European Journal of Taxonomy 961: 1–51
https://doi.org/10.5852/ejt.2024.961.2681
ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2024 · Das I. *et al.*

Monograph

urn:lsid:zoobank.org:pub:8E064900-1289-4648-BE9A-F17461CCF25C

Taxonomic revision of the king cobra *Ophiophagus hannah* (Cantor, 1836) species complex (Reptilia: Serpentes: Elapidae), with the description of two new species

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Abstract. The taxonomy of king cobras (*Ophiophagus*) was reevaluated using qualitative, mensural and meristic characters, based on 148 entire and five skeletal specimens, and supported by a recent molecular phylogenetic analysis. We provide nomenclatural synopses of both the genus and species-series nomina. We restrict the concept of *Ophiophagus hannah* s. str. to populations from eastern Pakistan, northern and eastern India, the Andaman Islands, Indo-Burma and Indo-China, south to central Thailand. The nomen *Ophiophagus bungarus* (Schlegel, 1837) comb. nov. is revived for the populations inhabiting the Sunda Shelf area, including the Malay Peninsula, the Greater Sunda Islands and parts of the southern Philippines. We describe two new species, *Ophiophagus kaalinga* Gowri Shankar, Das & Ganesh sp. nov. endemic to the Western Ghats of south-western India and *Ophiophagus salvatana* Gowri Shankar, Das & Wüster sp. nov., inhabiting the island of Luzon in northern Philippines. For the purpose of nomenclatural stability, we designate a neotype for *Hamadryas hannah* Cantor, 1836. A dichotomous identification key to the four species recognized here is provided.

Keywords. Elapidae, neotype designation, nomenclature, new species, systematics, taxonomy.

Das I., Gowri Shankar P., Swamy P., Williams R.C., Lalremsanga H.T., Prashanth P., Sahoo G., Vijayakumar S.P., Höglund J., Shanker K., Dutta S.K., Ganesh S.R. & Wüster W. 2024. Taxonomic revision of the king cobra *Ophiophagus hannah* (Cantor, 1836) species complex (Reptilia: Serpentes: Elapidae), with the description of two new species. *European Journal of Taxonomy* 961: 1–51. https://doi.org/10.5852/ejt.2024.961.2681

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Introduction

The king cobra *Ophiophagus hannah* (Cantor, 1836) is the longest extant venomous snake in the world, reportedly attaining a length of 5.6 m (Smith 1943; Burton 1950). The genus *Ophiophagus* Günther, 1864 is characterized by a number of unique characters, such as the consistent presence of a pair of occipital scales, dorsal banding (which is retained through adulthood in two of the four recognised species), a low midbody scale row count of 15; an unusual subcaudal scale arrangement typically comprising a series of divided and undivided scales; grooved palatine and dentary teeth; reduced number of pterygoid teeth; a proportionately longer and more deeply bifurcate hemipenes, compared to other elapids and large (reportedly reaching 5.6 m) total body length; 4/7 renal arteries; paired air sacs on dorsal side of body; a series of tracheal air sacs; lack of intrapulmonary bronchus and a relatively narrow braincase (Cope 1895; Boulenger 1896; Bogert 1943; Smith 1943; Underwood 1967, 1997). The species, as historically treated, has a distribution that extends from eastern Pakistan in the west (Parshad 1915), through India (including the Andaman Islands), Nepal, Bhutan, Bangladesh, up to China (including Hong Kong) in the east, to Indo-China (including Myanmar, Thailand, Laos, Cambodia and Vietnam), Indo-Malaya (including both the Malay Peninsula and the insular region of south-east Asia, such as the Sundaic islands of Sumatra, Java, Borneo, Bali, and east of Wallace's Line, on Sulawesi and the Philippines (Golay 1985; Golay *et al*. 1993)). Its distribution, in the Indian subcontinent, has been considered relictual (Minton 1981; Whitaker & Captain 2004), as it is largely restricted to forested regions, including highlands and their vicinity (Wall 1928), while in the more mesic Indochinese Peninsula and Sundaland it occurs as well in lowland forests, including dipterocarp forests and mangroves (Smith 1943; Wallach *et al*. 2014).

Although extensive geographic variation in king cobras has been documented (Charlton 2018), the taxonomy of *Ophiophagus* remains poorly understood. From 1836 to 1961, for nearly 125 years, from as far afield as Dehradun (in the western Himalaya) in the north-west, to Sulawesi in the south-east, across >4000 airline km of South and South-east Asia, a number of taxon descriptions and type designations have complicated the taxonomy of this species group. The single currently recognised species was originally described as *Hamadryas hannah* by Cantor (1836), based on three specimens collected from the "Sunderbuns" and a fourth from "jungle not far from Calcutta", in eastern India. Subsequent nomina of relevance include *Naja bungarus* Schlegel, 1837, from "Tjihao" (equivalent to Cihoe), West Java, Indonesia, and *Hamadryas ophiophagus* Cantor, 1838 (nom. subst. pro *Hamadryas hannah*), *Naja vittata* Elliot, 1840, based on a boxed specimen found floating in the sea off the coast of 'Madras' (sic), *Naja ingens* van Hasselt, "1857" 1858, from the island of Sumatra and *Hamadryas elaps* Günther, 1858, from Borneo, in Indonesia and *Dimeresurus boiei* Bleeker, 1858: 263 – type locality: "Westkust", namely the west coast of Sumatra, Indonesia; status: a nom. nud., containing no description. Deraniyagala (1960, 1961), in the most recent attempt at a revision of the complex, described four new subspecies and recognised three more under existing names (see below). However, through much of the 20th and early 21st centuries, these names remained relegated to the status of synonyms, and subsequent authors have not accepted Deraniyagala's classification and have instead maintained the king cobra as a single variable, widespread, monotypic species (Klemmer 1963; Taylor 1965; Leviton 1968; Wallach *et al.* 2014; Boundy 2020).

Gowri Shankar *et al.* (2021) conducted a species delimitation analysis based on a multilocus genetic dataset and multivariate morphometrics, and provided a mitochondrial phylogeny to highlight distinct phylogenetic lineages within *Ophiophagus* across its range. They identified four geographically separate lineages as confirmed candidate species (CCS). From west to east, these were an endemic Western Ghats lineage in India, a widespread Asian mainland lineage distributed from northern and eastern India to China and Thailand, a Malesian lineage distributed in the Malay Peninsula and the Greater Sunda Islands as well as part of the Philippines, and an isolated island lineage on Luzon Island, Philippines.

Here, as a follow up to Gowri Shankar *et al.*'s (2021) study, we present a formal taxonomic revision of the genus *Ophiophagus*, morphological diagnoses and descriptions of these four lineages, and describe two as new species. Our nomenclatural and taxonomic decisions have extensive implications for the content, diversity and distribution of members of this genus, as well as the management of snakebite, species conservation and prospects for future research.

Material and methods

We analysed the systematics of snakes referred to as *Ophiophagus hannah* through examination of morphological characters in preserved material and provide taxonomic data on the contents of the genus. Our sampling includes museum specimens from throughout its range, including many of historic importance, having been collected by pioneering field zoologists of the region, including John Anderson, Richard Beddome, William Blanford, Tom Harrisson, Malcolm Smith, William Theobald and Frank Wall. Unfortunately, it was not possible to examine specimens from the Sunderbans, a type locality of Cantor's (1836) *Hamadryas hannah*, nor from the following geographical areas (authors who reported the taxon from the area in parentheses), from where no major museums have specimens: eastern Pakistan (Parshad 1915), Kashmir (Faiz *et al.* 2017), north-eastern Bangladesh (Khan 1992), Cambodia (Saint-Girons 1972) and Bali (Mertens 1930).

Morphometric, pholidosis and miscellaneous variables recorded on members of the *Ophiophagus hannah* species complex are listed in 'Terminology for Character Analysis' below (see also Fig. 1). The general colouration was noted, including whether banded on the head and/or body and tail. Colour descriptions from photographs of live animals were compared with the swatches of Smithe (1975, 1981), as an attempt of standardisation of colour nomenclature, although we are aware of limitations such as ambient and introduced lighting conditions and possible seasonal changes in colouration. Measurements were taken with a Mitutoyo^{TM} vernier calliper (to 0.1 mm) for cephalic scales and landmarks on head, and with a plastic measuring tape (to 1.0 mm) for body lengths, including total length, measured from tip of snout to the tip of tail, and tail length, measured from centre of posterior edge of cloacal scute to tail tip. Tooth counts presented are ranges observed on right side of jaws.

In total, 153 (148 non-skeletal, five skeletal) specimens were examined. Nearly a third of the non-skeletal specimens examined were juveniles of SVL (snout-vent length) <600 mm, and about a tenth of wet specimens comprised heads, tails or skin only. Because members of the *Ophiophagus hannah* species complex lack easily discernable external sexual dimorphic features (see Leviton 1964), sex of adults could mainly be verified for specimens that were already dissected and/or were preserved with hemipenes everted. Of the specimens examined, 19 belong to this category, comprising seven males and 12 females, of which SVL and TL (tail length) were measured. Relative tail length (in %) was calculated by standardizing with Total length. Where the sex of a specimen was not ascertained, a "?" was used to express the uncertainty. Tooth counts (number of attached functional teeth and number of total tooth sockets) were recorded for the left maxilla, premaxilla and dentary in the series. In one case, the preserved holotype was scanned using a MeditronicsTM 100MA Human x-ray unit (model: Diagnox 100; equipment ID: G-XR-58599), at 50kVp/4.8 mAs. Teeth dimensions were measured using vernier calipers, to nearest 0.5 mm.

Geographical coordinates are from gazetteers of the respective countries produced by the Defense Mapping Agency, U.S. Board of Geographic Names, Washington, D.C., and from Rand McNally Atlases. Nomenclatural decisions comply with the fourth edition of the International Code of Zoological Nomenclature (ICZN 1999).

Description of characters used in analysis

Nomenclature of scalation, colour pattern and morphology relevant to the genus, as used in this paper, and remarks on variation encountered, are given below. Abbreviations are explained in the captions of Table 2 (page 33).

Body bands

Pale, partially encircling bands across body from the nuchal region to the level of cloacal scute.

Body width

Diameter at midbody, measured approximately at the middle portion of snout-vent length. Whenever possible, stomach contents were removed prior to measurement.

Cloacal scale

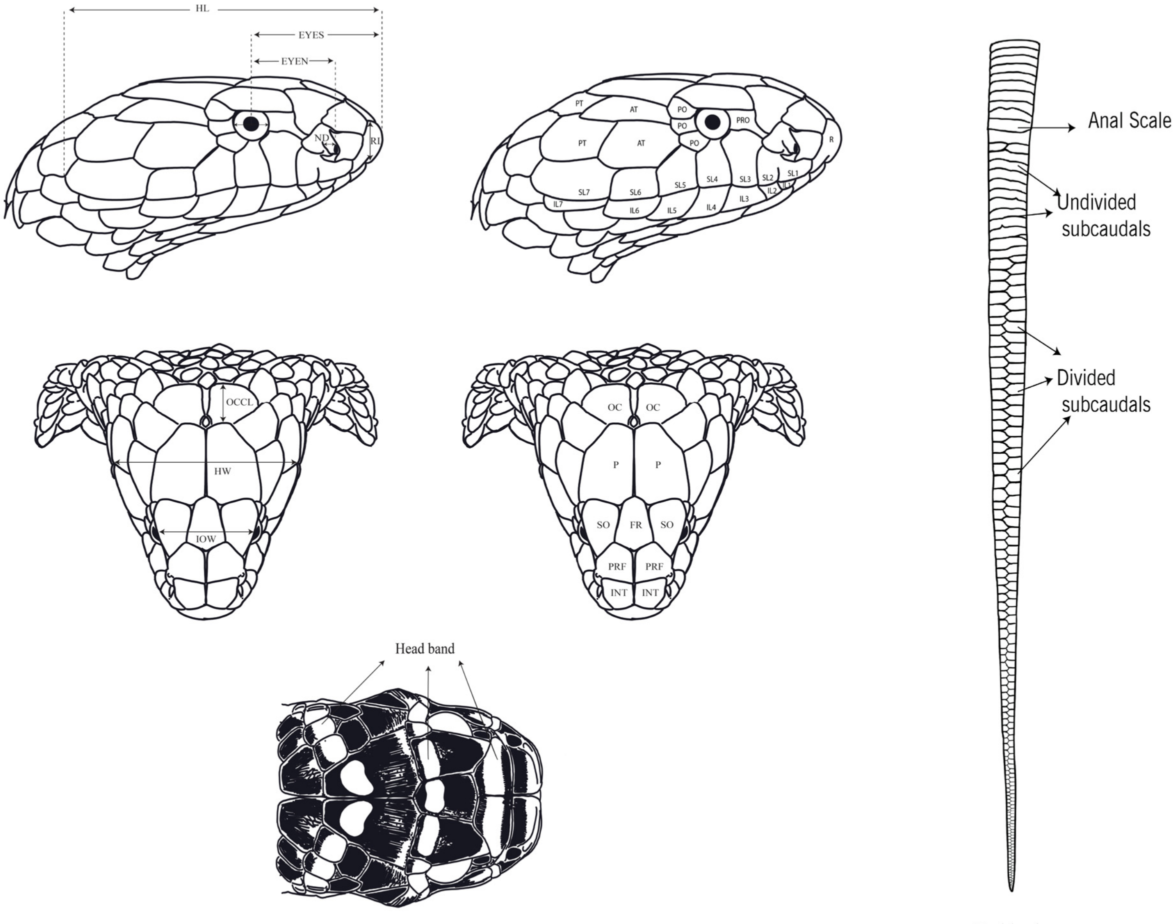
Scale covering the cloacal opening, and forming the terminal ventral scale (and excluded from ventral scale counts). In the species complex, the count was invariably 1.

Dental characters

Counts were made of maxilla, premaxilla, pterygoid and dentary teeth, when possible. Empty tooth sockets were included in the count in case of missing teeth.

Dorsal scale rows

Scales were counted obliquely one head length behind the head (DSR1), at approximately midbody (DSR2) and one head length before the vent (DSR3). In all members of the species complex, midbody scales are macroscopically smooth, subhexagonal, the vertebral series enlarged. To examine scale



Head bands in juvenile

Caudal scales

Fig. 1. Illustration of morphological characters and measurement landmarks used in the taxonomic descriptions of the *Ophiophagus hannah* species complex. Sketch by H.Vinod Kumar.

reductions (see Clark & Inger 1942; Dowling 1951b), transverse scale-row counts were taken along the nuchal, midbody and vent regions, by counting obliquely backwards to the vertebral row and then forward to the dorsal scale next to ventral on the opposite side. In the species complex, the typical count for DSR1, DSR2 and DSR3 were 19, 15 and 15, respectively, the range encountered being 17–21, 15 and 11–17, respectively.

Interoccipital scale

A small, unpaired scale occasionally present in members of the species complex, between the posterior corners of the parietals and the anterior corners of the occipitals, sometimes referred to as 'central scale'. First referred to as 'interoccipital' by Taylor (1965: 956).

Infralabials

The lower jaw scales that extend from the mental to the angle of the jaw. Scale counts were made from anterior to posterior, besides noting the contact of infralabial to genials and the relative sizes of each scale. In the species complex, the typical count was 8, the range seen 7–9; counts differing from 8 occurred in only 2–3 individuals.

Mental

The first, unpaired, subtriangular scale of the lower jaw, forming its tip, bordered on either side by Infralabial I. Measurements were made of greatest width and depth.

Nasals

The paired scales preceding the preoculars, separated by the nostril, which is located at the back of the anterior nasal.

Ocular ring

Scales bounding the eye, following the definition of Marx *et al.* (1987). In the complex, these include one preocular, three postoculars, one supraocular and two supralabials.

Parietals

Enlarged, paired scales at back of forehead, in contact with the frontal and supraoculars anteriorly, the anterior and posterior temporals laterally, and with the occipitals posteriorly.

Preocular

The single scale present between the anterior edge of the eye and the posterior nasal scale in members of the species complex, which is wider than high, following Powell *et al.* (1998).

Occipital

Paired, enlarged scales on the posterior forehead, and in broad contact with the parietals, that are unique to members of the species complex.

Postoculars

Scales present between the orbit and temporals.

Rostral

The first, unpaired, subtriangular scale of the upper jaw, forming the snout-tip. Measurements were made of greatest width and depth.

Subcaudals

Scales on the undersurface of the tail, between the cloacal scute and the tip of the tail (the terminal scute, which was not counted). In the species complex, fusion of the subcaudal scales is common. Members of the genus *Ophiophagus* are atypical among Serpentes, along with other Oriental snake lineages such as *Bungarus bungaroides* (Cantor, 1839) (Elapidae) and *Deinagkistrodon acutus* (Günther, 1888) (Viperidae), in displaying a mixture of divided and undivided subcaudals.

Supralabials

The upper jaw scales extending from the rostral to the angle of the jaws. Scale counts were made from anterior to posterior. In the species complex, the typical count was 7, the range seen was 6–8. Also noted were the contact of supralabial to nasals, orbit of eye, and the relative sizes of each scale.

Supraoculars

Enlarged scales, located on the dorsal side of orbit, which are distinct in members of the species complex.

Temporals

Paired, elongate or squarish scales located on the posterior lateral aspect of head, in contact with the postoculars, the parietals and the last two supralabials.

Ventrals

Enlarged scales across the venter, from chin scutes to before the cloacal scute. Counts were made using the Dowling (1951a) system.

Collections acronyms

The following institutional abbreviations (catalogue number prefix, if different) have been used (those not in Sabaj (2016, 2020) indicated with an asterisk):

AMNH = American Museum of Natural History, New York, USA
ANSP = Academy of Natural Sciences, Philadelphia, USA
BM* = Brunei Museum, Bandar Seri Begawan, Brunei Darussalam
BMNH = The Natural History Museum, London, UK
BNHS = Bombay Natural History Society, Mumbai, India
CAS = California Academy of Sciences (including specimens that were formerly in the Stanford University that bear the abbreviation CAS-SU)
CIB = Chengdu Institute of Biology, Chengdu, People's Republic of China
CSPT = Chennai Snake Park Trust, Madras, India
CUZM* = Chulalongkorn University, Zoological Museum, Bangkok, Thailand
FMNH = Field Museum of Natural History, Chicago, USA
IMR* = Institute of Medical Research, Kuala Lumpur, Malaysia
LSUMZ = Louisiana State University Museum of Natural Science, Baton Rouge, USA
MCBT* = Madras Crocodile Bank Trust, Vadanemmeli, India
MCZ = Museum of Comparative Zoology / Harvard Museum of Natural History, Harvard University, Cambridge, USA
MNHN = Muséum nationale d'Histoire naturelle, Paris, France
MZB = Museum Zoologicum Bogoriense, Cibinong, Indonesia
NKBP* = Nandan Kanan Biological Park Museum, Barang, Odisha, India
NMP = National Museum of the Philippines, Manila, Philippines
NRM = Swedish Museum of Natural History, Stockholm, Sweden
RMNH = Naturalis (formerly, Nationaal Natuurhistorisch Museum), Leiden, The Netherlands
SFRI* = State Forest Research Institute, Itanagar, Arunachal Pradesh, India
SM = Sarawak Museum, Kuching, Sarawak, Malaysia (currently under Forest Research Centre Sarawak)
SSM* = Sabah State Museum, Kota Kinabalu, Sabah, Malaysia

TNRC = Thailand National Reference Collection, Bangkok, Thailand
UF = Florida Museum of Natural History (formerly, Florida State Museum), University of Florida, Gainesville, USA
UPM* = University of the Philippines, Museum of Natural History, Los Baños, Philippines
USNM = National Museum of Natural History, Washington D.C., USA
ZMA = Zoological Museum of Amsterdam, Amsterdam, The Netherlands
ZMB = Zoologisches Museum, Berlin, Germany
ZRC* = Lee Kong Chian Natural History Museum, National University of Singapore, Singapore (following widespread usage; the abbreviation in Sabaj 2016, USDZ, has not been adopted here)
ZSI = Zoological Survey of India, National Zoological Collection, Kolkata, India
ZSIC* = Zoological Survey of India, Chennai, India
ZSIP* = Zoological Survey of India, Andaman and Nicobar Islands Regional Station, Port Blair, India

Results

Taxonomic accounts

Class Reptilia Laurenti, 1768
Order Squamata Oppel, 1811
Suborder Serpentes Linnaeus, 1758
Family Elapidae Boie, 1827

Genus ***Ophiophagus*** Günther, 1864

Hoplocephalus Wagler, 1830: 342 (in prevailing usage for Australian Broad-headed snakes).
Hamadryas Cantor, 1836: 187 (preoccupied; by *Hamadryas* Hübner, 1818).
Dendraspis Fitzinger, 1843: 28 (suppressed; for *Dendroaspis* Schlegel, 1848).
Ophiophagus Günther, 1864: 340. Official Generic Name No. 1599 Opinion 709 (ICZN 1964).

Type species

Hamadryas elaps Günther, 1858 fide Opinion 709 of ICZN (1964: 210).

Etymology

Greek, alluding to the snake-eating habits of member(s) of the genus, from the respective roots, '*ophis*' for 'snake' and '*phagos*' for 'eater'.

Nomenclatural remarks

The nomenclature of the generic name of the king cobra has been subject to considerable confusion. The original generic nomen, *Hamadryas* Cantor, 1836 was identified as preoccupied by *Hamadryas* Hübner, 1818 (Insecta: Lepidoptera) (see Bogert 1945; ICZN 1964; Smith & Chiszar 1989). Zhao & Adler (1993: 271) mentioned that Hübner (1806), usually cited as the source of the generic name, only used the plural form *Hamadryades.* The next oldest generic name, *Dendraspis* Fitzinger, 1843, was suppressed (ICZN 1964), due the likelihood of confusion with the genus *Dendroaspis* Schlegel, 1848.

Günther (1864: 340) established the genus *Ophiophagus*, with *Hamadryas elaps* Günther, 1858 as the sole included species, and hence the type species by monotypy. The specific epithet *elaps* has a confused history. Günther (1858, 1864) had erroneously attributed the name *elaps* to Lesson, 1829, as well as to Schlegel, 1837. In fact, Lesson did not use the specific epithet *elaps*, but instead described *Coluber ikaheca* Lesson, 1830 (now *Micropechis ikaheca*). The name *Naja elaps* was thus newly established by Schlegel (1837). The clear description and illustration in Schlegel (1844) leave no doubt that *Naja elaps* is a junior synonym of Lesson's *Coluber ikaheca* (see Mertens 1962). However, despite attributing the name *elaps* to Schlegel, in listing *Hamadryas elaps*, Günther (1858) provided an unmistakable description of the king cobra: the ventral and subcaudal scale counts lie outside the ranges for *Micropechis* Boulenger, 1896, the mixed single and divided subcaudals, a clear description of what are now called the occipital scales (the term 'occipital scales' was used by Günther and his contemporaries for what are now termed the parietal scales) and the size of the species are unambiguously characteristic of the king cobra. Günther's synonymy and chresonymy make clear that *O. elaps* is a chresonym of *Hamadryas elaps* Günther, 1858. The inclusion of *Naja elaps* Schlegel, 1837 in the synonymy of *O. elaps* is most probably a mistake of Günther, either a lapsus or a confusion with *Naja bungarus*, a taxon that is indeed a king cobra.

Mertens (1962) asked the ICZN to designate "*Hamadryas elaps* Günther, 1858 [equivalent to *hannah* Cantor, 1836]" as the type species of *Ophiophagus*. This was enacted by Opinion 709 of ICZN (1964: 210), fixing *Hamadryas elaps* Günther, 1858 as the type species of the genus *Ophiophagus* Günther, 1864.

While the nomenclature of the genus has been stable in the literature since ICZN Opinion 709 (ICZN 1964), several problematic issues have remained overlooked. Boie (1828a, 1828b) used the nomen *Naja bungaroides* for a juvenile (RMNH 1334; see below) from Java. We treat it as a nomen nudum, as the description, "due to the makeup of the scuta subcaudalia", does not constitute a "description or definition", as required by Article 12.1 of the Code (ICZN 1999) and defined in the Glossary therein (Mees 1957; David & Ineich 1999). Wagler (1830: 342) cited Boie's *Naja bungaroidea* (incorrect subsequent spelling of *Naja bungaroides*) and provided a diagnosis sufficient to make the name available. In the same publication, Wagler also proposed a new genus, *Hoplocephalus*, for *Naja bungaroides*. The consequence of this, overlooked ever since, is that the type species of the genus *Hoplocephalus* is *Naja bungaroides* Wagler, 1830, a king cobra, not the Australian broad-headed snake which Schlegel (1837) named *Naja bungaroides* (while also creating the name *Naja bungarus* for Boie's species). Schlegel's name *bungaroides* has been consistently applied to the Australian species since, while it is Schlegel's *Naja bungarus* that has long been associated with *Ophiophagus*. A strict interpretation of the Code would make *Hoplocephalus* the oldest available genus-group name for the king cobra, and *bungaroides* the oldest species-group name for any king cobra species. This would upend the nomenclature of two culturally iconic, medically important and IUCN Red-Listed genera of elapid snakes, each with a large associated body of literature.

A Case to the International Commission of Zoological Nomenclature is in preparation to preserve the prevailing usage of the genus-group names *Ophiophagus* and *Hoplocephalus* and of the binomen *Hoplocephalus bungaroides*. This will require setting aside the type of Wagler's *Naja bungaroides* and the designation of a neotype belonging to the Australian broad-headed snake. The action will make Wagler's name unavailable for any king cobra. In anticipation of a Commission Opinion in favour of this case, we have therefore refrained from using Wagler's name *bungaroides* for any king cobra species, and have used the next-oldest available name in all cases. In the interest of nomenclatural stability, all affected nomina should continue to be used in the prevailing manner pending resolution of the case by the Commission.

Nomenclatural histories of species-series nomina

The type species of *Ophiophagus*, Cantor's (1836) *Hamadryas hannah*, was from "Sunderbuns", equivalent to the Sunderbans of Bengal, a large deltaic region of mangrove forests at the confluence of the rivers Ganga, Brahmaputra and Padma, covering an area of ca 10 000 sq km in modern day India and Bangladesh, and "jungle not far from Calcutta" (since 2001, Kolkata, the administrative capital of

West Bengal State, eastern India), located ca 56 km NW of the Sunderbans. It is unclear where the four syntypes were deposited and these are considered not extant at present (Toriba 1993). Several other snake types of Cantor are unlocated, and a few are preserved either as specimens in the BMNH or depicted in numbered, coloured plates in the Bodleian Library of Oxford University, Oxford, United Kingdom. The original description, published in *Asiatick Researches* (later modified to '*Asiatic Researches*', its full form, '*Transactions of the Society Instituted in Bengal for Inquiring into the History and Antiquities, the Arts, Sciences and Literature of Asia*'), which was a short-lived (1798–1836) journal published by the Asiatic Society of Bengal from Calcutta. The original description contained a nine-line Latin diagnosis of the purported new genus *Hamadryas* Cantor, 1836, and a two-line diagnosis of the species, followed by five pages of description and reports on its behaviour, as reported by local inhabitants of the region. Three plates accompany the description, the first showing the head with neck expanded in anterior and posterior views (Cantor 1836: fig. 1), the second showing the cranium and mandible as well as dissected head showing cranial muscles as well as the venom glands (Cantor 1836: fig. 2), and finally, the head in dorsal and ventral views, showing close-ups of some scales and the posterior venter and tail, showing ventral and subcaudal scales (Cantor 1836: fig. 3).

About two years later, Cantor's (1838) redescription of the same species, as *Hamadryas ophiophagus*, was read out at the 12 June 1838 meeting of the Zoological Society of London, a somewhat rare case of synonymy involving the same author. The rationale for the action remains unknown, because Cantor (1838) alludes to his 1836 paper, and may either be on account of Cantor's desire to disseminate the information regarding his remarkable new species to a scholarly audience at home, and his realization of the transient nature of the *Asiatic Researches*.

Several names have been applied to members of the genus. The taxonomic and nomenclatural history is elaborated below. The nomina currently recognised as synonyms include *Naja bungarus* Schlegel, 1837; *Hamadryas ophiophagus* Cantor, 1838; *Naia vittata* Elliot, 1840; *Dimeresurus boiei* Bleeker, 1858 (a nomen nudum, carrying no description; the name [in the combination *Trimeresurus boiei*] was synonymised with *Naia bungarus* Schlegel, 1837 by Boulenger 1896: 396); and *Naja ingens* A.W.M. van Hasselt, 1858 (although Smith 1943 and Toriba 1993, incorrectly attributed this name to van Hasselt 1882).

In his review of the king cobra species complex (which he assigned to the genus *Dendraspis* Fitzinger, 1843), Deraniyagala (1960) established two new taxa, *D. hannah sinensis* (for the Chinese population) and *D. h. borneensis* (for the Bornean population), while also reviving the following names as subspecies: *vittata* (Elliot, 1840) for the south-western Indian population, and *bungarus* Schlegel, 1837, for the Sumatran population. In a subsequent paper, Deraniyagala (1961) described two further subspecies, *D. hannah nordicus* (from Mamgain, Dunda Lakhond, Dehra Dun, India and apparently also eastern Pakistan) and *D. hannah brunnea* (from the vicinity of Darjeeling, India).

The holotype of Cantor's (1836) *Hamadryas hannah* is erroneously mentioned as BMNH 1996.461 (ex RSL) by Wallach *et al.* (2014) and Leviton *et al.* (2018); this is instead the holotype of Elliot's (1840) *Naia vittata*, a subjective junior synonym of *Ophiophagus hannah*, a stuffed specimen, presumably once a 'gallery' specimen, which was rediscovered uncatalogued in the basement of the London collection during the course of this research in 1996. BMNH 1996.461 (ex RSL) appears to have been examined by Günther (1858) and Boulenger (1896), who list it in their respective catalogues.

The first use of the current combination for the nominate species, *Ophiophagus hannah*, is by Bogert (1945). A near complete synonymy for the Sunda region has been provided by David & Vogel (1996), and synonyms for populations from the Asian mainland have been listed in Smith (1943), Taylor (1965) and Zhao & Adler (1993). Leviton (1968) provided the most exhaustive chresonymy for *Ophiophagus hannah*.

Of the nine nomenclaturally valid nomina (Cantor 1836; Schlegel 1837; Cantor 1838; Elliot 1840; van Hasselt 1858; Deraniyagala 1960, 1961) that are currently allocated to *Opiophagus* sensu Günther, 1864, two (*Hamadryas hannah*; *Naja bungarus*) are shown in this paper to represent taxonomically valid species. An additional two populations, from the Western Ghats (India) and the island of Luzon (the Philippines) are described as new to science (see also Gowri Shankar *et al.* 2021).

Content

Four species, corresponding to the four Confirmed Candidate Species, CCS (sensu Padial *et al.* 2010) of Gowri Shankar *et al.* (2021):

Ophiophagus hannah s. str.: a widespread Asian mainland lineage, distributed from eastern Pakistan, northern and eastern India east to China and south to Myanmar, northern and central Thailand, Cambodia, Laos, Vietnam, as well as on the Andaman Islands. CCS2 of Gowri Shankar *et al.* (2021).

A Sundaland species from the Malay Peninsula, and islands of the Greater Sundas, including Sumatra, Borneo and Java, in addition to Mindoro (in the Philippines). CCS3 of Gowri Shankar *et al.* (2021). The nomen *Naja bungarus* originating from West Java, is the oldest available one for this form (read below).

A geographically isolated, unnamed species from the Western Ghats of south-western India. CCS1 of Gowri Shankar *et al.* (2021).

A second unnamed species, representing an isolated lineage from the island of Luzon (in the Philippines). CCS4 of Gowri Shankar *et al.* (2021).

Ophiophagus hannah (Cantor, 1836) s. str.

Figs 2–5, 7, 9A–C, 10A, 11A, 12A

Hamadryas hannah Cantor, 1836: 87.
Hamadryas ophiophagus Cantor, 1838: 187 (replacement name for *Hamadryas hannah*).
Naia Vittata Elliot, 1840: 41 (sic, for *vittata*).
Dendraspis hannah sinensis Deraniyagala, 1960: 62.
Dendraspis hannah nordicus Deraniyagala, 1961: 229.
Dendraspis hannah brunnea Deraniyagala, 1961: 229.

Common name

Northern king cobra.

Diagnosis (redefined herein)

A species of *Ophiophagus* inhabiting the Sub-Himalayas, eastern India, Myanmar, Indochina, southwards to the Isthmus of Kra, showing the following combination of characters: dark-edged yellow bands along body of adults (vs unbanded in adult *O. salvatana* Gowri Shankar, Das & Wüster sp. nov.; lacking dark edges to the pale bands in *O. kaalinga* Gowri Shankar, Das & Ganesh sp. nov. and, if present, in *O. bungarus*). Further, *O. hannah* differs from all other congeners in having a high pterygoid tooth count of 18–21 (vs 11 in *O. bungarus* and *O. salvatana* and 12 in *O. kaalinga*). Finally, juveniles of *O. hannah*, with 27–48 body bands, differ from *O. salvatana* (85–86) and *O. bungarus* (57–87); relative tail length ranging 21.7–26.4% with a mean of 24.05% (vs 19.3–25.1% [22.2%] in *O. bungarus*; vs 18.0–19.9% [18.95%] in *O. kaalinga*; vs 18.7–23.0% [20.85%] in *O. salvatana*).

Etymology

The source of the epithet *hannah* was not mentioned by Cantor (1836, 1838). More recently, Adler (2016) argued the same to be an eponym for Hannah Sarah Wallich (1820–1893), eldest daughter of Cantor's host and uncle, the celebrated botanist (and physician), Nathaniel Wallich (1786–1854), during his time in Calcutta, and at the time of description of the species.

Type material

Neotype (designated herein)

INDIA • ♀; West Bengal State, Kolkata, Howrah, Acharya Jagadish Chandra Indian Botanical Gardens; 22.55° N, 88.29° E; John Anderson leg.; ZSI 8292.

Remarks

The type series comprising four syntypes, of *Hamadryas hannah*, reported from "Sunderbuns" and "jungle not far from Calcutta", being lost or untraceable now (not mentioned in Boulenger 1896; Das *et al*. 1998), along with most of Cantor's zoological specimens (see Adler 2016), is the cause of some confusion, both in the past and presumably in the future. Indeed, there is no mention of the location of the types in other works that enumerate repositories of Asian snake types (e.g., Smith 1943; Golay 1985; Toriba 1993; David & Ineich 1999; McDiarmid *et al.* 1999; Iskandar & Colijn 2000).

Since it is evident that the type series of Cantor's *Hamadryas hannah* is currently not extant (Article 75.3.4), we invoke Article 75 of the Code (ICZN 1999) to designate ZSI 8292, an adult collected by John Anderson, Superintendent of the Indian Museum from the Indian Botanical Gardens, Howrah, Kolkata, India, as the neotype of *Ophiophagus hannah*, in the context of the revision of the genus, in order to clarify the taxonomic status of the species (Article 75.3.1) and describe the characters of the specimen (Article 75.3.2), the data and description of the same unequivocally diagnosing the taxon from its congeners (Article 75.3.3). The neotype matches the original description in all observed morphological characteristics (Article 75.3.5), and is drawn from the general geographical area of the type locality, in the north-western suburb of the township of Shibpur, ca 10 km from Kolkata (Article 75.3.6) and preserved in a globally-recognised systematic collection that dates back to the late 1800s (Article 75.3.7).

The members of the genus are widespread and appear morphologically conservative, with incorrect application of names for over a century and the possibility of parapatry or sympatry (such as in fragmented areas of central India, as well as in southern Thailand), and more intense sampling may reveal the existence of additional cryptic lineages within the complex. This is likely within the vast geographical range of *O. hannah*, as restricted here, as well as in the extreme eastern range of the group (Sulawesi) and the southern islands of the Philippines archipelago, as new material, including genetic samples, becomes available. Despite the long history of collections and research in the southern Bengal region (Das 2004), it is remarkable that no other topotypical specimen exists in a systematic institution, further necessitating the need to draw attention to this significant specimen (ZSI 8292).

On the identity and provenance of *Naia vittata*

Elliot (1840) erected the nomen *Naia vittata* based on a stuffed adult (see Günther 1858), a non-skeletal specimen sourced from southern India (Fig. 5). This nomen was however short-lived, as Cantor (1847) went on to synonymise Elliot's nomen under his own *Hamadryas ophiophagus* Cantor, 1838: the synonymy has been accepted by subsequent authors. Elliot (1840) in his original description states that the type specimen was given to him by a fisherman who found the live snake contained inside a floating box carried by a catamaran in mid-sea, off the coast of "St. Thome" (currently, Santhome, within Chennai City, Tamil Nadu State, southern India: 13.0303° N, 80.2788° E, 7 m a.s.l.). Thus, its true precise provenance remains unknown. The only other locality mentioned in the original description is Guindy (also in Chennai City: 13.0105° N, 80.2156° E; 14 m a.s.l.). By all evidence, there has never been any wild population(s) of *Ophiophagus* in either of the two localities mentioned in Elliot's description (Murthy 1978; Whitaker & Captain 2004). When Deraniyagala (1960) reinstated this nomen as a trinomial for a subspecies, he conferred it to the Western Ghats population. Our studies show that the description and figure of the holotype of *Naia vittata* are not in conformity with the Western Ghats population, in that the two-scale wide pale bands, distinct black borders of the pale bands and the progressive darkening of the dorsum posteriorly are unique to this nominal species. Thus, taking into account the morphology and the most plausible geographic scenario (see discussion), we treat *Naia vittata* Elliot, 1840 as a junior subjective synonym of *Hamadryas hannah*.

Material examined

BHUTAN • 1 ♀; Ronglong, Manas Valley; 26.79° N, 90.94° E; ZSI 22483.

CHINA (including Hong Kong) • 1 spec., holotype of *Dendraspis hannah sinensis* Deraniyagala, 1961; Fujian Province "Guling-Gu Shan", near Fuzhou Shi; 26.10° N, 119.28° E; AMNH 29944 • 1 ♀; New Territory, Hong Kong, Tai Po; 22.30° N, 113.95° E–22.45° N, 114.17° E; BMNH 1983.273 • 1 spec.; Guizhou Province Kowloon; 22.32° N, 114.18° E; BMNH 1955.1.4.69 • 2 specs; Xiuwen; 26.83° N, 106.59° E; CIB 21001, CIB 210002 • 1 ♂; Guizhou Province Xingyi; 25.09° N, 104.89° E;

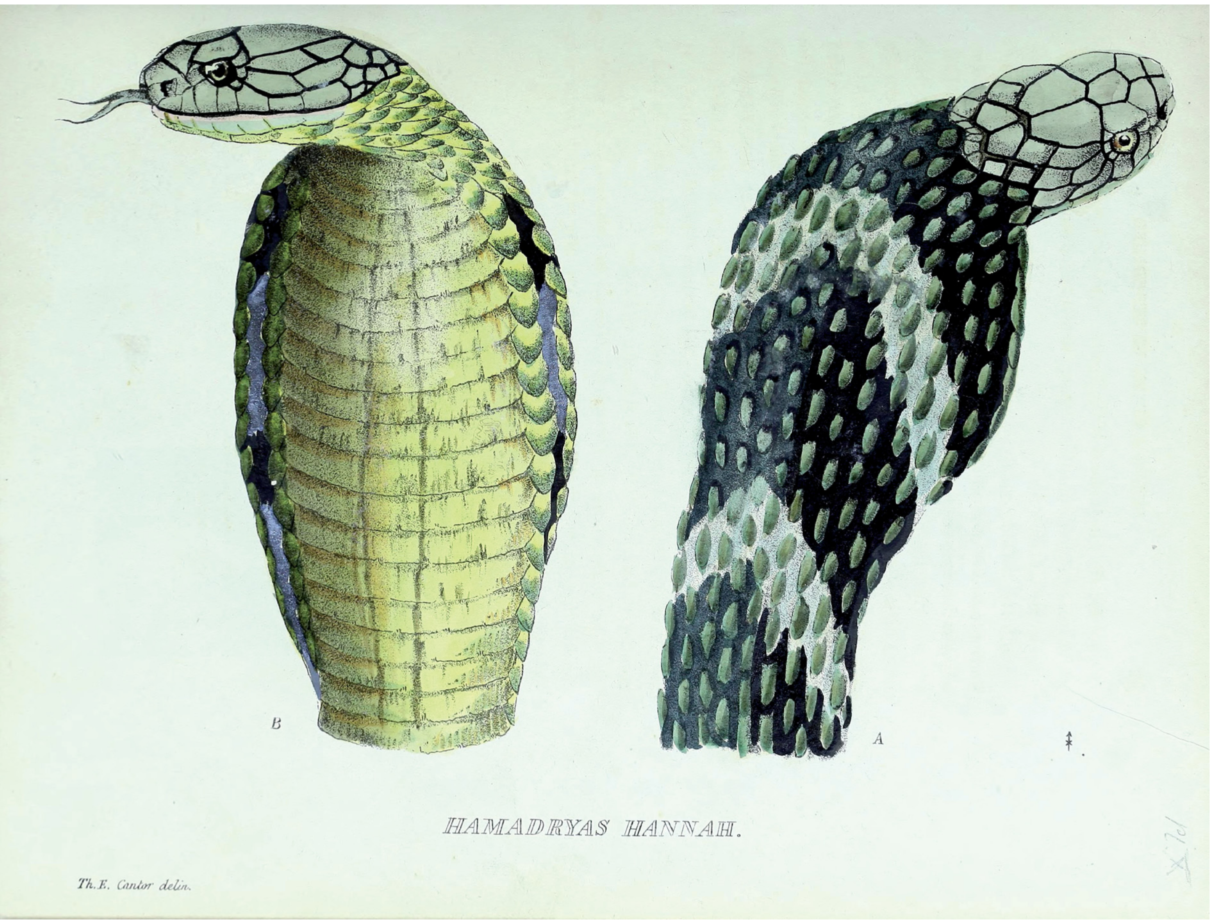


Fig. 2. Plate X from Cantor (1836), showing head with neck expanded in anterior and posterior views of a syntype of *Hamadryas hannah* Cantor, 1836.

CIB unregistered • 3 specs; Hong Kong Lantau Island i.e., Tai Yue Shan; 22.25° N, 113.93° E; MCZ 176539, MCZ 176540, MCZ 177105 • 1 spec.; Hong Kong New Territories, W slope of Tai Mo Shan; 22.42° N, 114.12° E; MCZ 176365.

INDIA • 1 ♀; Meghalaya State, Shillong'; 25.58° N, 91.89° E; BMNH 1907.12.16.21 • 1 ♀; same data as for preceding; ZSI 21703 • 1 ♂, holotype of *Naia vittata* Elliot, 1840; Tamil Nadu State, south-eastern India in Mylapore, coastal Chennai "St. Thome"; 13.03° N, 80.28° E; BMNH 1996.451 • 1 ♂; "Assam" [no further locality]; BNHS 2274 • 1 spec.; Assam State, Kokrajhar, Kachugaon; 26.38° N, 90.903° E; BNHS 2275 • 1 ♀, paratype of *Dendraspis hannah brunnea* Deraniyagala, 1961; West Bengal State, Tindharia; 26.85° N, 88.33° E; BNHS 2276 • 1 spec.; Sikkim State, Gangtok; 27.33° N, 88.612° E; BNHS 2270 • 1 spec.; Uttarakhand State, Nainital, Patwadangar; 29.38° N, 79.50° E; BNHS 2278 • 1 spec.; West Bengal State, Duars, ca 30 km area of floodplains in Himalayan foothills north of Brahmaputra; BNHS 2267 • 1 spec; South Andaman Island; ca 11.61° N, 92.61° E; CSPT/S-56 • 1 spec.; Odisha State, Bhitarkanika National Park; ca 20.75° N, 87.00° E; MCBT 152886 • 1 spec.; same data as for preceding; NKBP unreg. • 1 spec.; West Bengal State, Kalimpong, Tarkhola; 27.07° N, 88.48° E; MCZ 58258 • 1 spec.; Arunachal Pradesh, Itanagar; 27.07° N, 93.59° E; SFRI A-4 • 1 spec.; South Andaman Island, Port Blair [currently, Sri Vijaya Puram]; 11.62° N, 92.72° E; USNM 129748 • 1 ♂; South Andaman Island, Mathura; 11.72° N, 92.69° E; ZSIP 366 • 1 spec.; Uttarakhand State, Mussoorie; 30.45° N, 78.08° E; ZSI 12556 • 1 ♂, holotype of *Dendraspis hannah brunnea* Deraniyagala, 1961; West Bengal State, Darjeeling; 27.05° N, 88.3° E; ZSI 8294.

MYANMAR • 1 ♀; Bago Division, Bago or Pegu; 17.33° N, 96.48° E; BMNH 68.4.3.31 • 1 spec.; Shan State, Shweli, in a river; 23.67° N, 96.42° E; collection locality presumably in basin; BMNH 1925.12.22.18 • 1 ♀; Shan State, Mogok; 23.00° N, 96.42° E; BMNH 1900.9.20.19 • 1 spec.; Kachin State, Sumprabum Triangle; 26.55° N, 97.57° E; BMNH 1940.6.5.63 • 1 spec.; Magway Division, Thayet-myo; 19.32° N, 95.18° E; BNHS 2271 • 1 ♀; Sinlum Kaba or Sinlumkaba; ca 24° N, 97° E; BNHS 2273 • 1 spec.; Ayeyarwaddy Division, vicinity of Mwe Hauk village; 16.28° N, 94.77° E; CAS 206601 • 1 ♂; Mandalay Division, Mount Popa; 20.92° N, 95.25° E; MCZ 44699 • 1 ♀; Mandalay Division, Popa Mountain Park, Kyauk Pan Tawn; 20.87° N, 95.24° E; CAS 214017.

NEPAL • 1 spec.; Bagmati Province, Kathmandu; 27.72° N, 85.32° E; BNHS 2268 • 1 spec.; Bagmati Province, ca 14.5 km W of Hetauda, Rapti Bridge; ca 27.43° N, 85.00° E; BNHS 2269.

THAILAND • 1 spec.; Amphoe Pak Thong Chai, Nakhon Ratchasima Province [= Khorat Province], Sakaerat Environmental Research Station; 14.51° N, 101.93° E; FMNH 180215 • 1 spec.; Prachuap Khiri Khan Province, Koh Lak; 11.82° N, 99.80° E; BMNH 1969.1927 • 1 spec.; same data as for preceding; NRM 2532 • 1 spec.; Lampang Province, northern Thailand, Lakon, Lampang; 18.25° N, 99.50° E; BMNH 1921.4.1.44 • 1 spec.; Pak Nam Pho; 15.71° N, 100.13° E; BMNH 1968.836 • 1 spec.; north-western Thailand, Mae Hong Son Province; 19.25° N, 98.00° E; BMNH 1987.1160 • 1 spec.; Kanchanaburi Province, Sai Yok; 14.12° N, 99.14° E; BMNH 1987.1162 • 1 spec.; northern Thailand, Chiang Mai Province, Doi Suthep; 18.82° N, 98.89° E; FMNH 178405 • 1 spec.; Bangkok Province, Near Bangkok; ca 13.75° N, 100.52° E; MCZ 20331 • 1 spec.; Chiang Mai Province, Mount Angka, possibly Doi Angkei or Doi Angkhang; 19.00° N, 98.67° E; MCZ 20331 • 1 spec.; Khon Kaen Province, Khon Kaen, near Pong Neep Dam; 16.77° N, 102.59° E; TNRC 1120 • 1 spec.; Tak Province, Doi Hua Mod; 15.97° N, 98.85° E; USNM 101040 • 1 spec.; Nakhon Ratchasima Province, Pak Chong or Pak Jong; 14.75° N, 101.42° E; USNM 72726.

VIETNAM • 1 ♀; Dac Lak Province, Buon Ma Thuot City or Lac Giao; 12.67° N, 108.05° E; FMNH 26475 • 1 ♀; same data as for preceding; MCZ 43744 • 1 spec.; Thuan Pho Ho Chi Minh Province, Ho Chi Minh City or Saigon; 10.75° N, 106.67° E; LSUMZ 34904; 1 spec.; same data as for preceding;

MNHN 1975.127 • 2 specs; Ba Ria-Vung Tau Province, Vung Tàu or Cap Saint-Jacque; 10.35° N, 107.07° E; MNHN 1911.66, MNHN 1920.213 • 1 ♀; Lao Cai Province, Cha Pa or Chapa; 22.33° N, 103.83° E; MNHN 1935.108 • 1 spec.; "Cochinchine", [currently interpreted as south of Gianh River (Sông Gianh), southern Vietnam, no further data]; MNHN 1912.75 • 3 ♂♂; same data as for preceding; MNHN 3189, MNHN 7671, MNHN 5205.

Skeletal material

THAILAND • 1 spec.; Nakhon Ratchasima or Khorat Province, Pak Chong or Pak Jong; 101.42° E, 14.75° N; USNM 72726.

VIETNAM • 1 spec.; Lam Dong Province, Bao Loc; 11.42° N, 107.67°E; USNM 95105.

Description of neotype (ZSI 8292)

Venter with an incision, appears to be the specimen mentioned in Anderson (1871).

MEASUREMENTS. SVL 2085 mm, TL 462 mm, total 2547 mm.

HABITUS. Body relatively robust (midbody width 38.3 mm, 1.8% SVL), triangular in cross-section; transverse scales on body: DSR1 17; DSR2 15; DSR3 15; ventrals 240; subcaudals 91; cloacal 1; dorsal

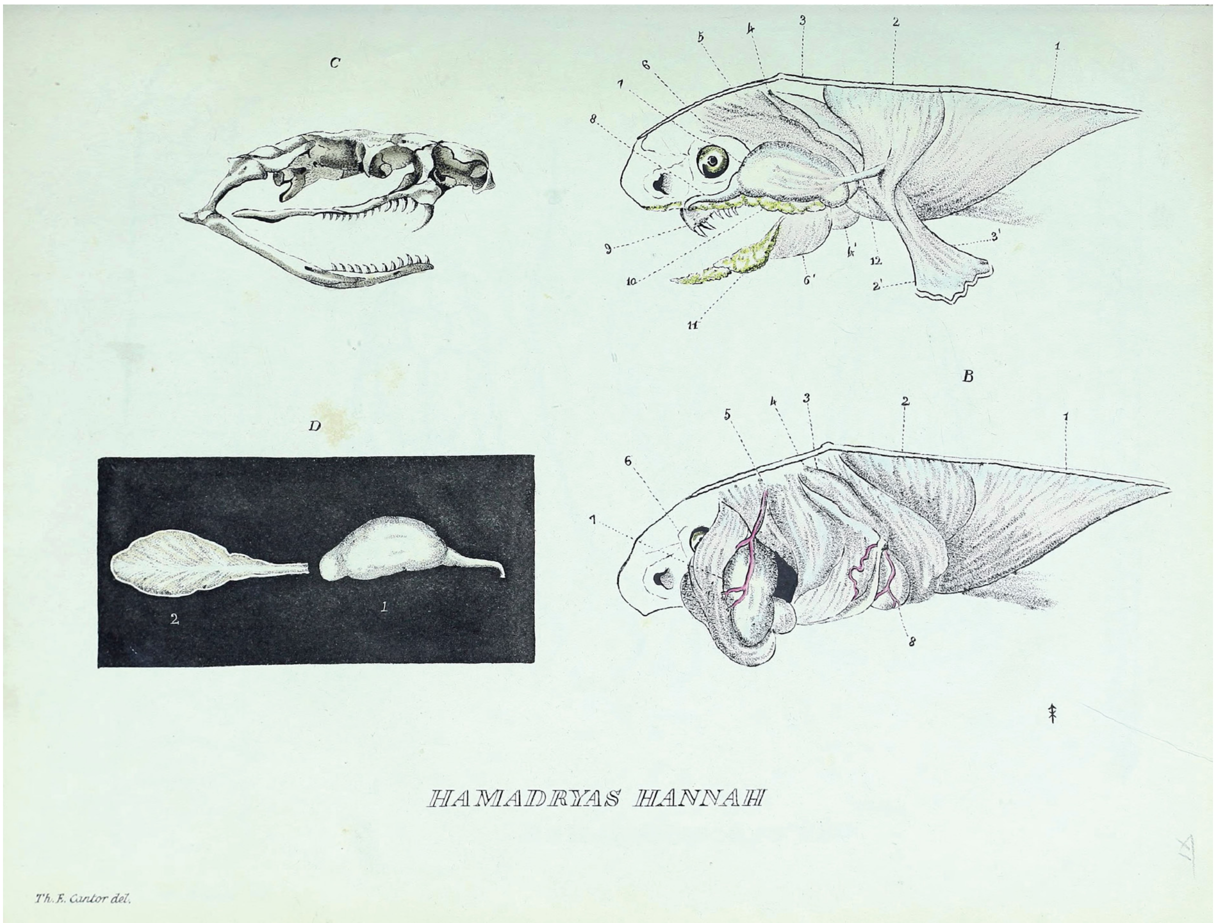


Fig. 3. Plate XI from Cantor (1836), showing cranium, mandible, dissected head and venom glands of a syntype of *Hamadryas hannah* Cantor, 1836.

scales smooth, the vertebral and outer two rows enlarged; ventral scales smooth; first four subcaudal scutes entire; tail short (22.1% SVL), cylindrical, tapering posteriorly.

Head. Head relatively large, head length 46.3 mm, head width 29.4 mm; head depth 25.8 mm; distinct from neck, flattened in the orbital region, rounded in the sagittal region, with a slight depression medially, snout projecting slightly beyond mandible; canthus rostralis sharply defined; eye diameter 7.4 mm; interorbital distance 19.3 mm; cephalic scales juxtaposed, smooth-edged, except parietals and occipitals, which are slightly imbricate; rostral trapezoid in shape, distinctly visible from above, over twice as long as wide, concave ventrally, rostral width 5.2 mm; rostral length 12.2 mm; eye to snout distance 15.0 mm; eye to nostril distance 7.0 mm; nostril diameter 5.3 mm; internasals large, subtrapezoidal, wider than long; internasal suture width 19.3 mm; preocular squarish, wider than high, separated from internasal by prefrontal; prefrontals trapezoid, wider than long; frontal trapezoidal, contacting prefrontals, supraoculars and parietals; frontal edge sinuous, short-sided posteriorly; supraocular subtrapezoidal, contacting prefrontal, frontal, parietal, orbit, preocular, upper postocular and two temporals; large paired occipitals, occipital length 13.0 mm; interoccipital scale present behind the suture between parietals; temporals 2/2 (L/R); in anterior pair, lower temporal larger than upper; in posterior pair, upper temporal longer than lower; first row of nuchals slightly enlarged compared to rest of dorsals; supralabials 7/7; III–IV (L/R) touching the eye; III (L/R) contacting preocular and I (L/R) contacting posterior nasal;

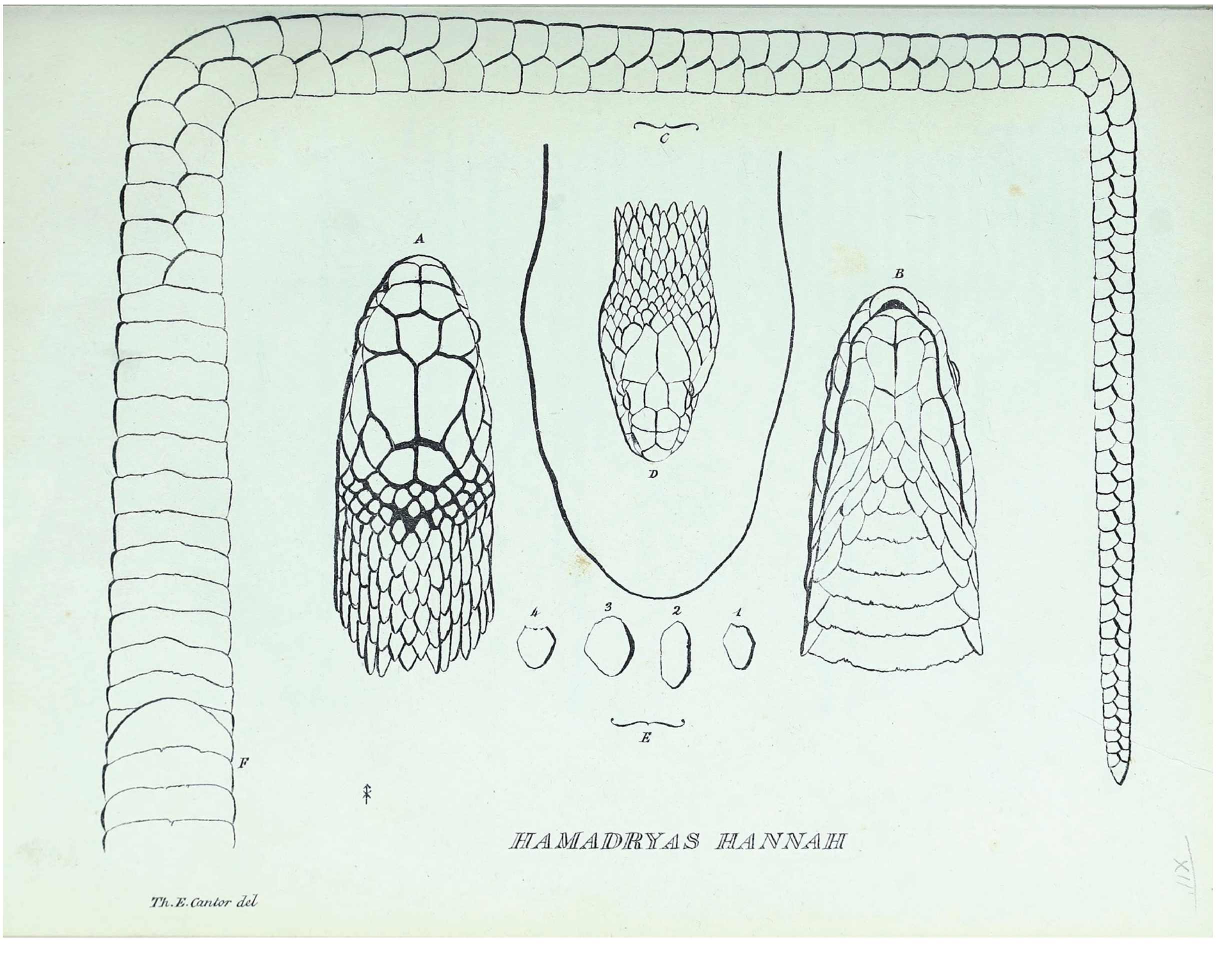


Fig. 4. Plate XII from Cantor (1836), showing head in dorsal and ventral views, scale closeups and the posterior venter and tail of a syntype of *Hamadryas hannah* Cantor, 1836.

supralabial I low; II high; III tallest; II and IV subequal; and VI and VII low, narrow and elongate; nostril lateral at posterior of a single concave nasal, horizontally elliptical, its greatest diameter along vertical axis; one preocular and three postoculars; eye large, contained in head length 0.16 times and head depth 0.29 times; pupil rounded; ocular ring (sensu Marx *et al.* 1987) comprising seven scales:

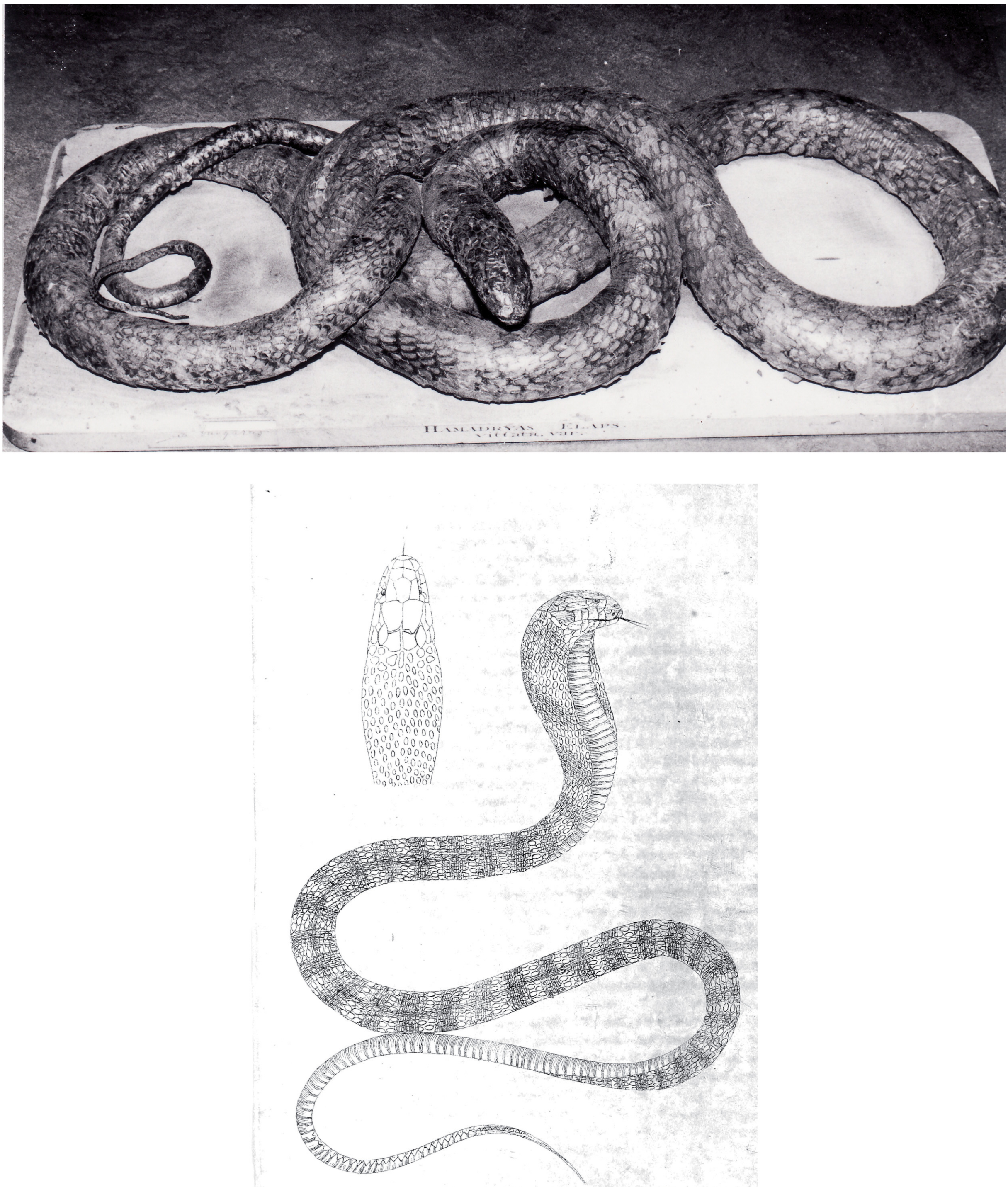


Fig. 5. Holotype of *Naia vittata* Elliot, 1840. **Top**. Photograph of the preserved holotype specimen BMNH 1996.451. **Bottom**. Plate I from Elliot (1840).

one preocular, three postoculars, one supraocular and two supralabials; suboculars absent; mental small, triangular, wider than deep (mental width 7.8 mm; mental depth 2.4 mm); infralabials 8/8 (L/R), first (L/R) contacting anterior genials; infralabial I contact anterior genial; infralabial IV (L/R) contact posterior genials; infralabial IV largest; cuneate scute on lower jaw absent; two elongate gular scales follow posterior mental; the anterior longer than posterior.

Dentition. Maxillary teeth recurved and stout, not compressed, gradually increasing in size posteriorly; fang length 4.0 mm; fang width at base 2.0 mm; tooth count obscured by gingivae.

Colouration. After over a century in preservative, neotype dorsum mahogany brown, almost band-less anteriorly with traces of mottled reticulation of dark-edged pale bands that become more visible from midbody to near tip of tail; venter similarly coloured as of dorsal ground colour, except posterior edge of each scute edged with pale grey; scutes of head midbrown, those on forehead distinctly edged with dark grey.

Hemipenis. Examined in SFRI A-4. Organ everted; distinctly bilobed, rather long and slender, its lengths (L/R) 97/85 mm and widths (L/R) 5.5/4.5 mm; extending up to 15/10 subcaudal scale; divided at level of first subcaudal scale; lobe head flat and rather circular near apex, with numerous, tiny spinules and flounces; asulcate side relatively less spinose compared to sulcate side; basal part of pedicel with dense congregation of large spines; bilobed tubular length of organ with series of circular whorls of spiny protuberances; sulcal lips not evident, sheath-like, completely surrounding apex base; sulcus spermaticus not evident.

Morphological variation

Six of 43 specimens (14%) examined have an interoccipital scute. The occurrence of divided and undivided subcaudals in members of the complex has been reported in the literature (e.g., Smith 1943: 436). All 43 specimens examined for this character have some undivided subcaudals, typically, the first and in succeeding subcaudals up to subcaudal 26, in what appears to be an irregular pattern, including about a third undivided subcaudals from Subcaudal 18 to 32, again without an apparent pattern that cannot be linked to either sex or geographical distribution. The total pale body band count made on 41 individuals was 27–48 (mean 39.6). Dorsum of more recently collected material examined is a shade of midbrown, Fawn Colour #25, forehead paler, Drab #27, interscale areas darker along body; distinct pale bands, Buff #124, numbering 27–48, each 2–3 scales wide, edged with darker grey, Blackish Neutral Gray #82 areas, about a scale wide, bands separated from each other by five scales; on nape region, the first two pale bands form distinct chevrons, the rest of the body bands less angular in adults; bands sometimes broaden on lower flanks; the largest scales of forehead, frontal, parietals, occipitals, upper temporals and postoculars with a distinct dark edge. Tail and posterior fourth of body nearly black, with 1–2 ivory-coloured scales on tail, separated from each other by 5–6 scales. Some large individuals are grey-black, the interscale regions appearing paler. Mandible and genial region Cream Colour, #54; the gular region to until Ventral 13–27 bright yellow, Warm Buff, #118, sometimes reported as a shade of orange, with two dark areas peripherally, comprising somewhat indistinct bands meeting Ventrals 13–27; and noticeably in larger, hooding individuals. Abdominal region as in gular region, but progressively darkening. Subcaudal region with pale scales, obscurely darkened throughout and with dark edges. Pupil rounded, black, iris brownish-red, Kingfisher Rufous #240, darkening peripherally, with a narrow, yellow ring. Tongue is blackish-grey, the oral cavity pink. Juveniles have ivory white bands, Buff, #124, including four on the head region, the first one in rostral position, a broad one covering rostral, as well as part of Supralabial 1, nasals, and internasals; the second in preocular position, narrower, and covering part of the prefrontals, preoculars and Supralabial III; the third one in postocular position, narrowest of the four bands, and covering part of the frontal and parietals, and comprising large, elongated marks arranged in a transverse series; and the fourth one on cephalic position, broader than the previous one, and covering part of the parietals and occipitals, and comprising large oval spots arranged in a transverse series. Body bands are of the same colour, about two scales in width, and number 35–48 between head bands and the caudal region above vent, and have 4–5 scale wide interband areas. Bands on tail relatively thick, with darker edges, both dorsally and ventrally; and the posterior third of body appears darker than the rest of the body.

Sample size and condition do not permit analysis of ontogenetic change of body bands, although the adult bands do appear to show reduced contrast on the dorsum, compared to hatchlings, and pale markings are absent on the forehead of adults. Individuals (n = 12) that permitted counts of tooth sockets have dentition thus: 15–16 dentaries; 18–21 pterygoids and 3 palatines.

Distribution

The geographical distribution of the nominate species, as restricted here, extends from extreme eastern Pakistan, across the sub-Himalayan region of Kashmir, northern India, Nepal, Bhutan, Tibet, and south to the Godavari-Mahanadi-Ganges deltas of the Circar Coast in eastern India, east to the eastern coast of China, including Hong Kong, the range extending south to Indo-China, including Myanmar, Laos, Vietnam, Cambodia and parts of Thailand, presumably north of the Isthmus of Kra (Pope 1935; Das 1999; Leviton *et al.* 2003; Whitaker & Captain 2004 [in part]; Ahmed *et al.* 2009; Nguyen *et al.* 2009; Sharma *et al.* 2013; Chandra *et al*. 2014; Ahsan *et al.* 2015; Faiz *et al*. 2017; Dolia 2018; Tshewang & Letro 2018; Francis 2021; Koirala *et al.* 2021). The records from the extreme west of the distributional range (including Lahore and Palanpur, in Pakistan) were considered by Wall (1928) to be introductions by snake charmers or the result of transport along rivers. However, old records of the occurrence of the snake in the extreme eastern part of Pakistan, discussed in this paper, appear to be reliable, although it is unknown if populations persist at present.

Ophiophagus bungarus (Schlegel, 1837) comb. nov.

Figs 6, 9D–F, 11B, 12B, 13B, 14

Naja bungaroides Boie, 1828a: 250 (nom. nud.).
Naja bungaroidea [sic] Wagler, 1830: 342.
Hoplocephalus bungaroides Wagler, 1830: 342, by implication.
Naja bungarus Schlegel, 1837: 184.
Naja ingens van Hasselt, 1858: 141.
Dimeresurus boiei Bleeker, 1858: 263 (nom. nud.).
Dendraspis hannah borneensis Deraniyagala, 1960: 61.

Nomenclatural comment

Due to the impending Case before the International Commission of Zoological Nomenclature and to future-proof the binomen of this species, we have not used Wagler's name for this species, but opted for the next-oldest available name, *Naja bungarus* Schlegel, 1837.

Common name

Sunda king cobra.

Diagnosis

A species of *Ophiophagus* inhabiting Malesia, south of the Isthmus of Kra (southern Thailand, peninsular Malaysia, Sunda Archipelago, east to parts of southern and central Philippines) and showing the following combination of characters: mostly unbanded in large individuals, occasionally with narrow pale bands, lacking darker edges, along body of adults (vs unbanded in adult *O. salvatana* sp. nov.; dark-edged pale band in *O. hannah*). It differs from *O. kaalinga* sp. nov. in having a brownish-yellow to mahogany dorsum, with or without (in large adults) slightly paler, narrow bands (vs dorsum dark grey with yellow bands that expand on lower flanks); dorsum ground colour showing little to no contrast at the meeting point of ventral scales at gular region (vs with a clear line of separation from ventrals in gular region). The higher body band counts (57–87) of juvenile *O. bungarus* separate it from those of *O. hannah* (27–48), and *O. kaalinga* (28–48). The pale body bands of juvenile *O. bungarus* are more rounded, the dark interband areas covering 4–9 scales (Fig. 12B), whereas they are extremely angular in *O. salvatana*, with the dark interband areas covering 2–3 scales (Fig. 12D); relative tail length ranging vs 19.3–25.1% with a mean of 22.2% (vs 21.7–26.4% [24.05%] in *O. hannah*; vs 18.0–19.9% [18.95%] in *O. kaalinga*; vs 18.7–23.0% [20.85%] in *O. salvatana*). Finally, *O. bungarus* differs from *O. hannah* in having a lower pterygoid tooth count of 11 (vs 18–21).

Etymology

The specific epithet probably alludes to either morphological (partially undivided subcaudals) or behavioural (ophiophagous) characters of kraits (genus *Bungarus*).

Material examined

Lectotype

INDONESIA • ♂, hatchling; Java, Java Barat Province, Tjihao or Cihoe or Tji Hoe; 6.43° S, 107.13° E; Apr. 1827; Heinrich Boie (1784–1827) and Heinrich Christian Macklot (1799–1827) leg. [see Troelstra 2016]; RMNH 1334.

Schlegel (1837) mentioned two specimens in his description of *Naja bungarus*: Boie's specimen (extant as RMNH 1334), and a specimen from Sumatra of unconfirmed whereabouts, but possibly RMNH 1338 (Wolfgang Denzer and Esther Dondorp in litt.; Wolfgang Wüster pers. obs.). Both of these are currently syntypes of the name. We hereby designate the extant specimen RMNH 1334 as the lectotype of *Naja bungarus* Schlegel, 1837 as per Art. 74 of the Code.

Other material examined

BRUNEI DARUSSALAM • 1 spec.; Dewan Museum, Kota Batu, Bandar Seri Begawan; 4.89° N, 114.97° E; BMNH 2.1979 • 1 ♂; Bandar Seri Begawan, Kampung Pinto Halim; 4.89° N, 114.97° E; BMNH 224.1991 • 1 ♂; Bandar Seri Begawan, Kampung Beribi, Gadong; 4.89° N, 114.89° E; BMNH 6.1998 • 1 spec.; Bandar Seri Begawan, Jalan Muara, Forest Hill; 4.90° N, 115.00° E; LSUMZ 55839 • 1 spec.; Bandar Seri Begawan, Kota Batu; 4.88° N, 114.97° E; BMNH 1984.80.

INDONESIA • 1 spec.; Jawa Barat, Pasir Banggoer Krawang; 6.42° S, 107.67° E; MZB 376 • 1 spec.; Jawa Barat, Batavia or Jakarta; 6.17° S, 106.78° E; MZB 368 • 1 spec.; Jawa Barat, Muara Karang; 6.12° S, 106.78° E; MZB 2206 • 1 spec.; Jawa Barat, Jakarta, Antjol or Ancol; 6.13° S, 106.83° E; MZB 402 • 1 spec.; Jawa Barat, Indramayu or Indramaju; 6.32° S, 108.32° E; MZB 399 • 1 spec.; Borneo, Kalimantan, Timur Province, Balikpapan; 1.24° S, 116.85° E; BMNH 1912.6.26.21 • 1 spec.; Borneo, Berau, Kalimantan Timur Province, Sambulajan, Sungei Segah; 2.17° N, 117.50° E; MZB 1339 • 1 spec.; Borneo, Central Kalimantan Province, Purukcahu or Puruktyau or Purukt Jahu; 0.58° S, 114.58° E; RMNH 7546 • 1 spec.; Borneo, East Kalimantan Province, Sebulu; 0.27° S, 117.00° E; USNM 200500 • 2 ♂♂; Sumatra, Bukit Tinggi or Fort de Kock; 0.32° S, 100.37° E; BMNH 1928.2.8.43, BMNH 1928.2.18.43 • 1 spec.; Sumatra, Siulakderas, Kerinchi or Korinchi; 1.92° S, 101.30° E; BMNH 1915.12.2.39 • 1 spec.; Sumatra, Langkat; 3.87° N, 98.31° E; RMNH 6351 • 1 spec.; Sumatra, Sinabang, Simeulue Island; 2.47° N, 96.37° E; RMNH 5192 • 1 spec.; Sumatra, Tarussan Bay or Teluk Tarusan; 1.2167° S, 100.42° E; USNM 35763 • 2 ♂♂; Sumatra, Labuhandeli or Deli Belawan; 3.75° N, 98.68° E; ZMA 13487, ZMA 17476 • 1 ♂; Sumatra, Klein Sungei, Karang Galang; 1.15° N, 104.18° E; ZMA

11235 • 1 spec.; Sumatra, Aceh Special District, Padang Miangatas Gunung Jago; 4.00° N, 97.06° E; MZB 401 • 1 spec.; Sumatra, Bengkulu Province, Kepahiang; 3.65° S, 102.57° E; USNM 070972 • 1 ♂; Sumatra, Bengkulu Province, Kepahiang; 3.65° S 102.57° E; ZRC 2.3212 • 1 spec.; Riau Archipelago, Pulau Galang; 0.75° N, 104.23° E; ZRC 2.3254-6 • 1 spec.; Bangka Belitung Province, Pulau Bangka, Pangkal Pinang; 2.12° S, 106.12° E; MZB 369 • 1 spec.; Bangka Belitung Province, Belitung, Kampung Rembikang, Tanjung Pandan; 2.75° S, 107.65° E; MZB 373.

MALAYSIA • 1 spec.; West Malaysia, Perak, Pulau Dinding; 4.23° N, 100.56° E; BMNH 1903.6.13.3 • 1 spec.; West Malaysia, Perak, in Gunung Korbu; 4.68° N, 101.30° E; BMNH 1957.1.11.40 • 1 ♂; West Malaysia, Selangor; 3.51° N, 101.50° E; IMR uncatalogued • 2 ♂♂; West Malaysia, Selangor, Kuala Langat, Bukit Mandol Forest Reserve; 2.95° N, 101.53° E; IMR 110487, IMR 5063 • 1 spec.; West Malaysia, Pulau Pinang; 5.40° N, 100.23° E–5.73° N, 103.00° E; MCZ 944 • 1 ♂; West Malaysia, Kuala Lumpur; 3.17° N, 101.70° E; MNHN 1899.172 • 1 spec.; East Malaysia (Borneo), Sarawak, Kuching; 1.55° N, 110.33° E; FMNH 67282 • 1 spec.; same data as for preceding; SM uncatalogued • 2 ♂♂; same data as for preceding; SM 5.45.25, SM 5.45.2 • 1 ♂; East Malaysia (Borneo) Sarawak, Subis Forest Reserve, Niah National Park; 3.80° N, 113.80° E; FMNH 128275 • 1 ♂; East Malaysia (Borneo), Sarawak, Bintulu Division, Labang Camp on Sungei Serin; 1.27° N, 110.45° E; FMNH 150891 • 1 spec.; East Malaysia (Borneo), Sarawak, Sungei Baram; 4.58° N, 113.97° E [collection locality presumably upriver]; FMNH 71659 • 1 spec.; East Malaysia (Borneo), Sarawak, Sibu; 2.30° N, 111.81° E; SM 5.45.2C • 1 ♂; East Malaysia (Borneo), Sabah, Lahad Datu, Danum Valley Field Centre; 5.02° N, 117.78° E; FMNH 233152 • 1 ♂; East Malaysia (Borneo), Sabah, Sandakan; 5.87° N, 118.07° E; FMNH 63566 • 2 ♂♂; East Malaysia, Sabah; 5.02° N, 117.78° E; SSM 0109, SSM 0096 • 1 ♂; East Malaysia (Borneo), Sabah, Sandakan; 5.87° N, 118.07° E; SSM 0360 • 1 ♂; "Malaysia" accidentally imported with logs; MCBT 152883.

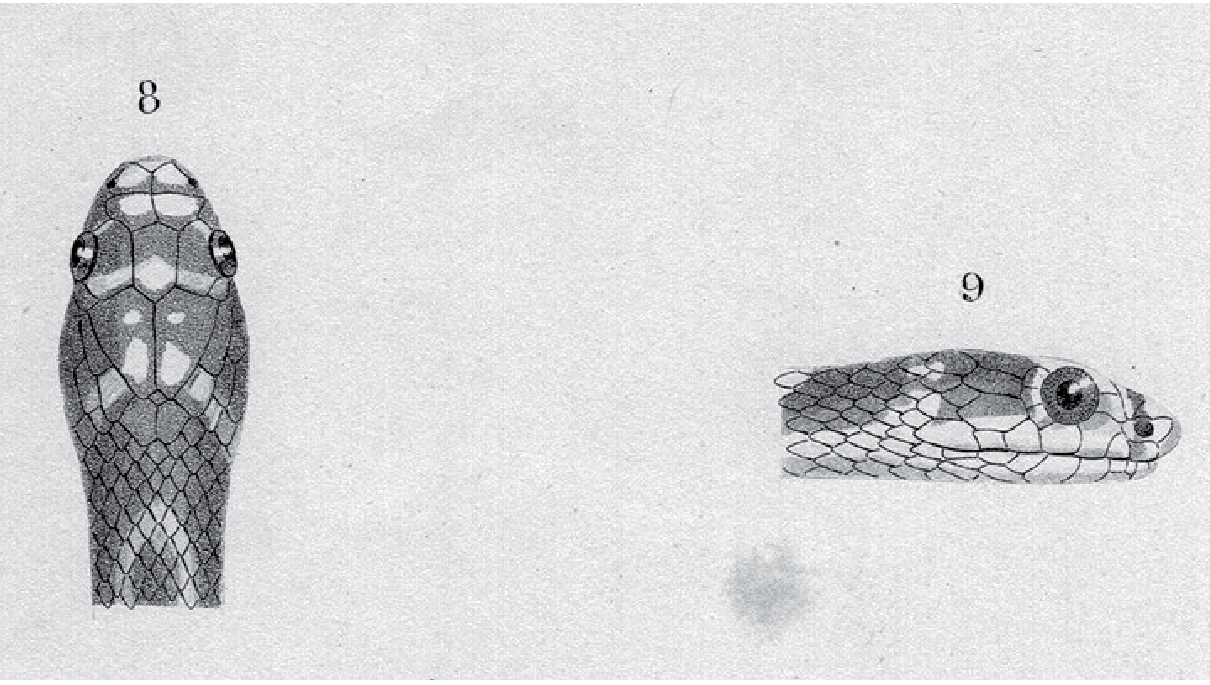


Fig. 6. Plate XVII, figures 8–9 from Schlegel (1837), showing head in dorsal and lateral views of lectotype of *Naja bungarus* Schlegel, 1837 (RMNH 1334).

PHILIPPINES • 1 ♂; 10 km SSW of Iwahig; 9.740° N, 118.66° E; CAS 129629 • 1 spec.; same data as for preceding; CAS 157468 • 1 spec.; Palawan, Tagup River, Brooke's Point, Borangbato, Mainit; 8.82° N, 117.78° E; NMP 2231.

SINGAPORE • 1 ♂; "Singapore", no further data; BMNH 82.11.29.1 • 1 ♂: "Singapore", no further data; CAS 16785 • 1 spec.; Mandai Lake Road; 1.42° N, 103.75° E; ZRC 2.2301.

THAILAND • 1 spec.; Yala Province, Betong; 5.75° N, 101.08° E; BMNH 1938.8.7.60 • 1 spec.; Pattani Province, Pattani Na Prado; 6.68° N, 101.14° E; CUZM unreg. • 1 spec.; Nakhon Si Thammarat Province, Nakhon Si Thammarat; 8.43° N, 99.97 °E; TNRC 1124 • 3 specs; Pattani Province, Pattani Na Prado; 6.68° N, 101.15° E; TNRC 1126, TNRC 1128, TNRC unreg. • 1 spec.; Trang Province, Trang; 7.56° N, 99.60° E; USNM 023014 • 1 spec.; Songkhla Province, Singora; 7.08° N, 100.50° E; USNM 079533 • 1 spec.; Trang Province, Trang [presumably also south of Isthmus of Kra]; 7.56° N, 99.60° E; USNM 220395 • 2 specs; "Southern Thailand"; AMNH 10046.1, AMNH 10046.2

Skeletal material

THAILAND • 1 spec.; Trang; 7.58° N, 90.50° E; USNM 220395.

Description of the lectotype (RMNH 1334)

Measurements. SVL 496 mm, TL 123 mm, total 619 mm.

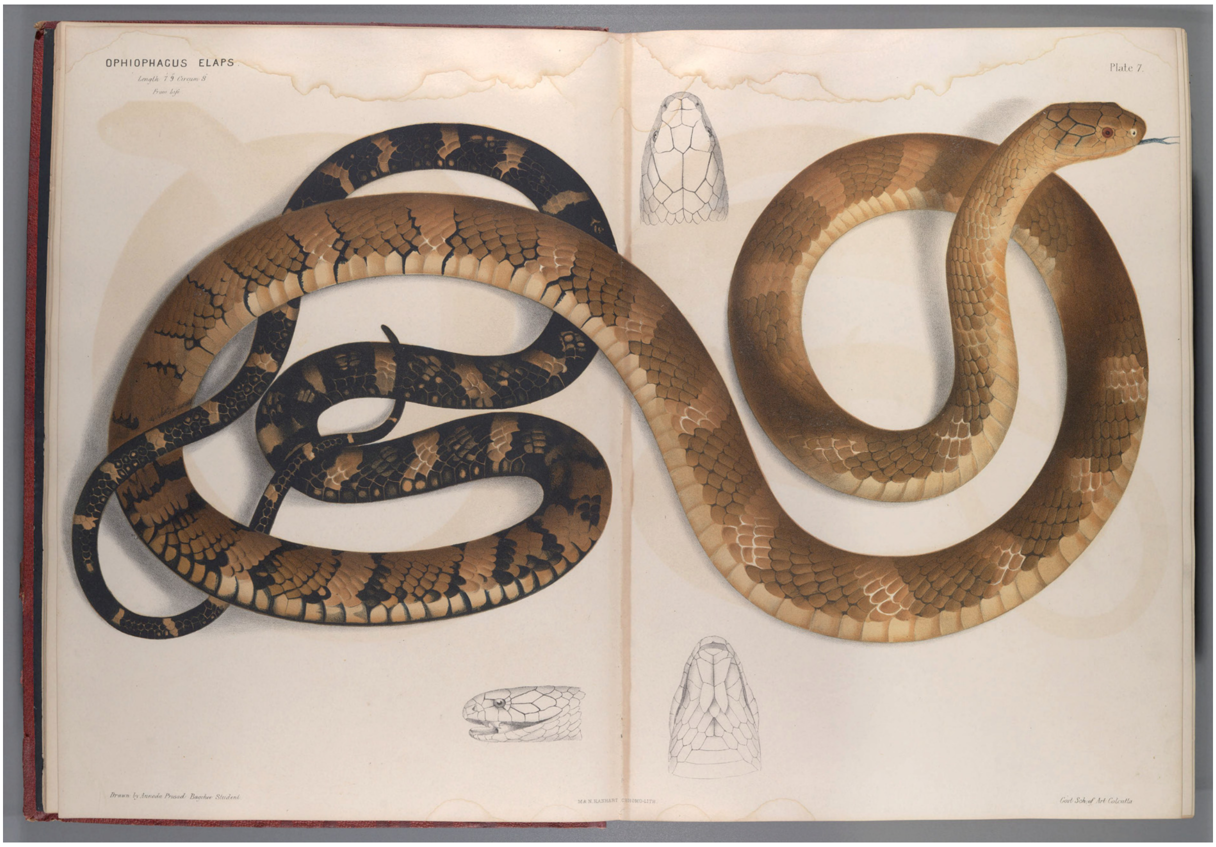


Fig. 7. Plate 7, figures 1–4 from Fayrer (1872), depicting *Ophiophagus elaps* (Günther, 1858), and corresponding to *Ophiophagus hannah* (Cantor, 1836) s. str., showing the body in dorsolateral view of an adult with a partially raised forebody. Also shown are line drawings of head in dorsal, ventral and lateral views.

HABITUS. Body relatively robust (midbody width 10.4 mm, 2.1% SVL), triangular in cross-section; Transverse body rows: DSR1 19; DSR2 15; DSR3 15; ventrals 253; subcaudals 108; supralabials 7; infralabials 8; anterior temporals 2; posterior temporals 2; cloacal 1; dorsal scales smooth, the vertebral and outer two rows enlarged; ventral scales smooth; subcaudals 1–28 entire, the rest divided; tail short (24.8% SVL), cylindrical, tapering posteriorly.

HEAD. Head relatively large, distinct from neck, head length 17.5 mm, head width 9.8 mm; head depth 7.3 mm; flattened in the orbital region, rounded in the sagittal region, with a slight depression medially, snout projecting slightly beyond mandible; canthus rostralis sharply defined; eye width 4.3 mm; interorbital distance 8.1 mm; cephalic scales juxtaposed, smooth-edged, except parietals and occipitals, which are slightly imbricate; rostral trapezoid in shape, distinctly visible from above, over twice as long as wide, concave ventrally, rostral width 0.8 mm; rostral width 1.5 mm; rostral length 4.4 mm; eye to snout distance 5.7 mm; eye to nostril distance 2.1 mm; nostril diameter 1.5 mm; internasals large, subtrapezoidal, wider than long; internasal suture width 1.0 mm; preocular squarish, wider than high, making a narrow contact with internasal; prefrontals trapezoid, wider than long; frontal trapezoidal, contacting prefrontals, supraoculars and parietals; frontal edge slightly sinuous, short-sided posteriorly; supraocular subtrapezoidal, contacting prefrontal, frontal, parietal, orbit, preocular, upper postocular but not the temporals; large paired occipitals; occipital length 3.5 mm; interoccipital scale present behind the suture between parietals; temporals 2/2 (L/R); in anterior pair, lower temporal broader but shorter than upper; in posterior pair, upper temporal longer than lower; first row of nuchals slightly enlarged compared to rest of dorsals; supralabials 7/7; III–IV (L/R) contact spectacle; III (L/R) contacting preocular and I and II (L/R) contacting posterior nasal; Supralabial I low; II high; III tallest; II and IV subequal; and VI and VII low, narrow and elongate; Supralabial IV does not contact preoculars; nostril lateral at posterior of a single concave nasal, horizontally elliptical, its greatest diameter along vertical axis; one preocular and three postoculars; eye large, contained in head length 0.24 times and head depth 0.6 times; pupil rounded; ocular ring comprises seven scales- one preocular, three postoculars, one supraocular and two supralabials; suboculars absent; mental small, triangular, wide than deep (mental width 0.43 mm; mental depth 0.14 mm); infralabials 8/8 (L/R), first (L/R) contacting anterior genials; infralabial IV (L/R) contact posterior genials; infralabial IV largest; one pair of genials; cuneate scute on lower jaw absent; two elongate gular scales follow posterior mental; the anterior longer than posterior.

DENTITION. Maxillary teeth recurved and stout, not compressed, gradually decreasing in size posteriorly; fang length 1.7 mm; fang width at base 0.5 mm; tooth count obscured by gingivae.

COLOURATION. The dorsum of the lectotype, a hatchling, is brownish-grey; cephalic and body bands ivory yellow, numbering 65 up to beginning of tail; throat and rest of venter unpatterned pale yellow, except the slightly darker edges of the ventral scales.

Morphological variation

Fourteen of 59 specimens (23.7%) examined have an interoccipital scute. Divided into geographical regions, the lowest occurrence of specimens with interoccipital scales were from Borneo and Palawan (11.5%; n = 26), followed by the Malay Peninsula (28.6%; n = 18) and Sumatra and Java (46.6%; n = 15).

Of 59 specimens examined for subcaudal imbrication character, 26 have one series of undivided subcaudals, in what appears to be an irregular pattern, the rest with up to eight series of undivided subcaudals, ranging from a single scute to 26 scutes, without an apparent pattern that cannot be linked to either sex, ontogeny or geographical distribution. Hatchlings and young adults bear multiple, narrow pale bands on body, pale body bands occasionally retained in presumed adult (>2000 mm) individuals. Specimens with intact dentition or those permitting counts of tooth sockets have dentition thus: 11–15 dentary sockets; 11–11 pterygoid sockets and 3 palatine sockets.

Dorsum is a shade of brown, dorsal surface of head darker, Kingfisher rufous #240, forebody ranging from Cinnamon, #139 to Buff, #124, interscale areas darker along body; the largest scales of forehead, frontal, parietal and occipitals and upper temporals with a distinct dark edge. Some large individuals are grey-black, the interscale regions appearing paler, while others appear to show pale transverse body bands, one scale wide, with 6–8 scales in interband areas. Isolated, irregular dark smudges may be present in such darker individuals on anterior part of gular scales. Mandible and genial region Buff, #124; the gular region to until Ventrals 12–28 bright yellow, Warm Buff, #118, with at least two dark areas peripherally, comprising somewhat indistinct bands meeting Ventrals 7–8 and 14–15; and noticeably in larger, hooding individuals, the first 5–6 nuchal scales are darker. Abdominal region as in gular region, but progressively darkening, initially from the peripheral region of the scales. Subcaudal region with pale scales, obscurely darkened throughout and with dark edges. Pupil rounded, black, iris brownish-red, Kingfisher Rufous #240, darkening peripherally, with a narrow, yellow ring. Tongue is blackish-grey, the oral cavity pink. Juveniles have ivory white bands, Buff, #124, including four on the head region, the first one in rostral position, broad one covering rostral, as well as part of Supralabial 1, nasals, and internasals; the second in preocular position, narrower, and covering part of the prefrontals, preoculars and Supralabial III; the third one in postocular position, narrowest of the four bands, and covering part of the frontal and parietals, and comprise large, elongated marks arranged in a transverse series; and the fourth one on cephalic position, broader than the previous one, and covering part of the parietals and occipitals, and comprise large oval spots arranged in a transverse series. Body bands are of the same colour, about two scales in width, and number 57–87 (65 in the lectotype), between head bands and the caudal region above vent, and have 4–5 scale wide interband areas. Bands on tail with relatively thick, dark, edges, both dorsally and ventrally; and the posterior third of body appears darker than the rest of the body.

Excluding hatchlings, which bear multiple, narrow pale bands on body, no pale body bands were seen in presumed adult (total length > 2,000 mm) individuals.

Distribution

The range of the species extends from south of the Isthmus of Kra, across the Malay Peninsula (including extreme southern Thailand, West Malaysia, Singapore, and offshore islands), Sumatra, Borneo, Java, Bali, and some of the islands of the southern Philippines Archipelago (David & Vogel 1996; David *et al.* 2006; Chanhome *et al.* 2011 [in part]; de Lang 2011, 2017; Stuebing *et al.* 2014; Das *et al.* 2015; Ismail *et al.* 2018).

Remarks

The king cobra genome sequenced by Vonk *et al.* (2013) came from a specimen of this species from Bali, Indonesia. Card *et al.* (2021) documented the genomic mechanisms of facultative parthenogenesis in this species (mitochondrial sequences included in Gowri Shankar *et al.* 2021).

Ophiophagus kaalinga Gowri Shankar, Das & Ganesh sp. nov.

urn:lsid:zoobank.org:act:84BAA541-67F1-4CE1-B72A-9832157B0267
Figs 8, 9G–I, 10C, 11C, 14

Common name

Western Ghats king cobra.

Diagnosis

A species of *Ophiophagus* endemic to the Western Ghats of the Indian peninsula, defined by the following combination of characters: possessing pale bands that lack darker edges, along body of adults (vs unbanded in adult *O. salvatana* sp. nov. and many *O. bungarus*; with dark edges to the pale bands in adult *O. hannah*). *Ophiophagus kaalinga* sp. nov. differs from *O. hannah* through a lower pterygoid teeth count (12 vs 18–21). Finally, juveniles of *O. kaalinga* have 28–48 body bands fewer than *O. salvatana*

Fig. 8. Plate 8, from Fayrer (1872) depicting the ‘Dusky variety’ of *Ophiophagus elaps* (Günther, 1858), and corresponding to *Ophiophagus kaalinga* Gowri Shankar, Das & Ganesh sp. nov., showing entire body of a hooding adult in mostly a dorsolateral view.

(85–86) and *O. bungarus* (57–87); relative tail length ranging 18.0–19.9% with a mean of 18.95% (vs 21.7–26.4% [24.05%] in *O. hannah*; vs 19.3–25.1% [22.2%] in *O. bungarus*; vs 18.7–23.0% [20.85%] in *O. salvatana* sp. nov.).

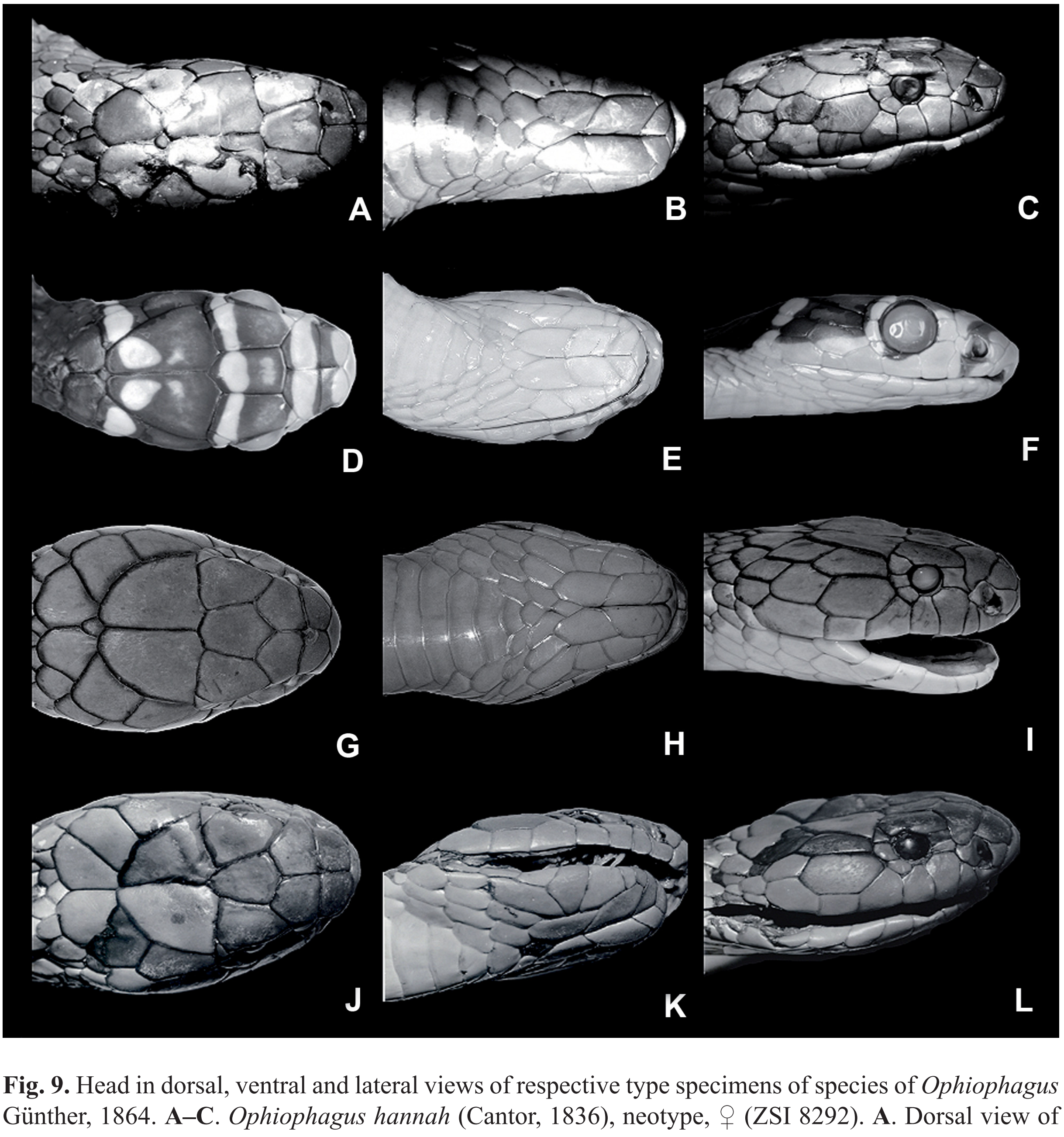


Fig. 9. Head in dorsal, ventral and lateral views of respective type specimens of species of *Ophiophagus* Günther, 1864. **A**–**C**. *Ophiophagus hannah* (Cantor, 1836), neotype, ♀ (ZSI 8292). **A**. Dorsal view of head. **B**. Ventral view of head. **C**. Left lateral view of head. **D**–**F**. *Ophiophagus bungarus* (Schlegel, 1837) comb. nov., lectotype, ♂ (RMNH 1334). **D**. Dorsal view of head. **E**. Ventral view of head. **F**. Left lateral view of head. **G**–**I**. *Ophiophagus kaalinga* Gowri Shankar, Das & Ganesh sp. nov., holotype, ♂ (BNHS 3655). **G**. Dorsal view of head. **H**. Ventral view of head. **I**. Left lateral view of head. **J**–**L**. *Ophiophagus salvatana* Gowri Shankar, Das & Wüster sp. nov., holotype, ♂ (CAS 61329). **J**. Dorsal view of head. **K**. Ventral view of head. **L**. Left lateral view of head.

Etymology

The specific epithet *kaalinga* is derived from Kannada language of Karnataka, India, alluding to the snake's dark colouration ('Kali' / 'Kari' = dark / black), an abbreviated form of 'Kaalinga Havu' / 'Sarpa' (see Das 1998), associated with Lord Shiva, as a demigod; here coined as a noun in apposition and hence invariable.

Type material

Holotype

INDIA • ♂; Karnataka State, Shivamogga District, Agumbe; 13.57° N, 75.10° E; 21 Apr. 2021; P. Gowri Shankar leg.; BNHS 3655.

Paratypes

INDIA • 1 ♀; Karnataka State, Uttara Kannada District, Dandeli Wildlife Sanctuary; 15.25° N, 74.57° E; ZSIC (ex-MCBT 152882) • 1 spec.; Kerala State, Quilon; 8.88° N, 76.6° E; BNHS 2280 • 1 spec.; Tamil Nadu State, Anaimalai or Annamalai; 10.30° N, 77.00° E; BMNH 61.12.30.83 • 1 spec.; Karnataka, Karwar District, Sirsi; 14.60° N, 74.90° E; MCBT 152884 • 1 spec.; Kerala State, Vanjikadavu, Kundurmadu; 10.39° N, 76.34° E; ANSP 35312.

Fig. 10. View of dorsum of entire body of respective type specimens of species of *Ophiophagus* Günther, 1864. **A**. *Ophiophagus hannah* (Cantor, 1836), neotype, ♀ (ZSI 8292). **B**. *Ophiophagus bungarus* (Schlegel, 1837) comb. nov., lectotype, ♂ (RMNH 1334). **C**. *Ophiophagus kaalinga* Gowri Shankar, Das & Ganesh sp. nov., holotype, ♂ (BNHS 3655). **D**. *Ophiophagus salvatana* Gowri Shankar, Das & Wüster sp. nov., holotype, ♂ (CAS 61329).

Description of holotype (BNHS 3655)

Laterally incised to access liver tissue; three ventral scales and two rib tips clipped as tissue samples.

Measurements. SVL 2475 mm, TL 530 mm, total 3005 mm.

Habitus. Body relatively robust (midbody width 43.2 mm, 1.6% SVL), triangular in cross-section; Transverse body rows: DSR1 19; DSR2 15; DSR3 15; ventrals 241; subcaudals 89; supralabials 7; infralabials 8; anterior temporals 2; posterior temporals 2; cloacal 1; dorsal scales smooth, the vertebral and outer two rows enlarged; ventral scales smooth; subcaudals 1–8 and 16–22 entire, the rest divided; tail short (20.4% SVL), cylindrical, tapering posteriorly.

Head. Head relatively large, head length 72.0 mm; head width 52.5 mm; head depth 30.0 mm; distinct from neck, flattened in the orbital region, rounded in the sagittal region, with a slight depression medially; eye diameter 8.0 mm; interorbital distance 27.0 mm; canthus rostralis sharply defined; cephalic scales juxtaposed, smooth-edged, except parietals and occipitals, which are slightly imbricate; rostral trapezoid in shape, distinctly visible from above, over twice as long as wide, concave ventrally, rostral width 7 mm; rostral length 16 mm; Eye to snout distance 25 mm; eye to nostril distance 11.5 mm; nostril diameter 6.0 mm; internasals large, subtrapezoidal, wider than long; preocular squarish, wider than high, separated from internasal by prefrontal; prefrontals trapezoid, wider than long; frontal trapezoidal, contacting prefrontals, supraoculars and parietals; frontal edge straight, short-sided posteriorly; supraocular subtrapezoidal, contacting prefrontal, frontal, parietal, orbit, preocular, upper postocular but not temporals; large paired occipitals; occipital length 10.6 mm; interoccipital scute present; temporals 2/2 (L/R); in anterior pair, upper temporal longer than lower; in posterior pair, upper temporal longer than lower; first row of nuchals slightly enlarged compared to rest of dorsals; supralabials 7/7; III–IV (L/R) touching the eye; IV (L/R) contacting preocular and I and II (L/R) contacting posterior nasal; supralabial I low; II and III progressively higher; III tallest; V and VI subequal; and VI and

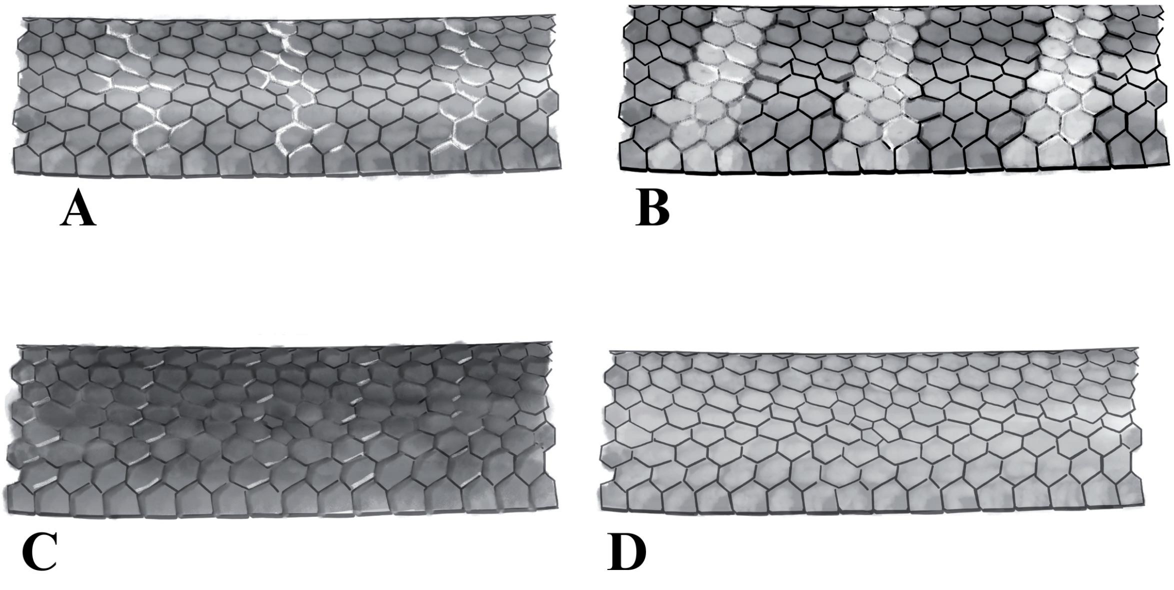


Fig. 11. Variation in dorsal bands in adults of the four species of *Ophiophagus* Günther, 1864 recognised in this study. **A**. *O. kaalinga* Gowri Shankar, Das & Ganesh sp. nov. **B**. *O. hannah* (Cantor, 1836). **C**. *O. bungarus* (Schlegel, 1837) comb. nov. **D**. *O. salvatana* Gowri Shankar, Das & Wüster sp. nov.

VII low, narrow and elongate; Supralabial III contacts preoculars; nostril lateral at posterior of a single concave nasal, horizontally elliptical, its greatest diameter at a vertical plane; one preocular and three postoculars; orbit large, pupil rounded; ocular ring comprises seven scales- one preocular, three postoculars, one supraocular and two supralabials; suboculars absent; mental small, triangular, wider than deep; infralabials 8/8 (L/R), first (L/R) contacting anterior genials; infralabial IV (L/R) contact posterior genials; infralabial IV largest; one pair of genials; cuneate scute on lower jaw absent; two elongate gular scales follow posterior mental; the anterior longer than posterior.

HEMIPENES. Organ partially everted on left side, fairly short and thick, length 24 mm and width 6 mm; extending to 3rd subcaudal scale; divided at level of 2nd subcaudal scale; divided lobe length 7 mm; divided lobe width 5 mm; lobe head forked near apex; lobe head with numerous tiny spinules and flounces; asulcate side rather smooth and less spinose; sulcate side with dense congregation of larger spines; sulcal lips not evident, sheath-like, completely surrounding apex base; sulcus spermaticus groove-like and rather straight than convoluted; pedicel more or less conical and tapering down towards its base.

DENTITION. Maxillary teeth recurved and stout, gradually enlarged posteriorly; fang length 9 mm; fang width at base 2 mm; a reserve fang present on left side.

COLOURATION. Dorsum dark grey, the ventrals paler. In life, the dorsal surface of the body Dark Brownish Olive (#129), darkening at the posterior third of body to Blackish Neutral Gray (#82); forehead Drab (#27), the largest scales of forehead, including frontal, parietal and occipitals and upper temporals with distinct dark edges; interscale areas of dorsum darker along body, distinctly yellowish when within the pale bands; dorsum and flanks with narrow, oblique, chevron-shaped Straw Yellow (#56) bands, covering a single scale on vertebral region, expanding to cover 4–5 scales on the lower flanks, and separated by 7–8 scales; mandible and genial region Straw Yellow (#56); gular region Buff-Yellow (#53), extending to 20th ventral scale, intervened by a 2-scale wide dark band at the level of 12–13 ventrals; abdominal region as in gular region, but progressively darkening, from Ventral 20 initially from the peripheral region of the scales. Subcaudal scales grey throughout, and with dark edges. Pupil rounded, black, iris brownish, darkening peripherally, with a narrow, yellow ring. Tongue dark red. Body bands Yellow Ocher (#123C), 1–2 scales in width, widening on lower flanks to 3–4 scales, 29 such bands present between head bands and the caudal region above vent, with 4–5 scale wide interband areas. The first two bands in nuchal region chevron-like. Bands on tail with relatively thick, dark, edges, both dorsally and ventrally; and the posterior third of body is darker than rest of body. In preservation, after over two years in alcohol, colouration generally the same, except the eye becoming dirty white to grey and venter becoming ivory coloured anteriorly to light ashy grey posteriorly.

Morphological variation

Two (ZSIC ex-MCBT 152882 and MCBT 152884) of four specimens examined had an interoccipital scute. Three of the specimens had intact tails to permit examination of subcaudal fusion pattern. One showed undivided subcaudals 1–7 (ZSIC ex-MCBT 152882), a second, 1–6 and 12–13 (BMNH 61.12.30.83) and the third, 1–8 and 10–11 (MCBT 152884). Wall (1919) reported slightly lower subcaudal (85) and ventral (239 and 241) counts, although it is unclear how these were made. Only two specimens permitted counts of body bands that number 28 and 48. Specimens that permitted counts of tooth and / or sockets had dentition thus: 12 dentary sockets and 3–4 palatine sockets. Juveniles have ivory white bands, Buff, #124, including four on the head region, the first one covering rostral, as well as part of Supralabial 1, nasals, and internasals; the second in preocular position, narrower, and covering part of the prefrontals, preoculars and Supralabial III; the third one in postocular position, narrowest of the four bands, and covering part of the frontal and parietals, and comprise large, elongated marks arranged in a transverse series; and the fourth one on cephalic position, broader than the previous one, and covering part of the parietals and occipitals, and comprise large oval spots arranged in a transverse series.

Distribution

Ophiophagus kaalinga sp. nov. is endemic to the Western Ghats of south-western India, covering parts of Tamil Nadu, Kerala, Karnataka, Goa and the adjacent border of Maharashtra States. The species is known from the Ashambu hills near Kanyakumari (formerly, Cape Comorin), through the Agasthyamalai and Devarmalai ranges, the Cardamom hills, the Meghamalai mountains, the Anamalai-Palni ranges, across the Palghat Gap, through Nilgiri-Waynad, on to the Malnad regions (Coorg-Agumbe-Sharavathi-Anshi), until about the Goa Gap, abutting Maharashtra State (Ishwar *et al.* 2001; Whitaker & Captain 2004 [part]; Khaire 2006; Hutton & David 2009; Ganesh *et al.* 2013, 2014; Yadav & Yankanchi 2015). It is essentially a hill-dwelling species, that is prevalent in mid-elevation (ca 500–900 m a.s.l.) rainforests, while extending lower to the very foothills (ca 100 m a.s.l.), in mesic windward western versant, or lower slopes (ca 300 m a.s.l.) in the drier leeward eastern versant, reaching up to the high elevation plateaus (ca 1800 m a.s.l.) covered with montane forests (unpubl. data).

Ophiophagus salvatana Gowri Shankar, Das & Wüster sp. nov.

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Figs 9J–L, 10D, 11D, 15

Common name

Luzon king cobra.

Diagnosis

A species of *Ophiophagus* inhabiting Luzon Island in the northern Philippines and exhibiting the following combination of characters: lacking pale bands along body of adults (vs with dark-edged, pale bands in *O. hannah*; lacking dark edges to the pale bands, if present, in *O. bungarus*, or with a pale band in *O. kaalinga* sp. nov.). Further, it differs from *O. hannah* in having fewer pterygoid teeth (11 vs 18–21). Finally, juveniles of *O. salvatana* sp. nov. have extremely angular pale body bands, with the dark intervening areas covering 2–3 scales (vs more rounded pale body bands, the intervening areas covering 4–9 scales in congeners). The new species, with 85–86 pale body bands, can be easily separated from *O. hannah* (27–48) and *O. kaalinga* (28–48); relative tail length ranging 18.7–23.0% with a mean of 20.85% (vs 21.7–26.4% [24.05%] in *O. hannah*; vs 19.3–25.1% [22.2%] in *O. bungarus*; vs 18.0–19.9% [18.95%] in *O. kaalinga*).

Etymology

The specific epithet *salvatana* is the Tagalog (a vernacular language spoken in Luzon and adjacent regions of the Philippines, of Austronesian origin) name for the king cobra in the Luzon region (northern Philippines), here coined as a noun in apposition and hence invariable.

Type material

Holotype

PHILIPPINES • ♂; Luzon, Benguet Province, Baguio; 16.40° N, 120.60° E; Edward H. Taylor leg.; CAS 61329.

Paratypes

PHILIPPINES • 1 spec.; Luzon, Isabella; 17.00° N, 122.00° E; BMNH 94.10.24.15 • 1 ♀; Luzon, Camarines Sur Province, Gota Beach Caramoan; 13.88° N, 123.70° E; UF 50927 • 1 ♂; Luzon, Camarines Sur Province, Caramoan Municipality, Tarago Base Camp; ca 13.82° N, 123.80° E; UF 55008 • 1 ♂; Luzon, Pampanga Province, Sapang Tagalog, Tarlac; 15.42° N, 120.59° E; UPM 1692 • 1 ♂; Luzon, Camarines Sur Province, San Pedro, Iriga; 13.49° N, 123.47° E; FMNH 53553.

Description of holotype (CAS 61329)

Measurements. SVL 2060 mm, TL 517+ mm, total 2577+ mm.

Habitus. Body relatively robust (midbody width 30.0 mm, 1.5% SVL), triangular in cross-section; Transverse body rows: DSR1 19; DSR2 15; DSR3 15; ventrals 252; subcaudals 95+; supralabials 7; infralabials 8; anterior temporals 2; posterior temporals 2; cloacal plate 1; dorsal and ventral scales smooth; subcaudals 1–26 and 31–37 undivided, the rest divided; tail short, cylindrical, tapering posteriorly, tail tip missing.

Head. Head relatively large, head length 52.2 mm; head width 31.7 mm; head depth 21.1 mm; distinct from neck, flattened in the orbital region, rounded in the sagittal region, with a depression medially, snout projecting slightly beyond mandible; canthus rostralis sharply defined; eye width 7.5 mm; interorbital distance 22.4 mm; cephalic scales juxtaposed, smooth-edged, except parietals and occipitals, which are slightly imbricate; rostral trapezoid in shape, distinctly visible from above, slightly under twice as high as wide, concave ventrally, rostral width 12.6 mm; rostral length 6.7 mm; eye to snout distance 19.7 mm; eye to nostril distance 9.4 mm; nostril diameter 5.4 mm; internasals large, subtrapezoidal, wider than long; internasal suture length 4.6 mm; internasal width 6.9 mm; prefrontals trapezoid, wider than long; prefrontal length 7.7 mm; prefrontal width 9.3 mm; prefrontal suture 5.8 mm; frontal lanceolate, contacting prefrontals, supraoculars and parietals, rectangular in shape, short-sided anteriorly; supraocular subtrapezoidal, contacting prefrontal, frontal, parietal, orbit, preocular and upper postocular; large paired occipitals; occipital length 12.4 mm; interoccipital scute absent; nuchals undifferentiated; supralabials 7/7; III–IV (L/R) touching the eye; II (L/R) contacting nasal and I, II and III (L/R) contacting posterior nasal; Supralabial I low; II high; III tallest; IV and V subequal; and VI and VII low, narrow and elongate; Supralabial IV does not contact preoculars; nostril lateral at posterior of a single concave nasal, oval in shape, its greatest diameter at a vertical plane; nasal irregularly triangular, one preocular and three postoculars; eye large, contained in head length 0.14 times and head depth 0.36 times; pupil rounded; ocular ring comprises seven scales – one preocular, three postoculars, one supraocular and two supralabials; suboculars absent; temporals 2/2 (L/R) + 3/3 (L/R); anterior upper temporal longer than lower temporal; mental small, triangular, wide than deep (mental width = 6.98 mm; mental depth = 3.64 mm); infralabials 8/8 (L/R); infralabial I–IV contact anterior genial; infralabial IV–V (L/R) contact posterior genials; infralabial IV largest; two pairs of genials, with the anterior larger than posterior; cuneate scute on lower jaw absent; three elongated gular scales follow posterior mental; the anterior longer than posterior.

Dentition. Maxillary teeth recurved and stout, not compressed, gradually increasing in size posteriorly; fang length 6.4 mm; fang width at base 1.8 mm; teeth count obscured by gingivae.

Colouration. Dorsum of holotype is yellowish-grey, each scale on forehead and body edged with pale grey, lacking distinct pale bands; the venter is paler, scales similarly dark-edged, edges progressively darker posteriorly.

Morphological variation

None of the six specimens examined have an interoccipital scute. All subcaudals were divided in the holotype, while other specimens examined have some undivided subcaudals, typically, the first, and some succeeding subcaudals, up to Subcaudal 26, in what appears to be an irregular pattern that cannot be linked to either sex, ontogeny or geographical distribution. Variations observed include undivided subcaudals 1–17, 20–25, 28, 30–35, 46 (UPMNH 1692); 1, 4–6, 25 (UF 50927); 1–18 (UF 55008); and 1–26, 31–37 (CAS 61329). In life, dorsal surface of body is Dark Neutral Gray #83, forehead and posterior fourth of body darker, especially on scale periphery, making the posterior of body darker than the rest; interscale areas dark along body; the largest scales of forehead, frontal, parietal and occipitals

Table 1. Summary of morphological characters associated with species of *Ophiophagus* Günther, 1864 recognised in this study. See 'Terminology for character analysis' for details. Note: pale dorsal bands are sometimes absent in adult *O. bungarus* (Schlegel, 1837) comb. nov. (in images of live specimens examined), and consistently absent in adult *O. salvatana* Gowri Shankar, Das & Wüster sp. nov. Further, juveniles of the latter show pale bands (in images of three live specimens examined; no voucher specimens of juvenile *O. salvatana* were available for study).

Characters	**Statistics**	***O. hannah*** s. str.	***O. bungarus*** comb. nov.	***O. kaalinga*** sp. nov.	***O. salvatana*** sp. nov.
Anterior dorsal scale rows (DSR1)	Mean	18.0	18.9	19.5	18.6
	Range	17–19	17–21	19–21	17–19
	(n)	15	46	4	5
Median dorsal scale rows (DSR2)	Mean	15.0	15.0	15.0	15.0
	Range	15–15	15–15	15–15	15–15
	(n)	15	12	4	4
Posterior dorsal scale rows (DSR3)	Mean	13.8	14.0	15.0	15.0
	Range	11–15	13–15	15–15	15–15
	(n)	13	12	4	4
Ventrals	Mean	244.0	250.12	247.8	251.0
	Range	226–267	253–268	241–251	247–256
	(n)	49	58	4	4
Subcaudals	Mean	89.0	106.8	88.0	93
	Range	80–112	71–125	86–90	74–112
	(n)	49	57	4	4
Precloacal	Mean	1.0	1.0	1.0	1.0
	Range	1–1	1–1	1–1	1–1
	(n)	49	63	4	4
Supralabials	Mean	6.9	7.0	7.4	7.0
	Range	6–7	7–7	7–8	7–7
	(n)	15	68	5	5
Infralabials	Mean	8.0	8.0	8.0	8.0
	Range	7–9	8–8	8–8	8–8
	(n)	15	68	5	5
Pale body bands	Mean	39.6	72.0	35.0	0
	Range	27–48	57–87	28–48	0
	(n)	41	51	3	5
Pterygoid teeth	Mean	19.3	11	12	11
	Range	18–21	11–11	12–12	11–11
	(n)	12	9	4	6

and upper temporals with a distinct dark edge; ventral scales, from Ventral I suffused with yellow, gradually turning entirely yellow with irregular patterned grey posterior edges; oval scales of the 2–3 lower-most row of dorsal scale rows meeting ventrals yellow; posterior third of body dorsum darkening due to increasing intensity and extent of dark edges of scales; tail dorsum nearly black, individual scales

Table 2. Summary of measurements (range [n], in mm) of species of *Ophiophagus* Günther, 1864 recognised in this study. See 'Terminology for character analysis' for details. Abbreviations: BW = Midbody diameter; ED = Eye width; EYEN = Eye to nostril distance; EYES = Eye to snout distance; FL = Fang length from base; FW = Maximum fang width; HD = Head depth; HL = Head length; HW = Head width; IORB = Interorbital width; NOD = Nostril diameter; OCCL = Occipital length; ROSL = Rostral length; ROSW = Rostral width; SVL = Snout-vent length; TL = Tail length (if entire).

Characters	***O. hannah*** s. str.	***O. bungarus*** comb. nov.	***O. kaalinga*** sp. nov.	***O. salvatana*** sp. nov.
SVL	233.0–3276.0 (37)	330.0–3790.0 (65)	496.0–2660.0 (4)	1490.0–2565.0 (4)
TL	84.0–875 (37)	111.0–845.0 (61)	109.0–542.0 (3)	343.0–770.0 (4)
RTL range (mean)	21.7–26.4% (24.05%)	19.3–25.1% (22.20%)	18.0–19.9% (18.95%)	18.7–23.0% (20.85%)
BW	6.7–45.9 (55)	12.5–64.5 (36)	11.7–60.0 (4)	28.1–45.9 (3)
HL	13.3–79.2 (61)	16.0–76.6 (68)	50.9–74.6 (4)	36.2–70.8 (5)
HW	10.9–53.5 (59)	7.1–60.4 (70)	10.5–54.7 (5)	22.9–57.2 (5)
HD	6.6–48.4 (54)	6.7–76.0 (70)	22.8–37.2 (4)	14.8–36.7 (5)
ED	3.7–10.5 (57)	4.1–9.8 (73)	4.2–9.7 (5)	6.3–11.1 (5)
EYES	4.4–27.6 (62)	5.2–26.3 (71)	18.5–25.2 (4)	12.1–21.6 (5)
EYEN	1.9–14.3 (62)	2.1–13.5 (71)	2.8–11.5 (5)	5.2–9.9 (5)
NOD	1.2–7.3 (61)	1.0–6.9 (71)	5.8–9.5 (4)	3.1–6.4 (5)
ROSL	3.1–19.9 (61)	3.2–18.7 (71)	12.0–16.6 (4)	8.6–15.6 (5)
ROSW	1.7–9.7 (60)	2.0–8.8 (71)	6.1–8.0 (4)	4.8–7.6 (5)
IORB	5.9–34.2 (61)	7.5–12.3 (71)	23.4–31.8 (4)	14.8–25.9 (5)
OCCL	2.7–24.0 (61)	3.4–19.9 (71)	3.8–18.3 (5)	9.6–21.3 (5)
FL	0.10–10.10 (48)	0.13–13.60 (50)	7.10–8.50 (4)	4.50–12.00 (4)
FW	0.04–4.80 (45)	0.01–4.50 (50)	1.90–2.40 (4)	1.10–3.30 (4)

with yellow centres. Mandible and genial region Buff Yellow, #53; the gular region brighter, Orange Yellow, #18, with darker areas peripherally. Abdominal region as in gular region, but progressively darkening, initially from the peripheral region of the scales. Subcaudal region with pale scales, obscurely darkened throughout and with dark edges. Pupil rounded, black, with pale yellow narrow ring; iris brownish-grey with a yellowish-brown ring. Tongue blackish-grey, oral cavity pink. Images of two hatchlings were examined for colour and pattern. The forehead of hatchlings is Light Neutral Gray (#85), including the posterior cephalic scales (including upper temporal, parietals and occipital), dark edged, Jet Black (#89), the dark areas of the latter pair extensive, separating the pale areas of the centre as eye-like spots; dorsum of body is Jet Black (#89), 2–3 scales across, with 101, extremely angular, Pale Neutral Gray (#86) bands, a single scale across; the pattern on back is undifferentiated posteriorly. Apart from two hatchlings, on which we counted 85–86 narrow pale bands on the body, the distinct pale bands seen in other species of the genus are absent in *O. salvatana* sp. nov. In preservative, forehead and dorsum of body are greyish-brown, with darker edges of scutes; no other patterns are discernable; venter is similarly coloured but slightly paler. Three individuals that permitted count of tooth and / or sockets have dentition thus: 15 dentaries; 11 pterygoids and 3 palatines.

Distribution

The range of the species is restricted to the Luzon islands in the northern Philippines (Diesmos *et al.* 2005; McLeod *et al.* 2011; Siler *et al.* 2011; Devan-Song & Brown 2012; Brown *et al.* 2013; Cruz & Afuang 2018; Cruz *et al.* 2018). The affinities of king cobras from other islands of the Philippine Archipelago remain to be confirmed.

Comparisons

Early attempts to understand variation in the complex suffered from a variety of shortcomings, due to the variation within (Figs 11–12) and among populations (Figs 13–16) and scarcity of vouchered specimens, especially entire specimens of adults. For instance, all four species recognised here demonstrate dramatic ontogenetic colour and pattern changes, with the banded juveniles losing the pattern in adults consistently in one species (*O. salvatana* sp. nov.) and sometimes in another (*O. bungarus* comb. nov.), retaining it into adulthood in a third population (*O. kaalinga* sp. nov.), and developing dark edges to the band in the fourth (*O. hannah*). Further, the allopatric populations of the four species recognized in this paper do not show categorical differences in the counts of the major scales that have been traditionally employed for taxonomic differentiation of species within snakes. However, a number of characters are useful to unequivocally diagnose the four species recognized here. Character states useful for identification and diagnosis of the members of the complex include dorsal ground colour and pattern, nature of body bands in adults (unbanded and banded, the bands with or without a dark edge) and pterygoid tooth/tooth socket counts.

Means, ranges and sample size of characters differentiating the four lineages identified in this study and supported by our mitochondrial phylogeny (see Gowri Shankar *et al.* 2021: 5) are shown in Table 1. Measurement data are in Table 2. Furthermore, we provide here a dichotomous identification key for the identification of the species of the genus *Ophiophagus* recognized here.

Key to the species of Ophiophagus Günther, 1864

1. More than 17 pterygoid tooth sockets; light body bands present at all ages, > 1.5 scales wide, with dark edges in most adults .... ***O. hannah*** (Cantor, 1836)
– 12 or fewer pterygoid tooth sockets, body bands not as above 2

2. Pale body bands always present, fewer than 55, > 1.5 scales wide; < 90 subcaudals .... ***O. kaalinga*** Gowri Shankar, Das & Ganesh sp. nov.

– Body bands absent or narrow (<1 scale wide), more than 55; often >90 subcaudals 3

3. Juveniles with 57–87 regular narrow light body bands, adults with faint narrow bands or unpatterned .... ***O. bungarus*** (Schlegel, 1837)
– Juveniles with >80 often irregular, highly angular narrow light bands, adults always without pale bands ....***O. salvatana*** Gowri Shankar, Das & Wüster sp. nov.

Discussion

In this work, following up on the recently published study by Gowri Shankar *et al.* (2021), we reanalysed morphological variation across the king cobra complex, and recognised and conferred names on four species of king cobras. Despite being undoubtedly one of the most iconic snakes in the world, *O. hannah* had remained under-studied for close to a century. Wall (1924) and Smith (1943) had

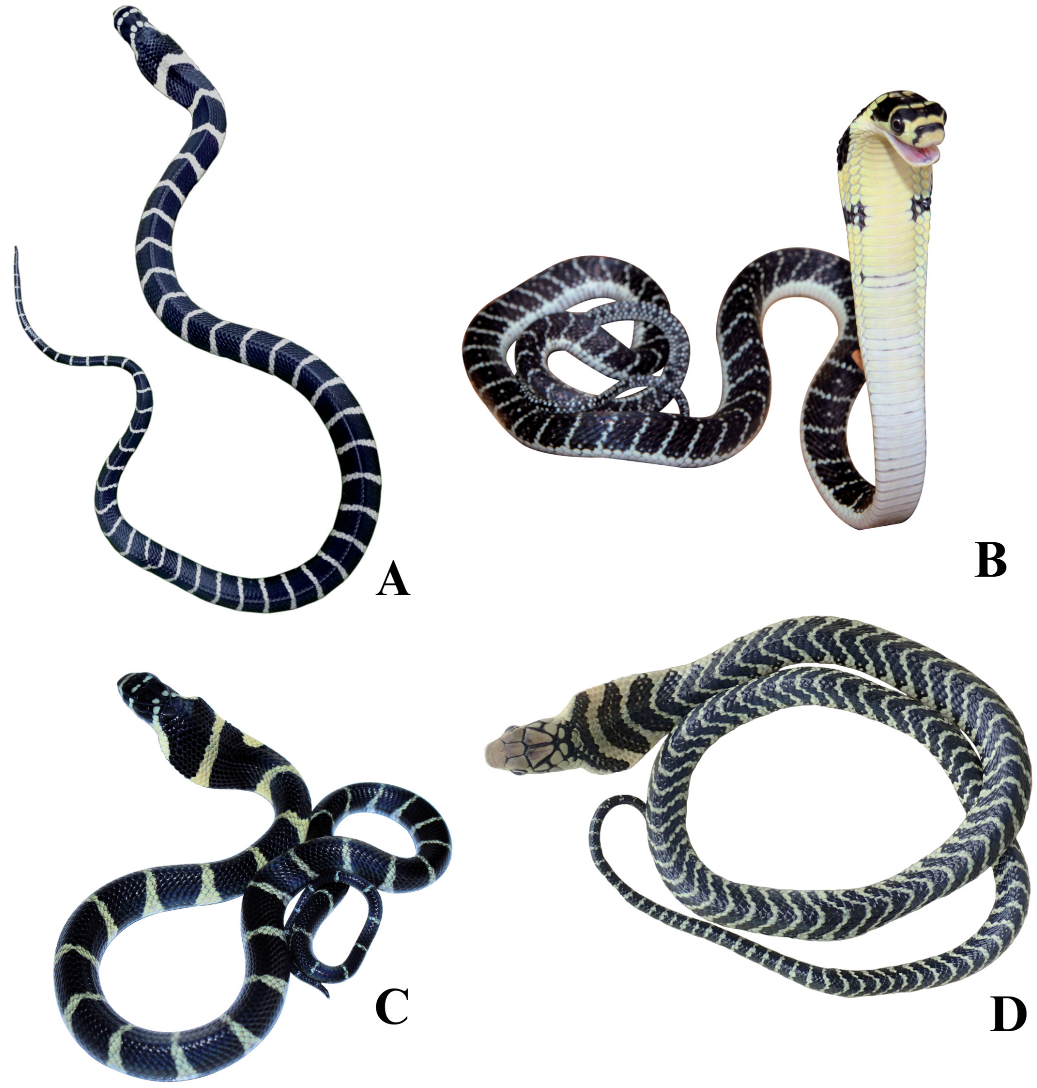

Fig. 12. Variation in dorsal body bands in juveniles of the four species of *Ophiophagus* Günther, 1864 recognised in this study. **A**. *O. hannah* (Cantor, 1836) (photo: H.T. Lalremsanga). **B**. *O. bungarus* (Schlegel, 1837) comb. nov. (photo: T. Charlton). **C**. *O. kaalinga* Gowri Shankar, Das & Ganesh sp. nov. (photo: P. Gowri Shankar). **D**. *O. salvatana* Gowri Shankar, Das & Wüster sp. nov. (photo: Bernard Tarun).

commented on its extensive synonymy and the varying morphologies across its vast geographic range, encompassing multiple biodiversity hotspots. Deraniyagala (1960, 1961) was the only author to address this issue directly and attempted to resolve the taxonomy of the king cobra across its range. However, his classification faced resistance from subsequent authorities (e.g., Taylor 1965). Deraniyagala (1960, 1961) recognised several subspecies, naming some and resurrecting others from synonymy. In 1960, he conferred new names or novel name combinations to populations he recognised as distinct, and a year later (Deraniyagala 1961), named three more new subspecies. However, we demonstrate here that all these are junior synonyms of earlier names.

It seems remarkable that the systematics of the *Ophiophagus hannah* species complex, comprising the largest venomous snakes of the world, has remained unsettled since 1836. Part of the reason has been a scarcity of comparative material at a single institution (that was often the case at the time), variation within populations including ontogenetic colour change and a highly conserved morphotype. Overlapping squamation characters, traditionally utilized in snake taxonomy, have contributed to obscuring the

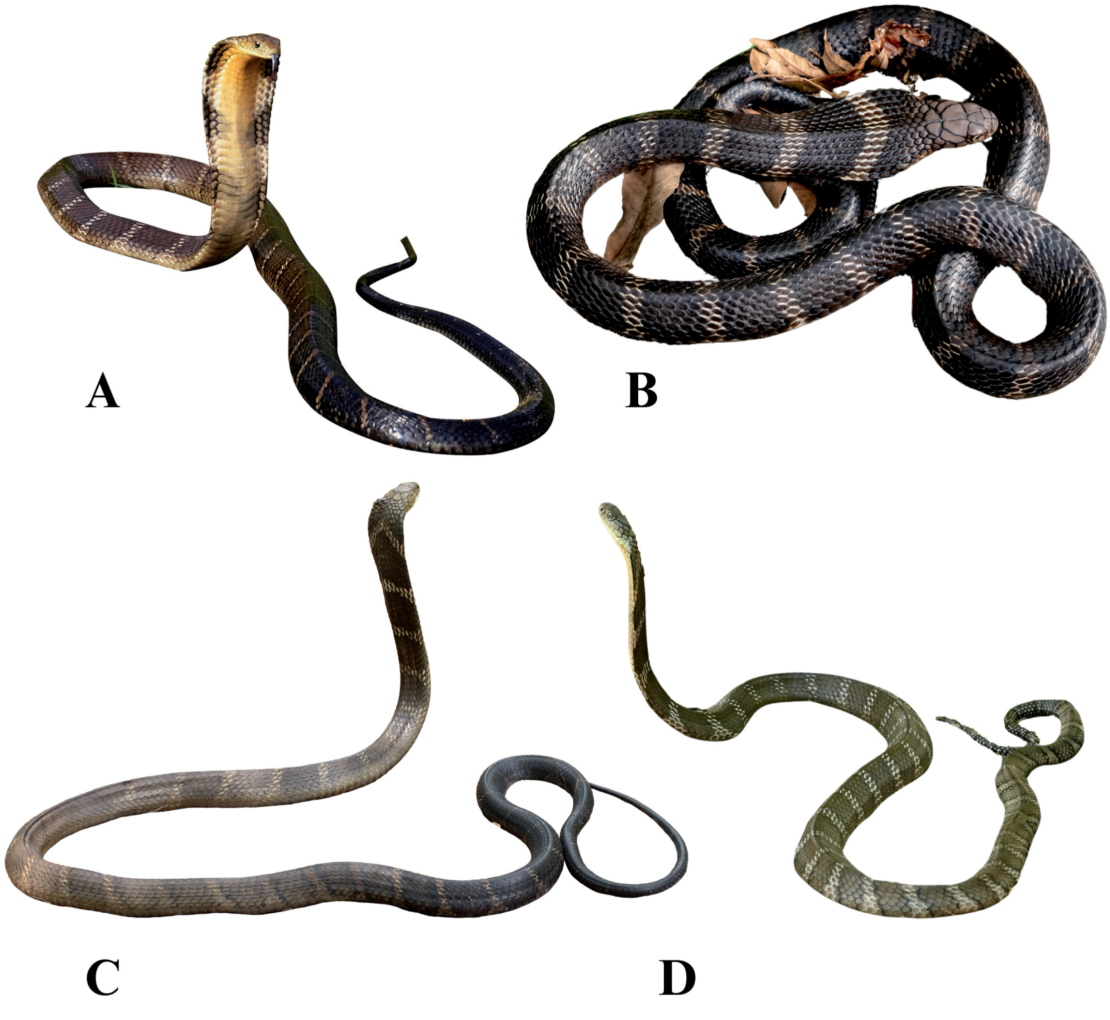

Fig. 13. Live unvouchered adults of *Ophiophagus hannah* (Cantor, 1836) showing variations in colour pattern. **A**. Mizoram, India (photo: H.T. Lalremsanga). **B**. China (Adam Francis). **C**. Thailand (photo: P. Gowri Shankar). **D**. Andaman Islands, India (photo: Aaron Fernandes).

identities of these species. However, other instances of large elapids with low morphological differences and significant genetic and other character differences are known (e.g., Wüster & Broadley 2007).

We note particularly the general rarity of material from islands in the Philippines archipelago and eastern Indonesia. The rarity of the species in most collections most likely reflects its relative rarity in most localities of occurrence, and the difficulties and dangers of capturing, transporting and preserving these large, dangerously venomous, snakes.

One character that was found to be taxonomically informative is the number of dorsal bands. Adults from the Luzon population, unlike juveniles, do not possess any discernible pale bands. In adult *O. salvatana* sp. nov., the bands in adults are faint and barely discernible, producing a mottled, near unbanded appearance. The northern lineage, *O. hannah*, shows a lower number of bands compared to *O. bungarus*, which possesses many more bands. Jerdon (1854) was perhaps the first to suspect cryptic speciation in the lineage, writing that a "magnificent snake that was 12 ½ feet long killed in the forest in the Waynaad (...) may be a different species from the Bengal serpent [*O. hannah*], for it was of an uniform dark olive colour above, without any appearance of bands", likely indicating a premolt individual of *O. kaalinga* sp. nov.

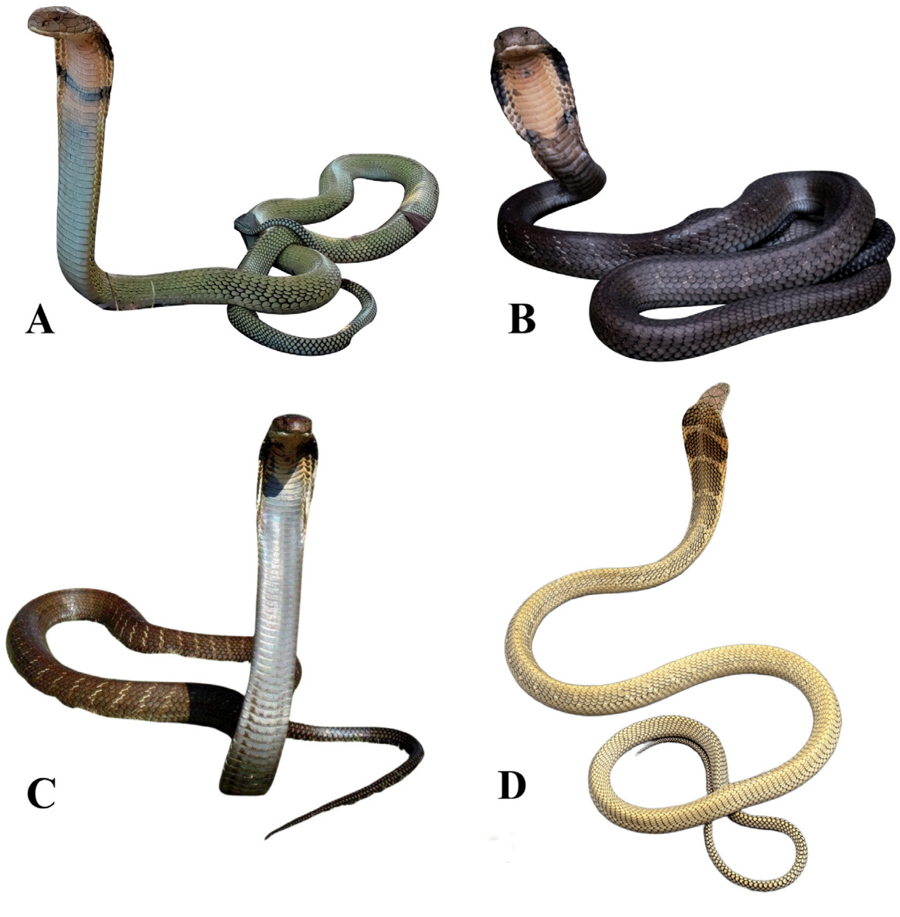

Fig. 14. Live unvouchered adults of *Ophiophagus bungarus* (Schlegel, 1837) comb. nov. showing variations in colour pattern. **A**. Peninsular Malaysia (photo: Ahmad Khaldun Ismail). **B**. Java, Indonesia (photo: Nathan Rusli). **C**. Bali, Indonesia (photo: Shinta Sukum). **D**. East Malaysia (photo: P. Gowri Shankar).

In our studies (Gowri Shankar *et al.* 2021; this paper), we have been able to sample representatives of the genus from most parts of the Asian mainland, and many islands of South-East Asia. Nevertheless, additional work is clearly needed. Further sampling in a follow-up phase of this work should focus on regions lacking representatives here. This includes, particularly, islands with a long history of isolation from each other and from the Asian mainland, and thus not connected during times of low sea levels during the Pleistocene, such as Sulawesi and some island groups in the Philippines (in particular the Mindanao and Panay-Negros groups). The likely contact area between *O. hannah* s. str. and *O. bungarus* in southern Thailand near the Isthmus of Kra would also benefit from additional sampling to test the possibility of a zone of intergradation. Among the four species, *O. hannah* s. str. displays considerable intraspecific genetic structure across its vast mainland range and the Andamans, which requires further research to identify Evolutionarily Significant Units for conservation (e.g., Behrooz *et al.* 2018) or potential cryptic speciation.

This, and future, taxonomic revisions of the king cobra are of particular importance for the conservation of these, the world's largest venomous snakes. Recognising biological diversity is crucial to its

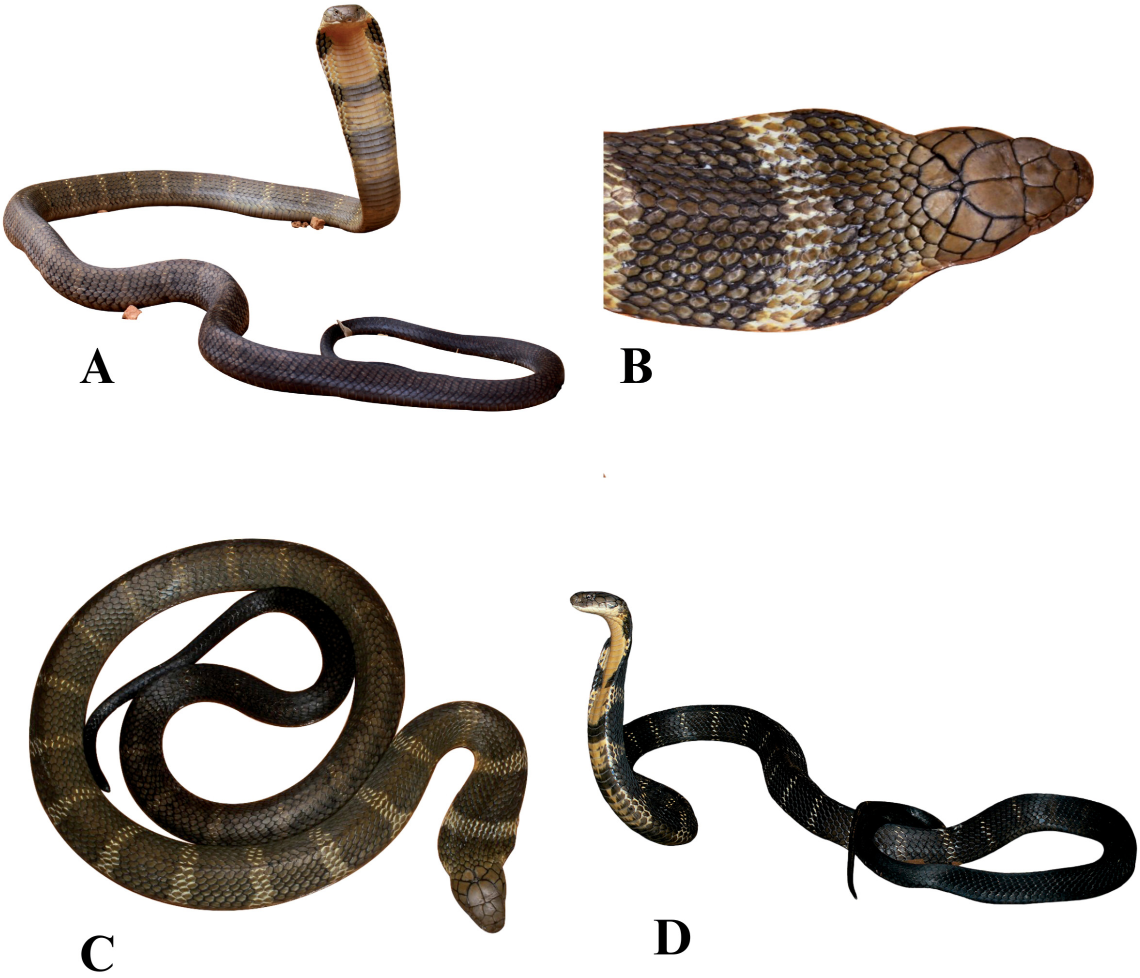

Fig. 15. Live unvouchered adults of *Ophiophagus kaalinga* Gowri Shankar, Das & Ganesh sp. nov. showing variation in colour pattern. **A**. Kalakkad-Mundanthurai Tiger Reserve, India (photo: Naveen Joseph). **B**–**C**. Agumbe, Karnataka, India (photo: P. Gowri Shankar). **D**. Goa, India (photo: P. Gowri Shankar).

assessment and conservation (May 1990; Mace 2004; Thomson *et al.* 2018; Garnett *et al.* 2020), and naming and listing species remains a typically essential precondition for conservation policy and action. In particular, failure to recognise units of biodiversity can potentially lead to their endangerment or extinction through neglect (May 1990).

The IUCN Red List status of *O. hannah* in its traditional sense is currently Vulnerable. However, this is an assessment of the risk of global extinction of king cobras across their entire vast range. This revision has shown that the king cobras consist of four distinct species, each requiring separate consideration. Understanding the taxonomy and species limits in a threatened clade is of critical importance for Red List Assessment, conservation prioritization in range states and the management of potential captive breeding programmes. Although two of the four species recognised here have relatively large, multinational distributions, the other two, *O. kaalinga* sp. nov. and *O. salvatana* sp. nov., are restricted to relatively small regions, the Western Ghats of India and the island of Luzon in the Philippines (Gowri Shankar *et al.* 2021). Both the Philippines and the Western Ghats are recognised as biodiversity hotspots, being home to a rich and generally threatened biodiversity, often subject to intense anthropogenic pressures, particularly habitat loss (Myers *et al.* 2000). Consequently, there is an urgent need to assess the conservation status of these two narrower endemics and formulate policies to ensure their survival. It is our hope that their status as unique regional representatives of an iconic genus will inspire local human populations to view them with pride, as is the case in some places already (e.g., Karnataka, India), rather than revulsion and fear.

One of the new species described here, *Ophiophagus kaalinga* sp. nov. is rather better researched than its congeners. Thanks to the field-based studies on the autecology of *O. kaalinga* in Agumbe, Central Western Ghats, a series of studies on various aspects of this species have been conducted. Bhaisare *et al.* (2010) reported on the foraging and feeding ecology of *O. kaalinga*, wherein instances of the snake feeding on small-sized (< 1 m) pit vipers were documented. Whitaker *et al.* (2011) reported on the first ever radio-telemetric studies on this genus. Barve *et al.* (2013) reported on the homing instincts and movement patterns of translocated individuals of *O. kaalinga*. Rao *et al.* (2013) reported on its habitat-use patterns in the agro-forest matrix. Gowri Shankar *et al.* (2013a) worked on the statistics of human encounters of *O. kaalinga*, while Gowri Shankar *et al.* (2013b) enumerated on the peoples' perception during such encounters. Gowri Shankar & Whitaker (2013) compiled instances of cannibalism in *O. kaalinga*. Finally, Whitaker *et al.* (2013) reported on its nesting ecology in captivity and the wild. The more widespread *O. hannah* has also been the subject of ecological studies, mostly in Thailand (but

Fig. 16. Live unvouchered adults of *Ophiophagus salvatana* Gowri Shankar, Das & Wüster sp. nov. showing colouration. **A**. Entire. **B**. Head close-up profiles, Luzon, Philippines (both photos Emerson Sy).

see Hrima *et al.* 2014), focusing on spatial ecology and threatening factors (Marshall *et al.* 2018, 2019, 2020; Silva 2018; Jones *et al.* 2022).

Members of the genus *Ophiophagus*, on account of their exceptionally large adult size and dramatic behaviour, are popular as live exhibits (Pfaff 1992). Understanding the systematics of the genus is therefore of importance to identify captive stocks, and particularly for ex-situ conservation programmes that plan reintroductions. Both *O. kaalinga* sp. nov. and *O. salvatana* sp. nov. are restricted to relatively small areas and highly threatened habitats, and at least some regional populations of the two more widespread species, *O. hannah* and *O. bungarus*, are declining in the face of habitat destruction and degradation, capture for food, skin, medicine, killing out of ignorance and fear (Somaweera & Somaweera 2010; Marshall *et al.* 2018; Devkota *et al.* 2021). Any captive breeding and reintroduction efforts must ensure that species are not allowed to hybridise, and that only the appropriate local species is released in any reintroduction programme.

A major nineteenth century publication that dealt with India's venomous snakes and their venom is Fayrer's (1872) monograph of the venomous snakes of India, which was published in a folio volume. It included two hand-painted lithographs of the king cobra, and had a second edition (in 1874). Fayrer's plate 7, figs 1–4 reproduced here as Fig. 7 and Fayrer's plate 8, here Fig. 8, were then identified as *Ophiophagus elaps*, following the nomenclature at the time. As now understood, these represent two species; Fig. 7 is here reidentified as *O. hannah* s. str. and Fig. 8 as *O. kaalinga* sp. nov., based on their respective diagnoses (including colouration and pattern). Besides the stunning imagery, Fayrer's (1872) volume presented early results of investigations on venom apparatus of the more familiar species.

Besides their conservation implications, our findings may also have implications for toxinology and snakebite treatment. Marked reduction in antivenom efficacy because of venom variation within species complexes with unresolved taxonomy has been noted in the past (Wüster & McCarthy 1996; Gutiérrez *et al.* 2006; Casewell *et al.* 2014). Although bites from *O. hannah* are rare, they are of medical significance, producing lethal neurotoxic effects and releasing large doses of venom, often leading to rapid death in human beings (Ganthavorn 1969; Pu & Wong 1995). Bites from members of the complex, though uncommon, have been recorded from virtually throughout the range, particularly from Myanmar (Evans 1902; Theobald 1924; Morris 1925; Swaroop & Grab 1954; Ganthavorn 1971; Muthusamy & Gopalakrishnakone 1990; Tin-Myint *et al.* 1991), and resolution of the systematics of the group will help develop appropriate antivenom for patients of snake-bite (see Ineich 1995 and references therein). Some population-specific venom profiling studies have been conducted, for example, from the Western Ghats population now referable to *O. kaalinga* sp. nov. (see Gowtham *et al.* 2012, 2014) and from the Indo-Malayan population now referable to *O. bungarus* (see Petras *et al.* 2015; Tan *et al.* 2015). Using the new taxonomy for these species may therefore be the first step to developing improved treatment of envenomation from *Ophiophagus* bites in the respective countries. Finally, the astounding fact is that the taxonomy of the world's largest and most iconic venomous snake has languished unstudied for over 60 years, and that at least two cryptic species have remained undetected until now. This starkly highlights the need for taxonomic knowledge to underpin our efforts to inventory the world's biodiversity and towards conservation policy and strategy.

Acknowledgements

Gowri Shankar and Kartik Shanker would like to acknowledge the Karnataka State Forest Department for granting permits to collect the holotype of the new species from the Western Ghats (Agumbe region: G.O.NO.FEE 119 FWL 2020, dated 12.10.2020). Gowri Shankar appreciates the support received from Malkhede Subhash (IFS), Arun Singegowda, Prasad Shivarudrappa, Raghunandan Ramanna and Sapthagiri Gowda in procuring permission to collect a holotype (for *O. kaalinga* sp. nov.) in Karnataka. GS would like to thank VL Hrima (Mizoram), Luke Yeomans (UK) and Maryline Dujeantieu (at

Paris Museum) for assisting during sample collection. H. Vinod Kumar (Figs 1, 11) and Sangeetha Kadur (Figs 2, 4–5) helped with the digitization and editing of images from Cantor and Elliot, Princia D'Souza helped edit geographical coordinates and Deepak P. helped with image edits. Additional images of live animals were provided by Tom Charlton and Adam Francis (China), Aaron Fernandes (Andaman), the late Naveen Joseph (Tamil Nadu), Ahmad Khaldun Ismail (Peninsular Malaysia), Shinta Sukum (Bali), Nathan Rusli (Java), Emerson Sy, and Bernard Tarun (Luzon). Curatorial staff of the following institutions (see Material and Methods for full forms of institutional abbreviations) provided facilities, data on specimens and/or loans of specimens to Indraneil Das: AMNH (D.R. Frost and L. Ford), ANSP (T. Daeschler and N. Gilmore), BM (M. Wong and Hj. Bakariah), BMNH (E.N. Arnold and C.J. McCarthy), BNHS (N. Chaturvedi, the late J.C. Daniel and A.G. Sekar), CAS (the late J.B. Slowinski and J.B. Vindum), CIB (S. Li, C. Wang, J.-P. Jiang and the late E.-M. Zhao), CSPT (the late B. Vijayaraghavan and V. Kalaiarasan), CUZM (K. Thirathupt and P.P. van Dijk), FMNH (H.K. Voris, the late R.F. Inger, A. Resetar and C. Redhed), IMR (the late B.L. Lim and R.M. Sapran), LSUMZ (D.A. Rossman and C.P. Kofron), MCBT (R. Whitaker and the late H.V. Andrews), MCZ (J.E. Cadle, J. Hanken, the late E.E. Williams and J.P. Rosado), MNHN (P. David, A. Dubois and I. Ineich), NMP (R. Sisson), MZB (I. Boeadi and I. Mumpuni), NKBP (S.K. Patnaik and S. Purohit), RMNH (M.S. Hoogmoed), SM (P. Kedit and C.M.U. Leh), NRM (E. Åhlander and S.O. Kullander), SSM (A. Wong), TNRC (the late J. Nabhitabhata), UF (D. Auth and F.W. King), UPM (P. Alveola and A.C. Diesmos), ZRC (P.K.L. Ng, K.K.P. Lim and C.M. Wang), USNM (W.R. Heyer, R.I. Crombie and G.R. Zug), ZMA (L. van Tuijl), ZSI (J.R.B. Alfred, S.K. Chanda, B. Dattagupta, K. Deuti, N.C Gayen, B.H.C. Murthy and D.P. Sanyal) and ZSIP (K. Chandra and P.V. Rajan). K. Adler, P. David, A. de Silva, K. Manamendra-Arachchi, C.J. McCarthy and V. Wallach supplied critical literature, and P. P. van Dijk helped with translations of the van Hasselt papers. For comments on the manuscript and information on localities, we thank K. Adler, D. Basu, A.M. Bauer, R.I. Crombie, P. David, A.C. Diesmos, C.P. Kofron, G.N. Martin, T. Nguyen, P.P. van Dijk, T. Vasaruchapong, Van Wallach and R. Whitaker. Ashok Captain, David Gower and an anonymous reviewer provided comments on previous drafts of the manuscript. Patrick David provided information on MNHN holdings and Arvin Diesmos, PNM provided vernacular names of species of the Philippines, and helped with specimen examination. Esther Dondorp, RMNH, provided Fig. 10B (image of the full body of the lectotype of *Naia bungarus*), and Lauren Scheinberg CAS, Fig. 10D (corresponding image of *Ophiophagus salvatana* sp. nov.). Museum visits were supported by Universiti Malaysia Sarawak, Universiti Brunei Darussalam, a Fulbright Fellowship at the Museum of Comparative Zoology, Harvard University, Centre for Herpetology / Madras Crocodile Bank Trust, a Raffles Museum Fellowship at the National University of Singapore, British Council and the Smithsonian Institution to Das. We warmly thank Glenn Shea, Wolfgang Denzer, Doug Yanega and Scott Thomson for last-minute help and advice on nomenclatural matters. Thanks are due to Masliadi Bin Asri, Mohamad Azwan Bin Abdullah and Chun Xing Wong for their help with king cobra sightings in East Malaysia.

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Manuscript received: 5 June 2023
Manuscript accepted: 12 April 2024
Published on: 16 October 2024
Topic editor: Magalie Castelin
Section editor: Aurélien Miralles
Desk editor: Pepe Fernández

Zeitschrift/Journal: European Journal of Taxonomy

Jahr/Year: 2024

Band/Volume: 0961

Autor(en)/Author(s): diverse

Artikel/Article: Taxonomic revision of the king cobra Ophiophagus hannah (Cantor, 1836) species complex (Reptilia: Serpentes: Elapidae), with the description of two new species 1-51