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Systematics and natural history of Southeast Asian Rock Geckos (genus *Cnemaspis* Strauch, 1887) with descriptions of eight new species from Malaysia, Thailand, and Indonesia

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Abstract

A well-supported and well-resolved phylogeny based on a concatenated data set from one mitochondrial and two nuclear genes, six morphological characters, and nine color pattern characters for 44 of the 50 species of the Southeast Asian Rock Geckos (genus *Cnemaspis* Strauch, 1887) is consistent with the previous taxonomy of *Cnemaspis* based solely on morphology and color pattern. *Cnemaspis* is partitioned into four major clades that collectively contain six species groups. The monophyly of all clades and species groups is strongly supported and they are parapatrically distributed across well-established, biogeographical regions ranging from southern Vietnam westward through southern Indochina, southward through the Thai-Malay Peninsula, then eastward to Borneo. Eight new species (*Cnemaspis omari* sp. nov. from the Thai-Malaysian border; *C. temiah* sp. nov. from Cameron Highlands, Pahang, Malaysia; *C. stongensis* sp. nov. from Gunung Stong, Kelantan, Malaysia; *C. hangus* sp. nov. from Bukit Hangus, Pahang, Malaysia; *C. sundagekko* sp. nov. from Pulau Siantan, Indonesia; *C. peninsularis* sp. nov. from southern Peninsular Malaysia and Singapore, and *C. mumpuniiae* sp. nov. and *C. sundainsula* sp. nov. from Pulau Natuna Besar, Indonesia) are described based on morphology and color pattern and all but *C. sundagekko* sp. nov. are included in the phylogenetic analyses. *Cnemaspis kendallii* is polyphyletic and a composite of six species. An updated taxonomy consistent with the phylogeny is proposed for all 50 species and is based on 25 morphological and 53 color pattern characters scored across 594 specimens. Cladogenetic events and biogeographical relationships within *Cnemaspis* were likely influenced by this group's low vagility and the cyclical patterns of geographical and environmental changes in Sundaland over the last 25 million years and especially within the last 2.5 million years. The phylogeny indicates that nocturnality, diurnality, substrate preferences, and the presence of ocelli in the shoulder regions have evolved independently multiple times.

Key words: *Cnemaspis*, Gekkonidae, Southeast Asia, new species, Sunda Shelf, biogeography, phylogeography

Introduction

Southeast Asia harbors 20–25% of the planet's terrestrial biodiversity in only 4% of its landmass. This makes it one of the great megadiverse hotspots of the world (Corlett 2009) even though much of its most prominent, geographic feature, the vast Sunda Plains, lie submerged beneath the South China Sea. Given that this is the second largest subareal margin of a continental shelf in the world (Parnell 2013) means that much of Sundaland's terrestrial biodiversity is in a refugial state being restricted to small, Sundaic islands on the southern Sunda Plains and the areal, continental fringes of the Sunda Shelf (Grismer *et al.* 2011a). Furthermore, the current geographic outline of Sundaland has existed intermittently for only 2% of the last 2.4 million years (Woodruff 2010) owing to multiple, glaciostatic driven, sea-level changes that have repeatedly exposed and submerged the Sunda Plains while uniting Indochina with Borneo, Java, Sumatra, and the Thai-Malay Peninsula. Therefore, the phylogeographic relationships of Sundaic species and many species from southern Indochina cannot be accounted for by current geography and ecology alone but reconciled only in the context of cyclical changes in sea levels and concomitant climatic fluctuations (Cannon *et al.* 2009; Bell *et al.* 2010, 2011; Loredó *et al.* 2013; Woodruff 2010).

One group that may offer insight into environmentally driven, cyclical speciation events in Sundaland is the monophyletic Southeast Asian branch of the polyphyletic gekkonid genus *Cnemaspis* Strauch (Gamble *et al.* 2012). *Cnemaspis* (*sensu* Smith 1933; Gamble *et al.* 2012) contains approximately 105 Afro-Asian scansorial species whose many morphological specializations are adaptations for moving about on flat, elevated surfaces during low levels of illumination. As such, the morphology within this genus appears to have been highly

Comments on genetic divergence with *Cnemaspis*

The genetic divergence based on ND2 seen among species of *Cnemaspis* greatly exceeds that seen among species within other gekkotan genera such as *Hemiphyllodactylus*, *Phyllopezus*, *Pseudogekko*, *Ptychozoon*, *Cyrtodactylus*.

Comments on integrative taxonomy

A general assumption concerning integrative taxonomic analyses is that currently recognized, widespread species are composed of morphologically cryptic species whose detection is possible only through the use of molecular analyses (see Grismer *et al.* 2013b for a discussion). On the contrary, the majority of integrative analyses result in demonstrating that diagnostic, morphological characters were present but overlooked by the last author(s) to revise the group and their subsequent discovery was simply prompted by the results of a molecular analysis (see references in Grismer *et al.* 2013b). Prior to 2003, *Cnemaspis* was known from 10 species. Between 2003 and this study, we and associated authors described 34 of the then 44 known species on the basis of morphology and color pattern alone (Das & Grismer 2003; Grismer & Das 2006; Grismer & Ngo 2007; Chan & Grismer 2008; Grismer & Chan 2008, 2009, 2010; Grismer *et al.* 2008a,b, 2009, 2010a,b,c; Grismer 2009; Chan *et al.* 2010; J. Grismer *et al.* 2010; Wood *et al.* 2013). The analysis herein indicated the only error made was that a geographically outlying specimen from southern Thailand (included as part of the type series of *C. chanardi*) and continental populations of *C. roticanai* actually constituted a new species, *C. omari* sp. nov., which turned out to be the sister species of *C. roticanai sensu stricto*. This mistake was made because Grismer *et al.* (2010a) and Grismer & Chan (2010) did not have all the material available on hand to compare. The molecular analysis indicated these were different taxa (Fig. 2), prompting a reexamination herein by comparing all the material together and in so doing, we discovered additional, diagnostic, morphological characters. Thus, integrative taxonomic analyses are not necessarily revealing cryptic species but rather highlighting less than efficient morphological analyses.

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