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Phylogenetic Analysis Reveals Additional Diversity within the *Dendrolagus dorianus* (Marsupialia: Macropodidae) Group from New Guinea

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ABSTRACT. The tree-kangaroos (genus *Dendrolagus*) are specialized arboreal macropodids now confined to the rainforests of New Guinea and northeastern Queensland, Australia. Within New Guinean *Dendrolagus*, a distinct Doria's group has been recognized since 1936. However, establishing the species limits and inter-relationships within the group has long been hampered by limited sampling. In this study we supplement published genetic data from high quality tissue samples with molecular data generated from museum specimens to improve taxon sampling and geographic coverage within the Doria's group to enhance our understanding of their evolutionary history. This included the addition of the previously unsampled *D. mayri* (holotype and only known specimen) and additional specimens of *D. dorianus* and *D. notatus*. DNA sequence data were generated from three mitochondrial loci and six distinct Doria's group lineages were identified: *D. dorianus, D. notatus, D. stellarum, D. scottae, D.* cf. *stellarum* and *D. mayri.* Phylogenetic analysis improved the resolution of relationships within the Doria's group, with *D. dorianus* being recovered as the sister to all other taxa. Surprisingly, *D. mayri* and *D.* cf. *stellarum* were monophyletic and formed a sister group to the three other species (*D. notatus, D. stellarum* and *D. scottae*). This indicates that the molecular affinities of *D.* cf. *stellarum,* from the Sudirman Range, Central Cordillera, lie with *D. mayri* (isolated on the Wondiwoi Peninsula to the west) rather than true *D. stellarum* from the Star Mountains further east along the Central Cordillera. The molecular divergence

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between *D.* cf. *stellarum* and *D. mayri* (3.8% sequence divergence) is less than that reported between other *Dendrolagus* species (≥ 4.7%). Therefore, *D.* cf. *stellarum* is best regarded as a differentiated population of *D. mayri* and should be referred to as *D.* cf. *mayri* pending further studies. This finding means that *D. stellarum* (*sensu stricto*) does not occur on the Maokop (Central Cordillera mountains east of the Baliem Valley, West Papua).

Introduction

Tree-kangaroos (*Dendrolagus*) are a group of specialized arboreal macropodids (kangaroos and wallabies) that originated in Australia, but have undergone several secondary radiations in the tropical forests of New Guinea (Flannery *et al.*, 1996; Martin, 2005; Eldridge *et al.*, 2018). Despite their biological interest, tree-kangaroos are poorly studied (Dabek *et al.*, 2021), and many taxa are only known from a handful of specimens (Flannery *et al.*, 1996; Eldridge & Coulson, 2015). The limited number of specimens available for study, lack of comprehensive geographic coverage and morphological variability has led to considerable taxonomic uncertainty (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 authors suggested that additional species could be recognized within New Guinea (Groves, 2005; Helgen, 2007; Eldridge *et al.*, 2018).

A distinct Doria's group within *Dendrolagus* was first proposed in 1936 (Rothschild & Dollman, 1936) and has subsequently been supported by most authors (Flannery *et al.*, 1996; Groves, 1982; Eldridge *et al.*, 2018). The Doria's group comprises a monophyletic lineage of medium/large (6–14.5 kg; Table 1), dark brown to black tree-kangaroos, with short, well-furred ears, short, broad feet, short tails (less than the head/body length), a variably positioned dorsal hair-whorl (often poorly expressed), significant sexual dimorphism and associated higher sociality (Table 1) (Rothschild & Dollman, 1936; Groves, 1982; Flannery, 1995; Flannery *et al.*, 1996). Doria's group species are considered the most derived tree-kangaroos, with the most highly modified feet and shortest tails (Flannery *et al.*, 1996; Eldridge *et al.*, 2018). Members of the Doria's group are widely distributed through the mountainous areas of New Guinea (except for the Vogelkop Peninsula; Fig. 1) and show considerable individual and geographic morphological variability (Groves, 1982; Flannery & Seri, 1990a; Flannery *et al.*, 1996). This has resulted in eight taxa attributable to this group being described, with the number of species recognized by various authors ranging from one to five (Table 2). This ongoing taxonomic instability continues to hamper research and effective conservation of this group, with all currently recognized taxa listed as threatened by the IUCN (Eldridge & Coulson, 2015). In New Guinea, most tree-kangaroo species are threatened by 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 (Eldridge & Coulson, 2015; Dabek *et al.*, 2021).

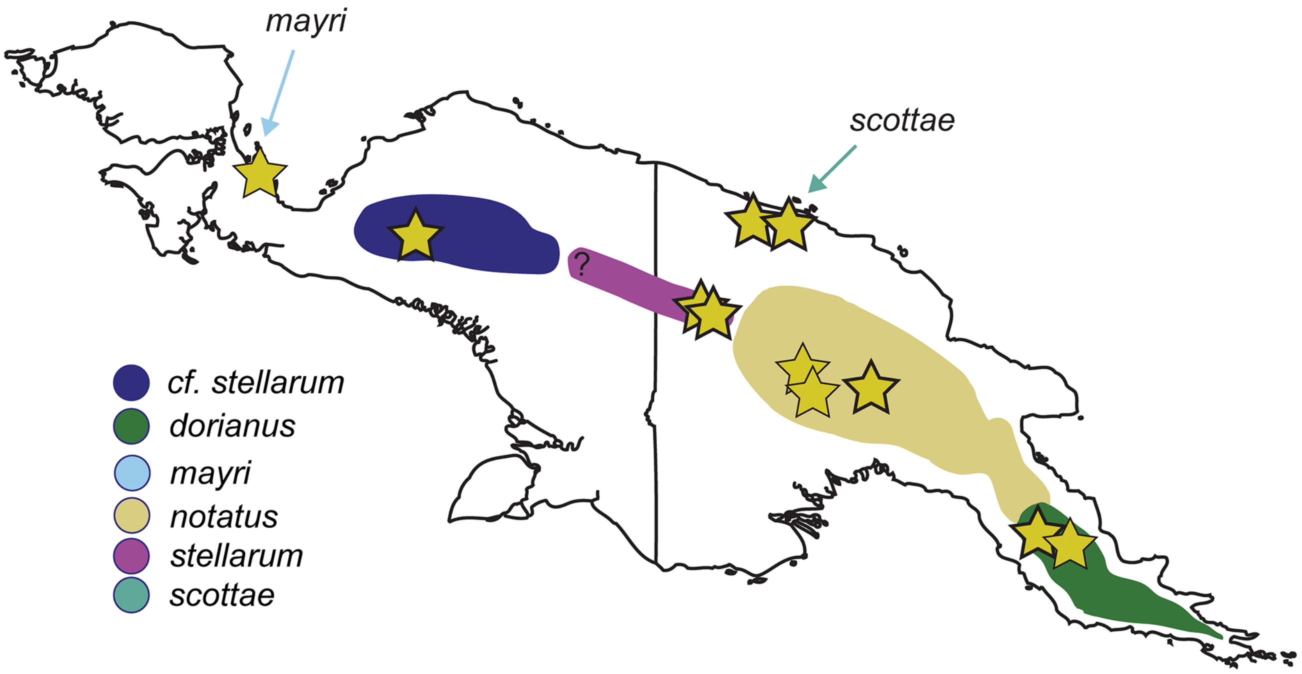

Figure 1. Distribution of *Dendrolagus* taxa of the Doria's group in New Guinea, with sampling sites indicated. Symbols for high quality tissue samples have bold outline, museum samples have normal outline. Note: *D.* cf. *stellarum* = *D.* cf. *mayri*.

The first Doria's group species to be scientifically described was *D. dorianus* in 1883 based on specimens from near Mt Astrolabe, south-eastern Papua New Guinea (Ramsay, 1883), followed in 1916 by *D. notatus* from the Schrader Mountains, Central Highlands, Papua New Guinea (Matschie, 1916). In 1933, a further species *D. mayri* was described from a single specimen (Fig. 2) collected in 1928 far to the west on the isolated Wondiwoi Peninsula on the northern coast of West Papua (Rothschild & Dollman, 1933) (Fig. 1). In the first comprehensive review of *Dendrolagus* taxonomy Rothschild & Dollman (1936) recognized, within the Doria's group, a single polytypic species; *D. dorianus* containing three subspecies; *D. d. dorianus* from the eastern Central Cordillera, *D. d. notatus* from the Central Highlands and *D. d. mayri* from the Wondiwoi Peninsula. They also described a local colour variant (*D. d. aureus*) from the Aroa River, southeastern Papua New Guinea (Rothschild & Dollman, 1936). In 1936, another two Doria's group taxa were described (Troughton & Le Souef, 1936); *D. d. profugus* and *D. d. palliceps*, another local colour variant, both from south-eastern Papua New Guinea. In 1954, Laurie and Hill recognized a single species, *D. dorianus* containing five subspecies (*dorianus, aureus, profugus*, *notatus, mayri*) (Table 2).

The next comprehensive revision of *Dendrolagus* taxonomy was conducted using morphology by Groves in 1982. Within the Doria's group a single polytypic species *D. dorianus* was recognized, containing three subspecies (Groves, 1982); *D. d. dorianus* (including *aureus, palliceps* and *profugus* as synonyms), *D. d. notatus* and *D. d. mayri*. In 1990, two new Doria's group taxa were described based on divergent morphology; *D. d. stellarum* from the Star Mountains and Telefomin area, western Papua New Guinea (Flannery & Seri, 1990a) and *D. scottae* from Mt Somoro, Torricelli Mountains in northern coastal Papua New Guinea (Flannery & Seri, 1990b) (Fig. 1). Subsequently, specimens attributable to *D. scottae* were also collected on nearby Mt Menawa and appearing morphologically and behaviourally distinct were thought to represent an undescribed subspecies (Flannery *et al.*, 1996). Finally, in 1995, another new tree-kangaroo species *D. mbaiso*, was described from the Tembagapura area in the Sudirman Range (Snow Mountains) from the western Central Cordillera, West Papua (Flannery *et al.*, 1995). This new species was also placed in the Doria's group on the basis of multiple shared features, although many differences were also noted (Flannery *et al.,* 1995; Flannery *et al.*, 1996). Additional specimens referred to *D. d. stellarum* were also collected from the Tembagapura area in the early 1990s, which significantly extended the range of this taxon 300 km westwards along the Central Cordillera into West Papua (Flannery *et al.*, 1996) (Fig. 1). This range extension went some way in closing the anomalous *ca*. 600 km gap that had previously existed within the distribution of *D. dorianus* between western Papua New Guinea (Star Mountains) and the Wondiwoi Peninsula in north-western West Papua (Fig. 1).

Thus, by the end of the 20th century, three species were recognized within the Doria's group: *D. mbaiso* and *D. scottae*, as well as polytypic *D. dorianus* (containing four subspecies *dorianus*, *notatus*, *stellarum* and *mayri*) (Flannery *et al.*, 1996). However, some authors subsequently suggested that some *D. dorianus* subspecies were sufficiently distinct to be considered separate species (Groves, 2005; Helgen, 2007; IUCN, 2008) and some limited mitochondrial DNA sequence

Table 1. Morphological measurements (range and average) for adult *Dendrolagus* from the Doria's group.

Taxon	Sex	Head-body (mm)	n	Tail (mm)	n	Hindfoot (mm)	n	Ear (mm)	n	Weight (kg)	n
D. dorianus	M	550–780 (672.8)	9	497–600 (552.6)	9	107–125 (116.3)	7	38–60 (52.9)	6	9.1–14.5 (11.8)	3
D. dorianus	F	596–770 (650.1)	13	450–662 (547.3)	13	100–120 (107.4)	9	45–58 (51.7)	11	8.2–11.8 (10.1)	10
D. notatus	M	580–690 (628.9)	9	435–565 (496.6)	9	100–115 (108.1)	8	45–58 (51.4)	8	7.0–9.1 (8.2)	3
D. notatus	F	515–630 (590.3)	9	430–540 (472.2)	9	90–109 (103.0)	8	45–59 (51.3)	8	6.0–6.5 (6.3)	2
D. stellarum	M	634–700 (667)	2	520–529 (524.5)	2	104–120 (112)	2	47–50 (48.5)	2	7.5–9.5 (8.5)	2
D. stellarum	F	610	1	490	1	100	1	50	1	6.75	1
D. cf. *stellarum*	M	645–673 (659)	2	510–570 (540)	2	100–112 (106)	2	52	1	8.5–9.0 (8.8)	2
D. cf. *stellarum*	F	626	1	585	1	98	1	50	1	6.5	1
D. mayri	M	635	1	570	1	112	1	53	1	9.3	1
D. scottae	M	720–750 (735.0)	2	520–590 (555)	2	108–119 (113.5)	2	50–55 (52.5)	2	9.5–11.5 (10.5)	2
D. scottae	F	565–725 (625.0)	4	520–540 (531.3)	4	104–115 (108)	4	45–55 (49.5)	4	6.8–9.5 (8.4)	3

Data from Flannery *et al*. (1996) and AM database.

Figure 2. Painting by Frederick William Frohawk [1861–1946] of *Dendrolagus mayri* holotype (NHMUK ZD 1939.2931) and only known specimen from Rothschild & Dollman (1936, plate XLII, pp. 518–519).

Table 2. Described *Dendrolagus* taxa in the Doria's group and their changing recognition by various authorities from 1936 to 2018.

Described Taxon	Rothschild & Dollman, 1936	Laurie & Hill, 1954	Groves, 1982	Flannery, 1995; Flannery *et al.*, 1996	Groves, 2005	Helgen, 2007; IUCN, 2008	Eldridge & Coulson, 2015	Eldridge *et al.*, 2018
D. dorianus Ramsay, 1883	*D. d. dorianus*	*D. d. dorianus*	*D. d. dorianus*	*D. d. dorianus*	*D. d. dorianus*	*D. dorianus*	*D. d. dorianus*	*D. dorianus*
D. dorianus aureus Rothschild & Dollman, 1936	*D. d. aureus*	*D. d. aureus*	*D. d. dorianus*	*D. d. dorianus*	*D. d. dorianus*	*D. dorianus*	*D. d. dorianus*	*D. dorianus*
D. dorianus palliceps Troughton & Le Souef, 1936	—	*D. d. dorianus*	*D. d. dorianus*	*D. d. dorianus*	*D. d. dorianus*	*D. dorianus*	*D. d. dorianus*	*D. dorianus*
D. dorianus profugus Troughton & Le Souef, 1936	—	*D. d. profugus*	*D. d. dorianus*	*D. d. dorianus*	*D. d. dorianus*	*D. dorianus*	*D. d. dorianus*	*D. dorianus*
D. notatus Matschie, 1916	*D. d. notatus*	*D. d. notatus*	*D. d. notatus*	*D. d. notatus*	*D. d. notatus*	*D. notatus*	*D. d. notatus*	*D. notatus*
D. mayri Rothschild & Dollman, 1933	*D. d. mayri*	*D. d. mayri*	*D. d. mayri*	*D. d. mayri*	*D. d. mayri*	*D. mayri*	*D. d. mayri*	*D. mayri*
D. dorianus stellarum Flannery & Seri, 1990b	—	—	—	*D. d. stellarum*	*D. stellarum*	*D. stellarum*	*D. d. stellarum*	*D. stellarum*
D. scottae Flannery & Seri, 1990a	—	—	—	*D. scottae*	*D. scottae*	*D. scottae*	*D. scottae*	*D. scottae*

data showed large divergences between (and within) some *D. dorianus* subspecies (Bowyer *et al.*, 2003).

More recently, a multi-locus (mitochondrial and nuclear) molecular analysis demonstrated that *D. mbaiso* represented a distinct evolutionary lineage with *Dendrolagus*, that was the sister to the Doria's group (Eldridge *et al.*, 2018), diverging from the group's common ancestor almost 5 mya. This study also provided some greater taxonomic clarity, within the Doria's group, supporting the specific distinction of *D. notatus* and *D. stellarum* from *D. dorianus*, but indicating that little genetic divergence was present between the Mt Somoro and Mt Menawa populations of *D. scottae* (Eldridge *et al.*, 2018). However, species level genetic divergence in both mitochondrial and nuclear DNA was also detected within *D. stellarum* between the type series from the Star Mountains, Papua New Guinea and the population sampled in the Tembagapura area of the Sudirman Range, West Papua, 300 km to the west (referred to as *D.* cf. *stellarum* hereafter) (Eldridge *et al.*, 2018). Although data from *D. d. mayri* was not included in this analysis, the pattern of divergence detected in the other Doria's group taxa suggested that it too is likely to represent a distinct species, (*D. mayri* hereafter) rather than a subspecies of *D. dorianus* (*sensu stricto*) which under these taxonomic changes is now a species restricted to the far east of New Guinea (Fig. 1). However, without data from *D. mayri* it could not be concluded if the Tembagapura specimens represent an additional new taxon or are an eastern population of *D. mayri* which occurs a further 300 km to the west on the Wondiwoi Peninsula. Since the type (and only known) specimen of *D. mayri* was collected in 1928 (Flannery *et al.*, 1996), this taxon had not been relocated until 2018 when an individual consistent with *D. mayri* was sighted and photographed on the Wondiwoi Peninsula (Dabek *et al.*, 2021).

Although greatly improving our understanding of *Dendrolagus* evolution, phylogenetic relationships and taxonomy, recent molecular analyses, utilizing high quality DNA, suffered from unavoidable sample size and geographic coverage limitations for most taxa. For example, within the Doria's group only 1–3 samples were available for most taxa, while a sample from *D. mayri* was not available (Eldridge *et al.*, 2018). Therefore, in the current study we have sought to extend the analysis of Eldridge *et al.* (2018) by utilizing museum specimens (both study skins and skeletal material) as an additional source of DNA for sequence analysis. This study increases geographic coverage for two taxa and also adds data for *D. mayri* to improve our understanding of taxon boundaries and inter-relationships within the Doria's group.

Materials and methods

Available sequence data

Published DNA sequence data, from high quality tissue samples, from 14 individuals of five Doria's group taxa (*D. dorianus* n = 1; *D. notatus* n = 3; *D. stellarum* n = 3; *D.* cf. *stellarum* n = 3; *D. scottae* n = 4) were included (Eldridge *et al.*, 2018) (Table 3). This included data from the holotype and/or paratypes of *D. scottae*, and *D. stellarum* (Table 3). Individuals of *D. bennettianus*, *Petrogale xanthopus, Petrogale concinna* and *Thylogale stigmatica* were included as out-groups. See Appendix 1 for GenBank numbers.

Table 3. Details of the *Dendrolagus* specimens used in this study.

Taxon	Specimen Voucher	Lab ID	Sample ID	Locality	DNA Source
D. dorianus	AM M.12854	—	ABTC42523	Kosipe, Mt Albert Edward, CP, PNG 1981	Eldridge *et al*., 2018
D. dorianus	AM M.32134	—	—	Lake Trist, MP, PNG 1995	Limb bones, skin
D. mayri	NHMUK ZD 1939.2931 Holotype	—	—	Wondiwoi Peninsula, West Papua, 1928	Dried tissue on skull
D. notatus	AM M.17374	S1618	ABTC46285	Mt Sisa, Bobole, HP, PNG 1985	Eldridge *et al*., 2018
D. notatus	AM M.17746	S1617	ABTC46283	Mt Sisa, Bobole, HP, PNG 1985	Eldridge *et al*., 2018
D. notatus	AM M.17153	S1613	ABTC46292	Bobole (Waro), HP, PNG 1985	Eldridge *et al*., 2018
D. notatus	AM M.7273	—	—	Mt Rentoul, SHP, PNG 1947	Skin
D. notatus	AM M.46213	S2873	—	Hegigio River, HP, PNG, 2013	Dried tissue on limb bone
D. stellarum	AM M.16699 Paratype	S1614	ABTC47179	Sol River Basin, WSP, PNG 1986	Eldridge *et al*., 2018
D. stellarum	AM M.17789 Holotype	—	EBU23021	Dokfuma Basin, Star Mts, WP, PNG 1987	Eldridge *et al*., 2018
D. stellarum	AM M.19463 Paratype	—	EBU23048	Dokfuma Basin, Star Mts, WP, PNG 1987	Eldridge *et al*., 2018
D. cf. *stellarum*	AM M.30720	S1607	EBU8059	Tempagapura area, West Papua 1994	Eldridge *et al*., 2018
D. cf. *stellarum*	AM M.30750	S1609	EBU8056	Tempagapura area, West Papua 1994	Eldridge *et al*., 2018
D. cf. *stellarum*	AM M.30753	S1608	EBU8052	Tempagapura area, West Papua 1994	Eldridge *et al*., 2018
D. scottae	AM M.19481 Holotype	S2087	EBU23412	Sweipini, Torricelli Mts, WSP, PNG 1988	Eldridge *et al*., 2018
D. scottae	AM M.21867	S2088	EBU25197	Mt Menawa, WSP, PNG 1990	Eldridge *et al*., 2018
D. scottae	AM M.22257	S2089	EBU25161	Mt Menawa, WSP, PNG 1990	Eldridge *et al*., 2018
D. scottae	AM M.23044	S2090	EBU25183	Mt Menawa, WSP, PNG 1990	Eldridge *et al*., 2018

CP = Central Province, HP = Hela Province, MP = Morobe Province, PNG = Papua New Guinea,
SHP = Southern Highland Province, WP = Western Province, WSP = West Sepik Province.

Tissue sampling and DNA extraction from museum specimens

Samples were collected from four museum specimens, including fragments of dried soft tissue remaining on prepared skeletal material or study skins, including from the holotype and only known specimen of *D. mayri*, as well as additional specimens of *D. dorianus* (n = 1) and *D. notatus* (n = 2) (Table 3). The following abbreviations are used: AM = Australian Museum, Sydney; NHMUK = Natural History Museum, London; EBU = Australian Museum tissue collection; ABTC = South Australian Museum tissue collection.

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 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 routinely included for each round of DNA extractions to detect reagent contamination. Dried tissue samples were initially hydrated 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 (*ca*. 100–200 bp) overlapping fragments (*COI*, 12 fragments; *Cytb,* 7 fragments; *ND2,* 4 fragments). For primer details see Appendix 2. 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; Eldridge *et al.*, 2024).

PCR-amplifications were carried out in 25 µL reactions with 100–400 ηg genomic DNA, 1×PCR Buffer II (Applied Biosystems), 0.2 mM each dNTP, 1.5–3.0 mM $MgCl_2$, 0.2 µmol each primer (Appendix 2) 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. See Appendix 1 for GenBank accession number of new sequences.

Sequence divergence and phylogenetic analysis

Uncorrected pairwise sequence divergence was estimated on aligned genes in MEGA v5 (Tamura *et al.*, 2011) between individuals and species. In addition, nucleotide diversity, polymorphic sites and parsimony informative sites were estimated in DnaSP v5.10 (Librado & Rozas, 2009).

A maximum likelihood analysis was performed on individual genes and the concatenated alignment of all three genes in RAxML v8.2.4 (Stamatakis, 2014). The nucleotide substitution model for each gene and the concatenated mitochondrial dataset was estimated using PartitionFinder (Lanfear *et al.*, 2012) based on the full search scheme allowing for all partitioning schemes. The raxml model of evolution was used and model selection was based on the BIC. Analysis was performed on individual genes as well as the concatenated mitochondrial dataset. For the concatenated dataset, data was partitioned by codon, with all codon 1 positions grouped together for the first partition (*ND2* + *COI* + *Cytb*), and similarly for codon 2, and two partitions for the third codon (*ND2* + *COI*) and *Cytb* separately (individual gene partitions available in supplementary results). Analysis was performed using the rapid bootstrap algorithm, the GTRGAMMA model, 100 bootstrap replicates and a random starting seed.

Results

Genetic Diversity

In total, 3116 bp of sequenced DNA was aligned from representative of all species currently recognized in the Doria's group: *D. dorianus*, *D. notatus*, *D. stellarum*, *D. scottae* and *D. mayri*—651 bp *ND2*, 1323 bp *COI* and 1142 bp *Cytb.* For the museum samples, 1.3–42.6% of the data were missing. There were 164 variable sites amongst the Doria's group taxa, 130 of which were parsimony informative (78–125 variable sites per gene; 62–99 parsimony informative). When including outgroup species, this increased to 263 variable sites and 172 parsimony informative sites with the highest variance for *COI*. Nucleotide diversity ranged from 0.049–0.061 for individual genes and was 0.059 for the concatenated data (0.081 with outgroups).

The average uncorrected pairwise sequence divergence (sd) amongst identified lineages within the Doria's group ranged from 3.8% between *D. mayri* and *D.* cf. *stellarum* to 7.9% between *D. stellarum* and *D. dorianus* (Table 4). Average sd between *D. stellarum* and *D.* cf. *stellarum* was 6.5% (Table 4). The largest divergences were for *Cytb* (4.1–9.0%) and the lowest were for *ND2* (3.5–7.4%) (Appendix 3). Within putative taxa, average divergence ranged from 0.0% within *D.* cf. *stellarum* to 1.4% within *D. dorianus* (Table 4). Average divergence comparisons with the outgroups (*D. bennettianus*, *P. concinna*, *P. xanthopus* and *T. stigmatica*) ranged from 10.5–14.8% (Table 4).

Phylogenetic analysis

The maximum likelihood analysis of the concatenated mitochondrial data resolved six lineages within the Doria's group: *D.* cf. *stellarum*, *D. mayri*, *D. notatus*, *D. stellarum*, *D. scottae* and *D. dorianus* (Fig. 3). The additional museum specimens of *D. notatus* (AM M.7273, M.46213) grouped tightly with their congeners, as did an additional museum specimen of *D. dorianus* (AM M.32134). The inclusion of *D. mayri* identified a well-supported relationship between this species and *D.* cf. *stellarum* separate from the remaining Doria's group taxa (Fig. 3). Aside from *D. mayri*, the phylogeny supported similar relationships amongst Doria's group lineages as previously reported (Eldridge *et al.*, 2018), with *D. stellarum* and *D. scottae* forming sister clades, followed by *D. notatus* (Fig. 3). However, the node connecting *D. dorianus* as sister to a clade of the five remaining Doria's group lineages showed only moderate support (70% bootstrap), which is consistent with varied results from previous mtDNA and nDNA+mtDNA analyses (Eldridge *et al.*, 2018). The bootstrap support at all remaining major nodes across the tree was strong (100%) (Fig. 3).

Table 4. Average uncorrected pairwise sequence divergence [and range] across three concatenated mtDNA loci between *Dendrolagus* taxa examined in this study, including within taxon divergences on the diagonal.

	dorianus	***notatus***	***stellarum***	**cf. *stellarum***	***scottae***	***mayri***	***bennettianus***	***P. concinna***	***P. xanthopus***
D. dorianus	0.014								
D. notatus	0.075 [0.069–0.080]	0.008 [0.000–0.019]							
D. stellarum	0.079 [0.075–0.087]	0.063 [0.057–0.075]	0.011 [0.000–0.017]						
D.* cf. *stellarum	0.072 [0.071–0.073]	0.069 [0.067–0.074]	0.065 [0.063–0.069]	0.000					
D. scottae	0.070 [0.067–0.071]	0.070 [0.067–0.073]	0.047 [0.043–0.050]	0.061 [0.058–0.062]	0.004 [0.000–0.008]				
D. mayri	0.075 [0.074–0.075]	0.071 [0.069–0.076]	0.065 [0.063–0.069]	0.038	0.063 [0.061–0.064]	—			
D. bennettianus	0.124 [0.122–0.126]	0.125 [0.125–0.126]	0.131 [0.130–0.133]	0.117	0.120 [0.120–0.121]	0.125	—		
P. concinna	0.129 [0.126–0.131]	0.132 [0.132–0.134]	0.130 [0.130–0.131]	0.133	0.120 [0.120–0.121]	0.126	0.118	—	
P. xanthopus	0.127 [0.125–0.128]	0.127 [0.126–0.130]	0.109	0.131	0.105 [0.103–0.105]	0.121	0.118	0.102	—
T. stigmatica	0.135 [0.132–0.137]	0.148 [0.147–0.150]	0.142 [0.140–0.147]	0.145 [0.138–0.141]	0.140	0.145	0.125	0.113	0.125

Discussion

The inclusion of genetic data in this study, obtained from museum specimens, has improved taxon and geographic sampling within the Doria's group. Six distinct Doria's group lineages were identified, enabling clarification of several long-standing phylogenetic and evolutionary questions within the group. Five of these lineages correspond to the currently recognized species within the group: *D. dorianus, D. notatus, D. stellarum, D. scottae* and *D. mayri*. An additional identified lineage represented sampled individuals of *D.* cf. *stellarum.*

Differentiation within the Doria's group

The first molecular data generated from the poorly known *D. mayri* has convincingly placed it within the Doria's group. Phylogenetically, *D. mayri* forms a strongly supported monophyletic lineage with the nearest sampled Doria's group population (*D.* cf. *stellarum*) from the Tembagapura area *ca*. 300 km to the east. Together, they form a sister group to three other species (*D. notatus, D. stellarum* and *D. scottae*). The *mayri*- cf. *stellarum* lineage is highly differentiated from all other Doria's group species, differing by 6.1–7.5% sd (Table 4). This demonstrates that the molecular affinities of *D.* cf. *stellarum* lie with *D. mayri* (isolated on the Wondiwoi Peninsula to the west) rather than true *D. stellarum* from the Star Mountains *ca*. 300 km to the east along the Central Cordillera.

The mtDNA sequence divergence detected between *D. mayri* and *D.* cf. *stellarum* (3.8%) is below the level of divergence detected between other closely related but clearly differentiated *Dendrolagus* species pairs, for example *D. scottae* and *D. stellarum* differ by 4.7% (Table 4), while *D. spadix* and *D. matschiei* differ by 5.1% (Eldridge *et al.*, 2024). However, divergences between two morphologically similar subspecies of Goodfellow's tree-kangaroo (*Dendrolagus goodfellowi*) are 7% (Eldridge *et al.*, 2024), while intra-taxon divergences reach a maximum of 1.4% in the Doria's group (Table 4) and 1.6% within Goodfellow's group (Eldridge *et al.*, 2024). Thus, the divergence detected between *D. mayri* and *D.* cf. *stellarum* sits in a grey-zone between reported intra- and inter-species divergences for this genus.

The high molecular divergence detected between *D. stellarum* and *D.* cf. *stellarum* is concordant with marked differences in pelage colouration and markings between these two populations (Fig. 4). In contrast, the pelage of *D.* cf. *stellarum* is most similar to that of the holotype of *D. mayri* (Fig. 4), although there are also some differences in colouration and markings (Fig. 4). The concordant moderate divergence between *D. mayri* and *D.* cf. *stellarum*

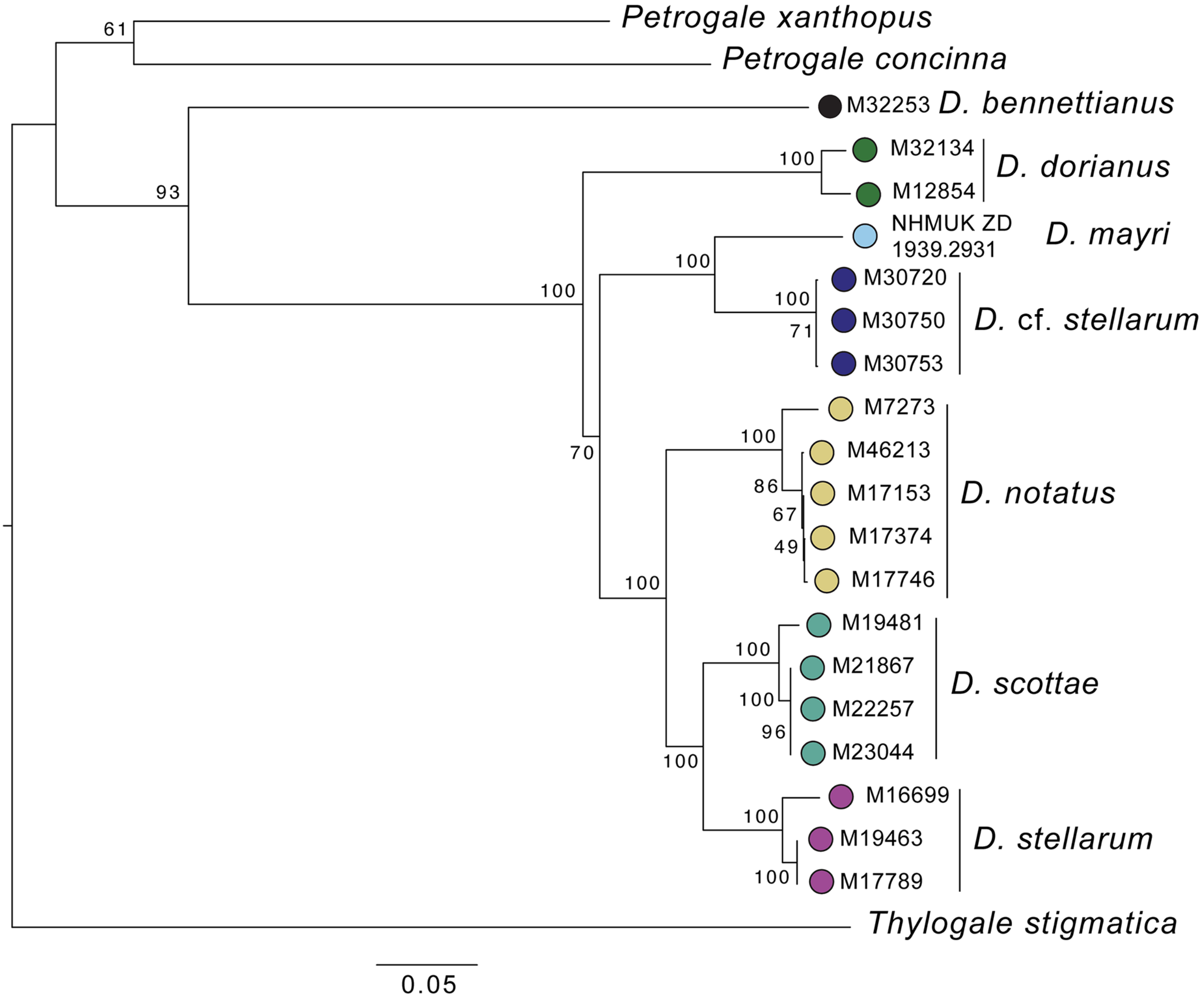

Figure 3. Phylogenetic relationships (ML) amongst mtDNA sequences from six sampled Doria's group taxa. Percentage bootstrap support is indicated.

in pelage morphology and genetics therefore suggests they are currently best regarded as differentiated subpopulations of *D. mayri*. However, mtDNA data can be misleading, as the increasing recognition of mito-nuclear discordance demonstrates (Firneno Jr *et al*., 2020; Potter *et al*., 2024). Therefore, this hypothesis requires testing with improved sampling, comparative nuclear DNA data and an analysis of skull morphology.

Phylogeography

Previous ancestral state reconstruction analysis (Eldridge *et al*., 2018) revealed that the ancestral lineage leading to the Doria's group and its sister taxon, *D. mbaiso,* was already associated with high elevation environments. The divergence of *D. mbaiso* from the Doria's group occurring almost 5 mya (Eldridge *et al*., 2018) when mountain building in New Guinea was well underway (van Ufford & Cloos, 2005). Subsequent diversification within the Doria's group occurred along the Central Cordillera 2–3 mya (late Pliocene, early Pleistocene) (Eldridge *et al.*, 2018), a period associated within ongoing mountain building of the Central Ranges (van Ufford & Cloos, 2005) and intensified climatic cycling (Byrne *et al.*, 2011). During these climatic cycles, the periodic expansion to lower altitudes and then contraction of mid-high elevation habitats would have facilitated the dispersal and differentiation of Doria's group species along the Central Cordillera. Currently the distribution of Doria's group species/lineages along the Central Cordillera appears associated with major high elevation mountain systems (southeast Peninsula, Central Highlands, Star Mountains, Snow Mountains) which are separated by lower elevation zones including major river valleys. These low elevation areas appear to form contemporary barriers to gene flow in the Doria's group and other groups of specialist mid-high elevation taxa including birds (Irestedt *et al.*, 2015), other mammals (Helgen & Helgen, 2009; Westerman *et al.*, 2012), and insects (Janda *et al.*, 2016).

Dendrolagus scottae appears to be a more recently derived species originating via a dispersal event (from the ancestral *D. stellarum* population) from the Central Cordillera to the Northern Coastal Ranges about 1.3 mya (Eldridge *et al.*, 2018). Given that *D. mayri* and *D.* cf. *stellarum* show less genetic divergence than *D. scottae* and *D. stellarum* (Table 4), we hypothesize that a more recent dispersal event from the western end of the Central

Figure 4. Comparison of pelage variation across Doria's group taxa. Top to bottom: *D. mayri* (NHMUK ZD 1939.2931, holotype), *D.* cf. *stellarum* (AM M.30720 = *D.* cf. *mayri*), *D. scottae* (AM M.24424), *D. stellarum* (AM M.16699, paratype), and *D. notatus* (AM M.16419). Photography of AM specimens by Ron Lovatt (AM Digivol). Photography of specimen from the collections of the Natural History Museum, London by Phaedra Kokkini.

Cordillera to the Wondiwoi Peninsula resulted in the differentiation of *D. mayri* on the Wondiwoi Peninsula from the ancestral Sudirman Range population. However, a better understanding of the distribution and evolution of *Dendrolagus* taxa in western New Guinea requires improved sampling and additional nuclear DNA data to test this assumption.

Conservation implications

Populations attributable to *D.* cf. *stellarum* are reported to be widespread in the western Central Cordillera (Sudirman Range), West Papua, Indonesia, being known from the Tembagapura and Kwiyauagai areas (Australian Museum specimens), Kamu Valley (Peabody Museum, Yale specimens) and Mt Mbinggela/Mt Dugudok area (Wild & Balke, 2018). They are therefore likely to be distributed from the Baliem Valley west to the Paniai Lakes near Pogapa. Further west, in the Weyland Mountains, tree-kangaroos appear to be absent (Flannery *et al.*, 1996).

Populations of *D.* cf. *stellarum* have previously been included within *D. stellarum* for description of biological attributes and conservation assessments (Flannery *et al.*, 1996; Helgen, 2007; Eldridge & Coulson, 2015; Leary *et al.*, 2016a). Since we have now shown that populations of *D.* cf. *stellarum* in the western Central Cordillera are more appropriately classified as a differentiated subpopulation of *D. mayri,* some reassessment will be required. These changes significantly reduce the known distribution of true *D. stellarum*, which is now restricted from the Telefomin area, through the Star Mountains and possibly west to the Baliem Valley. With this smaller distribution, *D. stellarum* may be more threatened than previously thought. *Dendrolagus stellarum* (*sensu lato*) is currently classified as Vulnerable by the IUCN (Leary *et al.*, 2016a). Conversely, these data significantly expand the known distribution of populations attributable to *D. mayri*, although there remains a major, but puzzling, gap in the distribution between the Wondiwoi Peninsula and western Central Cordillera subpopulations. Any reassessment of conservation status should take into account the differentiation apparent between the Sudirman Range and Wondiwoi Peninsula subpopulations of *D. mayri*, as well as their geographic isolation and large differences in distribution area / population size. *Dendrolagus mayri* (*sensu lato*) is currently classified as Critically Endangered by the IUCN (Leary *et al.*, 2016b).

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Appendix 1. GenBank accession numbers for *Dendrolagus* mtDNA data used in the analysis of Doria's group taxa.

Taxon	Specimen ID	*Cytb*	*ND2*	*COI*
D. dorianus	AM M.12854	MH197953	MH197919	MH197986
D. dorianus	AM M.32134	PX418938	PX418942	PX372088
D. mayri	NHMUK ZD 1939.2931 holotype	PX418939	PX418943	PX372089
D. notatus	AM M.17374	MH197954	MH197920	MH197987
D. notatus	AM M.17746	MH197955	MH197921	MH197988
D. notatus	AM M.17153	MH197956	MH197922	MH197989
D. notatus	AM M.7273	PX418936	PX418940	PX372086
D. notatus	AM M.46213	PX418937	PX418941	PX372087
D. stellarum	AM M.16699 paratype	MH197957	MH197923	MH197990
D. stellarum	AM M.17789 holotype	MH197958	MH197924	MH197991
D. stellarum	AM M.19463 paratype	MH197959	MH197925	MH197992
D. cf. *stellarum*	AM M.30720	MH197960	MH197926	MH197993
D. cf. *stellarum*	AM M.30750	MH197961	MH197927	MH197994
D. cf. *stellarum*	AM M.30753	MH197962	MH197928	MH197995
D. scottae	AM M.19481 holotype	MH197979	MH197945	MH198012
D. scottae	AM M.21867	MH197980	MH197946	MH198013
D. scottae	AM M.22257	MH197981	MH197947	MH198014
D. scottae	AM M.23044	MH197982	MH197948	MH198015
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

Appendix 2. 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	Eldridge *et al.*, 2024
	Den_CO1_F1	TCAATGCTTKCCTCAGC	Eldridge *et al.*, 2024
	Den_CO1_R2	ATAACATTATAAATCTG	Eldridge *et al.*, 2024
	Den_CO1_F2	CTTATTCGCGCAGAGCTCGG	Eldridge *et al.*, 2024
	Den_CO1_R3	TCGGGTGCGCCGATCATTAG	Eldridge *et al.*, 2024
	Den_CO1_F3	ATAATGTTATTGTRACRGCC	Eldridge *et al.*, 2024
	Den_CO1_R4	GTTCCTGCTCCYGCTTCTAC	Eldridge *et al.*, 2024
	Den_CO1_F4	CCTCCTTCTATTRGCATC	Eldridge *et al.*, 2024
	Den_CO1_R5	GTGATRAAGTTGATAGCTCC	Eldridge *et al.*, 2024
	Den_CO1_F5	CACGCTGGGGCTTCTGTAG	Eldridge *et al.*, 2024
	Den_CO1_R6	AAGGAGGAGAAGRACTGCTGT	Eldridge *et al.*, 2024
	Den_CO1_F6	ACCACCCGCYCTATCTCAATATC	Eldridge *et al.*, 2024
	Den_CO1_R7	CTTCTGGATGTCCRAAGAATCA	Eldridge *et al.*, 2024
	Den_CO1_F7	ACAATACTTTTAACAGACCG	Eldridge *et al.*, 2024
	Den_CO1_R8	TTACCAGAATAGTAGGTTAC	Eldridge *et al.*, 2024
	Den_CO1_F8	TGATTCTTYGGACATCCAGAAG	Eldridge *et al.*, 2024
	Den_CO1_R9	TAAGCTCGAGTGTCGACGTC	Eldridge *et al.*, 2024
	Den_CO1_F9	TTCACAGTCGGATTAGACG	Eldridge *et al.*, 2024
	Den_CO1_R10	ATAAATCCGAGAGCTCATAG	Eldridge *et al.*, 2024
	Den_CO1_F10	GTATTTAGTTGACTAGCAAC	Eldridge *et al.*, 2024
	Den_CO1_R11	CCTATRGATAGGACRTAGTGGAAGTG	Eldridge *et al.*, 2024
	Den_CO1_F11	CATGACACTTACTATGTA	Eldridge *et al.*, 2024
	M31(COA)	AGTATAAGCGTCTGGGTAGTC	Palumbi *et al.*, 1991
Cytb	L14724	CGAAGCTTGATATGAAAAACCATCGTTG	Pääbo, 1990
	Den_CB_R1	GCAGGCTCCTAGTAGTGA	Eldridge *et al.*, 2024
	Den_CB_F1	CACCCACTAATTAAAAT	Eldridge *et al.*, 2024
	Den_CB_R2	ATGAAGAATATGGATGCTC	Eldridge *et al.*, 2024
	Den_CB_F2	CCCACATCTGCCGAGAYGT	Eldridge *et al.*, 2024
	Den_CB_R3	CGATATAAGGAATAGCGGA	Eldridge *et al.*, 2024
	Den_CB_F3	GACAAATATCRTTCTGAGG	Eldridge *et al.*, 2024
	Den_CB_R4	GTATAGTACGGGTGGAATGG	Eldridge *et al.*, 2024
	Den_CB_F4	CTATTYCTACAYGAAAC	Eldridge *et al.*, 2024
	Den_CB_R5	CGGAGAATRGCATATGCAAA	Eldridge *et al.*, 2024
	Den_CB_F5	TTGCATAYGCYATYCTCCGATC	Eldridge *et al.*, 2024
	Den_CB_R6	AAGTATGAGATTGATGCT	Eldridge *et al.*, 2024
	Den_CB_F6	TGAATCGGAGGCCAACCAGTAG	Eldridge *et al.*, 2024
	Mr2	AGGGTGTTATACCTTCATTTTTGG	Bulazel *et al.*, 2007
ND2	mmND2.1	GCACCATTCCACTTYTGAGT	Osborne & Christidis, 2001
	Den_ND2_R1	GTTRAGTATGAGRAATAGGGTTAG	Eldridge *et al.*, 2024
	Den_ND2_F1	TCCTAGCCTACTCCTCTAT	Eldridge *et al.*, 2024
	Den_ND2_R2	CCTCCAAGRGATANAAGTGTGAG	Eldridge *et al.*, 2024
	Den_ND2_F2	AAATCACTRACAAACCTATG	Eldridge *et al.*, 2024
	Den_ND2_R3	GGAAATATAGTAAGTGTTGAG	Eldridge *et al.*, 2024
	Den_ND2_F3	GCCACCCTAATAGCACTYTCA	Eldridge *et al.*, 2024
	mrND2c	GATTTGCGTTCGAATGTAGCAAG	Osborne & Christidis, 2001

Appendix 3. Average uncorrected pairwise sequence divergence [and range] across the three mtDNA loci for *Dendrolagus* taxa examined in this study, including within taxon divergences on the diagonal.

COI	*dorianus*	*notatus*	*stellarum*	cf. *stellarum*	*scottae*	*mayri*	*bennettianus*	*P. concinna*	*P. xanthopus*
dorianus	0.010								
notatus	0.076 [0.072–0.078]	0.005 [0.000–0.009]							
stellarum	0.084 [0.081–0.087]	0.042 [0.040–0.045]	0.005 [0.000–0.008]						
cf. *stellarum*	0.076 [0.056–0.058]	0.057 [0.062–0.067]	0.064	0.000					
scottae	0.075 [0.073–0.077]	0.036 [0.035–0.039]	0.030 [0.028–0.033]	0.054 [0.000–0.005]	0.003				
mayri	0.086	0.073	0.071 [0.069–0.074]	0.037	0.062	—			
bennettianus	0.122 [0.121–0.123]	0.124 [0.123–0.125]	0.127	0.121	0.121	0.132	—		
P. concinna	0.136 [0.135–0.137]	0.127 [0.127–0.128]	0.130 [0.128–0.131]	0.126	0.120 [0.116–0.121]	0.131	0.126	—	
P. xanthopus	0.114	0.120 [0.119–0.121]	0.120 [0.118–0.121]	0.114	0.107	0.125	0.117	0.105	—
T. stigmatica	0.128 [0.126–0.130]	0.120 [0.119–0.122]	0.141	0.130	0.123	0.131	0.132	0.141	0.112

Cytb	*dorianus*	*notatus*	*stellarum*	cf. *stellarum*	*scottae*	*mayri*	*bennettianus*	*P. concinna*	*P. xanthopus*
dorianus	0.012								
notatus	0.084 [0.070–0.092]	0.011 [0.000–0.024]							
stellarum	0.090 [0.087–0.096]	0.075 [0.070–0.084]	0.013 [0.000–0.019]						
cf. *stellarum*	0.075 [0.072–0.077]	0.080 [0.080–0.082]	0.081 [0.080–0.084]	0.000					
scottae	0.067 [0.063–0.070]	0.066 [0.060–0.070]	0.047 [0.043–0.051]	0.065 [0.060–0.067]	0.004 [0.000–0.007]				
mayri	0.073 [0.070–0.075]	0.078 [0.077–0.080]	0.079 [0.077–0.082]	0.041	0.060 [0.058–0.060]	—			
bennettianus	0.130	0.144 [0.137–0.147]	0.149 [0.147–0.152]	0.130	0.130 [0.128–0.130]	0.130	—		
P. concinna	0.107 [0.106–0.108]	0.122 [0.118–0.125]	0.122 [0.120–0.125]	0.128	0.113 [0.111–0.113]	0.111	0.125	—	
P. xanthopus	0.106 [0.104–0.108]	0.110 [0.104–0.113]	0.097 [0.096–0.099]	0.113	0.086 [0.084–0.087]	0.101	0.108	0.089	—
T. stigmatica	0.134 [0.133–0.135]	0.147 [0.145–0.149]	0.150 [0.147–0.157]	0.142	0.140 [0.135–0.142]	0.130	0.125	0.096	0.113

ND2	*dorianus*	*notatus*	*stellarum*	cf. *stellarum*	*scottae*	*mayri*	*bennettianus*	*P. concinna*	*P. xanthopus*
dorianus	0.016								
notatus	0.066 [0.063–0.070]	0.006 [0.000–0.014]							
stellarum	0.068 [0.063–0.077]	0.051 [0.045–0.066]	0.009 [0.000–0.014]						
cf. *stellarum*	0.069 [0.068–0.070]	0.057 [0.054–0.068]	0.049 [0.047–0.054]	0.000					
scottae	0.073 [0.070–0.075]	0.074 [0.068–0.082]	0.047 [0.042–0.049]	0.056	0.005 [0.000–0.009]				
mayri	0.076 [0.075–0.077]	0.064 [0.061–0.075]	0.051 [0.049–0.056]	0.035	0.067 [0.063–0.068]	—			
bennettianus	0.119 [0.115–0.122]	0.107 [0.103–0.115]	0.114 [0.113–0.115]	0.103	0.111 [0.110–0.115]	0.120	—		
P. concinna	0.150 [0.146–0.153]	0.142 [0.141–0.146]	0.137 [0.136–0.138]	0.138	0.128 [0.127–0.131]	0.141	0.110	—	
P. xanthopus	0.147 [0.146–0.148]	0.145 [0.143–0.148]	0.121 [0.120–0.122]	0.148	0.122	0.141	0.127	0.115	—
T. stigmatica	0.135 [0.129–0.141]	0.149 [0.148–0.153]	0.135 [0.134–0.138]	0.148	0.141	0.160	0.124	0.129	0.136