

# Papers in Honour of Ken Aplin

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# Genetic Relationships of Long-nosed Potoroos *Potorous tridactylus* (Kerr, 1792) from the Bass Strait Islands, with Notes on the Subspecies *Potorous tridactylus benormi* Courtney, 1963

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**ABSTRACT.** Bass Strait is an important biogeographic barrier for Australian mammals, often resulting in significant genetic differentiation between populations on the mainland and Tasmania for species with a *trans*-Bassian distribution. King and Flinders Islands, in Bass Strait, are the largest remnants of the land bridge that once linked Tasmania with mainland Australia. Due to their remote locality and habitat loss on the islands since European settlement, little is known about the evolutionary movements of species across the former land bridge. Here we present genetic data, generated from museum skins, on the King and Flinders Island populations of Long-nosed Potoroo, *Potorous tridactylus* (Kerr, 1792) to investigate their affinities with other populations of this species. We also assessed the validity of the subspecies *Potorous tridactylus benormi* Courtney, 1963 described from King Island. Analysis of two partial mitochondrial DNA genes (*COI*, *ND2*) indicate that potoroos on King and Flinders Islands are more closely related to Tasmanian rather than mainland potoroo populations. Molecular and morphological data from the holotype and paratype of *Potorous tridactylus benormi* does not support separate taxonomic status and places it within the Tasmanian subspecies *Potorous tridactylus apicalis* (Gould, 1851).

## Introduction

Bass Strait is a 240 km expanse of ocean that separates Victoria on mainland Australia and the island of Tasmania. It is relatively shallow, mostly less than 100 m deep, and during glacial cycles, sea level drops have resulted in the exposure of a land bridge—“the Bassian Plain”—facilitating the dispersal of species between mainland Australia and Tasmania. This land bridge was most recently exposed from

around 43,000 years ago until around 14,000 years ago, including the period of the Last Glacial Maxima (Lambeck & Chappell, 2001) and since its most recent breakdown, has formed a biogeographic barrier for many species with a *trans*-Bassian distribution (Firestone, 1998; Symula *et al.*, 2008; Schultz *et al.*, 2007; Toon *et al.*, 2010).

Today, all that remains of this land bridge are over 50 islands in Bass Strait (Fig. 1). Along the western edge of the former Bassian Plain lies King Island (c. 1100 sq km) located

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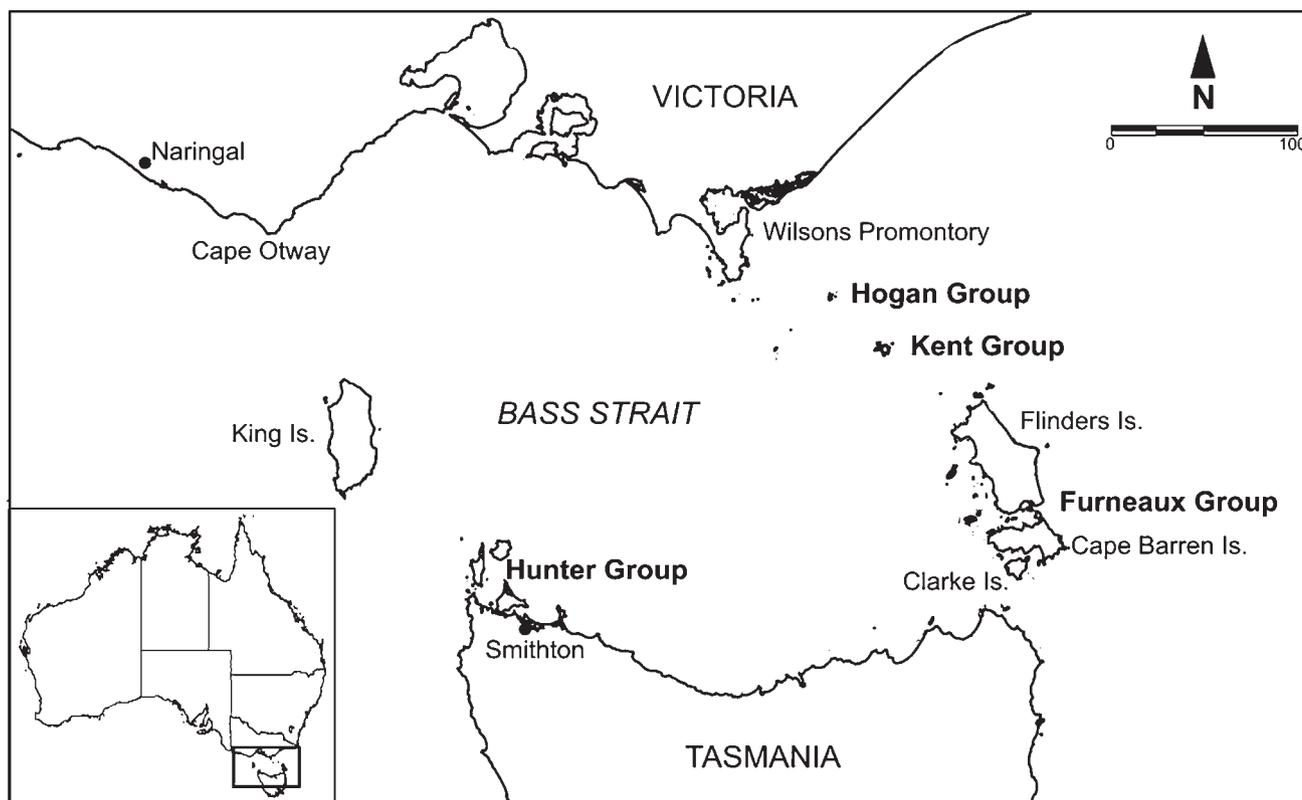


Figure 1. A map of Bass Strait and the Bass Strait Islands.

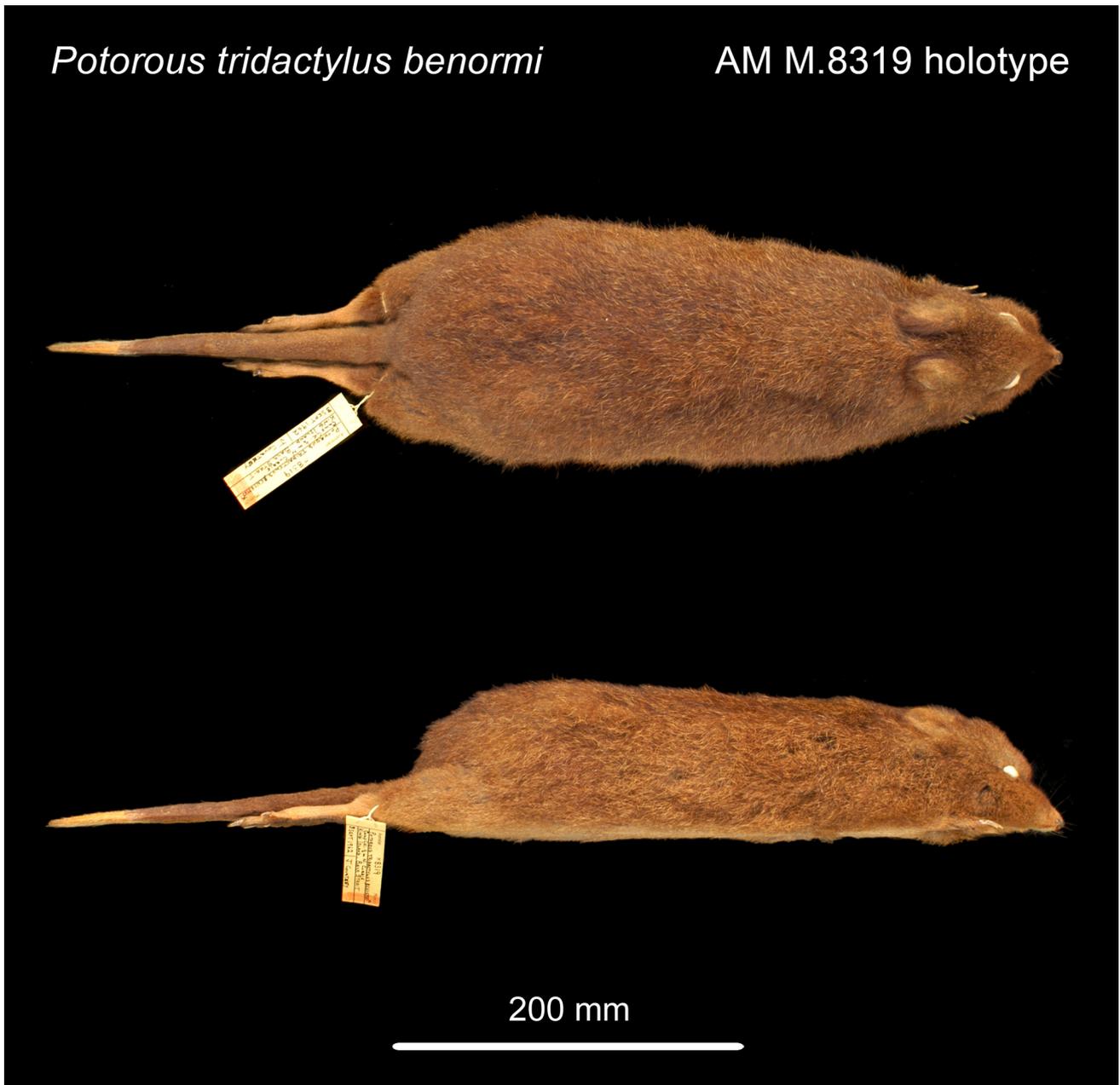
halfway between Cape Otway, Victoria and north-western Tasmania, as well as the Hunter Group, extending from the north-west tip of Tasmania. Along the eastern edge of the former Bassian Plain is a string of island groups running between Wilsons Promontory in Victoria and north-eastern Tasmania, including the Hogan, the Kent, and the Furneaux Groups (Fig. 1). Flinders Island (c. 1367 sq km) is the largest of the Bass Strait Islands and is part of the Furneaux Group (Abbott & Burbidge, 1995).

Due to the presence of seal colonies, settlement of the Bass Strait Islands by Europeans began as early as the late 18th century, thus these islands have a long history of settlement and habitat disturbance (Hope, 1973). Many of the islands have experienced extensive habitat loss and modification primarily from agricultural land practices (Courtney, 1963; Green & McGarvie, 1971; Hope, 1973), as well as the introduction of exotic and/or invasive species (Abbott & Burbidge, 1995). These changes have resulted in declines in native faunal assemblages, as well as the extinction of populations of several species, including Southern Elephant Seal (*Mirounga leonina*), Common Wombat (*Vombatus ursinus*), Spotted-tail Quoll (*Dasyurus maculatus*), and King Island Emu (*Dromaius novaehollandiae minor*) (Hope, 1973).

The loss of species from the Bass Strait Islands, coupled with the logistical difficulty of surveying the islands, means that specimens, and in particular tissue samples, from these islands are rare or absent from natural history collections, and therefore not available for inclusion in studies looking at the biogeography of the Australian mainland and Tasmania (Frankham *et al.*, 2016). Analyses of these populations would provide important insights into the evolutionary history of the Bassian Plain land bridge.

The Long-nosed Potoroo (*Potorous tridactylus*) (Kerr 1792) has a *trans*-Bassian distribution and has been recorded on many of the larger Bass Strait islands, including King Island, the Furneaux Group Islands (Flinders Island, Clarke Island, Cape Barren Island), the Kent Group Islands (Deal Island), as well as several in the Hunter Group (Robbins, Walker, and Three Hummock Islands) (Hope, 1963; Abbott & Burbidge, 1995). While considered reasonably common prior to the 1940s on King Island (Courtney, 1963), it has since declined, likely due to its sensitivity to habitat loss and disturbance (Frankham *et al.*, 2011; Holland & Bennett, 2009; Andren *et al.*, 2018). The last confirmed record of a Long-nosed Potoroo on the Bass Strait Islands was an individual trapped on Flinders Island in 1970 (Johnston, 1973). Johnston (1973) commented at the time, that the species was considered very rare on King Island, Flinders Island, and Clarke Island. Since the 1970s there has only been a handful of sightings (ALA, 2020) and these populations may be very rare or have gone extinct (Eldridge & Frankham, 2015).

Courtney (1963) assessed the size and pelage colouration of the Long-nosed Potoroos on King Island and designated this population a separate subspecies, *Potorous tridactylus benormi* Courtney, 1963, with the holotype lodged with the Australian Museum (AM M.8319) (Fig. 2), along with a paratype (AM M.8373). Subsequent authors have not considered the proposed King Island subspecies as valid or taxonomically distinct (Calaby & Richardson, 1988; Johnston, 2008; Jackson & Groves, 2015; Eldridge & Frankham, 2015). However, this proposed taxon has never been tested with molecular data, making this population of particular interest.



**Figure 2.** Holotype of *Potorous tridactylus benormi* AM M.8319 dorsal view (top) and lateral view (bottom). Photography by Sally Cowan.

Recent genetic studies by Frankham *et al.*, (2012; 2016) examined the phylogeography of the Long-nosed Potoroo across its range. These studies identified Bass Strait as a major biogeographic barrier within the species, suggesting that gene flow between mainland Australia and Tasmanian populations last occurred around 2.45 million years ago. Given the last confirmed trapping of a potoroo on a Bass Strait Island was in 1970 (Johnston, 1973), no tissue samples were available for inclusion in these studies, thus data from the Bass Strait island populations were not assessed.

In this study, we aimed to fill this gap to understand the evolutionary history of the species across the Bassian Plain by using genetic data generated from dried museum specimens. We aimed to examine the relationship of Long-nosed Potoroos from King Island and Flinders Island to determine if these shared a closer relationship with either

the mainland or Tasmanian populations. We also sampled the holotype and paratype of *Potorous tridactylus benormi* in order to assess its validity as a subspecies.

### Methods

Skin samples ( $2 \times 2$  mm) were taken with separate sterile scalpels from *Potorous tridactylus* study skins in the Australian Museum (AM) and Museum Victoria (NMV), including AM M.8319 (holotype of *benormi*) AM M.8373 (paratype of *benormi*) from King Island; AM M.4398 and NMV C.8859 from Flinders Island; and AM M.9138 and AM M.10788 from Cobargo, NSW. DNA extraction was undertaken in a designated low-template laboratory (with positive air pressure and HEPA filtered air handling

**Table 1.** Summary of primers designed to amplify *Cytochrome c oxidase subunit 1* and *NADH dehydrogenase subunit 2* for this study, those modified from or designed by previous studies are indicated.

forward	5'–3'	reverse	5'–3'
<i>Cytochrome c oxidase subunit 1</i>			
Pot_CO1_F5	CACGCAGGRGCYTCAGTAG	Pot_CO1_R6	GATAGTAGVAGMAGRACTGCTGT
Pot_CO1_F6	ACCACCCGCCCTRTCMCAATATC	Pot_CO1_R7	CTTCTGGGTGRCCRAAGAATCA
Pot_CO1_F7	ACYATRCTATTAACAGACCCG	Pot_CO1_R8	TTACCAGAGTAGTAAGTYAC
Pot_CO1_Cox_F8 <sup>a</sup>	TGATTCTTYGGYCACCCAGAAG	Pot_CO1_R9	TAGGCTCGGGTATCKACRTC
Pot_CO1_F9	ACAGTTGGACTRGAYGTAG	Pot_CO1_R10	ATRAATCCTAGGGCTCATAG
Pot_CO1_F10	GTTTTTCAGCTGRTTAGCAAC	Pot_CO1_R11	CCTATWGATAGGACGTAGTGGAAGTG
<i>NADH dehydrogenase subunit 2</i>			
Pot_ND2_F2	AAATCYTTAACCAACYTATG	Pot_ND2_R3	GGGAATATRGTGAGAGTTGAG
Pot_ND2_F3	GCWATCCTAATAGCYATATCA	mrND2c <sup>b</sup>	GATTTGCGTTCGAATGTAGCAAG

<sup>a</sup> Primer modified from M320 Schneider *et al.*, 1998.

<sup>b</sup> M636 from Osborne & Christidis, 2001.

system) at the Australian Centre for Wildlife Genomics at the Australian Museum. Prior to extraction samples were rehydrated in sterile phosphate buffered saline (PBS) on a gentle shake (300 rpm) overnight at 37°C. DNA was extracted using the QIAamp DNA Investigator Kit (QIAGEN) using the Isolation of Total DNA from Chewing Gum protocol following manufacturer's instructions, including the addition of Carrier RNA.

Primers were designed to amplify a series of overlapping short fragments (125–200 base pairs) for the partial regions of the mitochondrial DNA genes; cytochrome c oxidase subunit 1 (*COI*, 6 overlapping fragments) and NADH dehydrogenase subunit 2 (*ND2*, 2 overlapping fragments) (Table 1). PCRs were carried out in 25 µl reactions and comprised 100–400 ng genomic DNA, 1 × PCR Buffer II (Applied Biosystems), 0.2 mM each dNTP, 1.5–3.0 mM MgCl<sub>2</sub>, 0.2 µmol each primer (Table 1) and 1.0U *AmpliTaq Gold*<sup>TM</sup> polymerase (Applied Biosystems); negative controls were used for all PCR reactions. PCR reactions were conducted on an Eppendorf Thermocycler under the following conditions; 95°C for 9 minutes for one cycle, followed by 50 cycles of 94°C (60 s) denaturation, 50°C (60 s) annealing, and 60°C (60 s) extension, followed by a final cycle of extension at 60°C for 10 minutes. All PCR products were purified using Exo-SapIT (USB Corporation, Cleveland, Ohio, USA), and directly sequenced on an AB 3730xl Sequencer at the Australian Genome Research Facility, Sydney.

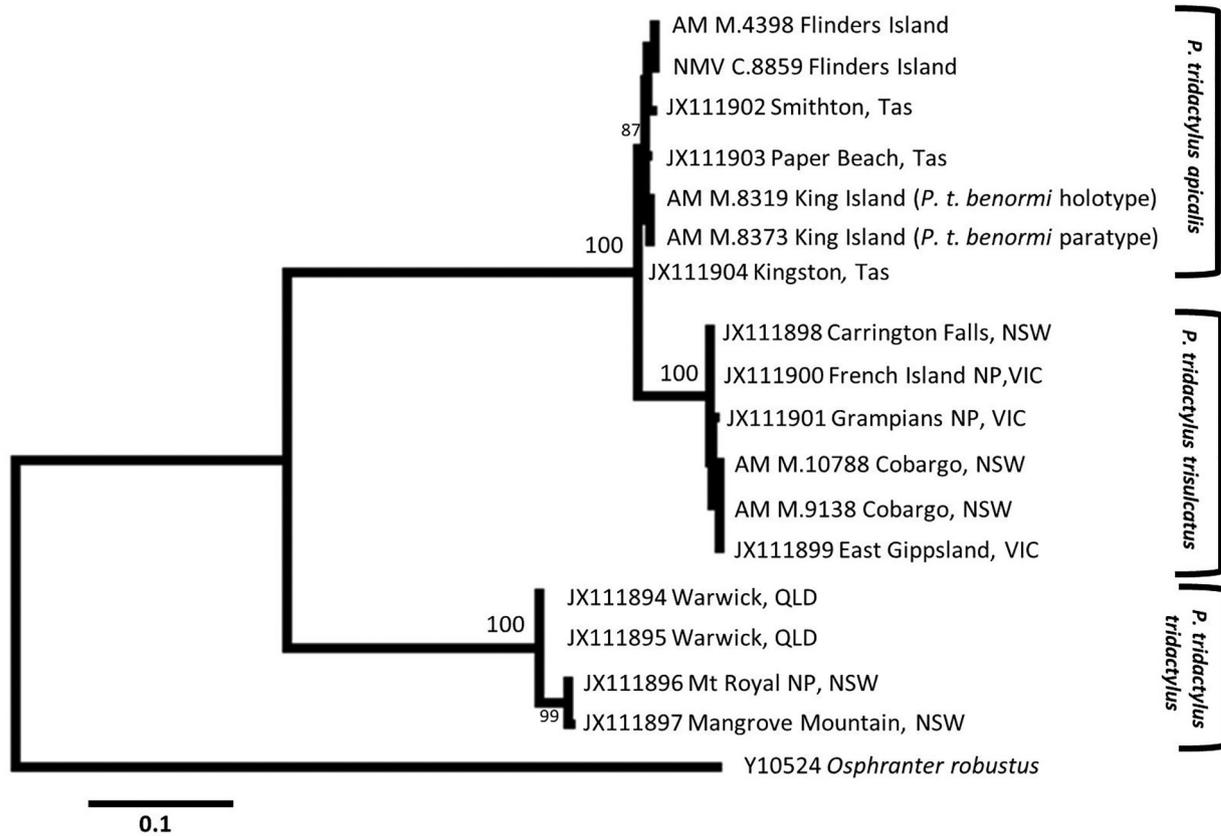
Sequences were visually checked with reference to chromatograms using SEQUENCHER version 5.2.4. Sequence alignments were carried out in MEGA version 6 with comparison to *COI* and *ND2* fragments generated by Frankham *et al.* (2012) (GenBank Accession numbers *COI*: JX111894–JX111903 and *ND2* JX104566–JX104576), *COI* and *ND2* sequences from the common wallaroo, *Osphranter robustus* (GenBank accession number Y10524) were used as outgroups. Phylogenetic relationships were estimated using both Bayesian inference (BI) and maximum likelihood (ML). MEGA version 6 (Nei & Kumar, 2000; Tamura *et al.*, 2013), was used to determine an appropriate model of evolution (HKY + Γ) based on the Bayesian Information Criterion (BIC scores) and Akaike information criterion, corrected (AICc scores). All phylogenetic analyses were carried out using this model. Bayesian Inference (BI) analysis was conducted in MRBAYES version 3.2 (Ronquist *et al.*, 2012).

Metropolis-Coupled Markov Chain Monte Carlo sampling was used to calculate posterior probabilities. The analyses were run using default settings for priors. Chains were run for 1 million generations and sampled every 100 generations to obtain 10,000 sampled trees. Maximum Likelihood was estimated using MEGA version 6 (Tamura *et al.*, 2013) with 1000 bootstrap replicates. TRACER version 1.7.1 (Rambaut *et al.*, 2018) was used to check for chain convergence and adequate effective sample size (> 200). Posterior probabilities (decimals) and bootstrap values (percentages) were used to assess the level of branch support.

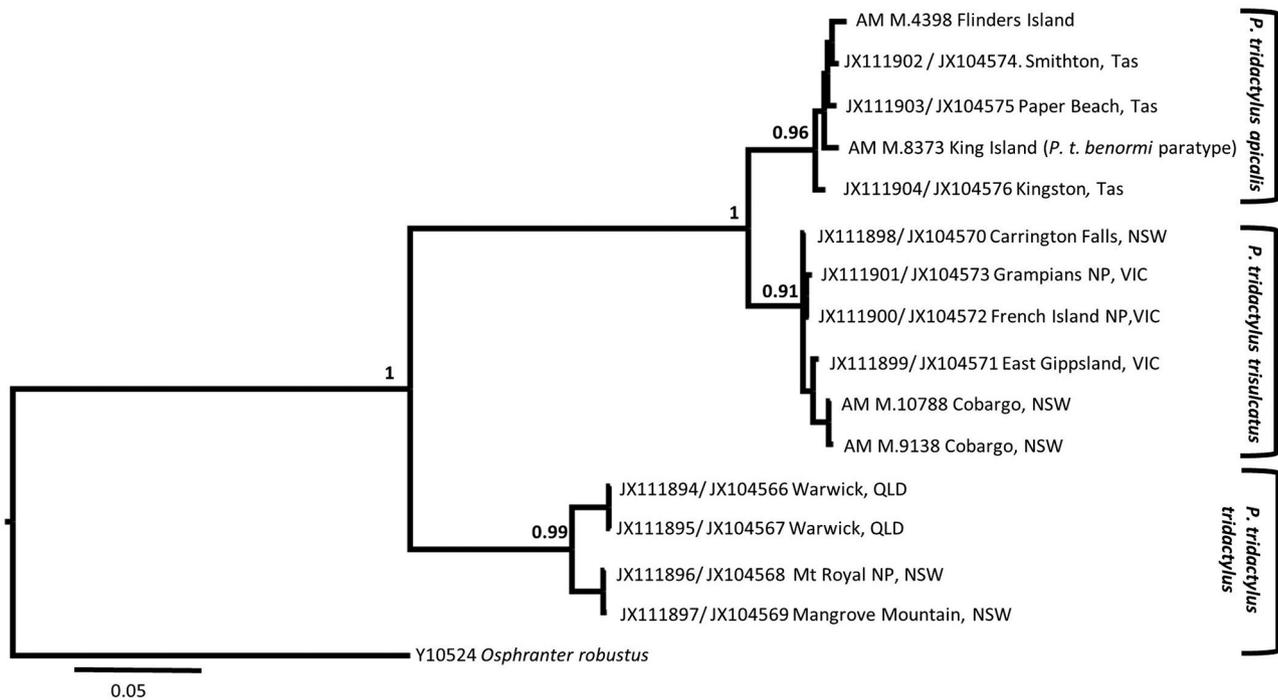
## Results

Partial *COI* and *ND2* fragments were recovered from specimens from both King and Flinders Islands with differing success. 695 bp of *COI* sequence was obtained from both King Island samples (AM M.8373, AM M.8319), from one Flinders Island sample (NMV C8859), and both Cobargo (NSW) samples (AM M.9138, AM M.10788). One of the overlapping *COI* sections failed to amplify in the remaining Flinders Island sample (AM M.4398) and only 490 bp of *COI* was recovered from this sample. A total of 344 bp of partial *ND2* were successfully amplified from one Flinders Island sample (AM M.4398) and one King Island sample (AM M.8373) and both Cobargo samples (AM M.9138, AM M.10788). Amplification failed in the remaining King (AM M.8319) and Flinders Island (NMV C8859) samples. Sequence data were deposited into GenBank (accession numbers, *COI*: MT422368–MT422373; *ND2*: MT431409–MT431412).

Phylogenetic analyses were carried out on two datasets, one with *COI* only in order to maximize the data available from the Bass Strait Islands, including investigating the placement of the *Potorous tridactylus benormi* holotype and paratype (Fig. 3), and one with *COI* and *ND2* concatenated in order to maximize the mtDNA data available for analyses (Fig. 4). The ML and BI trees for both data sets resolved trees of similar topology, with three well supported lineages concordant with currently recognized subspecies, the resolution however was superior in the concatenated dataset. The King and Flinders Island samples analysed in this study consistently grouped with samples of *Potorous tridactylus apicalis*, the Tasmanian subspecies, across all analyses.



**Figure 3.** Maximum Likelihood phylogenetic tree inferred from 695 bp of *COI* mtDNA sequence, including data from the *Potorous tridactylus benormi* Holotype (AM M.8319) and Paratype (AM M.8373). Bootstrap values for major lineages are shown. A similar tree topology was inferred from Bayesian inference.



**Figure 4.** Bayesian Inference phylogenetic tree inferred from 1039 bp of concatenated *COI* and *ND2* mitochondrial DNA sequence data. Posterior probabilities for major lineages are shown. A similar tree topology was also inferred from Maximum Likelihood.

## Discussion

Although only partial fragments (695 bp of *COI* [ $n = 4$ ] and 344 bp of *ND2* [ $n = 2$ ]) were available for analysis, these data consistently placed the individuals from both King and Flinders Islands within the Tasmanian subspecies *Potorous tridactylus apicalis*. The topology of the phylogenetic trees generated in this study were concordant with those describing three divergent potoroo subspecies generated by Frankham *et al.* (2012) who examined a longer mtDNA fragment of 2103 bp of *COI* and *ND2* from 11 potoroo samples, as well as 1893 bp of nuDNA. These subspecies were *Potorous tridactylus tridactylus* (distributed in New South Wales north of Sydney and in southeast Queensland), *Potorous tridactylus trisulcatus* (New South Wales south of Sydney, plus Victorian and South Australian populations) and *Potorous tridactylus apicalis* (Tasmanian populations). In addition, Frankham *et al.*, (2016) examined c. 630 bp of mtDNA control region from 347 individuals and resolved the same three lineages with the larger sample size from across the species distribution. The concordance of the current data with these previous studies lends confidence in the placement of the sequences obtained from the museum skins. The current study is limited to the examination of mtDNA (more reliably amplified from museum skins) and so does not allow for further investigation of nuDNA and the possibility of introgression between subspecies. However, Frankham *et al.* (2012) investigated both mtDNA and nuDNA and found no evidence of introgression and both nuDNA and mtDNA sequence data were able to distinguish between Tasmania and the mainland populations. Thus, we believe that mtDNA is a reliable indicator of subspecies boundaries in this species. This closer affinity with Tasmania is congruent with the few other molecular studies of small or specialist mammal species with a *trans*-Bassian distribution that have also included samples from the Bass Strait Islands, including, Southern Brown Bandicoots (*Isodon obesulus*) (Flinders Island only) (Cooper *et al.*, 2018) and Platypus (*Ornithorhynchus anatinus*) (King Island only) (Gongora *et al.*, 2012). A mtDNA study by Le Page *et al.* (2000) on the larger red-neck wallaby (*Notamacropus rufogriseus*) included samples from both King and Flinders Islands, as well as samples from Tasmania and mainland Australia (Warwick, QLD). Results from this study suggested Flinders Island samples grouped more closely with mainland Australia while King Island animals showed a closer affinity to Tasmanian samples. Historical connectivity between Tasmania and mainland populations and a lack of significant differentiation across Bass Strait have been shown in mtDNA studies for other generalist or larger more vagile species including Eastern Grey Kangaroos (*Macropus giganteus*) (Zenger *et al.*, 2003) and Emu (*Dromaius novaehollandiae*) (Thomson *et al.*, 2018).

While King and Flinders Islands are geographically closer to Tasmania (and associated islands) at present, the formation sequence of the Bassian Plain also supports the closer relationship between Tasmanian and Bass Strait Island potoroo populations. As the sea level fell during the last glacial maximum, the Furneaux Island Group would have first enlarged, merged, and formed a connection with north-eastern Tasmania, followed by a similar process exposing the land around King Island and forming a connection with north western Tasmania. These connections would have occurred

prior to the connection with mainland Australia (Hope, 1963; Lambeck & Chappell, 2001). This process, over thousands of years, would have allowed for the expansion northward of Tasmanian faunal populations, much earlier than mainland populations could move south. It was also suggested by Frankham *et al.*, (2016) that much of the Bassian Plain likely contained unsuitable habitat for Long-nosed Potoroos, which resulted in an extended period of genetic isolation (estimated 2.45 million years) between the Australian mainland and Tasmanian populations despite the periodic presence of a land bridge. Although molecular dating was not carried out for this study, the inclusion of individuals from the Bass Strait Islands in the analysis did not significantly alter the tree topology for either *COI* or *ND2* based on the data of Frankham *et al.* (2012). Therefore, it is likely that suitable habitat for dispersal was found along the northern coasts of Tasmania and into the Furneaux Island Group and King Island, but did not extend further north or into the central Bassian Plain, forming a barrier to dispersal and gene flow, and maintaining this deep divergence even during the last glacial maximum.

As part of this study we generated DNA sequence data from the holotype and paratype of *Potorous tridactylus benormi* Courtney, 1963, from King Island. This taxon was described on the basis of size and colour, being on average smaller and having a dark grey-brown belly compared to “the typical race” (Courtney, 1963). Sequences obtained from these specimens however, were similar to, and nested within the Tasmanian *Potorous tridactylus apicalis* lineage identified by Frankham *et al.* (2012). These genetic data indicate that subsequent authors were correct in not recognizing the proposed subspecies *Potorous tridactylus benormi* Courtney, 1963. The morphological measurements given for the male holotype of *Potorous tridactylus benormi* described by Courtney (1963, p. 19) as “rather old and very fat” with a mass of “2 lb 6 oz” (1.07 kg), are not smaller than male potoroos measured in Smithton, north west Tasmania or Naringal in Victoria (Fig. 1). Smithton males have been recorded weighing c. 800 g to over 1 kg (Heinsohn, 1968; unpublished data) and several studies on Naringal populations have recorded males average c. 780 g (Bennett, 1987; Long, 2001; unpublished data). Surveys of Long-nosed Potoroos across their range, which encompasses a variety of different habitats, soil and geology types, have documented morphological variation in pelage colour and morphometric measurements that includes the variation seen in the King Island population (e.g., hindfoot measurements). These data suggest the King Island potoroos described by Courtney (1963) were not significantly smaller overall, but instead that at the time of publication the extent of the morphological variation in potoroo populations across their range was still largely undocumented (Heinsohn, 1968; Johnston & Sharman, 1976; Bennett, 1987; Bryant, 1989; Mason, 1997; Long, 2001; Frankham *et al.*, 2011; Norton *et al.*, 2011).

Dried study skins from natural history collections are often the only representatives of rare or extinct populations, in this case, the last potoroo trapped on a Bass Strait Island was caught in 1970 (Johnston, 1973), predating the establishment of tissue collections in any Australian museum and routine tissue sampling as part of general survey methods. The availability of low template DNA extraction methods, meant that from these skins, ranging in age from 45 to 85 years old, we were able to amplify up to 1039 bp of mitochondrial

DNA allowing us to place with confidence Long-nosed Potoroos found on King and Flinders Island within the Tasmanian subspecies. These museum skins have provided valuable insights about Long-nosed Potoroo populations on the Bass Strait Islands and these data should guide any future conservation management decisions regarding these populations, e.g., any translocations or re-introductions should be sourced from Tasmanian populations. More broadly, the range of taxa represented in museum collections, coupled with continually-improving genomic techniques, means there is great museum-based potential for unlocking genetic information to continue to improve our knowledge of the evolutionary history of the Australian fauna (Eldridge *et al.*, 2020).

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