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Integrative taxonomic investigation of *Petaurus breviceps* (Marsupialia: Petauridae) reveals three distinct species

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The Australian sugar glider, *Petaurus breviceps s.l.*, is widely distributed across eastern and northern Australia. Examination of historical and contemporary collections of *Petaurus* specimens and phylogenetic analyses have revealed considerable taxonomic diversity within the genus. We aimed to utilize an integrative taxonomic approach, combining genetic and morphological evidence, to resolve the taxonomy of Australian gliders currently recognized as *Petaurus breviceps*. Herein, we confirm the existence of three distinct species: *P. breviceps*, ***P. notatus comb. nov.*** and ***P. ariel comb. nov.*** *Petaurus breviceps* and *P. notatus* are each represented by major mtDNA lineages in *P. breviceps*, while *P. ariel* forms a sister-lineage to *P. norfolcensis* and *P. gracilis*. Subtle morphological differences distinguish *P. breviceps* from the closely related *P. notatus*, while the morphological distinctions between *P. ariel* and its genetically similar sister-taxa, *P. norfolcensis* and *P. gracilis*, are more obvious. Given the purported broad geographic distribution of the taxon, *P. breviceps s.l.* was not listed as threatened, but dividing this taxon into three species has important conservation implications for all taxa in the group, particularly given the lamentable record for mammal extinctions in Australia. Concerted and targeted conservation efforts are necessary to preserve these distinct, newly described species.

ADDITIONAL KEYWORDS: Marsupialia – Diprotodontia – taxonomic revision – Australia – new species.

INTRODUCTION

Estimates of global extinctions suggests that the extinction rate for known taxa is currently ~1000 times the background rate (Pimm *et al.*, 2014), but it is likely that this rate is underestimated given the large number of taxa that remain undescribed (Raven & Yeates, 2007; Mora *et al.*, 2011; Costello *et al.*, 2013).

In Australia, the rapid decline in abundance and diversity of faunal species is testament to the global biodiversity crisis, with the loss of 30 endemic mammal species (Woinarski *et al.*, 2019). Widespread monitoring in northern Australia over the past 20 years has demonstrated the considerable extent of small-mammal declines in relatively intact landscapes. The declines have been linked to several factors, including changed fire regimes and increased predation by feral animals (Woinarski *et al.*, 2010; Ziembicki *et al.*, 2013; Fisher *et al.*, 2014; Woinarski, 2014).

Of particular concern is the fact that six of the nine species with most marked declines are arboreal (Fitzsimons *et al.*, 2010). Contemporary surveys

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have largely neglected the arboreal mammal fauna of the region and, consequently, these species may be under-represented in current status assessments. For example, despite being relatively well known from the savanna woodlands of the Northern Territory and reasonably well represented in museum collections, there have until recently been no targeted studies undertaken within the historical distribution of the sole gliding marsupial reconized in northern Australia, *Petaurus breviceps ariel* [*Belidea ariel* (Gould, 1842)]. Gliders have been detected on occasion by fauna monitoring programmes, but few programmes include targeted arboreal monitoring in their methods, so records are generally incidental (Woinarski *et al.*, 2010).

The genus *Petaurus* Shaw, 1791 (Marsupialia: Petauridae) comprises a group of marsupials characterized by a gliding membrane or patagium. Members of the genus occur throughout New Guinea and Australia and in parts of Indonesia, but it is likely that the group evolved in Australia (Flannery & Schouten, 1994; Malekian *et al.*, 2010b). Open forest became widespread in Australia during the Late Miocene to Pliocene (Archer & Hand, 1984), and gliding membranes are considered an adaptation of fauna to forests with an incomplete canopy, such as some eucalypt forests (Flannery & Schouten, 1994). Such adaptations restrict petaurids to forest areas and, consequently, these species are vulnerable to deforestation and habitat destruction (Rowston & Catterall, 2004).

The yellow-bellied glider (*Petaurus australis* Shaw, 1791), the squirrel glider [*P. norfolcensis* (Kerr, 1792)] and the mahogany glider [*P. gracilis* (De Vis, 1883)] are all endemic to the eastern parts of Australia (Strahan *et al.*, 2002). *Petaurus gracilis* is considered nationally Endangered and is restricted to coastal lowland woodland in northern Queensland (Environment Protection and Biodiversity Conservation Act, 1999). *Petaurus australis* is considered Vulnerable and *P. norfolcensis* is considered Endangered in the southern extent and Vulnerable in the centre of its distribution (New South Wales Biodiversity Conservation Act 2016; Victorian Flora and Fauna Guarantee Act 1988; Queensland Nature Conservation Act 1992). The sugar glider [*P. breviceps* (Waterhouse, 1838)] is the most widespread species of the genus, ranging from Tasmania, where it is thought to be introduced (Campbell *et al.*, 2018), through much of eastern and northern Australia and into New Guinea and several islands of Indonesia.

Three subspecies of *Petaurus breviceps* are currently recognized in Australia: *P. b. breviceps* (Waterhouse, 1838) ranges from southern Queensland, through eastern New South Wales and into Victoria and Tasmania, *P. b. longicaudatus* Longman, 1924 occurs in northern Queensland and *P. b. ariel* (Gould, 1842) occurs from near the Queensland–Northern Territory border, across the north of the continent (the 'top end') to north-west Western Australia (Fig. 1). The three subspecies are currently distinguished by subtle differences in colour and morphology, and by their geographic distributions (Gould, 1863; Smith, 1973; Jackson, 2012).

A recent molecular study that examined the systematics of the genus *Petaurus* highlighted our lack of knowledge of arboreal mammal fauna in northern Australia and divergence within recognized species of the genus (Malekian *et al.*, 2010a, b). The work demonstrated considerable mitochondrial DNA (mtDNA) divergence within the genus *Petaurus* and particularly within *P. breviceps*. Malekian *et al.* (2010a) identified two divergent mtDNA clades of *P. breviceps* distributed over distinct geographical ranges in eastern Australia. Intraspecific sequence divergence between these clades ranged from 10.4 to 12.2%, substantially greater than the interspecific divergence between *P. norfolcensis* and *P. gracilis* (1.8–2.2%) and similar to that between *P. breviceps* and *P. norfolcensis* (10.3–16.7%) (Malekian, 2007). The geographical distribution of these divergent clades is discordant with the recognized distribution of the two eastern subspecies of *P. breviceps*, and Malekian *et al.* (2007) supported the recognition of these lineages as distinct Evolutionarily Significant Units (Ryder, 1986) until their taxonomy could be revised. In addition to the divergence within *P. breviceps*, several samples obtained from the Northern Territory raised questions about the identity of the gliding marsupial found

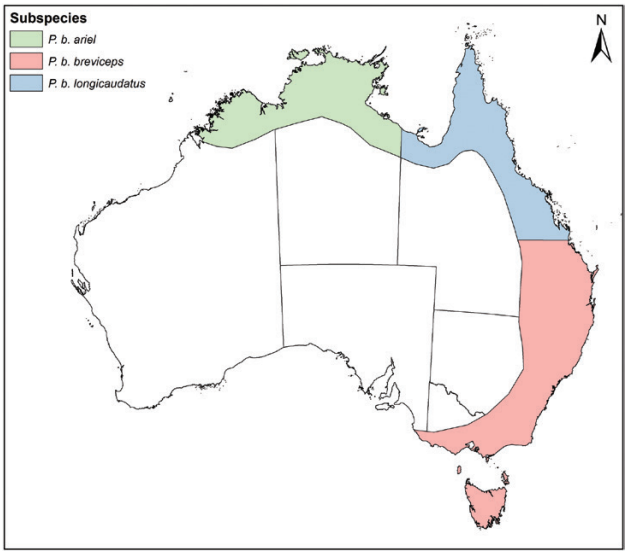

Figure 1. Currently recognized distribution of the three subspecies of *Petaurus breviceps* [modified from Smith (1973)].

in northern Australia that is currently recognized as a subspecies of *P. breviceps*, namely *P. b. ariel*. However, the genetic samples assayed did not group within *P. breviceps* but fell outside the *P. breviceps* mtDNA clades and showed a stronger affiliation with *P. norfolcensis* and *P. gracilis*. Malekian *et al.* (2010a), therefore, questioned the taxonomic identity of *P. b. ariel*. However, a lack of genetic and morphological material prevented further investigation at the time. New Guinean sugar gliders appear to have a more complex phylogenetic structure. Malekian *et al.* (2010b) identified five divergent clades from New Guinea forming a monophyletic group to the exclusion of the two clades identified within Australian *P. breviceps*. Malekian *et al.* (2010b) suggest the existence of cryptic diversity in New Guinea; an investigation of that is beyond the scope of the current revision.

Given the current setting of widespread small-mammal decline in northern Australia (Woinarski *et al.*, 2010), determining the identity of the marsupial glider found in northern Australia should be considered a matter of urgency. More broadly, there is a need to address the discordance between the current designation of *P. breviceps* subspecies and the proposed taxa using a combination of genetic and morphological information. Here, we investigate the taxonomic resolution of gliders currently identified as *P. breviceps* using a total evidence approach. We combine mtDNA and nuclear DNA sequence data from wild-caught and museum specimens with morphological examination of skulls (including type specimens) held in national and international collections. In particular, we aim to: (1) determine the taxonomic identity of gliders from northern Australia currently classified as *Petaurus breviceps ariel* and (2) incorporate morphological evidence to assess the divergent mtDNA lineages of *P. breviceps* on the east coast of Australia and resolve their taxonomy.

MATERIAL AND METHODS

Tissue samples

Skin samples ($N = 90$) were collected from live animals (trapping, nestboxes and opportunistic capture) from various locations across northern Australia (for details see Supporting Information, Table S1) for DNA analysis. Additional samples were obtained from tails ($N = 11$) of deceased gliders opportunistically encountered from the region following predation events. DNA was also extracted from museum specimens ($N = 49$), mostly from dried skins and alcohol-preserved liver samples. Additional DNA samples ($N = 87$) for petaurid gliders, representing the species *Petaurus abidi* Ziegler, 1981, *P. australis*, *P. breviceps* and *P. norfolcensis*, were sourced from the South Australian Museum [from the study of Malekian *et al.* (2010a); Supporting Information, Table S1]. *Petaurus abidi* was included in the analysis because it has a relatively stable taxonomic history (Flannery & Schouten, 1994) and is a sister-species, with strong support, to a monophyletic group comprising other Australian and New Guinean sugar and squirrel gliders, including *P. breviceps*, making it an ideal outgroup taxon (Malekian *et al.*, 2010a).

Genetic analyses

DNA was extracted from skin or liver tissue using the Gentra Puregene extraction kit and methods specified by the manufacturer (Gentra Systems Inc.). Previous molecular analyses of *P. breviceps* (Malekian *et al.*, 2010a, b) used a ~700-bp segment of the mtDNA NADH dehydrogenase subunit 2 gene (*ND2*) and, therefore, this gene marker was also utilized in the current study to assess species boundaries and relationships among taxa. *ND2* was PCR-amplified using the primers m635 (5'-GCACCATTCCACTTYTGAGT-3') and m636 (5'-GATTTGCGTTCGAATGTAGCAAG-3') (Osborne & Christidis, 2001). We also generated sequence data from two nuclear genes: the von Willebrand factor (*vWF*) gene and the *ω-globin* gene, both of which have been used in previous phylogenetic studies of petaurids (Malekian *et al.*, 2010a, b; Meredith *et al.* 2010). Data were also generated for the nuclear genes *BRCA1* (~570 bp) and *RAG-1* (~520 bp) for *4–6* NT specimens, but these sequences showed limited/no variation from orthologous sequences from *P. breviceps* and *P. norfolcensis*, and additional data for these genes were not generated (results not shown). A 945-bp fragment of *vWF* (exon 28) was amplified using primers 5'-GACTTGGCYTTYCTSYTGGATGG-3' and 5'-TTGATCTCATCSGTRGCRGGATTGC-3' (G807/G2526; Amrine-Madsen *et al.* 2003). A 700-bp segment of *ω-globin* was PCR amplified using primers G314 (5'-GGAATCATGGCAAGAAGGTG-3') and G424 (5'-CCGGAGGTGTTYAGTGGTATTTTC-3') (Wheeler *et al.*, 2001).

PCR amplifications were carried out in 25-μL volumes containing 0.1 U AmpliTaq Gold polymerase (Applied Biosystems), 1 × AmpliTaq Gold Buffer, 0.20 mM dNTPs, 2.5 mM $MgCl_2$, 0.5 μM of each primer and approximately 100 ng genomic DNA. Thermocycling conditions were: initial activation at 94 ℃ for 3 min; 35 cycles of denaturation at 94 ℃ for 30 s, annealing at 48 ℃ (*ND2*) or 55 ℃ (*vWF* and *ω-globin*) for 45 s and extension at 72 ℃ for 60 s; and a final extension at 72 ℃ for 3 min. PCR products were purified using Millipore MultiScreen PCR384Filter Plates (Millipore) and were capillary sequenced by the Australian Genome Research Facility (AGRF) using the ABI Prism Big Dye Terminator Cycle Sequencing

Kit (Applied Biosystems). Sequencing was carried out on an ABI 3700 DNA analyser and edited using SEQED v.1.0.3 (Applied Biosystems). Sequences were submitted to GenBank (Supporting Information, Table S1).

Phylogenetic and haplotype network analyses

DNA sequences were edited and aligned using the GENEIOUS alignment option within GENEIOUS v.9.1.2 (www.geneious.com). Pairwise distances among mitochondrial haplotypes were determined using GENEIOUS and the HKY-85 model of sequence evolution (Hasegawa *et al.*, 1985). GENEIOUS was also used to construct neighbour joining (NJ) trees using the HKY-85 distances. The robustness of nodes in the NJ trees was assessed by 1000 bootstrap replicates.

Identical *ND2* haplotypes were removed and the *ND2* data were phylogenetically analysed using maximum likelihood (ML) as implemented in the program RAxML v.7.2.8 (Stamatakis *et al.*, 2008) provided as a plugin for GENEIOUS (v.9.1.2). The program PartitionFinder v.1.1.1 (Lanfear *et al.*, 2012) was used to find an appropriate partitioning scheme and models of nucleotide evolution for each partition, considering first, second and third codon positions of *ND2* as distinct partitions. The best partitioning scheme based on the Bayesian information criterion suggested modelling first, second and third codon positions of each gene separately, each with the general time reversible (GTR) model (Rodriguez *et al.*, 1990) and with unequal variation at sites modelled using a Gamma (G) distribution (Yang, 1996). Robustness of branches on the tree was assessed using 500 bootstrap pseudoreplicates. Trees were visualized using FigTree (v.1.4.2; http://tree.bio.ed.ac.uk/), using a mid-point root. The mid-point root matched the position of the root given in analyses of *Petaurus* taxa by Malekian *et al.* (2010b) and in separate BEAST analyses of a reduced dataset including outgroup petaurid taxa (see details below).

The *vWF* and *ω-globin* sequence data showed low levels of divergence [20 single nucleotide polymorphic (SNP) sites for *vWF* and 13 SNP sites for *ω-globin*]. Therefore, a haplotype network approach was used to visualize the relationships among haplotypes from different species and geographic regions. Ambiguities in *vWF* sequences representing polymorphic variation were resolved manually into distinct haplotypes for each individual. No ambiguities were found for *ω-globin* data, but two sites within a *ω-globin* intron showed the presence of an insertion/deletion (indel) and to utilize these sites for phylogenetic analyses they were coded as a nucleotide difference. Unrooted NJ networks, based on HKY-85 distances (Hasegawa *et al.*, 1985) among haplotypes, were derived using GENEIOUS, exported as a NEWICK tree and then converted into haplotype networks using the program HAPLOVIEWER (developed by G. Ewing, http://www.cibiv.at/~greg/haploviewer).

Species delimitation analyses using *ND2* data

Under the unified species concept (USC; De Queiroz, 2007), the operational criteria we used for delimiting species were the presence of monophyletic groups of individuals that were genetically divergent (HKY-85 distances > 2%) from other groups and showing concordance for independent genetic markers and morphological data. The *COI* data were also analysed using the program Automated Barcode Gap Discovery (ABGD; Puillandre *et al.*, 2012). The parameters used in the analysis were: Pmin = 0.001, Pmax = 0.1, steps = 10, X (relative gap width) = 1.5 and the Kimura 2 parameter distance model (TS/TV = 2.0). We also utilized the Species Delimitation plugin in GENEIOUS (v.9.1.2), which implements a method that calculates the probability of reciprocal monophyly under a null model of random coalescence (Rosenberg, 2007). Using the NJ tree and a cut-off probability P(AB) of 0.05, we tested whether different sister-groups or species defined using ABGD may have arisen through random coalescence. We also used the Species Delimitation plugin to calculate pairwise average distances between these groups/lineages in the NJ tree with distances based on the HKY-85 model.

Molecular clock analyses

In order to estimate the coalescent time of petaurid mtDNA haplotypes, molecular clock analyses were conducted on the *ND2* sequence data using BEAST v.2.4.7 (Bouckaert *et al.*, 2014). Exemplar sequences from Australian *Petaurus* species, and the New Guinean *P. abidi*, were included in the analyses. The best partitioning scheme based on the PartitionFinder analyses (see above) of petaurid gliders involved separate partitions for first, second and third codon positions of *ND2* using the models HKY+G, HKY+G and TrN+G, respectively (Hasegawa *et al.*, 1985; Tamura & Nei, 1993; Yang, 1996). The program BEAUti was used to define the site substitution models for each partition, and to assign molecular clock models and tree and parameter priors for different analyses. To calibrate the molecular clock, a divergence time of 4.46 ± 0.1 Mya for the appearance of *Petaurus* in the fossil record was used as a minimum bound. These fossils were a mixed sample of teeth from deposits at Hamilton Victoria that were considered by Turnbull *et al.* (2003) to be similar in appearance to *P. australis*

and *P. norfolcensis*. Hence, the 4.46 Mya date was placed on the root of the phylogeny = common ancestor of all the known extant Australian *Petaurus* species (Malekian *et al.*, 2010b). A lognormal distribution with an offset of 4.46 Mya, a mean (m) = 1.0 and a standard deviation (SD) = 1.25 was used as the prior distribution for this node calibration. A birth–death tree prior, using estimated birth and death rates and default values for each parameter, was used in the analyses. Molecular clock models and trees were linked across each partition. To estimate the time to most recent common ancestor (tmrca) of the NT species and its sister-species *P. norfolcensis*, a uniform prior ranging between 0.0 and 4.46 Mya was placed on the node connecting the two species. Finally, two different molecular clock models were used for comparison: a strict clock model and an uncorrelated lognormal model. The prior distribution of the molecular clock rate under a strict clock model was given a Gamma distribution with alpha = 0.001 and beta = 1000; the prior distribution of the uncorrelated lognormal model used an exponential prior distribution with m = 10.0 for the mean and a Gamma prior distribution with alpha = 0.5396 and beta = 0.3819 for the standard deviation.

BEAST analyses were run for 10 million generations in multiple independent runs to test for convergence, sampling parameters and trees, sampling every 2000 generations, using the CIPRES Science Gateway (Miller *et al.*, 2010). The program TRACER [v.1.6; Rambaut *et al.* (2013)] was used to evaluate convergence of parameter estimates following a burnin of 10%. TREEANNOTATOR (v.2.4.7, included in the BEAST package) was used to generate a maximum clade credibility tree of the 5000 trees that were sampled, using a burnin of 10% (500 trees). Trees were visualized and initially prepared for publication using the program FigTree v.1.4.2 (available from http://tree.bio.ed.ac.uk/software/figtree/).

Skull morphometrics

A total of 17 cranial and dental measurements, based on Van Dyck (1990) and Malekian (2007) were taken from 304 adult skulls (241 representing *P. breviceps*; 51 representing *P. norfolcensis*; 12 representing *P. gracilis* based on availability of different taxa in museum collections) using Mitutoyo (Kawasaki, Japan) digital callipers (to the nearest 0.01 mm). Only animals of known sex and geographic location, and with fully-erupted, permanent molars (therefore, deemed to be adult), were included in the study to minimize age variation. Tooth nomenclature followed Thomas (1888). Skulls were sourced from the Northern Territory Museum and Art Gallery (MAGNT) (*N* = 8), Australian Museum (AMS) (*N* = 88), Queensland Museum (QM) (*N* = 45), Museum of Victoria (MV) (*N* = 62), Western Australia Museum (WAM) (*N* = 18), South Australia Museum (SAMA) (*N* = 21), Commonwealth Scientific and Industrial Research Organisation (CSIRO) Australian National Wildlife Collection (ANWC) (*N* = 43) and the Natural History Museum, London (NHMUK) (*N* = 19). An additional 12 skulls of unknown sex were also examined.

Of these 316 skulls, we were able to match 38 with tissue samples for individuals where all skull measures were available. Tissue samples were obtained either at the time of preservation or isolated from museum skins.

Measured craniodental variables included: MSL = maximum skull length; BL = basicranial skull length, including incisors; ZW = maximum zygomatic width; IOW = width of interorbital constriction where sutures meet orbital cavities; LW = width between outermost lachrymal sinus; NW = width of nasals at the nasal/premaxilla/maxilla junction; RH = rostral height at premolar 1 to point over rostrum level with nasal / premaxilla/maxilla junction; ROW = width of rostrum at insertion point of upper canines; I^1–P^4 = insertion point of upper incisor 1 to upper premolar 4; I^1–P^1 = insertion point of upper incisor 1 to upper premolar 1; I^1–M^4 = insertion point of upper incisor 1 to upper molar 4; UTR = full length of upper tooth row including front of upper incisor; UML = upper molar length M^1–M^4; RW = maximum ramal width; LML = lower molar length M_1–M_4; I_2–M_4 = lower incisor 2 to lower molar 4; M_1W = width of lower molar 1 (depicted in Fig. 2).

External morphology

Measurements of external morphology were included where they had been collected and recorded at the time of preservation. External measures recorded were: wt = body weight (g); hb = head body length (mm); tv = tail–vent length (mm) from mid-vent to tip of tail proper (excluding hair at tip); pes = hind foot length (mm) from behind heel to tip of longest extended toe (excluding claw); ear = ear length (mm) from extended ear tip to notch at rear base of tragus.

Type specimens

Types were examined following the type examination procedure adopted by Van Dyck (1990) and (Ziegler, 1981). Colour nomenclature used in the holotype pelage description followed Ridgway (1912). Skull and dentition were not described. Type specimens were available for *Petaurus breviceps* and *Petaurus breviceps ariel*, but the skull of the *Petaurus breviceps* type is

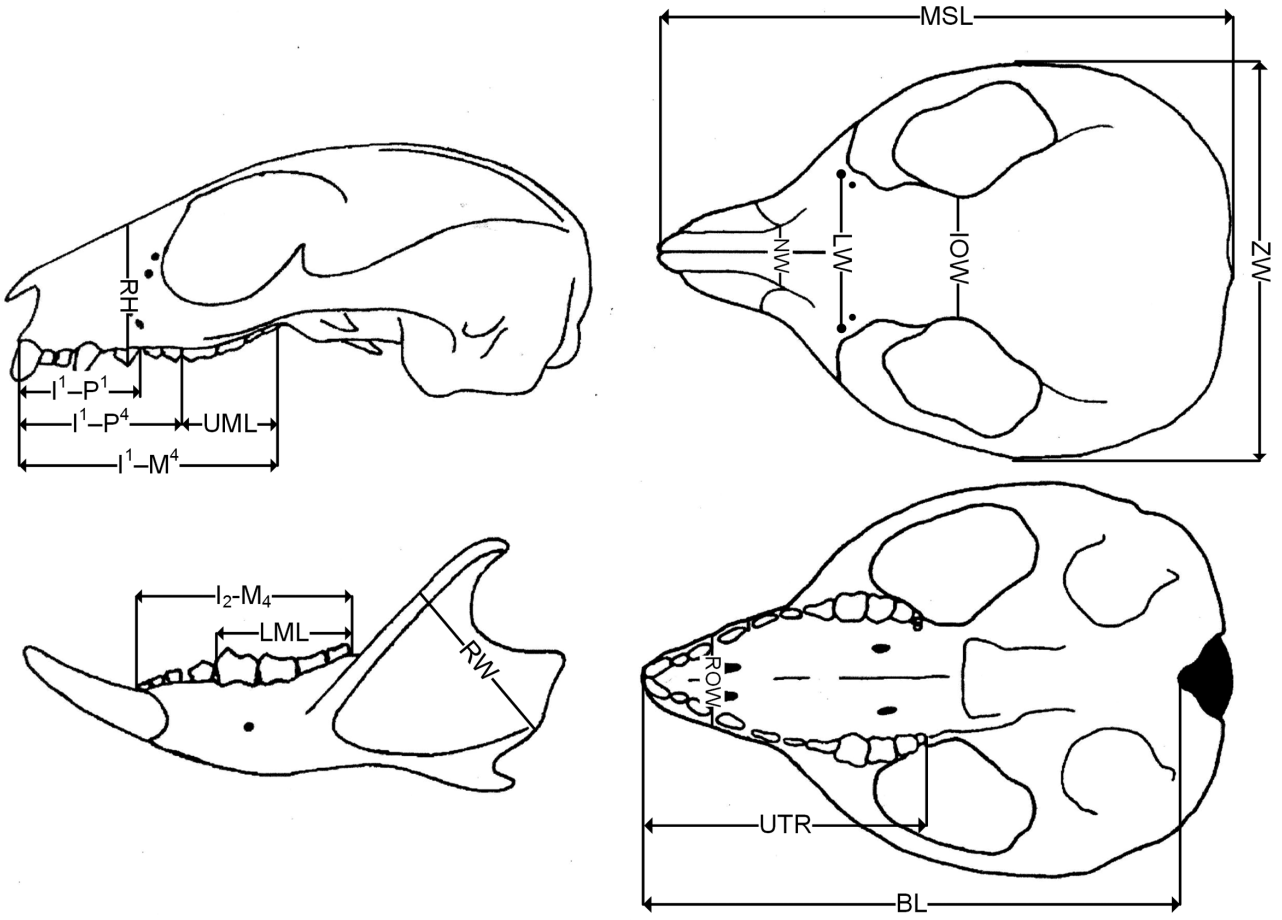

Figure 2. Craniodental measurements used in association with all *Petaurus* skulls. Abbreviation are described in the associated text.

missing (Tate, 1945). The type specimen of *Petaurus (Belideus) notatus* was held at the Royal Museum of Berlin, but documented as historically lost (McKay, 1988). The designated neotype for *Petaurus notatus* is held at the Victoria Museum.

Morphological statistical analyses

Statistical morphometric analyses were undertaken using the program SPSS v.24 (IBM, Armonk, NY). Univariate statistics (means, standard deviations, range minima and maxima) were compiled for craniodental and external measures for five Australian petaurid taxa (*P. b. ariel*, *P. b. breviceps*, *P. b. longicaudatus*, *P. gracilis* and *P. norfolcensis*). Samples were tested for normality and homogeneity of variance prior to subsequent analyses. Analysis of variance (ANOVA) was used to test for variation in means among the five Australian petaurid taxa examined. Post-hoc Tukey's HSD test was used to assess pairwise differences between species. All species were tested for sexual dimorphism, the results of which were inconsistent across species and variables. Given the widespread distribution of the species examined, we suspect that biogeographic/clinal variation has a stronger influence on morphological variation than sex. In most cases, we have analysed pairwise differences with the sexes combined.

Discriminant Function Analysis (DFA) was conducted using a reduced subset of variables to maximize inclusion of specimens with incomplete data due to specimen damage. Fifteen craniodental variables were included (BL and I_2–M_4 excluded). The exclusion of these characters also ensured that the *Petaurus breviceps ariel* lectotype skull (where specimen damage prevented the BL measurement) could be included in the analysis. A DFA was first performed using only those skulls with matching tissues. To achieve adequate sample size, males and females were pooled for analysis after confirming that the majority of craniodental characters were not significantly sexually dimorphic. We then conducted

a second DFA of skulls from *P.* ariel, *P. breviceps* and *P. notatus* without matching tissues. Here, we allocated skulls a priori to species groups based on their location. To allocate skulls, we constructed a species distribution map (Fig. 3), which was identified from genetic analysis. Due to uncertainty about their identity, skulls were excluded if they met any of the following criteria: Tasmanian specimens, South Australian specimens (without matching genetics) or specimens close to the geographic boundary for *P. breviceps* and *P. notatus* (without matching genetics).

RESULTS

MTDNA ANALYSES

The final *ND2* dataset comprised 173 sequences, of which 153 were newly generated for the current study (Fig. 4). These data included 107 sequences from Northern Territory gliders (106 new), seven new sequences from gliders of the Kimberley region in Western Australia, 15 sequences from *P. norfolcensis*/*P. gracilis* (11 new) and 44 from *P. breviceps* (29 new). The data were aligned and identical sequences removed to produce a *ND2* dataset of 124 unique sequences. NJ and ML analyses resulted in similar phenograms, with all NT specimens grouping to the exclusion of *P. breviceps*. The Northern Territory lineage, henceforth referred to as *P. ariel*, is a sister-lineage to a clade comprising *P. norfolcensis* and *P. gracilis*, supported by > 76% of bootstrap pseudoreplicates (Fig. 5). A third lineage comprising several individuals from the Central Kimberley region of Western Australia was also identified, which formed a sister-lineage to the *P.norfolcensis*/*P. gracilis*/*P. ariel* group, despite five samples from various locations across WA grouping within the *P. ariel* clade. Two major *ND2* lineages [referred to as AUS1 and AUS2 lineages by Malekian *et al.* (2010a)] were confirmed within *P. breviceps* specimens, each supported by high bootstrap values (75–100%; Fig. 5). Hereafter, the AUS1 and AUS2 lineages will be referred to by their proposed species names: *Petaurus breviceps* and *Petaurus notatus*, respectively. *Petaurus gracilis* grouped closely, but as a sister-lineage, to a group comprising *P. norfolcensis* individuals. However, an additional four specimens group with *P. gracilis* (see *P. gracilis* grp in Fig. 5), including one (NT007) that was collected from a location near Darwin and three from the Cape York Peninsula (C22465, DTC238 and DTC232). All were outside the current recognized geographic range of *P. gracilis*. We also measured skulls for these specimens; without a priori assignment to a species group, the DFA predicted group membership of all Cape York individuals within *P. breviceps*, while the single NT specimen was morphologically similar to *P. norfolcensis*.

Pairwise HKY-85 divergence estimates among the taxa and groups identified above range from 0.021 (between the *P. gracilis* group and *P. norfolcensis*) to 0.147 (between *P. norfolcensis* and *P. breviceps* clade). There was a low average intraspecific divergence distance within *P. ariel* (0.003) compared to an interspecies distance of 0.025 and 0.026 between *P. ariel* and *P. gracilis* or *P. norfolcensis*, respectively (Table 1).

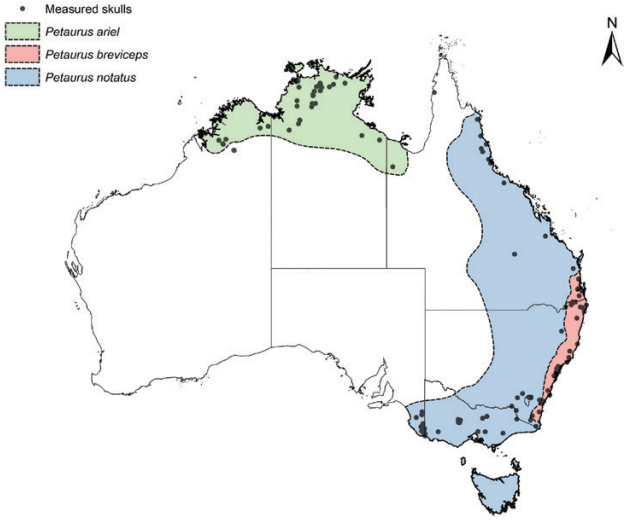

Figure 3. Proposed distribution of small *Petaurus* spp. in Australia constructed to enable allocation of skulls to proposed species groups. Skulls included in discriminant function analysis are shown as black circles.

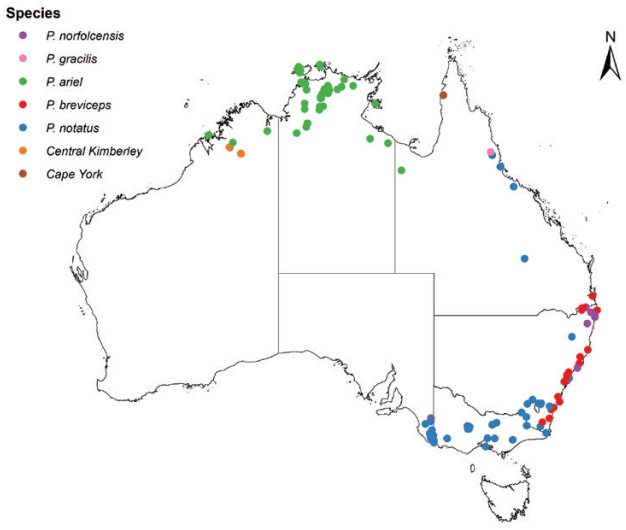

Figure 4. Schematic map of Australia showing the locality of the tissue samples used in the current study and their designated species based on *ND2* gene sequences.

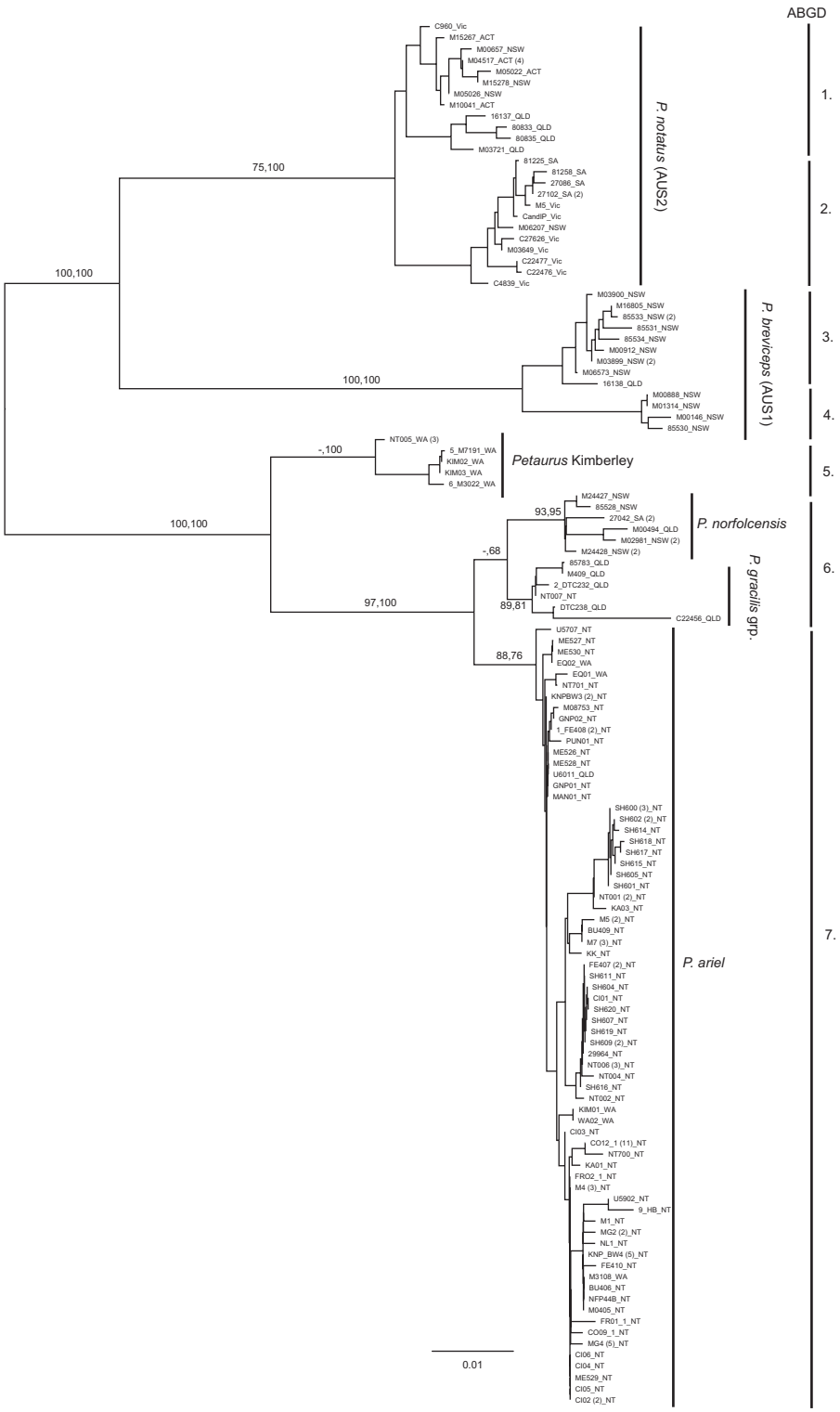

Figure 5. A neighbour joining phenogram of related petaurid species based on mitochondrial (*ND2*) gene sequences. A similar tree topology was obtained using maximum likelihood analyses (see Supporting Information, Fig. S1). The numbers on branches refer to bootstrap proportions as a percentage (left: ML; right: NJ). The seven groups, labelled in the tree, refer to groups identified using the ABGD species delimitation program, combined with the Roseberg (2007) test of random coalescence (see Material and methods).

Nuclear gene analyses

Sequence data from *vWF* were obtained from 70 specimens, of which 16 were found to be heterozygous for distinct *vWF* haplotypes. The final dataset comprised 86 *vWF* sequences, and 20 sites were found to have SNPs, resulting in 22 distinct haplotypes. Sequence data for *ω-globin* were obtained from 26 *P. ariel* specimens, and one Kimberley specimen, and were analysed with data from Malekian *et al.* (2010b) to give a dataset of 45 specimens. Overall, 11 SNPs and two indels were detected, which resolved into 13 distinct haplotypes. Haplotype networks for *vWF* and *ω-globin* data each showed the presence of fixed, or near fixed, haplotype differences among specimens of *P. ariel* compared to *P. breviceps*, *P. gracilis*, *P. norfolcensis* and *P. notatus* (Fig. 6). Six distinct *vWF* haplotypes were found in 46 *P. ariel* specimens, two of which were shared with the mitochondrially distinct Kimberley specimens. One *vWF* haplotype, present in a single individual from Melville Island NT, was also present in specimens of *P. breviceps*, *P. gracilis*, *P. norfolcensis* and *P. notatus*. This likely represents an ancestral haplotype (i.e. a haplotype present in the common ancestor of all species), rather than introgression among species (Kingman, 1982). A single *ω-globin* haplotype that occurred internally in the haplotype network, but not detected in any of the other glider species analysed, was present in the 25 *P. ariel* specimens and one mitochondrially distinct Kimberley specimen. In addition, *P. breviceps* and *P. notatus* specimens showed distinct *ω-globin* haplotypes and *P. breviceps* individuals showed numerous private (i.e. unique to the species) haplotypes compared to *P. notatus*.

Species delimitation analyses

ABGD analyses resulted in nine recursive groups being identified for the *ND2* data. Several of these groups were represented by one to three individuals with distinct sequences (C22456 from northern Queensland; NT005 from the Kimberley, WA), and when analysed using the Rosenberg (2007) test, as implemented in GENEIOUS, the null model of random coalescence was not rejected. Therefore, the combination of ABGD analyses and the Rosenberg (2007) test supported the presence of seven putative species groups, one of which was represented by all *P. ariel* individuals and a second group represented by the Kimberley individuals (Fig. 6). *Petaurus gracilis* and *P. norfolcensis* formed a single group, while *P. breviceps* and *P. notatus* were each found to comprise two groups.

Molecular clock analyses

Petaurid glider *ND2* data were further analysed using BEAST molecular clock analyses to estimate the coalescent time of mtDNA haplotypes from *P. ariel* relative to *P. norfolcensis*/*P. gracilis*. Estimated sample size (ESS) values for all parameters are > 263, suggesting that an adequate sample of the posterior distribution for each parameter had been obtained for all analyses. The Bayesian tree under the strict molecular clock model showing estimated dates of divergence and 95% confidence intervals on each node, is shown in Figure 7. Under this model, the time to most recent common ancestor (MRCA) estimate for the three taxa was 208 000 years [95% posterior distribution (PD) ranges from 106.4 to 328.2 thousand years]. Under an uncorrelated lognormal relaxed clock model, the estimate for the MRCA is 228 000 years (95% PD from 87.1 to 405 thousand years). MRCA estimate for *P. breviceps* and *P. notatus* was 1 million years (95% PD ranges from 600 thousand years to 1.4 million years). Similar values were obtained in independent analyses using these different molecular clock models (results not shown).

Morphological analyses

Discriminant function analysis (DFA) of 15 craniodental skull measurements from those gliders originally designated as *P. breviceps* with matching tissue samples indicate that 100% of individuals cluster distinctly into the three taxon groups identified from genetic analyses (Fig. 8).

A subsequent DFA of 126 skulls from Australian specimens using a priori grouping based on their

Table 1. Average pairwise sequence divergence (HKY-85 distance) for *ND2* within and among *Petaurus* taxa and groups

	1	2	3	4	5	6
1. *P. ariel*	0.003					
2. *P. gracilis*	0.025	0.010				
3. *P. norfolcensis*	0.026	0.021	0.008			
4. Central Kimberley	0.053	0.059	0.061	0.005		
5. *P. breviceps*	0.139	0.146	0.147	0.127	0.012	
6. *P. notatus*	0.119	0.125	0.127	0.107	0.102	0.010

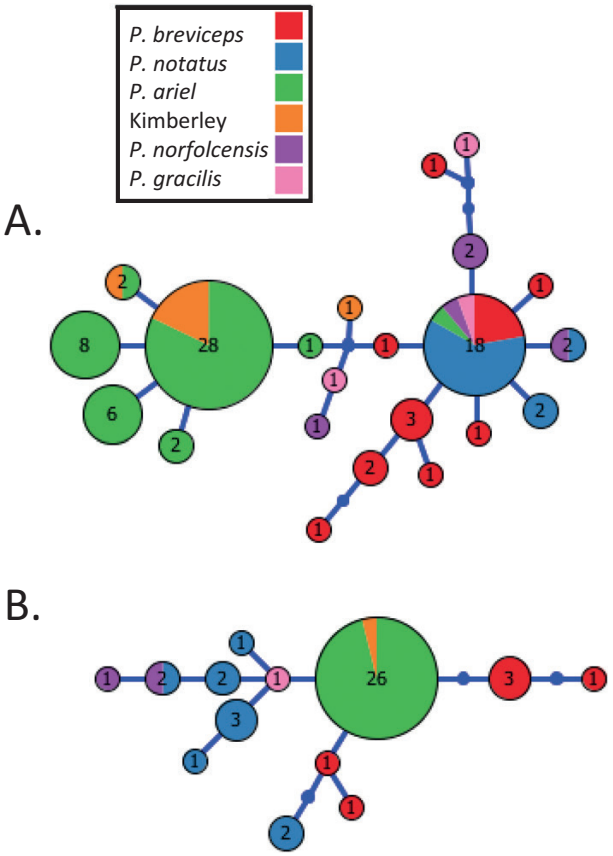

Figure 6. Unrooted neighbour joining haplotype networks based on (A) 20 SNP sites for *vWF* and (B) 13 SNP sites for *ω-globin*; node size is proportional to haplotype frequency and branch lengths to the number of substitutions.

location and analysed separately by sex, indicated that 98% of males and 96% females clustered into the three proposed Australian taxon groups (Fig. 9). With reference to the *P. ariel* type skull (NHMUK 1842.5.26.1), squared Mahalanobis distance to group centroid is 0.23 and probability of group membership within *P. ariel* based on skull morphology is $P = 0.997$. In the absence of a matching tissue sample we could still be confident, based on craniodental morphology, that the *P. breviceps ariel* lectotype conforms to the current form of *P. ariel* found across northern Australia. Furthermore, other tissue samples from the lectotype locality grouped with *P. ariel*. The designated *P. notatus* neotype skull fits within the *P. notatus* group with a squared Mahalanobis distance to group centroid of 1.013 and probability of group membership within *P. notatus* based on skull morphology $P = 0.999$. No type skull is available for *P. breviceps*.

To facilitate direct comparison of skull morphology, univariate statistics (means, SD, etc.) are shown for 17 craniodental and five external characters from the five Australian petaurids (*P. ariel*, *P. breviceps*, *P. gracilis*, *P. norfolcensis* and *P. notatus*) examined in this study (Tables 2–6). Despite a close genetic relationship between *P. ariel*, *P. norfolcensis* and *P. gracilis*, the three groups were separated by more obvious craniodental morphology differences (Fig. 10). To examine what were relatively subtle morphological differences between the three small Australian gliders, the larger gliders; *P. norfolcensis* and *P. gracilis* were removed from analyses comparing small Australian gliders.

Taxonomic summary

Based on genetic and morphological evidence suggesting substantial distinction of the species described here, the revised taxonomy should reflect relationships among species within the genus *Petaurus*. We recommend that all specimens previously described as *Petaurus breviceps ariel* be referred to the species *P. ariel*. This elevation to species level is supported by genetic distances between *P. ariel* and *P. breviceps* individuals and their morphological distinction from the more closely related *P. norfolcensis* and *P. gracilis*. Gliders on the east coast of Australia with a distribution extending from the south of Cape York Peninsula down to Tasmania, previously referred to *P. breviceps breviceps* and *P. breviceps longicaudatus*, should be redesignated to either *P. breviceps* or *P. notatus*, based on the geographic distribution of species outlined in Figure 3. The division of the latter two species was supported by both genetic distances and an apparent geographical barrier coincident with the Great Dividing Range. The nomination of *P. breviceps* and *P. notatus* was based on types collected from Sydney (NSW) and Port Phillip (Vic.), respectively. The type specimen locations fall clearly within the proposed distributions for these species, and the general morphological descriptions of the types in the taxonomic literature fit the morphological patterns observed in other specimens from proximate locations. Because the type skulls were missing, we could not confirm their morphological similarity. There is a holotype skin for *P. breviceps*, which we have described, but the entire type specimen (skin and skull) for *P. notatus* is missing. Thus, we have designated and described a neotype for the latter species, which is genetically and morphologically corroborated and selected from a proximate geographic location to the type specimen (see Systematics section).

Some taxonomic uncertainty surrounds gliders occurring in both Cape York Peninsula and the Central Kimberley region. The type locality for the subspecies *Petaurus breviceps longicaudatus* is Mapoon Mission, which is approximately 125 km north of Aurukun, the location of two genetic samples that group with *P. gracilis*, despite similar morphology to *P. breviceps*. Further voucher-based research will be required to determine their relationships.

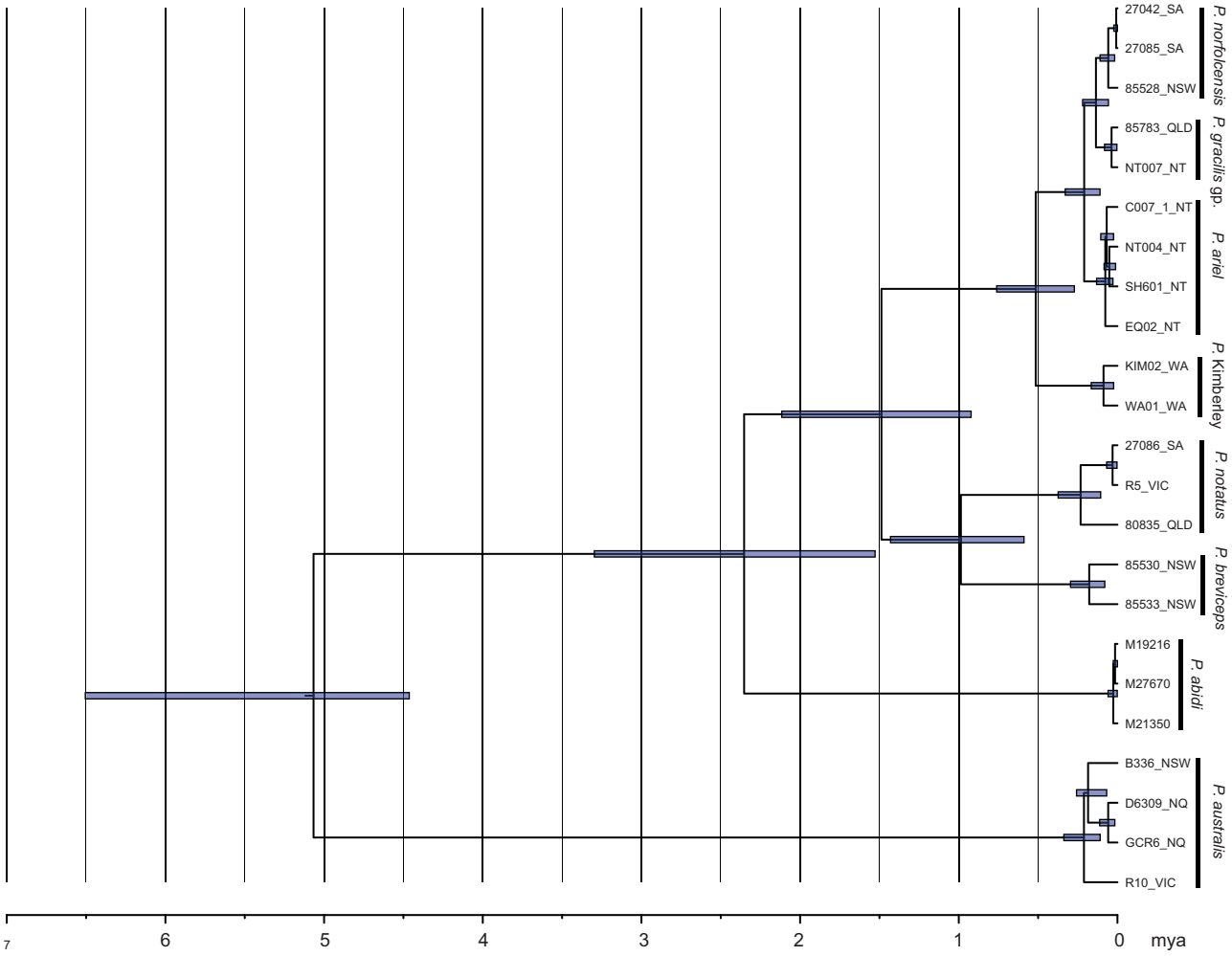

Figure 7. Bayesian tree under the strict molecular clock model, showing estimated dates of divergence and 95% confidence intervals on each node.

SYSTEMATICS

PETAURUS ARIEL (GOULD, 1842)

Recommended common name: Savanna glider.

Remarks: Originally designated as *Belidea ariel* by Gould (1842) before being synonymized within *breviceps* by Waterhouse (1846). *Petaurus breviceps ariel* was designated as a subspecies by Thomas (1922) and recognized by Iredale and Troughton (1934) and subsequent authors (summarized in: Jackson & Thorington, 2012).

Etymology: The species name *ariel* refers to 'a light and graceful spirit of the air', after a spirit in Shakespeare's play *The Tempest*.

Type specimen: Lectotype: NHMUK 1842.5.26.1, adult female skull, dentary and skin; lodged 26 May 1842 by John Gould from Port Essington, Northern Territory. Possibly collected by Mr Gilbert. Figure 11 depicts a photograph of the dorsal and ventral views of the specimen study skin and Figure 12 depicts features of the skull and dentary of the lectotype specimen.

Type locality: Port Essington is located within Garig Ganuk Barlu National Park on the Cobourg Peninsula. The peninsula is located on the north-west tip of Arnhem Land, 350 km east of Darwin in the Northern Territory, Australia (–11.335°, 132.138°). Live trapping was conducted near the lectotype locality as part of the present study, and we collected 11 tissue samples from wild caught individuals near the lectotype locality.

Distribution: The species is widely distributed across Northern Australia from the Gulf of Carpentaria to the Coast of the Kimberley and on several offshore islands. A specimen from Lawn Hill in Queensland

demonstrates the extent of the distribution of the species into western Queensland.

Diagnosis: Petaurus ariel displays substantial body size variation across its range. In the northern, more coastal parts of its range it is likely the smallest of all Australian *Petaurus* spp. However, in the southern, more arid parts of its range it can be more than double in size (Stobo-Wilson *et al.*, in press). *Petaurus ariel* appears to be the only species that occurs across the Top End of the Northern Territory and into Western Australia and thus it can be most easily distinguished based on location (Fig. 3). *Petaurus ariel* can be distinguished from its closest genetic relatives, *P. gracilis* and *P. norfolcensis*, by substantial size differences, with *P. ariel* being considerably smaller (Fig. 10). A distinctly cylindrical, thinly furred tail with little variation in fur length from the base to the tip also differentiates *P. ariel*. Compared to *P. breviceps*, and to a lesser extent *P. notatus*, *P. ariel* has a more clearly defined dorsal stripe, often extending all the way to a point between the hind legs. Throughout its range, *P. ariel* tends to have a stronger warm tone in its ventral fur when compared to *P. breviceps* and *P. notatus*.

The skulls of *P. ariel* have a significantly smaller maximum skull length, intra-orbital width, rostral height and rostral width than skulls of both *P. breviceps* and *P. notatus* (Table 4). A majority of tooth measurements were similar across all three species.

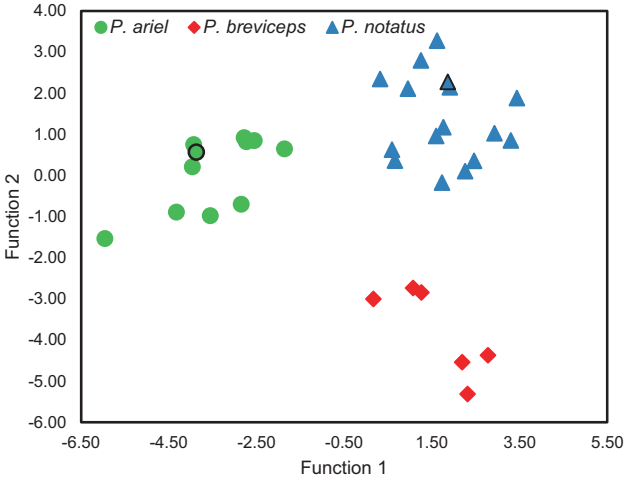

Figure 8. Scatterplot of canonical discriminant functions of small glider skulls with confirmed genetic species grouping via matching tissues. The position of the *Petaurus breviceps ariel* lectotype NHMUK 1842.5.26.1 and *Petaurus notatus* neotype MV C27626 are indicated with a black outline (○ and Δ, respectively); the skull for *P. breviceps* type is missing.

Description of lectotype 1842.5.26.1 of *Petaurus breviceps ariel*

External measurements: Hindfoot length: 22 mm; hand: 19 mm; head–body length: 155 mm; tail–vent length: 155 mm (tail appears incomplete, conversions from Gould's measurements suggest that the tail was 178 mm); ear length: 17 mm.

Pelage: Colours of the *Petaurus breviceps ariel* lectotype are as follows. Dorsal body coloration varies from light

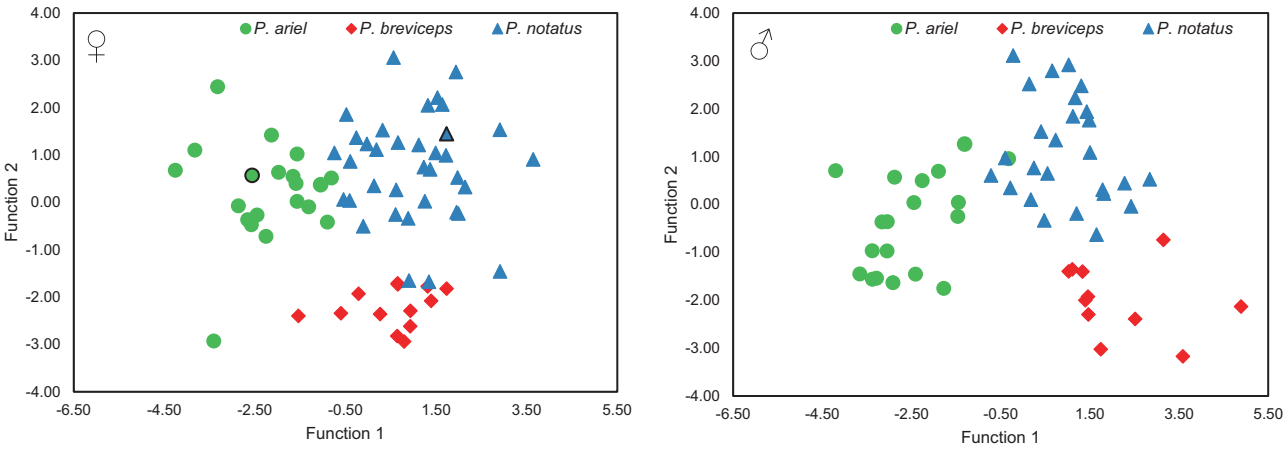

Figure 9. Scatterplot of canonical discriminant functions of female (♀) and male (♂) Australian glider skulls with a priori groupings based on location. The position of the *Petaurus breviceps ariel* lectotype NHMUK 1842.5.26.1 and *Petaurus notatus* neotype MV C27626 are indicated with a black outline (○ and Δ, respectively); the skull for *P. breviceps* type is missing.

Table 2. Univariate statistics: means, standard deviations (SD) and range minima and maxima of measured variables for *Petaurus breviceps*

	Males					Females				
	N	Mean	SD	Minimum	Maximum	*N*	Mean	SD	Minimum	Maximum
MSL	11	38.56	1.31	36.68	41.37	16	38.02	0.70	36.82	39.06
BL	11	34.03	1.33	32.43	37.02	15	33.17	1.08	30.87	34.62
ZW	12	26.81	0.84	25.35	28.41	16	25.94	0.73	24.17	27.31
IOW	12	8.62	0.75	7.36	9.72	16	8.84	0.28	8.18	9.25
LW	12	11.32	0.65	10.12	12.57	16	10.92	0.50	9.83	11.56
NW	12	4.80	0.52	3.92	5.39	15	4.63	0.28	4.28	5.28
RH	12	9.94	0.40	9.17	10.68	16	9.75	0.26	9.32	10.24
RoW	12	7.26	0.34	6.85	8.17	14	6.97	0.33	6.24	7.51
I^1–P^1	12	6.43	0.32	5.83	6.95	15	6.32	0.32	5.76	6.72
I^1–P^4	12	11.53	0.54	10.94	12.77	15	11.38	0.45	10.62	12.02
I^1–M^4	11	17.48	0.85	16.84	19.79	12	17.14	0.47	16.32	17.74
UTR	11	18.52	0.89	17.56	20.82	12	18.24	0.47	17.52	18.79
UML	11	6.63	0.37	6.23	7.57	12	6.49	0.15	6.27	6.77
I_2–M_4	9	11.03	0.79	10.41	12.93	12	10.95	0.34	10.39	11.46
LML	11	7.28	0.40	6.89	8.30	15	7.12	0.19	6.78	7.38
RW	12	9.16	0.55	8.23	10.29	16	8.67	0.33	8.05	9.31
M_1W	12	1.47	0.08	1.35	1.67	16	1.45	0.09	1.32	1.57
hb	4	168.25	6.99	160.00	175.00	2	163.00	11.31	155.00	171.00
tv	11	196.55	19.05	153.00	219.00	11	194.36	20.81	142.00	221.00
hf	12	26.81	2.22	23.00	30.00	11	25.73	2.49	21.00	29.00
e	12	27.17	2.59	23.00	30.00	11	27.18	1.83	23.00	29.00
wt	8	123.38	14.38	112.00	155.00	4	107.75	10.24	95.00	119.00

grayish olive to citrine drab. A mummy brown mid-dorsal stripe commencing at a point 4 mm posterior between the anterior edge of the eyes and extending posteriorly to a point over the rump, fading 25 mm from the base of the tail. The mid-dorsal stripe is irregular in width: 4 mm wide between the ears, 5 mm at mid-shoulder blades, 2 mm at the hips and fading over the rump. Fur of the mid-back is 12 mm long with colour varying over its length. The basal 8 mm is smoke grey, median 2 mm hair brown and apical 2 mm tipped pale smoke grey. The dorsal body is washed with olive buff with the wash being most pronounced over the rump but not giving a pronounced dappled appearance.

The head is furred with light greyish olive-citrine drab and a ring of fuscous black encircles the eye in a defined eye ring. Fuscous fur at the base of the pinna forms an incomplete circle, extending dorsally from the anterior edge of the pinna, adjoining the dark fur encircling the eye, to the ventral tragus. The inner surface and the distal 14 mm of the outer surface of the pinnae are sparsely furred with only scattered dark hairs visible. The pinnae of living animals are flesh-pink tending to fuscous black at the outer edge. A patch of deep olive buff fur on the posterior edge of the pinna forms a conspicuous tuft.

Dorsally, the gliding membrane or patagium is fringed along its length by a thickly furred 3–4 mm band of greyish olive fur (hairs 4 mm long). The patagium is sepia coloured and becomes interspersed with dorsal body fur closer to the medial surface of the patagium. Ventrally, the patagium is fringed in a 4 mm band of deep olive buff coloured fur from the claw of digit 5 to the ankle. More medially, this band is partially overlaid by drab fading to cream buff across the surface of the patagium with no distinct band. The soft ventral fur is cream buff lightened by a wash of light buff tending to chamois at the base of the throat.

A thin covering of fuscous hairs is present on the dorsal surface of the forefeet digits. Hindfeet are slightly more thickly covered chaetura drab, which gently contrasts with a less pronounced ‘mitten’ of sepia over the metatarsals extending up to the inner posterior region of the thigh in a triangular stripe almost to the top of the thigh. Longer drab fur (13-mm long hairs) forms a less pronounced fringe on the outer surface of the thighs.

The tail is thinly drab furred and may be incomplete in the specimen given its short length and abrupt tip (163 mm). The distal 53 mm tip of the tail is blackish brown on both dorsal and ventral surfaces. The

Table 3. Univariate statistics: means, standard deviations (SD) and range minima and maxima of measured variables for *Petaurus notatus*

	Males					Females				
	N	Mean	SD	Minimum	Maximum	*N*	Mean	SD	Minimum	Maximum
MSL	31	38.46	1.31	35.11	40.38	37	37.73	1.21	35.21	39.85
BL	31	33.76	1.20	30.21	35.73	37	33.05	1.21	30.39	35.21
ZW	31	26.90	0.93	24.37	28.41	36	26.36	0.71	24.91	27.81
IOW	31	9.18	0.58	7.70	10.35	37	9.29	0.53	8.15	10.67
LW	31	10.95	0.51	9.64	11.91	38	10.77	0.56	9.36	11.83
NW	31	4.15	0.67	2.89	5.57	38	4.10	0.46	3.02	5.01
RH	30	9.77	0.59	7.78	10.57	38	9.56	0.38	8.62	10.42
RoW	31	7.26	0.30	6.56	7.85	38	7.13	0.28	6.40	7.64
I^1–P^1	30	6.53	0.28	5.84	7.20	38	6.34	0.28	5.81	6.90
I^1–P^4	31	11.40	0.40	10.27	12.14	38	11.19	0.44	10.02	12.07
I^1–M^4	28	17.24	0.61	15.80	18.64	37	17.01	0.56	15.82	18.21
UTR	28	18.35	0.61	16.67	19.25	37	18.04	0.60	16.84	19.29
UML	28	6.66	0.28	6.07	7.19	37	6.57	0.20	6.16	6.99
I_2–M_4	29	11.02	0.37	10.06	11.83	34	11.04	0.32	10.17	11.57
LML	31	7.30	0.21	6.82	7.74	37	7.20	0.20	6.83	7.64
RW	31	9.13	0.48	7.83	9.99	37	8.81	0.46	7.71	9.62
M_1W	31	1.45	0.07	1.27	1.58	38	1.41	0.06	1.28	1.52
hb	5	171.90	11.49	160.00	188.00	6	165.50	8.12	157.00	177.00
tv	6	194.53	21.72	175.00	230.00	8	203.00	10.42	185.00	218.00
hf	6	26.73	2.37	24.00	30.00	8	26.66	2.65	22.00	31.50
e	6	27.80	2.66	24.90	31.00	7	26.09	1.63	24.00	29.00
wt	6	128.50	19.18	94.00	146.00	6	100.83	20.95	75.00	122.00

proximal 110 mm portion of the tail is dorsally coloured drab. The ventral surface of the tail is deep olive buff. Fur length 20 mm from the base of the tail is 16 mm long, and 40 mm from the tail tip is 11 mm long.

The lectotype skin is depicted in Figure 11. Note that males exhibit naked, ovoid glandular patches on the crown of the head within the black head stripe and at the base of the throat.

Vibrissae: Approximately 16 black mystacial vibrissae occur on each side and these are up to 23 mm long. Supra-orbital vibrissae (2); genals (3).

Pes and manus: The claws of the fore- and hindfeet are relatively large with maximum chord length of digit 4 and 5 claws approx. 9 mm. Digit 4 is the longest digit of manus or pes, and digit 4 > 5 > 3 > 2 > 1.

PETAURUS BREVICEPS (WATERHOUSE, 1838)

Recommended common name: Sugar glider.

Etymology: The species name *breviceps* derives from the Latin words *brevis*, short, and the suffix *-ceps*, headed.

Type specimen: Holotype NHMUK 1855.12.24.78, adult female skin (no skull located). The type skin is depicted in Figure 13.

Type locality: Jackson & Thorington (2012) lists the type locality as Sydney, NSW. However, we have been unable to locate any more specific locality information. The tag with the type specimens lists New South Wales and the texts of Waterhouse to accompany the specimen do not provide any evidence of a more specific type locality.

Distribution: Based on genetic and morphological evidence, the species distribution extends from the Victorian border in the south to north of Brisbane. The species occurs on the eastern or coastal side of the Great Dividing Range. Further research is needed to determine the extent of the distribution in southern coastal Queensland.

Diagnosis: Due to its more restricted, coastal distribution (Fig. 3), *P. breviceps* is the least variable of the small *Petaurus* spp. (Stobo-Wilson *et al.*, in press). *Petaurus breviceps* has a less clearly defined and often narrow dorsal stripe when compared to *P. ariel* and to

Table 4. Univariate statistics: means, standard deviations (SD) and range minima and maxima of measured variables for *Petaurus ariel*

	Males					Females				
	N	Mean	SD	Minimum	Maximum	*N*	Mean	SD	Minimum	Maximum
MSL	19	37.13	1.90	33.55	40.45	22	36.57	1.73	33.70	39.46
BL	20	32.78	1.81	29.08	35.59	20	32.34	1.65	29.44	34.60
ZW	20	25.86	1.37	23.57	29.10	23	25.59	1.15	23.10	27.09
IOW	20	8.42	0.58	7.27	9.51	23	8.42	0.61	7.16	9.53
LW	20	10.40	0.57	9.45	12.05	22	10.38	0.56	9.29	11.33
NW	20	4.14	0.41	3.22	4.84	22	4.11	0.64	3.22	5.65
RH	20	9.24	0.63	8.08	10.55	22	9.10	0.41	8.31	9.87
RoW	20	6.86	0.49	5.99	7.85	22	6.73	0.33	6.09	7.25
I^1–P^1	20	6.28	0.35	5.55	6.97	23	6.18	0.38	5.50	6.83
I^1–P^4	20	11.20	0.61	10.01	12.14	23	11.19	0.69	10.05	12.26
I^1–M^4	19	17.01	0.87	15.30	18.81	22	17.03	0.89	15.28	18.32
UTR	19	17.95	0.88	16.28	19.54	22	17.93	0.92	16.36	19.43
UML	19	6.59	0.42	5.86	7.35	22	6.57	0.32	5.93	7.11
I_2–M_4	16	10.63	0.55	9.36	11.38	20	10.72	0.60	9.76	11.57
LML	18	7.03	0.39	6.52	7.74	21	7.06	0.30	6.31	7.48
RW	19	8.91	0.51	8.02	9.87	22	8.77	0.63	7.75	9.96
M_1W	18	1.37	0.09	1.22	1.54	22	1.37	0.08	1.19	1.51
hb	3	178.00	14.11	163.00	191.00	7	168.71	24.51	140.00	214.00
tv	8	192.63	23.89	168.00	229.00	12	202.50	24.85	161.00	235.00
hf	8	25.90	1.87	24.00	30.00	11	25.86	2.27	23.00	31.00
e	8	25.61	2.31	23.00	28.90	12	23.86	3.05	16.00	27.00
wt	3	139.00	21.66	116.00	159.00	7	110.57	20.82	78.00	146.00

a lesser extent *P. notatus*. The stripe fades at a point before the hindlegs. The tail of *P. breviceps* is less attenuated than that of *P. notatus*.

The intraorbital width of *P. breviceps* skulls is significantly smaller than that of *P. notatus*, while the nasal width of *P. breviceps* is larger. There is a tendency for *P. breviceps* skulls to have a smaller zygomatic width. This is only significant in females, but may be attributable to a smaller sample size in males (Tables 2, 3). The skulls of *P. breviceps* and *P. notatus* were similar for all other measurements.

A geographic barrier appears to exist between *P. breviceps* and *P. notatus*, but given the close proximity of samples in the current study, it is possible that the species also co-occur. *Petaurus breviceps* co-occurs with *P. norfolcensis* but is distinguished by its significantly smaller size and blunt nose.

DESCRIPTION OF HOLOTYPE 1855.12.24.78 OF *PETAURUS BREVICEPS*

Specimen is poorly preserved. Fixed position of the specimen makes detailed description difficult. Observations were taken where possible.

External measurements: Hindfoot length: 24 mm; hand: 18 mm; head–body length: 155 mm; tail–vent length: 107 mm (partial, as tail damaged and incomplete); ear length: 14 mm (one missing).

Pelage: Colours of the *Petaurus breviceps* holotype are as follows. Dorsal body coloration varies from mouse grey to hairbrown. A bone-brown, mid-dorsal stripe commencing at a point posterior between the anterior edge of the eyes is only distinguishable over the ear and stops 13 mm posterior to the ears. The stripe is 4 mm wide between the ears. An indistinct stripe is visible as a slight darkening over the mid-back of the specimen, but it is not defined.

Fur of the mid-back is 10–12 mm long with colour varying over its length. The basal 7 mm is mouse grey, median 4 mm is olive brown and apical 1 mm tipped deep olive buff.

The head is furred mouse grey and a thin ring of fuscous-black encircles the eye as an eye ring. An indistinct mummy-brown ring forms an incomplete circle around the ear with a distinct thickening at the base of the ear. A patch of smoke grey fur on the posterior edge of the pinna forms a less conspicuous

Table 5. Univariate statistics: means, standard deviations (SD) and range minima and maxima of measured variables for *Petaurus norfolcensis*

	Males					Females				
	N	Mean	SD	Minimum	Maximum	*N*	Mean	SD	Minimum	Maximum
MSL	22	46.02	1.78	42.08	48.48	29	45.15	1.54	40.05	47.87
BL	21	41.08	2.04	36.14	44.49	29	40.35	1.61	35.18	43.48
ZW	21	30.80	1.22	27.78	32.84	29	29.87	1.20	26.96	32.15
IOW	22	9.54	0.75	7.94	10.96	29	9.36	0.85	7.65	11.35
LW	21	13.72	0.88	12.07	15.51	29	13.40	0.70	11.63	14.90
NW	20	4.62	0.49	3.42	5.45	28	4.30	0.51	3.11	4.96
RH	21	11.66	0.67	9.91	12.99	28	11.35	0.65	9.98	12.66
RoW	22	8.63	0.51	7.38	9.28	29	8.57	0.83	7.31	12.16
I^1–P^1	22	7.83	0.52	6.73	8.76	29	7.69	0.34	7.06	8.55
I^1–P^4	22	14.50	0.74	13.06	15.67	28	14.41	1.39	12.51	20.69
I^1–M^4	21	21.57	0.96	19.77	23.35	28	21.10	0.78	19.30	22.70
UTR	21	22.74	0.99	20.74	24.68	27	22.36	0.76	20.35	23.97
UML	21	8.08	0.32	7.42	8.70	26	8.02	0.24	7.52	8.49
I_2–M_4	17	13.60	0.46	12.78	14.33	22	13.48	0.45	12.49	14.78
LML	21	8.79	0.35	8.07	9.57	28	8.72	0.30	8.20	9.51
RW	21	11.27	0.58	10.35	12.19	29	10.91	0.54	9.56	11.86
M_1W	21	1.83	0.09	1.63	2.02	28	1.77	0.11	1.62	2.08
hb	10	197.50	20.47	150.00	226.00	15	202.93	9.40	184.60	220.00
tv	9	249.11	20.12	219.00	271.00	20	237.44	26.55	150.00	282.00
hf	9	32.49	0.97	31.20	34.00	20	31.15	4.98	23.00	47.00
e	9	30.32	3.74	26.00	37.00	17	29.12	2.49	24.10	33.50
wt	5	232.00	45.50	190.00	300.00	4	183.00	27.73	153.00	220.00

tuft, interrupting the ear ring. The gliding membrane is concealed by positioning of the specimen.

The soft ventral fur (12 mm long on the belly) is olive buff tending to drab, giving the ventral fur a dusty wash.

A thin covering of fuscous hairs is present on the dorsal surface of the forefeet digits, contrasting with a 'mitten' of mummy-brown fur extending to the shoulder and a strong forearm stripe. Hindfeet are slightly more thickly covered fuscous, which gently contrasts with a less distinct 'mitten' of olive brown over the metatarsals, extending up to the inner posterior region of the thigh in a triangular stripe almost to the top of the thigh.

The tail is furred sepia and is incomplete/broken in the specimen. The tail tip is absent.

Fur 20 mm from the base of the tail is 19 mm long.

Vibrissae: Approximately 12 black mystacial vibrissae occur on each side and these are up to 28 mm long. Supra-orbital vibrissae (2); genals (2).

Pes and manus: The claws of the fore and hindfeet are relatively large with maximum chord length of digit 4 claws approx. 12 mm. Digit 4 is the longest digit of manus or pes, and digit 4 > 5 > 3 > 2 > 1.

PETAURUS NOTATUS PETERS, 1859

Recommended common name: Krefft's glider.

Remarks: Originally described as *Petaurus* (*Belideus*) *notatus* by Peters (1859) and recognized in *Belideus* by Gould (1860), the species was later synonymized under *Petaurus breviceps* by Thomas (1888), Iredale and Troughton (1934) and all subsequent authors.

Etymology: The species name derives from the Latin *notatus*, marked.

Type specimen: The type was originally located in the Royal Museum of Berlin when described by Gould in 1860. However, the type was not found in 1980 (McKay, 1988), there is presently no record of it in the Royal Museum of Berlin and it is hence recorded as lost. Gould stated that he would have been inclined to regard the specimen as identical to *P. breviceps*, where it not for a white stripe on the dorsal tail and by its snow white tip. Further to this suggestion, the collector of the type suggested that *P. notatus* is equivalent to *P. breviceps* (Krefft, 1871). For a description of the type see Gould (1863). Our designated neotype, Victoria Museum C27626 adult

Table 6. Univariate statistics: means, standard deviations (SD) and range minima and maxima of measured variables for *Petaurus gracilis*

	Males					Females				
	N	Mean	SD	Minimum	Maximum	*N*	Mean	SD	Minimum	Maximum
MSL	8	50.42	1.67	47.52	52.04	4	50.55	1.33	49.03	51.81
BL	8	44.66	1.63	41.34	46.14	4	44.73	1.25	42.88	45.56
ZW	8	33.31	1.53	30.06	34.86	4	33.28	1.37	31.56	34.75
IOW	8	9.06	1.14	6.93	10.43	4	9.19	1.08	7.99	10.61
LW	8	14.90	0.65	13.93	15.75	4	15.41	0.98	14.07	16.17
NW	6	5.62	0.53	4.73	6.10	3	5.12	1.39	3.82	6.58
RH	7	13.21	0.86	11.90	14.18	3	12.75	1.22	11.70	14.09
RoW	8	9.47	0.33	9.09	10.01	4	9.30	0.43	8.66	9.56
I^1–P^1	8	8.49	0.26	8.13	8.91	4	8.42	0.27	8.03	8.60
I^1–P^4	8	15.59	0.35	15.07	16.19	4	15.42	0.65	14.47	15.97
I^1–M^4	7	23.49	0.34	23.11	24.17	4	22.98	0.67	22.05	23.63
UTR	7	24.43	0.35	24.02	24.87	4	24.22	0.52	23.47	24.66
UML	7	8.74	0.35	8.27	9.38	4	8.57	0.32	8.12	8.87
I_2–M_4	6	14.76	0.31	14.41	15.13	3	14.97	0.65	14.31	15.60
LML	8	9.48	0.31	8.94	10.02	3	9.28	0.05	9.25	9.34
RW	8	12.63	0.78	11.12	13.33	4	12.54	0.91	11.34	13.50
M_1W	8	1.90	0.11	1.65	2.00	4	1.83	0.10	1.72	1.96
hb	2	257.00	11.31	249.00	265.00	0				
tv	2	344.50	13.44	335.00	354.00	0				
hf	2	42.20	1.13	41.40	43.00	0				
e	2	35.45	0.78	34.90	36.00	0				
wt	2	380.00	42.43	350.00	410.00	0				

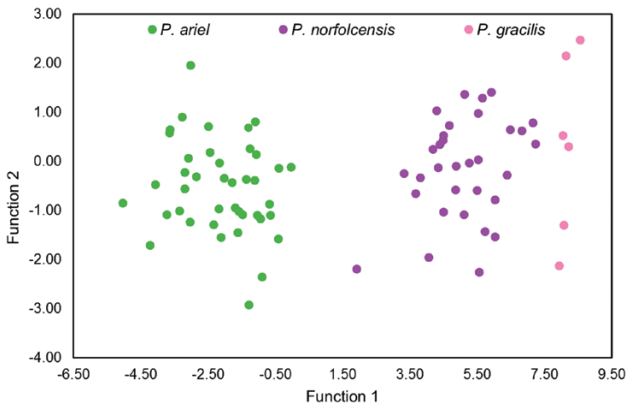

Figure 10. Scatterplot of canonical discriminant functions of *Petaurus ariel*, *P. norfolcensis* and *P. gracilis* with a priori groupings based on location. Sexes have been combined due to low sample size for *P. gracilis* (*N* = 6).

female skull, dentary and skin, is in excellent condition (see Figs 14 & 15 and description below).

Type locality: The type was collected by M. Gerard Krefft in the district of Victoria generally known as Port Phillip (Gould, 1863). The designated neotype was collected by A. J. Turnbull in 1988 from Warburton, VIC approximately 65 km from Port Phillip.

Distribution: Based on genetic and morphological evidence, the species distribution extends from South Australia to North Queensland. There is no evidence to suggest that the species co-occurs with *P. breviceps* except at the boundary of their distributions. It is likely that the species introduced into Tasmania is *P. notatus* (Campbell *et al.*, 2018) and we make that reference here (Fig. 3).

Diagnosis: Petaurus notatus is perhaps the most widely distributed of the Australian *Petaurus* spp. (Fig. 3). *Petaurus notatus* has a clearly defined mid-dorsal stripe fading between the hind legs. The tail of *P. notatus* is more attenuated than that of *P. breviceps* and *P. ariel*, with longer fur at the base of the tail, which shortens towards the tip. The intra-orbital width of *P. notatus* is the largest of the small *Petaurus* spp.

Skulls of *Petaurus notatus* have a smaller nasal width than *P. breviceps* and a tendency to have a larger zygomatic width (Tables 2, 3). The skulls of *P. breviceps* and *P. notatus* are similar for all other measurements.

Figure 11. *Petaurus ariel* lectotype (NHMUK 1842.5.26.1) specimen skin photographs.

A geographic barrier appears to exist between *P. breviceps* and *P. notatus* but, given the close proximity of samples in the current study, it is possible that the species also co-occur.

DESCRIPTION OF THE NEOTYPE C27626 OF *PETAURUS NOTATUS*

External measurements: Hindfoot length: 21 mm; hand: 20 mm; head–body length: 200 mm; tail–vent length: 202 mm; ear length: 19 mm.

Pelage: Colours for the *Petaurus notatus* neotype are as follows. Dorsal body coloration varies from smoke grey to pale smoke grey. An olive brown mid-dorsal stripe commences at a point 4 mm behind the tip of the nose and extends posteriorly to a point over the rump, fading 40 mm from the base of the tail. The mid-dorsal stripe is irregular in width and 11 mm wide between the ears, 5 mm at mid-shoulder blades and fades over the hips and rump.

Fur of the mid-back is 15 mm long with colour varying over its length. The basal 11 mm is pale mouse grey, median 2 mm hair brown and apical 2 mm tipped pallid mouse grey tending to white. The white-tipped fur over the dorsal body gives a subtle, dappled appearance to the fur.

The head is furred olive buff and a ring of fuscous-black encircles the eye in a defined but delicate eye ring. Fuscous fur at the base of the pinna forms an incomplete circle extending dorsally from the anterior edge of the pinna to the ventral tragus. The fuscous fur surrounding the pinna remains distinctly separate from the dark eye ring. The inner surface and the distal 14 mm of the outer surface of the pinna is sparsely furred with only scattered dark hairs visible. A patch of pale olive buff fur on the posterior edge of the pinna forms a conspicuous tuft.

Dorsally, the gliding membrane (or patagium) is fringed along its length by a thickly furred 3–4 mm

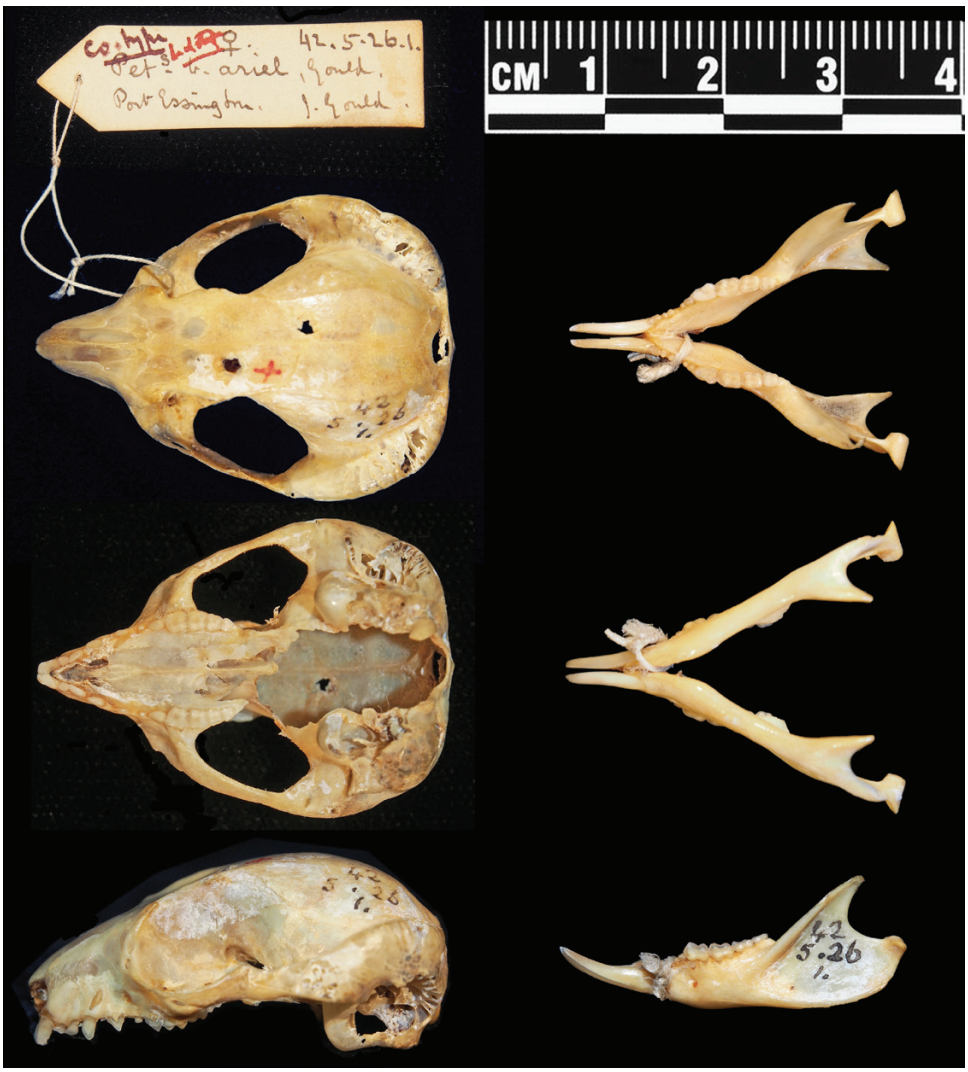

Figure 12. *Petaurus ariel* lectotype (NHMUK 1842.5.26.1) specimen photographs of skull and dentary.

band of pale olive buff fur (hairs 6 mm long). The patagium is olive brown and becomes interspersed with dorsal body fur closer to the medial surface of the patagium.

Ventrally the patagium is fringed in a fine band of pale olive buff tending to white coloured fur from the claw of digit 5 to the ankle. This band is formed by citrine drab fur with a distinct pale olive buff tip. More medially, the patagium is partially overlaid by drab fading to cream buff across the surface of the patagium with no distinct band.

The soft ventral fur is pale olive buff with a medial band of greyish olive giving a mottled appearance to the coat.

A thin covering of olive buff hairs is present on the dorsal surface of the forefeet digits. Hindfeet are slightly more thickly covered olive buff, which gently contrasts with a less pronounced 'mitten' of olive brown over the metatarsals extending up to the inner posterior region of the thigh in a triangular stripe almost to the top of the thigh.

The tail is furred smoke grey darkening distally to olive brown. The distal 15 mm tip of the tail is coloured white on both dorsal and ventral surfaces. There is a distinct light patch on the dorsal surface of the tail. The length of tail fur 20 mm from the base of the tail is 27 mm and 40 mm from the tip fur is 20 mm long.

Vibrissae: Approximately 16 black mystacial vibrissae occur on each side and these are up to 23 mm long. Supra-orbital vibrissae (2); genals (3).

Pes and manus: The claws of the fore and hindfeet are relatively large with maximum chord length of digit 4

Figure 13. *Petaurus breviceps*. holotype (NHMUK 1855.12.24.78) specimen skin photographs.

and 5 claws approx. 10mm. Digit 4 is the longest digit of manus or pes and digit 4 > 5 > 3 > 2 > 1.

DISCUSSION

The advancement of molecular systematics has revealed hidden diversity and undescribed mammalian taxa in a range of Australian genera (e.g., Malekian *et al.*, 2010a; Baker *et al.*, 2012, 2013; Aplin *et al.*, 2015; Potter *et al.*, 2015; Travouillon *et al.*, 2019). By combining molecular and morphological data, we have used a total evidence approach to provide a taxonomic revision and redescription of three species, all currently classified within *Petaurus breviceps*. The genetic evidence we have been able to obtain from live trapping and museum samples supports the existence of one lineage of glider in the NT, *Petaurus ariel*, and no evidence of its co-occurrence with *P. breviceps*. Despite being closely related to its two sister-lineages, *P. norfolcensis* and *P. gracilis*, with an average pairwise *ND2* sequence divergence of 2.6% and 2.5%, respectively, *P. ariel* displays obvious morphological differences from these species (Fig. 10). *Petaurus ariel* specimens also demonstrate distinctiveness for nuclear gene markers, with six unique *vWF* haplotypes and one unique *ω-globin* haplotype, and no *vWF* and *ω-globin* haplotypes shared with any of the other recognized Australian petaurid species (Fig. 6). The type locality of *Petaurus ariel* is Port Essington on the Cobourg Peninsula, well within the identified range of the proposed new species. Furthermore, morphology of the type skull indicates that it is nested within the cluster of *P. ariel* skulls (Figs 8, 9). Taken together, multiple lines of evidence from morphological data and multiple independent genetic loci support the recognition of *P. ariel* as a distinct species.

Petaurus ariel is geographically isolated from all other recognized Australian petaurids. The species appears restricted in the east by the Carpentarian Gap (MacDonald, 1969; Bowman *et al.*, 2010), with the easternmost specimen currently known from Lawn Hill (–18.697°, 138.526°). The clay plains that border the Gulf of Carpentaria are an essentially treeless habitat barrier that also delimits the geographic range of other northern Australian endemics, such as *Phascogale pirata* (Thomas, 1904) (Aplin *et al.*, 2015). *Petaurus ariel* extends its geographic range west into the Kimberley Region. Its distribution is not limited by the Ord Arid Intrusion, which has been identified as a barrier to other forest-adapted taxa of northern Australia (Bowman *et al.*, 2010). Similar distribution patterns to that of *P. ariel* have been observed historically for two other arboreal species that have now largely disappeared from mainland NT: brush-tailed rabbit-rats, *Conilurus penicillatus* (Gould, 1842) and golden-backed tree-rats, *Mesembriomys macrurus* (Peters, 1876) (McKenzie & Kerle, 1995; Firth *et al.*, 2010).

The current study provides further evidence for strong genetic divergence within *P. breviceps*. mtDNA evidence supports the existence of two divergent genetic clades (Fig. 5) distributed over distinct geographic regions (Figs 3, 4), corroborating the findings of previous work (Malekian *et al.*, 2010a). In addition to the deep genetic divergence, we here provide the first clear evidence for morphological distinction between the two lineages, with the two taxa forming statistically independent clusters in the discriminant function analysis (Figs 8, 9), justifying their designation as separate species.

The high level of genetic divergence between *P. breviceps* and *P. notatus* is best explained by their historical genetic separation. Based on the molecular clock presented in the present study (Fig. 7), a conservative time to the most recent common ancestor of *P. breviceps* and *P. notatus* is 1 million years, which includes several major climatic cycles. These cycles may have led to contractions of the species range to refugia (Hewitt, 1996), restricting gene flow and influencing the divergence of *P. breviceps* and

Figure 14. *Petaurus notatus* neotype (MV C27626) specimen skin photographs.

P. notatus. The two species identified here do not correspond to the recognized distribution of former *P. breviceps* subspecies (Figs 1, 3). *Petaurus breviceps*, as defined here, is a coastal species occurring < 130 km from the coast, approximately between the Sunshine Coast in Queensland (–26.98°, 152.93°) and Eden in far southern NSW (–37.08°, 149.86°). *Petaurus notatus* is evidently more widely distributed across eastern Australia, including Tasmania (Fig. 3). Based on these distributions, the Great Dividing Range (GDR) may have influenced patterns of gene flow during glacial maxima by blocking rainfall and contributing to the aridity of the Australian interior, while suitable forest habitat persisted for gliders to the east of the GDR (Malekian *et al.*, 2010a). Further sampling is required to determine the northern distribution of the range of *P. breviceps* in Queensland and to clearly define the species boundary between *P. notatus* and *P. breviceps*.

Gliders from the Cape York Peninsula (north of Coen –13.941667°, 143.2°) remain poorly understood. It is likely that Cape York Peninsula gliders are geographically isolated from *P. ariel* in the west by the Carpentarian Gap and from *P. notatus*, *P. norfolcensis* and *P. gracilis* in the south by the Laura Basin, a region of ancient alluvial lowlands separating Cape Melville from the wet tropics south of Cooktown, based on the apparent absence of gliders in these areas (Bryant & Krosch, 2016). Evidence from two genetic samples taken from vouchered skins (purportedly *P. breviceps*) indicates that the individuals are closely related to *P. gracilis*, falling within the same genetic clade (< 0.01 pairwise sequence divergence; Table 1). Despite this close genetic relationship, known *P. gracilis* are approximately four times larger than these Cape York Peninsula gliders. As a part of the present study we examined eight skulls from the region, one of which had a broken mandible and damage to the cranium and another of which was considered subadult due to the recent emergence of the upper third premolar tooth. The skulls examined demonstrated characters similar to *P. breviceps* and were notably different to *P. gracilis*. Given the close genetic relationship based on mtDNA, it is unclear whether the Cape York Peninsula gliders demonstrate extreme biogeographic variation within *P. gracilis* or whether the population should be recognized as a unique taxon.

To add to the complexity of the Cape York Peninsula gliders, the type locality for *P. breviceps longicaudatus* is Mapoon Mission, in the far north of the peninsula. Resolution of the taxonomy of gliders in this region will require collection of vouchers from various sites to enable a molecular and morphological species comparison and delimitation analysis. Although the *P. b. longicaudatus* type skull is damaged in key areas of the cranium, it will need to be compared to any vouchers that are collected to assess their status.

Figure 15. *Petaurus notatus* neotype (MV 27626) specimen photographs of skull and dentary.

The distinct lineage of five gliders sampled from the Central Kimberley region shows sequence divergence of at least 5.3% *ND2* from the nearest group (*P. ariel*). The phylogeny constructed in our study (Fig. 4) suggests that these samples represent a species group. However, no clear distinction was found for the two nuclear genes, with *P. ariel* found to share haplotypes with Kimberley specimens (Fig. 5). Sampling from the Kimberley region has been thus far limited and requires additional research as it appears individuals representing *P. ariel* and the distinct Kimberley lineage occur in close proximity to each other (< 10 km). Two of the five genetic samples included in the current study came from tail tissue collected opportunistically in the area and, therefore, have no matching morphological data. The three other samples were taken from live animals obtained via trapping and monitoring of nestboxes installed by Department of Biodiversity, Conservation and Attractions of Western Australia. We obtained measurements from one live adult female with matching tissue, and this animal exhibited obvious differences from *P. ariel* wild-caught specimens, particularly for weight, head length, ear length and tail length (Supporting Information, Table S2).

Despite taking tissue samples from 14 skins from the region at WAM, we could extract DNA from only one of these, which grouped with *P. ariel*. We have, therefore, been unable to obtain any craniodental measurements for this distinct lineage. Additional vouchers are required from this region if we are to clarify its genetic and morphological relationships. Two samples obtained from the King Leopold Ranges in the Kimberley are less than 5 km apart, but one sample groups genetically

with the central Kimberley lineage and the other with *P. ariel*. The habitat of these two locations is distinct: one is described as scree and the other as riparian. This may be an interesting site for further study to determine the possibility of co-occurrence. Similar genetic distinction in this region is also seen in northern quolls (How *et al.*, 2009; Hohnen *et al.*, 2016) where topographic complexity and the indirect effects of rainfall contribute to rates of gene flow.

CONCLUSION

The integrative taxonomic approach adopted here has identified and raised two additional species within what is currently designated as *Petaurus breviceps*. The recognition of distinct species is of particular importance given the current climate of biodiversity loss across northern Australia. Preliminary evidence has indicated that, as a unique taxon, the distribution of *Petaurus ariel* has declined by at least 35% since 1993 (Stobo-Wilson *et al.*, 2019). This has implications for the conservation status of the species. A comprehensive status assessment of *P. ariel* and the new taxa identified here (*P. breviceps and P. notatus*) are a matter of urgency. Furthermore, there is a need to understand the ecology of the taxa resolved here and how it may vary across the substantially changed geographic ranges of each species.

RECOGNITION OF INDIGENOUS KNOWLEDGE

Indigenous knowledge of the savanna glider, *Petaurus ariel*, has been an invaluable asset to our taxonomic investigation. We, therefore, formally recognize the scientific knowledge of the savanna glider that has been contributed to this research by local Aboriginal Australians. Among the people we have worked with, the savanna glider is recognized as 'rijinga' and 'rijingini' (female and male glider, respectively; Tiwi language: Tiwi Islands), 'lambalk' (Dalabon language, Arnhem Land), 'gardbug' and/or 'ngalmul' (Wardaman language, Victoria River region) and 'junggaluda' (Wunambul language: North Kimberley). The savanna glider is culturally significant and valued by people across multiple language groups in northern Australia and we are grateful to the Traditional Owners for sharing their knowledge of the species and its habitat.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Table S1. Complete list of tissue samples included in *ND2* and *vWF* analysis. Genbank accession numbers will be provided upon manuscript acceptance. Sequences created new for this study are indicated in the 'New' column.
Table S2. Comparison of measurement from a single specimen from Central Kimberley to average females within *P. ariel*.
Figure S1. Maximum likelihood tree of petaurid species based on RAxML analyses of mitochondrial *ND2* gene sequences. The numbers on branches refer to bootstrap proportions as a percentage of 500 pseudoreplicates.