: 41

Common name. Northern Brown Bandicoot

Emended species diagnosis. *Isoodon macrourus* differs from all species of *Isoodon* in being the largest in size. *Isoodon macrourus* differs from all species of *Isoodon* except *I. moresbyensis* in having no accessory fenestrae, I3 the same size as I2 or I4, a large anterior cingulum on M2, enlarged metacone on M4 (except *I. m. capensis*), preentocristid present on m4 (except *I. peninsulae*). *Isoodon macrourus* differs from all species of *Isoodon* except *I. f. fusciventer*, *I. f. halae* and *I. a. marchinbarensis* in having StC/D present on M4. *Isoodon macrourus* differs from all species of *Isoodon* except *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus* in having the postprotocrista on M4 end anterior to the most posterior end of the postparacrista. *Isoodon macrourus* differs from all species of *Isoodon* except *I. peninsulae*, *I. f. fusciventer* and *I. f. terrenus* in having a deep and wide submasseteric crest. *Isoodon macrourus* differs from all species of *Isoodon* except *I. f. fusciventer* in having no stylar crest connected to the metastyle on M1. *Isoodon macrourus* differs from *I. microtis*, *I. obesulus* and *I. peninsulae* in having the alisphenoid tympanic process terminating anterior to the transverse foramen. *Isoodon macrourus* differs from all other species except *I. f. fusciventer*, *I. f. dawensis*, *I. f. halae* and *I. auratus* in having a posterobuccally orientated preparacrista on M1. *Isoodon macrourus* differs from *I. auratus*, *I. obesulus* and *I. peninsulae* in having cristid obliqua of m1 terminating buccal to the

protocone. *Isoodon macrourus* differs from *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus*, *I. microtis*, *I. auratus*, *I. obesulus*, and *I. peninsulae* in having a well-developed lingual shelf on P3 that extends to the buccal side of the tooth. *Isoodon macrourus* differs from *I. microtis* and *I. obesulus* in having the posthypocristid oblique to the tooth row on m1. *Isoodon macrourus* differs from *I. f. fusciventer* and *I. f. dawensis* in having a canine-like I5, St A on M1 is small. *Isoodon macrourus* differs from *I. peninsulae* in having no St E or a remnant on M3. *Isoodon macrourus* differs from *I. microtis* in having small or no palatal fenestrae, larger bullae, the paraconid-metaconid distance shorter than the metaconid-protocristid distance on m1. *Isoodon macrourus* differs from *I. insulanus*, *I. f. nauticus* and *I. f. terrenus* in having a large entoconid on m4.

Isoodon macrourus macrourus (Gould, 1842)

Figure 19

urn:lsid:zoobank.org:act:F3736692-2239-40E0-B718-74150184B96E

Perameles macrourus Gould, 1842: 41

Holotype. NHMUK 1842.5.26.11, adult male, skin and skull

Type locality. Port Essington, Northern Territory

Emended subspecies diagnosis. *Isoodon m. macrourus* differs from all subspecies of *I. macrourus* in having the preentocristid on m4 oblique to the tooth row. *Isoodon m. macrourus* differs from *I. m. torosus* and *I. m. capensis* in having a large shelf between the base of the metacone and the metaconule on M3. *Isoodon m. macrourus* differs from *I. m. torosus* in having P1 as long as P2, the anterior cingulum of M1 not connected to the talon, StB and StC on M1 clearly identifiable as cusps, with StC larger than StB, having a large anterior cingulum on M4. *Isoodon m. macrourus* differs from *I. m. capensis* in having its nasals terminate well anterior to the anterior margin of the orbit, the postprotocrista of M1 ends at the lingual flank of the metastylar tip, a large anterior cingulum on M3, a large metacone on M4 expands the length of the tooth, p2 shorter than p3.

Remarks. No changes to this subspecies.

Distribution. Kimberley (Western Australia) and Top end (Northern Territory), Australia.

Isoodon macrourus torosus (Ramsay, 1877)

Figure 20

urn:lsid:zoobank.org:act:65CCE15C-C739-439D-8964-34E381CEB431

Perameles macroura var. *torosus* Ramsay, 1877: 12

Syntypes. MAMU M471, adult male, skin mount. MAMU M1153, skull, matching tentatively matched to M471 by Parnaby and Gill (2021).

Type locality. Near Cooktown, Queensland, Australia.

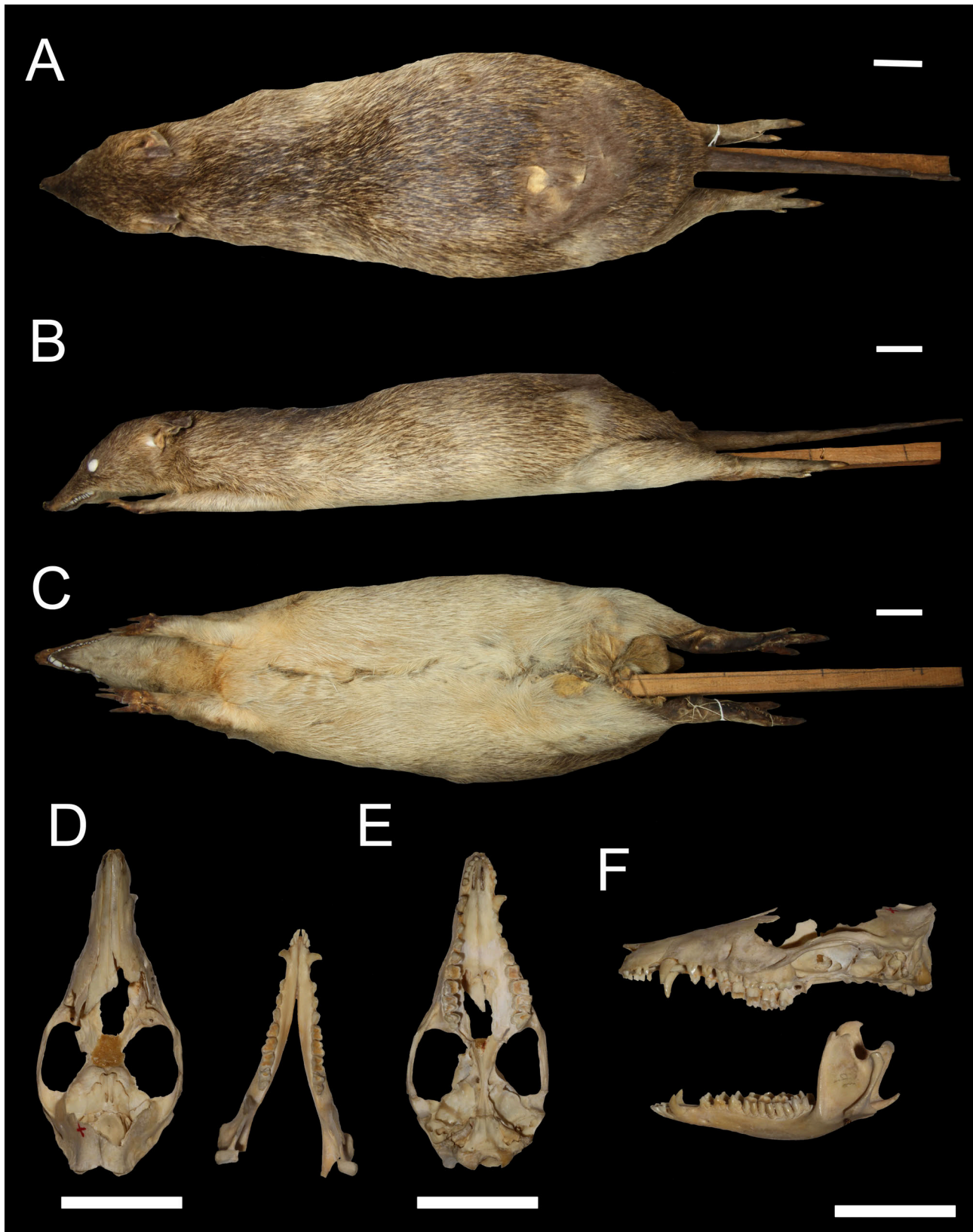


Figure 19. Holotype of *Isoodon macrourus*, NHMUK 1842.5.26.11. Study skin in dorsal (A), lateral (B) and ventral views (C). Skull and dentary in dorsal (D), ventral (E) and lateral views (F). Scale bar = 3cm.

Emended subspecies diagnosis. *Isoodon m. torosus* differs from all subspecies of *Isoodon macrourus* in having P1 longer than P2. *Isoodon m. torosus* differs from *I. m. macrourus* and *I. m. capensis* in having a small anterior cingulum on M4. *Isoodon m. torosus* differs from *I. m.*

macrourus in having a small shelf between the base of the metacone and the metaconule on M3, the preentocristid on m4 anteroposteriorly directed, the anterior cingulum of M1 connected to the talon, StB and StC on M1 undistinguishable as separate cusps. *Isoodon m.*

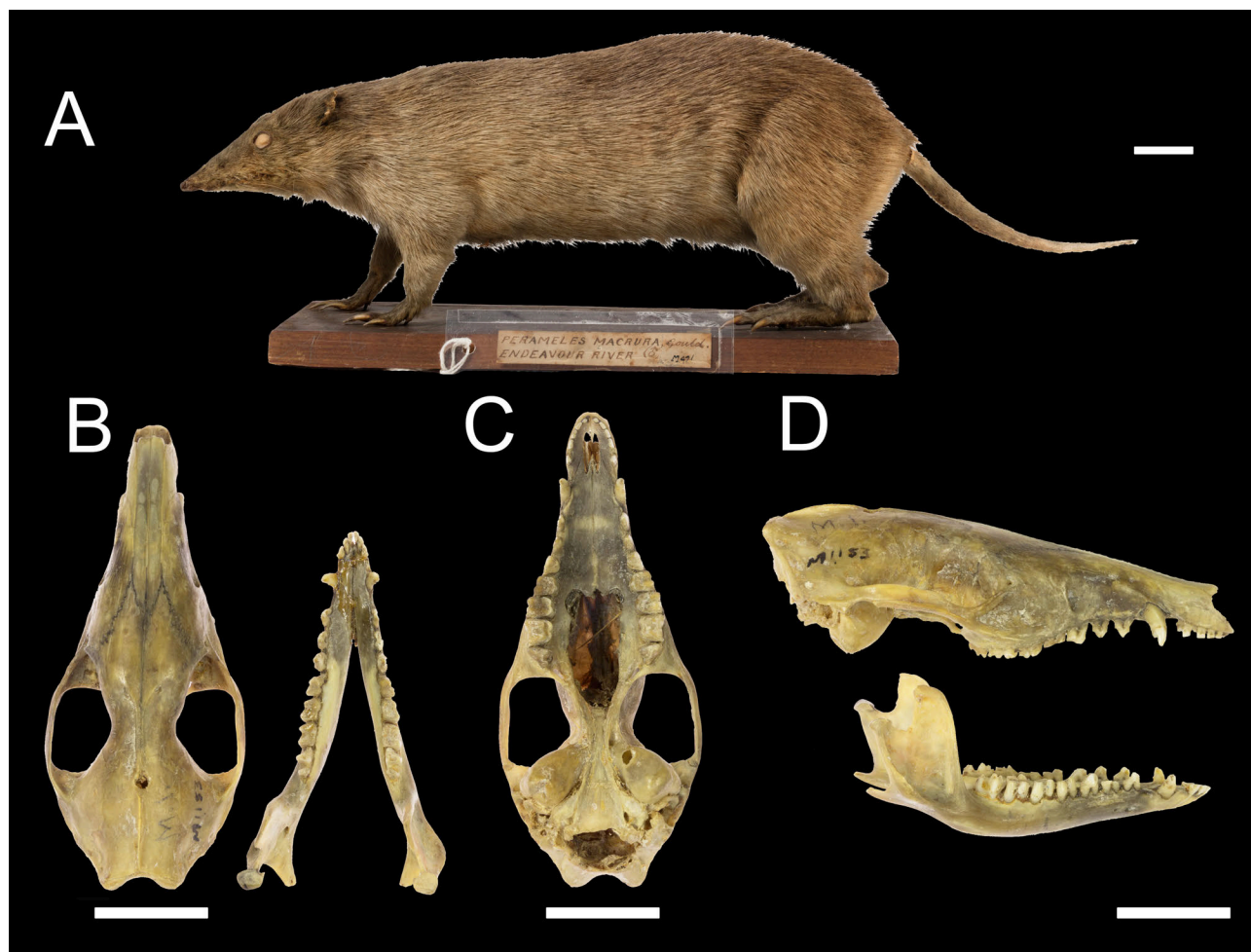


Figure 20. Syntype of *Isoodon macrourus torosus*, MAMU M471 (mounted skin) and MAMU M1153 (skull). Mounted skin in lateral view (A). Skull and dentary in dorsal (B), ventral (C) and lateral views (D). Scale bar = 3cm.

torosus differs from *I. m. capensis* in having its nasals terminate well anterior to the anterior margin of the orbit, the postprotocrista of M1 ends at the lingual flank of the metastylar tip, a large anterior cingulum on M3, a large metacone on M4 expands the length of the tooth, p2 shorter than p3.

Remarks. Parnaby and Gill (2021) identified skull MAMU M1153 as tentatively matched M471, considering it a syntype.

Distribution. East coast of Australia, from Sydney to Cooktown (south of Endeavour River).

Isoodon macrourus capensis new subsp.

Figure 21

urn:lsid:zoobank.org:act:9F5058F0-BAEE-44A5-B28F-69CF1C9E0993

Holotype. ANWC CM794, adult male, skin and skull.

Type locality. Iron Range, Cape York Peninsula, Queensland, Australia.

Paratype. QM JM14109, adult female, skull.

Etymology. Named after the type locality.

Diagnosis. *Isoodon m. capensis* differs from all other subspecies of *I. macrourus* in having a thin anterior cingulum on M3, the metacone on M4 is small, p2 longer than p3. *Isoodon m. capensis* differs from *I. m. macrourus* and *I. m. torosus* in having its nasals terminate just anterior to the anterior margin of the orbit, the postprotocrista of M1 ends posteriorly to the midpoint of the postmetacrista. *Isoodon m. capensis* differs from *I. m. macrourus* in having a small shelf between the base of the metacone and the metaconule on M3, the preentocristid on m4 anteroposteriorly directed. *Isoodon m. capensis* differs from *Isoodon m. torosus* in having P1 as long as P2, a large anterior cingulum on M4.

Description. The fur on the dorsal side of the skin is a mixture of dark brown, light brown, golden brown and black. The ventral fur is white. The tail is dark brown above and white below. Ears are dark brown on the outside, but as the ears are shrivelled, it is not possible to know what the inside colour is. Forefeet and hind feet are white on both sides. The overall size of the subspecies is the same as *I. m. macrourus* and *I. m. torosus*.

There is no difference in size of the skull compared to *I. m. macrourus* and *I. m. torosus*. In dorsal view, a sagittal crest is present in all males and some of the large-

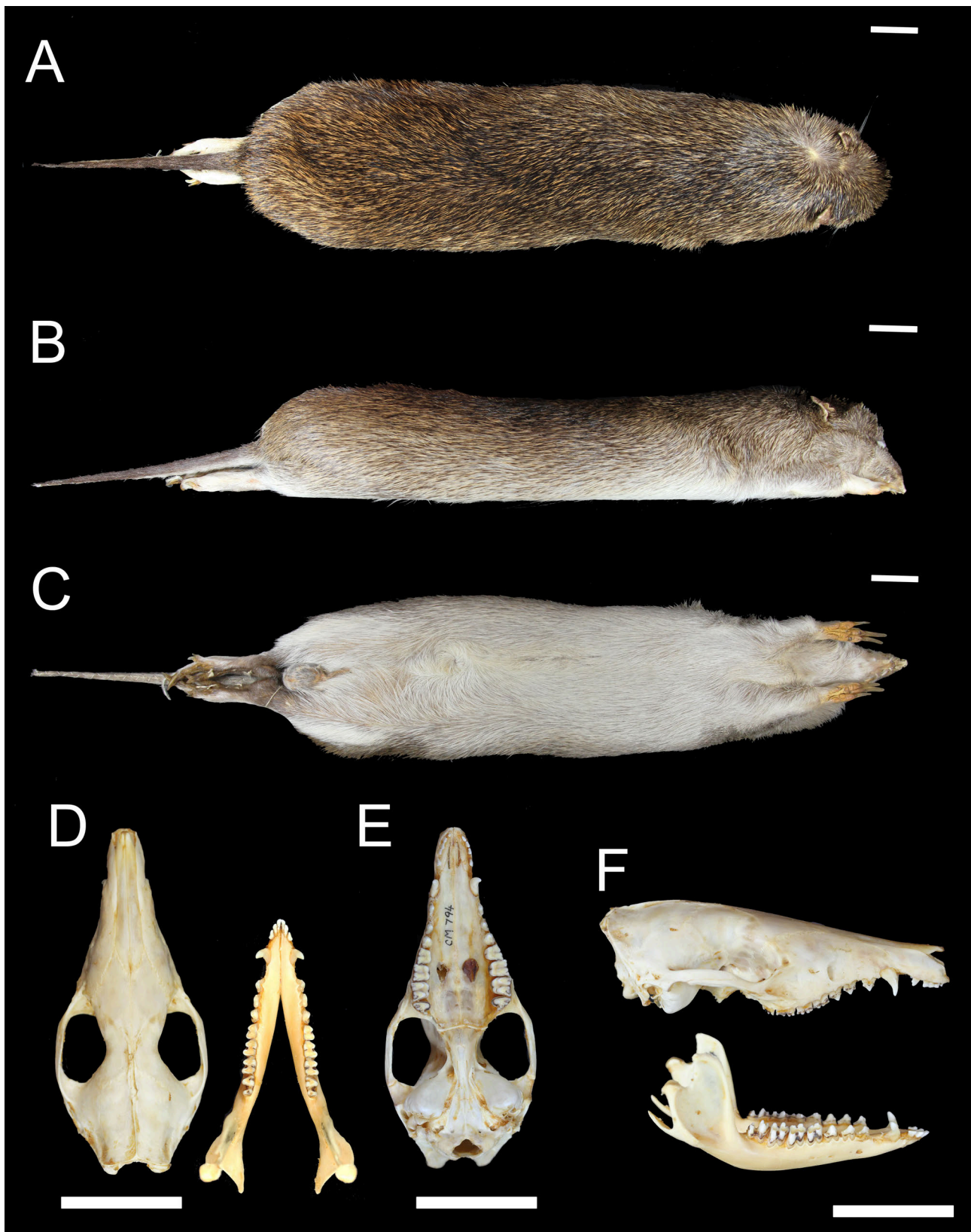


Figure 21. Holotype of *Isoodon macrourus capensis* new subsp., ANWC CM794. Study skin in dorsal (A), lateral (B) and ventral views (C). Skull and dentary in dorsal (D), ventral (E) and lateral views (F). Scale bar = 3cm.

er females may have a short one. The snout length (tip of snout to orbit) is slightly shorter than the cranium length (orbit to back of skull). The posterior end of the nasals terminates just anterior to the orbit, but terminate much more anteriorly in *I. m. macrourus* and *I.*

m. torosus. In lateral view, the infraorbital canal is long (longer than half the molar row). The bullae are large and of similar size to other subspecies of *I. macrourus*. In ventral view, accessory fenestrae are absent, as in all other subspecies of *I. macrourus*. The septa dividing the

maxillopalatine fenestrae is very thick (this can vary in thickness in *I. m. macrourus* and *I. m. torosus*). The maxillopalatine fenestrae are small, usually the level with the anterior and posterior ends of M2, but in some specimens extends a little anteriorly or posteriorly. In no cases does any specimen have the fenestrae as large as in other subspecies, which usually run from the anterior of M1 to the posterior of M2. The presence of palatal fenestrae is variable, from none to 4 small ones. The lateral walls of presphenoid/basisphenoid suture are present. The supraoccipital is as tall as it is wide. In the dentary, there are 3 mental foramina, one under the p1, one under the p3 and one under m1. These can vary in number and position between specimen as in all other subspecies of *I. macrourus*. The submasseteric crest is deep and wide.

The I5 is pointed and strongly canine as in other subspecies of *I. macrourus* but there is a diastema between the I4 and I5, which is not always present in other subspecies. Accessory cusps on C1 are absent. P1 is as long as P2, as in other subspecies except *I. m. torosus*. P2 is shorter than P3 as in other subspecies. The P3 has a well-developed lingual shelf that extends to the buccal side as in all other *I. macrourus*. On the M1, the postprotocrista ends posteriorly to the midpoint of the postmetacrista, unlike other subspecies which ends below the metastyle. On the M3, the anterior cingulum and posterior cingulum are smaller than in other subspecies. The shelf between the metacone and metaconule is small like in *I. m. torosus* (large in other subspecies). On M4, the anterior cingulum is large as in *I. m. macrourus* (small in other subspecies). The postparacrista is curved as in other subspecies. The metacone is small unlike other subspecies.

Accessory cusps on c1 are usually absent in males and present in females as in other subspecies. The p1 is shorter than p2 or p3, as in other subspecies. The p2 is longer than p3 unlike other subspecies. An anterior cusp is present on the p3 as in other subspecies. On the m3, the hypoconid is buccal to the protoconid as in other subspecies. On the m4, the preentocristid is anteroposteriorly directed, as in other subspecies except *I. m. macrourus*.

Remarks. Previously part of *I. m. torosus*.

Distribution. Cape York, north of Endeavour River.

Isoodon microtis new sp.

Figure 22

urn:lsid:zoobank.org:act:F1944572-4EDF-4761-BF77-D466339A7EE1

Holotype. SAMA M1981, adult. sex unknown (probably female due to smaller canines), skull only.

Type locality. Unknown, probably Eyre Peninsula, South Australia (see remarks).

Paratype. MV C33107, sex unknown (probably male due to larger canine), skull; MV ex C33107, sex unknown (probably

female), skull. SAMA SF347, two left adult dentaries with p1-3 (probably female), left subadult maxilla with C1, P1-2, M1-2 (probably male due to larger teeth), right adult maxilla fragment with M2 (probably male).

Etymology. *Microtis*, which is a noun, meaning small ear in Greek, in reference to the small inner ear bones (alisphenoid tympanic process) in the skull.

Species diagnosis. *Isoodon microtis* differs from all species of *Isoodon* in being the smallest in overall size and having very large posterior palatal fenestrae, much smaller bullae, no anterior cingulum on M2, paraconid-metaconid distance equidistant to metaconid-protocoid distance on m1. *Isoodon microtis* differs from all species of *Isoodon* except *I. obesulus* in having the posthypocristid perpendicular to the tooth row on m1. *Isoodon microtis* differs from *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus*, *I. macrourus* and *I. moresbyensis* in having the postprotocrista of M4 end level with the most posterior end of the postparacrista. *Isoodon microtis* differs from *I. macrourus*, *I. moresbyensis*, *I. peninsulae*, *I. f. fusciventer* and *I. f. terrenus* in having a moderately expanded submasseteric crest. *Isoodon microtis* differs from *I. auratus*, *I. obesulus*, *I. peninsulae*, *I. macrourus* and *I. f. fusciventer* in having a small lingual shelf on P3. *Isoodon microtis* differs from *I. auratus*, *I. obesulus* and *I. peninsulae* in having cristid obliqua of m1 terminating buccal to the protocone. *Isoodon microtis* differs from *I. auratus*, *I. fusciventer*, *I. macrourus* and *I. moresbyensis* in having the alisphenoid tympanic process terminating at the transverse foramen. *Isoodon microtis* differs from *I. auratus*, *I. f. fusciventer*, *I. f. halae*, *I. f. dawensis* and *I. macrourus* in having a buccally orientated preparacrista on M1. *Isoodon microtis* differs from *I. macrourus* and *I. f. fusciventer* in having a styler crest connected to the metastyle on M1. *Isoodon microtis* differs from *I. f. fusciventer* and *I. f. dawensis* in having a canine-like I5, anterior cingulum of M1 not connected to talon, St A on M1 is small. *Isoodon microtis* differs from *I. macrourus* and *I. moresbyensis* in having a pair of accessory fenestrae, I3 larger than I2 or I4, small metacone on M4, StC/D absent on M4, preentocristid absent on m4. *Isoodon microtis* differs from *I. peninsulae* in having no St E on M3. *Isoodon microtis* differs from *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus* in having a large entoconid on m4.

Description. There are no skins associated with any of the specimens. The skull is small compared to other species of *Isoodon*, as small as the smaller subspecies of *I. auratus*. In dorsal view, the distance between the tip of the snout and the orbit is equal to that of the orbit to foramen magnum. There is no sagittal crest present. In lateral view, the infraorbital canal is short, shorter than half the molar row. The bullae are extremely small for a species of *Isoodon*, similar sized to the larger species of *Perameles*, but not rounded in shape (in ventral view), ovoid as in all *Isoodon*. In ventral view, the incisive fenestrae are small, but the accessory fenestrae are large like in *I. auratus* and *I. peninsulae*. The maxillopalatine fenestrae are large but similar sized than in

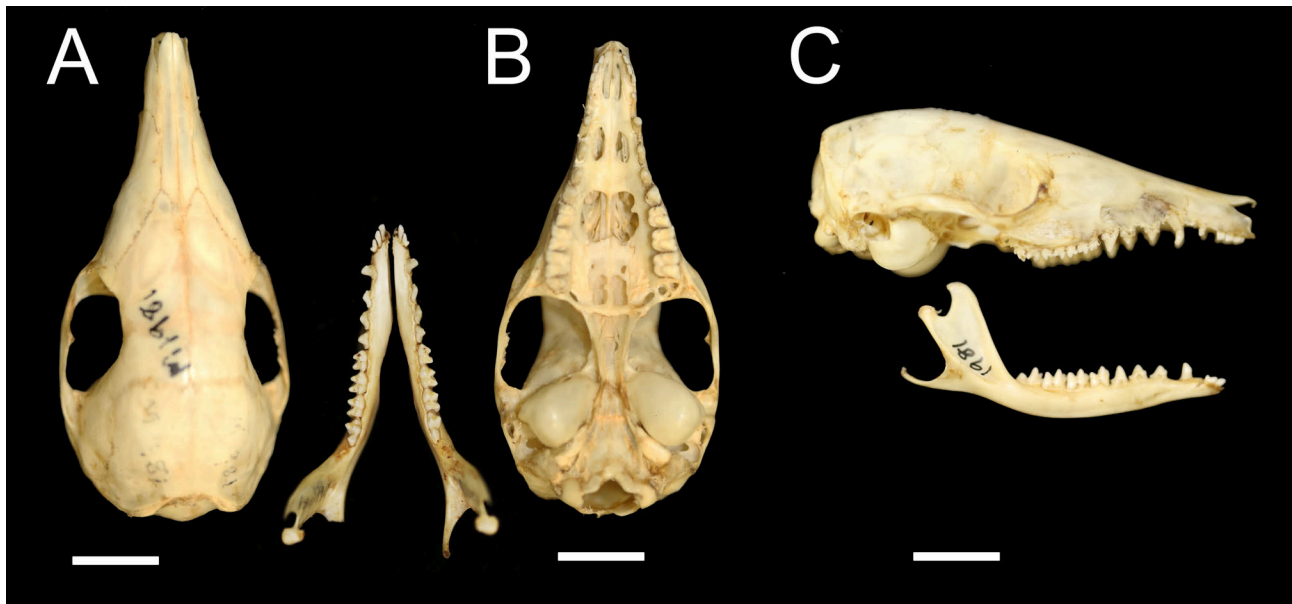


Figure 22. Holotype of *Isoodon microtis* new sp., SAMA M1981. Skull and dentary in dorsal (A), ventral (B) and lateral views (C). Scale bar = 1 cm.

I. auratus. The septa dividing the maxillopalatine fenestrae is broken but its anterior and posterior ends suggest it was very thin. There are 4 palatal fenestrae, two small anterior fenestrae and two large fenestrae, larger than in any other species of *Isoodon* (second largest in size is *Isoodon fusciventer nauticus*). Lateral walls are present bordering the lateral sides of the presphenoid-basisphenoid suture.

No accessory cusp on C1 is present. P1 is shorter than P2. The central cusp of P1 and P2 is inflated. P2 is shorter in length to P3. A small lingual shelf is present on the P3. The M1 has a small anterior cingulum which does not connect to the talon. StA is small. StB and StC are fused as a single cusp. The preparacrista is buccally orientated then change to a posterobuccal direction before connecting to StB. On the M2, there are no anterior cingulum present. StB is conical in shape and has no crest connection. On the M3, a small anterior cingulum is present and connected to talon. The posterior cingulum is narrow. The postprotocrista ends posteriorly to the midpoint of the postmetacrista. On M4, a small anterior cingulum is present and connected to the talon, StB is large. The postprotocrista ends posterior to the most posterior end of the postparacrista. StC/D is absent.

Accessory cusps on c1 are present in some specimens. The p1 is shorter than p2 or p3, with a short diastema between p1 and p2. The p2 is longer than p3. An anterior cusp is absent on the p3. There is no cusp within the hypoflexid of m1-3. The paraconid of the m1 is anterolabial to the metaconid. The paracristid connects the paraconid to the protoconid. The posthypocristid of m1-3 is perpendicular to the tooth row. On the m3, cristid obliqua terminates lingual to the midpoint of the tooth width on m3. The posthypocristid of m3 connects

to the hypoconulid, which is large in size. The cristid obliqua of m4 terminates lingual to the protocone, about midpoint to the tooth width. The posthypocristid of m4 is oblique to the tooth row. The entoconid is large.

Common name. Little Brown Bandicoot.

Remarks. The holotype is a skull donated by Mrs Symonds Clark in October 1920, after her husband had passed away on the 10th July 1920. Her husband was an aviculturist and ornithologist, but he sometimes collected mammal skulls, which he then donated to the South Australian Museum (Sutton, 1929). The holotype was collected by him, most likely between 1876 (the year he last donated specimens to the South Australian Museum, recorded in the museum database) and 1914 (the last entry in his diary, stored at the State Library of South Australia), somewhere in South Australia. None of the bandicoot specimens mentioned in his diary can be matched with certainty to the holotype. Between 1876 and 1914, the only trip he did outside of Adelaide was to Eyre Peninsula, which is also where the paratype SAMA SF347 came from. This is the most likely place where he could have acquired the holotype.

Both paratype MV C33107 and MV ex C33107 were exchanged from the South Australian Museum to Museum Victoria, with no data other than it was from Mr Waterhouse. Mr Frederick George Waterhouse was the first curator of the South Australian Museum in October 1861, which later opened in January 1862. He resigned in February 1882. These two skulls must have been collected and exchanged during that 20-year period (1862-1882). We searched the South Australian Museum archives and found in the Waterhouse reports one mention of two bandicoots being sent to Museum Victoria between November 1866 and January 1867, along with other specimens. This narrows down the period of col-

lection from 1862 to 1866. During that period, Waterhouse went on one major expedition, John McDouall Stuart's sixth expedition, which took him from Adelaide to Chambers Bay in the Northern Territory, via Gawler, Moolooloo, Chambers Creek, Newcastle Waters and Daly Waters (Kraehenbuehl, 1976). A species with small bullae is unlikely to have come from central Australia, as animals in the arid zone tend to have large bullae. As a result, it is unlikely that the two skulls were collected during this trip. Between this expedition and 1866, there are no records of Waterhouse collecting specimens. Instead, Waterhouse was receiving specimens donated to the museum. There are only 5 records of bandicoots being donated in the catalogue: on the 11th July 1864, Mr L. Clark donated a stuffed bandicoot; on the 10th January 1865, Dr Goldsmith donated 2 young bandicoots; on the 10th April 1865, Mr William Spencer donated a skin of a bandicoot from King George's Sound; on the 12th March 1866, Mr Withers donated two mounted bandicoots; and on the 8th June, Mr Andrews two skins of bandicoots. It is therefore impossible to narrow down the locality for these two specimens when localities haven't always been recorded.

In order to identify a locality for this new species, subfossil material in the collection of the South Australian Museum was examined. Of all the specimens registered in the collection, only one match the morphology of holotype, SAMA SF347. This specimen is a set of 3 dentaries and 2 maxillae, representing at least 3 individuals (based on dental wear), collected at South Block Site (near Edillilie, approximately 8km east of Coult, South Australia) on Eyre Peninsula, in an area that has not been cleared for agriculture. These specimens provide a locality for the species that the holotype and other paratypes can't provide.

Distribution. Eyre peninsula.

Isoodon moresbyensis (Ramsay, 1877) new stat.

Figure 23

urn:lsid:zoobank.org:act:1125C5C0-BB74-487D-ADE2-61CC18863572

Perameles moresbyensis Ramsay, 1877: 14

Syntype. AMS M2554, adult male, skin mount and skull.

Type locality. Port Moresby, Papua New Guinea.

Emended species diagnosis. *Isoodon moresbyensis* differs from all species of *Isoodon* except *I. macrourus* in having no accessory fenestrae, I3 the same size as I2 or I4, a large anterior cingulum on M2, enlarged metacone on M4 (except *I. m. capensis*), preentocristid present on m4 (except *I. peninsulae*). *Isoodon moresbyensis* differs from all species of *Isoodon* except *I. f. fusciventer*, *I. f. halae*, *I. macrourus* and *I. a. marchinbarensis* in having StC/D present on M4. *Isoodon moresbyensis* differs from all species of *Isoodon* except *I. f. insulanus*, *I. f. nauticus*

and *I. f. terrenus* and *I. macrourus* in having the postprotocrista on M4 end anterior to the most posterior end of the postparacrista. *Isoodon moresbyensis* differs from all species of *Isoodon* except *I. peninsulae*, *I. f. fusciventer*, *I. macrourus* and *I. f. terrenus* in having a deep and wide submasseteric crest. *Isoodon moresbyensis* differs from *I. microtis*, *I. obesulus* and *I. peninsulae* in having the alisphenoid tympanic process terminating anterior to the transverse foramen. *Isoodon moresbyensis* differs from *I. f. fusciventer* and *I. f. dawensis* in having a canine-like I5. *Isoodon moresbyensis* differs from *I. peninsulae* in having no St E or a remnant on M3. *Isoodon moresbyensis* differs from *I. microtis* in having small or no palatal fenestrae and larger bullae. *Isoodon moresbyensis* differs from *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus* in having a large entoconid on m4. *Isoodon moresbyensis* differs from *I. macrourus* in being smaller in size overall, having P2 subequal in length to P3, the lingual shelf of P3 not extending to the buccal side, buccal shelf on P3 is absent, postparacrista of M4 is straight, hypoconid of m3 is directly posterior to the protoconid.

Common name. New Guinea Brown Bandicoot.

Remarks. Parnaby and Gill (2021) identified additional possible syntypes, but the original description only mentions one animal in the description, suggesting only one syntype was used (Ramsay, 1877).

Distribution. Southern parts of Papua New Guinea.

Isoodon obesulus (Shaw, 1797)

urn:lsid:zoobank.org:act:3064B194-4268-4350-AEBA-A3369BC21B24

Didelphis Obesula Shaw, 1797: Text to Plate 298.

Common name. Southern Brown Bandicoot

Emended species diagnosis. *Isoodon obesulus* differs from *I. microtis*, *I. peninsulae* and *I. macrourus* in having a small anterior cingulum on M2 connected to the talon. *Isoodon obesulus* differs from all species of *Isoodon* except *I. microtis* in having the posthypocristid perpendicular to the tooth row on m1. *Isoodon obesulus* differs from *I. macrourus*, *I. moresbyensis*, *I. peninsulae*, *I. f. fusciventer* and *I. f. terrenus* in having a moderately expanded submasseteric crest. *Isoodon obesulus* differs from *I. microtis*, *I. macrourus*, *I. f. insulanus*, *I. f. nauticus* and *I. f. fusciventer* in having a well-developed lingual shelf on P3, not extending to the buccal side. *Isoodon obesulus* differs from *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus*, *I. macrourus* and *I. moresbyensis* in having the postprotocrista of M4 end level with the most posterior end of the postparacrista. *Isoodon obesulus* differs from *I. microtis*, *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus* and *I. macrourus* in having cristid obliqua of m1 terminating lingual to the protocone. *Isoodon obesulus* differs from *I. auratus*, *I. fusciventer*, *I. macrourus* and *I. moresbyensis* in having the alisphenoid tympanic process terminating at the transverse foramen. *Isoodon obesulus* differs from *I. auratus*, *I. f. fusciventer*, *I. f. halae*, *I. f. dawensis* and *I.*

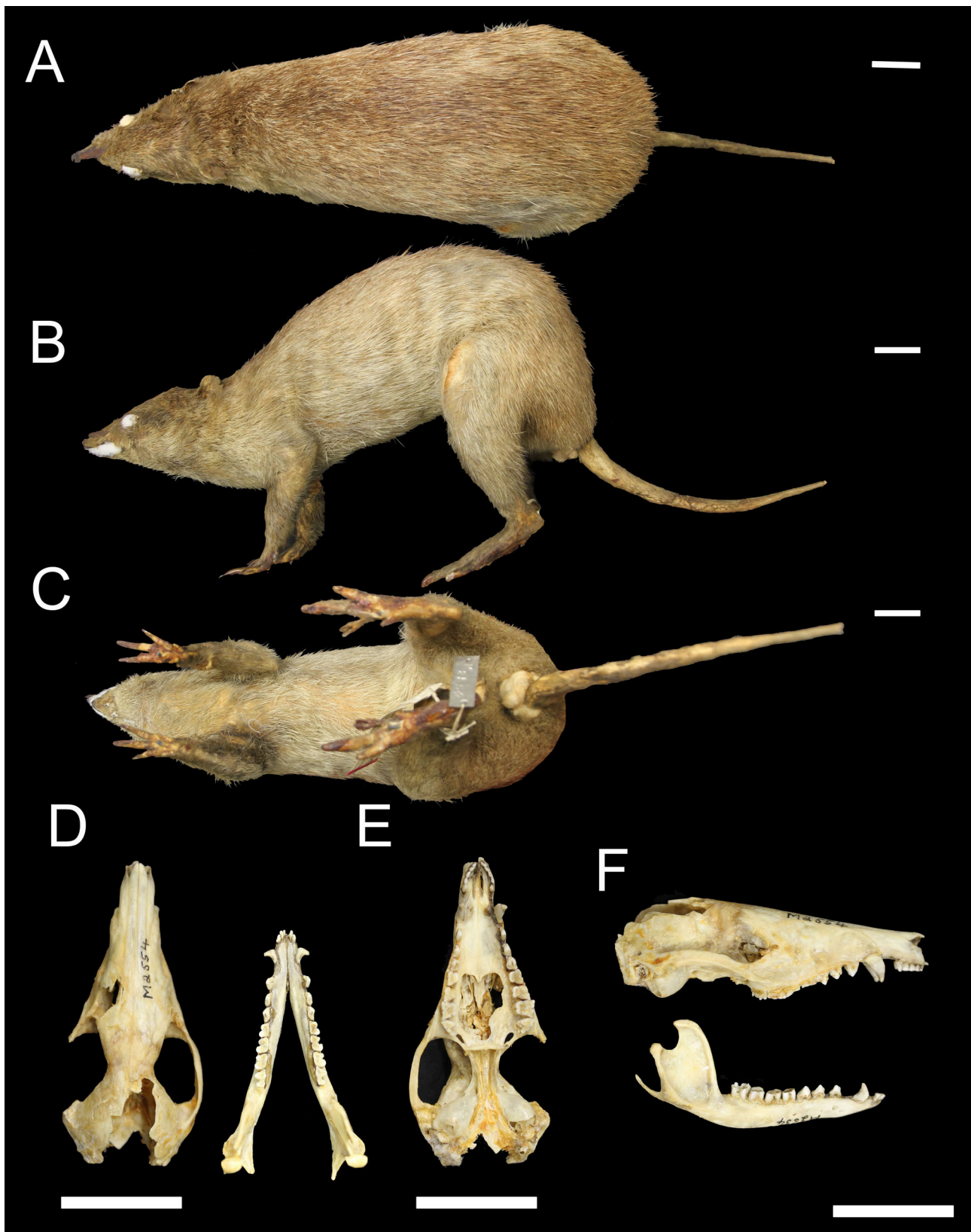


Figure 23. Syntype of *Isoodon moresbyensis*, AMS M2554. Mounted skin in dorsal (A), lateral (B) and ventral views (C). Skull and dentary in dorsal (D), ventral (E) and lateral views (F). Scale bar = 3cm.

macrourus in having a buccally orientated preparacrista on M1. *Isoodon obesulus* differs from *I. macrourus* and *I. f. fusciventer* in having a styler crest connected to the metastyle on M1. *Isoodon obesulus* differs from *I. f. fusciventer* and *I. f. dawsoni* in having a canine-like I5, ante-

rior cingulum of M1 not connected to talon, StA on M1 is small (except *I. o. affinis*). *Isoodon obesulus* differs from *I. macrourus* in being smaller in size. *Isoodon obesulus* differs from *I. macrourus* and *I. moresbyensis* in having a pair of accessory fenestrae, I3 larger than I2 or I4, small

metacone on M4 (except in some *I. o. obesulus*), StC/D absent on M4, preentocristid absent on m4. *Isoodon obesulus* differs from *I. peninsulae* in having no StE on M3. *Isoodon obesulus* differs from *I. microtis* in having small posterior palatal fenestrae, larger bullae, the paraconid-metaconid distance shorter than the metaconid-protocristid distance on m1. *Isoodon obesulus* differs from *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus* in having a large entoconid on m4.

Isoodon obesulus affinis (Waterhouse, 1846)

Figure 24

urn:lsid:zoobank.org:act:16045CDB-7500-4630-AEE6-8177D0C31E24

Perameles affinis Waterhouse, 1846: 373.

Holotype. NHMUK 1841.1173, juvenile, sex unknown, skin and skull.

Type locality. Kangaroo Point, near Hobart, Tasmania.

Emended subspecies diagnosis. *Isoodon obesulus affinis* differs from *I. o. obesulus* in having a long infraorbital canal (longer than half the molar row), StA on M1 is large, StB and StC are fused on M1, but not clearly identifiable as separate cusps, StB on M2 is oval with a stylar crest running through it, p1 shorter than either p2 or p3, the hypoconulid on m3 is large.

Remarks. It forms a monophyletic group in nuclear and mitochondrial trees, though is paraphyletic within *I. obesulus*.

Distribution. Tasmania.

Isoodon obesulus obesulus (Shaw, 1797)

Figure 25

urn:lsid:zoobank.org:act:3064B194-4268-4350-AEBA-A3369BC21B24

Didelphis Obesula Shaw, 1797: Text to Plate 298.

Neotype. AMS M1182, adult male, skin and skull, body in spirit.

Type locality. Ku-ring-gai Chase National Park, New South Wales.

Emended subspecies diagnosis. *Isoodon obesulus obesulus* differs from *I. o. affinis* in having a short infraorbital canal (shorter or equal to half the molar row), StA on M1 is small, StB and StC are fused on M1, but are clearly identifiable as separate cusps, StB on M2 is conical with no stylar crest connection, p1 as long as p2 or p3, the hypoconulid on m3 is small.

Remarks. Previously included population from Adelaide Hills and Kangaroo Island.

Distribution. Southeastern Australia, from Sydney to Victoria, and southern part of South Australia, on the south-eastern side of the Murray River.

Isoodon peninsulae Thomas, 1922

Figure 26

urn:lsid:zoobank.org:act:D92D1872-77F9-4DD8-8A1B-6A5C7CD79CAF

Isoodon peninsulae Thomas, 1922: 679.

Common name. Cape York Brown Bandicoot

Holotype. NHMUK 1915.3.5.71, adult male, skin and skull

Type locality. Utingu, Cape York, Queensland.

Emended species diagnosis. *Isoodon peninsulae* differs from all species of *Isoodon* except *I. auratus* in having a small anterior cingulum on M2 not connected to the talon. *Isoodon peninsulae* differs from all species of *Isoodon* except *I. f. fusciventer*, *I. f. halae*, *I. f. dawensis* in having a large StE on M3. *Isoodon peninsulae* differs from *I. microtis*, *I. macrourus*, *I. f. insulanus*, *I. f. nauticus* and *I. f. fusciventer* in having a well-developed lingual shelf on P3, not extending to the buccal side. *Isoodon peninsulae* differs from all species of *Isoodon* except *I. macrourus*, *I. moresbyensis*, *I. f. fusciventer* and *I. f. terrenus* in having a deep and wide submasseteric crest. *Isoodon peninsulae* differs from *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus*, *I. macrourus* and *I. moresbyensis* in having the postprotocrista of M4 end level with the most posterior end of the postparacrista. *Isoodon peninsulae* differs from *I. microtis*, *I. f. insulanus*, *I. f. nauticus*, *I. f. terrenus* and *I. macrourus* in having cristid obliqua of m1 terminating lingual to the protocone. *Isoodon peninsulae* differs from *I. auratus*, *I. f. fusciventer*, *I. macrourus* and *I. moresbyensis* in having the alisphenoid tympanic process terminating at the transverse foramen. *Isoodon peninsulae* differs from *I. auratus*, *I. f. fusciventer*, *I. f. halae*, *I. f. dawensis* and *I. macrourus* in having a buccally orientated preparacrista on M1. *Isoodon peninsulae* differs from *I. macrourus* and *I. f. fusciventer* in having a stylar crest connected to the metastyle on M1. *Isoodon peninsulae* differs from *I. microtis* and *I. obesulus* in having the posthypocristid oblique to the tooth row on m1. *Isoodon peninsulae* differs from *I. f. fusciventer* and *I. f. dawensis* in having a canine-like I5, anterior cingulum of M1 not connected to talon, StA on M1 is small. *Isoodon peninsulae* differs from *I. macrourus* and *I. moresbyensis* in being smaller in size and having a pair of accessory fenestrae, I3 larger than I2 or I4, StC/D absent on M4. *Isoodon peninsulae* differs from *I. microtis* in having small posterior palatal fenestrae, larger bullae, the paraconid-metaconid distance shorter than the metaconid-protocristid distance on m1. *Isoodon peninsulae* differs from *I. f. insulanus*, *I. f. nauticus* and *I. f. terrenus* in having a large entoconid on m4.

Remarks. No changes to this species.

Distribution. Cape York, Queensland.

The updated distribution of all the taxa above is shown in Fig. 27.

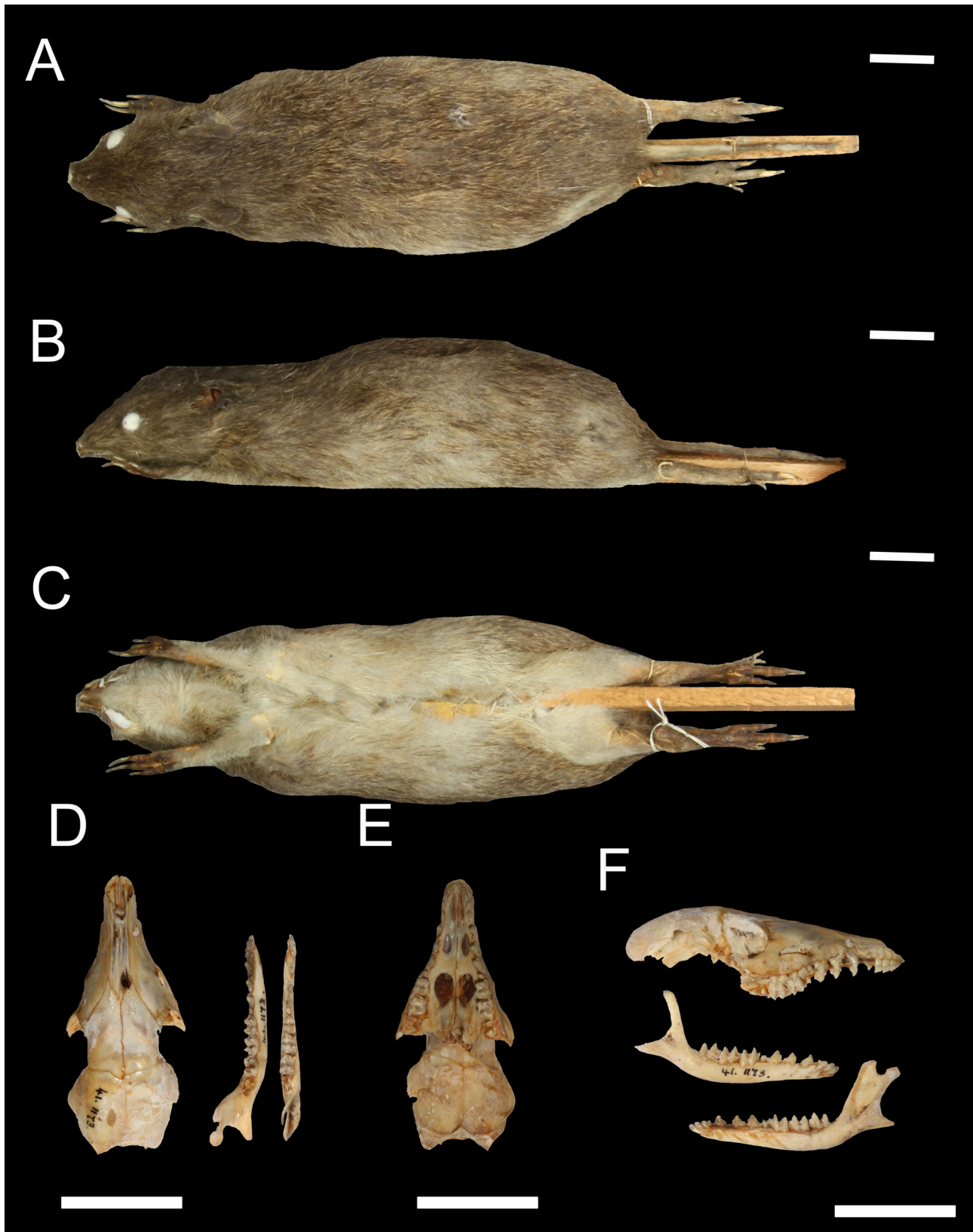


Figure 24. Holotype of *Isoodon obesulus affinis*, NHMUK 1841.1173. Study skin in dorsal (A), lateral (B) and ventral views (C). Skull and dentary in dorsal (D), ventral (E) and lateral views (F). Scale bar = 2cm.

Disclosures

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Travouillon, S. Cooper and T. Bertozzi) and the funding from Bioplatforms Australia through the Australian Government National Collaborative Research Infrastructure Strategy (NCRIS) for the Oz Mammals Genomics Initia-

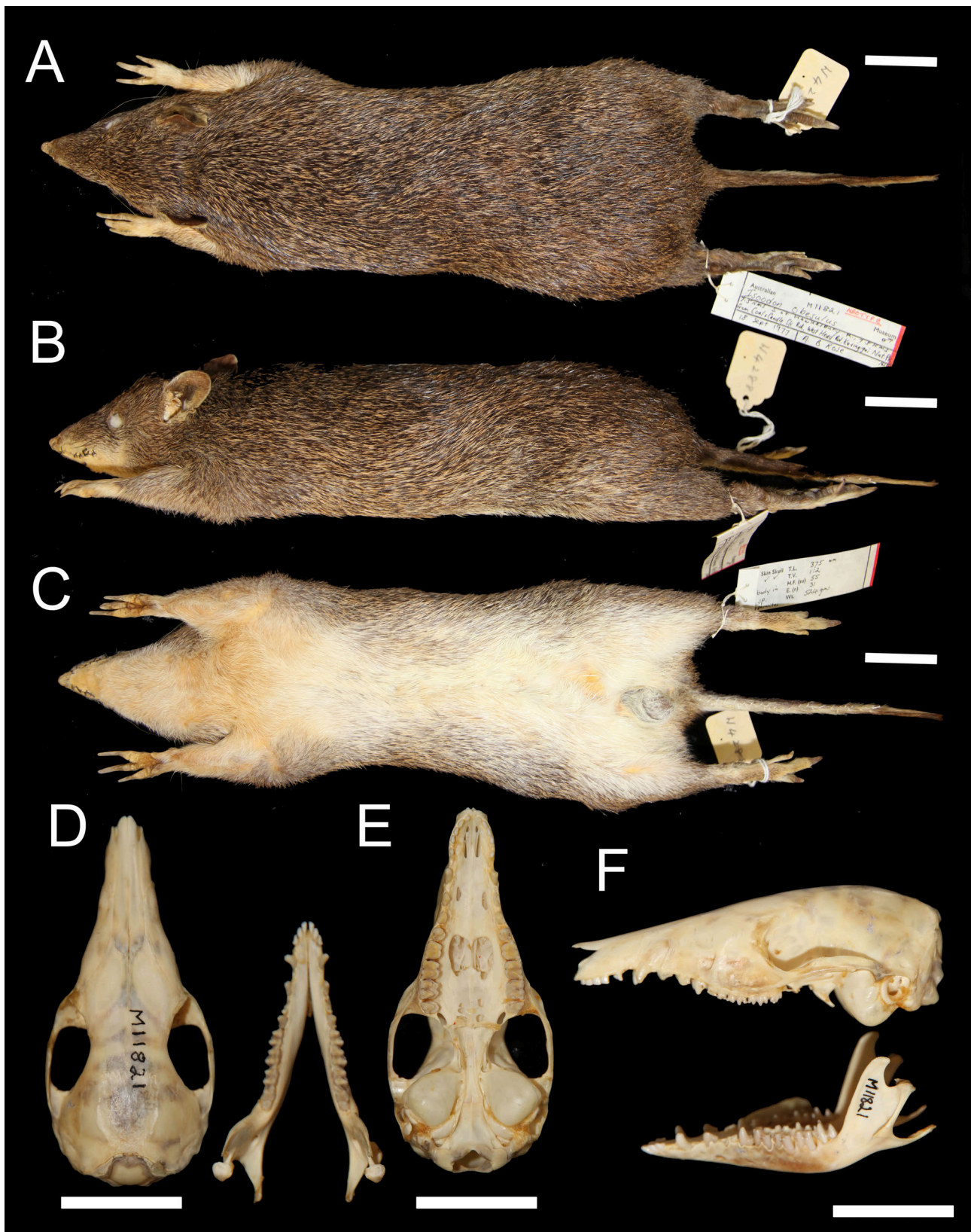


Figure 25. Neotype of *Isoodon obesulus*, AMS M1182. Study skin in dorsal (A), lateral (B) and ventral views (C). Skull and dentary in dorsal (D), ventral (E) and lateral views (F). Scale bar = 3cm (skin); 2cm (skull).

tive consortium (<https://ozmammalsgenomics.com/consortium/>).

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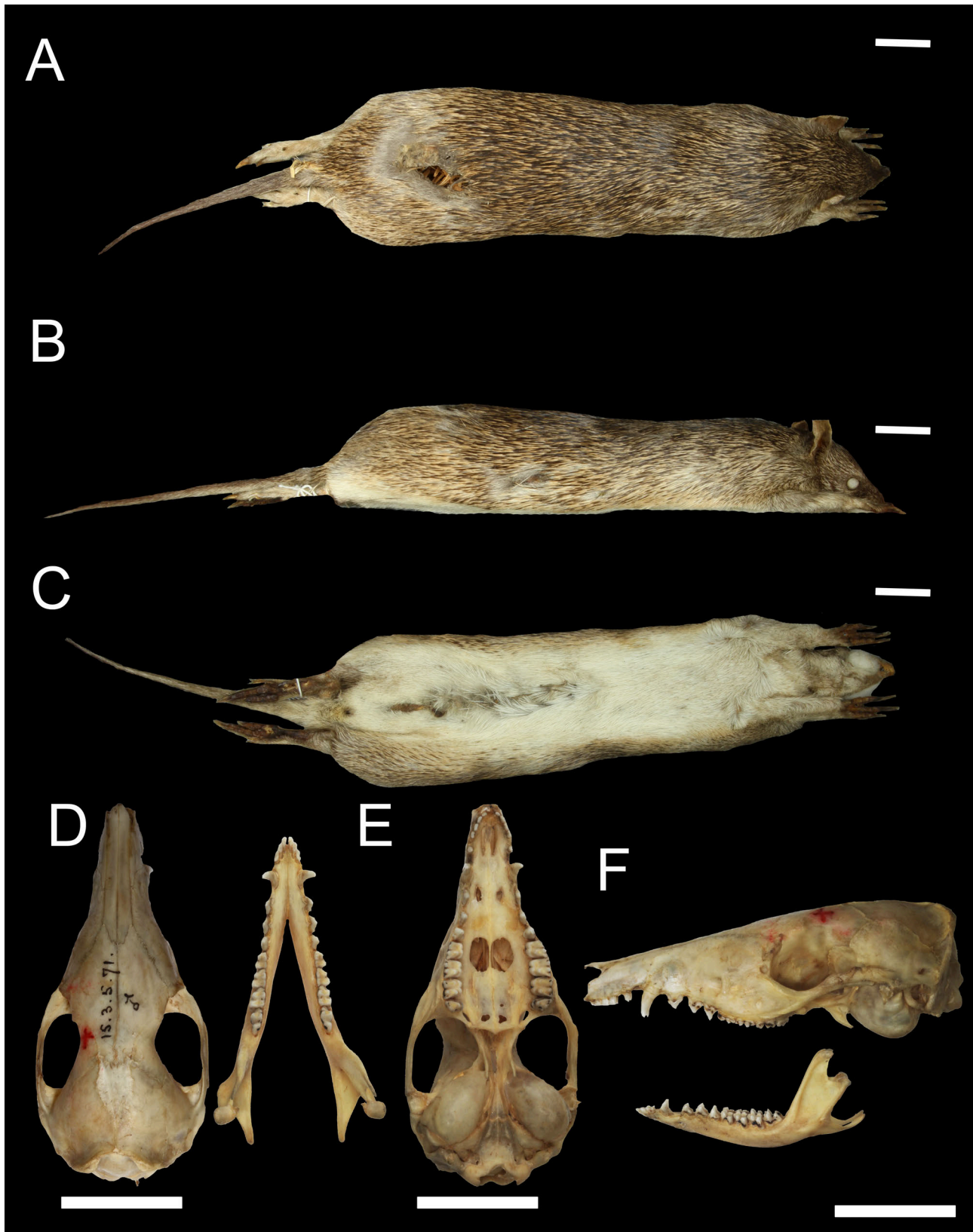


Figure 26. Holotype of *Isoodon peninsulae*, NHMUK 1915.3.5.71. Study skin in dorsal (A), lateral (B) and ventral views (C). Skull and dentary in dorsal (D), ventral (E) and lateral views (F). Scale bar = 3cm (skin); 2cm (skull).

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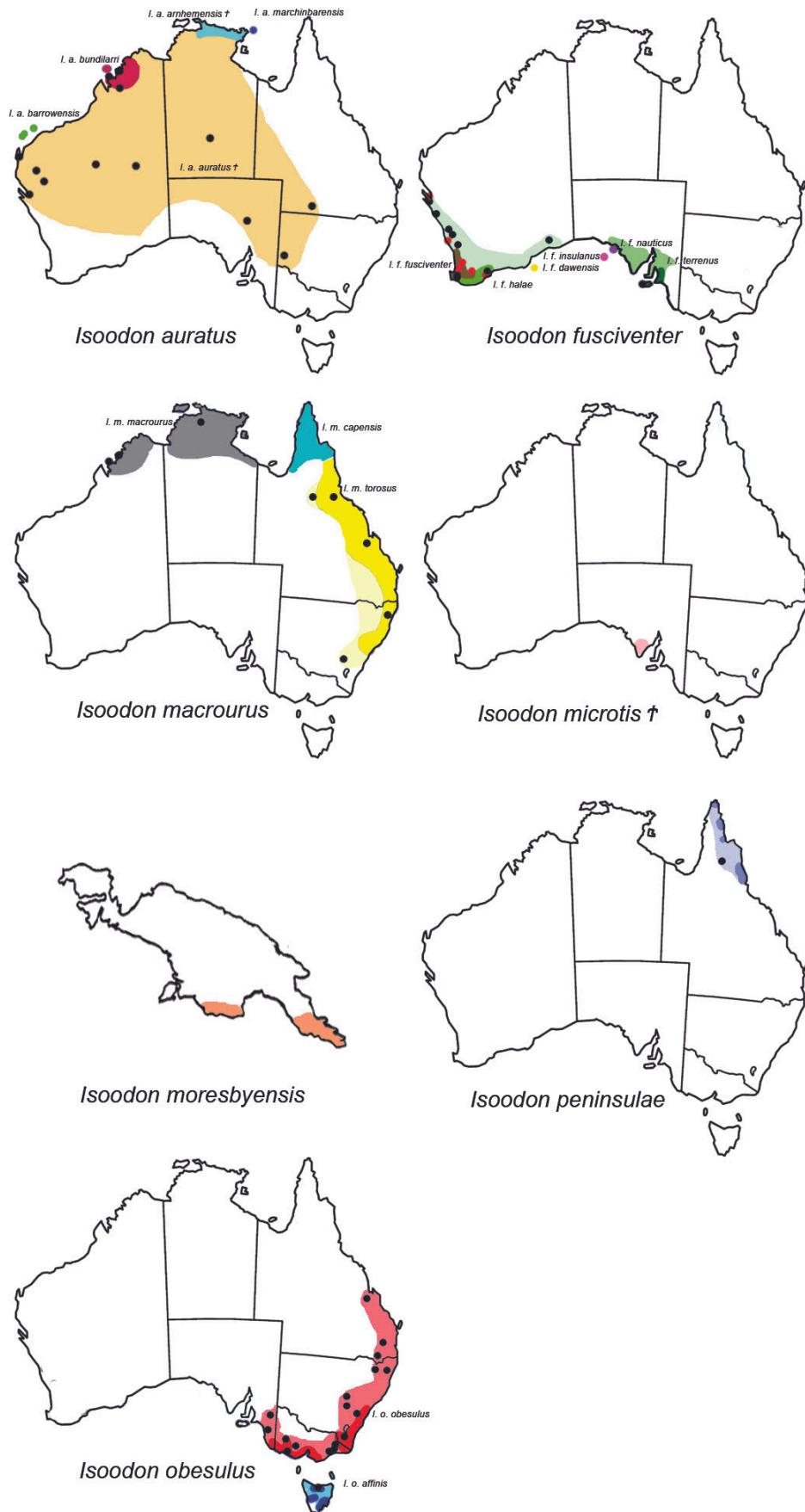


Figure 27. Updated distribution of species and subspecies of *Isodon*. Dark colour = current distribution; light colour = historical distribution at European arrival in Australia; black dots = subfossil sites; red dots = translocation sites.

Melbourne (Karen Roberts, Katie Date and Kevin Rowe), South Australian Museum in Adelaide, Flinders University Mammal Collection in Adelaide, Queensland Museum in Brisbane (Heather Janetzki), ANWC in Canberra (Leo Joseph and Chris Wilson), MAGNT in Darwin (Gavin Dally and Suzanne Horner), MacLay Museum in Sydney, Tasmanian Museum and Art Gallery in Hobart (Belinda Bauer), Queen Victoria Museum and Art Gallery in Launceston (David Maynard), NHMUK in London (Roberto Portela Miguez), MNHN in Paris (G  r  ldine V  ron, C  cile Callou and Aur  lie Verguin), MSN in Genoa (Giuliano Doria), Zoologische Staatssammlung M  nchen in Munich (Anneke H. van Heteren), Smithsonian Natural History Museum in Washington D.C. (Darrin Lunde), AMNH in New York (Eileen Westwig and Eleanor Hoeger) for providing access to the collection. We thank Linette Umbrello and Jenelle Ritchie for help during fieldwork at Normans Beach, collecting the type specimen for *I. f. halae*. We thank staff from DBCA's South Coast Region including Abby Martin, Tim Button, Emma Adams and Steve Butler for collections and data from Two Peoples Bay to Cape Arid National Park, and Bronte Van Helden for access to data for Albany. We thank Tom Vigilante and the Wunambal Gaambara rangers for their help with fieldwork on Mitchell's Plateau to collect the type specimen for *I. a. bundilarri*. and their approval to use a Wunambal Gaambara name as the scientific name for the subspecies.

Supplementary Data

Supplementary files (includes supplementary figures, supplementary tables, metadata for genetic samples and morphometric data): DOI: 10.5061/dryad.8gtht772x

References

- AMTC (2024). The Australian mammal taxonomy consortium Species List. Version 4.0. Available at <https://australianmammals.org.au/publications/amtc-species-list>. [accessed 21 October 2024]
- Andrews, S. (2010). FastQC: A quality control tool for high throughput sequence data. [Online]. Available at: <https://www.bioinformatics.babraham.ac.uk/projects/fastqc/>
- Aplin, K. P. & Archer, M. (1987). Recent advances in marsupial systematics with a new syncretic classification. In: Archer, M. (Ed.), *Possums and Opossums, Studies in Evolution*. Surrey Beatty and Sons, Sydney, pp. xv–lxxii.
- Bankevich, A., Nurk, S., Antipov, D., Gurevich, A. A., Dvorkin, M., Kulikov, A. S., Lesin, V. M., Nikolenko, S. I., Pham, S., Prjibelski, A. D., Pyshkin, A. V., Sirotkin, A. V., Vyahhi, N., Tesler, G., Alekseyev, M. A. & Pevzner, P. A. (2012). SPAdes: A new genome assembly algorithm and its applications to single-cell sequencing. *Journal of Computational Biology*, 19(5), 455–477.
- Baverstock, P. R., Flannery, T., Aplin, K., Birrell, J. & Krieg, M. (1990). Albumin immunologic relationships of the bandicoots (Peramelidae: Marsupialia) – a preliminary report. In: Seebeck, J. H., Brown, P. R., Wallis, R. L. & Kemper, C. M. (Eds.), *Bandicoots and Bilbies*. Surrey Beatty and Sons, Sydney, pp. 13–18.
- Bi, K., Linder  th, T., Vanderpool, D., Good, J. M., Nielsen, R. & Moritz, C. (2013). Unlocking the vault: Next-generation museum population genomics. *Molecular Ecology*, 22(24), 6018–6032.
- Black, J. G., Cooper, S. J. B., Schmidt, T. L. & Weeks, A. R. (2024). Simulating genetic mixing in strongly structured populations of the threatened southern brown bandicoot (*Isodon obesulus*). *Evolutionary Applications*, 17, e70050. <https://doi.org/10.1111/eva.70050>.
- Bolger, A. M., Lohse, M. & Usadel, B. (2014). Trimmomatic: a flexible trimmer for illumina sequence data. *Bioinformatics*, 30, 2114–2120.
- Bragg, J. G., Potter, S., Bi, K., Catullo, R., Donnellan, S. C., Eldridge, M. D. B., Joseph, L., Keogh, J. S., Oliver, P., Rowe, K. C. & Moritz, C. (2017). Resources for phylogenomic analyses of Australian terrestrial vertebrates. *Molecular Ecology Resources*, 17(5), 869–876.
- Burbidge, A. A. (2024). Australian terrestrial mammals: how many modern extinctions? *Australian Mammalogy*, 46(1), <https://doi.org/10.1071/am23037>.
- Chou, J., Gupta, A., Yaduvanshi, S., Davidson, R., Nute, M., Mirarab, S. & Warnow, T. (2015). A comparative study of SVDquartets and other coalescent-based species tree estimation methods. *BMC Genomics*, 16(Suppl 10), S2. <https://doi.org/10.1186/1471-2164-16-S10-S2>
- Close, R. L., Murray, J. D. & Briscoe, D. 1990. Electrophoretic and chromosome surveys of the taxa of short-nosed bandicoots within the genus *Isodon*. In: Seebeck, J. H., Wallis, R. L., Brown, P. R., Kemper, C. M. (Eds.), *Bandicoots and Bilbies*. Surrey Beatty and Sons, Sydney, pp. 19–27.
- Cooper, M. L. (1998). Geographic variation in size and shape in the southern brown bandicoot, *Isodon obesulus* (Peramelidae: Marsupialia), in Western Australia. *Australian Journal of Zoology*, 46, 145–152.
- Cooper, M. L. (2000). Temporal variation in skull size and shape in the southern brown bandicoot, *Isodon obesulus* (Peramelidae: Marsupialia) in Western Australia. *Australian Journal of Zoology*, 48, 47.
- Cooper, S.J.B., Ottewell, K., Macdonald, A. J., Adams, M., Byrne, M., Carthew, S. M., Eldridge, M. D. B., Li, Y., Pope, L. C., Saint, K. M., & Westerman, M. (2020). Phylogeography of southern brown and golden bandicoots: Implications for the taxonomy and distribution of endangered subspecies and species. *Australian Journal of Zoology*, 66, 379.
- Criscuolo, A. & Gribaldo, S. (2010). BMGE (Block Mapping and Gathering with Entropy): a new software for selection of phylogenetic informative regions from multiple sequence alignments. *BMC Evolutionary Biology*, 10, 210. <https://doi.org/10.1186/1471-2148-10-210>.

- Desmarest, A. G. (1817). Nouveau Dictionnaire d'Histoire Naturelle, appliquée aux arts, à l'agriculture, à l'économie rurale et domestique, à la médecine, etc. Par une société de naturalistes et d'agriculteurs. Nouvelle édition presque entièrement refondue et considérablement augmentée. Chez Deterville, Paris, 595pp.
- Dixon, J. M. (1981). Selection of a neotype for the southern short-nosed (brown) bandicoot, *Isoodon obesulus* (Shaw and Nodder, 1797). *Victorian Naturalist*, 98(3), 130–135.
- Eldridge, M. D. B., Deakin, J. E., MacDonald, A. J., Byrne, M., Fitzgerald, A., Johnson, R. N., Moritz, C., Palmer, S. & Young, A. (2020). The Oz Mammals Genomics (OMG) initiative: developing genomic resources for mammal conservation at a continental scale. *Australian Zoologist*, 40(3), 505–509.
- Gordon, G. & Hulbert, A. J. (1989). Peramelidae. In: Walton, D.W. (Ed), *Fauna of Australia*. Australian Government Publishing Service, Canberra, Australia, pp. 603–624.
- Gould, J. (1842). On some new species of Australian mammals. *Proceedings of the Zoological Society of London*, 10, 10–14.
- Gray, J. E. (1825). Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently appertaining to each tribe. *Annals of Philosophy (New Series)*, 10, 337–344.
- Gray, J. E. (1841). Contributions towards the geographical distribution of the Mammalia of Australia, with notes on some recently discovered species, in a letter addressed to the Author. Appendix C. In: Grey, G. (Ed.), *Journals of Two Expeditions of Discovery in North-west and Western Australia, During the Years 1837, 38 and 39, Under the Authority of Her Majesty's Government. Describing many newly discovered, important, and fertile districts, with observations on the moral and physical condition of the aboriginal inhabitants, &c., & c.* T. & W. Boone, London, pp. 397–414.
- Gray, J. E. (1843). *List of the Specimens of Mammalia in the Collection of the British Museum*. British Museum, London.
- Gruber, B., Unmack, P. J., Berry, O. F. & Georges, A. (2018). Dartr: An R package to facilitate analysis of SNP data generated from reduced representation genome sequencing. *Molecular Ecology Resources*, 18(3), 691–699.
- Hale, M. (2000). Inheritance of geographic variation in body size, and countergradient variation in growth rates, in the southern brown bandicoot *Isoodon obesulus*. *Australian Mammalogy*, 22, 9–16.
- Hammer, Ø., Harper, D. A. T. & Ryan, P. D. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4, 1–9.
- Iredale, T. & Troughton, E. G. (1934). A check-list of the mammals recorded from Australia. *Memoirs of the Australian Museum*, 6, i–xii, 1–122.
- IUCN (2024). The IUCN red list of threatened species. Available at <https://www.iucnredlist.org>. [accessed 21 October 2024].
- Jackson, S. & Groves, C. (2015). *Taxonomy of Australian Mammals*. CSIRO Publishing.
- Joseph, L., Boussès, P., Wilke, T. & Austin, J. J. (2016). Ancient DNA resolves the subspecific identity of the holotype of the galah *Eolophus roseicapilla*, a widespread Australian cockatoo. *Emu - Austral Ornithology*, 116(4), 472–475.
- Katoh, K. & Standley, D. M. (2013). MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. *Molecular Biology and Evolution*, 30(4), 772–780. <https://doi.org/10.1093/molbev/mst010>.
- Kirsch, J. A. W. (1968). Prodrum of the comparative serology of Marsupialia. *Nature*, 217, 418–420.
- Kirsch, J. A. W., Springer, M. S., Krajewski, C., Archer, M., Aplin, K. & Dickerman, A. W. (1990). DNA/DNA hybridization studies of the carnivorous marsupials. I: The intergeneric relationships of bandicoots (Marsupialia: Peramelidae). *Journal of Molecular Evolution*, 30, 434–448. <https://doi.org/10.1007/BF02101115>.
- Kirsch, J. A. W., Lapointe, F. J. & Springer, M. S. (1997). DNA-hybridisation studies of marsupials and their implications for metatherian classification. *Australian Journal of Zoology*, 45, 211–280.
- Kraehenbuehl, D. N. (1976). Waterhouse, Frederick George (1815–1898). *Australian Dictionary of Biography*. Canberra: Australian National University.
- Legge, S., Woinarski, J. C. Z., Burbidge, A. A., Palmer, R., Ringma, J., Radford, J. Q., Mitchell, N., Bode, M., Wintle, B., Baseler, M., Bentley, J., Copley, P., Dexter, N., Dickman, C. R., Gillespie, G. R., Hill, B., Johnson, C. N., Latch, P., Letnic, M., Manning, A., McCreless, E. E., Menkhorst, P., Morris, K., Moseby, K., Page, M., Pannell, D. & Tuft, K. (2018). Havens for threatened Australian mammals: the contributions of fenced areas and offshore islands to the protection of mammal species susceptible to introduced predators. *Wildlife Research*, 45, 627–644. <https://doi.org/10.1071/wr17172>.
- Li, Y., Lancaster, M. L., Carthew, S. M., Packer, J. G., Cooper, S. J. B. (2014). Delineation of conservation units in an endangered marsupial, the southern brown bandicoot (*Isoodon obesulus obesulus*), in South Australia/western Victoria, Australia. *Australian Journal of Zoology*, 62, 345–359.
- Louys, J., Cramb, J., Ferguson, K., Kemp, J., Wood, R., Miszkiewicz, J. J., Dias Guimarães, N. R., Higgins, P., Trouvillon, K. J., Hocknull, S. A., Webb, G. E. & Price, G. J. (2023). Interim report on the vertebrate deposits recovered

- from the Capricorn Caves, Rockhampton, Queensland. *Alcheringa: An Australasian Journal of Palaeontology*, 47, 562–589. <https://doi.org/10.1080/03115518.2022.2157486>
- Lyne, A. G. & Mort, P. A. (1981). A comparison of skull morphology in the marsupial bandicoot genus *Isoodon*: Its taxonomic implications and notes on a new species, *Isoodon arnhemensis*. *Australian Mammalogy*, 4, 107–133.
- Meyer, M. & Kircher, M. (2010). Illumina sequencing library preparation for highly multiplexed target capture and sequencing. *Cold Spring Harb Protoc*, 2010(6), <https://doi.org/10.1101/pdb.prot5448>.
- Newman-Martin, J., Travouillon, K. J., Warburton, N., Barham, M. & Blyth, A. J. (2023). Taxonomic review of the genus *Dasyercus* (Dasyuromorphia: Dasyuridae) using modern and subfossil material; and the description of three new species. *Alcheringa: An Australasian Journal of Palaeontology*, 47, 624–661. <https://doi.org/10.1080/03115518.2023.2262083>.
- Nguyen, L. -T., Schmidt, H. A., Von Haeseler, A. & Minh, B.Q. (2015). IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32, 268–274. <https://doi.org/10.1093/molbev/msu300>.
- Ottewell, K., Dunlop, J., Thomas, N., Morris, K., Coates, D. & Byrne, M. (2014). Evaluating success of translocations in maintaining genetic diversity in a threatened mammal. *Biological Conservation*, 171, 209–219.
- Padial, K. M., Miralles, A., De la Rica, I. & Vences, M. (2010). The integrative future of taxonomy. *Frontiers in Zoology*, 7, 16. <https://doi.org/10.1186/1742-9994-7-16>
- Parnaby, H. & Gill, A. C. (2021). Mammal type specimens in the Macleay Collections, University of Sydney. *Zootaxa*, 4975(2), 201–252.
- Parrott, M. L., Coetsee, A. L., Hartnett, C. M. & Magrath, M. J. L. (2017). New hope for the Eastern barred bandicoot *Perameles gunnii* after 27 years of recovery effort. *International Zoo Yearbook*, 51(1), 154.
- Phillips, M. J., Cascini, M. & Celik, M. (2022). Identifying complex DNA contamination in pig-footed bandicoots helps to clarify an anomalous ecological transition. *Diversity*, 14, 50352. <https://doi.org/10.3390/d14050352>.
- Pope, L., Storch, D., Adams, M., Moritz, C. & Gordon, G. (2001). A phylogeny for the genus *Isoodon* and a range extension for *I. obesulus peninsulae* based on mtDNA control region and morphology. *Australian Journal of Zoology*, 49, 411–434.
- Rambaut, A. (1996). SE-AL: Sequence Alignment Editor. <http://evolve.zoo.ox.ac.uk/>.
- Ramsay, E. P. (1877). The mammals of the Chevert Expedition, part 1. *Proceedings of the Linnean Society of New South Wales*, 2, 7–15.
- Ramsay, E. P. (1887). Description of three new species of mammals from north west Australia. *Abstract of Proceedings of the Linnean Society of New South Wales*, 1887, vi.
- Rannala, B. & Yang, Z. (2007). Inferring speciation times under an episodic molecular clock. *Systematic Biology*, 56, 453–466.
- Rick, K., Byrne, M., Cameron, S., Cooper, S. J. B., Dunlop, J., Hill, B., Lohr, C., Mitchell, N. J., Moritz, C., Travouillon, K. J., von Takach, B. & Ottewell, K. (2023). Population genomic diversity and structure in the golden bandicoot: a history of isolation, extirpation, and conservation. *Heredity*, 131, 374–386. <https://doi.org/10.1038/s41437-023-00653-2>
- Ride, W. D. L. (1970). *A Guide to the Native Mammals of Australia*. Oxford University Press: Melbourne.
- Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A. & Huelsenbeck, J. P. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542. <https://doi.org/10.1093/sysbio/sys029>.
- Roycroft, E. J., Moussalli, A. & Rowe, K. C. (2020). Phylogenomics uncovers confidence and conflict in the rapid radiation of Australo-Papuan rodents. *Systematic Biology*, 69(3), 431–444.
- Roycroft, E., Moritz, C., Rowe, K. C., Moussalli, A., Eldridge, M. D. B., Portela Miguez, R. Piggott, M. P. & Potter, S. (2022). Sequence Capture From Historical Museum Specimens: Maximizing Value for Population and Phylogenomic Studies. *Frontiers in Ecology and Evolution*, 10. <https://doi.org/10.3389/fevo.2022.931644>.
- Shaw, G. (1797). The Naturalist's Miscellany: Or coloured figures of natural objects, drawn and described immediately from nature. F.P. Nodder & Co., London, Volume 8.
- Strahan, R. (1983). *The Complete Book of Australian Mammals*. Angus and Robertson, Sydney.
- Strahan, R. (1995). *The Mammals of Australia*. Reed Books, Sydney.
- Sutton, J. (1929). Extracts from the Late Mr. M. Symonds Clark's Diaries. *South Australian Ornithologist*, 10(4), 144–153.
- Tate, G. H. H. (1948). Results of the Archbold Expeditions, no 60. Studies in the Peramelidae (Marsupialia). *Bulletin of the American Museum of Natural History*, 92, 317–346.
- Thavornkanlapachai, R., Levy, E., Li, Y., Cooper, S. J. B., Byrne, M. & Ottewell, K. (2021). Disentangling the genetic relationships of three closely related bandicoot species across Southern and Western Australia. *Diversity*, 13(1), 2. <https://doi.org/10.3390/d13010002>.
- Thomas, O. (1888). *Catalogue of the Marsupialia and Monotremata in the Collection of the British Museum (Natural History)*. British Museum, London.

- Thomas, O. (1901). On some kangaroos and bandicoots from Barrow Island, N.W. Australia, and the adjoining mainland. *Novitates Zoologicae*, 8, 394–396.
- Thomas, O. (1904). On a collection of mammals made by Mr. J. T. Tunney in Arnhem Land, Northern Territory of South Australia. *Novitates Zoologicae*, 11, 222–229.
- Thomas, O. (1922). LXXXIV.–The bandicoots of Nuyts Archipelago, S. Australia, and of Cape York, N. Queensland. *Journal of Natural History*, 9, 677–679.
- Travouillon, K. J., Louys, J., Price, G. J., Archer, M., Hand, S. J. & Muirhead, J. (2017). A review of the Pliocene bandicoots of Australia, and descriptions of new genus and species. *Journal of Vertebrate Paleontology*, 37(5), e1360894. <https://doi.org/10.1080/02724634.2017.1360894>.
- Travouillon, K. J. & Phillips, M. J. (2018). Total evidence analysis of the phylogenetic relationships of bandicoots and bilbies (Marsupialia: Peramelemorphia): reassessment of two species and description of a new species. *Zootaxa*, 4378, 224–256. <https://doi.org/10.11646/zootaxa.4378.2.3>.
- Travouillon, K. J., Simões, B. F., Miguez, R. P., Brace, S., Brewer, P., Stemmer, D., Price, G. J., Cramb, J. & Louys, J. (2019). Hidden in plain sight: reassessment of the pig-footed bandicoot, *Chaeropus ecaudatus* (Peramelemorphia, Chaeropodidae), with a description of a new species from central Australia, and use of the fossil record to trace its past distribution. *Zootaxa*, 4566, 1–69. <https://doi.org/10.11646/zootaxa.4566.1.1>
- Troughton, E. (1967). *Furred Animals of Australia*. Angus and Robertson, Sydney. 9th ed.
- Warburton, N. M. & Travouillon, K. J. (2016). The biology and taxonomy of the Peramelemorphia: a review of current knowledge and future research directions. *Australian Journal of Zoology*, 64, 151–181.
- Waterhouse, G. R. (1838). *Catalogue of the Mammalia Preserved in the Museum of the Zoological Society of London*. R. Taylor & J.E.Taylor, London, 42 pp.
- Waterhouse, G. R. (1846). *A Natural History of the Mammalia. Volume 1. Containing the Order Marsupialia, or Pouched Animals*. Bailliere, London, 553 pp. + 22pls.
- Westerman, M. & Krajewski, C. (2000). Molecular relationships of the Australian bandicoot genera *Isoodon* and *Perameles* (Marsupialia: Peramelina). *Australian Mammalogy*, 22, 1–8.
- Westerman, M., Kear, B. P., Aplin, K., Meredith, R. W., Emerling, C. & Springer, M. S. (2012). Phylogenetic relationships of living and recently extinct bandicoots based on nuclear and mitochondrial DNA sequences. *Molecular Phylogeny and Evolution*, 62, 97–108.
- Woinarski, J. C. Z., Burbidge, A. A. & Harrison, P. L. (2015). Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences USA*, 112, 4531–4540. <https://doi.org/10.1073/pnas.1417301112>.
- Woinarski, J. C. Z., Braby, M. F., Burbidge, A. A., Coates, D., Garnett, S. T., Fensham, R. J., Legge, S. M., McKenzie, N. L., Silcock, J. L. & Murphy, B. P. (2019). Reading the black book: The number, timing, distribution and causes of listed extinctions in Australia. *Biological Conservation*, 239, 108261.
- Yang, Z. (2007). PAML 4: Phylogenetic analysis by maximum likelihood. *Molecular Biology and Evolution*, 24, 1586–1591. <https://doi.org/10.1093/molbev/msm088>.
- Xi, Z., Liu, L. & Davis, C. C. (2015). Genes with minimal phylogenetic information are problematic for coalescent analyses when gene tree estimation is biased, *Molecular Phylogenetics and Evolution*, 92, 63–71. <https://doi.org/10.1016/j.ympev.2015.06.009>
- Xu, H., Luo, X., Qian, J., Pang, X., Song, J., Qian, G. & Chen, S. (2012). FastUniq: A fast de novo duplicates removal tool for paired short reads. *PLoS ONE*, 7(12), e52249. <https://doi.org/10.1371/journal.pone.0052249>.
- Zenger, K. R., Eldridge, M. D. B. & Johnston, P. G. (2005). Phylogenetics, population structure and genetic diversity of the endangered southern brown bandicoot (*Isoodon obesulus*) in south-eastern Australia. *Conservation Genetics*, 6, 193–204.
- Zhang, C., Rabiee, M., Sayyari, E. & Mirarab, S. (2018). ASTRAL-III: polynomial time species tree reconstruction from partially resolved gene trees. *BMC Bioinformatics*, 19(Suppl 6), 153. <https://doi.org/10.1186/s12859-018-2129-y>



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