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Underestimated diversity of *Cnemaspis* Strauch, 1887 (Sauria: Gekkonidae) on karst landscapes in Sarawak, East Malaysia, Borneo

Izneil Nashriq [1] & Indraneil Das [2]

[1,2] Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, 94300 Kota Samarahan, Sarawak, Malaysia.
[1] izneilnshrq@gmail.com, [2] idas@unimas.my (corresponding author)

Abstract: The paraphyletic group of Old World rock gecko genus *Cnemaspis*, currently comprises ~180 described species from Africa and Asia. The south-east Asian clade with 63 described species, is most diverse on the Thai-Malay Peninsula, with just five species known from Borneo, an island biodiversity hotspot. Karst regions are known as centres for species endemism, and vast areas of caves and karst exist across northern Borneo. Fieldwork from 2017 to 2020 recovered additional undescribed species of *Cnemaspis* from areas of karst forests in western and northern Sarawak. These discoveries emphasize the importance of preserving areas of limestone karst within rainforest areas for maintaining species diversity, as well as accelerating research on documenting the biota.

Keywords: Biodiversity, rock gecko, systematics.

Bahasa Malaysia: Kumpulan paraphyletic cicak batu genus *Cnemaspis* dari Dunia Lama, kini dianggarkan mempunyai ~180 spesis dikenal pasti dari Afrika dan Asia. Klad Asia tenggara dengan 63 spesis terhurai, dilihat lebih pelbagai di semenanjung Thai-Malay, dengan hanya lima spesis dikenal pasti dari Borneo, sebuah pulau kaya dengan kepelbagaian hidupan. Kawasan batu kapur diketahui sebagai kawasan tumpuan spesis endemik, dengan jumlah bilangan kawasan gua dan batu kapur yang besar di utara Borneo. Kerja lapangan daripada 2017 hingga 2020 telah menambahkan bilangan spesis Cnemaspis dari kawasan hutan batu kapur di barat dan utara Sarawak. Penemuan ini menekankan kepentingan memelihara kawasan batu kapur dalam hutan hujan tropika untuk menjaga kepelbagaian spesis, serta meningkatkan kajian dan dokumentasi biota.

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Author details: Izneil Nashriq holds an MSc in Animal Systematics from the Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak. His fields of interest include taxonomy, ecology and biogeography. Since 2016, he have been a member of the Herpetofaunal Biology Lab, assisting with project involving herpetofaunal conservation. Indraneil Das has a DPhil in Animal Ecology from the University of Oxford, and was a Fulbright Fellow at the Museum of Comparative Zoology, Harvard University. He is currently Professor at the Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, where he pursues his research and teaching interests in ecology, systematics and conservation biology.

Author contributions: ID conceived, designed and obtained funding. ID and IN collected field data and wrote the manuscript.

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INTRODUCTION

Sarawak State of East Malaysia, located on the northwestern region of the island Borneo, can be divided into two mineralization zones, corresponding to geological provinces, namely, West Sarawak that hosts important metalliferous mineral deposits, which geologically forms part of the Sunda Shield; and central-northern Sarawak, which is renowned for fossil fuels, such as oil, gas and coal deposits. Limestone outcrops cover 520km^2 (or 0.4%) of Sarawak, and are reported to be shallow marine deposits ranging from Upper Carboniferous to Miocene (Gendang et al. 2008). Older limestone deposits are located in western Sarawak, while the younger one are found in central and northern Sarawak. Karstic regions have been regarded as biodiversity reservoirs that can be used as stock for repopulating degraded environments during ecosystem reassembly (Schilthuizen 2004). Past research conducted on karst formations and adjacent limestone forests in the Sundas have resulted in improved knowledge of endemic species of flora and invertebrates, as well as better appreciation of their endemicity. Microendemic karst-dwelling species of squamate reptiles too have been identified and described from such landscapes (Ellis & Pauwels 2012; Grismer et al. 2015).

In Borneo, recent discoveries of lizard species have been made, especially in areas with forest cover, including species of *Cnemaspis* (Grismer & Chan 2009; Kurita et al. 2017), *Cyrtodactylus* (Hayden et al. 2019), and *Lygosoma* (Karin et al. 2018), highlighting the underestimated nature of the diversity. At the same time, the landscape of Borneo is experiencing rapid change through deforestation from activities such as large- to small-scale agriculture and colonization, unsustainable logging, fires, mining and construction of infrastructure (Bennet 2017), resulting in the degradation of the ecosystem. *Cnemaspis* Strauch, 1887 is a lizard genus allocated to the family Gekkonidae, comprising ~180 described species from tropical Africa and Asia (Uetz et al. 2021), making it one of the most speciose Old World gekkonid genera. As currently constituted, the genus has been shown to be polyphyletic (Gamble et al. 2012; Grismer et al. 2014). Members of the genus in Asia occupy habitats ranging from lowland dipterocarp forests to primary and old-growth forests, often within karst, granite or sandstone landscapes (Das & Bauer 1998; Iskandar et al. 2017).

The south-east Asian *Cnemaspis* group has been reported from areas of Myanmar, Thailand, Vietnam, Cambodia, Laos, Peninsular Malaysia, Singapore, Sumatra, Borneo, and Java, in addition to numerous small and mid-sized islands off some of these landmasses. With its distribution extending from the subtropical eastern Himalaya and Indo-China, to tropical areas of Sundaland, the highest diversity is encountered on the Thai-Malay Peninsula (Kurita et al. 2017). Phylogenetic analyses of south-east Asian *Cnemaspis* have revealed two divergent lineages: the southern Vietnamese insular endemics and a lineage containing three major clades referred to as the Pattani, northern Sunda, and southern Sunda clades distributed sporadically along the northern, western and southern edges of the Sunda Shelf, extending from southern Vietnam, Cambodia and Thailand, southward through the Thai-Malay Peninsula, to Borneo (Grismer et al. 2014, 2015; Kurita et al. 2017; Wood et al. 2017). The Pattani clade, restricted to the southernmost portion of peninsular Thailand, is sister to the northern Sunda and southern Sunda sister clades. The northern Sunda clade extends from Vietnam to central Peninsular Malaysia, while the southern Sunda clade extends from southern Peninsular Malaysia and Singapore, eastward through the Seribuat, Anambas, and Natuna archipelagos to northwestern Borneo.

The first member of the genus *Cnemaspis* on Borneo was reported by Gray (1845), described as *Heteronata kendallii*, based on two specimens presented to the British Museum of Natural History by Captain Edward Belcher, with locality given simply as "Borneo". Smith (1925) described the second Bornean species, *Gonatodes nigridius*, from "Mt. Gading" (= Gunung Gading). Dring (1979) subsequently discovered that one of Gray's syntypes was a juvenile *Cnemaspis nigridia* (Smith, 1925), and designated the other as the lectotype of *Cnemaspis kendallii*. Das & Bauer (1998) described *Cnemaspis dringi* from Labang Camp, Bintulu, Sarawak and Grismer & Chan (2009) recorded the first karst-endemic species on Borneo, *Cnemaspis paripari* from Gua Pari Pari (Fairy Cave) and Gua Angin (Wind Cave), in the Bau region of Sarawak. The most recent discovery was by Kurita et al. (2017), who described *Cnemaspis leucura* from Gunung Penrissen, Sarawak. These five species currently represent the known diversity of the genus on Borneo. Bornean *Cnemaspis* are represented by two major lineages (the *nigridia* group and the *kendallii* group); however, Kurita et al. (2017) recovered a basal polytomy of *Cnemaspis dringi*, the *nigridia* group, and the *kendallii* group, suggesting multiple origins of the Bornean *Cnemaspis*.

During recent fieldwork, we discovered additional populations of *Cnemaspis* in areas of limestone formations which, on the basis of morphological

characters and phylogenetic divergence, we regard as new species. We here describe the distribution and habitats of these geckos.

MATERIALS AND METHOD

Inventories were conducted between 2017 and 2020, and collections were made during both day and night at a number of localities in Sarawak. A hand-held Global Positioning System Garmin, GPSMap 76CS receiver (datum WGS 84) was used for georeferencing. We used Google Maps and Google Earth Pro to identify areas for sampling, prioritizing the presence of intact vegetation with a greater possibility of the occurrence of members of the genus. Sites inspected included national parks, nature reserves and other areas within karst formations, as well as non-karst areas. The visual encounter survey method was used to locate individuals, and macro- and micro-habitat features were identified. Specimens were photographed using a Nikon D600 DSLR camera and 105mm Micro-Nikkor f/2.8 D lens, illuminated by a speedlight flash unit (SB800), using a Lastolyte softbox. Temperature and humidity of the study sites were recorded using CENTER 315 humidity temperature meter. Specimens were collected manually, euthanized with the use of sodium pentobarbital, fixed in 10% buffered formalin prior to storage in 70% ethanol in the collection of the museum of the Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak (UNIMAS). Tissue samples were taken and preserved in 95% ethanol for DNA analysis.

Study sites

We obtained research permit for collection and permission to enter national parks and conduct studies from the Sarawak Forest Department for multiple localities. Habitat associations of members of the

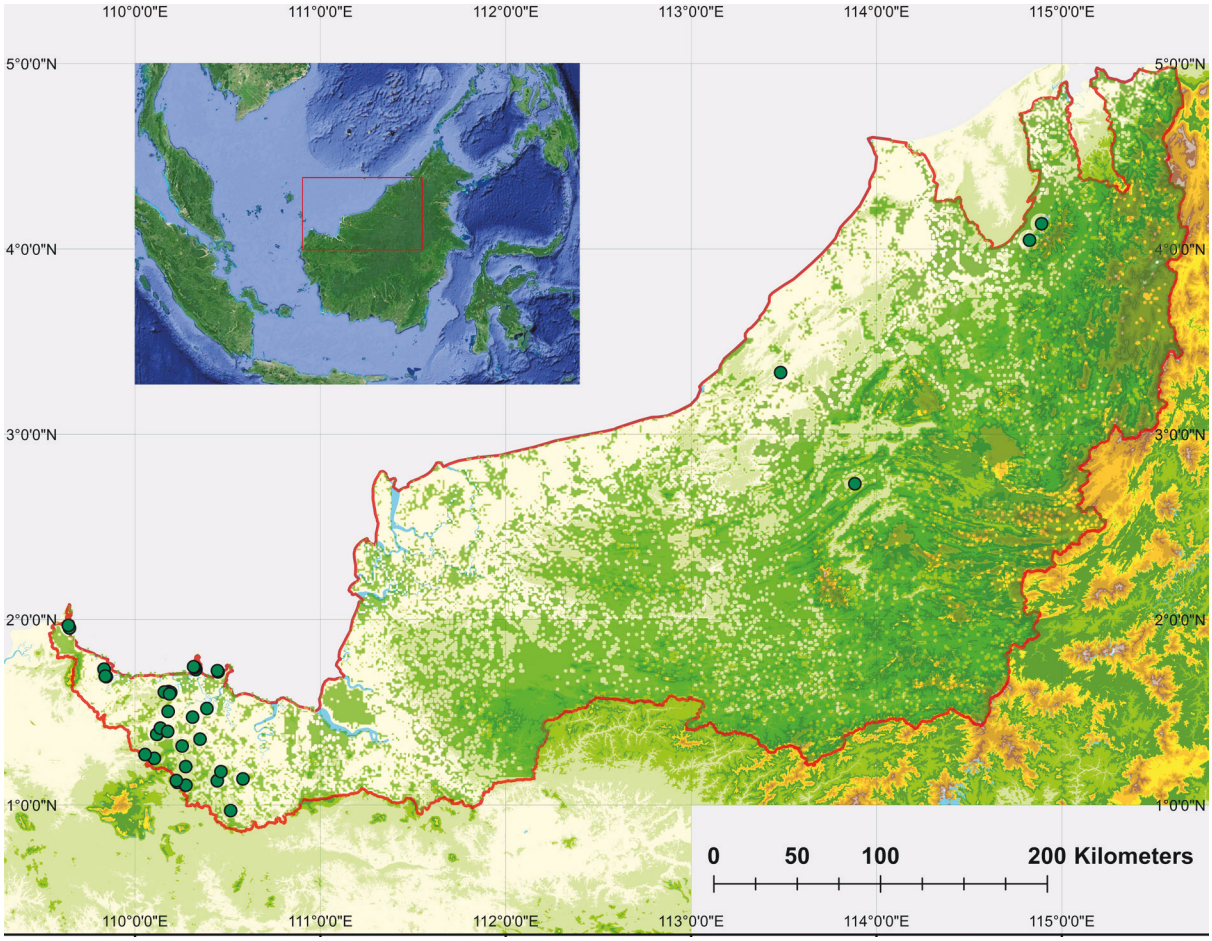

Image 1. Forest cover and records of *Cnemaspis* species in Sarawak, East Malaysia. Insert: Map of Borneo and adjacent regions in south-east Asia showing the enlarged area below. Vector tile of Sarawak Forest Cover 2019 by Sarvision. Updated as of October 2020. Developed for Heart of Borneo (HoB) initiative by WWF-Netherlands, WWF-Indonesia and WWF-Malaysia.

lineage and habitat assessments were conducted by day, while collections of specimens were conducted between 2000–2300 h. A total of 27 areas were surveyed during the present study (Table 1), including primary and secondary forests. Sites included the Kayan Plateau sandstone of Bako National Park; Kayan sandstone of Gunung Gading National Park, the Serapi Range, Kubah National Park, Santubong National Park, and on the Pedawan Formation of Gunung Penrissen. The Bau Limestone which includes karst towers and formations, such as Fairy Cave and Wind Cave Nature Reserve, and Dered Krian National Park; Kedadom and Pedawan limestone formations in Siburan and Serian District, consisting of multiple karst hills and caves, such as Gua Raya, Gua Rabus, Gua Silabur, Gua Simadang and Gua Sireh; the Belaga Formation of central Sarawak, Pelagus National Park; the Nyalau/Sibuti Formation of Niah National Park; and also the Melinau Limestone and Mulu Formation of the Gunung Mulu National Park, northern Sarawak.

Limestone hills are characteristically steep-sided, with subvertical to overhanging cliffs. The base of limestone hills exhibit deep horizontal notches or undercuts due to dissolution by streams, groundwater or swamp water, and the collapse of the limestone cliffs contributing to the reduction in size of limestone hills. Mazed with numerous caverns and cave systems, limestone hills range in height and size, and provide multiple microclimates.

RESULTS

In western Sarawak, habitats occupied by *Cnemaspis* are present both within the protected areas network (such as national parks) and in unprotected ones. Additional populations were recorded within the Siburan and Serian districts. The deposits of Kedadom and Pedawan formations are of Late Jurassic – Late Cretaceous age. The karst towers of these regions reach elevation of approximately 700m, and are dominated by mesophytic flora. Streams, often originate from these formations. Some of the karstic areas are bounded by human activities such as orchards and plantations, limestone mining and land development. Individuals were found usually on ground level spatially constrained to an area with multiple degree of surfaces. In northern Sarawak, the habitat of *Cnemaspis* is located within the Melinau Limestone formation, within the protected boundaries of Gunung Mulu National Park. Deposited in the Eocene to the Miocene, this geological formation reaches a height of approximately 1,700m. Specimens were found at ground level, on stalactites and on walls of the cave entrance.

Substrate identified associated with *Cnemaspis* can be classified into granite, limestone, sandstone and vegetation. *Cnemaspis kendallii* is here considered the most generalized species, being observed on multiple substrates, and showing overlapping distribution (= syntopic) with *C. nigridia*, *C. paripari*, and *C. leucura*. *C. kendallii* may persist in disturbed areas such as the detached forest patch of Sama Jaya Nature Reserve, which serves as a rainforest park in an urban setting. Covering 38ha, the population is disconnected from the major forest region. Another example of persistency is observed in the population of *C. paripari* from the Fairy Cave Nature Reserve which occurs as an isolated karst hill measuring about 4ha, detached from the major Bau Limestone formation by 800 m of lowland. Members of the genus are often found syntopic with other gecko species, especially Bent toed geckos, *Cyrtodactylus*.

Rock crevices act as shelters into which geckos typically retreat when threatened. Furthermore, crevices also serve as a nursery for eggs. Egg-clutches were observed in pairs, embedded within depressions of mineral formations in such moisture-laden microhabitats. For the first two species, communal nesting, as evidenced from multiple egg-scars on rocks, was noticed. Habitat descriptions of Bornean *Cnemaspis* are summarised in Table 2.

DISCUSSION

The discovery of undescribed *Cnemaspis* reveals the poorly-known nature of the herpetofauna of Borneo. Based on surveys and satellite imagery, sites of occurrence tend to be isolated and restricted to mineral formations and intact secondary to primary forests. Although environmental conversion can occur naturally, human activities have intensified the decline of many habitats. Major conservation concerns that can be identified from this study are major and minor agricultural practices, mining of limestone for industry and deforestation. These factors seriously influence the quality and extant of *Cnemaspis* habitats in Sarawak.

Populations of *Cnemaspis* geckos are fragmented by human intervention. The hills of the Bau Limestone stretching to the Pedawan formation and along with Kedadom and Sadong formations comprise karst outcrops of which some parts are mined for industrial uses such as cement production. Shifting agriculture and

Table 1. Study sites in Sarawak State, East Malaysia (Borneo), with reference to geological formations and general habitat descriptions. Asterix indicates locality where species of *Cnemaspis* have been recorded.

	Localities, Division	Coordinates	Geological Formation and General Habitat Type
1*	Bako National Park, Kuching	1.7179°N, 110.446°E	Plateau Sandstone Formation ~ 200m. Coastal forest, swamp forest, mixed dipterocarp forest
2*	Bengoh Range, Bau	1.252°N, 110.102°E	Kayan Sandstone Formation ~ 900m. Mixed dipterocarp forest, with agriculture and human settlements on foothills
3*	Borneo Highlands at Gunung Penrissen, Padawan	1.135°N, 110.221°E	Kayan Sandstone Formation ~ 1,000m. Mixed dipterocarp forest, submontane forest
4*	Dered Krian National Park, Bau	1.3802°N, 110.163°E	Bau Limestone Formation ~ 400m. Karst formation, dominated by herbaceous plants and mid-sized trees; conversion to commercial plantation on foothills
5*	Gua Angin, Bau	1.416°N, 110.133°E	Bau Limestone Formation ~ 50m. Cave systems, dominated by herbaceous plants and mid-sized trees
6*	Gua Pari Pari, Bau	1.381°N, 110.117°E	Bau Limestone Formation ~ 250m. Cave systems, dominated by herbaceous plants and mid-sized trees
7*	Gua Rabus, Temurang, Padawan	1.207°N, 110.273°E	Pedawan Formation ~ 500m. Cave system dominated by herbaceous plants and mid-sized tree; natural vegetation hemmed by horticulture
8	Gua Raya, Kampung Chupak, Serian	1.285°N, 110.429°E	Sadong Formation ~ 600m. Abandoned bird-nest harvesting operations in cave system, broken plank walks, dominated by herbaceous plants and mid-sized trees
9*	Gua Silabur, Lobang Batu, Tebakang, Serian	0.969°N, 110.516°E	Sadong Formation ~ 50m. Cave system dominated by herbaceous plants to mid-sized trees and bounded by local horticulture.
10*	Gua Simadang, Temurang, Padawan	1.207°N, 110.274°E	Pedawan Formation ~ 500m. Cave system dominated by herbaceous plants to mid-sized trees and bounded by local horticulture.
11*	Gua Sireh, Kampung Bantang, Serian	1.180°N, 110.463°E	Sadong Formation ~ 350m. Archaeological site. Cave system dominated by herbaceous plants and mid-sized trees, hemmed in by horticulture
12*	Gunung Gading National Park, Lundu	1.691°N, 109.845°E	Gading Formation ~ 850m. Mixed dipterocarp forest, with granite boulders and scree at foothills
13*	Kampung Mambong, Siburan	1.355°N, 110.351°E	Bau Limestone Formation ~ 100m. Weathered limestone hills, dominated by herbaceous plants and mid-sized trees, hemmed in by horticulture
14*	Kampung Puak, Bau	1.358°N, 110.141°E	Bau Limestone Formation ~ 400m. South of Dered Krian and Fairy Cave, its sharp limestone ridges dominated by herbaceous vegetation and mid-sized trees; small stream present
15*	Kampung Skio, Bau	1.396°N, 110.176°E	Bau Limestone Formation ~ 250m. Outcrops connected to Dered Krian formation; cave opening with small stream
16*	Kubah National Park, Kuching	1.612°N, 110.196°E	Kayan Sandstone Formation ~ 850m. Mixed dipterocarp forest; forest stream originate from upper elevation
17*	Lambir Hills National Park, Miri	4.198°N, 114.042°E	Lambir Formation ~ 450m. Mixed dipterocarp forest, with steep slope
18*	Limestone Hills of Jambusan-Samadang, Siburan	1.319°N, 110.255°E	Pedawan Formation ~ 300m. Karst formation, bounded by river and oil palm plantation
19*	Limestone hills, Serian-Tebedu, Serian	1.130°N, 110.444°E	Kedadom Formation ~ 300m. Karst formation, dominated by herbaceous vegetation; presence of small stream
20*	Gunung Mulu National Park, Miri	4.041°N, 114.812°E	Melinau Limestone Formation ~ 1,750 m; Mulu Formation ~2,376m. Massive karst formation, submetamorphic slates and hard sandstones, mixed dipterocarp forests at points of sampling; other vegetation types at higher elevations or other sites within the National Park
21	Nanga Pelagus, Belaga	2.169°N, 113.056°E	Pelagus Formation Low sandstone hills; small forest streams
22	Niah National Park, Miri	3.824°N, 113.761°E	Subis Limestone ~ 350m. Karst formation within lowland mixed dipeterocarp forest
23	Pelagus National Park, Belaga	2.188°N, 113.056°E	Pelagus Formation Mixed dipterocarp forest at edge of Rajang River
24*	Ranchan Pool Forest, Serian	1.143°N, 110.584°E	Sadong Formation ~ 800m. Sandstone hill with forest stream, frequented as recreational area
25*	Sama Jaya Nature Reserve, Kuching	1.522°N, 110.387°E	Alluvium flat ~ 0m. Forest reserve within city of Kuching, comprising Kerangas (Bornean heath) forests with blackwaters and mixed dipterocarp forest
26*	Gunung Santubong National Park, Kuching	1.743°N, 110.317°E	Kayan Sandstone Formation ~ 800m. Mixed dipterocarp forest, with streams and waterfalls
27	Tinbarap Oil Palm Plantation, Miri	4.055°N, 114.238°E	High Value Conservation forest ~ 0m. Conserved forest patch; blackwater swamp forest

Table 2. Summary of *Cnemaspis* habitat use and activity on Borneo.

Species	Active period	Preferred substrate			
		Granite	Limestone	Sandstone	Vegetation
kendallii	Diurnal	+	+	+	+
nigridia	Nocturnal	+	-	-	-
dringi	NA	NA	NA	NA	+
paripari	Nocturnal	-	+	-	-
leucura	Nocturnal	-	-	-	-
Species 1	Nocturnal	-	+	-	-
Species 2	Nocturnal	-	+	-	-
Species 3	Nocturnal	-	+	-	-

Image 2. Karsts habitat for *Cnemaspis* in Sarawak: Top and bottom left—limestone hills in Serian District | Top right—egg scars within crevices of limestone formation | Bottom right—*Cnemaspis* gecko on limestone substrate. © Izneil Nashriq

mining activities are both widespread and sometimes intense in Sarawak, which, if not mitigated or done sustainably, not only affect these geckos, but in a wider context, result in loss of biological diversity as a whole.

CONCLUSION

The accretion of species of *Cnemaspis* on Borneo has been somewhat sluggish, starting with *C. kendallii* in 1845, *C. nigridia* in 1925, *C. dringi* in 1998, *C. paripari* in 2009, and most recently, *C. leucura* in 2017. The effort of locating specimens may be thwarted by their occupancy of relatively inaccessible areas and microhabitats,

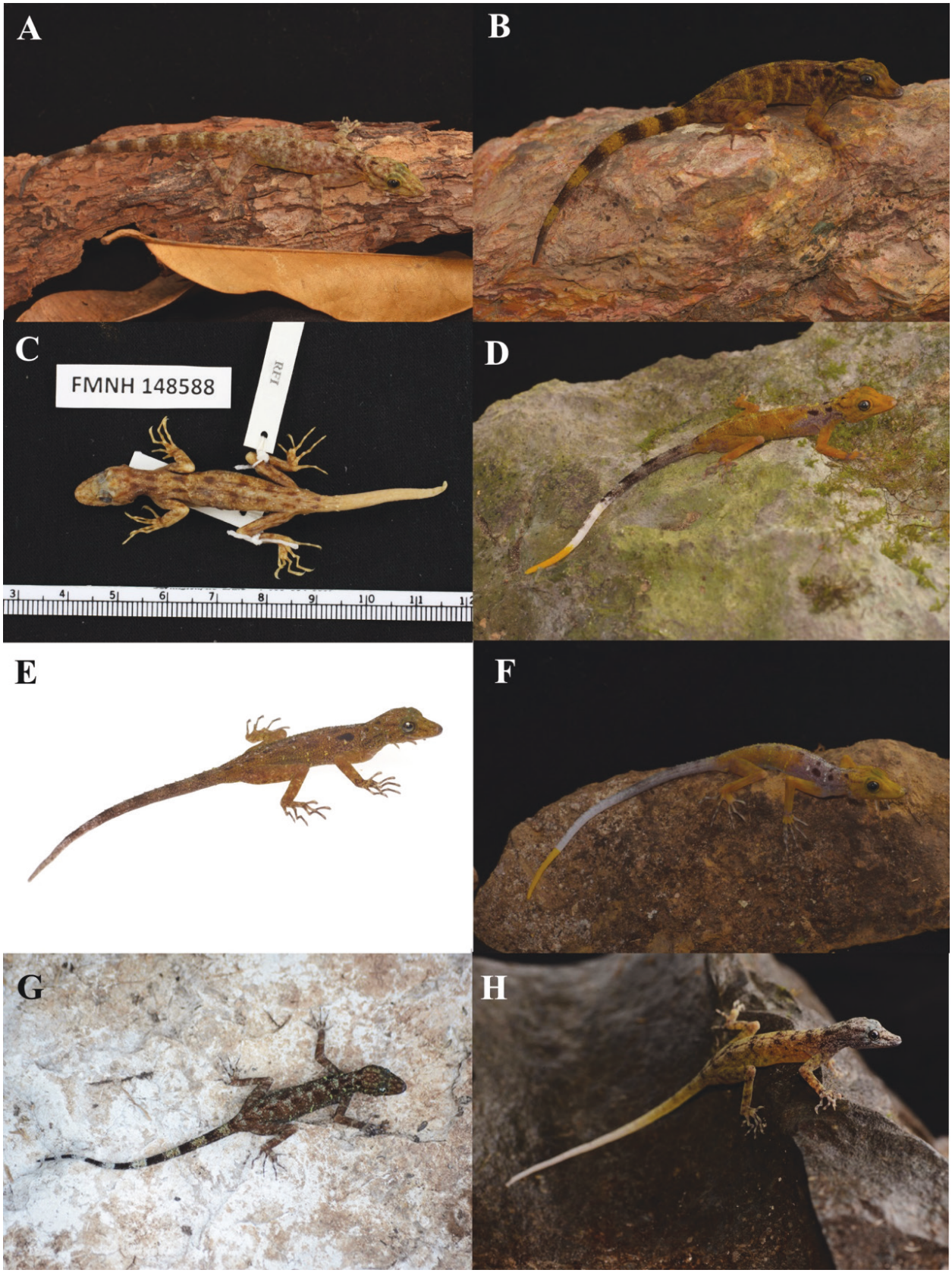

Image 3. Bornean species of rock geckos. A—*Cnemaspis kendallii* | B—*Cnemaspis nigridia* | C—*Cnemaspis dringi* | D—*Cnemaspis paripari* | E—*Cnemaspis leucura* | F—*Cnemaspis* Sp. 1 | G—*Cnemaspis* Sp. 2 | H—*Cnemaspis* Sp. 3. © A, B, D, F, H—Indraneil Das; C—Joshua Matta; E—Pui Yong Min; G—Hayden Davis

besides the ecologically cryptic nature of these species. In addition to the described species, four from western Sarawak, and one in central Sarawak, morphological and genetical data reveal the existence of three additional species from western and northern Sarawak. Mineral formations of Sarawak are home to a disproportionate number of *Cnemaspis*, all except one showing rupicolous adaptations. Only *C. kendallii* inhabits forested areas, and is sylvicolous. On the other hand, *C. nigridia* is restricted to granite formations; *C. paripari* endemic to limestone formations; and *C. leucura* from sandstone formations. All three undescribed species reported in this study inhabit separate limestone formations. This brings the number of species to a total of eight occurring on the island of Borneo, an increase of 60% of the fauna.

The study was focused largely in western Sarawak. The formations in western Sarawak are relatively more accessible compared to those of central and northern Sarawak. Future efforts should be directed in finding species of *Cnemaspis* in these latter areas, especially along regions of limestone karst.

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