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Systematics and phylogeography of the widely distributed African skink *Trachylepis varia* species complex

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ABSTRACT

A systematic study of the *Trachylepis varia* complex was conducted using mitochondrial and nuclear DNA markers for individuals sampled across the species range. The taxonomic history of *T. varia* has been complicated and its broad geographic distribution and considerable phenotypic variation has made taxonomic revision difficult, leading earlier taxonomists to suggest that *T. varia* is a species complex. We used maximum likelihood and Bayesian inference to estimate gene trees and a multilocus time-tree, respectively, and we used these trees to identify the major clades (putative species) within *T. varia*. Additionally, we used morphological and color pattern data to distinguish and revise the taxonomy of the southern African clades. The major clades recovered in the multilocus time-tree were recovered in each of gene trees, although the relationships among these major clades differed across gene trees. Genetic data support the existence of at least eight species within the *T. varia* complex, each of which originated during the mid to late Miocene or early Pliocene. We focus our systematic discussion on the southern African members of the *T. varia* complex, revive *Trachylepis damarana* (Peters, 1870) and *T. laevigata* (Peters, 1869), and designate lectotypes for *T. damarana* and *T. varia*.

1. Introduction

1.1. Background

Trachylepis (Lygosominae) is a large group (> 80 species) of skinks occurring in Sub-Saharan Africa and Madagascar that likely includes multiple species complexes (Mausfeld et al., 2000; Karin et al., 2016; Metallinou et al., 2016; Uetz and Hallermann, 2016). The phylogenetic position of *Trachylepis* within the *Mabuya* group (Lygosominae) was recently inferred from a multilocus DNA dataset (Karin et al., 2016), but species-level relationships are not well understood within *Trachylepis*. Furthermore, relatively few studies have used genetic data to resolve relationships within *Trachylepis* species complexes (Mausfeld-Lafdhiya et al., 2004; Jesus et al., 2005; Ceriaco et al., 2016; Lima et al., 2013; Sindaco et al., 2012; Portik et al., 2011; Portik and Bauer, 2012). Nevertheless, morphological data suggest that several wide-ranging species, including *Trachylepis affinis*, *T. maculilabris*, and *T. varia*, are each composed of multiple species (Broadley, 1966; Jacobsen, 1989). Phylogeographic studies using genetic and phenotypic data are needed to clarify species relationships within taxa that are suspected of being species complexes and to aid future studies examining species relationships within *Trachylepis*.

The Variable Skink (*Trachylepis varia*) is broadly distributed across Sub-Saharan Africa, has been considered a species complex (Jacobsen, 1989), and has six junior synonyms (Peters, 1869, 1870, 1871; Bocage, 1867, 1872; Loveridge, 1953). Loveridge (1920, 1933) noted that *T. varia* populations frequently differ in color pattern and morphology, but this species' large range (Fig. 1) prevented earlier taxonomists from conducting a comprehensive phylogeographic study. Peters (1867) described *T. varia* (as *Euprepes varius*) and three additional *Trachylepis* that were later synonymized with *T. varia* by Loveridge (1957), including *Euprepes laevigatus* Peters, 1869 (type locality: “ebbenfalls in Gerlachshoop” [northern Limpopo Province, South Africa]; holotype: ZMB 6224); *Euprepes damaranus* Peters, 1870 (type locality: “Damaraland” [Namibia]; syntypes: ZMB 6153 and NRM 2149); and *Euprepes isselii* Peters, 1871 (type locality: “Keren, im Bogoslande” [Eritrea]; syntypes: ZMB 7272 (9 specimens) and MSNG 27778 (23 specimens)). Additionally, Boulenger (1887) synonymized *Euprepes Olivierii* var. *albopunctatus* Bocage, 1867 (type localities: Benguella and Catumbella, Angola; type specimens destroyed by fire) and *Euprepes angolensis* Bocage, 1872 (type localities: Biballa and Dondo, Angola; syntypes: five individuals, including two individuals collected by Anchieta from Biballa and three individuals collected by Bayão from Dondo, destroyed by fire) with *T. varia*, an arrangement with which Bocage (1895) later concurred. Broadley (1966) synonymized *Mabuya varia nyikae* Loveridge, 1953 (type locality: “Nyika Plateau above Nchenachena, at

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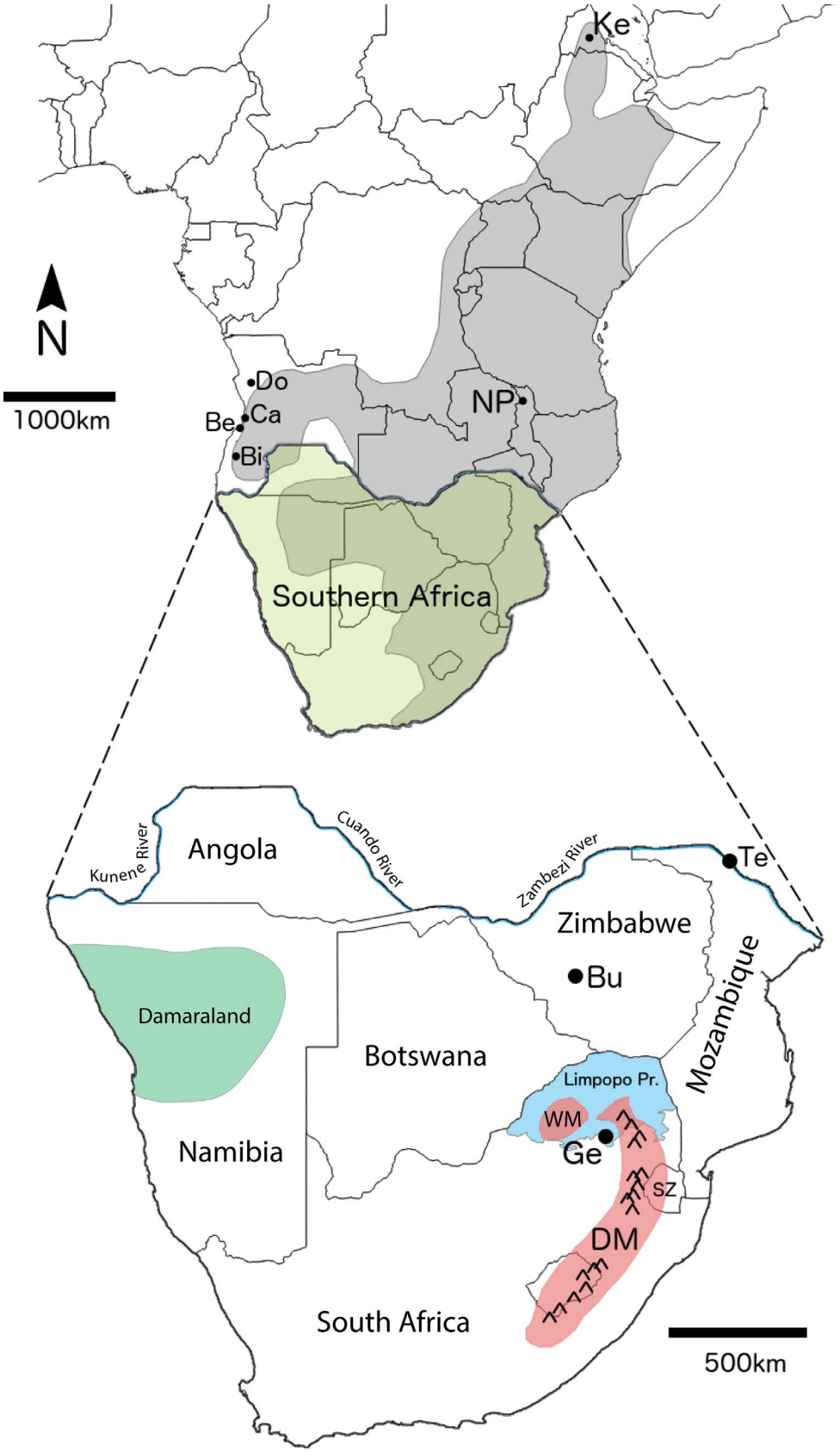

Fig. 1. Map of the study area. Gray shading indicates the distribution of the *Trachylepis varia* complex, based on occurrences reported by Bates et al. (2014), Broadley (1966), Jacobsen (1989), Largen and Spawls (2010), Parker (1942), Pietersen et al. (2013), Pietersen (2014), Spawls et al. (2004), and Scortecci (1928, 1930, 1931). Abbreviations: *Angola*: Benguella (Be); Biballa (Bi), Catumbella (Ca), Dondo (Do); *Eritrea*: Keren (Ke); *Malawi*: Nyika Plateau (NP); *Mozambique*: Tete (Te); *South Africa*: Drakensberg Mountains (DM), Gerlachshoop (Ge), Waterberg Massif (WM); *Swaziland* (SZ); *Zimbabwe*: Bulawayo (Bu). Southern Africa traditionally does not include Angola, but we chose to include southeastern Angola in this study to capture additional occurrence records for Maxent analyses. Damaraland is approximated for when Peters (1870) described *Euprepes damaranus* (= *Trachylepis damarana*).

7000 feet, northwest of Lake Nyasa, Nyasaland" [Malawi]; holotype: MCZ R-50860) with *T. varia*.

Jacobsen (1989) recognized an additional species that he considered to be closely related to *Trachylepis varia* and morphologically intermediate between *T. varia* and *Trachylepis lacertiformis*. Although Jacobsen (1989) collected specimens of this new species (which he referred to as "*Mabuya* sp. aff. *M. lacertiformis*" or "*Mabuya* sp. nov.") from northeastern South Africa and provided a species account in his