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SYSTEMATICS AND BIOGEOGRAPHY OF BORNEAN GECKOS OF THE GENUS *CNEMASPIS* STRAUCH, 1887 (SAURIA: GEKKONIDAE), WITH THE DESCRIPTION OF A NEW SPECIES

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ABSTRACT. - Three species of the gekkonid genus *Cnemaspis,* one of them new, are shown to occur on Borneo. The ranges of the species appear to hug the north-western coast of Borneo, all species being recorded from Sarawak State, East Malaysia. Such a distribution is similar to that reported for a lineage of the Dipterocarpaceae, with affinities in peninsular Malaya and the Rhiau Archipelago. It is thought that the present day distribution of the gekkonids may be influenced by the drainage of the ancient river basins of Sundaland which presumably stopped their dispersal into central and eastern Borneo.

KEYWORDS. - Geckos, *Cnemaspis*, Gekkonidae.

INTRODUCTION

The tropical Old World (Africa and Asia) gekkonid genus *Cnemaspis* Strauch, 1887, currently contains 36 valid species in the Oriental region (Kluge, 1996; Das, 1993). Three nominal species of the genus *Cnemaspis* have been reported from the island of Borneo: *Cnemaspis kendallii* (Gray, 1845),*Cnemaspis affinis* (Stoliczka, 1870) and *Cnemaspis nigridius* (Smith, 1925b). Dring (1979) reported a fourth species from Bintulu District, Sarawak, but did not formally describe it. The purpose of this paper is to refine the description of the contents of the genus *Cnemaspis* from Borneo. In the process, one new species from Sarawak, north-western Borneo, is described, and the biogeography of the Sundaic species of the genus discussed.

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MATERIALS AND METHODS

The following measurements were taken with dial vernier calipers (to the nearest 0.1 mm): snout-vent length (SVL; from tip of snout to vent); tail length (TL; from anus to tip of tail); tail width (TW; width of tail at base); tibia length (TBL; distance between heel to knee); forearm length (FA; distance between elbow and palm); head length (HL; distance between angle of jaws and snout-tip); head width (HW; measured at angle of jaws); head depth (HD; maximum height of head, from occipital region to throat); body width (BW; greatest width of body); axilla to groin length (A-G; distance between posterior edge of forelimb and anterior edge of hindlimb); eye diameter (ED; greatest diameter of orbit); eye to nostril distance (E-N; distance between anterior-most point of orbit and nostrils); eye to snout distance (E-S; distance between anterior-most point of orbit and tip of snout); eye to ear distance (E-E; distance from anterior edge of ear opening to posterior corner of eyes); maximum ear diameter (EL; greatest diameter of ear opening); interorbital distance (IO; least distance between upper eyelids); and internasal distance (IN; distance between nares). Lamellae on digits were counted from the enlarged basal plate-like scansors to the tips.

Institutional abbreviations follow Leviton et al. (1985). Sources of geographical coordinates, unless otherwise mentioned, are Anon (1970; 1982a; 1982b). Referred materials are in Appendix I.

SYSTEMATICS

Cnemaspis kendallii (Gray, 1845)

(Figs. 1, 2, 7A)

Heteronota Kendallii J. E. Gray. 1845. Cat. Species Lizards Coll. Brit. Mus.: 174. Type locality: Borneo.
Gonatodes kendallii G. A. Boulenger. 1885. Cat. Lizards Brit. Mus. 1: 63.
Cnemaspis kendallii M. A. Smith. 1930. Bull. Raffles Mus. 3: 16.

History. - *Heteronota Kendallii* was described from Borneo (without precise locality) by Gray (1845), based on two specimens presented to the BMNH by Captain Edward Belcher. Dring (1979) subsequently found that one of the syntypes (BMNH XXII.92b) was actually a juvenile *Cnemaspis nigridius* (Smith, 1925a), and designated the other (BMNH XXII.92a) as the lectotype of *Cnemaspis kendallii.*

Cnemaspis kendallii Gray was reported from localities in peninsular Thailand, such as Patiyu (Smith, 1916a), and from Khao Wang Hip, Nakhon Sithammarat and Maprit (Smith, 1916b), although Smith (1925b) subsequently assigned these specimens to the species *C. siamensis* (Smith, 1925b). *Cnemaspis kendallii* was reported from the Malay peninsula for the first time by Smith (1922), noting that specimens from this area differ from Bornean populations of the species in possessing six to eight preanal pores arranged in an obtuse series. Subsequently, Smith (1925b) referred them to *Gonatodes affinis* (under which name Shelford, 1901, had earlier reported material from Mt. Penrissen). Boulenger (1885) examined an additional example of *C. kendallii* from "Matang" (01° 36'N; 110° 11'E; near Kuching, Sarawak, East Malaysia). There are few Bornean specimens with precise locality records. Besides the Matang record by Boulenger (1885), both Bartlett (1895) and Smith (1925b) reported it from Kuching (01° 33'N; 110° 20'E), and the BMNH has four examples from Bidi, 01° 23'N; 110° 08'E, Sarawak (BMNH 1902.12.12.12) and Baii (BMNH 1911.1.30.7-

9 [without any further information: Anon., 1970, gives the coordinates for Sungai Bai {note variation in spelling} as 01° 21'N; 111° 37'E; 02° 13'N; 113° 02'E; 02° 25'N; 113° 26'E; 01° 10'N; 110° 14'E; and 03° 50'N; 114° 18'E). Shelford (1901) noted the following localities: Santubong (01° 43'N; 110° 18'E) and Simatan [also spelt Sematan], 01° 48'N; 109° 46'E. De Rooij (1915) gave the following additional Bornean localities: Mount Penrissen (in Sarawak, East Malaysia, 01° 07'N; 110° 13'E; spelt Gunung Penerisan in Indonesia and Simatau (not located in gazetteer, and possibly a typographical error for Simatan). Das & Charles (1993) recorded the species from Bako National Park (02° 05' N; 109° 39'E), First Division, Sarawak, East Malaysia.

There are several records of the taxon from the Malay peninsula, including, Bukit Timah, Singapore, 01° 21'N; 103° 46'E (Ridley, 1899; Flower, 1896; 1899; Smith, 1925b; Sworder, 1925; Lim & Lim, 1992), Larut Hills of Perak, West Malaysia, 04° 47'N; 100° 45'E to 05° 00'N; 100° 53'E (Flower, 1896; 1899) and Bukit Lanjan, Selangor, West Malaysia, 03° 11'N; 101° 36'E (FMNH 184424). The records from the archipelago north of Sumatra and Borneo include Great Natunas (= Pulau Natuna Besar), 04° 00'N; 108° 15'E (Smith, 1925b), Tambelan Island, Pulo Bunoa, 00° 58'N; 107° 34'E (USNM 26573), St. Barbe Island (at present, Pulau Pedjantan), 00° 07'N; 107° 14'E (USNM 26555), Pulo Siantan, Anambas Archipelago, 03° 10'N; 106° 15'E (Smedley, 1928; also USNM 26547-26549), Bunguran, Natunas Islands, 04° 00'N; 108° 15'E (USNM 28139-28140), Pulo Lingga, Natunas Islands, 00° 12'S; 104° 35'E (USNM 28145), and Sirhassen (also spelt Siraisan), Natunas Islands, 01° 06'N; 99° 37'E (USNM 28149). In addition, Hendrickson (1966) tentatively assigned to this species several specimens collected from Pulau Tioman (where specimens were earlier taken by Smith, 1930) and Pulao Tulai, which apparently differed from the description of the species in their smaller size (51-53 mm) and relatively weak canthal ridges. The size range in the species has been found to be highly variable (see 'Variation') and the development of the canthal ridge, a subjective criterion within these gekkonids at best, is relatively more developed in older individuals (unpubl. obs.).

McCann (1955) recorded three specimens of *Cnemaspis kendallii* from a ship which brought a cargo of scrap metals to New Zealand from New Guinea and New Britain. An examination of these specimens, deposited in the National Museum of New Zealand (NMNZ, formerly Dominion Museum, bearing registration numbers of Dominion Museum R298-300), indicates that these are *Nactus pelagicus* (Girard, 1857).

Redescription **(based on BMNH XXII.92a [lectotype of *Cnemaspis kendallii*; an adult male with a partially regenerated tail; measurements in Table 1]). -** Snout-vent length 55.9 mm; head oblong, large (HL/SVL ratio 0.16), narrow (HW/SVL ratio 0.14), depressed (HD/HL ratio 0.65), distinct from neck; interorbital region distinctly depressed; snout long (E-S/HW ratio 0.77), longer than the eye diameter (ED/E-S ratio 0.62); scales on snout and forehead tuberculate, with the posterior portion of each scale raised; scales on snout larger than those on the occipital region; eye large (ED/HL ratio 0.46); orbits of eyes with 'extra-brillar fringes' (sensu Underwood, 1954); pupil round; 22 enlarged supraciliaries on the top half of the orbit; tympanum deep, oval shaped, its greatest diameter vertically, fairly narrow (EL/HL ratio 0.14); eye to ear distance less than the diameter of the eyes (E-E/ED ratio 1.05); a ridge of warts run from the posterior of the orbit to the postero-venter of the tympanum; and second from the antero-dorsum of the tympanum to the nape; rostral divided by the rostral groove which meets the anterior of the snout, rostral half as deep as wide, contacted posteriorly by two nasals and two semi-circular supranasals that are separated by a single scale. Ventro-posteriorly, the rostral is in contact with supralabial I. Nostrils oval,

situated within the nasals, and oriented dorsally; nasals in narrow contact with supralabial I. Six postnasals bound the nasal; mental subtriangular, much deeper than wide, paired postmentals that are semicircular, smaller than the mental, narrowly contact each other. Posteriorly, each postmental is bounded by five (on left) and four (right) rounded and juxtaposed scales that possess a single keel. A series of 10 enlarged scales separate the infralabials from the chin shields. Tongue narrowly elongate, lacking a median cleft.

Body slender, elongate (A-G/SVL ratio 0.48); scales on the dorsum at midbody approximately equal to those of the ventrum at the same level; the smallest scales on the dorsum at the same level being along the vertebral region, which shows a weak spinous process. Paravertebral rows of tubercles on the dorsum smooth and without keels. Pectoral and abdominal scales distinctly elongated and imbricate, bearing a single keel; no preanal or femoral pores; no preanal groove. Scales on palm and sole smooth, rounded; scales on inner surface of the forearm smooth, those on the distal aspect of the upper arm unicarinate; scales of the dorsal surface of the thighs, tibia; upper arm and forearm weakly tricarinate. Presacral vertebrae 25.

Forelimbs moderately long, slender; forearm short (FA/SVL ratio 0.18); tibia short (TBL/ SVL ratio 0.22). Digits elongate, all bearing claws that are slightly recurved; subdigital scansors entire, except for the two to three fragmented ones at the base, unnotched; an enlarged scansor towards the base of the digits, which is more than twice the width of the other scansors; interdigital webbing absent. Relative length of digits (finger): 4 (8.0) > 3 (7.8) > 2 (7.2) > 5 (6.4) > 1 (5.5); (toe): 4 (8.5) > 5 (7.5) > 3 (7.3) > 2 (6.0) > 1 (3.5). Subdigital lamellae (fingers) I (13); II (15); III (20); IV (21); V (16); (toes) I (11); II (15); III (22); IV (19); V (17).

Regenerated tail long, tail base distinctly swollen; tail segmented with enlarged flattened scales forming conical whorls of nine enlarged scale, each enlarged scale is separated from the other by one to seven smaller scales, and each whorl is separated from the other by six to nine scale rows. Two conical postcloacal spurs present. Tail with a distinct pair of furrow ventro-laterally. Ventral surface of tail with a median interrupted series of single, enlarged keeled scales, separated by three to four smaller scales. Scales on the postanal region and at the proximal part of the tail base tricarinate, the rest of the subcaudals unicarinate.

Scutellation. - Supralabials (to midorbit position) 11; infralabials 11; interorbital scale rows (at midpoint of orbit) 9; midbody scale rows at belly to lowest row of tubercles 40.

Colouration (in preservative). - The holotype is discoloured, but shows dark brown blotches on the dorsum and cross bars on the dorsal surfaces of the limbs. The following details are from MCZ 157158: dorsum pale brown, with dark brown oblong spots forming seven interrupted bands, each composed of three spot, across the dorsal surface of the torso between the nuchal and caudal regions. The pale brown areas of the dorsum are reticulated with lighter shades of yellow-brown, which form a spot-like pattern on the upper surfaces of the fore and hind limbs. Tail dorsum with nine dark brown bands on the tail dorsum and somewhat narrower light intervening areas. There are three dark brown radiating lines from the posterior edge of the orbit to the nape region, a second to the ear hole, and a third to beyond the end of the supralabials. The top of snout is with four dark brown longitudinal stripes, one pair across the nostrils, and one over the edge of the canthal ridge. Labials are indistinctly dark-mottled. The ventral surfaces of the body, including the chin, throat, chest and abdomen are cream-coloured.

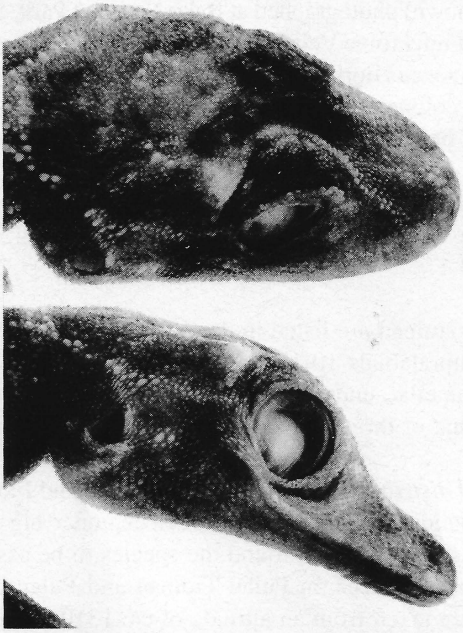

Fig. 1. Dorsal (1.1) and lateral (1.2) views of the head of the holotype of *Cnemaspis kendallii* (BMNH XXII.92a). Bars = 5 mm.

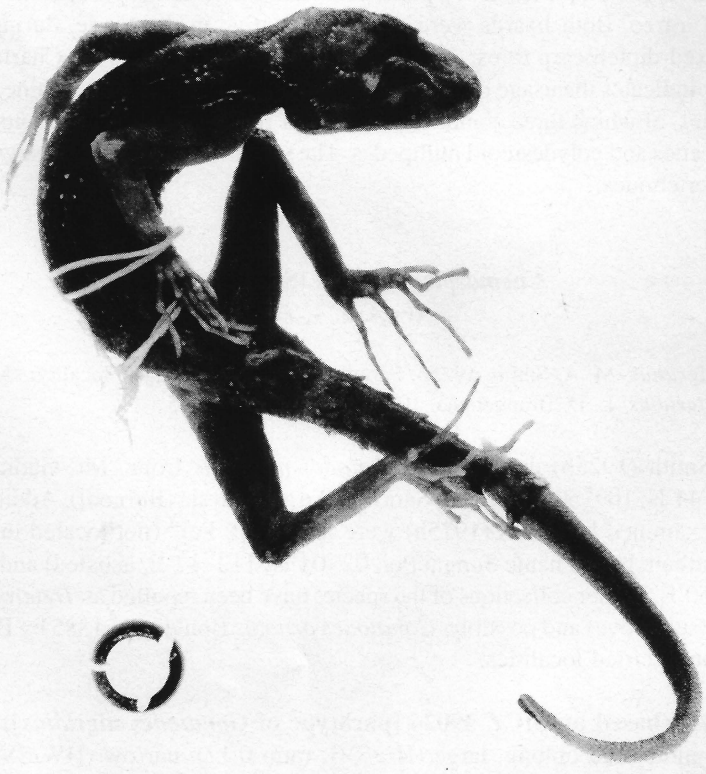

Fig. 2. Dorsal view of of the holotype of *Cnemaspis kendallii* (BMNH XXII.92a). Bar = 15 mm.

A live individual (sex unknown) photographed at Bako National Park, Sarawak, East Malaysia (colour description from a Fujichrome Velvia 50 ASA transparency; nomenclature after Smith, 1975, 1981) was deep vinaceous dorsally, with the darker spots being dark greyish brown. There is a series of flesh coloured spots on the vertebral region that are joined. The tail is banded with dark greyish brown and flesh coloured.

Measurements **.** - (in mm) of the holotype (BMNH XXII.92A): SVL 55.9; FA 10.2; TBL 12.5; TL 60.7; TW 6.1; A-G 27.0; HL 9.1; HW 8.2; HD 5.9; ED 4.2; E-E 4.4; E-S 6.3; E-N 4.7; IO 1.3; EL 1.3; IN 1.7.

Variation. - Non-types examined are listed in Appendix I. The following is a summary of the major scale counts: supralabials 10-12, infralabials 8-11, scales across snout between supralabial VIII 34-36, lamellae under toe IV 19. SVL of seven males measured ranged between 44.1-56.8 mm; that of three females between 50.7-79.5 mm.

Natural history notes and distribution. - Both Ridley (1899) and Flower (1896) mentioned that these lizards were found during the day in crevices under big rocks at Bukit Timah, Singapore. Hendrickson (1966) however found the species to be associated with trees and dead wood rather than rock surfaces on Pulau Tioman and Pulau Tulai. At Larut, in the Malay peninsula, they were taken from an altitude of ca. 1310 m (Flower, 1896), whereas the Bukit Timah specimens were found under 152 m (Flower, 1899). The records from Bako, Kuching, Bidi, Baii and Matang indicate a great variation in the vertical distribution of the species. Both Ridley (1899) and Lim & Lim (1992) reported that the species curls its tail over its back. In the vicinity of Telok Asam, within Bako National Park, two examples were observed active, one on the trunk of a palm tree, circa 2 m from the ground, the other amongst the roots of a tree. Both lizards were apparently active in the shade, during the midday, within a mixed-dipterocarp forest. The locality lies at sea level (Das & Charles, 1993). The Bau locality indicates the usage of limestone regions. Bullock (1966) examined six stomachs of this species, of which three contained remains of food, which included ants, earthworms, scarabeid beetles and polydesmoid millipedes. The small sample examined suggests the usage of litter invertebrates.

Cnemaspis nigridius (Smith, 1925b)

(Figs. 3, 4, 7B)

Gonatodes nigridius M. A. Smith. 1925b. Sarawak Mus. J. 3: 22. Type locality: "Mt. Gadin".
Cnemaspis nigridius L. D. Brongersma. 1934. Zool. Med. 17: 165.

History. - Smith (1925b) described *Gonatodes nigridius* from "Mt. Gadin" (= Gunung Gading, 01° 44'N; 109° 50'E, western Sarawak, East Malaysia [Borneo]). Additional Bornean specimens examined by Smith (1925b) were from "Mt. Poi" (not located in Anon., 1970, although a stream by the name Sungai Poi, 02° 04'N; 112° 17'E, is listed) and "Lundu", 01° 41'N; 109° 50'E. Earlier collections of the species have been reported as *Heteronota Kendallii* Gray, 1845 (see above) and possibly *Gonatodes ornatus* Boulenger, 1885 by Bartlett (1895), both from unspecified localities.

Redescription **(based on MCZ 39024 [paratype of *Gonatodes nigridius*]).** - Snout-vent length 69.0 mm; head oblong, large (HL/SVL ratio 0.17), narrow (HW/SVL ratio 0.18), depressed (HD/HL ratio 0.13), distinct from neck; interorbital region distinctly depressed;

snout long (E-S/HW ratio 0.69), shorter than the eye diameter (ED/E-S ratio 0.44); scales on snout and forehead tuberculate, with the posterior portion of each scale raised; scales on snout larger than those on the occipital region; eye large (ED/HL ratio 0.32); orbits of eyes with 'extra-brillar fringes'; pupil round; enlarged supraciliaries, especially on the top half of the orbit; tympanum deep, oval shaped, its greatest diameter vertically, fairly narrow (EL/HL ratio 0.13); eye to ear distance greater than the diameter of the eyes (E-E/ED ratio 1.76); a ridge of tubercles runs along the mandible; and a second one that is weakly developed from the antero-dorsum of the tympanum to the nape; rostral divided by the rostral groove which meets the anterior of the snout, rostral is less than half as deep as wide, contacted posteriorly by two nasals and two semi-circular supranasals that are widely in contact. Ventro-posteriorly, the rostral is in contact with supralabial I. Nostrils oval, situated within the nasals, and oriented dorsally; nasals in narrow contact with supralabial I. Five postnasals bound the nasal; Mentals subtriangular, much deeper than wide; paired postmentals that are semicircular, smaller than the mental and failing to contact each other. Posteriorly, each postmental is bounded by four rounded and smooth scales. Tongue narrowly elongate, lacking a median cleft.

Body slender, elongate (A-G/SVL ratio 0.43); ventrally, the scales increase in size from the chin region to the gular, pectoral and abdominal regions. Scales on the dorsum at midbody smaller than those of the ventrum at the same level; the smallest scales on the dorsum at the same level being along the vertebral region, which shows a weak spinous process. Scattered rows of tubercles on the dorsum, each tubercle keeled. Pectoral and abdominal scales circular and tricarinate; no preanal or femoral pores; no preanal groove. Scales on palm and sole smooth, rounded; scales on inner surface of the forearm keeled, those on the distal aspect of the upperarm smooth; scales of the dorsal surface of the thighs, tibia; upperarm and forearm tricarinate.

Forelimbs moderately long, slender; forearm short (FA/SVL ratio 0.21); hindlimbs relatively short; tibia short (TBL/SVL ratio 0.26). Digits elongate, all bearing claws that are slightly recurved; subdigital scansors entire, except for the one to two fragmented ones at the base, unnotched; an enlarged scansor towards the base of the digits, which is more than twice the width of the other scansors; interdigital webbing absent. Relative length of digits (finger): 4 (11.4) > 3 (9.8) > 2 (8.9) > 5 (7.8) > 1 (6.5); (toe): 4 (11.7) > 3 (10.7) > 5 (9.7) > 2 (7.6) >1 (5.1). Subdigital lamellae (fingers) I (13); II (14); III (19); IV (18); V (15); (toes) I (11); II (14); III (19); IV (19); V (17).

Partially regenerated tail long, slightly shorter than snout-vent length (TL/SVL ratio 0.95); tail base distinctly swollen; tail segmented with enlarged flattened scales forming conical whorls of enlarged scale, each enlarged scale is separated from the other by one to six smaller scales, and each whorl is separated from the other by one to six scale rows. One (on left) and two (on right) conical postcloacal spurs present. Tail with a distinct pair of furrow ventro-laterally. Ventral surface of tail with a median uninterrupted series of single, enlarged smooth scales. Scales on the postanal region and at the proximal part of the tail base unicarinate, the rest of the subcaudals smooth.

Scutellation. - Supralabials (to midorbit position) (11); infralabials (12); interorbital scale rows (at midpoint of orbit) (40); midbody scale rows at belly to lowest row of tubercles (68).

Colouration. - (based on MCZ 39024 and 15250; both in preservatives). Brownish dorsally,

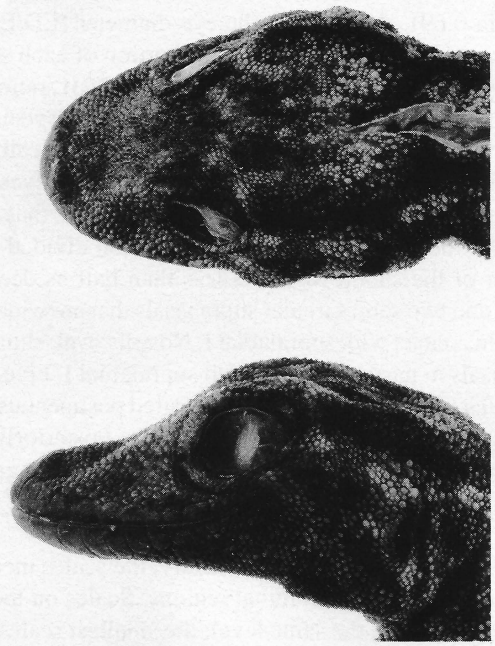

Fig. 3. Dorsal (3.1) and lateral (3.2) views of the head of a paratype of *Cnemaspis nigridius* (MCZ 39024). Bars = 5 mm.

Fig. 4. Dorsal view of a paratype of *Cnemaspis nigridius* (MCZ 39024). Bar = 15 mm.

with paler blotches, especially on the vertebral region in MCZ 15250; the white arranged in the form of transverse bars in MCZ 39024. Two dark brown lines radiate from the posterior of the orbit of eyes to the nape, where they fail to meet. Two pairs of dark brown elongated spots on nape and axilla; a single elongated spot on the vertebral region. Limbs are dark-banded. Ventrally, the gular, pectoral and abdominal regions unpatterned grey.

Measurements. - (in mm) of the paratype (MCZ 39024): SVL 69.0; BW 13.7; FA 14.3; TBL 18.1; TL 65.5; TW 9.2; A-G 29.7; HL 11.9; HW 12.4; HD 8.9; ED 3.8; E-E 6.7; E-S 8.6; E-N 6.2; IO 4.6; EL 1.6; IN 2.1.

Variation. - The only non-type examined, an adult male, MCZ 15250 (from Mt. Lundu, Sarawak, East Malaysia), shows seven pairs of preanal pores and a SVL of 69.8 mm.

Natural history notes and distribution. - There is little in the literature on the natural history of this taxon. The localities from where the species has been recorded (see above) suggests hills of low elevations (< 500 m above msl).

The species of *Cnemaspis* being described here as new is Dring's (1979: 222-223) "species B". Collected in 1963, only one subsequent specimen (FMNH 221478) has come to light, and given the destruction of tropical forests in Sarawak (see Hurst, 1990) and the fact that a knowledge of biodiversity can help in the protection of these fragile ecosystems, it was thought important to describe this highly distinctive species.

Cnemaspis dringi, new species

(Figs. 5, 6, 7C)

Holotype. - FMNH 148588 (FMNH FS 19914), Labang Camp (03° 20'N; 113° 29'E), Bintulu District, Fourth Division, Sarawak, East Malaysia, Borneo. Collected by W. Hosmer & J. Bacon, 26 Dec.1963.

Paratype. - FMNH 221478 (FMNH FS 34321), Sungai Segaham (02° 44'N; 113° 53'E), Belaga District, Seventh Division, Sarawak, East Malaysia, Borneo. Collected by Paul Walker, 24 May.1984.

Diagnosis. - A small species of *Cnemaspis* (SVL 43.18-45.5 mm), differing from congeneric species in showing the following characters: snout-vent length up to 45.5 mm; five postnasals; pectoral and abdominal scales distinctly elongated, imbricate and smooth; three pairs of preanal pores; no femoral pores; no preanal groove; no postcloacal spur; gular, pectoral and abdominal regions dark pigmented; flanks of body with distinct white patches.

***Description* (from holotype, an adult male).** - Snout-vent length 45.5 mm; head oblong, large (HL/SVL ratio 0.19), narrow (HW/SVL ratio 0.15), depressed (HD/HL ratio 0.11), distinct from neck; interorbital region distinctly depressed; snout long (E-S/HW ratio 0.83), longer than the eye diameter (ED/E-S ratio 0.53); scales on snout and forehead tuberculate, with the posterior portion of each scale raised; scales on snout larger than those on the occipital region; eye large (ED/HL ratio 0.35); orbits of eyes with 'extra-brillar fringes'; pupil round; enlarged supraciliaries on the top half of the orbit; tympanum deep, oval shaped, its greatest diameter vertically, fairly narrow (EL/HL ratio 0.14); eye to ear distance greater than the diameter of the eyes (E-E/ED ratio 1.07); rostral divided by the rostral groove which meets

the anterior of the snout, rostral less than half as deep as wide, contacted posteriorly by two nasals and two semi-circular supranasals that are separated by a single scale. Nostrils oval, situated within the nasals, and oriented dorsally; nasals in narrow contact with supralabial I. Five postnasals bound the nasal; mental subtriangular, much deeper than wide, 10 small blunt-keeled postmentals border the mental; chin scales meet the infralabials; tongue narrowly elongate, lacking a median cleft.

Body slender, elongate (A-G/SVL ratio 0.46); scale size does not decrease dorsally after the thorax; ventrally, the scales do not decrease in size from the chin region to the gular, pectoral and abdominal regions. Scales on the dorsum at midbody approximately equal to those of the ventrum at the same level; vertebral scales not reduced; three pairs of paravertebral rows of tubercles on the dorsum, each tubercle smooth and without keels; pectoral and abdominal scales distinctly elongated, imbricate and smooth; three pairs of preanal pores; no femoral pores; no preanal groove. Scales on palm and sole smooth, rounded; scales on inner surface of the forearm and distal aspect of the upperarm with a blunt keel; scales of the dorsal surface of the thighs, tibia; upperarm and forearm tricarinate. The holotype shows 27 presacral vertebrae (the count on the paratype is 26).

Forelimbs moderately long, slender; forearm short (FA/SVL ratio 0.19); tibia short (TBL/SVL ratio 0.24). Digits elongate, all bearing claws that are slightly recurved; subdigital scansors entire, except for the fragmented ones at the base, unnotched; an enlarged scansor towards the base of the digits, which is more than twice the width of the other scansors; interdigital webbing absent. Relative length of digits (finger): 4 (8.4) > 3 (7.5) > 5 (5.5) > 2 (5.3) > 1 (4.2); (toe): 4 (8.7) > 3 (7.4) > 5 (7.5) > 2 (4.9) > 1 (3.1). Subdigital lamellae (fingers) I (12); II (15); III (20); IV (21); V (14); (toe) I (19): II (19): III (19); IV (13); V (12).

Regenerated tail short, shorter than snout-vent length (TL/SVL ratio 0.69); tail base distinctly swollen; tail segmented with enlarged flattened scales forming conical whorls of enlarged scale. No postcloacal spurs present. Tail with a distinct pair of furrow ventro-laterally. The nature of subcaudal scales (i.e., median series enlarged/not enlarged and interrupted/continuous) is unknown, as the tail is broken through the autotomy plane of the seventh postsacral vertebra; scales on the postanal region and at the proximal part of the tail base tricarinate, the rest of the subcaudals unicarinate.

Scutellation (holotype followed by paratype in parentheses). - Supralabials (to midorbit position) 11 (11); infralabials 11 (11); interorbital scale rows (at midpoint of orbit) 10 (10); midbody scale rows at belly to lowest row of tubercles 40 (39).

Colouration (in preservative). - Dorsum, pale brown, with a dark brown parallel dark linear series along the paravertebral region that run from the nape to beyond the caudal constriction; an irregular series of markings along the vertebral midline, flanked by the dark brown linear series; two dark brown radiating lines radiate from the posterior of orbit of eye towards the ear holes. Upper surface of the fore and hind limbs dark-banded. Upperlips with indistinct dark reticulations. The gular, pectoral and abdominal regions pale brown with scattered clusters of off-white scales, giving a very weakly mottled appearance; flanks of body very dark brown with distinct white spots of varying size.

Measurements. - (in mm) of the holotype (FMNH 148588), followed by the paratype (FMNH 211478; with original tail) in parentheses: SVL 45.5 (43.3); BW 7.9 (7.3); FA 8.5 (7.6);

Fig. 5. Dorsal (5.1) and lateral (5.2) views of the head of the holotype of *Cnemaspis dringi* (FMNH 148588). Bars = 5 mm.

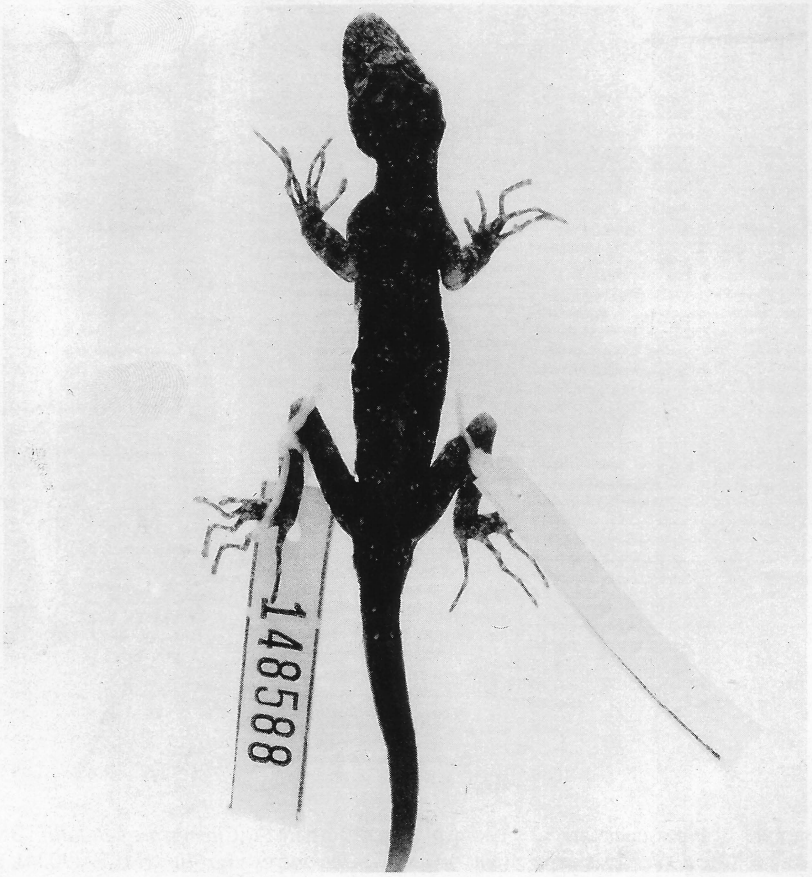

Fig. 6. Dorsal view of the holotype of *Cnemaspis dringi* (FMNH 148588). Bar = 15 mm.

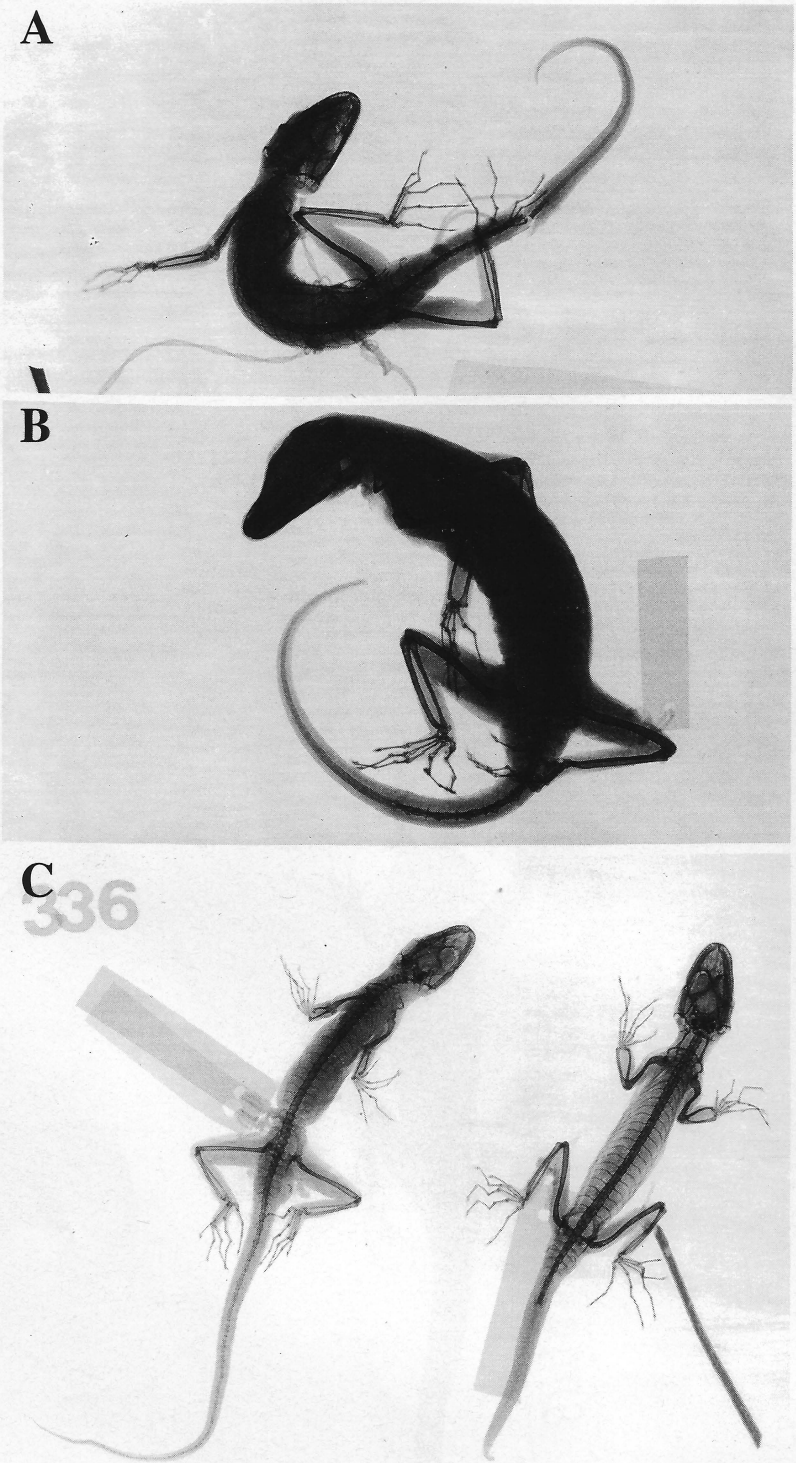

Fig. 7. Radiographs of type specimens of *Cnemaspis* from Borneo. A. *Cnemaspis kendallii* (BMNH XXII.92a), x-ray setting 40 seconds exposure at 40 kV; B. *Cnemaspis nigridius* (MCZ 39024), x-ray setting 40 second exposure at 40 kV; and C. *Cnemaspis dringi* (FMNH 221478 on left; FMNH 148588 on right), x-ray setting 45 seconds exposure at 45 kV.

TBL 10.9 (10.0); TL 31.4 (62.7); TW 4.9 (4.7); A-G 20.9 (19.4); HL 8.6 (8.4); HW 6.9 (7.0); HD 5.0 (4.5); ED 3.0 (2.6); E-E 3.2 (3.0); E-S 5.7 (5.5); E-N 4.4 (4.3); IO 2.9 (2.9); EL 1.2 (0.9); IN 1.7 (1.6).

Natural history notes and distribution. - A map of Borneo showing the location of the site from where the holotype of the new species can be found in Inger & Voris (1993). Of its natural history, nothing is on record, except that the paratype was taken from a log.

Comparisons. - *Cnemaspis dringi*, new species, is compared with nominal species of *Cnemaspis* from south-east Asia. Only characters that separate them from the new species have been listed. *Cnemaspis kandianus* (males with femoral pores; proximal subdigital lamellae greatly enlarged relative to the distal lamellae under the toes; 11-12 lamellae under toe IV; maximum SVL 35.0 mm); *C. boulengeri* (presence of a series of shield-like subtibial scales; subcaudals as wide as tail; preanal pores absent; 16-18 lamellae under toe IV; maximum SVL 66.0 mm); *C. kumpoli* (8 preanal pores; smooth ventrals; 21-24 lamellae under toe IV; maximum SVL 51.0 mm); *C. nigridius* (16 preanal pores in males from Borneo, preanal pores absent in specimens from Pulau Tioman; enlarged postmentals; median subcaudals smooth; maximum SVL 85.0 mm); *C. kendallii* (preanal pores absent; venter lightly

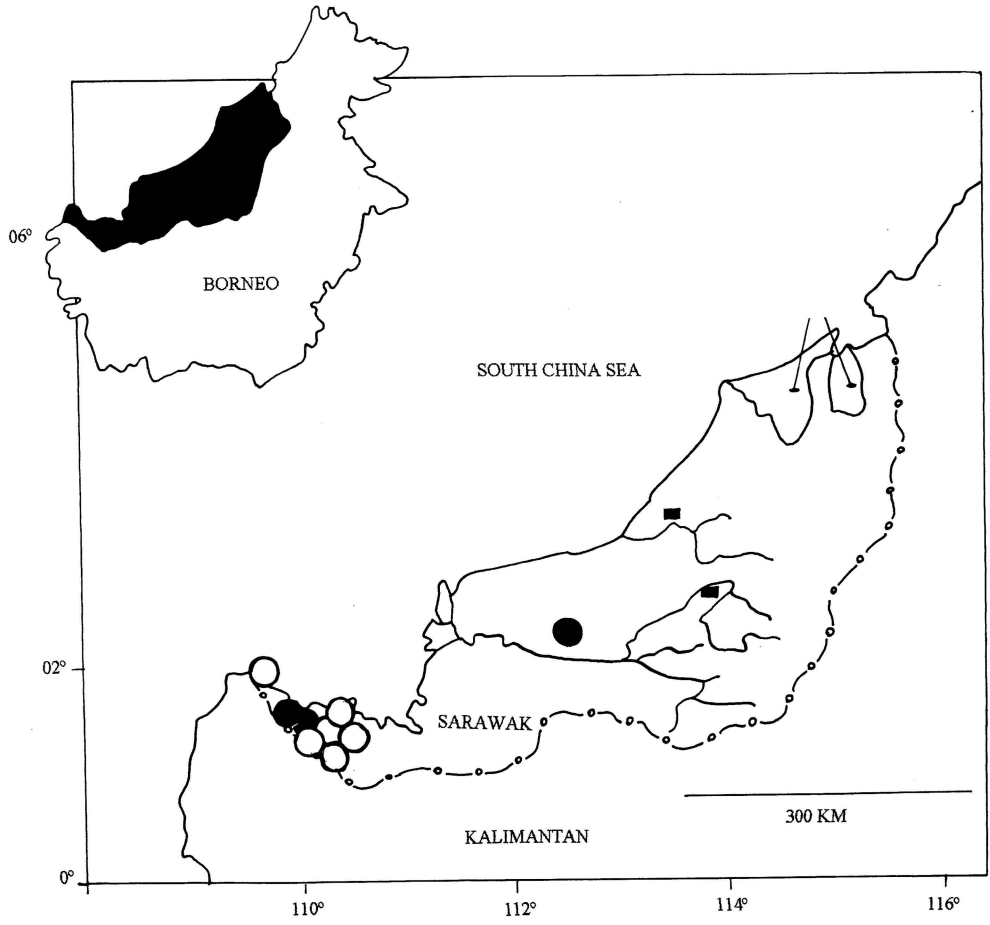

Fig. 8. The known distribution of *Cnemaspis* species in Borneo, based on museum specimens and literature records (see text for details). Open circles, *Cnemaspis kendallii;* closed circles, *Cnemaspis nigridius*; square, *Cnemaspis dringi.*

pigmented; no black areas on flanks; enlarged postmentals; maximum SVL 79.5 mm); *C. argus* (10 preanal pores; 22-24 lamellae under toe IV; no black areas on flanks; venter pale pinkish-grey; maximum SVL 65.3 mm); *C. affinis* (two postcloacal spurs; no black areas on flanks; venter unpigmented; maximum SVL 46.7 mm). Dring (1979) recognised two distinct populations of *C. siamensis* that are diagnosable. The northern population differs from *C. dringi* in the following features: preanal pores absent; no black areas on flanks; maximum SVL 38.0 mm; while the southern population differs in showing 4-8 preanal pores, no black areas on flanks; and maximum SVL 39.7 mm.

BIOGEOGRAPHIC NOTES

Oriental species of *Cnemaspis* show a curious distribution in insular south-east Asia, with large disjunctions in range, no species being recorded from some of the intervening islands of the Sundas (McCann, 1953; Das, 1993). On the island of Borneo, the distribution is restricted to the north-western tip of Sarawak. No specimens have been found elsewhere, despite intensive fieldwork conducted in other parts of northern Borneo, which are areas of high herpetological diversity, such as Mount Kinabalu in Sabah (Boulenger, 1891; Malkmus, 1991; 1992; 1994a; 1994b; Manthey, 1982; Manthey & Denzer, 1982a; 1982b; Smith, 1925a), Batu Apoi in Brunei Darussalam (Das, 1995), and other parts of northern Borneo (van Lidth de Jeude, 1893; Lloyd et al., 1968; Matsui et al., 1985; Mocquard, 1890; Smith, 1925a) that are suspected to be areas of Pleistocene refugia (Ashton, 1972; 1992), or indeed elsewhere on Borneo (Andersson, 1923; Boulenger, 1892; de Rooij, 1915; Lidth de Jeude, 1905). The distribution is similar to that reported by Ashton (1972) for tree species of the Dipterocarpaceae, with affinities in peninsular Malaya and the Riau Archipelago.

The distribution shown by these taxa is suggestive of a vicarious event during the Quaternary. Current geological evidence suggests sea level drops of as much as 120 m below present levels during the Pleistocene (Gascoyne et al., 1979), which united the Malay Peninsula to the Sundaic Islands of Sumatra, Borneo, Java and Bali, as well as the smaller associated islands (Molengraaff, 1921b; Morley & Flenley, 1987). The land mass exposed, termed 'Sundaland', was drained by several river systems, including the North Sunda River, which drained parts of western Borneo, eastern Sumatra and the eastern slopes of the Malay Peninsula (Molengraaff, 1921b) and the southern Indo-China River, which drained the area south of the Mekong delta, emptying about 240 km north of the North Sunda River (Molengraaff, 1921b; Krempf & Cheney, 1933). Further support for the contact of the North Sunda River to the Mekong drainage in Indo-China lies in the present day distribution of a lineage of the silurid cat fish, *Hemisilurus*. Sister species of a taxon of the silurid from the middle Mekong are extant in Borneo and Sumatra, rather than in the intervening areas on the Asian mainland. Vicariant events during the Quaternary, including the sea level rise that drowned ancients rivers, have been attributed to the disjunct distribution of the present day ichthyofauna of these regions by Bornbusch & Lundberg (1989). As suggested for the dipterocarps and silurid fishes, the distribution of the gekkonid genus is reflective of the connection of the Malay Peninsula with the Sundaic Islands of eastern Sumatra and western Borneo, formed by the basins of the North Sunda River and a proto-Mekong.

Weber (1921b) hypothesized that the ancient drainage system of Mussi ('Moesi', in the earlier Dutch literature) River on the east coast of Sumatra, may have been connected to the Kapuas River of western Borneo. Support for such an idea comes from the similarities of the ichthyofauna of the Kapuas River to those of the rivers of eastern Sumatra, rather than to

those of the adjacent Mahakham, southern Borneo, western Sumatra, Java or the Malay Peninsula. Within this Rhiao Province (of Ashton, 1992), species were stopped by the Mussi-Mahakham on the south-east and the Baram that drains the north-west of Borneo into the South China Sea, on the north-west, but including what are now islands of the Rhiao Archipelago and the southern-most point of peninsular Malaya, including Singapore. In summary, the distribution of the geckos of the genus *Cnemaspis* on the island of Borneo is reflected by the history of the drainage of the ancient, now drowned, rivers, which presumably stopped their dispersal into central and eastern Borneo.

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APPENDIX I

Cnemaspis affinis (Stoliczka, 1870): ZMA 11987, Penang, West Malaysia.

Cnemaspis boulengeri Strauch, 1887: MCZ 39014-39023, Pulo Condore (= Con Dao), Vietnam.

Cnemaspis gordongekkoi Das, 1993: USDZ 2.3380 and 2.3381 (holotype and paratype, respectively, of *Cnemaspis gordongekkoi* Das, 1993) Sendanggila Falls, Lombok, Nusa Tenggara District, Indonesia.

Cnemaspis kandianus (Kelaart, 1852): MCZ 162896 and 162899, Madras (at present a city in south-eastern India; in the past Madras Presidency referred to much of southern India); MCZ 4138 and 26719, "Ceylon" (= Sri Lanka);

Cnemaspis kendallii (Gray, 1845): BPBM 7494, Alag Sungei Ayer, Pulau Tioman, Pahang, West Malaysia; BMNH XXII.92a, "Borneo" (holotype of *Heteronota kendallii*); BMNH 1902.12.12.12, Bidi, Sarawak, East Malaysia (Borneo); BMNH 1911.1.20.7-9 (three examples), Baii, Sarawak, East Malaysia (Borneo); FMNH 184424, Bukit Lanjan, Selangor, West Malaysia; FMNH 223201, Bako National Park, First Division, Sarawak, East Malaysia; MCZ 157158-59 (two examples), Bako National Park, First Division, Sarawak, East Malaysia; UF 78463, Borneo; USDZ 2.1101, Jerantut, Pahang, West Malaysia; USDZ 2.1102, Gunung Rokan, Pulau Tioman, West Malaysia; USDZ 2.1103, Sedagong, Pulau Tioman, West Malaysia; USDZ 2.1109-10 (two examples), Pulau Siantan, Anamba Archipelago, Indonesia; USDZ 2.1112-13 (two examples), Sungai Ulu, Great Natuna, Natunas Archipelago, Indonesia; USDZ 2.3014, Bukit Timah, Singapore; USDZ 2.3015, Gunung Ladang, Malacca, West Malaysia; USNM 26573, Pulau Bunoa, Tambelan Islands, Indonesia; USNM 26555, St. Barbe Island, Indonesia; USNM 26547-49 (three examples), Pulau Siantan, Anambas Archipelago, Indonesia; USNM 28139-40 (two examples), Bunguran, Natunas Archipelago, Indonesia; USNM 28145, Pulau Lingung, Natuna Archipelago, Indonesia; USNM 28149, Sirhassen, Natunas Archipelago, Indonesia; ZSI 14767 and 19637, "Borneo".

Cnemaspis nigridius (Smith, 1925): MCZ 39024 (paratype of *Gonatodes nigridius* Smith, 1925b), "Mt. Gadin" (= Gunung Gading, Sarawak, East Malaysia, Borneo); MCZ 15250, Lundu, Sarawak, East Malaysia, Borneo.

Cnemaspis siamensis (Smith, 1925): MCZ 39025, Maprit, Patiyu, peninsular Thailand; MCZ 39694, Klong Bang Lai, peninsular Thailand.