Records of the Australian Museum (2024)
vol. 76, issue no. 2, pp. 105–129
https://doi.org/10.3853/j.2201-4349.76.2024.1864

Records of the Australian Museum
a peer-reviewed open-access journal
published by the Australian Museum, Sydney
communicating knowledge derived from our collections
ISSN 0067-1975 (print), 2201-4349 (online)

Molecular systematics of the *Dendrolagus goodfellowi* species group (Marsupialia: Macropodidae)

MARK D. B. ELDRIDGE[1], SALLY POTTER[1,2], RENAE PRATT[1], REBECCA N. JOHNSON[1,4],
TIM F. FLANNERY[1,3] AND KRISTOFER M. HELGEN[1]

[1] Australian Museum Research Institute, Australian Museum,
1 William Street, Sydney, NSW 2010, Australia

[2] School of Natural Sciences, Macquarie University, NSW 2109, Australia

[3] Melbourne Sustainable Society Institute, Melbourne University, Parkville, Vic 3010, Australia

[4] Current address: National Museum of Natural History, District of Columbia,
Washington, 20560 United States of America

ABSTRACT. Tree-kangaroos (genus *Dendrolagus*) are a morphologically distinctive genus of specialized, arboreal macropodids confined to the wet forests of New Guinea and northeast Australia. A distinct Goodfellow's group, containing up to four species, has long been recognized. Resolving the relationships of taxa within the group has been hampered by limited samples of most taxa. Here we supplement published genetic data from high quality tissue samples with molecular data generated from museum specimens to improve taxon and geographic coverage. This includes specimens of the previously unsampled *D. g. goodfellowi*, the holotype and paratype of *D. deltae*, and additional specimens of *D. matschiei*, *D. spadix* and *D. g. buergersi*. DNA sequence data were generated from three mitochondrial loci. Phylogenetic analysis improved the resolution of relationships within the Goodfellow's group, with the morphologically similar *D. g. goodfellowi* and *D. g. buergersi* being recovered as sister taxa, while *D. pulcherrimus* was the sister to the closely related, but morphologically and ecologically distinct, *D. spadix* and *D. matschiei*. Despite being sister to *D. g. buergersi*, *D. g. goodfellowi* was highly divergent. However, the two are morphologically very similar and we recommend retaining the taxonomic status quo (recognizing them as two subspecies of a single species) until improved sampling and a more thorough analysis is possible. The problematic *D. deltae* was confirmed as a junior synonym of *D. matschiei*.

Keywords: New Guinea; mammal; taxonomy; morphology; genetics; museum
ZooBank registration: urn:lsid:zoobank.org:pub:449837A3-37C8-4F17-9A9C-D940F4698F25
ORCID iD: Eldridge 0000-0002-7109-0600 | Potter 0000-0002-5150-7501 | Pratt 0009-0004-1248-7351 | Johnson 0000-0003-3035-2827 | Flannery 0000-0002-3005-8305 | Helgen 0000-0002-8776-4040
Corresponding author: Mark Eldridge **Email**: Mark.Eldridge@Australian.Museum
Submitted: 5 October 2023 **Accepted**: 15 February 2024 **Published**: 15 May 2024 (in print and online simultaneously)
Publisher: The Australian Museum, Sydney, Australia (a statutory authority of, and principally funded by, the NSW State Government)
Citation: Eldridge, M. D. B., S. Potter, R. Pratt, R. N. Johnson, T. F. Flannery, and K. M. Helgen. 2024. Molecular systematics of the *Dendrolagus goodfellowi* species group (Marsupialia: Macropodidae). *Records of the Australian Museum* 76(2): 105–129. https://doi.org/10.3853/j.2201-4349.76.2024.1864

Introduction

Tree-kangaroos (genus *Dendrolagus*) are a morphologically distinctive, highly specialised group of arboreal macropodid (kangaroos and wallabies) marsupials confined to the wet tropical forests of northeast Queensland, Australia and New Guinea (Flannery *et al*., 1996; Martin, 2005). Despite major morphological differences, tree-kangaroos are most closely related to rock-wallabies (*Petrogale*), sharing a common ancestor ~10 million years ago (mya) (Kirsch *et al*., 1997; Meredith *et al*., 2008; Potter *et al*., 2012). Subsequently within a relatively short time, tree-kangaroos have undergone marked morphological change associated with their shift to arboreality (Flannery *et al*., 1996; Martin, 2005). Tree-kangaroos appear to have originated in Australia, but have undergone a series of secondary radiations within New Guinea (Flannery *et al*., 1996; Martin, 2005; Eldridge *et al*., 2018).

Although tree-kangaroos have long fascinated and intrigued biologists, their secretive nature and occurrence in dense habitat in rugged and remote terrain has resulted in most species being little studied. They remain amongst the most poorly known of all macropodids (Dabek *et al*., 2021). Many taxa are only known from a handful of specimens (Flannery *et al*., 1996). Tree-kangaroos were amongst the last large mammal species described from Australia, while in New Guinea additional taxa continue to be discovered, with four having been described since 1990 (Eldridge & Coulson, 2015). It is likely that additional taxa await recognition. The limited number of specimens available for study, lack of comprehensive geographic coverage and morphological variability within and amongst localities has led to considerable taxonomic uncertainty and speculation as to the number of tree-kangaroo species (Groves, 1982; Flannery *et al*., 1996). In 1996, 10 tree-kangaroo species were recognized, two in Australia and eight in New Guinea (Flannery *et al*., 1996), although several subsequent authors have suggested that additional species should be recognized within New Guinea (Groves, 2005; Helgen, 2007a). A recent molecular phylogenetic analysis confirmed that species diversity had been underestimated and that at least three additional New Guinean species should be recognized (Eldridge *et al*., 2018). In addition, they demonstrated that living *Dendrolagus* comprise six distinct lineages, the two Australian species (*D. lumholtzi*, *D. bennettianus*), and from New Guinea *D. inustus*, *D. ursinus*, *D. mbaiso*, a Doria's group and a Goodfellow's group (Eldridge *et al*., 2018).

A distinct Goodfellow's group within *Dendrolagus* was first proposed in 1936 (Rothschild & Dollman, 1936) and has subsequently been widely supported (Flannery *et al*., 1996; Groves, 1982; Eldridge *et al*., 2018). The Goodfellow's group comprises a lineage of medium-sized (7–9 kg), red-brown tree-kangaroos with yellow markings, long tails (1–1.2 times the head/body length), large ears, a mid-dorsal hair-whorl and little sexual dimorphism (Rothschild & Dollman, 1936; Groves, 1982; Flannery, 1995; Flannery *et al*., 1996) (Appendix 1). Although skull morphology is relatively conserved within the group (Groves, 1982), pelage colouration and markings are highly variable (Flannery, 1993; Flannery *et al*., 1996). As a consequence, nine species/subspecies attributable to this group have been described, with the number of species recognized by various authors ranging from one to four (Table 1). This ongoing taxonomic instability continues to hamper research and effective conservation: all taxa are currently listed as threatened by the IUCN (Eldridge & Coulson, 2015). In New Guinea, increased subsistence hunting, as well as by habitat loss and degradation associated with human population growth, as well as expanding agriculture, mining and petroleum exploration and exploitation are all threats (Eldridge & Coulson, 2015; Beehler *et al*., 2021a, 2021b; Pattiselanno *et al*., 2021; Valentine *et al*., 2021).

The first Goodfellow's group taxon to be described by Western science was *D. matschiei* in 1907 from the Rawlinson Mountains, Huon Peninsula, north-eastern Papua New Guinea (Förster & Rothschild, 1907), followed in 1908 by *D. goodfellowi* from the Owen Stanley Range, south-eastern Papua New Guinea (Thomas, 1908). In 1912, two further taxa were described, *D. buergersi* from the Upper Sepik of north-western Papua New Guinea and *D. matschiei flavidior* also from the Rawlinson Mountains, Huon Peninsula (Matschie, 1912).

In the first comprehensive review of *Dendrolagus* taxonomy Rothschild and Dollman (1936) recognized two species within the Goodfellow's group; *D. matschiei* and *D. goodfellowi*. *Dendrolagus matschiei* was confined to the Huon Peninsula, and contained two subspecies (*matschiei,* with *flavidior* as a synonym, and added a new taxon *xanthotis*) (Rothschild & Dollman, 1936). *Dendrolagus goodfellowi* was distributed along the Central Cordillera of Papua New Guinea and contained three subspecies found sequentially east to west (*goodfellowi* in the southeast peninsula, the newly described *shawmayeri* from the Central Highlands, and *buergersi*, in the west) (Rothschild & Dollman, 1936) (Table 1). Also in 1936, two additional Goodfellow's group species were described (Troughton & Le Souef, 1936): *D. spadix* and *D. deltae* (Table 1). *Dendrolagus spadix* was described from a flat skin (Fig.1) collected in the southern lowlands of Papua New Guinea (Fig. 2) and *D. deltae* from skins and skulls (Figs 3 and 4) of two captive animals reportedly from Mt Pratt, south-western Papua New Guinea (Fig. 2). However, almost all subsequent authors have regarded this locality as erroneous and synonymised *D. deltae* with *D. matschiei* (Table 1). However, the Mt Pratt area has not been well surveyed so this conclusion may be premature (Helgen *et al*., 2011). Troughton and Le Souef (1936) also synonomised *flavidior* with *matschiei* but in contrast to Rothschild and Dollman (1936) regarded *buergersi* as a subspecies of *D. matschiei,* not *D. goodfellowi*. Laurie and Hill (1954) recognized four Goodfellow's group species, monotypic *D. matschiei*, *D. spadix* and *D. deltae*, as well as a polytypic *D. goodfellowi* containing three subspecies (*goodfellowi*, *shawmayeri, buergersi*) (Table 1). In 1977, Kirsch and Calaby recognised only two Goodfellow's group species, having synonymised *D. deltae* with *D. matschiei,* and *D. spadix* with *D. goodfellowi* (Kirsch & Calaby, 1977).

The next comprehensive morphological taxonomic revision of *Dendrolagus* was by Groves (1982). Within the Goodfellow's group a single polytypic species, *D. matschiei* was recognized, containing five subspecies (Groves, 1982); *D. m. matschiei* from the Huon Peninsula (including *flavidior* and *xanthotis* as synonyms), *D. m. spadix* from the southern lowlands, and three additional subspecies from the Central Cordillera (*goodfellowi, shawmayeri* and *buergersi*) (Table 1). In 1990, *D. spadix* and *D. goodfellowi* were separated

Table 1. Described *Dendrolagus* taxa in the Goodfellow's group and their changing recognition by various authorities from 1936 to 2015.

Described Taxon	Rothschild & Dollman, 1936	Troughton & Le Souef, 1936	Laurie & Hill, 1954	Kirsch & Calaby, 1977	Groves, 1982	Flannery, 1990	Flannery, 1993, 1995; Flannery *et al.*, 1996	Groves, 2005	Helgen, 2007; IUCN, 2008	Eldridge & Coulson, 2015
D. matschiei Förster & Rothschild, 1907	*D. m. matschiei*	*D. m. matschiei*	*D. matschiei*	*D. matschiei*	*D. m. matschiei*	*D. matschiei*	*D. matschiei*	*D. matschiei*	*D. matschiei*	*D. matschiei*
D. matschiei xanthotis Rothschild & Dollman, 1936	*D. m. xanthotis*	—	*D. matschiei*	*D. matschiei*	*D. m. matschiei*	*D. matschiei*	*D. matschiei*	*D. matschiei*	*D. matschiei*	*D. matschiei*
D. matschiei flavidior Matschie, 1912	*D. m. matschiei*	*D. m. matschiei*	*D. matschiei*	*D. matschiei*	*D. m. matschiei*	*D. matschiei*	*D. matschiei*	*D. matschiei*	*D. matschiei*	*D. matschiei*
D. deltae Troughton & Le Souef, 1936	—	*D. deltae*	*D. deltae*	*D. matschiei*	*D. m. matschiei*	*D. matschiei*	*D. matschiei*	*D. matschiei*	*D. matschiei*	*D. matschiei*
D. goodfellowi Thomas, 1908	*D. g. goodfellowi*	*D. goodfellowi*	*D. g. goodfellowi*	*D. goodfellowi*	*D. m. goodfellowi*	*D. g. goodfellowi*	*D. g. goodfellowi*	*D. g. goodfellowi*	*D. goodfellowi*	*D. g. goodfellowi*
D. buergersi Matschie, 1912	*D. g. buergersi*	*D. m. buergersi*	*D. g. buergersi*	*D. goodfellowi*	*D. m. buergersi*	*D. g. buergersi*	*D. g. buergersi*	*D. g. buergersi*	*D. goodfellowi*	*D. g. buergersi*
D. goodfellowi shawmayeri Rothschild & Dollman, 1936	*D. g. shawmayeri*	—	*D. g. shawmayeri*	*D. goodfellowi*	*D. m. shawmayeri*	*D. g. shawmayeri*	*D. g. buergersi*	*D. g. buergersi*	*D. goodfellowi*	*D. g. buergersi*
D. goodfellowi pulcherrimus Flannery, 1993	—	—	—	—	—	—	*D. g. pulcherrimus*	*D. pulcherrimus*	*D. pulcherrimus*	*D. g. pulcherrimus*
D. spadix Troughton & Le Souef, 1936	—	*D. spadix*	*D. spadix*	*D. goodfellowi*	*D. m. spadix*	*D. spadix*	*D. spadix*	*D. spadix*	*D. spadix*	*D. spadix*

Figure 1. AM M.4561, holotype flat skin of *D. spadix* Troughton & Le Souef 1936. An image of this specimen has not previously been published.

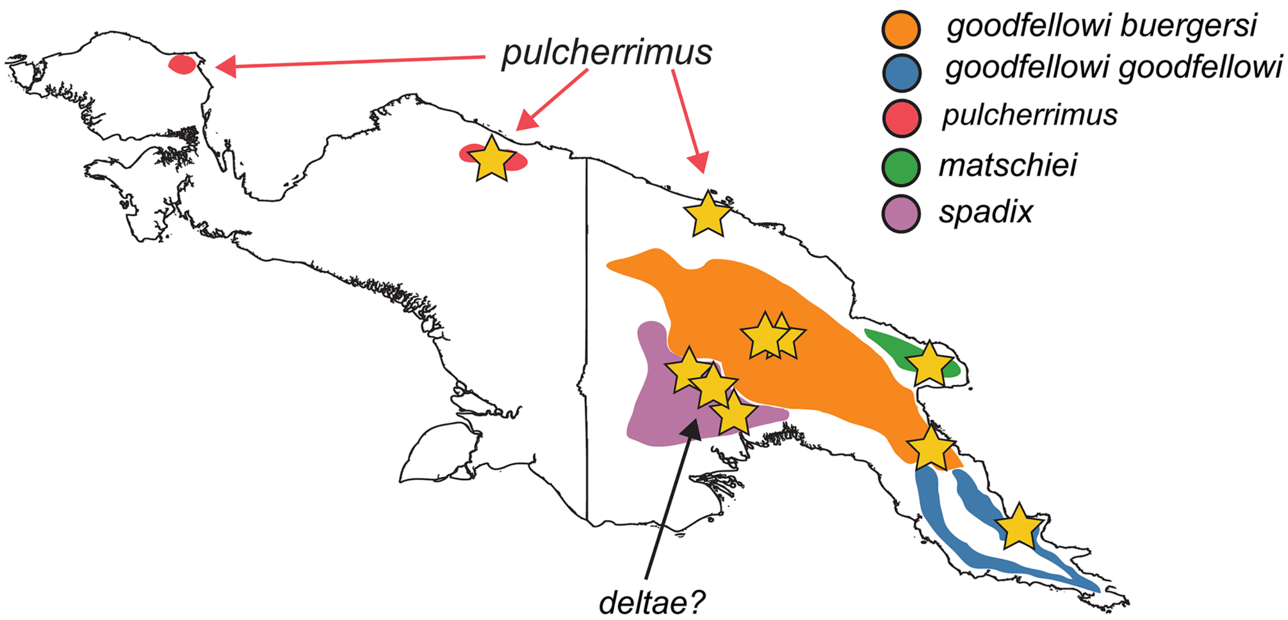

Figure 2. Distribution of *Dendrolagus* taxa of the Goodfellow's group in New Guinea, with sampling sites indicated.

from *D. matschiei* as full species, and three subspecies were recognized within *D. goodfellowi* (*goodfellowi*, *shawmayeri, buergersi*) (Flannery, 1990). In 1993 a morphological analysis of *D. goodfellowi* was conducted which resulted in the description of a new taxon (*D. g. pulcherrimus*) from the Torricelli Mountains of northern coastal Papua New Guinea, and synonomised *D. g. shawmayeri* with *D. g. buergersi* (Table 1) (Flannery, 1993). Subsequently, the presence of *D. g. pulcherrimus* has also been confirmed in the Foja Mountains of West Papua (Fig. 2) (Eldridge & Coulson, 2015). Remains of a tree-kangaroo in the Goodfellow's group, most likely *D. g. pulcherrimus*, have been reported from late Quaternary deposits from the Vogelkop Peninsula (Aplin *et al*., 1999; Helgen, 2007a).

By the end of the 20th century three species were recognized within the Goodfellow's group; monotypic *D. matschiei* and *D. spadix*, as well as polytypic *D. goodfellowi* (containing three subspecies: *goodfellowi*, *buergersi* and *pulcherrimus*) (Flannery, 1995; Flannery *et al*., 1996). However, some authors subsequently suggested that *D. g. pulcherrimus* was sufficiently distinct morphologically to be considered a separate species (Groves, 2005; Helgen, 2007a). Subsequently, the first comprehensive multilocus molecular analysis of *Dendrolagus* confirmed the specific distinctness of *D. pulcherrimus* (Eldridge *et al*., 2018).

Although greatly improving our understanding of *Dendrolagus* evolution and taxonomy, the recent phylogenetic analyses utilizing high quality DNA (Eldridge *et al*., 2018), suffered from unavoidable sample size and geographic coverage limitations. For example, within the Goodfellow's group only 1–2 samples were available for all taxa, while samples from the nominate *D. g. goodfellowi* were not available (Eldridge *et al*., 2018). In the current study we extend the analysis of Eldridge *et al*. (2018) by including museum specimens (study skins) as an additional source of DNA for sequence analysis. This increased geographic coverage for some taxa and enabled data for *D. g. goodfellowi* and the type series of *D. deltae* to be included. Therefore, the aim of this study, with the inclusion of *D. g. goodfellowi* and *D. deltae*, was to improve our understanding of taxon boundaries and inter-relationships within the Goodfellow's group and to test the validity of *D. deltae* as a species.

Materials and Methods

DNA sequence data

Mitochondrial DNA (mtDNA) sequence data, generated from high quality tissue samples, from six individuals of four Goodfellow's group taxa (*D. goodfellowi buergersi* n = 1; *D. pulcherrimus* n = 2; *D. matschiei* n = 2; *D. spadix* n = 1) were available from Eldridge *et al*. (2018), including data from the holotype of *D. pulcherrimus* (Table 2; Fig. 2.). Individuals of *D. bennettianus*, *Petrogale xanthopus, Petrogale concinna* and *Thylogale stigmatica* were included as out-groups. See Appendix 2 for GenBank numbers.

Tissue sampling and DNA extraction from museum specimens

Samples were collected from museum specimen study skins of seven individuals. Samples included *D. g. goodfellowi* (n = 1), the holotype and paratype of *D. deltae* (n = 2), as well as additional specimens of *D. matschiei* (n = 1), *D. spadix* (n = 1) and *D. g. buergersi* (n = 2) which extended taxon sampling and geographic coverage (Table 2; Fig. 2).

Subsequent DNA extraction and PCR amplification was undertaken in a designated ultraclean low-template DNA extraction laboratory (with positive air pressure and HEPA filtered air handling system) at the Australian Centre for Wildlife Genomics, Australian Museum Research Institute. Neither *Dendrolagus* DNA nor tissue samples had previously been handled in this laboratory facility. Reagent blank controls and no-template PCR controls were included for each round of DNA extractions to detect reagent contamination. Dried tissue samples were initially hydrated

Figure 3. AM M.5418 the holotype study skin of *D. deltae* Troughton & Le Souef 1936. An image of this specimen has not previously been published.

Figure 4. AM M.5418, the holotype cranium and dentaries of *D. deltae* Troughton & Le Souef 1936. An image of this specimen has not previously been published.

in sterile phosphate buffered saline (PBS) solution at 37˚C for 24–30 hours. We then aspirated the PBS and DNA extracted from both the supernatant and tissue with a QIAamp Micro Extraction kit (QIAGEN) following the "Isolation of total DNA from chewing gum" protocol.

PCR and sequencing

Three mitochondrial gene segments, cytochrome oxidase c subunit 1 (*COI*), cytochrome *b* (*Cytb*) and NADH dehydrogenase subunit 2 (*ND2*), were PCR amplified using a series of short (~150–200 bp) overlapping fragments (*COI*, 12 fragments; *Cytb,* seven fragments; *ND2,* four fragments) due to the degraded nature of the DNA extracted from museum skins. Details of primers are given in Appendix 3. These genes were chosen due to their proven utility in resolving relationships within marsupials (Osborne & Christidis, 2001; Meredith *et al*., 2008; Malekian *et al*., 2010; Potter *et al*., 2012) including *Dendrolagus* (Eldridge *et al*., 2018).

PCR-amplifications were carried out in 25µL reactions with 100–400 ηg genomic DNA, 1 x PCR Buffer II (Applied Biosystems), 0.2 mM each dNTP, 1.5–3.0 mM $MgCl_2$, 0.2 µmol each primer (Appendix 3) and 1.0U Ampli*Taq* Gold^{TM} polymerase (Applied Biosystems). A negative control was included for each batch of amplifications and for each primer set.

PCR conditions were: initial denaturation at 95°C for 9 min, then 40–50 cycles of 94°C for 1 min, annealing for 1 min at 45–50°C and extension at 60°C for 1 min, and a final extension at 60°C for 10 min. PCR products were purified using ExoSap-IT© (USB Corporation) and directly sequenced on a AB 3730xl at the Australian Genome Research Facility (AGRF), Sydney. Forward and reverse strands were combined and sequences checked for errors with SEQUENCHER (version 5.2.4) (Genecodes). Only samples that provided clear and unambiguous sequence were subject to further analysis.

Sequence divergence and phylogenetic analysis

We calculated nucleotide diversity, polymorphic sites and parsimony informative sites in DnaSP v5.10 (Librado & Rozas, 2009) for the concatenated mitochondrial dataset as well as individual genes. Uncorrected pairwise sequence divergence was estimated between individuals and species in MEGA v5 (Tamura *et al*., 2011).

A maximum likelihood analysis was performed in RAxML v8.2.4 (Stamatakis, 2014) on the concatenated mitochondrial alignment, as well as individual genes. Nucleotide substitution models were estimated using PartitionFinder (Lanfear *et al*., 2012), using the raxml model of evolution, a full search scheme allowing for all partitioning schemes and the BIC model selection. The best partition model included four partitions: the first combining codon 1 positions (*ND2* + *COI* + *Cytb*), the second combining codon 2 positions (*ND2* + *COI* + *Cytb*), the third combining codon 3 for *ND2* and *COI*, and the fourth representing codon 3 for *Cytb*. The rapid bootstrap algorithm was used in the RAxML analysis with 100 bootstrap replicates, the GTRGAMMA model for partitions and a random starting seed.

Table 2. Details of the *Dendrolagus* specimens used for the molecular analysis in this study.

Taxon	Specimen Voucher	Sample ID	Locality	DNA Source
D. goodfellowi goodfellowi	AM M.29227	—	Kwin River, e Mt Victory, OP, PNG 1992	skin
D. goodfellowi buergersi	AM M.52279	S-1606	Captive, Taronga Zoo, NSW, Australia 1998	Eldridge *et al*., 2018
	AM M.6509	—	Wau, MP, PNG 1938	skin
	AM M.7221	—	Mt Jaka, ne Mount Hagen, WHP, PNG 1946*	skin
D. pulcherrimus	AM M.21717 holotype	EBU25198	Mt Sapau, near Sibilanga, SP, PNG 1990	Eldridge *et al*., 2018
	ANWC M38950	ABTC92102	Foja Mountains, West Papua 2005	Eldridge *et al*., 2018
D. matschiei	—	S-1621	Captive, National Zoo, Washington DC 1998	Eldridge *et al*., 2018
	ARK900073	S-1625	Captive, Perth Zoo, WA, Australia 1998	Eldridge *et al*., 2018
	AM M.4195	—	Rawlinson Range, MP, PNG 1927*	skin
D. spadix	AM M.17212	ABTC44698	Fogamaiyu, SHP, PNG 1985	Eldridge *et al*., 2018
	AM M.15720	—	Mt Sisa, HP, PNG 1986	skin
D. deltae	AM M.5418 holotype	—	Mt Pratt, SHP, PNG 1933*	skin
D. deltae	AM M.5420 paratype	—	Mt Pratt, SHP, PNG 1934*	skin

* Ex-captive, Taronga Zoo, Sydney, NSW, Australia. AM = Australian Museum, Sydney; ANWC = Australian National Wildlife Collection, Canberra; EBU = Australian Museum tissue collection; ABTC = South Australian Museum tissue collection. HP = Hela Province, MP = Morobe Province, OP = Oro Province, PNG = Papua New Guinea, SP = Sandaun Province; SHP = Southern Highland Province, WHP = Western Highlands Province.

Results

Genetic diversity

A total of 3116 bp of mtDNA was sequenced and aligned (*ND2* – 651 bp, *COI* – 1323 bp, *Cytb* – 1142 bp). Excluding *D. spadix* M.15720 (77.1% missing data), the museum samples had on average 21% missing data (11.0–37.4%). Within the Goodfellow's group there were 119 variable sites and 76 parsimony informative sites. When including the outgroups, there were 219 variable sites, 133 of which were parsimony informative. The nucleotide diversity ranged from 0.031–0.063 (*COI* and *ND2* respectively). The nucleotide diversity for the concatenated mtDNA dataset was 0.054 (0.085 including outgroups).

Average uncorrected pairwise sequence divergence between taxa within the Goodfellow's group ranged from 5.1% between *D. matschiei* and *D. spadix*, to 7.6% between *D. g. goodfellowi* and *D. pulcherrimus* (Table 3). The two currently recognized subspecies of *D. goodfellowi* differed by 7.0% (Table 3). Within taxon sequence divergences ranged from 0.2% within *D. g. buergersi* to 1.6% within *D. pulcherrimus* (Table 3). The two samples of *D. deltae* had identical sequences and differed from the three sampled *D. matschiei* by an average of 0.8%. The average uncorrected pairwise divergences were greatest for *ND2* and lowest for *COI* (Appendix 4). Average sequence divergence with outgroups (*D. bennettianus*, *P. concinna*, *P. xanthopus* and *T. stigmatica*) ranged from 11.8–14.4% (Table 3).

Phylogenetic analysis

The maximum likelihood phylogenetic analysis of the concatenated mitochondrial data resolved five lineages within the Goodfellow's group: *D. goodfellowi goodfellowi*, *D. g. buergersi*, *D. matschiei* (including *D. deltae*), *D. pulcherrimus* and *D. spadix* (Fig. 5). These relationships were mostly well resolved (73–100% bootstrap support), in particular the node separating the two *D. goodfellowi* subspecies from *D. matschiei*, *D. pulcherrimus* and *D. spadix*. The additional museum specimens all grouped with conspecifics, except for *D. g. goodfellowi* which was the only sample of this taxon. The two *D. deltae* samples grouped within the *D. matschiei* clade which formed a monophyletic lineage. *D. spadix* formed the sister clade to *D. matschiei* (+ *D. deltae*) but with the lowest clade support (73%), followed by *D. pulcherrimus* (96% support). Phylogenetic analysis of a reduced dataset containing no missing data was unable to resolve most relationships.

Discussion

The improved taxon and geographic sampling used in this study by including genetic material from museum specimens resulted in the identification of five distinct Goodfellow's group lineages. Incorporation of these samples from museum specimens enabled the clarification of several long-standing questions within the Goodfellow's group. A sample of nominotypical *D. g. goodfellowi* was found to be divergent from all other Goodfellow's group taxa, the problematic *D. deltae* was confirmed as a junior synonym of *D. matschiei* and the resolution of the phylogenetic relationships of the Goodfellow's group was improved.

This study is the first to obtain genetic data for the poorly known nominotypical *D. g. goodfellowi* which was resolved as a sister lineage to *D. g. buergersi* (Fig. 5), consistent with their morphological similarity (Fig. 6) (Flannery, 1993; Flannery *et al*., 1996). The two monophyletic *D. goodfellowi* subspecies were then sister to the remaining three species (Fig. 5). Of these three, *D. pulcherrimus* was resolved as the sister lineage to *D. spadix* and *D. matschiei*, as had been previously reported (Eldridge *et al*., 2018). The sister relationship between *D. spadix* and *D. matschiei*, which are also the most closely related of all the Goodfellow's group species (5.1% sd) is curious as they have very different pelage patterns and ecological associations (Flannery *et al*., 1996), as well as distributions widely separated by the Central Ranges of New Guinea (Figs 2 & 6). *Dendrolagus spadix* is distributed in the southern lowlands, while *D. matschiei* occurs in high altitude forests of the Huon Peninsula in northeast New Guinea (Flannery *et al*., 1996). *Dendrolagus spadix* and *D. matschiei* are also the only species in the Goodfellow's group to lack (or have markedly reduced) highly contrasted distinct markings on the rump and tail (Fig. 6), suggesting these distinct markings are ancestral in the Goodfellow's group but were lost in *D. spadix* and *D. matschiei*. Indeed, the faint remnants of pale rump and tail markings can be seen in some *D. spadix* specimens.

The genetic data obtained from the single sampled specimen of nominotypical *D. g. goodfellowi*, revealed a high level of sequence divergence (7%) from its sister subspecies *D. g. buergersi* and all the other sampled taxa (Table 3). Indeed, the two *D. goodfellowi* subspecies were more divergent than the sampled species *D. spadix* and *D. matschiei* (Table 3). The high molecular divergence of the two *D. goodfellowi* subspecies contrasts with their morphological similarity (Flannery, 1993; Flannery *et al*., 1996) (Fig. 6), although the few specimens available for *D. g. goodfellowi* are consistently larger than those of *D. g. buergersi*, especially in the length of the skull. This poses a taxonomic dilemma as to whether *D. g. buergersi* and *D. g. goodfellowi* should each be recognized as full species. Recognizing species based solely on divergent mtDNA is not recommended (Frankham *et al*., 2017), especially given the increasing recognition of mito-nuclear discordance (Firneno Jr *et al*., 2020). Nevertheless, the southeastern Papuan Peninsula, where *D. g. goodfellowi* occurs is a well-established biogeographic region in New Guinea and supports a range of endemic taxa in many groups (Beehler & Pratt, 2016; Aplin *et al*., 2010), including the Doria's group of tree-kangaroos (Flannery *et al*., 1996). Pending improved sampling and more comprehensive data, we believe that maintaining the status quo is the best option.

Currently, *D. goodfellowi* is assessed for conservation status and managed as a single species (Leary *et al*., 2016a). The confirmation in this study that *D. goodfellowi* comprises two divergent lineages (here recognized as subspecies pending further research) warrants some reassessment. Most knowledge of the species, and the current global captive population is derived from *D. g. buergersi* (Flannery *et al*., 1996; Blessington *et al*., 2021), with *D. g. goodfellowi* being very poorly known and potentially more threatened.

The addition of sequence data from museum specimens for several taxa allowed a better understanding of intraspecific variation to be obtained. Overall, intra-taxon sequence divergence was low, ranging from 0.2% within

Table 3. Average uncorrected pairwise sequence divergence [and range] across three concatenated mtDNA loci between *Dendrolagus* taxa examined in this study.

Taxa	*D. g. goodfellowi*	*D. g. buergersi*	*D. pulcherrimus*	*D. spadix*	*D. matschiei*	*D. bennettianus*	*P. concinna*	*P. xanthopus*
D. g. buergersi	0.070 [0.070–0.071]	0.002 [0.001–0.003]	—	—	—	—	—	—
D. pulcherrimus	0.076 [0.075–0.077]	0.066 [0.064–0.068]	0.016	—	—	—	—	—
D. spadix	0.073 [0.071–0.074]	0.074 [0.071–0.077]	0.069 [0.067–0.071]	0.011 —	—	—	—	—
D. matschiei	0.070 [0.068–0.072]	0.068 [0.061–0.075]	0.056 [0.054–0.058]	0.051 [0.044–0.058]	0.009 [0.000–0.018]	—	—	—
D. bennettianus	0.128 —	0.124 [0.123–0.125]	0.131 [0.130–0.132]	0.128 —	0.121 [0.118–0.122]	—	—	—
P. concinna	0.128 —	0.118 [0.118–0.119]	0.123 [0.122–0.123]	0.134 [0.132–0.136]	0.120 [0.112–0.122]	0.104 —	—	—
P. xanthopus	0.129 —	0.125 [0.125–0.126]	0.121 [0.119–0.123]	0.129 —	0.125 [0.125–0.126]	0.118 —	0.102 —	—
T. stigmatica	0.140 —	0.142 [0.142–0.143]	0.144 [0.140–0.148]	0.142 —	0.133 [0.128–0.135]	0.123 —	0.106 —	0.125 —

D. g. buergersi to 1.6% between widely geographically separated samples of *D. pulcherrimus* (Table 3, Fig. 2). DNA sequences from the two type series specimens of *D. deltae* were identical and differed from the three sampled *D. matschiei* by an average of 0.8% sd (Table 3). This limited divergence is well within the intra-taxon range detected in the other species. In addition, the *D. deltae* haplotype was nested within the well supported *D. matschiei* clade (Fig. 5), providing molecular support for *D. deltae* being a junior synonym of *D. matschiei*, as most previous authors had recommended (Table 1). The pelage of the *D. deltae* specimens is also consistent with that of *D. matschiei* (Figs 3 & 6). This suggests that the collection locality of Mt Pratt (on the southern side of the Central Ranges), given as the type locality for *D. deltae* (Troughton & Le Souef, 1936) was likely erroneous and that the specimens (then in captivity at Taronga Zoo, Sydney) described as *D. deltae* had been sourced from the natural range of *D. matschiei* on the Huon Peninsula on the northern side of the Central Ranges. Indeed, Troughton himself subsequently expressed doubts about the validity of *D. deltae* as a taxon and the published collection locality of the type. In an undated type-written note added as a footnote to the first page of a reprint of his Troughton and Le Souef 1936 paper (held in the Mammal section at the Australian Museum) Troughton states "Note: Dendrolagus spadix is recognized as valid, but D. deltae remains uncertain owing to the doubtful locality provided for Zoo specimens by co-author Le Souef" (Parnaby *et al*., 2017). The alternative explanation, that the original published type locality is correct, would require a genetically and morphologically undifferentiated population of *D. matschiei* to occur at Mt Pratt. Given the distances and topography involved, the recent dispersal or translocation of *D. matschiei* individuals from the Huon Peninsula across the Central Ranges to Mt Pratt seems unlikely.

Although this study has benefited from access to molecular data obtained from museum specimens of Goodfellow's group taxa, the number of specimens available for research from most, especially *D. spadix, D. pulcherrimus* and *D. g. goodfellowi*, remains severely limited. A more complete understanding of this group will only be possible with significantly improved access to material obtained from across the range of each taxon to enable a comprehensive morphological and molecular assessment. But obtaining additional material is challenging. All members of the Goodfellow's group have been profoundly impacted by hunting by people and many remaining populations occur in relatively inaccessible locations.

The apparent absence of any member of the Goodfellow's group from most (if not all) of the Central Cordillera in West Papua (Flannery & Seri, 1990; Flannery, 1993) remains puzzling. Questioning of local hunters at both Etna Bay and in the Timika area, on the southern slopes of the Central Cordillera in West Papua, reveal that the Goodfellow's group is unknown there. Likewise, the Third Archbold Expedition to New Guinea by the American Museum of Natural History failed to detect any representatives on the northern fall of the Central Cordillera (Archbold *et al*., 1942). We suspect that the absence of the Goodfellow's group from the Central Cordillera west of 141° longitude, at least in the border region of Papua New Guinea, and West Papua, is real. Hunting by people is unlikely to explain this absence, as the population

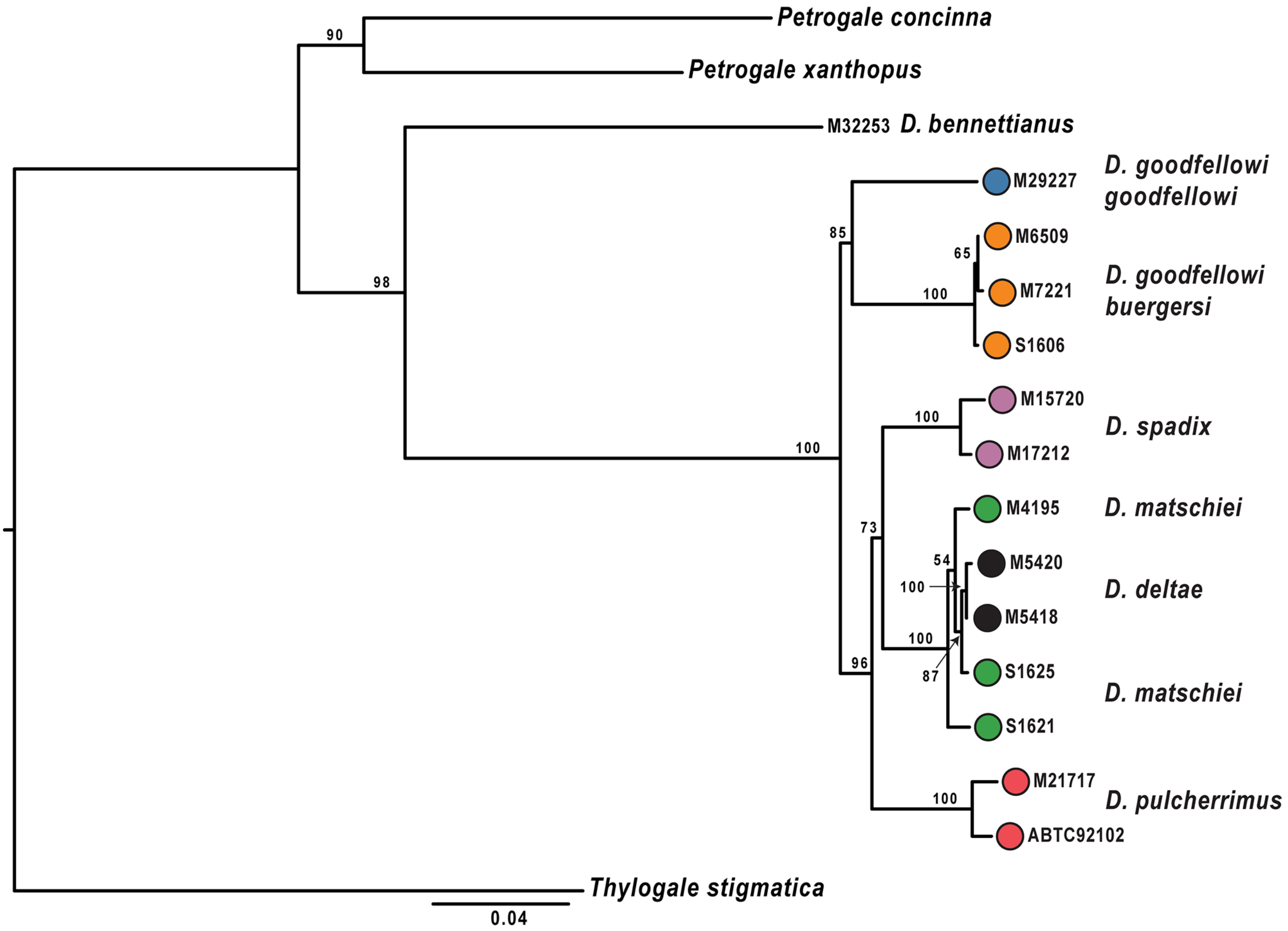

Figure 5. ML tree showing phylogenetic relationships amongst mtDNA sequences from six sampled Goodfellow's group taxa. Percentage bootstrap support is indicated.

density of people is low over most of the suitable habitat in the region. No ecologically similar species exists in the area, so intraspecific competition cannot explain the gap. A plausible explanation is that a zoogeographic barrier exists (or has existed until recently) in the vicinity of the headwaters of the Fly and Sepik Rivers, which has prevented members of the Goodfellow's group complex from spreading west along the Central Cordillera. Nevertheless, a "war bonnet" (from the anthropological collections in the Museum fur Volkenkunde, Berlin, No VI 50 932) collected in 1973 at Angguruk in Yali territory on the Central Cordillera to the east of the Baliem River, West Papua, is made of rich red tree-kangaroo fur (Flannery *et al*., 1996) and deserves closer study; it may represent an additional occurrence of the group in the highlands of western New Guinea. In addition, in May 1994, TF interviewed an Amungme man from the Tembagapura area of the Sudirman (Snow) Mountains, West Papua, who indicated that three species of tree-kangaroos occurred in the area. The two of the species were readily identifiable as *D. stellarum* ('naki') and *D. mbaiso* ('nemenaki'), while the third known as 'mbisop' was described as smaller than 'naki' and coloured yellow, white and chocolate. The size and colouration of 'mbisop' would be consistent with a member of the Goodfellow's group which is currently unknown by Western science in this area.

The progress reported here in resolving relationships within the Goodfellow's group enables the evolution of the group, as it is currently understood, to be explored for the first time. Unusually, for New Guinean mammals the Goodfellow's group has a predominately eastern distribution (Fig. 2). In many groups of New Guinean vertebrates, the most divergent lineages are found in western New Guinea and on the Vogelkop Peninsula in particular (Flannery *et al*., 2022).

Vicariance events within the Goodfellow's group remain perplexing. Ancestral state recontraction analysis suggests that the ancestor of the group inhabited mid-montane forest (Eldridge *et al*., 2018), and most taxa in the group primarily inhabit hill forest. This mid-montane habitat would have been more widespread during cooler glacial cycles than today, with the expansion and contraction of this preferred habitat potentially facilitating the spread and diversification of the Goodfellow's group. Previous phylogenetic analysis suggested that major diversification within the Goodfellows group occurred 1.6–2.4 mya during the early Pleistocene (Eldridge *et al*., 2018). The first split (*goodfellowi – pulcherrimus/ spadix/ matschiei*) suggests an origin in eastern New Guinea as has also been reported in the bird-of-paradise genus *Paradisaea* (Stelbrink *et al*., 2022). The second split (*pulcherrimus - spadix/ matschiei*)

Figure 6. Comparison of pelage variation across taxa in the Goodfellow's group. Left to right: *D. g. buergersi* (AM M.17213), *D. g. goodfellowi* (AM M.29227), *D. pulcherrimus* (AM M.21717), *D. matschiei* (AM M.6062), and *D. spadix* (AM M.17212).

involved the group reaching the North Coastal Ranges (which must have involved a crossing of the Sepik River), from whence *D. pulcherrimus* spread westwards to the Foja Mountains and then to the Vogelkop Peninsula. Alternatively, a widespread ancestral population may have diverged across the barrier formed by the Sepik River. The final split of *spadix* - *matschiei* is particularly perplexing, as these closely related, but morphologically divergent species are widely separated geographically by the high mountains of the Central Cordillera. This separation suggests a potential role for the rapid mountain building of the Central Cordillera, which commenced uplift ~10 mya (Stelbrink *et al*., 2022), in driving their isolation and divergence as has been reported in many other groups including phalangerid marsupials (Colgan & Flannery, 1993), turtles (Georges *et al*., 2014), fishes (Unmack *et al*., 2013) and birds (Bruxaux *et al*., 2018). However, separation of *D. spadix* and *D. matschiei* appears more recent, at ~1.6 mya (Eldridge *et al*., 2018). This suggests that either a relatively recent dispersal event occurred across the Central Cordillera, or that the ancestral *D. spadix* population occurred more widely throughout the southeastern lowlands of New Guinea and subsequently became extinct in most of its distribution after giving rise to *D. matschiei* on the rapidly uplifting Huon Peninsula which became a more montane-adapted taxon.

The mtDNA data also suggests an early split within *D. goodfellowi*, resulting in the large genetic divergence between the morphologically similar *D. g. goodfellowi* and *D. g. beurgersi* in eastern Papua New Guinea. This is likely to coincide with major river valleys that dissect the Central Cordillera in south-east New Guinea and appear to form major contemporary barriers to gene flow in *Dendrolagus* (Eldridge *et al*., 2018) and other groups of mid-high evaluation taxa including birds (Irestedt *et al*., 2009; Irestedt *et al*., 2015), other mammals (Meredith *et al*., 2010; Westerman *et al*., 2012; Helgen & Helgen, 2009) and insects (Janda *et al*., 2016; Toussaint *et al*., 2014).

Since taxonomic changes have occurred and much new information has become available since the last formal morphologically based taxonomic review of the Goodfellow's group (Groves, 1982), we here present an updated systematic review of the group and the first to include molecular data. The following standard museum abbreviation are used: AM, Australian Museum, Sydney; AMNH, American Museum of Natural History, New York; ANWC, Australian National Wildlife Collection, Canberra; BBM, Bernice P. Bishop Museum, Honolulu; BMNH, Natural History Museum, London; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; NMV National Museum of Victoria, Melbourne; PNGM, Papua New Guinea National Museum and Art Gallery, Port Moresby; RMNH, National Museum of Natural History (Naturalis Biodiversity Center), Leiden; UPNG, University of Papua New Guinea, Port Moresby; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; and ZMB, Zoologisches Museum, Berlin.

Systematics

Dendrolagus goodfellowi goodfellowi Thomas, 1908

Common name. Goodfellow's Tree-kangaroo

Holotype. BMNH 8.10.10.1, adult male, skin and damaged skull. Mt Obree, Owen Stanley Range, Papua New Guinea.

Other material examined. AM M.29227, BMNH 50.1433; PNGM 22888 (see below).

Distribution. *Dendrolagus goodfellowi goodfellowi* is patchily distributed in south-eastern Papua New Guinea, where it is recorded from Central, Oro, and Milne Bay Provinces, in lowland and mid-montane forest from sea-level to 2,400 m elevation (Flannery, 1993; Flannery *et al*., 1996). The subspecies appears uncommon and is very poorly represented in museum collections. Its distribution is likely to have been profoundly restricted by hunting by people.

The type is from 2,400 m elevation on Mt Obree in the Central Cordillera (Thomas, 1908), today located in the border area of Central and Oro (Northern) Provinces of Papua New Guinea. It is absent from the Central Cordillera north of Mt Obree, between English Peaks in the Kokoda area and the Wharton Range (Flannery *et al*., 1996). This may well mean there is a geographic gap between the range of *D. g. goodfellowi* and the south-eastern limit of the distribution of *D. g. buergersi*, which is situated in Morobe Province (Groves 1982). Other records apparently from Central Province include "armlets" made for a boy, collected in Kalo, Central Province, presumably representing *D. g. goodfellowi* (in the anthropological collections at the University Museum in Cambridge; Flannery *et al*., 1996: 184), and a captive individual that was held at Moitaka and later accessioned at PNGM (PNGM 22888). Most records are from outlying ranges and isolated peaks on the northern margins of the Central Cordillera in Oro Province, including from the Ajule Kajale Range (a low range lying north of, and isolated from the Central Cordillera by the Mambare River, north of Kokoda) (Flannery *et al*., 1996), Mt. Victory (AM M.29227) and Cape Nelson. On a visit to Cape Nelson in January 2011 one of us (TF), was informed by villagers that the species existed at sea level in deeply shaded rainforest on steep limestone slopes and cliffs at the heads of drowned river valleys on the Cape. Much of Cape Nelson is anthropogenic grassland, with rainforest remnants in the valleys and coastal margin, so the survival of *D. goodfellowi* there is notable. In Milne Bay Province it is recorded from "mountains of SE New Guinea, behind the island of" Samarai, which is located off the far southeastern tip of mainland New Guinea (BMNH 50.1433; Laurie, 1952), and one of us (KMH) saw an individual of *D. g. goodfellowi* held captive in Alotau in January 2003.

Description. *Dendrolagus g. goodfellowi* is morphologically similar to *D. g. buergersi* but appears to be larger, possibly with a longer tail (Table 4), and is paler and less distinctly marked (Fig. 6) (Eldridge & Coulson, 2015).

Remarks. As a species *D. goodfellowi* is listed as 'Endangered' on the IUCN Red List (Leary *et al*., 2016a). The nominate subspecies is rarely reported, poorly represented in museum collections and little is known of its biology.

Dendrolagus goodfellowi buergersi Matschie, 1912

Dendrolagus goodfellowi shawmayeri Rothschild and Dollman, 1936

Common names. Ornate Tree-kangaroo, Timboyok, Buergers' tree-kangaroo

Holotype. MZM 22155, adult male, skin and skull. Hunstein Range, upper August River, Papua New Guinea.

Other material examined. AM M.6509, AM M.7221, AM M.7416, AM M.7417, AM M.7497, AM M.7535, AM M.7536, AM M.7574, AM M.7575, AM M.7580, AM M.7586, AM M.7598, AM M.7620, AM M.9145, AM M.17222, AM M.17213, AM M.19579, AM M.23548, AM M.23632, AM M.24631, AM M.29690, AM M.46657, AMNH 190992, AMNH 190993, AMNH 192145, AMNH 192147, BBM-NG 21091, BBM-NG 24500, BBM-NG 51218, BMNH 1939.2930, BMNH 50.1429, BMNH 50.1430, BMNH 50.1814, MVZ 129784, MVZ 129785, PNGM 24127, PNGM 24129, PNGM 24130, PNGM 24496, PNGM 24670, PNGM 24752, PNGM 24754, PNGM 24755, UPNG 1950, UPNG 1956, UPNG 1959, UPNG 2393, UPNG 3186, UPNG 3215, UPNG 3268, USNM 586105–586107.

Many of the AM specimens are ex-Taronga Zoo animals, mostly listed as coming from Mt Hagen, but as the major commercial centre in the Central Highlands this would most likely have been the locality from which they were exported to Australia not necessarily the locality at which they were captured (Groves, 1982).

Distribution. *Dendrolagus goodfellowi buergersi* occurs in the central highlands of Papua New Guinea, from the Bubu River and the vicinity of Wau in Morobe Province in the east, west to Mt Bubiari near the West Papuan border, in mid-montane forest from 700 to 2865 m elevation (Groves, 1982; Flannery *et al*., 1996; the lowest record we note is UPNG 3215, a skull from Hagahai, 700 m, Madang Province). Many of the well-provenanced museum specimens are from Morobe Province, including specimens from the Bubu/Waria River (BMNH), Mt. Missim (BBM-NG), Bulldog Track (AMNH), and Wau (BBM-NG). Further to the west it is recorded from the Kratke Range (BMNH), and areas along the northern margin of the central highlands including Mt. Wilhelm (AMNH), Kerowagi (BBM-NG), and Mt. Jaka (AM; Groves, 1982). The holotype of *D. g. buergersi* is from the Hunstein Range, which lies to the north of, and is completely isolated from, the Central Cordillera, ~125 km northwest of the area surveyed by Flannery and Seri (1990). Further east, *D. g. buergersi* was reported present on the Western Schrader Range (the northern margin of the Central Cordillera) including the Jimi and Simbai Valleys, by Majnep and Bulmer (2007). It was however, absent from the Kaironk Valley (which bounds the Schrader Range to the south) "presumably due to the density of human occupation" (Majnep & Bulmer, 2007).

At its westernmost distributional limit, in Sandaun Province, *D. g. buergersi* is restricted to the outlying ranges north of the Central Cordillera, with the Sepik River forming a barrier (Flannery & Seri, 1990). On the Thurnwald Range (where *D. dorianus* is absent) *D. g. buergersi* extends to above 2,000 m (and possibly to the summit at 2,600 m). Its extreme western limit is Mt Bubiari, an isolated limestone

Table 4. The mean (and range) of body measurements from taxa in the Goodfellow's group.

	Head-body (mm)	n	Tail (mm)	n	Hindfoot (mm)	n	Ear (mm)	n	HB/T	n	Weight (kg)	n
D. g. goodfellowi	688 (640–770)	3	838 (815–855)	3	121 (113–125)	3	63 (59–66)	1	1.23 (1.10–1.34)	3	9.5	1
D. g. buergersi	596 (500–750)	26	699 (585–784)	25	117 (105–128)	21	60 (46–73)	19	1.18 (0.93–1.45)	25	7.5 (5.6–9.3)	10
D. pulcherrimus	602 (585–630)	3	735 (710–770)	3	115 (110–120)	3	55 (54–58)	3	1.22 (1.13–1.31)	3	6.9 (6.7–7.1)	3
D. spadix	638 (500–745)	5	715 (616–810)	5	129 (123–135)	2	57 (53–61)	3	1.13 (0.97–1.26)	5	8.1 (7.0–9.1)	2
D. matschiei	620 (512–740)	16	588 (455–685)	15	116 (99–126)	14	56 (45–64)	14	0.95 (0.81–1.10)	15	7.9 (4.5–10.5)	9

Since sexual dimorphism is limited in this group (Flannery *et al*., 1996), data from both sexes has been combined. For measurements separated by sex see Appendix 1.

massif rising from the Sepik lowlands to around 1,000 m (Flannery & Seri, 1990).

Dendrolagus g. buergersi is also present in the valley of the southwards flowing Om River (which lies north of Telefomin and flows into the Strickland River). The Hak-Om divide is one of the lowest points on the Central Cordillera, being a steep ridge at 1,560 m (Flannery & Seri, 1990). During a visit to the Ok Tedi mine in 2001 one of us (TF) saw two captive individuals which were reportedly captured on the southern slopes of the Central Cordillera in the vicinity of Tabubil-Kiunga, Western Province, which may be its western limit on the south side of the Cordillera. From here *D. g. buergersi* occurs eastward across the southern margins of the Central Cordillera, including in Hela Province at Mt. Sisa (UPNG) and in the Wanakipa area of Hewa (USNM; Helgen *et al*. 2011; see also Helgen [2007b], who found it was familiar to hunters at elevations below Porgera in Enga Province), in Southern Highlands Province at Arakubi near Lake Kutubu (Woxvold & Legra, 2019; Woxvold *et al*., 2021), and in Chimbu Province below 1,500 m on Mt Karimui, (UPNG; Hide *et al*., 1984).

Description. *Dendrolagus g. buergersi* can be distinguished from other members of the Goodfellow's group by its dark brown body and head, prominent bright yellow paired neck and rump stripes, strongly contrasting pale limbs and patterned tail (Fig. 6). Chestnut to dark brown dorsally, including the upper limbs, the ventral surface is paler and more sparsely furred. A dark brown mid-dorsal stripe of variable prominence and thickness runs from the top of the head to the base of tail. A single hair whorl occurs on the dorsal midline on mid-lower back. Prominent paired yellow to gold stripes occur on the rump and fainter paired stripes are present on the neck and back of head. The lower limbs are yellow to gold, contrasting strongly with upper limbs/body, although the digits are often dark. The head is of similar colour to the body or paler, especially on face and cheeks. The dark brown tail is longer than the head/body (Table 4), well covered with short hair, often paler ventrally and proximally, as well as mottled with highly variable yellow to gold rings and blotches along its length (Eldridge & Coulson, 2015).

Remarks. As a species *D. goodfellowi* is listed as 'Endangered' on the IUCN Red List (Leary *et al*., 2016a).

Dendrolagus matschiei
Förster and Rothschild, 1907

Dendrolagus matschiei flavidior Matschie, 1912
Dendrolagus deltae Troughton and Le Souef, 1936
Dendrolagus matschiei xanthotis Rothschild and Dollman, 1936

Common Names. Huon Tree-kangaroo, Matschie's Tree-kangaroo

Holotype. BMNH1939.2027, adult male, skin. Rawlinson Mountains, Huon Peninsula, Papua New Guinea.

Other material examined. AM M.3799, AM M.4032, AM M.4195, AM M.4205, AM M.4320, AM M.4326, AM M.5418 (holotype of *D. deltae*), AM M.5420 (paratype of *D. deltae*), AM M.6062, AM M.6751, AM M.6812, AM M.7869, AM M.7999, AM M.19579, AM M.39754, AMNH 190990, AMNH 194792, AMNH 194798, AMNH 194800, AMNH 194792, AMNH 236864, AMNH 236955, BMNH 14.2.18.2, BMNH 46.131, NMV 12642, MVZ 133135, PNGM 24141, PNGM 24289, PNGM 24518, PNGM 25376, RMNH 325, UPNG 581, USNM 521044, USNM 582438, USNM 582898, 598003.

Distribution. *Dendrolagus matschiei* occurs in the mountain ranges of the Huon Peninsula, in north-eastern New Guinea (Morobe and Madang Provinces of Papua New Guinea), including the Finisterre, Cromwell, Saruwaged, and Rawlinson Ranges, in mid- to upper-montane tropical rainforest, 1000 to 3300 m elevation (Flannery *et al*., 1996; Valentine *et al*., 2021). It also occurs on Umboi Island, where it may have been introduced in prehistory (Heinsohn, 2003). Previously thought to also have been introduced to Mt Agulupella in West New Britain (Flannery *et al*., 1996), but recent photographic evidence indicates that the species on New Britain appears to be more like *D. goodfellowi*.

Given the morphological (Groves, 1982) and genetic resemblance of the type series of *D. deltae*, supposedly from Mt. Pratt on the southern margin of the Central Cordillera, to *D. matschiei*, we confidently identify *deltae* as a synonym of *D. matschiei* and regard these specimens as mislabelled animals that originally must have come from the Huon Peninsula, firmly resolving an old riddle in New Guinea mammalogy (Helgen *et al*., 2011).

Description. *Dendrolagus matschiei* can be distinguished from other members of the Goodfellow's group by its relatively short tail (Table 4), dense fur, uniformly pale-yellow tail and dark dorsal stripe (Fig. 6). Warm brown dorsally and around the neck, paler on rump; underfur yellowish brown. A prominent dark brown mid-dorsal stripe runs from the top of the head to the base of tail. Paired hair whorls are present on either side of dorsal midline on the mid-lower back. The throat, chest, abdomen, inside of limbs, lower limbs, paws, feet and tail are pale yellow to gold. The head and face are brown, but with pale yellow to gold colouration, highly variable in extent, on the muzzle, forehead, around eyes and on ears. The tail is the same length as the head/body or shorter (Table 4) and is densely covered with short hairs. Typically, there is an abrupt colour change dorsally from the yellow tail base to the brown rump, but occasionally in some specimens it can intergrade more gradually (Eldridge & Coulson, 2015).

Remarks. Listed as 'Endangered' on The IUCN Red List (Ziembicki & Porolak, 2016). *Dendrolagus matschiei* has been a major focus of a community-based conservation program run by the Tree Kangaroo Conservation Program (TKCP) (Schwartz *et al.,* 2021; TKCP, 2023), including the establishment of the YUS protected area (Dabek & Wells, 2021).

Dendrolagus pulcherrimus Flannery, 1993

Common name. Golden-mantled Tree-kangaroo, Weimang

Holotype. AM M.21717, adult female, skin and skull. Mt Sapau, near Sibilanga, Torricelli Mountains, Sandaun Province, Papua New Guinea.

Paratypes. AM M.22173, unsexed, partial trophy skull. Parkop, near Sibilanga, Torricelli Mountains, Sandaun Province, Papua New Guinea. AM M.23423, adult female, body in alcohol – now missing (Parnaby *et al*., 2017). Macholp area, Torricelli Mountains, Sandaun Province, Papua New Guinea.

Other material examined. ANWC M38950, adult female, skin and skull, from "Bog Camp", Foja Mountains, West Papua. AM M.35029, AM M.38062: two sets of trophy jaws, purchased on 7 October 1992 at Pin-nai Village, 3 hours walk from Mokwam on the track to Jeu'te village in the Arfak Mountains, West Papua. The animals had been caught by Botor, brother of Benjamin of Jeu'te Village, on Gunung Minika, which lies to the west of Pin-nai. Botor had bad knees, so they may have been caught some time prior to the purchase, when Botor was more able.

Distribution. Disjunct populations in the Torricelli Range, Papua New Guinea, and the Foja Mountains and Vogelkop Peninsula, West Papua, Indonesia. It is recorded from mid-montane forest, 680–1700 m elevation (Flannery *et al*., 1996).

In the North Coastal Ranges it is very rare, being restricted to the easternmost part of the Torricelli Mountains. Accounts collected from the oldest hunters in the Lumi area (men in their 80s) in the late 1980s–1990s confirm that as late as the 1930s it was present throughout the North Coastal Ranges. It has thus become extinct in around 95% of its distribution between the 1930s and 1990s (Flannery *et al*., 1996). It is absent from the Mt Menawa block and the ranges adjacent to the Indonesian border in PNG, as well as the Cyclops Ranges north of Lake Sentani in West Papua.

In the Foja Mountains of West Papua, which are uninhabited by people at higher elevations, this species was first observed by Jared Diamond in 1981 (Flannery, 1993; Diamond, 2021). In 2005, one of us (KMH) working with hunters from the village Kwerba, obtained a voucher specimen from 1500 m during a biological survey in the Foja Mountains (ANWC M38950) and sighted and camera trapped other individuals in these mountains in 2008.

On the Vogelkop Peninsula it is known only as a subfossil from the Ayamaru Lakes area (Aplin *et al*., 1999) and from two trophy jaws (AM M.35029, AM M.38062) from the Arfak Mountains.

Description. *Dendrolagus pulcherrimus* can be distinguished from other members of the Goodfellow's group by its striking colouration and markings: a pale golden yellow head and upper back, contrasting with dark reddish-brown body (Fig. 6). Dark reddish-brown flanks becoming paler and more reddish dorsally; paler and more sparsely furred ventrally. Pale yellow to golden orange face, head, neck and upper back. A dark mid-dorsal stripe runs from the top of head to the lower back becoming broader and less defined distally. The ear margins are white. The upper limbs are also dark reddish brown but becoming paler on the paws and feet. A single hair whorl is present on the dorsal midline on the mid-lower back. Paired brownish-yellow stripes are present on the rump but are not as prominent as in *D. goodfellowi*. The tail is longer than the head/body (Table 4) and a paler brown than the flanks. It is well covered with short hair, often paler ventrally and proximally, with variable mottling of pale yellow to white rings and blotches along its length (Eldridge & Coulson, 2015).

Remarks. Listed as 'Critically Endangered' on the IUCN Red List (Leary *et al*., 2016b), however this could be reassessed now that a wider recent distribution has been documented. The species is poorly represented in museum collections and almost nothing is known of its biology. *Dendrolagus pulcherrimus* has been the major focus of a community-based conservation program in the Torricelli Mountains run by the Tenkile Conservation Alliance (Schwartz *et al*., 2021; TCA, 2023), and a focal species of the Foya Mamberamo Protected Area, including the Foja Mountains.

Dendrolagus spadix Troughton and Le Souef, 1936

Common name. Lowland Tree-kangaroo

Holotype. AM M.4561, adult male, skin (Fig. 1). Between Upper Awarra and Strickland Rivers, Western Province, Papua New Guinea.

Paratype. AM M.5978, subadult, unsexed, skin and skull. Bamu, Western Province, Papua New Guinea.

Other material examined. AM M.10789 (skin, adult, precise locality unknown, Papua New Guinea), AM M.15720 (skin and skull, juvenile female) and AM M.15721 (adult, skull, Mt. Sisa, Hela Province); AM M.17212 (skin and skull, adult male, Fogamaiyu, Southern Highlands Province); PNGM 22707 (skin, adult male, Mt. Bosavi, Southern Highlands Province); UPNG 2807(1943), UPNG 2808(1529) (flat skins, adults, labelled as from "Rio Tura south of Yuro", Karimui area, Chimbu Province, which appears to be where they where purchased at a market but UPNG 2808 was collected from Gurimata, Purari River, Gulf Province), UPNG 3244 (skull and skeleton, adult, Kesigi, Balimo subdistrict, Western Province); USNM 586436 (trophy jaw, Siona Falls, near Fogamaiyu, Southern Highlands Province); uncatalogued specimen formerly at the Papua New Guinea Institute of Biological Research, Goroka, Papua New Guinea (skull, between Wabo and Haia, Chimbu Province).

Leary and Seri (1997) mentioned trophy specimens referred to this species from Kopi in the Kikori Basin (Southern Highlands Province). Additional tree-kangaroo specimens described by Leary and Seri (1997) from the Kikori Basin in Southern Highlands Province, from the localities of Mt. Faru (reported as *D. goodfellowi* with weakly defined rump stripes), Mt. Kemenagi, and Wasi Falls, probably also represent this species. Two hunters' skins from Babeio in the Uro Creek Catchment of the Kikori Basin, southern Gulf Province, photographed and referred to *D. goodfellowi* by Kale *et al.* (2018a), are dark red over their entire body and tail and in fact represent *D. spadix*. Kale *et al.* (2018b) also discussed the possibility that *D. spadix* occurs in the Wau Creek Catchment of the Kikori Basin.

Distribution. *Dendrolagus spadix* inhabits sections of the Purari, Kikori and Strickland River catchments, south-central Papua New Guinea, in primary lowland tropical rainforest (small and large crowned hill forest) on limestone and other sedimentary geologies and uplifted alluvial plains, from sea level to 800 m elevation (Flannery, 1995; Flannery *et al*., 1996). It is recorded from Western, Hela, Southern Highlands, Gulf, and Chimbu Provinces of Papua New Guinea (Leary, 2004). Wright *et al*. (1998:181) suggested it may occur in the Lakekamu Basin in the lowlands in the border region of Gulf, Central, and Morobe Provinces, which would represent the easternmost occurrence. In the west, it may extend into the Trans-Fly region of Papua Province (Indonesia), where it as yet unrecorded. It is presumably geographically and elevationally parapatric with *D. goodfellowi* along the southern slopes of the Central Cordillera, occurring at lower elevations.

Most records for the species come from rugged karst terrain on the Papuan Plateau, extending to the coast in Gulf Province, and uninhabited swamp forest southeast of Lake Murray on the Fly River. These regions have little in common except for the fact that people are either absent or exist in extremely low density. Flannery *et al*. (1996) noted that 'its distribution hardly overlaps at all with people'. Apparently suitable habitat for *D. spadix* occurs across a vast area of southern New Guinea, and it seems likely that hunting by people has eliminated the species from much of its potential range.

Captain G.F.W. Zimmer, who collected the type specimen, reported that it came from "unknown and uninhabited country" (Troughton & Le Souef, 1936). The people of Lake Murray report that the vast uninhabited region lying southeast of Lake Murray was originally inhabited, but was depopulated as a result of *D. spadix*, which they believe hunts much as people do (Flannery *et al*., 1996). The species' dangerous reputation doubtless provides some protection.

Description. *Dendrolagus spadix* can be distinguished from other members of the Goodfellow's group by its largely unornamented dark brown colouration and short, sparse fur (Fig. 6). Uniformly, dark chestnut-brown dorsally, paler ventrally and on limbs and face. The ventral surface is sparsely furred. A faint dark mid-dorsal stripe runs from the head to the rump. Very faint paired pale stripes (of similar dimensions to those seen prominently in *D. goodfellowi*) occur on the rump in some specimens. A single hair whorl is present on the dorsal midline on the mid-lower back. The tail is longer than the head-body (Table 4) and dark brown, with occasional small yellowish markings, more common ventrally (Eldridge & Coulson, 2015).

Remarks. Listed as 'Vulnerable' on the IUCN Red List (Leary *et al*., 2016c). The species is poorly represented in museum collections and almost nothing is known of its biology.

ACKNOWLEDGEMENTS. We thank the Hermon Slade Foundation and the Australian Museum for funding. Kristin Stewardson, Cassie Vockler, Linda Neaves and Greta Frankham are thanked for expert technical assistance. Abram Powell is thanked for specimen photography. Staff at the Australian Museum (Sandy Ingleby, Anja Divljan, Harry Parnaby), American Museum of Natural History, New York (Eileen Westwig), Australian National Wildlife Collection https://ror.org/059mabc80 (Leo Joseph), Bernice P. Bishop Museum, Hawaii, Museum of Vertebrate Zoology (Allen Allison and Molly Hagemann), University of California, Berkeley (Jim Patton), National Museum of Victoria, Melbourne (Karen Roberts), Natural History Museum, London (Roberto Portela Miguez), Naturalis Biodiversity Center, Leiden (Chris Smeenk), Papua New Guinea National Museum and Art Gallery (Bulisa Iova and Jim Anamiato) and University of Papua New Guinea (Paulus Kei) are thanked for providing access to specimens.

References

Aplin, K. P., K. M. Helgen, and D. P. Lunde. 2010. A review of *Peroryctes broadbenti*, the giant bandicoot of Papua New Guinea. *American Museum Novitates* 3696: 1–41. https://doi.org/10.1206/3696.2

Aplin, K. P., J. M. Pasveer, and W. E. Boles. 1999. Late Quaternary vertebrates from the Bird's Head Peninsula, Irian Jaya, Indonesia, including descriptions of two previously unknown marsupial species. *Records of the Western Australian Museum, Supplement* 57: 351–387.

Archbold, R., A. L. Rand, and L. J. Brass. 1942. Results of the Archbold Expeditions. No. 41. Summary of the 1938–1939 New Guinea expedition. *Bulletin of the American Museum of Natural History* 79: 197–288.

Beehler, B. M., N. Kemp, and P. L. Shearman. 2021a. Threats to New Guinea's tree kangaroos. In *Tree Kangaroos: Science and Conservation*, ed. L. Dabek, P. Valentine, J. Blessington, and K. R. Schwartz, pp. 43–48. London: Academic Press. https://doi.org/10.1016/B978-0-12-814675-0.00008-7

Beehler, B. M., N. Kemp, and P. L. Shearman. 2021b. Opportunities for tree kangaroo conservation on the island of New Guinea. In *Tree Kangaroos: Science and Conservation*, ed. L. Dabek, P. Valentine, J. Blessington, and K. R. Schwartz, pp. 129–133. London: Academic Press. https://doi.org/10.1016/B978-0-12-814675-0.00018-X

Beehler, B. M., and T. K. Pratt. 2016. *Birds of New Guinea. Distribution, Taxonomy and Systematics*. Princeton, NJ: Princeton University Press. https://doi.org/10.1515/9781400880713

Blessington, J., J. Steenberg, K. R. Schwartz, U. Schurer, B. Smith, M. Richardson, R. Jaffar and C. Ford. 2021. Tree kangaroo popualtions in managed facilities. In *Tree Kangaroos: Science and Conservation*, ed. L. Dabek, P. Valentine, J. Blessington, and K. R. Schwartz, pp. 249–269. London: Academic Press. https://doi.org/10.1016/B978-0-12-814675-0.00020-8

Bruxaux, J., M. Gabrielli, H. Ashari, R. Prŷs-Jones, L. Joseph, B. Milá, G. Besnard, and C. Thébaud. 2018. Recovering the evolutionary history of crowned pigeons (Columbidae: *Goura*): Implications for the biogeography and conservation of New Guinean lowland birds. *Molecular Phylogenetics and Evolution* 120: 248–258. https://doi.org/10.1016/j.ympev.2017.11.022

Bulazel, K., G. C. Ferreri, M. D. B. Eldridge, and R. J. O'Neill. 2007. Species-specific shifts in centromere sequence composition are coincident with breakpoint reuse in karyotypically divergent lineages. *Genome Biology* 8 (8): R170. https://doi.org/10.1186/gb-2007-8-8-r170

Colgan, D. J., and T. F. Flannery. 1993. Electrophoretic and morphological analysis of the systematics of the *Phalanger orientalis* (Marsupialia) species complex in Papua New Guinea and the Solomon Islands. *Australian Journal of Zoology* 41: 355–378.
https://doi.org/10.1071/ZO9930355

Dabek, L. and Z. Wells. 2021. Creating the first conservation area in Papua New Guinea to protect tree kangaroos. In *Tree Kangaroos: Science and Conservation*, ed. L. Dabek, P. Valentine, J. Blessington, and K. R. Schwartz, pp. 135–151. London: Academic Press.
https://doi.org/10.1016/B978-0-12-814675-0.00032-4

Dabek, L., P. Valentine, J. Blessington, and K. R. Schwartz. 2021. *Tree Kangaroos: Science and Conservation*. London: Academic Press.

Diamond, J. 2021. Foreword: the charisma of tree kangaroos. In *Tree Kangaroos: Science and Conservation*, ed. L. Dabek, P. Valentine, J. Blessington, and K. R. Schwartz, pp. xxvii–xxxi. London: Academic Press.
https://doi.org/10.1016/B978-0-12-814675-0.00033-6

Eldridge, M. D. B., and G. M. Coulson. 2015. Family Macropodidae (kangaroos and wallabies). In *Handbook of the Mammals of the World. Volume 5. Marsupials and Monotremes*, ed. D. E. Wilson, and R. A. Mittermeier, 630–735. Barcelona: Lynx Edicions.

Eldridge, M. D. B., S. Potter, K. M. Helgen, M. H. Sinaga, K. P. Aplin, T. F. Flannery, and R. N. Johnson. 2018. Phylogenetic analysis of the tree-kangaroos (*Dendrolagus*) reveals multiple divergent lineages within New Guinea. *Molecular Phylogenetics and Evolution* 127: 589–599.
https://doi.org/10.1016/j.ympev.2018.05.030

Firneno Jr, T. J., J. R. O'Neill, D. M. Portik, A. H. Emery, J. H. Townsend, and M. K. Fujita. 2020. Finding complexity in complexes: assessing the causes of mitonuclear discordance in a problematic species complex of Mesoamerican toads. *Molecular Ecology:* 29: 3543–3559.
https://doi.org/10.1111/mec.15496

Flannery, T. F. 1990. *Mammals of New Guinea*. Sydney: Reed Books.

Flannery, T. F. 1993. Taxonomy of *Dendrolagus goodfellowi* (Macropodidae: Marsupialia) with description of a new subspecies. *Records of the Australian Museum* 45: 33–42.
https://doi.org/10.3853/j.0067-1975.45.1993.128

Flannery, T. F. 1995. *Mammals of New Guinea. 2nd edition*. Sydney: Reed Books.

Flannery, T. F., R. Martin, and A. L. Szalay. 1996. *Tree-kangaroos. A Curious Natural History*. Melbourne: Reed Books.

Flannery, T. F., T. H. Rich, P. Vickers-Rich, T. Ziegler, E. G. Veatch, and K. M. Helgen. 2022. A review of monotreme (Monotremata) evolution. *Alcheringa* 46: 3–20.
https://doi.org/10.1080/03115518.2022.2025900

Flannery, T. F., and L. Seri. 1990. The mammals of the southern West Sepik Province, Papua New Guinea: their distribution, abundance, human use and zoogeography. *Records of the Australian Museum* 42: 173–208.
https://doi.org/10.3853/j.0067-1975.42.1990.114

Förster, F., and W. Rothschild. 1907. Description of a new tree-kangaroo. *Novitates Zoologicae* 14: 506.
https://doi.org/10.5962/bhl.part.25383

Frankham, R., J. D. Ballou, K. Ralls, M. D. B. Eldridge, M. R. Dudash, C. B. Fenster, R. C. Lacy, and P. Sunnucks. 2017. *Genetic Management of Fragmented Animal and Plant Populations.* Oxford, UK: Oxford University Press.
https://doi.org/10.1093/oso/9780198783398.001.0001

Georges, A., X. Zhang, P. J. Unmack, B. N. Reid, M. Le, and W. P. McCord. 2014. Contemporary genetic structure of an endemic freshwater turtle reflects Miocene orogenesis of New Guinea. *Biological Journal of the Linnean Society* 111: 192–208.
https://doi.org/10.1111/bij.12176

Groves, C. P. 1982. The systematics of tree kangaroo (*Dendrolagus;* Marsupialia, Macropodidae). *Australian Mammalogy* 5(3): 157–186.
https://doi.org/10.1071/AM82017

Groves, C. P. 2005. Order Diprotodontia. In *Mammal Species of the World: A Taxonomic and Geographic Reference. Third Edition*, ed. D. E. Wilson, and D. M. Reeder, pp. 43–70. Baltimore: Johns Hopkins University Press.

Heinsohn, T. E. 2003. Animal translocation: long-term human influences on the vertebrate zoogeography of Australasia (natural dispersal versus ethnophoresy). *Australian Zoologist* 32 (3): 351–376.
https://doi.org/10.7882/AZ.2002.014

Helgen, K. M. 2007a. A taxonomic and geographic overview of the mammals of Papua. In *The Ecology of Papua,* ed. J. A. Marshall, and B. M. Beehler, pp. 689–749. Singapore: Periplus Editions.

Helgen, K. M. 2007b. The mammal fauna of the Kaijende Highlands, Enga Province, Papua New Guinea. In *A Rapid Biological Assessment of the Kaijende Highlands, Enga Province, Papua New Guinea*, ed. S. J. Richards, pp. 52–68. Arlington, Virginia: Conservation International.

Helgen, K. M. and L. E., Helgen. 2009. Biodiversity and biogeography of the moss-mice of New Guinea: a taxonomic revision of *Pseudohydromys* (Rodentia: Murinae). *Bulletin of the American Museum of Natural History* 331: 230–312.
https://doi.org/10.1206/582-8.1

Helgen, K. M., M. D. Opiang, and W. H. Thomas. 2011. The mammal fauna of Wanakipa, Southern Highlands Province, Papua New Guinea. In *Rapid Biological Assessments of the Nakanai Mountains and the Upper Strickland Basin: Surveying the Biodiversity of Papua New Guinea's Sublime Karst Environments*, ed. S. J. Richards, and B. G. Gamui, pp. 246–258. Arlington, VA: Conservation International.

Hide, R. L., J. C. Pernetta, and T. Senabe. 1984. Exploitation of wild animals. In *The Research Report of the Simbu Land Use Project, Vol. 4. South Simbu: Studies in Demography, Nutrition and Subsistence*, ed. R. L. Hide, 291–380. Port Moresby: IASER.

Irestedt, M., K. A. Jønsson, J. Fjeldsa, L. Christidis, and P. G. P. Ericson. 2009. An unexpectedly long history of sexual selection in birds-of-paradise. *BMC Evolutionary Biology* 9: 235.
https://doi.org/10.1186/1471-2148-9-235

Irestedt, M., H. Batalha-Filho, C. S. Roseelaar, L. Christidis, and P. G. P. Ericson. 2015. Contrasting phylogeographic signatures in two Australo-Papuan bowerbird species complexes (Aves: Ailuroedus). *Zoologica Scripta* 45 (4): 365–379.
https://doi.org/10.1111/zsc.12163

Janda, M., P. Matos-Maraví, M. Borovanska, J. Zima Jr., E. Youngerman, and N. E. Pierce. 2016. Phylogeny and population genetic structure of the ant genus *Acropyga* (Hymenoptera : Formicidae) in Papua New Guinea. *Invertebrate Systematics* 30 (1): 28–40.
https://doi.org/10.1071/IS14050

Kale, E., K. N. Armstrong, P. Amick, and I. A. Woxvold. 2018a. Mammals of the Uro Creek catchment, Gulf Province, Papua New Guinea. In *Rapid Biological Assessments of Wau Creek , Uro Creek, and Lake Kutubu: Documenting Biodiversity Values to Promote Forest Conservation in the Kikori River Basin, Papua New Guinea,* pp. 243–268. Port Moresby: ExxonMobil PNG Limited.

Kale, E., K. N. Armstrong, P. Amick, and I. A. Woxvold. 2018b. Mammals of the Wau Creek proposed Wildlife Management Area, Gulf Province, Papua New Guinea. In *Rapid Biological Assessments of Wau Creek , Uro Creek, and Lake Kutubu: Documenting Biodiversity Values to Promote Forest Conservation in the Kikori River Basin, Papua New Guinea*, pp. 119–145. Port Moresby: ExxonMobil PNG Limited.

Kirsch, J. A. W., and J. H. Calaby. 1977. The species of living marsupials: an annotated list. In *The Biology of Marsupials*, ed. B. Stonehouse, and D. Gilmore, pp. 9–26. London: MacMillan Press.
https://doi.org/10.1007/978-1-349-02721-7_2

Kirsch, J. A. W., F. J. Lapointe, and M. S. Springer. 1997. DNA-hybridisation studies of marsupials and their implications for metatherian classification. *Australian Journal of Zoology* 45 (3): 211–280.
https://doi.org/10.1071/ZO96030

Lanfear, R., B. Calcott, S. Y. W. Ho, and S. Guindon. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Biological Evolution* 29: 1695–1701.
https://doi.org/10.1093/molbev/mss020

Laurie, E. M. O. 1952. Mammals collected by Mr. Shaw Mayer in New Guinea, 1932–1949. *Bulletin of the British Museum (Natural History) Zoology* 1: 271–318.
https://doi.org/10.5962/bhl.part.21635

Laurie, E. M. O., and J. E. Hill 1954. *List of Land Mammals of New Guinea, Celebes and Adjacent Islands 1758-1952*. London: British Museum (Natural History).
https://doi.org/10.5962/bhl.title.112425

Leary, T. 2004. *Mammal Survey of Darai Plateau, Gulf Province and Libano Sok, Southern Highlands Province July – August, 2003*. Report to WWF – Kikori Integrated Conservation and Development Project.

Leary, T., and L. Seri. 1997. An annotated checklist of mammals recorded in the Kikori River Basin, Papua New Guinea. *Science in New Guinea* 23: 79–100.

Leary, T., L. Seri, D. Wright, S. Hamilton, K. Helgen, R. Singadan, J. Menzies, A. Allison, R. James, C. Dickman, K. Aplin, T. Flannery, R. Martin, and L. Salas. 2016a. *Dendrolagus goodfellowi,* Goodfellow's tree kangaroo. *The IUCN Red List of Threatened Species 2016: e.T6429A21957524* 2016 [cited 11 April 2022].

Leary, T., D. Wright, S. Hamilton, K. Helgen, R. Singadan, K. Aplin, C. Dickman, L. Salas, T. Flannery, R. Martin, and L. Seri. 2016b. *Dendrolagus pulcherrimus,* golden-mantled tree kangaroo. *The IUCN Red List of Threatened Species 2016: e.T136696A21957219* 2016 [cited 11 April 2022].

Leary, T., L. Seri, D. Wright, S. Hamilton, K. Helgen, R. Singadan, J. Menzies, A. Allison, R. James, C. Dickman, K. Aplin, L. Salas, T. Flannery, and F. Bonaccorso. 2016c. *Dendrolagus spadix,* lowland tree kangaroo. *The IUCN Red List of Threatened Species 2016: e.T6436A21956250* 2016 [cited 11 April 2022].

Librado, P. and J. Rozas. 2009. DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* 25: 1451–1452.
https://doi.org/10.1093/bioinformatics/btp187

Majnep, I. S., and R. Bulmer. 2007. *Animals the Ancestors Hunted: An Account of the Wild Mammals of the Kalam Area, Papua New Guinea*. Bathurst: Crawford House Publishing.

Malekian, M., S. J. B. Cooper, and S. M. Carthew. 2010. Phylogeography of the Australian sugar glider (*Petaurus breviceps*): evidence for a new divergent lineage in eastern Australia. *Australian Journal of Zoology* 58: 165–181.
https://doi.org/10.1071/ZO10016

Martin, R. W. 2005. *Tree-kangaroos of Australia and New Guinea*. Melbourne: CSIRO Publishing.
https://doi.org/10.1071/9780643093126

Matschie, P. 1912. Zwei neue rassen des roten baumkänguru aus Deutsch-Neuguinea. *Sitzungbericht der Gesellschaft Naturforschender Freunde Zu Berlin* 1912: 568–572.

Meredith, R. W., M. Westerman, and M. S. Springer. 2008. A phylogeny and timescale for the living genera of kangaroos and kin (Macropodiformes: Marsupialia) based on nuclear DNA sequences. *Australian Journal of Zoology* 56(6): 395–410.
https://doi.org/10.1071/ZO08044

Meredith, R. W., M. A. Mendoza, K. K. Roberts, M. Westerman, and M. S. Springer. 2010. A phylogeny and timescale for the evolution of Pseudocheiridae (Marsupialia: Diprotodontia) in Australia and New Guinea. *Journal of Mammalian Evolution* 17: 75–99.
https://doi.org/10.1007/s10914-010-9129-7

Osborne, M. J., and L. Christidis. 2001. Molecular phylogentics of Australo-Papuan possums and gliders (Family Petauridae). *Molecular Phylogenetics and Evolution* 20(2): 211–224.
https://doi.org/10.1006/mpev.2001.0960

Pääbo, S. 1990. Amplifying ancient DNA. In *PCR Protocols: A Guide to Methods and Applications*, ed. M. A. Innes, D. H. Gelfand, J. J. Sninsky, and T. J. White, pp. 159–166. San Diego: Academic Press.
https://doi.org/10.1016/B978-0-12-372180-8.50024-X

Palumbi, S. R., A. P. Martin, S. Romano, W. O. McMillan, L. Stice, and G. Grabowski. 1991. *The Simple Fool's Guide to PCR, Version 2.0*. Honolulu: University of Hawaii.

Parnaby, H., S. Ingleby, and A. Divljan. 2017. Type specimens of non-fossil mammals in the Australian Museum, Sydney. *Records of the Australian Museum* 69(5): 277–420.
https://doi.org/10.3853/j.2201-4349.69.2017.1653

Pattiselanno, F., J. F. Koibur, and A. Y. S. Arobaya. 2021. Status of tree kangaroo science and conservation in Indonesian New Guinea. In *Tree Kangaroos: Science and Conservation*, ed. L. Dabek, P. Valentine, J. Blessington, and K. R. Schwartz, pp. 237–246. London: Academic Press.
https://doi.org/10.1016/B978-0-12-814675-0.00019-1

Potter, S., S. J. B. Cooper, C. J. Metcalfe, D. A. Taggart, and M. D. B. Eldridge. 2012. Phylogenetic relationships within *Petrogale* (Marsupialia: Macropodidae) and their biogeographic history within Australia. *Molecular Phylogenetics and Evolution* 62 (2): 640–652.
https://doi.org/10.1016/j.ympev.2011.11.005

Rothschild, W., and G. Dollman. 1936. The genus *Dendrolagus*. *Transactions of the Zoological Society of London* 21: 477–548.
https://doi.org/10.1111/j.1096-3642.1936.tb00459.x

Schwartz, K.R., O. Byers, P. Miller, J. Blessington and B. Smith. 2021. The role of zoos in tree kangaroo conservation: Connecting ex situ and in situ conservation action. In *Tree Kangaroos: Science and Conservation*, ed. L. Dabek, P. Valentine, J. Blessington, and K. R. Schwartz, pp. 329–361. London: Academic Press.
https://doi.org/10.1016/B978-0-12-814675-0.00026-9

Stelbrink, B., T. Von Rintelen, K. Richter, K. Finstermeier, S. Frahnert, J. Cracraft, and M. Hofreiter. 2022. Insights into the geographical origin and phylogeographical patterns of *Paradisaea* birds-of-paradise. *Zoological Journal of the Linnean Society* 196: 1394–1407.
https://doi.org/10.1093/zoolinnean/zlac010

Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei, M. and S. Kumar. 2011. MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* 28: 2731–2739.
https://doi.org/10.1093/molbev/msr121

Tenkile Conservation Alliance (TCA). 2023. Tenkile Tree Kangaroo. https://tenkile.com/ [accessed 4 October 2023]

Thomas, O. 1908. A new tree-kangaroo from British New Guinea. *Annals and Magazine of Natural History* 2(8): 452–453.
https://doi.org/10.1080/00222930808692512

Toussaint, E. F. A., R. Hall, M. T. Monaghan, K. Sagata, S. Ibalim, H. V. Shaverdo, A. P. Vogler, J. Pons, and M. Balke. 2014. The towering orogeny of New Guinea as a trigger for arthropod megadiversity. *Nature Communications* 5: 4001.
https://doi.org/10.1038/ncomms5001

Tree Kangaroo Conservation Program (TKCP). 2023. Accessed 4 October 2023.
https://www.zoo.org/tkcp

Troughton, E. Le G., and A. S. Le Souef. 1936. Two new tree kangaroos from Papua, with notes on allied forms. *Australian Zoologist* 8 (3): 193–197.

Unmack, P. J., P. J. Allen, and J. B. Johnson. 2013. Phylogeny and biogeography of rainbowfishes (Melanotaeniidae) from Australia and New Guinea. *Molecular Phylogenetics and Evolution* 67: 15–27.
https://doi.org/10.1016/j.ympev.2012.12.019

Valentine, P., L. Dabek, and K. R. Schwartz. 2021. What is a tree kangaroo? Evolutionary history, adaptation to life in the trees, taxonomy, genetics, biogeography, and conservation status. In *Tree Kangaroos: Science and Conservation*, ed. L. Dabek, P. Valentine, J. Blessington, and K. R. Schwartz, pp. 3–16. London: Academic Press.
https://doi.org/10.1016/B978-0-12-814675-0.00010-5

Westerman, M., B. P. Kear, K. Aplin, R. W. Meredith, C. Emerling, and M. S. Springer. 2012. Phylogenetic relationships of living and recently extinct bandicoots based on nuclear and mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 62: 97–108.
https://doi.org/10.1016/j.ympev.2011.09.009

Woxvold, I. A., and L. Legra. 2019. Camera trap monitoring of terrestrial mammals and birds. In *Results of the Second PMA3 Biodiversity Monitoring Survey of the PNG LNG Upstream Project Area, 10–31 May 2017*, ed. S. J. Richards, pp. 63–120. Port Moresby: ExxonMobil PNG Limited.

Woxvold, I. A., S. Tulai, S. Yama, and A. Mani. 2021. Camera trap monitoring of terrestrial mammals and birds. In *Results of the Third PMA3 Biodiversity Monitoring Survey of the PNG LNG Upstream Project Area, 8 August-2 September 2019*, ed. S. J. Richards, pp. 53–111. Port Moresby: ExxonMobil PNG Limited.

Wright, D. D., S. Balagawi, T. T. Raga, and R. T. Ipu. 1998. Mammals. In *A Biological Assessment of the Lakekamu Basin, Papua New Guinea*, ed. A. L. Mack, pp. 67–71, 181–184. Washington, D.C.: Conservation International (Rapid Assessment Program Working Papers 9).

Ziembicki, M., and G. Porolak. *Dendrolagus matschiei*, Huon tree kangaroo. The IUCN Red List of Threatened Species 2016: e.T6433A21956650 2016 [cited 11 April 2022].
https://www.iucnredlist.org/species/6427/21957392

Appendix 1. The mean (and range) of body measurements from taxa in the Goodfellow's group separated by sex.

	Sex	Head-body (mm)	n	Tail (mm)	n	Hindfoot (mm)	n	Ear (mm)	n	HB/T	n	Weight (kg)	n
D. g. goodfellowi	M	705 (640–770)	2	850 (845–855)	2	125 (124–125)	2	59	1	1.22 (1.10–1.34)	2	9.5	1
D. g. goodfellowi	F	655	1	815	1	113	1	66	1	1.24	1	—	—
D. g. buergersi	M	611 (500–750)	13	714 (645–760)	12	120 (110–128)	10	60 (46–73)	10	1.18 (0.93–1.45)	12	7.7 (6.4–9.3)	6
D. g. buergersi	F	585 (535–654)	17	688 (585–784)	17	115 (105–126)	15	60 (55–68)	13	1.18 (1.04–1.32)	17	7.4 (5.6–0–8.6)	5
D. pulcherrimus	F	602 (585–630)	3	735 (710–770)	3	115 (110–120)	3	55 (54–58)	3	1.22 (1.13–1.31)	3	6.9 (6.7–7.1)	3
D. spadix	M	573 (500–645)	2	661 (616–705)	2	135	1	57 (53–61)	2	1.16 (1.09–1.23)	2	8.1 (7.0–9.1)	2
D. spadix	F	681 (573–745)	3	751 (720–810)	3	123	1	56	1	1.11 (0.91–1.26)	3	—	—
D. matschiei	M	659 (615–740)	4	596 (555–620)	4	119 (111–124)	3	58 (57–59)	3	0.91 (0.81–0.98)	4	8.4 (7.1–10)	3
D. matschiei	F	608 (512–672)	12	585 (455–685)	11	115 (99–126)	11	55 (45–64)	11	0.97 (0.89–1.10)	11	7.7 (4.5–10.5)	6

Data from Flannery *et al*. (1996), supplemented with additional data from the AM, BMNH, PNGM, UPNG, BBM and F. Vejmelka (*pers. comm.*).

Appendix 2. GenBank accession numbers for *Dendrolagus* mtDNA data used in the analysis of Goodfellow's group taxa.

Taxon	Specimen ID	Cytb	ND2	COI
D. g. goodfellowi	AM M.29227	PP379018	PP379025	PP395866-67*
D. g. buergersi	AM M.52279	JQ042137	JQ042160	JQ042183
	AM M.6509	PP379014	PP379021	PP379027
	AM M.7221	PP379013	PP379020	PP379026
D. pulcherrimus	AM M.21717	MH197963	MH197929	MH197996
	ABTC92102	MH197964	MH197930	MH197997
D. matschiei	S-1621	MH197995	MH197941	MH198008
	900073	MH197996	MH197942	MH198009
	AM M.4195	PP379015	PP379022	PP379028
D. spadix	AM M.17212	MH197978	MH197944	MH198011
	AM M.15720	PP393684-85	PP379019	—
D. 'deltae'	AM M.5418	PP379017	PP379024	PP379030
	AM M.5420	PP379016	PP379023	PP379029
D. bennettianus	AM M.32253	MH197950	MH197916	MH197984
P. concinna	S-315	JQ042124	JQ042147	JQ042170
P. xanthopus	S-359	JQ042136	JQ042159	JQ042181
T. stigmatica	S-1101	JN202479	JQ042163	JQ042186

* For M.29227 an additional short fragment from the 5' end of COI was included in the analysis but could not be uploaded to GenBank: atgttcattaatcgttgattgttttcaaccaatcacaaagacattggcacgttatactta.

Appendix 3. Primers used to amplify segments of the *COI, Cytb* and *ND2* genes from *Dendrolagus* taxa.

Gene	Primer		Reference
COI	M134	GTATTTATCCTGCTTACTCTTAGTTAACAGC	KN Armstrong, unpubl. data
	Den_CO1_R1	CCTACTATTCCTGCTCARGCRCCGAATAG	this study
	Den_CO1_F1	TCAATGCTTKCCTCAGC	this study
	Den_CO1_R2	ATAACATTATAAATCTG	this study
	Den_CO1_F2	CTTATTCGCGCAGAGCTCGG	this study
	Den_CO1_R3	TCGGGTGCGCCGATCATTAG	this study
	Den_CO1_F3	ATAATGTTATTGTRACRGCC	this study
	Den_CO1_R4	GTTCCTGCTCCYGCTTCTAC	this study
	Den_CO1_F4	CCTCCTTCTATTRGCATC	this study
	Den_CO1_R5	GTGATRAAGTTGATAGCTCC	this study
	Den_CO1_F5	CACGCTGGGGCTTCTGTAG	this study
	Den_CO1_R6	AAGGAGGAGAAGRACTGCTGT	this study
	Den_CO1_F6	ACCACCCGCYCTATCTCAATATC	this study
	Den_CO1_R7	CTTCTGGATGTCCRAAGAATCA	this study
	Den_CO1_F7	ACAATACTTTTAACAGACCG	this study
	Den_CO1_R8	TTACCAGAATAGTAGGTTAC	this study
	Den_CO1_F8	TGATTCTTYGGACATCCAGAAG	this study
	Den_CO1_R9	TAAGCTCGAGTGTCGACGTC	this study
	Den_CO1_F9	TTCACAGTCGGATTAGACG	this study
	Den_CO1_R10	ATAAATCCGAGAGCTCATAG	this study
	Den_CO1_F10	GTATTTAGTTGACTAGCAAC	this study
	Den_CO1_R11	CCTATRGATAGGACRTAGTGGAAGTG	this study
	Den_CO1_F11	CATGACACTTACTATGTA	this study
	M31(COA)	AGTATAAGCGTCTGGGTAGTC	(Palumbi *et al*. 1991)
Cytb	L14724	CGAAGCTTGATATGAAAAACCATCGTTG	(Pääbo 1990)
	Den_CB_R1	GCAGGCTCCTAGTAGTGA	this study
	Den_CB_F1	CACCCACTAATTAAAAT	this study
	Den_CB_R2	ATGAAGAATATGGATGCTC	this study
	Den_CB_F2	CCCACATCTGCCGAGAYGT	this study
	Den_CB_R3	CGATATAAGGAATAGCGGA	this study
	Den_CB_F3	GACAAATATCRTTCTGAGG	this study
	Den_CB_R4	GTATAGTACGGGTGGAATGG	this study
	Den_CB_F4	CTATTYCTACAYGAAAC	this study
	Den_CB_R5	CGGAGAATRGCATATGCAAA	this study
	Den_CB_F5	TTGCATAYGCYATYCTCCGATC	this study
	Den_CB_R6	AAGTATGAGATTGATGCT	this study
	Den_CB_F6	TGAATCGGAGGCCAACCAGTAG	this study
	Mr2	AGGGTGTTATACCTTCATTTTTGG	(Bulazel *et al*. 2007)
ND2	mmND2.1	GCACCATTCCACTTYTGAGT	(Osborne and Christidis 2001)
	Den_ND2_R1	GTTRAGTATGAGRAATAGGGTTAG	this study
	Den_ND2_F1	TCCTAGCCTACTCCTCTAT	this study
	Den_ND2_R2	CCTCCAAGRGATANAAGTGTGAG	this study
	Den_ND2_F2	AAATCACTRACAAACCTATG	this study
	Den_ND2_R3	GGAAATATAGTAAGTGTTGAG	this study
	Den_ND2_F3	GCCACCCTAATAGCACTYTCA	this study
	mrND2c	GATTTGCGTTCGAATGTAGCAAG	(Osborne and Christidis 2001)

Appendix 4. Average uncorrected pairwise sequence divergence [and range] across the three mtDNA loci for *Dendrolagus* taxa examined in this study.

COI	*D. g. goodfellowi*	*D. g. buergersi*	*D. pulcherrimus*	*D. spadix*	*D. matschiei*	*D. bennettianus*	*P. concinna*	*P. xanthopus*
D. g. buergersi	0.044	0.000	—	—	—	—	—	—
D. pulcherrimus	0.050 [0.048–0.051]	0.036 [0.034–0.038]	0.004 —	— —	— —	— —	— —	— —
D. spadix	0.048 —	0.040 —	0.034 [0.032–0.036]	— —	— —	— —	— —	— —
D. matschiei	0.048 [0.046–0.050]	0.038 [0.036–0.040]	0.036 [0.032–0.040]	0.026 [0.024–0.028]	0.003 [0.000–0.006]	— —	— —	— —
D. bennettianus	0.121 —	0.107 —	0.115 [0.113–0.117]	0.113 —	0.098 [0.097–0.099]	— —	— —	— —
P. concinna	0.141 —	0.123 —	0.125 [0.123–0.127]	0.133 —	0.131 [0.129–0.133]	0.113	— —	— —
P. xanthopus	0.115 —	0.095 —	0.101 [0.099–0.103]	0.099 —	0.100 [0.099–0.101]	0.107	0.079 —	— —
T. stigmatica	0.103 —	0.097 —	0.101 [0.099–0.103]	0.109 —	0.106 [0.105–0.107]	0.115 —	0.127 —	0.095 —

Cytb	*D. g. goodfellowi*	*D. g. buergersi*	*D. pulcherrimus*	*D. spadix*	*D. matschiei*	*D. bennettianus*	*P. concinna*	*P. xanthopus*
D. g. buergersi	0.067 [0.066–0.069]	0.004 [0.003–0.006]	— —	— —	— —	— —	— —	— —
D. pulcherrimus	0.078 [0.075–0.080]	0.055 [0.053–0.058]	0.011 —	— —	— —	— —	— —	— —
D. spadix	0.074 [0.072–0.075]	0.065 [0.061–0.069]	0.057 [0.053–0.061]	0.008 —	— —	— —	— —	— —
D. matschiei	0.062 [0.058–0.066]	0.049 [0.042–0.055]	0.048 [0.044–0.053]	0.042 [0.036–0.047]	0.009 [0.000–0.019]	— —	— —	— —
D. bennettianus	0.136 —	0.134 [0.133–0.136]	0.128 [0.125–0.130]	0.132 [0.130–0.133]	0.121 [0.119–0.122]	— —	— —	— —
P. concinna	0.111 —	0.109 [0.108–0.111]	0.100 —	0.104 [0.102–0.105]	0.094 [0.080–0.100]	0.102 —	— —	— —
P. xanthopus	0.125 —	0.117 [0.116–0.119]	0.102 —	0.101 [0.100–0.102]	0.103 [0.100–0.105]	0.102 —	0.083 —	— —
T. stigmatica	0.13 —	0.131 [0.130–0.133]	0.136 [0.133–0.139]	0.126 [0.125–0.127]	0.111 [0.102–0.116]	0.122 —	0.091 —	0.122 —

Appendix 4. *Continued...*

Appendix 4. *Continued.*

ND2	*D. g. goodfellowi*	*D. g. buergersi*	*D. pulcherrimus*	*D. spadix*	*D. matschiei*	*D. bennettianus*	*P. concinna*	*P. xanthopus*
D. g. buergersi	0.073	0.000	—	—	—	—	—	—
D. pulcherrimus	0.075	0.077	0.020	—	—	—	—	—
	[0.073–0.076]	[0.076–0.078]	—	—	—	—	—	—
D. spadix	0.072	0.083	0.081	0.015	—	—	—	—
	[0.070–0.073]	[0.081–0.084]	[0.076–0.087]	—	—	—	—	—
D. matschiei	0.078	0.087	0.066	0.061	0.010	—	—	—
	[0.076–0.081]	[0.081–0.096]	[0.061–0.070]	[0.052–0.067]	[0.000–0.017]	—	—	—
D. bennettianus	0.119	0.113	0.136	0.124	0.121	—	—	—
	—	—	[0.134–0.137]	[0.122–0.125]	[0.116–0.125]	—	—	—
P. concinna	0.145	0.139	0.147	0.166	0.147	0.105	—	—
	—	[0.128–0.154]	[0.145–0.148]	[0.163–0.169]	[0.145–0.148]	—	—	—
P. xanthopus	0.134	0.139	0.141	0.159	0.148	0.134	0.122	—
	—	[0.128–0.154]	[0.137–0.145]	[0.157–0.160]	[0.145–0.151]	—	—	—
T. stigmatica	0.151	0.139	0.153	0.159	0.155	0.125	0.122	0.128
	—	[0.128–0.154]	[0.148–0.157]	[0.156–0.160]	[0.151–0.157]	—	—	—