



Genomic analysis of Bornean geckos (Gekkonidae: *Cyrtodactylus*) reveals need for updated taxonomy

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Abstract

Using molecular genetic data, recognised diversity within the gecko genus *Cyrtodactylus* has more than doubled, with many lineages that were once thought to be wide-ranging being delimited into multiple independent species. On the Southeast Asian island of Borneo, there has been a recent renewed focus on reptile taxonomy, as genetic data have demonstrated a high amount of unrecognised biodiversity. We herein advance this taxonomic trend by delimiting three distinct species within the *Cyrtodactylus consobrinus* species complex: *C. consobrinus*, *C. kapitensis* sp. n., and *C. hutan* sp. n. To do so, we use a combination of ddRAD-seq and single-locus data, and morphological data. Using genomic data, we test species and population boundaries within the *consobrinus* species complex and show minimal population structure but high species-level diversity. Despite not finding uniquely diagnostic morphological characters to delimit the new species, we suggest a combination of characters that can be used to identify each lineage. Lastly, we use our data to comment on the status of *C. malayanus*, with indications that this lineage is also better considered a species complex. These data highlight the prevalence of unrecognised lineages on Borneo, many of which face threats due to increasing deforestation and other anthropogenic pressures.

KEYWORDS

ddRADseq, morphology, multispecies coalescent, population genetics, Southeast Asia, species delimitation

1 | INTRODUCTION

The gecko genus *Cyrtodactylus* (Gekkonidae) has been the focus of many molecular systematic and taxonomic studies in the past decade, resulting in an expanded knowledge of the group and many recently recognised species (Chan et al., 2023; Chomdej et al., 2021; Davis et al., 2020; Grismer et al., 2018, 2020, 2021; Luu et al., 2016; O'Connell et al., 2019; Oliver et al., 2018; Wood et al., 2012). Studies on the Southeast Asian island of Borneo have revealed similar patterns, in which there is a high amount of genetic diversity present but a comparatively low number of recognised species (Davis et al., 2020). Unveiling this hidden diversity led to the recognition of five new species in two years, and molecular phylogenetic methods have highlighted abundant population-level diversity (Davis et al., 2019; Davis et al., 2021; Riyanto et al., 2021). However, the combination of having limited molecular genetic data available and highly conserved interspecific morphology among Bornean *Cyrtodactylus* has hindered taxonomic progress (Davis et al., 2021; Hikida, 1990). Despite these difficulties, 12 species are recognised on Borneo, of which 11 are endemic, with *C. consobrinus* being the sole species also occurring extraliminally.

Despite evidence that *Cyrtodactylus consobrinus* (Peters, 1871) and its sister taxon *C. malayanus* (De Rooij, 1915) may comprise species complexes rather than biological species (Davis et al., 2020), updating their taxonomies within and beyond Borneo has proved difficult for a diversity of reasons. First, all lineages currently identified as *C. consobrinus* bear strong morphological resemblance to one another and have high intra-lineage morphological variation. The noted variation impedes taxonomic changes due to difficulty establishing diagnostic characters. Second, the geographic distributions of *C. consobrinus* and *C. malayanus* are not well-defined. As a result, genetic and museum records are often mislabeled, thus suggesting largely overlapping geographic distributions for the species (Asad et al., 2015; Das, 2007; Hikida, 1990). Although existing molecular genetic data for the *C. malayanus* group are limited, they suggest that the species primarily occurs in the Indonesian portion of Borneo (Kalimantan). Third, the limited number of herpetofaunal studies conducted in Kalimantan, which comprises approximately two-thirds of the island, has hindered taxonomic progress within the group. In total, only two *Cyrtodactylus* species (*C. malayanus* and *C. hamidyi* Riyanto et al., 2021) are known from Kalimantan, neither of which are considered endemic to the region. Lastly, *C. consobrinus* has a type locality of Gunung Matang, Kuching Division, Sarawak, but *C. malayanus* lacks a specific type locality. The designated type locality for the *C. malayanus* is “Indo-Australian Archipelago”

(De Rooij, 1915). Establishing a more precise type locality is essential to avoid recognising a “new species” from the *malayanus* complex that actually represents *C. malayanus sensu stricto*.

Confounding identifications for *Cyrtodactylus consobrinus* and *C. malayanus* is not unexpected, as they are closely related phylogenetically, share similar morphological and life history characteristics, and lack precise information of their geographic distributions. Based on the type series, both species are large-bodied geckos bearing dorsal body bands and a reticulated pattern on the occiput. However, type material for *C. malayanus* has a vertebral line that separates the dorsal bands – a pattern lacking in *C. consobrinus*. The two species are further distinguished by the larger size of *C. consobrinus* and often the presence of enlarged femoral scales, although this character has variability (Hikida, 1990). The morphological features of *C. malayanus* also generally overlap with *C. ingeri*, which has a type locality of Poring Hot Springs, Ranau District, Sabah, with the key distinguishing features being a different colour pattern and a more slender body (Hikida, 1990). Few publications have documented the ecology of *C. malayanus* (Inger & Greenberg, 1966; van Rooijen & van Rooijen, 2002), and we show herein that those records are likely for lineages of the *consobrinus* complex rather than *C. malayanus*.

Determining species boundaries among morphologically cryptic lineages adds complexity to species delimitation, often requiring large datasets to accurately interrogate (Singhal et al., 2018). To address the uncertainties within and between the two focal species of this study, we use genomic data spanning the *consobrinus* and *malayanus* complexes. We bolstered this dataset with samples of *Cyrtodactylus* sp. and *C. limajalur* Davis et al., 2019, which form a clade sister to the *consobrinus/malayanus* clade, to infer a species tree (Davis et al., 2020). Further, we use the genomic data to identify genetically distinct populations and assess whether distinct lineages in the *consobrinus* complex are admixed. We supplement the genomic analyses with morphological data for each population and conduct multivariate statistics to determine whether the lineages occupy distinct regions of morphospace. Combining these data, we give specific recognition to two lineages comprising the genetic diversity of the *consobrinus* complex. Lastly, we provide recommendations for making future taxonomic changes within *C. malayanus* in a responsible manner. This study compounds the need to conduct substantially more herpetofaunal studies on Borneo using molecular genetic data to obtain accurate estimates of the island's endemism. With Borneo experiencing increasing habitat fragmentation, many lineages that remain unrecognised, due to being lumped within morphologically cryptic or conserved species complexes,