RECORDS OF THE WESTERN AUSTRALIAN MUSEUM 40 001–046 (2025) DOI: 10.18195/issn.0312-3162.40.2025.001-046

Molecular and morphological assessment of the widely distributed legless gecko *Delma tincta* Kluge (Squamata: Pygopodidae), including a taxonomic revision

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ABSTRACT – The pygopodid lizard *Delma tincta* is widely distributed across Australia, including the arid zone, eastern seaboard and monsoon tropics. *Delma* is morphologically extremely conservative, and the highly cryptic *D. tincta* species complex presents a particular taxonomic challenge. Here, we use a large SNP molecular dataset and a detailed morphological dataset to evaluate variation in *Delma tincta* across its range. Our SNP data strongly support eight monophyletic populations, which we allocate to four species, based on a combination of morphological and genetic distinctiveness. Two of these species, including type *D. tincta*, have largely overlapping distributions over a vast area in central and northern Australia. The type specimen of *D. tincta* from Normanton in Queensland was collected 140 years ago and is in very poor condition. In the absence of other information, we elected to assign the name *tincta* to one of the two clades for which a tissue-sampled specimen was nearest to the type location. A specimen for which we had a sequence was collected 50 km from this locality, and we allocate the name *D. tincta* to this lineage. The other lineage we name *D. hades* sp. nov., with a sequenced specimen occurring as close as 200 km to the type location of *D. tincta*. These sympatric lineages, which are not each other's closest relatives, are morphologically cryptic and cannot be distinguished from one another without nuclear molecular data. Such cryptic species are a challenge for field ecologists and collection managers, and we provide recommendations for how to treat such taxa. We redescribe the lineage that occurs in eastern Queensland as *Delma reticulata* Garman. *Delma reticulata* is also challenging to distinguish from the two sympatric central species, but differs morphologically where they are geographically close to each other in southern Queensland. The most morphologically distinctive lineage is *Delma branchia* sp. nov., which occurs in the Pilbara and Gascoyne regions of Western Australia and is readily identified by a series of ventrolateral transverse bars that continue down the neck. The four species can be diagnosed from all congeners by unique fixed differences in nuclear SNPs and by aspects of colouration in some instances. Deep genetic structure and significant numbers of fixed and private allelic differences suggest additional species-level diversity may be present within three of the four taxa in the *D. tincta* species-group, requiring more detailed sampling in future. We comment on ecological and evolutionary patterns in *Delma*, including problematic patterns of introgression as observed here and in other groups. These new taxa bring the number of *Delma* species to 25, accounting for nearly half the species diversity of enigmatic pygopods.

KEYWORDS: Australian arid zone, monsoon tropics, cryptic species, molecular genetics, SNPs, gecko, Pygopodidae, Wet Tropics biogeographic barriers, fixed differences

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INTRODUCTION

Australia harbours one of the most diverse lizard assemblages on the planet (Webb et al. 2015). In particular, geckos have undergone remarkable diversification in the arid zone, which supports the highest species richness across all four major gecko families found in the country (Norris et al. 2021). It was long assumed the superficially featureless deserts comprised young radiations with limited genetic diversity over vast areas (see Byrne et al. 2008). However, in recent decades, it has become clear that species with extremely wide distributions spanning

much of the arid zone comprise significant unrecognised taxonomic diversity (Oliver et al. 2009, 2014; Melville et al. 2021). The past two decades have seen integrative taxonomic revisions of many arid zone gecko groups, including *Heteronotia* (Pepper et al. 2013), *Diplodactylus* (Doughty et al. 2007; Hutchinson et al. 2009; Oliver et al. 2014), *Rhynchoedura* (Pepper et al. 2011), *Gehyra* (Doughty et al. 2018a; Kealley et al. 2018), *Lucasium* (Eastwood et al. 2020), *Nephrurus* (Oliver et al. 2022), *Oedura* (Oliver and Doughty 2016) and *Crenadactylus* (Doughty et al. 2016). In contrast to the deserts, the monsoon tropics of northern Australia are relatively depauperate of geckos, with the exception of the Kimberley region in Western Australia, which is a hotspot of gekkonine species richness (Norris et al. 2021). Indeed, intensive sampling across the monsoon tropics in recent years has identified many deeply divergent gecko lineages in *Gehyra* (Doughty et al. 2012, 2018b; Ashman et al. 2018; Oliver et al. 2020) and *Heteronotia* (Moritz et al. 2016). Together, these studies across central and northern Australia have resulted in the identification and description of dozens of new gecko species. Many of these newly described species differ only subtly in morphology. In the past, this variation was usually attributed to intraspecific variation within a wide-ranging taxon. However, integrative studies using a combination of molecular and morphological data and denser sampling often reveal a more complex picture with multiple taxa present, with many of these 'cryptic' species having, in hindsight, clear diagnostic morphological features.

The limbless pygopodid geckos are a group of 47 extant species that diversified in Australia (with two species occurring in New Guinea) (Brennan et al. 2016; Jennings 2021) and reach their highest species richness in the arid zone (Norris et al. 2021). With an elongate snake-like body plan, they bear little resemblance to their four-limbed relatives; however, several morphological characters such as fixed spectacles, fleshy tongues and two eggs per clutch have long suggested a close affinity with geckos (Kluge 1974). Molecular data have established that pygopods are an ancient sister lineage to the carphodactylid geckos (Jennings et al. 2003; Han et al. 2004; Oliver and Sanders 2009; Brennan et al. 2016), a relationship that is also supported by morphology (Daza and Bauer 2012).

Of the eight genera of pygopods, *Delma* is the most speciose, with 22 described taxa, many of which have geographically large distributions in the arid zone. One of the most widespread species is *Delma tincta* De Vis, occurring across central and northern Australia, and inhabiting a variety of semi-arid to arid habitats in far Western Australia (WA), the Northern Territory (NT) and Queensland (QLD), as well as occurring in northern South Australia (SA) and New South Wales (NSW) (Kluge 1974; Wilson and Swan 2021; Atlas of Living Australia). The species appears to be absent from the Great Sandy and Great Victoria deserts of WA, where the closely related *D. desmosa* replaces it; as such, the WA populations of *D. tincta* are geographically disjunct from those to the east. In his comprehensive revision of the genus *Delma*, Kluge (1974) found no significant morphological differences among populations of *D. tincta* across its vast distribution. Similarly, Shea (1991) examined many *D. tincta* specimens from central Australia and neighbouring regions and did not remark on any observable differences. However, the near continent-wide distribution of this taxon and the prevalence of cryptic species in other groups in the arid zone, as well as *D. tincta* being one of the oldest recognised pygopod species (De Vis 1888) warrants a genetic assessment of *D. tincta* populations from across its distribution.

Here, we use a combination of genetic data in the form of nuclear Single Nucleotide Polymorphisms (SNPs), as well as morphological evidence drawn from material collected across the geographic range of *D. tincta*, spanning nearly the entire arid zone and adjacent monsoon tropics. We found four deeply diverged lineages within *D. tincta* (*sensu lato*) and further structure within these main groups. Although the western lineage possesses useful diagnostic morphological characters, straightforward identification of the eastern taxa is problematic. They are highly conservative in traditional morphological characters used in pygopods, including meristic characters and size, and each exhibits significant intraspecific colour variation across their range and ontogenetic variation in head colour and pattern. The two most genetically divergent taxa are found in broad sympatry across the central and eastern arid zone, rendering geography an unreliable guide for species identification. We used a genotyped specimen collected ~50 km away from the type locality of *D. tincta* of Normanton, Queensland, to apply the name *tincta* to one of these lineages. Based on the strength of our molecular data, we raise *D. reticulata* Garman from north-eastern Australia from synonymy and describe two new species: a cryptic species that overlaps extensively with true *D. tincta* and another species from the Pilbara and Gascoyne regions of Western Australia. We also suggest ways for field workers and collection managers to cope with what appear to be truly cryptic species in the absence of genetic information to identify specimens.

MATERIALS AND METHODS

DNA ANALYSIS

Taxonomic sampling

We sampled 114 *D. tincta* tissues from collections of the Western Australian Museum (WAM), the South Australian Museum (SAMA), the Australian Museum (AMS), the Queensland Museum (QM) and the Museum and Art Gallery Northern Territory (MAGNT) to provide the broadest geographic sampling possible. We used *D. borea,* the sister taxon to *D. tincta* (Jennings 2021), as the outgroup for analyses.

SNP genetic data

We used the DArTseq (Diversity Array Technology sequencing) platform designed by Diversity Arrays Technology, Canberra, Australia (DArT) for genomic analysis and SNP genotyping. This technique involves a complexity reduction process that uses specific restriction enzymes to fragment the DNA, which is then sequenced using the Illumina HiSeq2500 system (for details on this method, see Kilian et al. [2012] and Georges et al. [2018]). The generated data includes thousands of 69 bp-long fragments associated with restriction sites and their accompanying SNPs. The utility of DArTseq data in assessing phylogeographic patterns and defining species boundaries is well-documented across multiple reptile studies (e.g. Melville et al. 2017; Georges et al. 2018; Zozaya et al. 2019; Chaplin et al. 2020; Esquerré et al. 2021; Pavon-Vazquez et al. 2022).

Preliminary phylogenetic analysis had identified some misidentified individuals that were not part of the *D. tincta* complex, so these were removed from the dataset (NTM R22310, WAM R174757, SAMA ABTC6580, SAMA R22934, SAMA ABTC60831 and SAMA ABTC60820) before filtering. We used the 'dartR 2.9.7' R package (Gruber et al. 2018) to filter our dataset as follows (in order). We first excluded SNPs that were found in the same fragment as other SNPs (to avoid linkage), and then excluded individuals with more than 60% missing data as a first pass to remove the poorest samples. We then excluded SNPs that had a reproducibility below 0.99, had a read depth below 4 or above 40, were missing in more than 90% of samples and whose minor allele was found in only one individual. Subsequently, we excluded individuals with more than 70% missing data. The following samples were excluded due to not meeting the individual call rate threshold: QM J80509, QM J84129, QM J90118, SAMA R22934, SAMA R67717, SAMA R42944, SAMA R42945, WAM R141584, WAM R141273, WAM R116545, WAM R138078, WAM R151060. In the Taxonomy section, holotypes and paratypes are denoted with '*'.

Phylogenetic analyses

Phylogenetic tree reconstruction on our filtered SNP dataset was conducted using two methods. We inferred the maximum likelihood (ML) tree in the program iq-tree 2.2.2.6 (Nguyen et al. 2015). We ran 10,000 ultrafast bootstrap replicates (Minh et al. 2013) and 10,000 replicates of the SH-like approximate likelihood ratio test (SH-aLRT; Guindon et al. 2010). Model selection was completed using Model Finder Pro with ascertainment bias correction (Kalyaanamoorthy et al. 2017). We also used the SNPs to model a lineage tree based on the multi-species coalescent. We used the program SVDQuartets (Chifman and Kubatko 2014), implemented in PAUP v.4.0 (Swofford 2003), assessing branch support with 10,000 bootstrap replicates.

Population structure

To infer population genetic structure and potential admixture, we used the Bayesian admixture analysis sNMF (Frichot et al. 2014) in the 'LEA 2.8.0' R package (Frichot and François 2015) to estimate ancestry coefficients (the proportion of an individual's genome that originates from a set of inferred ancestral populations). We tested nine combinations of the regularisation (α) and tolerance (ε) parameters, choosing that with the lowest cross-entropy. In these test runs, we performed ten repetitions for each value of K (number of theoretical populations) between 1–12. We then performed 100 repetitions for each of the 12 values of K with the best combination of α (1000) and ε (0.00001). We obtained the optimal value of K and individual ancestry coefficients from the run with the lowest cross-entropy. We also characterised population structure by performing a principal component analysis (PCA) with the 'gl.pcoa' function of 'dartR'.

Molecular species delimitation

The fixed difference at a locus occurs when two populations share no alleles, and as such, an accumulation of fixed differences between populations is a strong indicator of reproductive isolation (Georges et al. 2018). An important characteristic of fixed differences is that they enable clear identification of an individual's origin from a particular population or species, and alleles that are fixed and different between two populations are diagnostic characters. This ability to clearly distinguish between populations is especially useful in species delimitation studies (Georges et al. 2018; Unmack et al. 2019). We evaluated whether there are fixed allelic differences in the populations identified by sNMF and populations grouped into major lineages using the 'gl.fixed.diff' function of 'dartR'. We performed 1,000 simulation iterations where we identified true positives based on a threshold of 0.02 for the true minor allele frequency. We first performed this analysis on the four major groups ([P1–2, P7]; [P3–4, P6]; [P5]; [P8]) in pairwise comparisons to demonstrate their uniqueness. We then looked for fixed differences unique to each of these four major lineages by comparing each one to the other three lineages combined (e.g. P8 vs. P1, P2, P3, P4, P5, P6, P7). This latter analysis identifies diagnosable sequences that exclusively occur in a particular lineage. We filtered our data only to include sequences that occurred in more than 80% of the samples and excluded sequences shorter than 25 base pairs (because the probability of a sequence of 25 base pairs occurring more than once in a 2GB genome is $<10^{-6}$).

MORPHOLOGICAL ANALYSIS

Taxonomic sampling

We took linear measurements and counted meristic features in 142 specimens of *D. tincta* from across its distribution, which included all individuals genotyped in our SNP dataset that had associated specimens as well as high-quality specimens for which no tissue sample was available (Appendix 1 and type lists in the Taxonomy section). All specimens were from WAM, SAM, AMS and QM. A previous detailed assessment of *D. tincta*

and closely related species found sexual dimorphism in some linear measurements and meristic traits (Maryan et al. 2007), whereas an earlier study found little sexual dimorphism other than the number of ventral scales (Kluge 1974). We did not record sex and based our analyses on interspecific comparisons.

Morphological measurements and analysis

The following linear measurements are reported in mm and were taken with digital callipers, plastic ruler or string (for tails): snout-vent length (SVL) measured from tip of snout to vent, tail length (TailL) measured from tip of tail to vent and including both potentially original and regenerated tails (see further comments below), head depth (HeadD) measured from dorsal surface of head and ventral surface of throat at point immediately behind eye, head length (HeadL) measured from tip of snout to posterior margin of ear, head width (HeadW) measured from the widest point between the ears, snout length (SnoutL) measured from tip of snout to anterior margin of transparent spectacle and eye width (EyeW) horizontal distance measured from anterior to posterior extremities of transparent spectacle (measurement not including the circumocular granules). Three meristic counts were taken: number of 'hindlimb' (i.e. reduced 'flap') scales (HLS) counted from distal extreme and origin with body, number of midbody scale rows (MBS) counted entirely midway around body and number of ventral scales (VS) counted from immediately behind mental scale to vent. We exclude tail length from our summary descriptive statistics and analyses, as many tails were either recently broken or regenerated, as indicated by a clear break in colouration. For the formal descriptions, we provide only the original TailL for the longest TailL/SVL recorded in each species.

Colour and pattern were difficult to score as wide natural variation was coupled with variable fading in museum specimens. In general, hatchlings and juveniles always have a darkly marked head which fades with age to varying degrees among populations (Maryan et al. 2007; pers. obs.; see Results). Given the materials available to us, we examined available photographs of animals in life and preserved museum specimens to provide the best summation of colour and pattern possible.

We collected morphological data from genotyped specimens and did exploratory morphological analyses based on results from the genetic analyses. We excluded specimens smaller than 55 mm SVL to ensure we were measuring adult specimens (Maryan et al. 2007). These preliminary analyses of linear measurements and meristic data demonstrated that members of this species group are extremely morphologically conservative, as previously noted by Kluge (1974) and Shea (1991). We supplemented our morphological data set with additional non-genotyped specimens to maximise geographic coverage. Unfortunately, owing to the two central taxa's highly conservative morphology and sympatry, 52 specimens could not be confidently assigned to a taxon and were excluded from our analyses. However, we were able to include seven individuals of *D. reticulata,* which could be unambiguously assigned to this taxon based on geography and the lectotype of *D. tincta*. We did not record the sex of individuals, but our primary interest was in the differences between putative species. Therefore, our statistical analyses focus on differences between taxa. We did analyses of variance (ANOVA) to test for differences among putative species means for linear measurements, ventral scale number and relative sizes (ratios) of head length as a proportion of snout-vent length and relative head width, head depth, snout length and eye width as a proportion of head length.

RESULTS

DNA ANALYSIS

Preliminary phylogenetic analyses, including all *Delma* for which we had SNP data (*D. tincta*, *D. borea*, *D. desmosa*, *D. nasuta*, *D. butleri*, and *D. australis*), confirmed the monophyly of *D. tincta* (*sensu lato*). For all *D. tincta* samples, DArT scored 213,459 polymorphic SNPs. After filtering, 5020 SNPs and 96 individuals were retained and used for downstream analyses. Museum accession numbers and collection localities are given in Appendix 1.

Phylogenetic analyses

The ML analysis of the SNP dataset inferred *D. tincta* to be monophyletic with strong support (bootstrap = 100) (Figure 1). In addition, *D. tincta* individuals cluster within eight major lineages (P1–P8) that further cluster into four distinct, well supported clades: Pilbara-Gascoyne (P5; bootstrap = 100), QLD coast (P3–4, P6; bootstrap = 100), and two largely overlapping central/eastern desert clades (P1–2, P7; bootstrap = 99, P8; bootstrap = 100). The Pilbara-Gascoyne lineage was recovered as a sister to one of the central lineages (P8) with good support (bootstrap = 100), with the other central lineage (P1–2, P7) inferred as sister to these (bootstrap = 99). The QLD coast lineage (P3–4, P6) was recovered as sister to these three main lineages (bootstrap = 100). The coalescent lineage tree inferred using SVDquartets, where the lineages were defined *a priori* using the ML tree and the sNMF results (below), provided strong support for the grouping of populations 3, 4 and 6 (QLD coast), 1, 2 and 7 (central/eastern desert lineage 1), and the sister relationship between population 8 (central/eastern desert lineage 2) and 5 (Pilbara-Gascoyne) (Figure 2). However, the relationships among these major lineages were not strongly supported (bootstrap = 67).

In addition to the SNP dataset, we also collected Sanger sequenced data for the mitochondrial locus ND2 for the same individuals (unpublished data). These data showed rampant mito-nuclear discordance in line with ancient and recent hybridisation events between many lineages within the *D. tincta* species complex, as well as with the sister taxon *D. borea,*

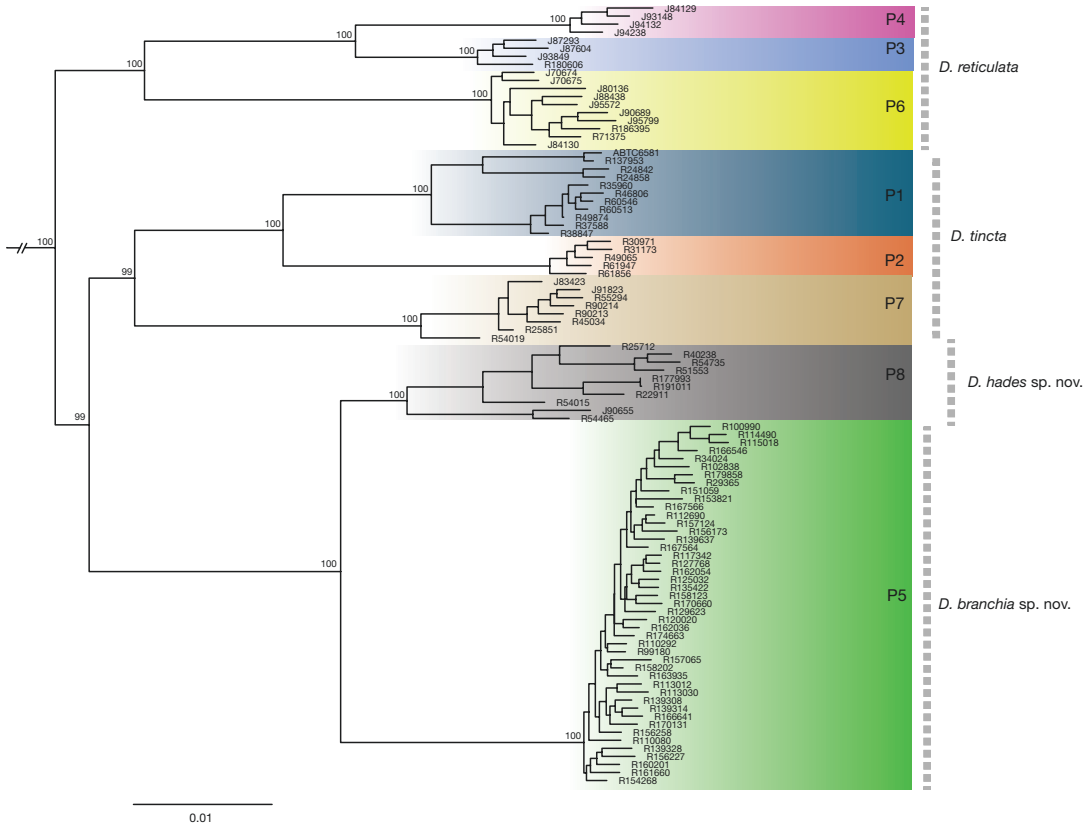

FIGURE 1 Maximum likelihood phylogeny of the *D. tincta* species complex inferred with IQ-Tree using 5020 SNPs. Branch support values correspond to ultrafast bootstraps. The outgroup is not shown. P1–P8 refer to the populations identified in the sNMF analysis.

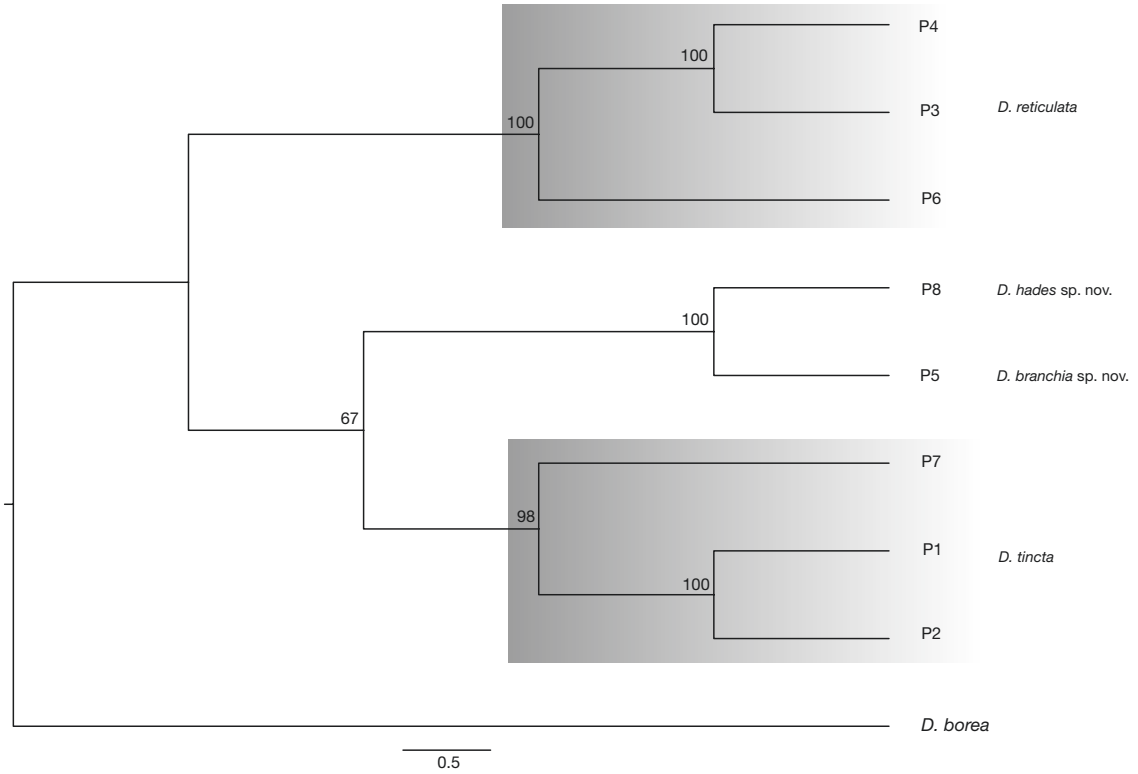

FIGURE 2 Nuclear DNA lineages of the *D. tincta* species complex based on a species tree (inferred with SVDQuartets).

and will be published elsewhere. Multiple instances of mitochondrial introgression have been identified within *Delma*, likely associated with the high frequency of sympatry, particularly between hypothesised sister taxa, and low morphological diversity (Brennan et al. 2016). Given this result, we do not refer to these ND2 data further and do not use these results to inform our species delimitation.

Population genetic analyses

Population genetic structure is highly concordant with our phylogenetic results. The best fitting model in our sNMF analysis indicated K = 8, with very little admixture between these clusters (Figure 3). This large number of populations reflects the significant deep structure within three of the four main lineages identified in the ML phylogenetic analysis. These clusters are readily identifiable in the PCoA plot of the first two PCs, which account for 36.2% and 13.4% of the variation, respectively (Figure 4).

Molecular species delimitation

The first fixed difference analysis comparing all six combinations of the four major groups revealed that all four lineages identified in the phylogenetic analyses have between 72 and 311 fixed differences between them (Table 2), far greater than the expected count of false positives for each comparison. For species diagnoses, we then report the diagnostic fixed differences unique to each lineage compared to all other groups (Appendix 2). The ICZN (International Code of Zoological Nomenclature) allows for any set of characters (including molecular ones) to serve as distinguishing features, provided they enable clear differentiation of taxa. We provide the diagnosable sequences and the position of the SNP, and if aligned, the position on the reference genome of *Gekko japonicus* in Appendices 2–3.

Morphological measurements and analysis

We present summary statistics and results of ANOVA analyses of the morphological data in Table 1. As anticipated, the analyses demonstrate these lineages are highly morphologically conservative in linear body measurements and meristic characters, conforming to a generalised *D. tincta* morphology. While several linear measurements show statistically significant differences in mean values among the four lineages (SVL, HeadL, HeadD, SnoutL), there is still extensive overlap in these values, rendering them of limited use for diagnostic traits. Body size did differ significantly, with the two central lineages reaching larger average body sizes than the western and eastern lineages; however, maximum SVLs were similar except for *D. reticulata,* which was smaller (Table 1). Analyses of relative HeadL and relative SnoutL show no significant differences, while relative HeadW and EyeW show significant differences. This is likely driven by a higher mean HeadW to HeadL ratio in the QLD lineage relative to the other putative species, but again, there is considerable overlap in values. Follow-up PCAs on linear measurements and ventral scale number, which do not identify groups a priori, showed near complete overlap among putative species and a DFA, with putative species identified, only reliably identified *D. reticulata* and *D. hades* sp. nov. at 85% and 86% accuracy, respectively, and performed more poorly on *D. branchia* sp. nov. (68%) and very poorly on *D. tincta,* with less than half of the individuals correctly identified (including the lectotype). Taken together, these analyses demonstrate that these taxa are morphologically extremely similar.

Cryptic species and criteria for species recognition

As discussed by De Queiroz (2007), different species concepts agree that the primary definition of a species is a group of metapopulations that are evolving independently; Maddison and Whitton (2023) also emphasise the persistence of a reproductive community through time with a recent history not shared by other lineages. Diagnosing such separately evolving entities for taxonomy is an issue for truly cryptic taxa that have no apparent morphological differences compared to close relatives (Bickford et al. 2007; Jörger and Schrödl 2013). Despite the prevalence of cryptic species across all animal phyla (Pérez-Ponce de León and Poulin 2016), they are often identified and differentiated but typically remain undescribed; they are '…the worst-case scenario of taxonomic incompleteness' (Delic et al. 2017). Nonetheless, there is strong agreement in the scientific community that cryptic species warrant thorough attention and appropriate taxonomic treatment, including naming them formally (see Delic et al. 2017).

Our SNP analyses identified four major lineages within what is currently recognised as *D. tincta* (Figure 5). Following the Generalized Lineage Concept (GLC; de Queiroz 1998), we consider each of these lineages as independently evolving entities and apply multiple criteria — including morphological and colour pattern differences, reproductive isolation and genetic divergence — to diagnose them as distinct species. In addition to clear phylogenetic and population genetic evidence (although not as deep as some eastern lineage differences), we found that colour and head pattern variation distinguish the western taxon, which is also geographically isolated from eastern populations by the western deserts. Taxonomic delineation is far from straightforward for the three remaining eastern populations (including *D. tincta* [*sensu stricto*]). The molecular evidence for divergent evolution, lack of admixture between groups and fixed allelic differences at a significant number of loci establishes the existence of metapopulations that no longer engage in reticulate evolution with neighbouring populations. That the two central taxa are not each other's closest relatives, and exist in broad geographic sympatry, presents a robust argument for valid biological species — the accumulation of many fixed differences between these lineages is a result of long-standing reproductive isolation. Further sampling in northern NSW and southern QLD may identify additional sympatry with the adjacent QLD lineage in the southern part of its distribution. Complicating this matter for field

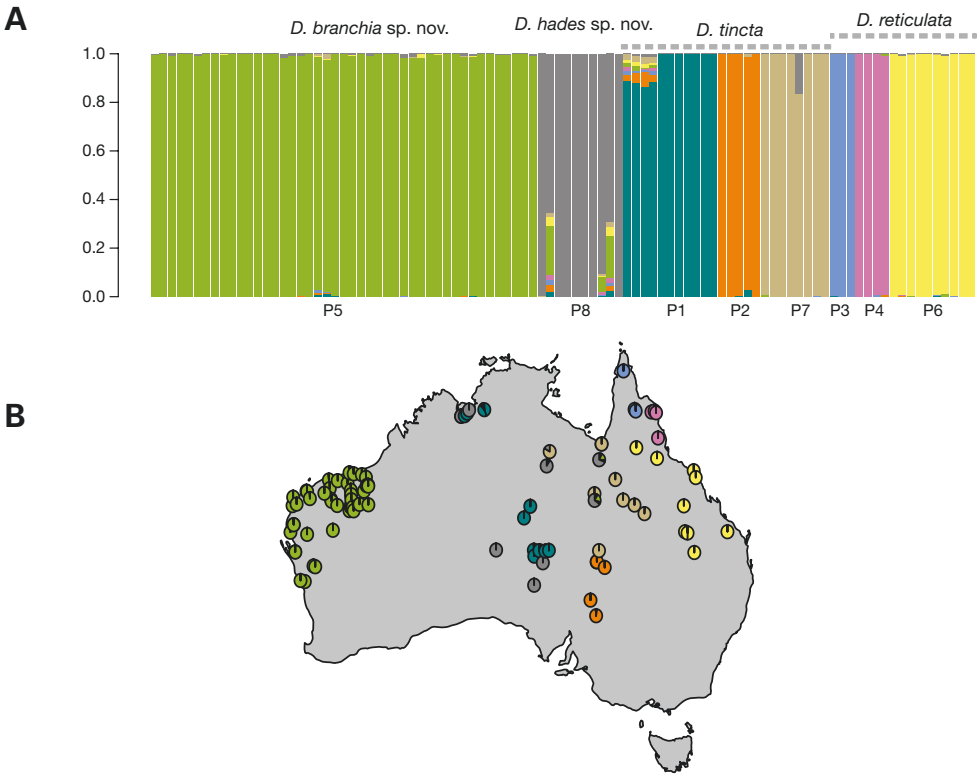

FIGURE 3 A) Ancestry coefficients of each of the eight identified genetic populations (K) for the *D. tincta* species complex, sorted by species. B) Distribution map of the genotyped specimens displayed as pie charts of their ancestry coefficients, to visualise the lack of geographic admixture.

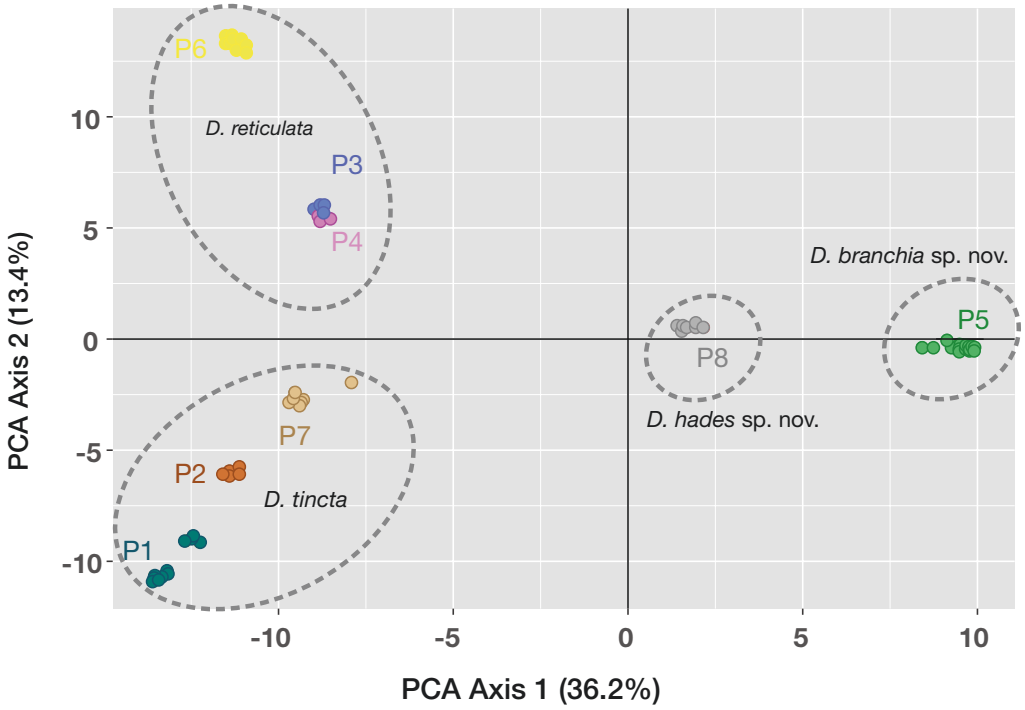

FIGURE 4 Principal coordinates analysis (PCoA) plot of genetic structure based on genetic distances among the 8 populations within the *D. tincta* species complex. Percentages of genetic variation explained by each PCoA axis are shown in parentheses.

TABLE 1 Summary statistics for characters and ratios measured for members of the *D. tincta* species complex. Mean ± SD (range) See text for abbreviations of characters used.

Character	*D. hades* sp. nov.	*D. reticulata*	*D. tincta*	*D. branchia* sp. nov.	Statistics
Sample size	8	13	17	42	
SVL	78 ± 13 (56–95)	69 ± 10 (55–84)	76 ± 12 (56–96)	70 ± 8 (55–93)	F3,80=3.177, P=0.0288
HeadL	8.3 ± 1.0 (6.6–9.2)	7.3 ± 0.8 (6.0–8.1)	7.8 ± 0.7 (6.4–8.8)	7.5 ± 0.6 (6.3–8.8)	F3,80=4.212, P=0.0082
HeadD	3.9 ± 0.6 (2.6–4.6)	3.4 ± 0.4 (2.6–4.1)	3.4 ± 0.5 (2.6–4.4)	3.3 ± 0.4 (2.6–4.3)	F3,80=5.052, P=0.0030
HeadW	4.9 ± 0.6 (3.7–5.5)	4.6 ± 0.7 (3.3–5.6)	4.7 ± 0.8 (3.4–6.0)	4.3 ± 0.5 (3.3–5.6)	F3,80=2.6537, P=0.0546
SnoutL	3.3 ± 0.4 (2.7–3.6)	2.9 ± 0.3 (2.3–3.2)	3.1 ± 0.3 (2.5–3.5)	3.0 ± 0.3 (2.1–3.5)	F3,80=4.4369, P=0.0063
EyeW	1.1 ± 0.1 (1.0–1.3)	1.2 ± 0.1 (0.9–1.4)	1.1 ± 0.1 (1.0–1.4)	1.2 ± 0.1 (1.0–1.4)	F3,80=0.0797, P=0.9708
HeadL/SVL	0.1 ± 0.0 (0.1–0.1)	0.1 ± 0.0 (0.1–0.1)	0.1 ± 0.0 (0.1–0.1)	0.1 ± 0.0 (0.1–0.1)	F3,80=1.657, P=0.1848
HeadW/HeadL	0.6 ± 0.0 (0.6–0.6)	0.6 ± 0.1 (0.6–0.7)	0.6 ± 0.1 (0.5–0.7)	0.6 ± 0.0 (0.5–0.6)	F3,80=4.3382, P=0.0071
SnoutL/HeadL	0.4 ± 0.0 (0.4–0.4)	0.4 ± 0.0 (0.4–0.4)	0.4 ± 0.0 (0.4–0.4)	0.4 ± 0.0 (0.3–0.4)	F3,80=0.9396, P=0.4259
EyeW/HeadL	0.1 ± 0.0 (0.1–0.2)	0.2 ± 0.0 (0.1–0.2)	0.2 ± 0.0 (0.1–0.2)	0.2 ± 0.0 (0.1–0.2)	F3,80=5.6045, P=0.0016
VS	67.8 ± 2.9 (63–72)	64.9 ± 2.5 (61–69)	69.7 ± 4.2 (63–78)	68.8 ± 2.9 (61–75)	F3,79=6.6280, P=0.0005
MBS	14 (100%)	14 (84.6%), 15 (15.4%)	14 (100%)	13 (14.6%),14 (82.9%), 15 (2.4%)	
HLS	2 (14.3%), 3 (85.7%)	3 (100%)	2 (6.3%), 3 (62.5%), 4 (31.3%)	3 (100%)	
Supralabial scales (R)	6 (100%)	5 (18.2%), 6 (81.8%)	5 (5.9%), 6 (94.1%)	5 (2.4%), 6 (95.2%), 7 (2.4%)	
Infralabial scales (R)	7 (100%)	4 (18.2%), 5 (72.7%), 6 (9.1%)	4 (11.8%), 5 (88.2%)	4 (23.8%), 5 (76.2%)	
Supralabial scales (L)	6 (100%)	5 (8.3%), 6 (83.3%), 7 (8.3%)	6 (100%)	6 (100%)	
Infralabial scales (L)	4 (14.3%), 5 (85.7%)	4 (8.3%), 5 (91.6%)	4 (5.9%), 5 (94.1%)	4 (7.1%), 5 (90%), 6 (2.4%)	

identification in central Australia, our morphological data indicate widely overlapping characters with no clear way to diagnose an ungenotyped individual reliably. In addition, multiple instances of mito-nuclear discordance identified in preliminary mtDNA analyses also render mtDNA barcoding an unreliable tool for species identification (unpublished data). Thus, for this truly cryptic species complex, we have relied heavily on the substantial molecular evidence from the nuclear SNPs and the diagnostic fixed differences for recognising the three eastern taxa (Table 2 and Appendices 2–3). While several deeply divergent lineages exist within three of the four major lineages, our current genetic sampling is geographically limited, and few genotyped specimens are available for morphological assessment, particularly in remote central Australia. In addition, small sample sizes can lead to an excess of fixed differences. Therefore, we grouped lineages together so each was represented by at least 10 samples. Until broader geographic and genetic sampling can clarify their evolutionary and ecological distinctiveness, we conservatively retain them within our proposed framework of four species in the *D. tincta*

TABLE 2 The fixed differences between the major lineages identified by the phylogenetic analyses, showing the number of fixed differences is far greater than the expected count of false positives for each comparison.

Lineage 1	Lineage 2	N1	N2	Fixed differences	False positives
D. branchia sp. nov. (P5)	*D. hades* sp. nov. (P8)	45	10	108	28.6
D. branchia sp. nov. (P5)	*D. reticulata* (P3–4, P6)	45	17	311	41.5
D. branchia sp. nov. (P5)	*D. tincta* (P1–2, P7)	45	24	207	67.9
D. hades sp. nov. (P8)	*D. reticulata* (P3–4, P6)	10	17	254	51.4
D. hades sp. nov. (P8)	*D. tincta* (P1–2, P7)	10	24	118	79.7
D. reticulata (P3–4, P6)	*D. tincta* (P1–2, P7)	17	24	72	23.1

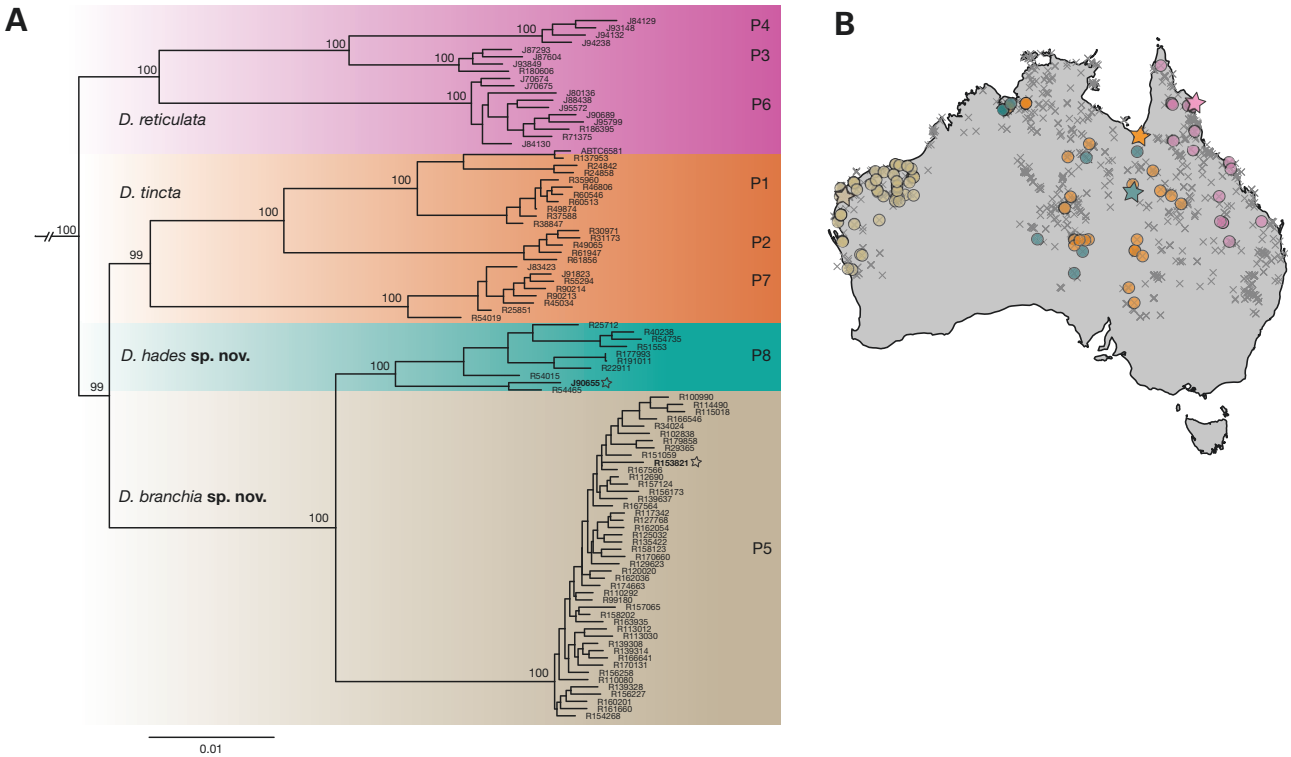

FIGURE 5 Maximum likelihood phylogeny from Figure 4 reflecting the new taxonomy of the *D. tincta* species complex. P1–P8 refer to the populations identified in the sNMF analysis. The map is colour-coded to match the phylogeny, and the stars indicate the location of the holotype or lectotype for each taxon. The grey Xs indicate ALA records for *D. tincta* (*sensu lato*).

species group.

The lectotype for *D. tincta* is from Normanton near the coast of the Gulf of Carpentaria, Qld, where two taxa occur in sympatry. The lack of genetic material for this specimen and the lack of diagnosable characters to definitively assign the lectotype to one of two possible sympatric taxa are problematic. The *D. tincta* lectotype is in poor condition, given its age and state of preservation (Figure 6), and our DFA analysis could not assign this specimen to a lineage. One of our genotyped specimens (SAMA R25851) was collected from within 50 km of Normanton, whereas the closest genotyped specimen from the other lineage was ~200 km away. Here, we have applied the name *D. tincta* (*sensu stricto*) to the genetic lineage with the genotyped specimen that is ~50 km away from Normanton. Although the distribution of each cryptic species ranges for thousands of km across the arid zone, this somewhat arbitrary criterion for designating the name *tincta* to a lineage is at least clear in the absence of other compelling information.

The designation of type specimens to particular species based on genetic proximity to a known reference population carries inherent risks, particularly when geographic sampling is limited. We recognise the downstream implications of misidentifying the type locality and remain cautious in our interpretations, acknowledging the potential for future revisions as additional samples are incorporated.

TAXONOMY

Pygopodidae Boulenger, 1884

Delma Gray, 1831

Type species: *Delma fraseri* Gray, 1831, by monotypy.

DIAGNOSIS

Delma differs from all other pygopod lizard genera in possessing the following combination of characters: head scales, including the parietals, enlarged and symmetrical; anterior nasal scales nearly always in contact; first pair of lower labials in contact behind mental scale; nostril usually bordered by more than two scales (except in some *D. impar*); external ear opening large; 20 or fewer midbody scale rows; dorsal and ventral scales smooth; precloacal pores absent; tail about three times as long as body (Kluge 1974).

Delma tincta species-group vs. *D. tincta* species complex

DIAGNOSIS

Based on the molecular analysis from this study, as well as the published mtDNA and nDNA study of Brennan et al. (2016) and the work of Shea (1991) and Maryan et al. (2007), we redefine a monophyletic '*D. tincta* species-group', comprised of *D. tincta*, *D. borea*, *D. pax*, *D. elegans*, *D. tealei*, *D. desmosa*, *D. reticulata*, *D. branchia* sp. nov. and *D. hades* sp. nov. The original group of Shea (1991), which has been added to by Maryan et al. (2007), is no longer a cohesive entity but rather a morphologically variable group that is supported by genetic data. Morphological characteristics shared by all members of this species-group are: relatively small to moderate size (SVL to 98 mm); one or two pairs of supranasal scales; eye above third or fourth supralabial; 14 to 18 midbody scale rows. Colour is usually brown with shades of olive and orange; banding on the head and neck is prominent on small individuals, but, depending on the species, fades in larger adults.

The '*Delma tincta* species complex' refers to the four species within *D. tincta* (*sensu lato*): *D. tincta*, *D. reticulata*, *D. branchia* sp. nov. and *D. hades* sp. nov. All are redescribed or described as new, below.

Delma tincta De Vis, 1888

Excitable Delma (lineage P1–2, P7)

(Figures 6, 7A)

1888. *Delma tincta* De Vis, Proc. Linn. Soc. N.S.W., 2: 824.

MATERIAL EXAMINED

Lectotype

Australia: *Queensland*: QM J241. Type locality: 'Normanton, Gulf of Carpentaria' [donated by M.

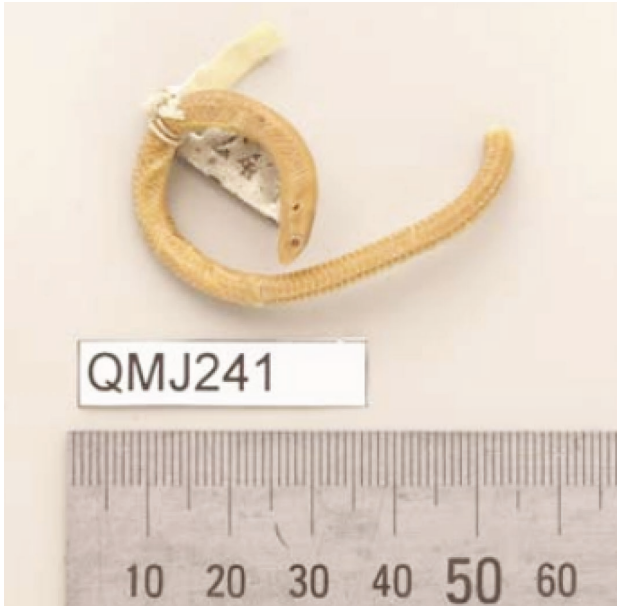

FIGURE 6 Lectotype of *Delma tincta* from Normanton in the Gulf of Carpentaria, Queensland, donated by M. Comley.

FIGURE 7 Photos of the four *D. tincta* species complex members from near the collection location of the holotypes: A) *D. tincta* (Doomagee, Queensland; photo: S. Macdonald); B) *Delma reticulata* (Laura, Queensland; photo: A. Zimny); C) *D. hades* sp. nov. (Julia Creek, Queensland; photo: A. Zimny); D) *D. branchia* sp. nov. (Bullara Station, Western Australia; photo: B. Maryan).

Comley]. Lectotype designation by Kluge (1974), who also restricted the type locality to Normanton.

Paralectotypes

Australia: *Queensland:* specimens lost before the lectotype designation of Kluge (1974) (Covacevich 1971). Collected from 'Springsure, Central Queensland' [donated by M. Comley].

Other material examined

A full list of the material examined is provided in Appendix 4.

DIAGNOSIS

A moderately-sized *Delma* (SVL to 55–96 mm; tail length up to 280 mm long) with one pair of supranasals, third labial below eye and 14 midbody scale rows. Differs from *D. reticulata* by adults lacking a boldly patterned head and neck, where these species come into near-contact in northern Queensland. It differs from *D. branchia* sp. nov. by lacking the series of ventrolateral transverse bars on the neck and posterior edge of ear opening, usually in contact or narrowly separated from the dark nuchal band. If present, pale band separating the crown and nuchal band is twice as wide as the one between the ocular and the crown bands.

Genetically diagnosed from all other members of the *D. tincta* species-group by 11 unique fixed differences (see Appendix 2), and from the sympatric *D. hades* sp. nov. by 118 fixed SNP differences (see Table 2). Appendices 2–3 show the diagnostic positions and sequences for all comparisons and the position on the reference chromosome where it aligns to *Gekko japonicus*.

DESCRIPTION

Snout-vent length 55–96 mm; tail length to 280 mm (up to 300% of SVL). Usually one pair of supranasals. Loreals 1–7. Third upper labial below eye. Midbody scale rows 14.

Head short, narrowing to rounded tip of snout, neck slightly constricted compared to head and forebody; ear opening ovoid, narrowing on either end, ear sloping backwards on a 30° angle bordered above by a narrow scale anteriorly and a large triangular scale posteriorly, and below by more numerous granular scales (~5–12); in profile, snout tapering gradually to rounded tip, gular region flat; body elongate and circular in cross-section but with ventrum flatter; hind flaps small and narrowing to a rounded point, covered by 3–5 scales; tail relatively long (to 300% SVL), tapering gradually to a fine point.

Head scales smooth, non-imbricate and heterogeneous;

top of rostral coming to a point dorsally, wider than long, not in contact with nostril; one pair of supranasals in broad contact; nostril positioned behind anterior extension of supranasal, postnasal and first upper labial; one postnasal, wider than high, angled posteroventrally and in contact with first loreal, excluded from second upper labial; prefrontals in contact; supraloreal 2–3 times as high as wide, in contact ventrally with loreals; 2–3 loreals in contact with supralabials, the anteriormost slightly larger; three supraciliaries; two supraoculars of similar size; two frontals, the anteriormost slightly wider and larger; frontoparietals large and in broad medial contact; two parietals, long with inner edge in contact with interparietal; 3–4 temporals; six upper labials, third widest and positioned below eye; five lower labials; mental width similar to length and coming to a point; first infralabials elongate and in contact; second infralabials elongate and separated by scale. Dorsal and lateral scales smooth, non-imbricate and homogeneous; ventral scales 1.5–2.0 times wider than body scales; three precloacal scales.

Pattern in life: Body typically light brown but with variation including olive hues and grey; head with 2–4 darkish bands: faint loreal band present; dull ocular band through black eyes and continuing as smudge on lower labial; band on crown to upper jaw; if present, nuchal band posterior to ear opening continuing to level of mouth; pale bands on head pale cream; ventrum pale cream. Sides of neck lacking dark markings.

VARIATION

Table 1 presents the individual measurements and meristic counts for all the *D. tincta* examined.

DISTRIBUTION AND SYMPATRY

The following account is based on genotyped specimens. *Delma tincta* occurs across a wide area of central Australia: from the eastern Kimberley, south and east to the Lake Frome region in SA, inland Queensland to near the Gulf of Carpentaria and through the central Northern Territory. Kimberley specimens belong to either *D. tincta* or *D. hades* sp. nov., but not *D. branchia* sp. nov., based on the absence of the diagnostic neck markings in the latter. Genotyping of Top End specimens is necessary to determine whether *D. tincta* occurs there.

Overlaps *D. hades* sp. nov. broadly in central NT and the western edge of inland Queensland. It appears to be allopatric with *D. reticulata* to the east and is entirely allopatric with *D. branchia* sp. nov., which occurs in western WA. Further sequencing of available specimens could result in more precise estimates of distribution and potential sympatry (especially with *D. reticulata*).

HABITAT

Detailed habitat notes are unavailable; however, it is likely to be a terrestrial generalist, sheltering under logs and moving through vegetation to actively hunt prey.

REMARKS

Owing to the lectotype's poor quality, it was not possible to morphologically assign the type to either of the two central lineages recovered in the genetic analyses. Hence, we used the criterion of the closest genotyped individual to the type location of Normanton, which proved to be a choice of ~50 km vs. ~200 km distance. As all species considered here occur over thousands of kilometres, this may or may not indicate the lineage to which the lectotype of *D. tincta* belongs. To resolve the matter, ancient DNA from the lectotype is the best option; a second option is to petition for the type to be set aside and choose a neotype with an available tissue sample, both of which are beyond the scope of this paper. Hence, we regard our allocation of names to the two central lineages as provisional at this stage.

***Delma reticulata* Garman, 1901**

Coastal Queensland Delma (lineage P3–4, P6)

(Figure 7B)

1901. *Delma reticulata* Garman, Bull. Mus. Comp. Zool. Harv., 39: 5, pl. 2, figs. 1-la–f.

MATERIAL EXAMINED

Holotype

Australia: *Queensland*: MCZ 6486 collected from near Cooktown in 1896 by E.A.C. Olive.

Other material examined

A full list of the material examined is provided in Appendix 4.

DIAGNOSIS

A relatively small (to 84 mm SVL) member of the *D. tincta* species-group. In the north of its distribution, it differs from the adjacent two species to the west (where they nearly come into contact) by being boldly patterned on the head whereas *D. tincta* and *D. hades* sp. nov. are plain (however, these taxa may be boldly patterned elsewhere within their distribution). However, in the inland southern part of its distribution, *D. reticulata* is also plain, resembling the plain *D. tincta* and/or *D. hades* sp. nov. It differs from *D. branchia* sp. nov. by lacking the series of ventrolateral transverse bars on the neck and posterior edge of ear opening usually in contact or narrowly separated from the dark nuchal band. Pale band separating the crown and nuchal band narrow (similar thickness to band separating occipital and crown band).

Genetically diagnosed from all other *D. tincta* species complex taxa by 39 unique fixed differences (Appendix 2). Appendix 2 shows the diagnostic positions and sequences for all comparisons as well

as the position on the reference chromosome where it aligns to *Gekko japonicus*.

DESCRIPTION

Snout-vent length 55–84 mm; tail length to 246 mm (up to 293% of SVL). Usually one (occasionally two) pair of supranasals. Loreals 1–7. Third (rarely fourth) upper labial below eye. Midbody scale rows usually 14 (occasionally 13 or 15).

Head short, narrowing to rounded tip of snout, neck is slightly constricted compared to head and forebody; moderately small ear opening ovoid, narrowing on either end, ear sloping backwards on a 30° angle bordered above by a narrow scale anteriorly and a large triangular scale posteriorly, and below by more numerous granular scales (~5–12); in profile, snout tapering gradually to rounded tip, gular region flat; body elongate and circular in cross-section but with ventrum flatter; hind flaps small and narrowing to a rounded point, covered by 3–5 scales; tail relatively long (up to 293% of SVL), tapering gradually to a fine point.

Head scales smooth, non-imbricate and heterogeneous; top of rostral coming to a point dorsally, wider than long, not in contact with nostril; one pair of supranasals in broad contact; nostril positioned behind anterior extension of supranasal and in contact with postnasal and first upper labial; one postnasal, wider than high, angled posteroventrally and in contact with first loreal, excluded from second upper labial; prefrontals in contact; supraloreal 2–3 times as high as wide, in contact ventrally with loreals; 2–3 loreals in contact with supralabials; three supraciliaries; two supraoculars of similar size; two frontals, the anteriormost slightly wider and larger; frontoparietals large and in broad medial contact; two parietals, long and inner edge in contact with interparietal; 3–4 temporals; six upper labials, third the widest and positioned below eye; five lower labials; mental width similar to length and coming to a point; first infralabials elongate and in contact; second infralabials elongate and separated by scale. Dorsal and lateral scales smooth, non-imbricate and homogeneous; ventral scales 1.5–2.0 times wider than body scales; three precloacal scales.

Pattern in life: Body typically light brown to olive brown; head with four prominent dark bands: weakly-defined loreal band continuing as dark smudge on lower labial; ocular band through black eyes and continuing as dark smudge on lower labial; band on crown continuing to lower jaw; nuchal band posterior to ear opening continuing to level of mouth; pale bands on head can range from pale cream to orange; posterior to nuchal band, at most one black mark ventrolaterally; ventrum pale cream. Black banding on head fades in southern inland adults.

VARIATION

Table 1 presents the individual measurements and meristic counts for all the *D. reticulata* examined. In the north, individuals possess prominent dark headbands, whereas in the south, in large adults, these bands fade.

HABITAT AND ECOLOGY

Little known but recorded from dry habitats and is likely a terrestrial generalist.

DISTRIBUTION AND SYMPATRY

Based on genotyped specimens, it occurs in eastern Queensland from the tip of the Cape to Brisbane. It may extend into northern New South Wales. In central Queensland, it comes into near contact with *D. tincta* and/or *D. hades* sp. nov.

REMARKS

This species appears to be largely allopatric to the other three species in the species complex. The Cape York population is deeply diverged genetically from more southern populations of *D. reticulata*, and this area receives far greater annual rainfall as part of the Wet Tropics region.

***Delma hades* sp. nov.**

Hellish Excitable Delma (lineage P8)

(Figures 7C, 8)

urn:lsid:zoobank.org:act:0510C87E-A9F2-47DE-A8EC-72670C19A8BC

MATERIAL EXAMINED

Holotype

Australia: *Queensland*: QM J90655*, collected from Two Rivers Homestead (-22.3964°, 139.9572°) on 22 April 2010 by M. Hutchinson, P. Oliver and D. Rabosky.

Paratypes

Australia: ***Queensland*:** SAMA R54465*, Burke and Wills Roadhouse dump, Queensland (-19.2264°, 140.3481°). ***Northern Territory*:** SAMA R54015*, Barkly Roadhouse, Northern Territory (-19.7114°, 135.8278°).

Other material examined

A full list of the material examined is provided in Appendix 4.

DIAGNOSIS

A moderately-sized (to 95 mm SVL) member of the *D. tincta* species-group. In the eastern part of its distribution, it differs from the geographically adjacent *D. reticulata* by a plain head (vs. boldly patterned); elsewhere, it is indistinguishable from *D. reticulata*. Indistinguishable morphologically from *D. tincta*. It differs from *D. branchia* sp. nov. by lacking the series

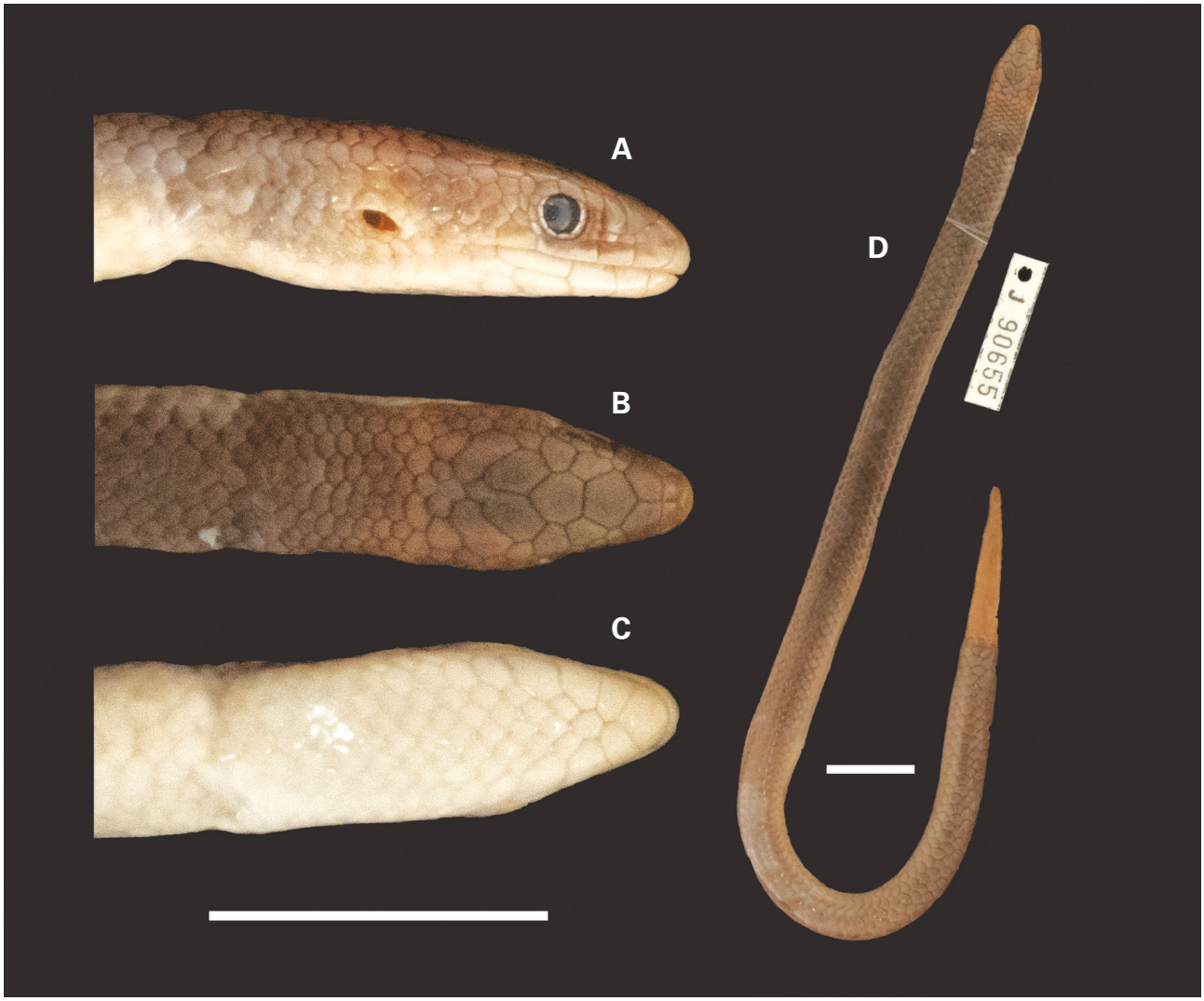

FIGURE 8 *Delma hades* sp. nov. holotype (QM J90655): A) lateral, B) dorsal, and C) ventral views of head, scale = 10 mm; D) whole body, scale = 10 mm.

of ventrolateral transverse bars on the neck.

Genetically diagnosed from all other members of the *D. tincta* species complex by 11 fixed differences (Appendix 2). Appendices 2–3 show the diagnostic positions and sequences for all comparisons as well as the position on the reference chromosome where it aligns to *Gekko japonicus*.

DESCRIPTION

Snout-vent length 55–95 mm; tail length to 292 mm (up to 307% of SVL). Usually, one pair of supranasals. Loreals 1–7. Third upper labial below eye. Midbody scale rows 14.

Head short, narrowing to rounded tip of snout, neck is slightly constricted compared to head and forebody; ear opening ovoid, narrowing on either end, ear sloping backwards on a 30–45° angle bordered above by 2–3 scales, and below by more numerous granular scales (~5–12); in profile, snout tapering gradually to rounded tip, gular region flat; body elongate and circular in cross section but with ventrum flatter; hind flaps small and narrowing to a rounded point, covered by 3–5 scales; tail relatively long (to 307% SVL), tapering gradually to a fine point.

Head scales smooth, non-imbricate and heterogeneous; top of rostral coming to a point dorsally, wider than long, not in contact with nostril; one pair of supranasals in broad contact; nostril positioned behind anterior extension of supranasal, postnasal and first upper labial; one postnasal, wider than high, angled posteroventrally and in contact with first loreal, excluded from second upper labial; prefrontals in contact; supraloreal 2–3 times as high as wide, in contact ventrally with loreals; 2–3 loreals of equal size in contact with supralabials; three supraciliaries; two supraoculars of similar size; two frontals, the anteriormost slightly wider and larger; frontoparietal large and in broad medial contact; two parietals, long and inner edge in contact with interparietal; 3–4 temporals; six upper labials, third the widest and positioned below eye; five lower

labials; mental width similar to length and coming to a point; first infralabials elongate and in contact; second infralabials elongate and separated by scale. Dorsal and lateral scales smooth, non-imbricate and homogeneous; ventral scales 1.5–2.0 times wider than body scales; three precloacal scales.

Pattern in life: Body typically light brown but with variation including olive to orange hues; head with 2–4 dark bands: weakly-defined loreal band continuing as dark smudge on lower labial, ocular band through black eyes and continuing as dark smudge on lower labial, band on crown continuing to lower jaw, nuchal band posterior to ear opening continuing to level of mouth; pale bands on head are pale cream; in large individuals, bands faded with little contrast of dark and light elements; ventrum pale cream.

MEASUREMENTS

Holotype (in mm or counts): SVL 95, HeadD 4.26, HeadL 9.2, HeadW 5.26, SnoutL 3.61, EyeW 1.3, MBS 14, VS 72.

VARIATION

Table 1 presents the individual measurements and meristic counts for all the *D. hades* examined.

HABITAT AND ECOLOGY

Unknown. Likely a habitat generalist.

DISTRIBUTION AND SYMPATRY

The following account is based on genotyped specimens. *Delma hades* sp. nov. occurs across a wide area of central Australia: from the eastern Kimberley, south to central SA, inland Queensland to near the Gulf of Carpentaria and through central NT.

Overlaps *D. tincta* broadly in central NT and the western edge of inland Queensland. Allopatric with *D. reticulata* to the east and allopatric with *D. branchia* sp. nov. in the west. Further sequencing could result in more precise estimates of distribution and potential sympatry (perhaps with *D. reticulata*).

Genotyping of Top End specimens is necessary to determine if *D. hades* sp. nov. occurs there. In the Kimberley, it is unknown if *D. tincta* species complex animals are *D. hades* sp. nov. or *D. tincta* without further genetic information (mtDNA results are equivocal; unpublished data). It may also occur in northern New South Wales.

ETYMOLOGY

The specific name *hades* is derived from the Greek god of the Underworld (or hell), in reference to the distribution of this taxon in broad sympatry, i.e. lying 'underneath', the distribution of *D. tincta* and the 'hellish' difficulty of distinguishing the two taxa in the absence of morphological markers.

REMARKS

As noted above, future work could more firmly establish that this is a newly-named taxon if the lectotype of *D. tincta* can be demonstrated to be a member of the non-*D. hades* lineage through ancient DNA or some other kind of analysis of the type specimen. Field workers and collection managers in museums may simply have to denote non-genotyped individuals as '*D. tincta/hades*' until reliable morphological identifiers are discovered, or the specimen is identified with SNP or other kinds of genetic data.

***Delma branchia* sp. nov.**

Western Excitable Delma (lineage P5)

(Figures 7D, 9)

urn:lsid:zoobank.org:act:32F21DDA-4F0D-4B1C-82CE-E31D08DCE2C1

Holotype

Australia: *Western Australia*: WAM R153821*, male, collected from Bullara Station (-22.8091°, 113.9442°) on 10 September 2003 by Brad Maryan and David Algaba.

Paratypes

Australia: *Western Australia*: WAM R112690*, 5.5 km SE Onslow (-21.6758°, 115.1450°); WAM R114490*, male, Wicherina Dam (-28.73°, 115.00°); WAM R115018*, Spalding Park, Geraldton (-28.65°, 114.63°); WAM R116545, Depot Hill (-29.13°, 115.35°); WAM R151059*, 10 km E Carnarvon (-24.883°, 113.767°); WAM R162054*, 5.5 km NE Giles Point (-23.214°, 119.202°); WAM R166546* Meka Station, (-27.5797°, 115.8992°).

Other material examined

A full list of the material examined is provided in Appendix 4.

DIAGNOSIS

A small to medium-sized *Delma* (to 93 SVL and 370 mm long) with one pair of supranasals, third labial below eye and 14 midbody scale rows. Pattern differs from other *D. tincta* species-group members by the presence of ventrolateral markings posterior to dark bands of head; anteriorly they resemble a continuation of head banding but fade to checker-like patterns posteriorly on forebody (to 2–3 head lengths down the body). Ear opening not in contact with dark bands on head. Pale band separating the crown and nuchal band thick (twice as wide as band separating occipital and crown band). Large adults do not lose banding on head.

Genetically diagnosed from all other *D. tincta* species complex taxa by 49 fixed differences (Table 2). Appendix 2 shows the diagnostic positions and sequences for all comparisons as well as the position

on the reference chromosome where it aligns to *Gekko japonicus*.

DESCRIPTION

Snout-vent length 55–93 mm; tail length to 260 mm (up to 280% of SVL). Usually one (occasionally two) pair of supranasals. Loreals 1–7. Third (rarely fourth) upper labial below eye. Midbody scale rows usually 14 (occasionally 13 or 15).

Head short, narrowing to rounded tip of snout, neck is slightly constricted compared to head and forebody; ear opening ovoid, narrowing on either end, ear sloping backwards on a 30–45° angle bordered above by a narrow scale anteriorly and a large triangular scale posteriorly, and below by more numerous granular scales (~5–12); in profile, snout tapering gradually to rounded tip, gular region flat; body elongate and circular in cross section but with ventrum flatter; hind flaps small and narrowing to a rounded point, covered by 3–5 scales; tail relatively long (to 280% SVL), tapering gradually to a fine point.

Head scales smooth, non-imbricate and heterogeneous; top of rostral coming to a point dorsally, wider than long, not in contact with nostril; one pair of supranasals in broad contact; nostril positioned behind anterior extension of supranasal and in contact with postnasal and first upper labial; one postnasal, wider than high, angled posteroventrally and in contact with first loreal, excluded from second upper labial; prefrontals in contact; supraloreal 2–3 times as high as wide, in contact ventrally with loreals; 2–3 loreals in contact with supralabials, the anteriormost slightly larger; three supraciliaries; two supraoculars of similar size; two frontals, the anteriormost slightly wider and larger; frontoparietals large and in broad medial contact; two parietals, long and inner edge in contact with interparietal; 3–4 temporals; six upper labials, third the widest and positioned below eye; five lower labials; mental width similar to length and coming to a point; first infralabials elongate and in contact; second infralabials elongate and separated by 1–2 scales. Dorsal and lateral scales smooth, non-imbricate and homogeneous; ventral scales 1.5–2.0 times wider than body scales; three precloacal scales.

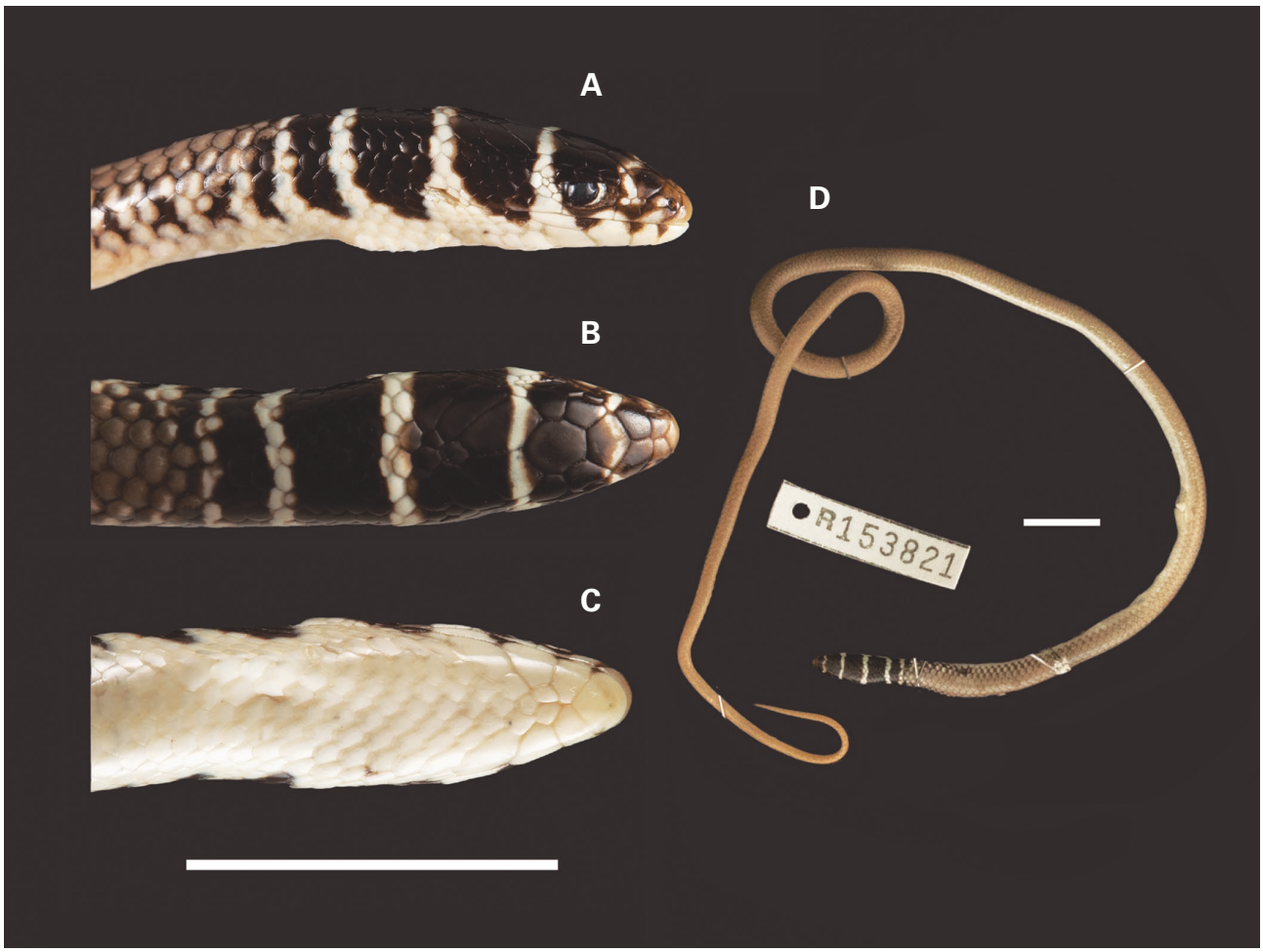

FIGURE 9 *Delma branchia* sp. nov. holotype (WAM R153821): A) lateral, B) dorsal, and C) ventral views of head, scale = 10 mm; D) whole body, scale = 10 mm.

Pattern in life. Body typically light brown but with variation including olive to orange hues; head with four prominent dark bands: weakly-defined loreal band continuing as dark smudge on lower labial; ocular band through black eyes and continuing as dark smudge on lower labial; band on crown continuing to lower jaw; nuchal band posterior to ear opening continuing to level of mouth; pale bands on head can range from pale cream to rich orange; posterior to nuchal band, a ventrolateral series of alternating pale and dark bands that taper and fade 2–3 head lengths along forebody, posteriorly regressing to a checked pattern; ventrum pale cream.

MEASUREMENTS

Holotype (in mm or counts): SVL 64, HeadD 2.87, HeadL 6.94, HeadW 3.78, SnoutL 2.85, EyeW 0.96, MBS 13, VS 72.

VARIATION

Table 1 presents the individual measurements and meristic counts for all the *D. branchia* sp. nov. examined.

ETYMOLOGY

The specific name *branchia* is derived from the Latin noun *branchiae*, meaning gills, alluding to the broken banding and checkered pattern that continues down the side of the neck.

DISTRIBUTION AND SYMPATRY

Delma branchia sp. nov. is distributed throughout the Pilbara and Gascoyne regions, south to near Kalbarri National Park. Scattered records along the western coast and inland (e.g. Ashburton region) indicate it likely occurs throughout these regions as well. Ungenotyped individuals from the Kimberley lack the barring on the neck and are therefore unlikely to belong to this species. *Delma tincta* and/or *D. hades* sp. nov. comes into near sympatry in the Broome region of the Kimberley to the north of this species' distribution.

HABITAT

Mainly heavy red soils including sand, clay and gibber. WAM database habitat notes mention under rocks (limestone and exfoliated granite), inside spinifex clumps and among debris or leaf litter. Several specimens were captured from rubbish tips; one specimen was retrieved from a burrow.

REMARKS

This species adds to the growing list of western endemic reptiles from the Pilbara and Gascoyne regions (McKenzie et al. 2000; Doughty et al. 2008). Owing to the dense survey effort in the Pilbara region, it appears to occur throughout the region, which features a mixture of rocks, clay and sand. Of the four species treated here, *D. branchia* sp. nov. is the easiest to identify and the least likely to be confused with other species owing to its isolation and distinctive patterning on the side of the neck.

DISCUSSION

Our study provides the first range-wide genetic assessment of *Delma tincta* (*sensu lato*). With data from thousands of SNP markers, and a comprehensive assessment of morphological variation, we find evidence for four evolutionarily distinct taxa within this species complex. This brings the number of *Delma* species to 25, making it significantly larger than the next most speciose pygopod genus *Aprasia*, with 15 described species.

A conundrum for field workers and collection managers for the deeply divergent, yet morphologically identical, sympatric species of *D. tincta* and *D. hades* sp. nov., is how to categorise an individual specimen if the essential genetic data are lacking — in this case, only SNP data usefully resolved species identification as mtDNA were insufficient to adjudicate between the two species owing to rampant introgression (unpublished data). There are two options in this case. One is to recognise all such individuals as the originally described name of *D. tincta*. This default option would be straightforward for collection managers with many older specimens that lack tissue samples. In contrast, confidently genotyped *D. hades* sp. nov., would be labelled as such. Another option is to identify the remaining non-genotyped specimens as '*D. tincta/hades*'. Doing so is more conservative in that it is not possible to know the true identity. This leaves open the possibility that future work (genetics, internal morphology) may eventually confidently identify such specimens. This problem is not unique to this group: it will be increasingly common as modern systematic investigations of species groups reveal more and more morphologically cryptic species that are indistinguishable from one another.

The sNMF population structure analysis identified eight populations with very little admixture between them, even in regions of potential contact or broad sympatry. The fixed difference analysis identified significant numbers of fixed allelic differences between all the lineages. Despite this strong evidence of reproductive isolation, we have decided against elevating each to a new species, pending the collection of more genetic data and examining additional material to improve sample sizes. Species tree analysis supports the monophyly of the three central populations (P1–2 and P7) to which we have assigned *D. tincta sensu stricto*, the monophyly of the QLD coastal populations (P3–4 and P6) for which we resurrect the name *D. reticulata*, and the sister relationship of the other central population (P8), which we name *D. hades* sp. nov., and the WA taxon (P5), which we name *D. branchia* sp. nov. The relationships between these major lineages are not strongly supported in this analysis.

Almost all the diversity within the *D. tincta* species

complex is in eastern Australia, with three of the four species (encompassing 7 of the 8 sNMF populations), found almost exclusively in the eastern Australian states (except for a small number of individuals that occur over the WA border in the far north and into Broome). In contrast, the exclusively WA species, *D. branchia* sp. nov., has a broad distribution throughout the Pilbara and the Gascoyne to the south, with little genetic structure across this range. Such contrasting genetic diversity between the eastern and western deserts is seen in several arid zone taxa (i.e. *Geyhra variegata* [Duckett and Stow 2013] and *Centipeda* [Nylinder et al. 2014]) and may relate to the influence of historical hydrological change (discussed in Pepper and Keogh 2021). Increased availability of water due to the large river systems of the eastern arid zone may have enhanced the ability of populations to persist in these deserts following more extreme aridification in the late Miocene. Higher effective population sizes over long periods of time are expected to leave a signature of high nucleotide diversity within populations and species, with relatively constant diversification rates and an overall even topology, a pattern which is typified in the eastern *D. tincta* species complex populations. In contrast, the drier and more arid landscapes in the western deserts may have led to higher rates of extinction, with relatively low effective population sizes and consequently lower levels of nucleotide diversity within populations and species, as seen in the western taxon *D. branchia* sp. nov. A dated phylogenetic analysis from Brennan et al. (2016) of *Delma* and other pygopods suggests the split between *D. borea* and *D. tincta* (*sensu lato*) occurred in the late Miocene (~7 mya) which is consistent with speciation events within the *D. tincta* species complex (and within *Delma* more generally) being late Miocene/Pliocene in age.

Despite a continent-wide distribution, relatively high species richness, deep molecular divergences, and adaptation to a variety of habitat types, the genus *Delma* remains remarkably conservative in morphology, microhabitat and diet (see Brennan et al. 2016). Along with broadly overlapping ranges of closely related species (Jennings et al. 2003) and numerous instances of ancient and recent mitochondrial introgression (Brennan et al. 2016), it is unsurprising that there has been confusion in taxonomy and interspecific relationships within *Delma*. The two closely related *D. tincta* and *D. hades* sp. nov. provide another example of the prevalence of this pattern of closely related sympatric species within *Delma*. Additional finer-scale sampling within central Australia would clarify the degree of sympatry, and fieldwork could determine whether these taxa exist in ecological syntopy. Furthermore, given the taxa in the *D. tincta* species complex are morphologically conservative yet show deep genetic divergence, chemical communication, particularly pheromones, may play an important role in reproductive isolation, as seen in other cryptic lizard species (Zozaya et al. 2019). Pheromone divergence has been shown to drive behavioural isolation in morphologically similar species and may be a key, yet currently unexplored, mechanism facilitating species boundaries in *Delma*.

Despite the overall morphological conservatism across the *D. tincta* species complex in traditional linear measurements and meristic characters, we found significant variation in head colour and pattern within each of the three eastern taxa across their respective distributions (ranging from bold and banded to plain). It has been suggested that the prominent head pattern in other *Delma* (including *D. tincta*) is a characteristic of juveniles and becomes obscure in older individuals (Maryan et al. 2007). However, we have identified many adult-sized individuals that retain the prominent head markings in *D. tincta, D. reticulata* and *D. hades* sp. nov. in some parts of their ranges. In his taxonomic revision of the Pygopodidae, Kluge (1974) referred to individuals of *D. tincta* observed in the lab that were buried in sand or loose gravel and only had their black and white-banded heads projecting above the substrate. Such behaviour was thought to be related to camouflage, as the projecting head was hard to distinguish from small rocks and pebbles. Little is known about the ecology and habitat use of these *D. tincta* species complex members, but the broad habitats occupied by the species vary considerably across each of their ranges. There is a particularly stark contrast between the *Eucalyptus* woodland-dominated landscapes of the coastal Queensland species, *D. reticulata*, and the arid tussock grasslands and mulga habitats of the inland taxa, *D. tincta* and *D. hades* sp. nov. Where these species come into contact between Barcaldine in central QLD and the Gulf of Carpentaria, the morphological disparity is at its greatest, with the heads of *D. reticulata* being highly banded, while those of the neighbouring *D. tincta* and *D. hades* sp. nov. are plain. This morphological distinction will be a useful character for distinguishing between taxa in this part of the continent.

We did not have SNP data from Broome, for which there are specimens with tissues, which are separated from Pilbara *D. branchia* by Dampierland along the Great Sandy Desert and those in the eastern Kimberley (*D. tincta*/*D. hades* sp. nov.). We examined the morphology and colour pattern for a number of individuals from this region, and they do not possess the diagnostic neck pattern of *D. branchia* sp. nov. The closest SNP genotyped individuals from the eastern Kimberley belong to both *D. tincta* and *D. hades,* which are sympatric here and across most of their distribution. Preliminary (unpublished) mtDNA data suggest these Broome individuals are divergent but most closely related to the WA *D. branchia* sp. nov.; however, a more thorough genetic assessment that includes nuclear SNPs is warranted. The same situation is true for *D. tincta* species complex individuals from the remote Top End in the NT, where no genetic material exists.

Compared to other widely distributed *Delma* that show little genetic variation across the continent (i.e. *D. borea*, *D. butleri* and *D. nasuta*; M. Pepper, unpublished data), the multiple and deep lineage divergences within the *D. tincta* species complex, particularly in the arid zone, highlight an evolutionary history characterised by long-term persistence. This geographic pattern of species richness is in line with what is known from geckos more broadly, and pygopods more specifically (Norris et al. 2021). Our discovery of three deeply diverged lineages within the resurrected *D. reticulata* is surprising, given that north Queensland is not recognised as a hotspot of diversity for this group. The distributions of these lineages closely mirror the well-known biogeographic barriers of the Laura Basin and the Burdekin Gap (Bryant and Krosch 2016) and underscore the historical significance of these lowland landscapes in driving and maintaining genetic divergence within and across taxa.

ACKNOWLEDGEMENTS

We acknowledge the Traditional Custodians of the lands across Australia where *Delma tincta* has been collected and studied. We pay our respects to Elders past and present, and recognise their enduring connection to Country and the ongoing significance of their culture and knowledge.

This work could not have been done without support in the form of a research grant from the Australian Biological Resources Study (ABRS) (Activity ID 4-EHPVS3D). An ARC DECRA also supported MP during this project (DE230100014). We thank the herpetology staff at the museums that loaned us material and kindly provided access to vouchers and/or tissue samples. In particular, we are grateful to Andrew Amey and Jessica Worthington-Wilmer from the QM, Sally South, Ralph Foster and Steve Donnellan from SAMA, Gavin Dally from NTM, Dane Trembath and Jodi Rowley from AMS, Joanna Sumner and Jane Melville from Museum Victoria, and Kailah Thorn and Brad Maryan from WAM. Stephen Zozaya and Kailah Thorn generously gave their time to take specimen photos. We thank Ian Brennan for his thoughts and *Delma* expertise the whole way through this project, Bernd Gruber for his help with the population genetics analyses and for proposing the use of fixed genetic differences as diagnostic molecular characters in accordance with ICZN requirements, and Brian Jennings for discussing ideas while carrying out morphological measurements at WAM. We thank Glenn Shea for extensive background information on the provenance of type specimens. Aaron Bauer and Paul Oliver kindly reviewed the manuscript and provided valuable comments that greatly improved the paper. We are grateful for a grant from Bioplatforms Australia as part of the Australian Amphibian and Reptile Genomics project that funded the sequencing costs, and to Sophie Mazzard for facilitating this.

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MANUSCRIPT RECEIVED 3 SEPTEMBER 2024; ACCEPTED 3 JULY 2025.

APPENDIX 1 Museum accession numbers and collection localities.

Species	Museum	Tissue No.	Specimen	Population	Latitude	Longitude	State	Locality	Morphology	Genetics
D. branchia sp. nov.	WAM		R179858	P5	-26.4139	114.1728	Western Australia	Hamelin Pool Rd, 4 km N Denham-Hamelin Rd Intersection, road verge	N	Y
D. branchia sp. nov.	SAMA	ABTC52154	R29365	P5	-26.43	114.18	Western Australia	Hamelin Homestead	Y	Y
D. branchia sp. nov.	SAMA	ABTC11679	R34024	P5	-25.05	115.2	Western Australia	Gascoyne Junction	N	Y
D. branchia sp. nov.	SAMA	ABTC104823	R100990	P5	-27.5166	115.75	Western Australia	19 km SE New Forest	N	Y
D. branchia sp. nov.	WAM		R102838	P5	-22.1502	113.9978	Western Australia	Cape Range National Park	Y	Y
D. branchia sp. nov.	WAM		R110080	P5	-20.808	117.073	Western Australia	8 km SW Roebourne	Y	Y
D. branchia sp. nov.	WAM		R110292	P5	-22.7073	119.709	Western Australia	12 km NE Mile Camp	Y	Y
D. branchia sp. nov.	WAM		R112690	P5	-21.6758	115.145	Western Australia	5.5 km SE Onslow	Y	Y
D. branchia sp. nov.	WAM		R113012	P5	-20.2472	118.8472	Western Australia	Lesley Salt Works	Y	Y
D. branchia sp. nov.	WAM		R113030	P5	-20.2472	118.8472	Western Australia	Lesley Salt Works	Y	Y
D. branchia sp. nov.	WAM		R114490	P5	-28.7333	115	Western Australia	Wicherina Dam	Y	Y
D. branchia sp. nov.	WAM		R115018	P5	-28.65	114.6333	Western Australia	Spalding Park, Geralton	Y	Y
D. branchia sp. nov.	WAM		R117342	P5	-22.9458	119.125	Western Australia	Hope Downs	Y	Y
D. branchia sp. nov.	WAM		R120020	P5	-22.4666	117.3	Western Australia	Brockman, 3.5 km NE Mount Brockman	Y	Y
D. branchia sp. nov.	WAM		R125032	P5	-22.7205	118.9906	Western Australia	Yandicoogina	Y	Y
D. branchia sp. nov.	WAM		R127768	P5	-22.7969	117.7889	Western Australia	5 km S Mount Tom Price Mine	Y	Y
D. branchia sp. nov.	WAM		R129623	P5	-22.9166	118.95	Western Australia	120 km NW Newman	Y	Y
D. branchia sp. nov.	WAM		R135422	P5	-22.3105	117.2522	Western Australia	Mount Brockman	Y	Y
D. branchia sp. nov.	WAM		R139308	P5	-21.2447	120.3222	Western Australia	Meentheena	Y	Y
D. branchia sp. nov.	WAM		R139314	P5	-21.2177	120.4556	Western Australia	Meentheena	Y	Y

Species	Museum	Tissue No.	Specimen	Population	Latitude	Longitude	State	Locality	Morphology	Genetics
D. branchia sp. nov.	WAM		R139328	P5	-21.2816	120.4661	Western Australia	Meentheena	Y	Y
D. branchia sp. nov.	WAM		R139637	P5	-22.6891	114.2936	Western Australia	Giralia Station	Y	Y
D. branchia sp. nov.	WAM		R151059	P5	-24.8833	113.7667	Western Australia	10 km E Carnarvon	Y	Y
D. branchia sp. nov. (holotype)	WAM		R153821	P5	-22.8091	113.9442	Western Australia	Bullara Station	Y	Y
D. branchia sp. nov.	WAM		R154268	P5	-22.0675	118.9953	Western Australia	Fortescue Marsh	Y	Y
D. branchia sp. nov.	WAM		R156173	P5	-24.733	117.4186	Western Australia	Waldburg Station	Y	Y
D. branchia sp. nov.	WAM		R156227	P5	-20.6033	120.2642	Western Australia	Cattle Gorge	Y	Y
D. branchia sp. nov.	WAM		R156258	P5	-21.7116	115.1969	Western Australia	Onslow Area	Y	Y
D. branchia sp. nov.	WAM		R157065	P5	-21.9538	118.9958	Western Australia	Fortescue Marsh	Y	Y
D. branchia sp. nov.	WAM		R157124	P5	-23.1991	118.8469	Western Australia	West Angelas	Y	Y
D. branchia sp. nov.	WAM		R158123	P5	-22.3469	119.01	Western Australia	1.5 km NE Cowra Line Camp	Y	Y
D. branchia sp. nov.	WAM		R158202	P5	-22.7419	120.4731	Western Australia	55.2 km W Roy Hill	Y	Y
D. branchia sp. nov.	WAM		R160201	P5	-21.6785	120.088	Western Australia	56.3 km N Nullagine	Y	Y
D. branchia sp. nov.	WAM		R161660	P5	-20.3256	119.211	Western Australia	32.5 km W Goldsworthy	Y	Y
D. branchia sp. nov.	WAM		R162036	P5	-22.2554	115.437	Western Australia	21.5 km NE Mount Mary	Y	Y
D. branchia sp. nov.	WAM		R162054	P5	-23.2136	119.202	Western Australia	5.5 km NE Giles Point	Y	Y
D. branchia sp. nov.	WAM		R163935	P5	-20.3908	119.909	Western Australia	41 km ESE Goldsworthy	Y	Y
D. branchia sp. nov.	WAM		R166546	P5	-27.5797	115.8992	Western Australia	Meka Station	Y	Y
D. branchia sp. nov.	WAM		R166641	P5	-20.8572	117.8342	Western Australia	Mons Cupri Mine	Y	Y
D. branchia sp. nov.	WAM		R167564	P5	-24.2952	114.0442	Western Australia	76 km NE Carnarvon	N	Y
D. branchia sp. nov.	WAM		R167566	P5	-24.2952	114.0444	Western Australia	76 km NE Carnarvon	N	Y
D. branchia sp. nov.	WAM		R170131	P5	-21.0717	118.68	Western Australia	11 km N Wodgina	Y	Y
D. branchia sp. nov.	WAM		R170660	P5	-21.8397	116.683	Western Australia	11.5 km W Mount Elvire	Y	Y
D. branchia sp. nov.	WAM		R174663	P5	-21.47673	117.14898	Western Australia	Millstream National Park	Y	Y

Species	Museum	Tissue No.	Specimen	Population	Latitude	Longitude	State	Locality	Morphology	Genetics
D. branchia sp. nov.	WAM		R99180	P5	-21.6097	118.9622	Western Australia	Woodstock Station	Y	Y
D. tincta	WAM		R137953	P1	-15.5888	128.9833	Western Australia	35 km NNE Kununurra	N	Y
D. tincta	SAMA		R37588	P1	-22.860833	134.418167	Northern Territory	Alcoota Station	N	Y
D. tincta	SAMA	ABTC441	R35960	P1	-26.3	136.02	South Australia	Alka Seltzer Bore	Y	Y
D. tincta	SAMA	ABTC6581	ABTC6581	P1	-15.7905	128.7661	Western Australia	Kununurra	N	Y
D. tincta	SAMA	ABTC67965	R24842	P1	-15.320667	130.457333	Northern Territory	Bradshaw Station	N	Y
D. tincta	SAMA	ABTC67988	R24858	P1	-15.320667	130.457333	Northern Territory	Bradshaw Station	N	Y
D. tincta	SAMA	ABTC12058	R38847	P1	-23.77	133.88	Northern Territory	Camel Farm, Ross River Hwy, Alice Springs	Y	Y
D. tincta	SAMA	ABTC36156	R46806	P1	-26.3575	135.7075	South Australia	0.2 km W Anvil Hole Native Well, Witjira	Y	Y
D. tincta	SAMA	ABTC58700	R49874	P1	-26.2869	134.7244	South Australia	Eringa Waterhole	Y	Y
D. tincta	SAMA	ABTC88012	R60513	P1	-26.7511	134.7622	South Australia	31.5 km W Hamilton Homestead	Y	Y
D. tincta	SAMA	ABTC88082	R60546	P1	-26.3181	135.2008	South Australia	Witjira National Park	Y	Y
D. tincta	SAMA	ABTC23937	R30971	P2	-27.18	140.15	South Australia	Coongie	Y	Y
D. tincta	SAMA	ABTC51994	R31173	P2	-27.2	140.13	South Australia	Cooper Creek area	Y	Y
D. tincta	SAMA	ABTC37312	R49065	P2	-27.6325	140.8294	South Australia	7.2 km SW Table Hill, Innamincka Area	Y	Y
D. tincta	SAMA	ABTC132053	R61856	P2	-31.4014	140.0886	South Australia	3.5 km NE Billeroo West Homestead	Y	Y
D. tincta	SAMA	ABTC132086	R61947	P2	-30.1825	139.6033	South Australia	29.6 km ENE Arkaroola Village	Y	Y
D. tincta	SAMA	ABTC6492	R90213	P7	-22.375	142.412	Queensland	63km W Winton	N	Y
D. tincta	SAMA	ABTC6493	R90214	P7	-22.764	143.391	Queensland	55km SE Winton	N	Y
D. tincta	SAMA	ABTC70822	R25851	P7	-18	140.55	Queensland	Road junction, Inverleigh Station	N	Y

Species	Museum	Tissue No.	Specimen	Population	Latitude	Longitude	State	Locality	Morphology	Genetics
D. tincta	SAMA	A009149	J91823	P7	-20.7681	141.7417	Queensland	12 km S Julia Creek	Y	Y
D. tincta	SAMA	A001706	J83423	P7	-23.4318	144.2511	Queensland	Gin Creek, Longreach	Y	Y
D. tincta	SAMA	ABTC34964	R45034	P7	-26.3181	140.3361	South Australia	6.2 km SSE Elbow Well	Y	Y
D. tincta	SAMA	ABTC72712	R54019	P7	-18.5922	136.0894	Northern Territory	Brunette Downs Racecourse	Y	Y
D. tincta	SAMA	ABTC82403	R55294	P7	-21.8769	139.9456	Queensland	Phosphate Hill, Grassland Site	Y	Y
D. tincta (lectotype)	QM		J241	-			Queensland	Normanton, Gulf of Carpentaria	Y	N
D. reticulata	QM	A013415	J94238	P3	-15.4242	143.4947	Queensland	Killarney Station Homestead	Y	Y
D. reticulata	QM		J93148	P3	-12.293889	142.444167	Queensland	Steve Irwin Wildlife Reserve	N	Y
D. reticulata	QM	A013311	J94132	P3	-15.3000	143.4000	Queensland	Olkola area	N	Y
D. reticulata	AMS		R180606	P4	-17.53	145.42	Queensland	1 km S Kaban	Y	Y
D. reticulata	QM	A005376	J87604	P4	-15.5652	145.2511	Queensland	Killarney, 15 km S Cooktown	N	Y
D. reticulata	QM	A012124	J93849	P4	-15.5014	144.8497	Queensland	Kings Plains Station	Y	Y
D. reticulata	QM	A005047	J87293	P4	-15.4297	145.1189	Queensland	Jensen's Crossing Via Cooktown	Y	Y
D. reticulata	QM	A002121	J70675	P6	-24.9450	147.9606	Queensland	Carnarvon National Park, Mount Moffatt Section, near Marlong Creek	Y	Y
D. reticulata	QM	A002120	J70674	P6	-24.9450	147.9606	Queensland	Carnarvon National Park, Mount Moffatt Section, near Marlong Creek	Y	Y
D. reticulata	AMS		R186395	P6	-20.082243	148.489181	Queensland	Hydeaway Bay	N	Y
D. reticulata	QM	A000261	J80136	P6	-26.4658	148.5433	Queensland	Donnybrook Rd, 15.6 km NW Warrego Hwy	Y	Y
D. reticulata	QM	A007889	J90689	P6	-18.2900	143.5489	Queensland	Georgetown	Y	Y
D. reticulata	QM	A006522	J88438	P6	-22.8243	147.6411	Queensland	Clermont, Herschel Street	Y	Y
D. reticulata	QM	A014574	J95572	P6	-24.8431	151.3969	Queensland	Goondicum, Near Monto	Y	Y

Species	Museum	Tissue No.	Specimen	Population	Latitude	Longitude	State	Locality	Morphology	Genetics
D. reticulata	QM	A003140	J84130	P6	-24.8464	147.7408	Queensland	Carnarvon	Y	Y
D. reticulata	QM	A014749	J95799	P6	-19.1206	145.3350	Queensland	Christmas Creek Station	Y	Y
D. reticulata	WAM	ABTC149823	R71375	P6	-20.61817	148.6658	Queensland	Laguna Quays Driveway	Y	Y
D. reticulata	QM		J56465	-	-16.5333	145.1333	Queensland	Mount Carbine, town area	Y	N
D. reticulata	QM		J57250	-	-16.8167	145.6833	Queensland	Cairns	Y	N
D. reticulata	QM		J75298	-	-20.1667	149.0833	Queensland	Whitsundays	Y	N
D. reticulata	QM		J77978	-	-21.1925	147.9433	Queensland	Newlands Coal Mine	Y	N
D. reticulata	QM		J78002	-	-21.1914	147.9025	Queensland	Newlands Coal Mine	Y	N
D. reticulata	QM		J81285	-	-19.0833	146.4167	Queensland	Toomulla Beach Rd, Clemant State Forest, 3 km WNW Bruce Hwy	Y	N
D. reticulata	QM		J88170	-	-15.5652	145.2511	Queensland	Kallarney Station, 15 km S Cooktown	Y	N
D. hades sp. nov.	WAM		R191011	P8	-15.832345	128.46196	Western Australia	34.6 km W Kununurra, Victoria Highway	Y	Y
D. hades sp. nov.	SAMA	ABTC30108	R22911	P8	-15.3461	129.1514	Northern Territory	Spirit Hills, Keep River	N	Y
D. hades sp. nov.	SAMA	ABTC70681	R25712	P8	-19.652	134.184	Northern Territory	Tennant Creek	N	Y
D. hades sp. nov. (holotype)	SAMA	ABTC113677	J90655	P8	-22.3964	139.9572	Queensland	8.5 km SW Two Rivers Homestead	Y	Y
D. hades sp. nov.	SAMA	ABTC35520	R40238	P8	-27.27	135.5	South Australia	14 km WSW Macumba Homestead	Y	Y
D. hades sp. nov.	SAMA	ABTC42381	R51553	P8	-26.27	131.4767	South Australia	36 km ESE Amata	Y	Y
D. hades sp. nov.	SAMA	ABTC72709	R54015	P8	-19.7114	135.8278	Northern Territory	Barkly Roadhouse	Y	Y
D. hades sp. nov.	SAMA	ABTC72877	R54465	P8	-19.2264	140.3481	Queensland	Burke and Wills Roadhouse Dump	Y	Y
D. hades sp. nov.	SAMA	ABTC73397	R54735	P8	-29.02	134.75	South Australia	Coober Pedy	Y	Y
D. hades sp. nov.	WAM		R177993	P8	-15.832	128.462	Western Australia	Victoria Highway	Y	Y

APPENDIX 2 The sequences of diagnostic fixed differences between the four taxa in the *D. tincta* species complex with the SNP in [bold] and corresponding coordinates provided for the reference genome (*Gekko japonicus* v1.1) where alignments were possible.

Sequence	Length	SNP alleles	Diag. allele	SNP pos	RefChrom	Chrom pos
***D. hades* sp. nov. vs rest**						
TGCAGTTAGAGTGACCAACTGTCCCAGTTTGCCC**[A]**GGAGAGTCCCAGATTGAAGGGTGGTTGTCCTGCA	69	G>A	A	35		
TGCAGAAATA**[A]**GGCAGGTGAAGTTTTCCTGGTTAAGAAACCTGCACCTGACACACAACAGCTCTTAAAC	69	A>G	A	11		
TGCAGGCAACACCATTTGGCAGCCA**[T]**TAATATATTCCTTCTGACTTCTTTTTCTGCATG	59	C>T	T	26	NW_015170280.1_scaffold203	1324869
TGCAGCTATTTTGCAAG**[C]**ACAGGGAAATGCATG	33	T>C	C	18		
TGCAGGCACGGGAAAC**[T]**TTGGTTTAGGCCCAAGGCATG	38	T>C	T	17		
TGCAGTGTCTGCACAGCGTGCTAATCAAAATATGCACCAATTCCCAAATACAACATTTTTAAA**[C]**CCATT	69	C>T	C	64		
TGCAGGGAGTTGGACTAGATGATCCTTGTGGTCCCTTCCAGCTCTAATATTCTATGATTC**[G]**TTGATGCT	69	G>T	G	61	NW_015170918.1_scaffold929	169621
TGCAGTGTGTAATCAGCAAAGGAAGAAGGAAAAGTCTTTAGGTAGCTCCCTG**[G]**ACAACAAAATGGAAAG	69	G>T	G	53		
TGCAGT**[T]**CCTGACCATTTGTTCTGCATG	28	C>T	T	7		
TGCAGCATA**[A]**CCCTGTGCATGAGCGGTTCAGCAGGAATGCCGAGACCGATCTCGTATGCCGTCTTCTGC	69	G>A	A	10		
TGCAGATAGGCAGGTGTTCTGTGTAGGTATGGCTATATAAAGCTTTCA**[A]**AGCAGCAGTTCTAAAAAGAG	69	G>A	A	49		
***D. branchia* sp. nov. vs rest**						
TGCAGGGCTGCAAGACAGTGAGACTAGCAAGATTTGCCCTTGTCTGG**[C]**TGTAATCTTTTATCAGCATGA	69	T>C	C	48	NW_015176056.1_scaffold2651	33328
TGCAGATTTGCCCT**[T]**ACTTAGTTTAAGGCATG	32	G>T	T	15		
TGCAGGTATGAAGGATTTGTATGTAATAG**[G]**ACCTTGAACTGTGGCCAATAAATGATGAGCAACCAATGG	69	G>T	G	30		
TGCAGGT**[T]**ACTATCCTACCACCCTATTGCATG	32	T>G	T	8		
TGCAGC**[T]**TTGCTTTGAGAGTCAAAATGGATAGTAGCCCCTGATCTCTTCTAGAAGATTGTTCCAGAGGC	69	T>C	T	7		
TGCAGTAGGGGTGTGTGCA**[T]**TCAGAATGTGGATTTCTGCATG	42	T>C	T	20		
TGCAGATTTGCCACCAGCATATTGGAGAGGCTGGTTGTTACAGAACTGA**[C]**ATATGAAACTGGTTGGCAG	69	A>C	C	50		

Sequence	Length	SNP alleles	Diag. allele	SNP pos	RefChrom	Chrom pos
TGCAGAA**[C]**AGTTACACACATATTCAGGAGAATCAGTGGAGTGGTTCCTTCATTCTTAATCTCTTTTATC	69	T>C	C	8		
TGCAGATTTCCTGTCA**[C]**TGCATATTGTTTGAACCCTAAGCTTGATGGTGAAACATGGACTTGCATGAGC	69	T>C	C	17		
TGCAGTGCTTCAAGCAGTGTACGAGAGTCATAATGTGAGGGTTGTCCCTTTGTAGTTG**[A]**TAATGACTCT	69	T>A	A	59		
TGCAGGTTTGAGCTAGAAAGCAGAACATGAGGCAAGGAAACAGAGAATATCAACTTTTAAAGA**[T]**ATTTA	69	G>T	T	64		
TGCAGGATCACAGCACTATC**[A]**CAATTGCTGTTGGTGCCACTATGGCCCACGAAATGGGCCATAACTTTG	69	G>A	A	21		
TGCAGAGCCTGCAAAGTTAAACTATTCTGTTGAGCTTT**[T]**AGTACTTGAACTGGGACAGCTTGGCCAAAC	69	C>T	T	39		
TGCAGTCTACCCTTCCCTTTCAGTTA**[T]**CCCCTGGCACACCATTTGCATG	49	T>C	T	27		
TGCAG**[A]**AAAACCATCTAATAGATCTGTTACATAATTCATGATGGGGCTTGTAGTTTTAAAACTCTACCA	69	G>A	A	6		
TGCAGTGAGATGAGAGCACCCTGCCATCACTGGCATAAAAGGA**[A]**TTGCTACTGCAAATGCATG	63	G>A	A	44	NW_015159712.1_scaffold84	1219696
TGCAGGCCCCACAGCAAGGTCAAGGGG**[A]**TGCCGCCCGCCAATGGGGGGCCCTTGCATG	58	A>C	A	28		
TGCAGGTCAAATTTGTTGGCTAGTTTGT**[G]**TTGTCCTCTGAAGTGCTAAAAGAAGCGTAGCATG	63	A>G	G	29		
TGCAGACCA**[A]**GTGTTCCCATTCTCTGTCTGCATTGGCATG	40	T>A	A	10		
TGCAGTCTGTGCCTATTCTGG**[C]**GCATG	27	A>C	C	22		
TGCAGAGCTGTGGTAGGCATGAGGCTGGGAG**[T]**GGGCATG	39	T>G	T	32		
TGCAGACCTTAAATAACTTGTGTTCAGAGTATCCAAAAGACTTT**[A]**TCTGCATATATAAATATCCTCAGG	69	C>A	A	45		
TGCAGGATGGATGTTTTCTTGGAAATGGGAGGAGGTGGATTTAGATTGCTTCCATGATCAAAC**[A]**TAATG	69	A>G	A	64		
TGCAGTTAGTTTTTATTCAT**[G]**TGAGTAGTTCTATTGAACCTAGAGAGCCTCTTACATTGCAAAAGCATC	69	A>G	G	21		
TGCAG**[A]**GGATGGGATCCAGCATCCTGCCTGTAGCATG	37	A>G	A	6		
TGCAGTCCA**[G]**TTAATGAACTTTGTTTAAGGTTTACTATTTGTGTTCTCTGAGCCTTTTTGCATG	64	G>A	G	10		
TGCAGAAACATTTCTTGTGAATTTGACAGGCA**[A]**TCATGTTGCATG	45	A>G	A	33		
TGCAGC**[C]**GTAACTTAAATGTTCAACAGAAACCCCACAGAGGTTGGCTTGGTGGATTTCCTAAAGCACTT	69	C>A	C	7		
TGCAGGTGGAG**[A]**TTGCAGTGGCATG	25	A>C	A	12		
TGCAGGCCCTCCTCAGCCACAGGGTCTGGAAA**[A]**AAATCCAGCAGACAACCTTCAAGCCATGGCTCTGAG	69	C>A	A	33		
TGCAGACCCAAGAAAGATTTGATTTGCCAGGGTAAGTCTTGACCTTAGATTT**[A]**GCATG	58	A>G	A	53		

Sequence	Length	SNP alleles	Diag. allele	SNP pos	RefChrom	Chrom pos
TGCAGAAAAGTGGCATATGATCCTGCCATGGAAATAATAAATTAA**[T]**CCTTAATGGCTAAACCAAGCCTC	69	T>C	T	46		
TGCAGGAATCTTGGCTTTCAAAGTTTCAGAATTTGATGTA**[T]**CTTATTTGTAAAGCATG	58	C>T	T	41		
TGCAGGGCAAAAAAACAGACCATTTTGGCATGA**[A]**ATCAGCATG	43	A>G	A	34		
TGCAGAGGTATCTTTCCAAAGTATGCATGAAAACCTAAGTGATAAGGGAATCTCCTGTGCAT**[A]**GGGACA	69	G>A	A	63		
TGCAGTCAGCTAACACGTCACAGAAATGACTGAAACCCTTGGTGTAATCCATCATA**[G]**GACAAAAACCTT	69	G>C	G	57		
TGCAGTCTAAACTTTGAGAACTAT**[G]**AAATAGTCTTGCAGGTATGCAATGCTGCATG	56	G>A	G	25		
TGCAGT**[A]**TTGTTGCTTGGCATGTTGCATATGTGTGCATG	39	A>G	A	7		
TGCAGAATTCAATAAAA**[C]**TCTTACCTTTGGTGCATG	36	C>T	C	18		
TGCAGTGTCAGGGTTCTTTCTC**[T]**TCCTCCTTTTGTCCTCAACACCATCTCTGCATG	56	T>A	T	23		
TGCAGATGAATAGGTGCCTT**[T]**CAGATTCAGCAGTTCCCACCAGCCACTCTTGCCTAACCAGGAGTGAGT	69	G>T	T	21		
TGCAGGC**[T]**CCTCTAACCAATAAAGGCATG	29	T>C	T	8		
TGCAGTCAATAGGCATAAGGGGGACTCTCTGTGGTGAGTTAATGCCTGAAAAGTGCATGACATCAGAA**[T]**	69	C>T	T	69		
TGCAGAATGACTTGCTCTAGAAACAGGTTTTAAAGTCCAC**[A]**AAATCAACACACAGATACATATATTTTC	69	A>T	A	41		
TGCAGGCTGCATCACAC**[A]**GGTCGGTCGTTTATAGCTCAGCACCCAATCAGCTGAGCATG	59	G>A	A	18		
TGCAGCTCTCCACCCACAT**[T]**GCTTGGATTGGCTCGCATG	39	T>G	T	20		
TGCAGTTTATGGGATTACATCCTTTTCAAAGTGCCTGT**[T]**AGTTAATAACTACCTGTGAGTGGGGAAAGT	69	T>G	T	39		
TGCAGGTGGAACAG**[A]**TGCTTGATGCGCCCTGGGGGCACTTGCATG	45	A>G	A	15		
TGCAGTAACTCTGCATACAACACTACTGTTAAA**[A]**TGACCTGGAGCATCATCTGCATGATTTCTGTGCAT	69	A>C	A	34		
***D. reticulata* vs rest**						
TGCAGTGGGGATTCAGAACAGTCTTTCTGAGCCAGTGGGTGGGGTGGGGTGGGCA**[C]**ATTCTAGTGTGGT	69	C>T	C	56		
TGCAGTCA**[T]**CTGCCTTTTCAGTTTGTGTTCTGTTTAGACAGTGTAGGTTTAACATAGATCTCTATTGGC	69	T>G	T	9		
TGCAGCAATGGCTGTGAGGCATCCTTGCGGCTCAGGGGAAATAT**[T]**ATGTGACACTGGCATG	61	T>G	T	45		
TGCAGC**[A]**AGAAATGCTTCCAGCATG	25	G>A	A	7		

Sequence	Length	SNP alleles	Diag. allele	SNP pos	RefChrom	Chrom pos
TGCAGAAAAAATG**[C]**TCAGAAAATTGTCTCTCAGGAATTAAATTGGGATCGGTCAAATGCTAAGAATTAG	69	A>C	C	14		
TGCAGCTGGCA**[T]**GACAGCACTGCTTGACTGAAAGTAACCTGTGTGTATGCAAAAATATGTTTTGAAATA	69	C>T	T	12		
TGCAGTTTAGCTATTACTGAGAGCTACATG**[G]**GGCATG	37	T>G	G	31		
TGCAGTCTTAAAA**[T]**GGCTACATTTCACAATCGTCAGAGCAGCAGGTAGCAAAGTCGCCCACACATGATG	69	T>A	T	14		
TGCAGCCTAC**[G]**ATATTGGAATATGGCATG	29	A>G	G	11		
TGCAGGTTCTCAGGAGGAGCCAATGGAACTGAGGATGAAAATAT**[G]**ATTTTGTTTTATTCTAAAAGCCTT	69	G>T	G	45		
TGCAGCCTGGGGCATGGGATGGGTGGGGCC**[A]**CAGCATG	38	A>C	A	31		
TGCAGGTTAAGAGGATTTTCCAGGAAAAACTCAGATGAAGTACCACATGG**[T]**GCATG	56	T>C	T	51		
TGCAGTGGATTCAAGGAAGACACAAGGG**[C]**AATGTGTAGTAGAAATTTACAAGGTATATATGTATGGCAT	69	C>T	C	29		
TGCAGG**[A]**GACAGGGAGAAGTGCTGTGTGCCTTTGGCATG	39	A>G	A	7		
TGCAGGT**[G]**CCCATACCGCGATGAAAGCACTGATGGAAGAAAGACTTCCTCATTCTGACACGCATG	65	G>A	G	8		
TGCAGGGACAGCTCAGCTT**[T]**AGACACTTCAAAGAACTTAGAAGGGATACACAAAACACTCAATCTCTTT	69	T>C	T	20		
TGCAGTAATGCACTCTGTGTAGGTCTCC**[T]**CTTGAAATCTGTTCTGACTCCAGTTGGTACTGTCTGGTGG	69	T>C	T	29		
TGCAGAAGCTTAT**[T]**TCACTTGGTCATCTGAGACAATCCACTTGGGAAGTCTAATGGGGAGTAAATAGAA	69	T>C	T	14		
TGCAG**[T]**GCTTGTTTCAGAAAACTCATGTGAAGGAGTGTTTCATGCATGTAGGTTTCCAGGTTTCTACAT	69	T>A	T	6		
TGCAGATAATGCGAGTTCTGAATCTGCT**[A]**GCTGTGTCTCTGGCTTTCTTTTAGGTTTTCTGCCCCCACG	69	G>A	A	29		
TGCAGCCAACACTTGATCATGGGACACACTTAAAAAC**[T]**CCTTTTCCATCAGAATATAAACAGCATGAGC	69	T>C	T	38		
TGCAGAGCCCACCCCTCCCCTTGC**[T]**TCCTGCATG	34	C>T	T	25		
TGCAGCTAGACAATAACTTTGAGGTTTGTGCTTACCTCTCTTGCCCC**[G]**TCTTTATTGCAGGTTCTTCCC	69	G>A	G	48		
TGCAGTGTATGAGAACTGAGACTGTGGTGGAATTGGGTGTGGTTCTTCCCCCTCTGAA**[C]**ATTTGCAGTG	69	T>C	C	59		
TGCAGTAAGTGACAATCCTGATC**[A]**GAGCTCTTGAATAAAAGGTCAGTGCAGCCAAGGATGAGGCTGCAT	69	A>G	A	24		
TGCAGACAGACACAAGCTAATTTATTAC**[A]**GTTTTGCATTGCAATGTTTTATCTAAGAGACTGAGCACAG	69	T>A	A	29		
TGCAGCATGGATAAGGGCTCATTGAAGTTAACCTGGGGGCAAAAGCAGCAAGTTACAGCCAGAAGA**[T]**CT	69	C>T	T	67	NW_015171552.1_scaffold1660	412461
TGCAGTTAAAGCTGG**[C]**ACACAAGAATGTCCACAAAAAAGCATG	43	G>C	C	16		

Sequence	Length	SNP alleles	Diag. allele	SNP pos	RefChrom	Chrom pos
TGCAGCTCACCTCCTTCACTTGGGTGTGAAGGATACTCTTGGTCTGGGTT**[A]**CAAGGAGAAGCCCACATG	69	A>C	A	51		
TGCAGA**[G]**ACATGGTCATACAGTTTGGATCATTTCAATGCATG	42	A>G	G	7		
TGCAGCCTTTCTTGGGCAGAAAAGATC**[T]**GGTCAATGTGGTGCATG	45	T>A	T	28	NW_015165318.1_scaffold2512	191827
TGCAGGTT**[C]**AGCACATTCCCACCTGCATG	29	T>C	C	9		
TGCAGAAACTTGAAACCAAGCGTCATCTGAACAAAGC**[T]**TAAGAATTAAATTTGACAATGCAGAGCATGA	69	T>A	T	38		
TGCAGGTTTAAGGCCATCCTGACTTC**[T]**CCTCCCAGAGGGAAGCACTGATTATCCCAGGAAACAGATATC	69	T>C	T	27		
TGCAGCATTTTGGACTAATTGAAGATTATGAACACTTTTCAAGAGCAGCCTTTCATAGTGTTTTG**[A]**AGT	69	A>G	A	66		
TGCAGAGCAGAAAA**[T]**AGTAAACCAATTCTTGCATTTTTCTAGGACCAGTCATGAGAGCAGTGTGCGGGA	69	T>C	T	15	NW_015163115.1_scaffold956	268489
TGCAGTCCCAAAGACAACACATATT**[T]**AGCATG	32	C>T	T	26		
TGCAGATGCCATGGTCTGAACCTA**[C]**GACCTTCTGCATG	38	C>G	C	25		
TGCAGAGGACAGATACTGAGGAGAAA**[A]**GCCTGGTCTCTCCTGAGCATG	48	A>G	A	27		
***D. tincta* vs rest**						
TGCAGAGGCAGGGGAAGAAGATGGATGAGATGGTCAAAAGT**[G]**GATCAGGAAATGCATG	58	G>A	G	42		
TGCAGCTCTCCTGGCA**[C]**AGGTCTTTCCCATCCCTGCCACCATAGATTCTTTCTTCAATTGGCAAGGCAA	69	C>G	C	17		
TGCAGATTGGTTTTTAACTCTGGGAGATCTCCAGGTACCACCTGGAACTTGGCAAGCCTAG**[C]**TCATGGG	69	C>T	C	62		
TGCAGTTAACACCACCTTCTTGCCTGCCTTAATTCTCAGCTG**[A]**TATTTATTGGTGGTGGTGGAATCTGC	69	A>T	A	43		
TGCAGGACATAA**[A]**GCTTTGGTGTTATGCATG	31	T>A	A	13		
TGCAGAGGGGGTACCTACT**[A]**CCTAATGCATG	31	A>G	A	20		
TGCAGACCACATAAAAGAGTTTTTGGAAATCGGTTAG**[T]**TATTTAACACCTGTCATAAGTTTCACAGAAA	69	C>T	T	38		
TGCAGTGCTTTGCACAACACGTGCATTGACAGGAATGTAAGTTGAGCAAAATGGTTCTGTG**[G]**TCCAGCA	69	A>G	G	62		
TGCAGCTTTGA**[C]**GTACAGGCATGAGCGGTTCAGCAGGAATGCCGAGACCGATCTCGTATGCCGTCTTCT	69	T>C	C	12		
TGCAGGCTCTGCACTCCTGACCCTTCATTGCTACTGCTTTACTGGA**[T]**CTTAAACCATGTAATGCACTGT	69	T>G	T	47		
TGCAGCACTATTTTCCTGACCTGGGAAAGGGTGCCATTTGACCCACAGTAACTCAGCAGT**[T]**TTTATGCA	69	T>G	T	61		

APPENDIX 3 The sequences of diagnostic fixed differences between the sympatric *D. tincta* and *D. hades* sp. nov., with corresponding coordinates provided for the reference genome (*Gekko japonicus* v1.1) where alignments were possible.

Sequence	Length	SNP alleles	Diag. allele	SNP pos	Ref Chrom	Chrom pos
D. hades* sp. nov. vs *D. tincta						
TGCAGAGGCAGGGGAAGAAGATGGATGAGATGGTCAAAAGT**[A]**GATCAGGAAATGCATG	58	G>A	A	42		
TGCAGATTTTTCACATGATTATGT**[C]**TACTTTCTTGTGTGTATGTGGCATG	50	C>T	C	25		
TGCAGCAGGTGCTGCTGACTAGTGCACCTTTCCTTGAAGCCTCAC**[C]**TGGCTACAGAAGACAGAGGCGAT	69	T>C	C	46		
TGCAGCCCAGAA**[A]**TGTATCCCCCATCCAGTATGCATG	37	G>A	A	13	NW_015170301.1_scaffold882	395551
TGCAGCCTCAAGACACTGT**[T]**TGCTTGTGCATG	32	C>T	T	20		
TGCAGATTCATGCTGCACAGAAAGTGTGATAAAAAG**[C]**AAAATTGGAAAGATGGAAAGATTCAGGCATAC	69	T>C	C	37		
TGCAGTTAGAGTGACCAACTGTCCCAGTTTGCCC**[A]**GGAGAGTCCCAGATTGAAGGGTGGTTGTCCTGCA	69	G>A	A	35		
TGCAGCCCTACTGCTACTA**[A]**GAAATAGGTAGAGCATG	37	A>G	A	20		
TGCAGCAGCTCTAATTTTTCC**[G]**CAAGGGTATGGCCCCAGTATGATCAGAACACCAGCATG	60	G>A	G	22		
TGCAGTTTCTGGGGGCTTTTTGCATACATGGGGAACAAGAGTTGACCTCACTAATGAGGAATGCGCTT**[C]**	69	C>T	C	69	NW_015165830.1_scaffold15	131044
TGCAGATAACACAAAATTGGAGGGCCTGGCTAACACCCAGGTTGACAGAAGGAAA**[A]**TGCCTCAACAGGT	69	G>A	A	56		
TGCAGGAGTCCCACCC**[G]**CAAAATGCCTCTCAGATCCATGTGAAACGGGAAGAGCTTGTTGCAAACTGGG	69	G>T	G	17		
TGCAG**[T]**GGCATTTGGAGCATGAGCGGTTCAGCAGGAATGCCGAGACCGATCTCGTATGCCGTCTTCTGC	69	C>T	T	6		
TGCAGACTGTCATCTC**[T]**GACAGCATG	26	A>T	T	17		
TGCAGTGCAC**[A]**TGTTTCCTTATTCCCTCTGGACAGAAAATAGGAGCATAGAATCTCTGCTGGCCATGTG	69	A>G	A	11		
TGCAGATTCTGCTACTAAGACTAATGCACGTAGGAG**[G]**AGCATGGAAATAAAGCTAGAAATAAAAGCAGC	69	G>C	G	37		
TGCAGTGATGGATCACAGATGTACTGATTTGTTCTGGACATGCCCCTACTGCAACC**[A]**AGCATG	63	A>G	A	57		
TGCAGCTGTCAGAAACTTTATTTATCAGTT**[A]**CTAGCAAAACCACCATCATTATCCAGGGAGAGATGGCC	69	A>T	A	31	NW_015166440.1_scaffold634	539315
TGCAGCATTCCAATTTAGGCAGTCATCTG**[C]**CTGGCAAGTCCACCCTGCTCACAGGCATG	59	C>T	C	30		
TGCAGAAAGGAAAGG**[A]**AAAAATCCTGTAGAAAGGGAGAGAGGGAGATAGGTAAGTAAGTAATGTGGTTC	69	T>A	A	16		
TGCAGAACAC**[G]**GCCGGAAGACATGGGGACAACCTACGCAACATCAGGCAGGAGATTCAAGAGCTGACCA	69	G>A	G	11		
TGCAGGGTAGAGCATAGAGAGGGAGGTGATCCCTCAG**[A]**TATGAAGGACCAAGTCTATGAAAGGCTTTGT	69	G>A	A	38		
TGCAGGAAGTGGTGCATC**[T]**AAACTATTGGTGGTGGTCAGGGGTAAGGGGATTGGAACAAACACTAATTG	69	C>T	T	19		

Sequence	Length	SNP alleles	Diag. allele	SNP pos	Ref Chrom	Chrom pos
TGCAGCTCTCCTGGCA**[G]**AGGTCTTTCCCATCCCTGCCACCATAGATTCTTTCTTCAATTGGCAAGGCAA	69	C>G	G	17		
TGCAGTCTT**[A]**TATAGGGAGTTTCCCTACAGGGGCTACTGGGTTCCAAGCTAGGTTCTTCTTCTTAAGAT	69	G>A	A	10		
TGCAGGTGC**[T]**AGGGATTGAACCTGGGACCTCTGGCATG	38	T>C	T	10		
TGCAGTTCAGGCAC**[G]**GCCATCAAAACAAATATATTCTTTGGCATTCTTGAAAACTGTGGGAAAGCAGGG	69	A>G	G	15	NW_015172036.1_scaffold1095	224085
TGCAGGCTGAGCAGGAAACTGTTGGTCAT**[A]**TTTTCAGTGAAAGGGTAGACATTCCTGATGGTGTCAATT	69	G>A	A	30		
TGCAGGCACTTCTTCCTAGGCTAATATTCT**[T]**CTCTGAATAAGAATATAACTAAATTTAAAGGTGCATAA	69	C>T	T	31		
TGCAGCCATTTTACCTC**[C]**TCAAAAGGCATAGTTTTGTGCATG	42	A>C	C	18		
TGCAGACTAAT**[A]**ATACCCAGTGTGAGGCCACCCTCTGAGTAACCAAGTCCACTATATGGTTTTGCAGAA	69	A>G	A	12		
TGCAGAAATA**[A]**GGCAGGTGAAGTTTTCCTGGTTAAGAAACCTGCACCTGACACACAACAGCTCTTAAAC	69	A>G	A	11		
TGCAGGCAGAGAG**[A]**TAAAGGCAGAGATAGATCTCGGAGGAATCACTGTATCACTGCACCAGAACTCTCT	69	T>A	A	14		
TGCAGCAGGAGACAGAGAAAGTCAGGCTAAATGTTACAGCTTGGCAGCCCACA**[G]**TTTCCCTCCTGCTGA	69	G>A	G	54		
TGCAGA**[G]**TATGTGTCTGTTTATAGCATG	28	A>G	G	7		
TGCAGTCAGGAGGGTGTGCCAGGAGGGACATCATAGACAAATTGCTGATAAGTG**[C]**CCTTGACATTTGCA	69	C>T	C	55		
TGCAGACAGGGAAGGATCAGGATCAGCTCCTGAGCTGGG**[T]**GGAACGGGCATG	52	C>T	T	40		
TGCAGTGC**[G]**CCAGGACCAGGCAACATCTCTGGTCGCATG	39	A>G	G	9		
TGCAGTATAGTTTTGTTATAACAGACTATGATTGCTGGGTAAAGTGTTTCTTTTTAGA**[T]**AATTTTATAA	69	C>T	T	59		
TGCAGATTGGTTTTTAACTCTGGGAGATCTCCAGGTACCACCTGGAACTTGGCAAGCCTAG**[T]**TCATGGG	69	C>T	T	62		
TGCAGCT**[T]**TAACCACACATTAAGTGCACTAGGTTGACTCCATTGTGCATG	50	A>T	T	8		
TGCAG**[G]**CGCTGTAACCTTTGGCTCTCCAAATACAGACTGATGAACCATGCTCATGTGCTCATAAACTAT	69	A>G	G	6	NW_015175360.1_scaffold153	367239
TGCAGTGGGAGGAAA**[T]**GCATGAGCGGTTCAGCAGGAATGCCGAGACCGATCTCGTATGCCGTCTTCTGC	69	G>T	T	16		
TGCAGTTTGT**[C]**ATCTTATCTCTATACCTTGGCATG	35	C>T	C	11		
TGCAGACAGATAATGAAACTTTTGAAAAA**[C]**TAAGCATTCTGTAGGATACAGTGCTTCATAAAAATGTTT	69	C>A	C	30		
TGCAGAAACAAAAATAAATCACTTTTAAAT**[T]**ATTGCATG	39	G>T	T	31		
TGCAGCCTGC**[G]**GCAGGGCAGCTTTGTTTGGATTTCCCAGCATG	43	G>A	G	11		
TGCAGTGGAGTGAGTTATGTGCTGTTGTATGTGCCCACCTAATGAA**[C]**AGATTGTATTGTTCACTTTCAA	69	T>C	C	47		
TGCAGCTTGCTCATCCCTTGCTTCTGA**[G]**CTTCCACATGCATG	42	G>A	G	28		

Sequence	Length	SNP alleles	Diag. allele	SNP pos	Ref Chrom	Chrom pos
TGCAGACTTTTCTCTTTTCTCTACATTTCTCTGCACACT**[G]**TCTTCAGAGCAGAAGGCAGCAGCAGTCAG	69	G>A	G	40		
TGCAG**[G]**TACTGTCAGAAGCCAGATGGTGCATG	32	G>C	G	6		
TGCAGATTCTGGACTTCTGCTCCAGTCTTGCCATGTTCTGTGCCTCTGTGGCTAC**[A]**GTGGTCAAACTCA	69	G>A	A	56		
TGCAGGTATCTCTGTAGATGGCACCAAGGA**[G]**AGCATG	37	A>G	G	31		
TGCAGTTTCCC**[A]**GGTTGTCATCCTTCCCTTTTTTGAAGATTGGGATAACATTCTTCCTCCGTCAGTATT	69	A>G	A	12		
TGCAGCAGAACTATAACAATATTTTAAAGCATTGCTTTTGAAGTTATCTTATTCTAAAT**[A]**AAAAAGCAT	69	C>A	A	60		
TGCAGTTAACACCACCTTCTTGCCTGCCTTAATTCTCAGCTG**[T]**TATTTATTGGTGGTGGTGGAATCTGC	69	A>T	T	43		
TGCAGGG**[T]**ATGTATTTTGTCTCTTCAGTACTTCTGATTCGGATGAGCATG	50	T>G	T	8	NW_015161459.1_scaffold1869	41294
TGCAGGACATAA**[T]**GCTTTGGTGTTATGCATG	31	T>A	T	13		
TGCAGCTAGTTTGTTG**[A]**AGAAGCATG	26	A>G	A	17		
TGCAGTGGCCATGGTGGGTGCATCCTTGTCCAGTTGCAG**[G]**AGCAGCTATGGCTCCACAGGGGCTAAGGA	69	G>C	G	40		
TGCAGCTT**[A]**ATGTTAAAACCCATGTGTTGCATG	33	A>T	A	9		
TGCAGTGAGGTATGATACATGTATATGGAAGTGCAGAGGAG**[A]**AGCACTGTCTTGTAGGCAGCAGCAACA	69	G>A	A	42		
TGCAGGCAACACCATTTGGCAGCCA**[T]**TAATATATTCCTTCTGACTTCTTTTTCTGCATG	59	C>T	T	26	NW_015170280.1_scaffold203	1324869
TGCAGAGGGGGTACCTACT**[G]**CCTAATGCATG	31	A>G	G	20		
TGCAGTCATGGCACAACAAACCCTATGGCTGAGGACCTG**[A]**CAGGCCAACTTCCATTTGAGGGCCATCCT	69	G>A	A	40		
TGCAGTTGACC**[C]**GGCAGATGAAATAGTAGATGTGTATATGATTCTAGGCATG	52	C>T	C	12		
TGCAGACCACATAAAAGAGTTTTTGGAAATCGGTTAG**[C]**TATTTAACACCTGTCATAAGTTTCACAGAAA	69	C>T	C	38		
TGCAGAGATAACTCAAAGCAAGTTTGCATTTTAACTGTCTTTTTATGCAACTGT**[G]**ACCATTTGATTTTA	69	T>G	G	55		
TGCAGTGCTTTGCACAACACGTGCATTGACAGGAATGTAAGTTGAGCAAAATGGTTCTGTG**[A]**TCCAGCA	69	A>G	A	62		
TGCAGCTATTTTGCAAG**[C]**ACAGGGAAATGCATG	33	T>C	C	18		
TGCAGCC**[A]**CAATTAAACAGGTTGCTTACCTGTAACTGTTGTTCTCAAGTGGTCATTTGTGCACTTACAT	69	A>C	A	8	NW_015173673.1_scaffold34	1086238
TGCAGTGCATGAATTCAGT**[C]**TTGTATTGCATG	32	C>G	C	20		
TGCAGAATCTTCCTTGGTGGCCTCCCATGCAAGGACTGA**[T]**CCTGCTTAGCTTCTGAGATCTGACAAGAT	69	T>C	T	40	NW_015177026.1_scaffold612	249092
TGCAGCCAGACAG**[T]**CCTCTCCAATCGTTTTCTTGAGCTGCAATCATCTGATCACAACCAAATAGCTTGA	69	C>T	T	14	NW_015166447.1_scaffold825	529383
TGCAGG**[A]**CTGAGAAAGATCTTGGCTTAAGGTTTAAGAGAACTGCTTTCAAGTAGAATAAAGGCATGAGC	69	A>G	A	7		

Sequence	Length	SNP alleles	Diag. allele	SNP pos	Ref Chrom	Chrom pos
TGCAGCCTAATGAAGGACTTTTCTCATCTGTTACAG**[C]**TTTATCAAGAAAGCCAGGAACATGCAAGTGCA	69	T>C	C	37	NW_015165873.1_scaffold1783	18546
TGCAGCAGAGTTGCCCACATA**[T]**GCTGCAACCAGCACTCAGCATG	44	T>C	T	22		
TGCAGATCCA**[G]**TTTGTGAAGAAAAGATGCATG	32	A>G	G	11	NW_015169778.1_scaffold39	1181212
TGCAGGCACGGGAAAC**[T]**TTGGTTTAGGCCCAAGGCATG	38	T>C	T	17		
TGCAGAACTAGAAG**[C]**TGGGGGCATG	25	C>T	C	15		
TGCAGAAGCCTATGACACTTGTACAGGAGCTAGAAAATTCTCAAAGCTCACAG**[T]**TGCTTGAGCATATTA	69	T>C	T	54		
TGCAGTGTCTGCACAGCGTGCTAATCAAAATATGCACCAATTCCCAAATACAACATTTTTAAA**[C]**CCATT	69	C>T	C	64		
TGCAGGTGTCATAGCTGAAATTGCCCTGCTTCAGAATGTACTC**[A]**TTTTGCTTCTGCACATGCCCAGAGC	69	G>A	A	44	NW_015175365.1_scaffold337	121076
TGCAGGGGCATTCTGTATGTAGTTGCA**[C]**AGATCAGTGTAGAACTTGCTCTTTTCTTCAGGATTTGCTTG	69	C>T	C	28		
TGCAGCTTTGA**[T]**GTACAGGCATGAGCGGTTCAGCAGGAATGCCGAGACCGATCTCGTATGCCGTCTTCT	69	T>C	T	12		
TGCAGGGAGTTGGACTAGATGATCCTTGTGGTCCCTTCCAGCTCTAATATTCTATGATTC**[G]**TTGATGCT	69	G>T	G	61	NW_015170918.1_scaffold929	169621
TGCAGTAGCTCATTTAATTTTGTTTCCAGATGCCCCATCAGTCA**[T]**GGCACAAAGACTGAAGCCTTTCAA	69	G>T	T	45		
TGCAGAATTCCTGTTCTGCTAAGAGCAACTCCA**[C]**GGTAGCATG	43	T>C	C	34		
TGCAGAACTGCTTGTCAAAAATAGAAAGGGGGTAGGTTCATGTAAGCTCTTCTCACCTCTAG**[C]**TCCCAT	69	C>A	C	63		
TGCAGACA**[T]**AAGTGGTGAGAATCAAGGCAAACCACAAAATGTGAATAAATCATAAATTTTATAGGCATT	69	G>T	T	9		
TGCAGGCTCTGCACTCCTGACCCTTCATTGCTACTGCTTTACTGGA**[G]**CTTAAACCATGTAATGCACTGT	69	T>G	G	47		
TGCAGCAGGTTGGAGTATCAGCAAAAATCACATTCTC**[C]**TTGCATG	45	C>T	C	38		
TGCAGGAAAATTTACT**[C]**TTTTCTCACTATGGATTTGGGTGCATG	44	C>G	C	17		
TGCAGAATGGAAGTGATGTTACCCTAGTGGCTTGGGGCAC**[T]**CAGGTTAGTATGACTGTTGTGAGATACC	69	A>T	T	41		
TGCAGTGTGTAATCAGCAAAGGAAGAAGGAAAAGTCTTTAGGTAGCTCCCTG**[G]**ACAACAAAATGGAAAG	69	G>T	G	53		
TGCAGGTGACCCATGTTCTGAGGAC**[G]**AAAGATGCATG	37	A>G	G	26		
TGCAGCAGGGTATGTTAGAGCACATAGCTCCTGCTAGCACACATGG**[T]**AGCTTCCTCAACAATGTGTTTC	69	G>T	T	47		
TGCAGTTGTGTTCTAAGTCAGATTTGGCAC**[C]**ATAATAAAGTCTCAAAGCCAACAGCAGGGTCAAAAGTC	69	T>C	C	31		
TGCAGA**[C]**CTGGAGGAGGTGGTGAGCAGCATG	31	C>G	C	7		
TGCAGT**[G]**CCGACTTTGATCTTCATGCAATCTGACAGAAGCATG	43	A>G	G	7		
TGCAGTTTCTCTTTGTCTAGTGCTCTGTTCTGCATCCTCCTGTGGAGAC**[C]**TGGTGATTTTCTGTGAACT	69	C>T	C	50		

Sequence	Length	SNP alleles	Diag. allele	SNP pos	Ref Chrom	Chrom pos
TGCAGCACTATTTTCCTGACCTGGGAAAGGGTGCCATTTGACCCACAGTAACTCAGCAGT**[G]**TTTATGCA	69	T>G	G	61		
TGCAGAACAGGTCAGAAGAAAAACAGGAAGAGAGGGTAGAAAGTAATGCAATGTAGTAGGTT**[A]**ACAGAG	69	G>A	A	63		
TGCAGT**[T]**CCTGACCATTTGTTCTGCATG	28	C>T	T	7		
TGCAGTTTAAGAAATAAATAAGA**[G]**TGGTGATTGATGAATGTGGATGTGAACAGCATCTGTTTTATTTCT	69	T>G	G	24		
TGCAGTG**[T]**GCTTGCTCATTCCTTCTGACAACATAAGATGCTTGTATGCACCTTACAGTCAGCAACCCAC	69	C>T	T	8		
TGCAGACAAGTCAGATGCTATGATGAGGTAACA**[C]**TGTGGTATGGAGTGCTATGAAACATCCAAAAATAT	69	G>C	C	34	NW_015170309.1_scaffold1106	373447
TGCAGTTTCATAAAACTTCCAGCTGTCGACCAAAGGATTTGTAGCTGAATTAATCACCTGCCATTTAG**[T]**	69	T>C	T	69		
TGCAGTATTGTGTACCGTTCTGGAGACCTTGCTTCAAAAAG**[A]**ATGTGGGCAAATCAGTACCATTGTTAG	69	G>A	A	42		
TGCAGAGCTAGGAACCTCAGGACAAA**[A]**AACAGCCAAGGCATG	42	A>G	A	27		
TGCAGGAACTAAA**[T]**CCACGTGCATG	25	T>A	T	14		
TGCAGCATA**[A]**CCCTGTGCATGAGCGGTTCAGCAGGAATGCCGAGACCGATCTCGTATGCCGTCTTCTGC	69	G>A	A	10		
TGCAGACCTGCCAAACACAGTGATAACAGAATTGTCACACAGAAACTTCCAAG**[A]**GTCAGATCTAGGTAC	69	A>G	A	54		
TGCAGATAGGCAGGTGTTCTGTGTAGGTATGGCTATATAAAGCTTTCA**[A]**AGCAGCAGTTCTAAAAAGAG	69	G>A	A	49		
TGCAGGGG**[C]**AGAACATCTTCTTGGCATG	28	C>T	C	9		
***D. tincta* sp. nov. vs *D. hades* sp. nov.**						
TGCAGAGGCAGGGGAAGAAGATGGATGAGATGGTCAAAAGT**[G]**GATCAGGAAATGCATG	58	G>A	G	42		
TGCAGATTTTTCACATGATTATGT**[T]**TACTTTCTTGTGTGTATGTGGCATG	50	C>T	T	25		
TGCAGCAGGTGCTGCTGACTAGTGCACCTTTCCTTGAAGCCTCAC**[T]**TGGCTACAGAAGACAGAGGCGAT	69	T>C	T	46		
TGCAGCCCAGAA**[G]**TGTATCCCCCATCCAGTATGCATG	37	G>A	G	13	NW_015170301.1_scaffold882	395551
TGCAGCCTCAAGACACTGT**[C]**TGCTTGTGCATG	32	C>T	C	20		
TGCAGATTCATGCTGCACAGAAAGTGTGATAAAAAG**[T]**AAAATTGGAAAGATGGAAAGATTCAGGCATAC	69	T>C	T	37		
TGCAGTTAGAGTGACCAACTGTCCCAGTTTGCCC**[G]**GGAGAGTCCCAGATTGAAGGGTGGTTGTCCTGCA	69	G>A	G	35		
TGCAGCCCTACTGCTACTA**[G]**GAAATAGGTAGAGCATG	37	A>G	G	20		
TGCAGCAGCTCTAATTTTTCC**[A]**CAAGGGTATGGCCCCAGTATGATCAGAACACCAGCATG	60	G>A	A	22		
TGCAGTTTCTGGGGGCTTTTTGCATACATGGGGAACAAGAGTTGACCTCACTAATGAGGAATGCGCTT**[T]**	69	C>T	T	69	NW_015165830.1_scaffold15	131044
TGCAGATAACACAAAATTGGAGGGCCTGGCTAACACCCAGGTTGACAGAAGGAAA**[G]**TGCCTCAACAGGT	69	G>A	G	56		

Sequence	Length	SNP alleles	Diag. allele	SNP pos	Ref Chrom	Chrom pos
TGCAGGAGTCCCACCC**[T]**CAAAATGCCTCTCAGATCCATGTGAAACGGGAAGAGCTTGTTGCAAACTGGG	69	G>T	T	17		
TGCAG**[C]**GGCATTTGGAGCATGAGCGGTTCAGCAGGAATGCCGAGACCGATCTCGTATGCCGTCTTCTGC	69	C>T	C	6		
TGCAGACTGTCATCTC**[A]**GACAGCATG	26	A>T	A	17		
TGCAGTGCAC**[G]**TGTTTCCTTATTCCCTCTGGACAGAAAATAGGAGCATAGAATCTCTGCTGGCCATGTG	69	A>G	G	11		
TGCAGATTCTGCTACTAAGACTAATGCACGTAGGAG**[C]**AGCATGGAAATAAAGCTAGAAATAAAAGCAGC	69	G>C	C	37		
TGCAGTGATGGATCACAGATGTACTGATTTGTTCTGGACATGCCCCTACTGCAACC**[G]**AGCATG	63	A>G	G	57		
TGCAGCTGTCAGAAACTTTATTTATCAGTT**[T]**CTAGCAAAACCACCATCATTATCCAGGGAGAGATGGCC	69	A>T	T	31	NW_015166440.1_scaffold634	539315
TGCAGCATTCCAATTTAGGCAGTCATCTG**[T]**CTGGCAAGTCCACCCTGCTCACAGGCATG	59	C>T	T	30		
TGCAGAAAGGAAAGG**[T]**AAAAATCCTGTAGAAAGGGAGAGAGGGAGATAGGTAAGTAAGTAATGTGGTTC	69	T>A	T	16		
TGCAGAACAC**[A]**GCCGGAAGACATGGGGACAACCTACGCAACATCAGGCAGGAGATTCAAGAGCTGACCA	69	G>A	A	11		
TGCAGGGTAGAGCATAGAGAGGGAGGTGATCCCTCAG**[G]**TATGAAGGACCAAGTCTATGAAAGGCTTTGT	69	G>A	G	38		
TGCAGGAAGTGGTGCATC**[C]**AAACTATTGGTGGTGGTCAGGGGTAAGGGGATTGGAACAAACACTAATTG	69	C>T	C	19		
TGCAGCTCTCCTGGCA**[C]**AGGTCTTTCCCATCCCTGCCACCATAGATTCTTTCTTCAATTGGCAAGGCAA	69	C>G	C	17		
TGCAGTCTT**[G]**TATAGGGAGTTTCCCTACAGGGGCTACTGGGTTCCAAGCTAGGTTCTTCTTCTTAAGAT	69	G>A	G	10		
TGCAGGTGC**[C]**AGGGATTGAACCTGGGACCTCTGGCATG	38	T>C	C	10		
TGCAGTTCAGGCAC**[A]**GCCATCAAAACAAATATATTCTTTGGCATTCTTGAAAACTGTGGGAAAGCAGGG	69	A>G	A	15	NW_015172036.1_scaffold1095	224085
TGCAGGCTGAGCAGGAAACTGTTGGTCAT**[G]**TTTTCAGTGAAAGGGTAGACATTCCTGATGGTGTCAATT	69	G>A	G	30		
TGCAGGCACTTCTTCCTAGGCTAATATTCT**[C]**CTCTGAATAAGAATATAACTAAATTTAAAGGTGCATAA	69	C>T	C	31		
TGCAGCCATTTTACCTC**[A]**TCAAAAGGCATAGTTTTGTGCATG	42	A>C	A	18		
TGCAGACTAAT**[G]**ATACCCAGTGTGAGGCCACCCTCTGAGTAACCAAGTCCACTATATGGTTTTGCAGAA	69	A>G	G	12		
TGCAGAAATA**[G]**GGCAGGTGAAGTTTTCCTGGTTAAGAAACCTGCACCTGACACACAACAGCTCTTAAAC	69	A>G	G	11		
TGCAGGCAGAGAG**[T]**TAAAGGCAGAGATAGATCTCGGAGGAATCACTGTATCACTGCACCAGAACTCTCT	69	T>A	T	14		
TGCAGCAGGAGACAGAGAAAGTCAGGCTAAATGTTACAGCTTGGCAGCCCACA**[A]**TTTCCCTCCTGCTGA	69	G>A	A	54		
TGCAGA**[A]**TATGTGTCTGTTTATAGCATG	28	A>G	A	7		
TGCAGTCAGGAGGGTGTGCCAGGAGGGACATCATAGACAAATTGCTGATAAGTG**[T]**CCTTGACATTTGCA	69	C>T	T	55		
TGCAGACAGGGAAGGATCAGGATCAGCTCCTGAGCTGGG**[C]**GGAACGGGCATG	52	C>T	C	40		

Sequence	Length	SNP alleles	Diag. allele	SNP pos	Ref Chrom	Chrom pos
TGCAGTGC**[A]**CCAGGACCAGGCAACATCTCTGGTCGCATG	39	A>G	A	9		
TGCAGTATAGTTTTGTTATAACAGACTATGATTGCTGGGTAAAGTGTTTCTTTTTAGA**[C]**AATTTTATAA	69	C>T	C	59		
TGCAGATTGGTTTTTAACTCTGGGAGATCTCCAGGTACCACCTGGAACTTGGCAAGCCTAG**[C]**TCATGGG	69	C>T	C	62		
TGCAGCT**[A]**TAACCACACATTAAGTGCACTAGGTTGACTCCATTGTGCATG	50	A>T	A	8		
TGCAG**[A]**CGCTGTAACCTTTGGCTCTCCAAATACAGACTGATGAACCATGCTCATGTGCTCATAAACTAT	69	A>G	A	6	NW_015175360.1_scaffold153	367239
TGCAGTGGGAGGAAA**[G]**GCATGAGCGGTTCAGCAGGAATGCCGAGACCGATCTCGTATGCCGTCTTCTGC	69	G>T	G	16		
TGCAGTTTGT**[T]**ATCTTATCTCTATACCTTGGCATG	35	C>T	T	11		
TGCAGACAGATAATGAAACTTTTGAAAAA**[A]**TAAGCATTCTGTAGGATACAGTGCTTCATAAAAATGTTT	69	C>A	A	30		
TGCAGAAACAAAAATAAATCACTTTTAAAT**[G]**ATTGCATG	39	G>T	G	31		
TGCAGCCTGC**[A]**GCAGGGCAGCTTTGTTTGGATTTCCCAGCATG	43	G>A	A	11		
TGCAGTGGAGTGAGTTATGTGCTGTTGTATGTGCCCACCTAATGAA**[T]**AGATTGTATTGTTCACTTTCAA	69	T>C	T	47		
TGCAGCTTGCTCATCCCTTGCTTCTGA**[A]**CTTCCACATGCATG	42	G>A	A	28		
TGCAGACTTTTCTCTTTTCTCTACATTTCTCTGCACACT**[A]**TCTTCAGAGCAGAAGGCAGCAGCAGTCAG	69	G>A	A	40		
TGCAG**[C]**TACTGTCAGAAGCCAGATGGTGCATG	32	G>C	C	6		
TGCAGATTCTGGACTTCTGCTCCAGTCTTGCCATGTTCTGTGCCTCTGTGGCTAC**[G]**GTGGTCAAACTCA	69	G>A	G	56		
TGCAGGTATCTCTGTAGATGGCACCAAGGA**[A]**AGCATG	37	A>G	A	31		
TGCAGTTTCCC**[G]**GGTTGTCATCCTTCCCTTTTTTGAAGATTGGGATAACATTCTTCCTCCGTCAGTATT	69	A>G	G	12		
TGCAGCAGAACTATAACAATATTTTAAAGCATTGCTTTTGAAGTTATCTTATTCTAAAT**[C]**AAAAAGCAT	69	C>A	C	60		
TGCAGTTAACACCACCTTCTTGCCTGCCTTAATTCTCAGCTG**[A]**TATTTATTGGTGGTGGTGGAATCTGC	69	A>T	A	43		
TGCAGGG**[G]**ATGTATTTTGTCTCTTCAGTACTTCTGATTCGGATGAGCATG	50	T>G	G	8	NW_015161459.1_scaffold1869	41294
TGCAGGACATAA**[A]**GCTTTGGTGTTATGCATG	31	T>A	A	13		
TGCAGCTAGTTTGTTG**[G]**AGAAGCATG	26	A>G	G	17		
TGCAGTGGCCATGGTGGGTGCATCCTTGTCCAGTTGCAG**[C]**AGCAGCTATGGCTCCACAGGGGCTAAGGA	69	G>C	C	40		
TGCAGCTT**[T]**ATGTTAAAACCCATGTGTTGCATG	33	A>T	T	9		
TGCAGTGAGGTATGATACATGTATATGGAAGTGCAGAGGAG**[G]**AGCACTGTCTTGTAGGCAGCAGCAACA	69	G>A	G	42		
TGCAGGCAACACCATTTGGCAGCCA**[C]**TAATATATTCCTTCTGACTTCTTTTTCTGCATG	59	C>T	C	26	NW_015170280.1_scaffold203	1324869

Sequence	Length	SNP alleles	Diag. allele	SNP pos	Ref Chrom	Chrom pos
TGCAGAGGGGGTACCTACT**[A]**CCTAATGCATG	31	A>G	A	20		
TGCAGTCATGGCACAACAAACCCTATGGCTGAGGACCTG**[G]**CAGGCCAACTTCCATTTGAGGGCCATCCT	69	G>A	G	40		
TGCAGTTGACC**[T]**GGCAGATGAAATAGTAGATGTGTATATGATTCTAGGCATG	52	C>T	T	12		
TGCAGACCACATAAAAGAGTTTTTGGAAATCGGTTAG**[T]**TATTTAACACCTGTCATAAGTTTCACAGAAA	69	C>T	T	38		
TGCAGAGATAACTCAAAGCAAGTTTGCATTTTAACTGTCTTTTTATGCAACTGT**[T]**ACCATTTGATTTTA	69	T>G	T	55		
TGCAGTGCTTTGCACAACACGTGCATTGACAGGAATGTAAGTTGAGCAAAATGGTTCTGTG**[G]**TCCAGCA	69	A>G	G	62		
TGCAGCTATTTTGCAAG**[T]**ACAGGGAAATGCATG	33	T>C	T	18		
TGCAGCC**[C]**CAATTAAACAGGTTGCTTACCTGTAACTGTTGTTCTCAAGTGGTCATTTGTGCACTTACAT	69	A>C	C	8	NW_015173673.1_scaffold34	1086238
TGCAGTGCATGAATTCAGT**[G]**TTGTATTGCATG	32	C>G	G	20		
TGCAGAATCTTCCTTGGTGGCCTCCCATGCAAGGACTGA**[C]**CCTGCTTAGCTTCTGAGATCTGACAAGAT	69	T>C	C	40	NW_015177026.1_scaffold612	249092
TGCAGCCAGACAG**[C]**CCTCTCCAATCGTTTTCTTGAGCTGCAATCATCTGATCACAACCAAATAGCTTGA	69	C>T	C	14	NW_015166447.1_scaffold825	529383
TGCAGG**[G]**CTGAGAAAGATCTTGGCTTAAGGTTTAAGAGAACTGCTTTCAAGTAGAATAAAGGCATGAGC	69	A>G	G	7		
TGCAGCCTAATGAAGGACTTTTCTCATCTGTTACAG**[T]**TTTATCAAGAAAGCCAGGAACATGCAAGTGCA	69	T>C	T	37	NW_015165873.1_scaffold1783	18546
TGCAGCAGAGTTGCCCACATA**[C]**GCTGCAACCAGCACTCAGCATG	44	T>C	C	22		
TGCAGATCCA**[A]**TTTGTGAAGAAAAGATGCATG	32	A>G	A	11	NW_015169778.1_scaffold39	1181212
TGCAGGCACGGGAAAC**[C]**TTGGTTTAGGCCCAAGGCATG	38	T>C	C	17		
TGCAGAACTAGAAG**[T]**TGGGGGCATG	25	C>T	T	15		
TGCAGAAGCCTATGACACTTGTACAGGAGCTAGAAAATTCTCAAAGCTCACAG**[C]**TGCTTGAGCATATTA	69	T>C	C	54		
TGCAGTGTCTGCACAGCGTGCTAATCAAAATATGCACCAATTCCCAAATACAACATTTTTAAA**[T]**CCATT	69	C>T	T	64		
TGCAGGTGTCATAGCTGAAATTGCCCTGCTTCAGAATGTACTC**[G]**TTTTGCTTCTGCACATGCCCAGAGC	69	G>A	G	44	NW_015175365.1_scaffold337	121076
TGCAGGGGCATTCTGTATGTAGTTGCA**[T]**AGATCAGTGTAGAACTTGCTCTTTTCTTCAGGATTTGCTTG	69	C>T	T	28		
TGCAGCTTTGA**[C]**GTACAGGCATGAGCGGTTCAGCAGGAATGCCGAGACCGATCTCGTATGCCGTCTTCT	69	T>C	C	12		
TGCAGGGAGTTGGACTAGATGATCCTTGTGGTCCCTTCCAGCTCTAATATTCTATGATTC**[T]**TTGATGCT	69	G>T	T	61	NW_015170918.1_scaffold929	169621
TGCAGTAGCTCATTTAATTTTGTTTCCAGATGCCCCATCAGTCA**[G]**GGCACAAAGACTGAAGCCTTTCAA	69	G>T	G	45		
TGCAGAATTCCTGTTCTGCTAAGAGCAACTCCA**[T]**GGTAGCATG	43	T>C	T	34		
TGCAGAACTGCTTGTCAAAAATAGAAAGGGGGTAGGTTCATGTAAGCTCTTCTCACCTCTAG**[A]**TCCCAT	69	C>A	A	63		

Sequence	Length	SNP alleles	Diag. allele	SNP pos	Ref Chrom	Chrom pos
TGCAGACA**[G]**AAGTGGTGAGAATCAAGGCAAACCACAAAATGTGAATAAATCATAAATTTTATAGGCATT	69	G>T	G	9		
TGCAGGCTCTGCACTCCTGACCCTTCATTGCTACTGCTTTACTGGA**[T]**CTTAAACCATGTAATGCACTGT	69	T>G	T	47		
TGCAGCAGGTTGGAGTATCAGCAAAAATCACATTCTC**[T]**TTGCATG	45	C>T	T	38		
TGCAGGAAAATTTACT**[G]**TTTTCTCACTATGGATTTGGGTGCATG	44	C>G	G	17		
TGCAGAATGGAAGTGATGTTACCCTAGTGGCTTGGGGCAC**[A]**CAGGTTAGTATGACTGTTGTGAGATACC	69	A>T	A	41		
TGCAGTGTGTAATCAGCAAAGGAAGAAGGAAAAGTCTTTAGGTAGCTCCCTG**[T]**ACAACAAAATGGAAAG	69	G>T	T	53		
TGCAGGTGACCCATGTTCTGAGGAC**[A]**AAAGATGCATG	37	A>G	A	26		
TGCAGCAGGGTATGTTAGAGCACATAGCTCCTGCTAGCACACATGG**[G]**AGCTTCCTCAACAATGTGTTTC	69	G>T	G	47		
TGCAGTTGTGTTCTAAGTCAGATTTGGCAC**[T]**ATAATAAAGTCTCAAAGCCAACAGCAGGGTCAAAAGTC	69	T>C	T	31		
TGCAGA**[G]**CTGGAGGAGGTGGTGAGCAGCATG	31	C>G	G	7		
TGCAGT**[A]**CCGACTTTGATCTTCATGCAATCTGACAGAAGCATG	43	A>G	A	7		
TGCAGTTTCTCTTTGTCTAGTGCTCTGTTCTGCATCCTCCTGTGGAGAC**[T]**TGGTGATTTTCTGTGAACT	69	C>T	T	50		
TGCAGCACTATTTTCCTGACCTGGGAAAGGGTGCCATTTGACCCACAGTAACTCAGCAGT**[T]**TTTATGCA	69	T>G	T	61		
TGCAGAACAGGTCAGAAGAAAAACAGGAAGAGAGGGTAGAAAGTAATGCAATGTAGTAGGTT**[G]**ACAGAG	69	G>A	G	63		
TGCAGT**[C]**CCTGACCATTTGTTCTGCATG	28	C>T	C	7		
TGCAGTTTAAGAAATAAATAAGA**[T]**TGGTGATTGATGAATGTGGATGTGAACAGCATCTGTTTTATTTCT	69	T>G	T	24		
TGCAGTG**[C]**GCTTGCTCATTCCTTCTGACAACATAAGATGCTTGTATGCACCTTACAGTCAGCAACCCAC	69	C>T	C	8		
TGCAGACAAGTCAGATGCTATGATGAGGTAACA**[G]**TGTGGTATGGAGTGCTATGAAACATCCAAAAATAT	69	G>C	G	34	NW_015170309.1_scaffold1106	373447
TGCAGTTTCATAAAACTTCCAGCTGTCGACCAAAGGATTTGTAGCTGAATTAATCACCTGCCATTTAG**[C]**	69	T>C	C	69		
TGCAGTATTGTGTACCGTTCTGGAGACCTTGCTTCAAAAAG**[G]**ATGTGGGCAAATCAGTACCATTGTTAG	69	G>A	G	42		
TGCAGAGCTAGGAACCTCAGGACAAA**[G]**AACAGCCAAGGCATG	42	A>G	G	27		
TGCAGGAACTAAA**[A]**CCACGTGCATG	25	T>A	A	14		
TGCAGCATA**[G]**CCCTGTGCATGAGCGGTTCAGCAGGAATGCCGAGACCGATCTCGTATGCCGTCTTCTGC	69	G>A	G	10		
TGCAGACCTGCCAAACACAGTGATAACAGAATTGTCACACAGAAACTTCCAAG**[G]**GTCAGATCTAGGTAC	69	A>G	G	54		
TGCAGATAGGCAGGTGTTCTGTGTAGGTATGGCTATATAAAGCTTTCA**[G]**AGCAGCAGTTCTAAAAAGAG	69	G>A	G	49		
TGCAGGGG**[T]**AGAACATCTTCTTGGCATG	28	C>T	T	9		

APPENDIX 4 Morphological measurements taken for all specimens in this study. See text for abbreviations of characters used.

Museum	Specimen	Species	Population	SVL	HeadD	HeadL	HeadW	SnoutL	EyeW	VS	MBS	TL	HLS (R)	Supralabial scales (R)	Infralabial scales (R)	Supralabial scales (L)	Infralabial scales (L)	sex
SAMA	42945	not genotyped		70	3.58	7.66	4.51	3.16	1.18	67	14	108	3	6	5	6	5	
SAMA	67717	not genotyped		80	3.89	8.40	5.18	3.47	1.29	68	14	126	3	6	5	6	5	
QM	J80509	not genotyped		48	1.90	3.86	3.45	2.05	0.92	74	14	84	-	5	4	5	5	juv
SAMA	10377	not genotyped		81	5.07	8.86	6.08	3.65	1.37	66	14	-	3	6	5	6	5	
SAMA	14498	not genotyped		75	3.94	8.01	4.94	3.77	1.20	64	14	174	3	6	5	6	5	
SAMA	15189	not genotyped		70	4.75	8.37	5.08	3.52	1.08	-	-	249	3	6	5	6	5	
SAMA	18254	not genotyped		75	3.54	8.09	5.05	3.46	1.21	66	14	134	3	6	5	6	5	m
SAMA	32453	not genotyped		79	4.26	8.22	5.29	3.32	1.21	67	14	129	3	6	5	6	5	
SAMA	34447	not genotyped		71	3.48	7.90	4.87	3.04	0.91	65	14	183	3	6	5	6	5	
SAMA	42946	not genotyped		75	3.90	8.02	4.63	3.07	1.20	67	14	231	3	6	4	6	5	
SAMA	44804	not genotyped		64	2.71	7.06	3.91	2.70	1.11	69	14	-	3	6	5	6	5	
SAMA	45033	not genotyped		51	3.08	6.32	3.09	2.58	0.99	66	14	-	2	5	5	6	5	juv
SAMA	57467	not genotyped		43	2.40	5.88	3.45	2.26	1.04	67	14	77	2	6	5	6	5	juv
SAMA	60966	not genotyped		86	4.20	8.16	5.23	3.62	1.40	72	14	155	4	6	5	6	6	
SAMA	72368	not genotyped		79	4.11	8.03	4.80	3.11	1.06	69	14	109	4	6	5	6	5	
SAMA	72376	not genotyped		74	4.00	7.77	4.17	2.95	1.10	69	14	234	4	6	5	6	5	
SAMA	72372	not genotyped		90	4.13	8.22	5.24	3.44	1.16	68	14	126	4	6	5	6	5	
QM	J241	not genotyped		63	3.38	6.75	4.06	2.84	0.97	66	14	-	3	6	5	6	5	
SAMA	7875	not genotyped		66	4.75	7.98	5.15	3.36	1.07	68	14	-	3	6	5	6	5	
SAMA	18571	not genotyped		77	4.70	8.40	5.28	3.32	1.18	70	14	175	3	6	5	6	5	
WAM	93701	not genotyped		44	2.36	5.43	3.11	2.28	0.84	71	14	-	3	6	4	6	5	
WAM	114391	not genotyped		69	3.06	7.66	4.37	2.96	1.13	69	14	96	3	6	5	6	5	

Museum	Specimen	Species	Population	SVL	HeadD	HeadL	HeadW	SnoutL	EyeW	VS	MBS	TL	HLS (R)	Supralabial scales (R)	Infralabial scales (R)	Supralabial scales (L)	Infralabial scales (L)	sex
WAM	114392	not genotyped		67	3.44	7.89	4.31	3.17	1.14	65	14	238	3	6	5	6	5	m
WAM	116439	not genotyped		76	2.71	7.39	4.04	2.94	0.92	72	14	105	3	6	5	6	5	
WAM	146890	not genotyped		80	3.41	8.94	4.86	3.40	1.05	73	15	284	3	6	5	6	5	
WAM	146957	not genotyped		82	2.50	8.34	4.51	3.42	1.21	72	14	93	3	6	5			
WAM	168506	not genotyped		54	2.69	6.40	3.29	2.32	1.06	65	14	178	3	6	5	6	5	
WAM	168507	not genotyped		70	3.28	7.54	4.23	2.96	1.15	70	14	126	3	7	5	6	5	
WAM	168520	not genotyped		70	3.09	7.90	4.33	3.14	1.17	69	15	160	3	6	5	6	5	
WAM	168521	not genotyped		46	2.16	6.11	2.82	2.41	0.89	66	14	-	3	6	5	6	5	
WAM	176401	not genotyped		77	3.80	8.26	5.09	3.41	1.16	71	14	282	3	6	5	6	5	
WAM	180214	not genotyped		84	4.02	8.58	4.89	3.57	1.24	74	14	305	3	6	4	6	4	
SAMA	4978	not genotyped		75	4.30	8.34	5.38	3.39	1.13	70	14	241	-	-	-	-	-	
QM	21786	not genotyped		75	3.84	7.69	4.38	2.93	1.25	69	14	217	3	6	5	6	5	
QM	51530	not genotyped		53	3.26	6.98	4.19	2.60	0.97	71	14	-	-	6	5	6	5	
QM	54476	not genotyped		70	2.69	6.92	3.86	2.76	0.88	72	14	200	-	6	5	6	5	
QM	59911	not genotyped		81	3.59	8.70	4.57	3.39	1.17	69	14	-	3	6	5	6	5	
QM	70487	not genotyped		75	3.44	7.06	4.40	2.72	0.99	67	14	235	3	6	5	6	5	
QM	81877	not genotyped		81	4.49	8.36	5.32	3.41	1.24	69	14	-	-	6	5	6	5	
QM	82226	not genotyped		74	2.91	7.10	4.25	2.66	1.13	73	14	-	3	6	5	6	5	
QM	83469	not genotyped		87	4.02	8.47	5.29	3.36	1.38	74	15	218	3	6	5	6	5	
QM	84099	not genotyped		67	4.08	7.25	4.44	2.93	1.21	66	14	-	4	6	5	6	5	
QM	86155	not genotyped		65	2.85	6.46	2.91	2.76	0.88	72	14	-	3	6	5	6	5	
QM	97651	not genotyped		78	3.81	8.06	5.56	3.09	1.36	70	16	195	3	6	5	6	6	
QM	97653	not genotyped		74	3.76	7.97	4.92	3.26	1.39	64	14	-	3	6	5	6	5	
WAM	117215	not genotyped		74	3.29	7.99	4.74	3.11	1.18	69	14	-	3	6	4	6	4	

Museum	Specimen	Species	Population	SVL	HeadD	HeadL	HeadW	SnoutL	EyeW	VS	MBS	TL	HLS (R)	Supralabial scales (R)	Infralabial scales (R)	Supralabial scales (L)	Infralabial scales (L)	sex
WAM	157704	not genotyped		70	3.25	7.28	4.34	2.9	1.19	70	14	197	3	6	5	6	5	m
QM	46687	not genotyped		74	3.11	7.23	3.56	2.84	1.17	74	14	118	3	6	5	6	5	
QM	56465	not genotyped		77	3.34	8.00	5.36	3.23	1.03	63	14	98	-	6	5	6	5	
QM	57250	not genotyped		56	3.41	6.35	3.85	2.54	0.94	63	14	155	3	6	5	6	5	
QM	69324	not genotyped		60	3.04	6.72	4.10	2.37	0.93	63	14	-	3	6	5	6	5	
QM	75298	not genotyped		74	3.59	7.87	5.62	3.14	1.17	67	14	132	3	6	5	6	5	
QM	76459	not genotyped		67	4.07	6.81	4.03	2.98	1.05	61	14	104	3	6	5	6	5	
QM	77978	not genotyped		64	3.55	6.65	4.85	2.51	1.17	66	14	186	3	5	6	6	5	
QM	78002	not genotyped		78	3.81	7.69	4.69	3.17	1.25	68	14	-	3	6	5	6	5	
QM	81285	not genotyped		57	3.31	6.72	4.11	2.80	1.21	62	15	187	3	6	5	7	5	
QM	83188	not genotyped		63	3.41	6.87	4.03	2.71	1.13	64	14	176	3	6	5	6	5	
QM	88170	not genotyped		78	3.41	8.10	5.22	3.09	1.17	66	14	-	-	-	-	6	5	
QM	97844	not genotyped		75	3.47	7.63	4.42	3.13	1.22	68	14	-	3	6	5	6	5	
SAMA	35960	*D. tincta*	P1	65	3.44	7.80	4.86	3.19	1.16	66	14	-	3	6	5	6	4	
SAMA	38847	*D. tincta*	P1	87	3.57	8.55	6.02	3.22	1.3	74	14	237	3	6	5	6	5	
SAMA	46806	*D. tincta*	P1	80	4.24	8.23	5.77	3.39	1.23	68	14	248	4	6	5	6	5	
SAMA	49874	*D. tincta*	P1	83	4.36	8.79	5.89	3.44	1.35	70	14	158	4	6	5	6	5	
SAMA	60513	*D. tincta*	P1	41	2.10	5.57	2.81	1.97	0.94	64	14	101	3	6	4	6	4	juv
SAMA	60546	*D. tincta*	P1	56	2.97	6.90	4.05	2.73	1.04	64	14	84	2	6	5	6	5	
WAM	137953	*D. tincta*	P1	80	3.73	8.35	4.25	3.32	1.12	73	-	-	-	6	5	6	5	m
SAMA	30971	*D. tincta*	P2	75	3.40	7.60	4.67	2.87	1.07	67	14	182	3	6	5	6	5	
SAMA	31173	*D. tincta*	P2	64	2.81	7.22	4.65	2.97	1.12	63	14	135	3	6	5	6	5	
SAMA	49065	*D. tincta*	P2	74	3.57	8.33	4.94	3.10	1.25	65	14	151	4	6	5	6	5	
SAMA	61947	*D. tincta*	P2	96	3.76	8.71	5.28	3.54	1.3	71	14	143	4	6	5	6	5	

Museum	Specimen	Species	Population	SVL	HeadD	HeadL	HeadW	SnoutL	EyeW	VS	MBS	TL	HLS (R)	Supralabial scales (R)	Infralabial scales (R)	Supralabial scales (L)	Infralabial scales (L)	sex
SAMA	61856	*D. tincta*	P2	85	3.56	8.60	5.29	3.28	1.05	71	14	125	4	5	4	6	5	
SAMA	45034	*D. tincta*	P7	69	3.19	7.10	3.53	2.61	1.11	70	14	151	3	6	4	6	5	
SAMA	54019	*D. tincta*	P7	93	3.81	8.25	4.55	3.15	1.18	78	14	280	3	6	5	6	5	
SAMA	55294	*D. tincta*	P7	89	3.01	7.57	4.19	2.91	1.01	77	14	237	3	6	5	6	5	
QM	90118	*D. tincta*	P7	59	2.63	6.35	3.44	2.45	1.12	70	14	156	3	6	5	6	5	
QM	J83423	*D. tincta*	P7	71	3.34	7.11	3.97	3.08	0.95	70	14	-	3	6	5	6	5	
QM	J91823	*D. tincta*	P7	71	3.17	7.11	4.61	2.67	1.08	68	14	146	3	6	5	6	5	
SAMA	40238	*D. hades*	P8	76	4.55	8.67	4.92	3.64	1.19	67	14	-	2	6	5	6	5	
SAMA	51553	*D. hades*	P8	90	4.44	9.03	5.44	3.58	1.24	66	14	-	3	6	5	6	5	
SAMA	54015	*D. hades*	P8	79	4.10	8.70	5.53	3.40	1.18	69	14	292	3	6	5	6	4	
SAMA	54465	*D. hades*	P8	76	4.12	8.29	4.79	3.41	1.06	63	14	263	3	6	5	6	5	
SAMA	54735	*D. hades*	P8	85	3.79	8.89	5.09	3.50	1.15	71	14	145	3	6	5	6	5	
QM	90655	*D. hades*	P8	95	4.26	9.20	5.26	3.61	1.30	72	14	-	3	6	5	6	5	
WAM	177993	*D. hades*	P8	56	2.62	6.59	3.74	2.67	1.05	68	14	190	3	6	5	6	5	
WAM	99180	*D. branchia*	P5	67	3.49	7.32	4.25	2.89	1.14	13	-	107	3	6	5	6	5	
WAM	102838	*D. branchia*	P5	61	3.21	6.74	4.07	2.60	1.10	66	14	205	3	6	5	6	5	
WAM	110080	*D. branchia*	P5	78	3.80	7.76	4.72	3.04	1.25	73	14	174	3	6	5	6	5	
WAM	110292	*D. branchia*	P5	75	3.41	7.60	4.13	3.08	1.13	61	13		3	6	5	6	5	
WAM	112690	*D. branchia*	P5	55	2.96	6.34	3.81	2.49	1.13	69	14	182	3	6	5	6	5	
WAM	113012	*D. branchia*	P5	72	3.84	8.04	5.15	3.25	1.21	67	14	211	3	6	5	6	6	
WAM	113030	*D. branchia*	P5	78	3.13	7.92	4.90	3.14	1.07	69	14	123	3	6	5	6	5	m
WAM	114490	*D. branchia*	P5	71	2.92	7.87	4.55	2.98	1.18	68	13	183	3	6	4	6	4	m
WAM	115018	*D. branchia*	P5	68	3.11	7.27	4.53	2.90	1.23	70	14	155	3	6	5	6	5	m
WAM	116545	*D. branchia*	P5	85	3.41	8.33	4.63	3.35	1.19	70	14	221	3	6	5	6	5	

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WAM	117342	*D. branchia*	P5	61	2.56	6.63	3.69	2.60	1.00	68	14	155	3	6	4	6	5	
WAM	120020	*D. branchia*	P5	75	3.16	7.45	4.19	3.24	1.19	67	14	188	3	6	4	6	5	
WAM	125032	*D. branchia*	P5	65	3.02	7.31	4.09	2.70	1.10	70	13	130	3	6	4	6	5	
WAM	127768	*D. branchia*	P5	58	2.96	6.45	3.51	2.67	1.04	71	14	153	3	6	5	6	5	
WAM	129623	*D. branchia*	P5	70	3.44	7.78	4.00	2.94	1.12	72	14	219	3	5	4	6	5	
WAM	135422	*D. branchia*	P5	70	3.21	7.43	4.34	2.89	1.27	68	13	166	3	6	5	6	5	
WAM	138078	*D. branchia*	P5	93	4.34	8.84	5.62	3.52	1.28	73	14	274	3	6	4	6	5	
WAM	139308	*D. branchia*	P5	44	2.19	5.89	3.05	2.45	1.06	65	14	122	3	6	5	6	5	
WAM	139314	*D. branchia*	P5	75	3.73	8.13	4.97	3.31	1.29	69	14	191	3	6	5	6	5	
WAM	139328	*D. branchia*	P5	71	3.37	7.77	4.55	3.05	1.36	64	14	126	3	6	5	6	5	
WAM	139637	*D. branchia*	P5	57	3.62	6.96	3.97	2.97	1.04	62	14	210	3	6	5	6	5	
WAM	141273	*D. branchia*	P5	66	3.21	7.32	4.04	2.73	1.00	75	15	236	3	6	5	6	5	
WAM	151059	*D. branchia*	P5	72	2.95	8.06	4.80	3.10	1.22	68	14	212	3	6	4	6	5	
WAM	151060	*D. branchia*	P5	72	3.56	8.44	4.60	3.47	1.22	68	14	107	3	6	5	6	5	m
WAM	153821	*D. branchia*	P5	64	2.87	6.94	3.78	2.85	0.96	72	13	220	3	6	5	6	5	m
WAM	154268	*D. branchia*	P5	67	2.94	7.63	4.30	2.84	1.19	68	14	92	3	6	5	6	5	
WAM	156173	*D. branchia*	P5	75	2.99	7.90	4.78	3.26	1.25	68	14	260	3	6	5	6	4	
WAM	156227	*D. branchia*	P5	65	3.72	7.08	4.49	3.05	1.20	69	14	172	3	6	5	6	5	m
WAM	156258	*D. branchia*	P5	71	3.10	7.19	4.15	2.82	1.16	70	14	136	3	6	5	6	5	
WAM	157065	*D. branchia*	P5	58	2.99	6.44	3.30	2.13	1.07	66	14	176	3	6	5	6	5	
WAM	157124	*D. branchia*	P5	64	3.29	6.59	3.45	2.58	1.02	72	14	180	3	6	4	6	5	
WAM	158123	*D. branchia*	P5	63	3.04	6.90	4.02	2.65	1.05	68	14	-	3	6	4	6	4	
WAM	158202	*D. branchia*	P5	79	3.42	7.75	4.32	2.87	1.24	75	14	-	3	7	5	6	5	
WAM	160201	*D. branchia*	P5	62	2.95	6.95	3.94	2.55	1.12	68	14	166	3	6	4	6	5	

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WAM	161660	*D. branchia*	P5	63	3.11	7.23	4.36	2.84	1.11	66	14	176	3	6	5	6	5	
WAM	162036	*D. branchia*	P5	70	3.16	7.93	4.35	3.03	1.10	68	14	130	3	6	5	6	5	
WAM	162054	*D. branchia*	P5	74	3.30	7.29	4.63	2.94	1.08	69	13	230	3	6	5	6	5	
WAM	163935	*D. branchia*	P5	70	2.95	7.38	4.23	2.82	1.15	71	14	232	3	6	5	6	5	
WAM	166546	*D. branchia*	P5	75	4.06	8.22	5.10	3.22	1.18	67	14	257	3	6	5	6	5	
WAM	166641	*D. branchia*	P5	75	3.78	8.02	4.51	3.21	1.19	69	14	185	3	6	5	6	5	
WAM	170131	*D. branchia*	P5	76	3.28	8.40	4.46	3.29	1.21	66	14	146	3	6	5	6	5	
WAM	170660	*D. branchia*	P5	77	3.47	7.80	4.27	3.07	1.22	71	14	134	3	6	5	6	5	
WAM	174663	*D. branchia*	P5	51	2.53	6.48	3.13	2.37	1.07	67	14	151	3	6	5	6	4	
SAMA	29365	*D. branchia*	P5	67	2.79	7.578	4.48	3.20	0.95	70	14	-	3	6	5	6	5	
SAMA	71375	*D. reticulata*	P6	51	2.66	5.95	4.17	2.20	0.84	63	14	76	3	6	5	6	5	
QM	90689	*D. reticulata*	P6	45	2.57	6.11	3.30	2.99	1.00	65	14	-	-	6	5	6	5	
QM	95572	*D. reticulata*	P6	49	2.26	5.76	3.62	2.31	-	66	14	-	-	-	-	-	-	
QM	J70674	*D. reticulata*	P6	84	4.08	7.89	4.81	3.19	1.21	67	14	199	3	5	4	5	4	
QM	J70675	*D. reticulata*	P6	70	3.81	7.16	4.21	2.75	1.04	63	15	125	3	6	5	6	5	
QM	J80136	*D. reticulata*	P6	51	2.50	6.02	3.42	2.30	0.98	63	15	123	3	6	5	6	5	
QM	J84130	*D. reticulata*	P6	54	3.02	6.15	3.21	2.26	-	66	14	-	3	6	5	6	5	
QM	J88438	*D. reticulata*	P6	52	2.44	6.55	3.81	2.44	1.16	73	14	146	3	6	5	6	5	
QM	J95799	*D. reticulata*	P6	80	3.58	8.13	5.34	3.14	1.36	63	14	246	3	6	4	6	5	
QM	84129	*D. reticulata*	P4	56	2.64	6.01	3.29	2.30	1.23	65	14	-	-	-	-	-	-	
QM	J94238	*D. reticulata*	P4	55	2.69	6.43	3.79	2.63	0.97	69	14	168	3	6	5	6	5	
QM	93849	*D. reticulata*	P3	33	2.34	4.99	2.62	1.99	0.97	62	14	-	-	5	5	5	4	juv
QM	J58918	*D. reticulata*	P3	66	3.37	7.26	4.05	2.80	1.34	61	14	213	3	6	5	6	5	
QM	J87293	*D. reticulata*	P3	48	2.83	6.89	3.38	2.68	1.15	62	14	-	-	5	4	5	4	