SALAMANDRA **57**(2): 219–228
15 May 2021 | ISSN 0036–3375

SALAMANDRA
German Journal of Herpetology

New data on the distribution, morphology, and molecular systematics of two venomous snakes, *Bungarus niger* and *Bungarus lividus* (Serpentes: Elapidae), from north-east India

Lal Biakzuala[1], Jayaditya Purkayastha[2], Yashpal Singh Rathee[3] & Hmar Tlawmte Lalremsanga[1]

[1)] Developmental Biology and Herpetology Laboratory, Department of Zoology, Mizoram University, 796004 Tanhril, Mizoram, India

[2)] Help Earth, 781007 Guwahati, Assam, India

[3)] Herpsmitten, Umroi Military Station,793103 Umiam, Meghalaya, India

Corresponding author: Hmar Tlawmte Lalremsanga, e-mail: htlrsa@yahoo.co.in

Manuscript received: 1 December 2020
Accepted: 9 March 2021 by Arne Schulze

Abstract. This paper provides new information on the two medically important snakes, *Bungarus niger* and *B. lividus* from northeastern India. Included are morphological data on both the species and for the first time, genetic data (cytb) on *B. lividus* and establishing the genetic relation of the species to its congeners. We also provide brief descriptions of hemipenial morphology and new distributional records for both the species, along with notes on their natural history.

Key words. Squamata, Assam, greater black krait, lesser black krait, Meghalaya, Mizoram, natural history, phylogeny.

Introduction

Elapid snakes belonging to the genus *Bungarus* Daudin, 1803 are represented by 17 species known to occur throughout most of the Oriental region (Kuch et al. 2005, Abtin et al. 2014, Wallach et al. 2014, Sunagar et al. 2021). India is home to eight species of *Bungarus* (Kraits) and north-east (NE) India harbours four of them, namely, *B. bungaroides* (Cantor, 1839), *B. fasciatus* (Schneider, 1801), *B. lividus* (Cantor, 1839) and *B. niger* (Wall, 1908). Throughout their respective ranges, kraits are nocturnal and active predators, and are among the most medically important snakes (Warrell 1999). Brahmaputra Basin, south of the Himalayas was noted as part of the ranges of both *B. lividus* and *B. niger* (Wall 1908). Smith (1943) agrees to Wall (1908) in recognizing *B. lividus* as a species distinct from *B. niger* but added that the ventrals of both the species to be white with distinct dark mottling at the base of the ventral and subcaudal scales. Furthermore, Smith (1943) stated the total maximum size of *B. lividus* and *B. niger* to be 1,020 mm and 1,200 mm, respectively. According to Smith (1943), *B. lividus* is recorded from Rangpore (=Rangpur, in the Republic of Bangladesh), Jalpaiguri and Darjeeling (West Bengal State, India), and Dibrugarh (Assam State, India), and *B. niger* from Darjeeling (West Bengal State, India), Dibrugarh, Sadiya and Sibsagar (Assam State, India), Garo Hills (Meghalaya State, India).

A morphology-based phylogenetic analysis of *Bungarus* species by Slowinski (1994) included *B. andamanensis* Biswas & Sanyal, 1978, *B. bungaroides*, *B. caeruleus* (Schneider, 1801), *B. candidus* (Linnaeus, 1758), *B. ceylonicus* Günther, 1864, *B. fasciatus*, *B. flaviceps* Reinhardt, 1843, *B. lividus*, *B. magnimaculatus* Wall & Evans, 1901, *B. multicinctus* Blyth, 1861, *B. niger*, and *B. sindanus* Boulenger, 1897. Slowinski (1994) used six parameters, namely, relative size of the vertebral scales, presence or absence of postzygapophysial processes, structure of choanal process of the palatine, subcaudals structure (divided or entire), demarcation between calyculate and spinose zone of hemipenis, and colour pattern. According to his model, *B. lividus* and *B. niger* were found to be sisters to each other sharing five of the six characters considered for the analysis. Both the species differed from each other in only relative size of the vertebral scales: *B. niger* has vertebral scales which are strongly enlarged compared to other dorsal scales, whereas in *B. lividus* the posterior vertebral scales are only slightly enlarged. Both the species together were placed as the sister group to a clade comprising *B. andamanensis, B. caeruleus, B. candidus, B. ceylonicus, B. magnimaculatus*, *B. multicinctus* and *B. sindanus*. Although the morphology-based taxonomic procedure is considered as an effective method for identifying snakes (Burbrink & Crother 2011, Wallach et al. 2014), differences between life stages and sexes can lead to misidentification (Laopichienpong et al. 2016). Consequently, the use of molecular tools are valuable in assisting rapid species identification, phylogenetic reconstruction, biodiversity research, and population genetics (Burbrink & Lawson 2007, Castoe et al. 2012). There has been rather limited molecular studies on Indian snakes, especially of those found in northeastern India. Despite the relative abundance in the region of the two closely related sympatric species, *B. niger* and *B. lividus*, their conservation status and distribution pattern in the country are poorly documented (Ahmed et al. 2009). Herein, we attempt to provide additional data on their morphology, distributional records and natural history of the two species of black kraits in northeastern India, and also establish their phylogenetic relationship with the congeners using mitochondrial cytochrome *b* (cytb) marker gene.

Materials and methods

Field surveys and sampling were conducted in Mizoram State, northeastern India, with permission (No.A.33011/2/99-CWLW/225) from the Chief Wildlife Warden of Environment, Forests and Climate Change Department, Government of Mizoram, and in Meghalaya State after obtaining the permission (No. FWC/G/173/Pt-V/2377-87) from the Forest Department, Meghalaya State Government. Tissue samples were stored in 95% ethanol at –20˚C for molecular-based investigation. The voucher specimens were fixed in 10% formalin, subsequently transferred to 70% ethanol, and deposited in the Departmental Museum of Zoology, Mizoram University, India (MZMU). The localities were recorded with a Garmin, Montana 650 GPS unit, and maps created using QGIS 3.10.8.

Morphometric measurements were taken with a Mitutoyo™ slide-calliper (505–671) to the nearest 0.01 mm. We followed the scalation terminology of Campbell & Lamar (2004), Dowling (1951) for counting ventrals (Ve), and the hemipenis terminology by Dowling & Savage (1960). The terminal scute is excluded from the number of subcaudals (Sc). Snout–vent length (SVL) and tail lengths (TaL) were measured to the nearest millimetre. The numbers of dorsal scale rows (DSR) are given at one head length behind head, at midbody (i.e., at half of SVL), and at one head length before vent, respectively. Values for symmetric head characters are given in left/right order. Sex was determined by using a metal sexing probe in live specimens, whereas in preserved specimens, it was determined by making an incision at the base of the tail followed by establishing the presence or absence of hemipenes. Other abbreviations used in the text are as follows: MZMU (Departmental Museum of Zoology, Mizoram University), YSR (collection of Yashpal Singh Rathee), TL (total length), RTaL (relative tail length), ED (eye diameter), END (eye–nostril distance), IOD (inter–orbital distance), IND (inter–narial distance), SW (snout width), SL (snout length), HL (head length), HW (head width), SL (supralabials), SLE (supralabials touching eye), IF (infralabials), Tem (temporals), ATem (anterior temporal), PTem (posterior temporal), PoO (postoculars), PrO (preoculars), As (anal shield), a.s.l. (above sea level), WL (Wildlife Sanctuary), NP (National Park).

Genomic DNA was extracted from the tissue samples using a DNeasy Blood and Tissue Kit (Qiagen™, Valencia, California, USA) following the standard protocol provided by the manufacturer. We amplified and sequenced the partial cyt*b* gene using primers L14910 and H16064 (Burbrink et al. 2000). The newly generated sequence data was added to a dataset of previously published sequence data (Kuch 2003, Kuch 2007, Pyron et al. 2013). Sequences (maximum of 768 base pairs) were aligned in MEGA X software (Kumar et al. 2018) using the MUSCLE algorithm with default parameter settings (Edgar 2004). Maximum Likelihood (ML) phylogenetic reconstruction was performed in MEGA X software (Kumar et al. 2018) with 2,000 bootstrap replicates using the model GTR+I+gamma, which was selected based on the lowest Bayesian Information Criterion (Nei & Kumar 2000). For the Bayesian inference (BA) phylogeny, GTR+I+gamma was also selected as the optimal model of nucleotide evolution using Mr.Modeltest 2.4 (Nylandar 2004) under the Akaike Information Criterion. Bayesian analysis was run for 20 million generations sampling one tree each 1,000 generations using Mr.Bayes 3.2.5 (Ronquist & Huelsenbeck 2003). Burn-in was set to 25%, and stationarity was considered to be reached when the average standard deviation of split frequencies was less than 0.01.Uncorrected p-distance was calculated in MEGA X (Kumar et al. 2018).

Results and discussion

Bungarus niger Wall, 1908
(Type locality: Tindharia, eastern Himalayas, India)

Morphology. *Bungarus niger* commonly known as greater black krait, is a species morphologically similar to *B. lividus.* It was originally described from Tindharia, Darjeeling District of West Bengal in India by Wall (1908). According to the original diagnosis by Wall (1908), the species is distinguished from *B. lividus* in the vertebral row of dorsal scales, where they were much enlarged and were broader than long (vs. vertebral row of dorsal scales feebly enlarged and not broader than long in *B. lividus*); greater number of Ve (216–231 vs. 209–221 in *B. lividus*) and Sc (49–56 vs. 35–43 in *B. lividus*) and larger body size i.e 1,200 mm in *B. niger* vs. 1,020mm in *B. lividus* (Smith 1943).

We provide updated morphological data based on 27 specimens examined in this study (male = 23, female = 4) in Fig. 1 and Supplementary Table 1. It is a moderately sized snake (SVL max: 1,170 mm), males (Tal/TL: 0.11–0.16, avg. 0.14±0.012) with slightly longer relative tail length than females (Tal/TL: 0.14–0.16, avg. 0.15±0.008); head not distinct from the neck, longer than broad (HW/HL: 0.68–0.90, avg. 0.79±0.062 in male; 0.67–0.85, avg. 0.77±0.084 in female). Eye around 14% of the HL in sex pooled (ED/HL: 0.11–0.18, avg.0.14±0.017 in male; 0.14–0.16, avg. 0.15±0.010 in female), pupil round; SL and IF 7 in number, 3rd and 4th touching the eyes; PrO1, and 2 PoO (except MZMU 1418 with single PrO); ATem 1, PTem 2. In males, Ve214–228 (avg. 220.7±3.62) and Sc 48–56 (avg. 51.9±2.09); in females, Ve 220–225 (avg. 221.8±2.22) and Sc 48–54 (avg. 51.8±2.63). Hemipenis vaguely bilobed; about one-third of the distal part is calyculate, followed by spinose from mid region with the size of spines decreasing as they approach to the proximal area with ill-defined demarcation between calyculate and spinose region (Fig. 1E–F).We noted a peculiar nape colouration in a juvenile specimen (MZMU 1809); it was mottled with light patches at both sides from the rim of posterior temporals up to part of the first dorsal scale (Fig. 2A–B). Our data on *B. niger* extends the previously known lower limit of Ve count (214–228 vs. 216–231 in Smith 1943), and the upper limit of the range of Sc (48–58 vs. 47–57 in Purkayastha 2013).

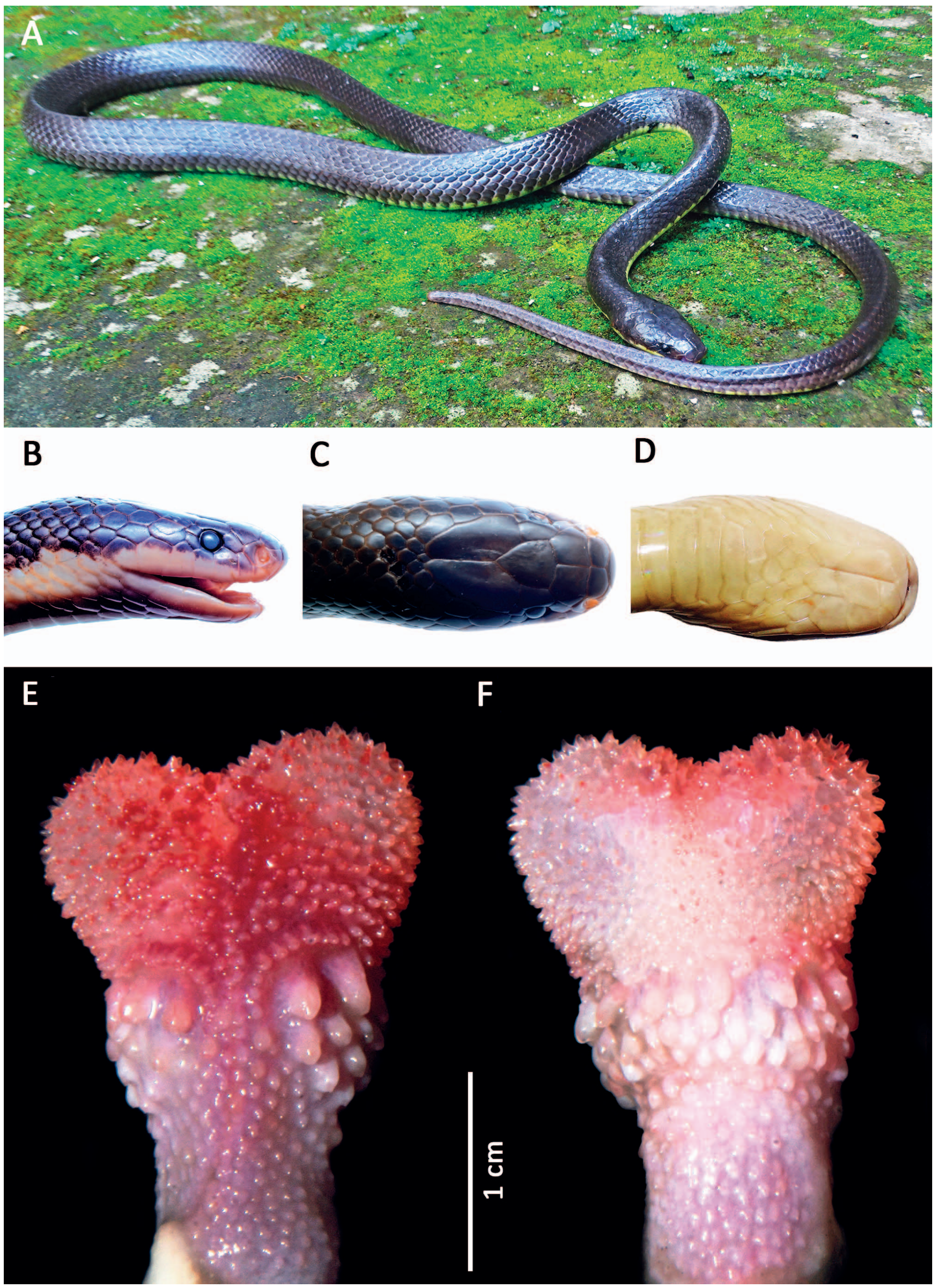

Figure 1. *Bungarus niger.* (A) Adult male from Reiek Community Reserve Forest, Mizoram, NE India; (B–D) lateral, dorsal and ventral views of the head; (E) sulcate, and (F) asulcate view of the everted hemipenis.

Distribution. In this study, we provide new distributional records (n=56) for *B. niger* from the State of Mizoram and Meghalaya, NE India at the elevation range of 50–1,433 m a.s.l. These records are represented by six individuals recorded from Umroi Military Station, Ri Bhoi District in Meghalaya State, and 55 localities from eight Districts in Mizoram State. Detailed specimens collection data is given in Supplementary Table 2. In addition, we compiled the following distributional records from published data (Wall 1908, Wall 1924, Smith 1943, Bauer & Günther 1992, Pawar & Birand 2001, Tillack & Grossmann 2001, Grosselet et al. 2004, Khan 2004, Athreya 2005, Borang et al. 2005, Dasgupta & Raha 2006, Leviton et al. 2008, Theophilus et al. 2008, Faiz et al. 2010, Lalremsanga et al. 2011, Sharma et al. 2013, Pandey et al. 2016, Ahsan & Rahman 2017, Das 2018, Lalbiakzuala et al. 2019). Bangladesh: Chittagong Division–Chandanaish, Khagrachhari, Fatikchhari, Dighinala, Chittagong University, Dudpukuria-Dhopachari WS, Teknaf WS, Baraiyadhala NP, Bandarban, Rangamati, Kaptai NP, Cox's Bazar; Mymensingh Division–Sherpur, Jamalpur; Sylhet Division–Habiganj, Moulvibazar, Lawachara NP; Dhaka Division–Savar. Bhutan: Chuka District–Phuntsholing. India: Assam–Dibrugarh, Margherita, Sadiya, Sivasagar, Guwahati, Nameri NP, Nambor WS, Borail WS, Maruacherra, Silkuri, Assam University campus; Tripura–Damcherra; Arunachal Pradesh–NERIST campus, Itanagar, Mehao WS, Pakke Khellong in Eaglenest WS; Changlang,

Figure 2. *Bungarus niger.* (A) Juvenile (MZMU 1809) from Tanhril, Mizoram; (B) dorso-lateral view of the head of a juvenile *B. niger*; (C) adult male of *B. niger* preying on adult *Smithophis atemporalis* at Paikhai road, Mizoram, NE India.

Namdapha NP; Meghalaya–Garo Hill, Selbelgiri, Balpakram; Mizoram–Ngengpui WLS, Aizawl, Kolasib, Mamit and Siaha, Buhchangphai and Champhai Vengsang; Uttarakhand–Bungapani; West Bengal–Tindharia, Jalpaiguri; Nagaland (no locality record available). Nepal: Province No. 1–Golbasti, Ilam municipality; Gandaki Pradesh–Naudana, and in Kaski District. Myanmar: Chin and Rakhine States.

Natural history notes. *Bungarus niger* is known to be an ophiophagus and nocturnal species of snake, typically encountered between ca. 18:00 hrs and 02:00 hrs, and rarely by day. It is known to inhabit evergreen and moist deciduous forests, grasslands, plantations, and human settlements (Ahmed et al. 2009) at the elevation of 42–1,646 m a.s.l. (Lalbiakzuala et al. 2019). In the wild, we observed a male individual preying on an adult *Smithophis atemporalis* on 23 September 2020 at ca. 22:00 hrs on a tarmac road at Paikhai road, Mizoram, India (23.560556°N, 92.832222°E; ca. 806 m a.s.l.; Fig. 2C). It was also reported to feed on *Coelognathus radiatus* in the wild (Lalbiakzuala et al. 2019). In captivity, we observed the species feeding on *Argyrophis diardi*, adult *Psammodynastes pulverulentus*, sub-adult *Trimeresurus erythrurus* and *Oligodon albo-*

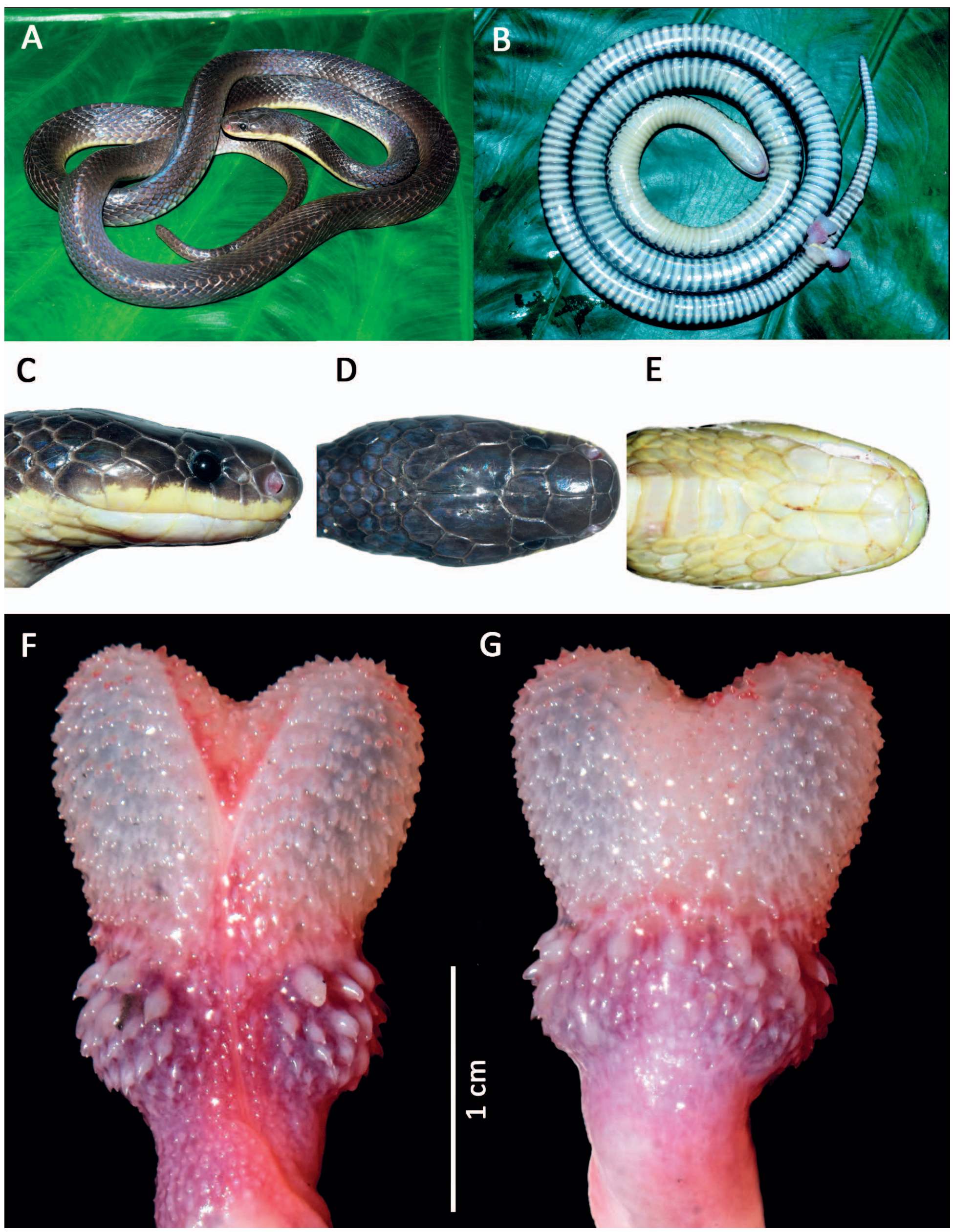

Figure 3. *Bungarus lividus*. (A) A sub-adult male (YSR 187) from Baridua, Meghalaya; (B) ventral view of the specimen; (C–D) lateral, dorsal and ventral views of the head; (F) sulcate, and (G) asulcate view of the everted hemipenis.

cinctus. Another species recorded in the diet of the snake is *Trachischium tenuiceps* (Wall 1923). Moreover, we inferred that females are seemingly more secretive, or naturally rarer than the males, as only around 18% of our randomly collected specimens during this study period (2009–2020) were of the female.

Bungarus lividus Cantor, 1839
(Type locality: Assam, India)

Morphology. Cantor (1839) described *B. lividus* (Lesser Black Krait) based on a single specimen from Assam, India. According to the original description, the snake was blackish-blue dorsally, yellowish-white ventrally with 221 Ve and 56 Sc. Subsequently, Boulenger (1890, 1896) added to the knowledge on the species and defined the species in having the rostral nearly as high as broad, visible from above; internasal shorter than prefrontal; frontal longer than broad, shorter than parietals; one PrO and two PoO; Tem 1+2; seven SL, third and fourth SLE; two pairs of chin shields, anterior longer and is in contact with three IF; DSR with 15 at the midbody; vertebral row of dorsal scales feebly enlarged and not broader than long; Ve 212–225 and Sc 37–56 in number. Uniform black or brown dorsal surface in colour, and ventral surface white or pale brown in colour.

In this study, we provide the morphological data based on three male specimens collected from Baridua, Meghalaya (Fig. 3, Supplementary Table 1). It is a moderately sized snake (SVL max: 335 mm), Average relative tail length (Tal/TL) in male is 0.23–0.25 (avg. 0.24±0.012); head not distinct from the neck, longer than broad (HW/HL: 0.68–0.76, avg. 0.72±0.04). Eye around 16% of the HL (ED/HL: 0.15–0.17, avg. 0.16±0.01), pupil round; SL and IF 7 in number, 3rd and 4th touching the eyes; PrO1, PoO2; ATem 1, PTem 2. In males, Ve 213–228 (avg. 218.3±8.38) and Sc 33–36 (avg. 34.7±1.53); Hemipenis extends up to 6–8 Sc, vaguely bilobed; at about one third from the base strongly spinosed rim present. Above the spinosed rim till the apex, the hemipenis is with small homogenous spines. The sulcus spermaticus bifurcates at two-third of the length of hemipenis and enters the lobe in a "V" shaped structure; the base of the organ is relatively smooth (Fig. 3F–G).

Distribution. During the study, we documented *B. lividus* from Azara in Assam State, and Baridua in Meghalaya State which were all within north-eastern India (Supplementary Table 2). We also compiled the following distributional records from published data (Wall, 1908, Wall, F. 1924, Smith 1943, Khan 1992, Sharma et al. 2003, Kuch et al. 2011, Ahsan & Rahman 2017, Bhattarai et al. 2018, Das 2018, Tshewang & Letro, 2018, Ray & Pandey, 2020): Arunachal Pradesh–Pakke; West Bengal–Tindharia, Darjeeling, Jalpaiguri (Raikatpara Area); Assam–Dibrugarh, near Tezpur, Guwahati. Bangladesh: Rangpur Division–Rangpur, Carmichael University College campus,

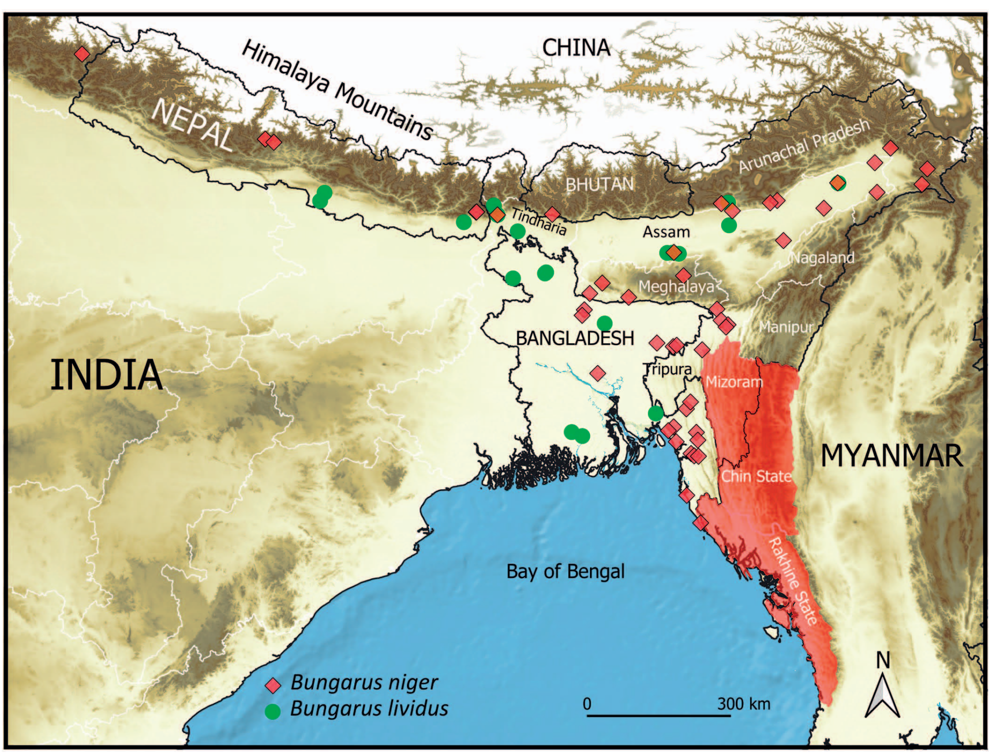

Figure 4. Distributional records of *Bungarus niger* (in red diamond and red shaded) and *Bungarus lividus* (in green dots). Distribution in Myanmar (Chin and Rakhine States), and Mizoram State, NE India is based on Leviton et al. (2008) and Lalbiakzuala (2019), respectively.

Dinajpur; Mymensingh division–Mymensingh district; Chittagong Division–Feni District; Barisal Division–Pirojpur; Khulna Division–Bagerhat. Nepal: Province No. 1–Beldangi I Refugee Camp near Damak in Jhapa District; Province No. 2–Amlekhganj and Bhata-Hattisar in Parsa NP. Bhutan: Langthel in Jigme Singye Wangchuck NP (Fig. 4).

Natural history notes. *Bungarus lividus* is also a night-active species, which is known to occur at an elevation range up to 340 m a.s.l. (Wallach et al. 2014). All the individuals were encountered between 19:00 hrs and 23:00 hrs. In one occasion, an individual after being rescued from a residential area bit itself on its lower lip and soon after died (Purkayastha et al. in press).

Phylogenetic relationship. For this study, the partial cyt*b* gene was amplified and sequences were generated from two individuals for *B. niger* (MZMU 975, GenBank accession no. MW596473; MZMU 1809, GenBank accession no. MW596474), and single individual each for *B. lividus* (YSR 187, GenBank accession no. MW596472) and *B. fasciatus* (MZMU 978, GenBank accession no. MW596475). The BA and ML inferred trees largely congruent except for the position of *B. flaviceps*. This species was resolved as the sister lineage to the cluster consisting of *B. bungaroides* + *B. slowinskii* in the BA analysis, but to *B. fasciatus* in the ML tree (not shown). Our generated sequence of *B. fasciatus* clustered with conspecific sequences from Thailand and Java by strong Bayesian posterior probability (BPP=1.0) and bootstrap value (100). Our analyses clearly nested *B. lividus* among the kraits of Indian subcontinent, and retrieved as a sister taxa of *B. caeruleus* and *B. ceylonicus* with a significant BPP (1.0) and bootstrap value (99), whereas *B. niger* formed a sister taxa to the clade of Southeast Asian endemic kraits (*B.multicinctus* + *B.candidus*) (BPP=0.73;

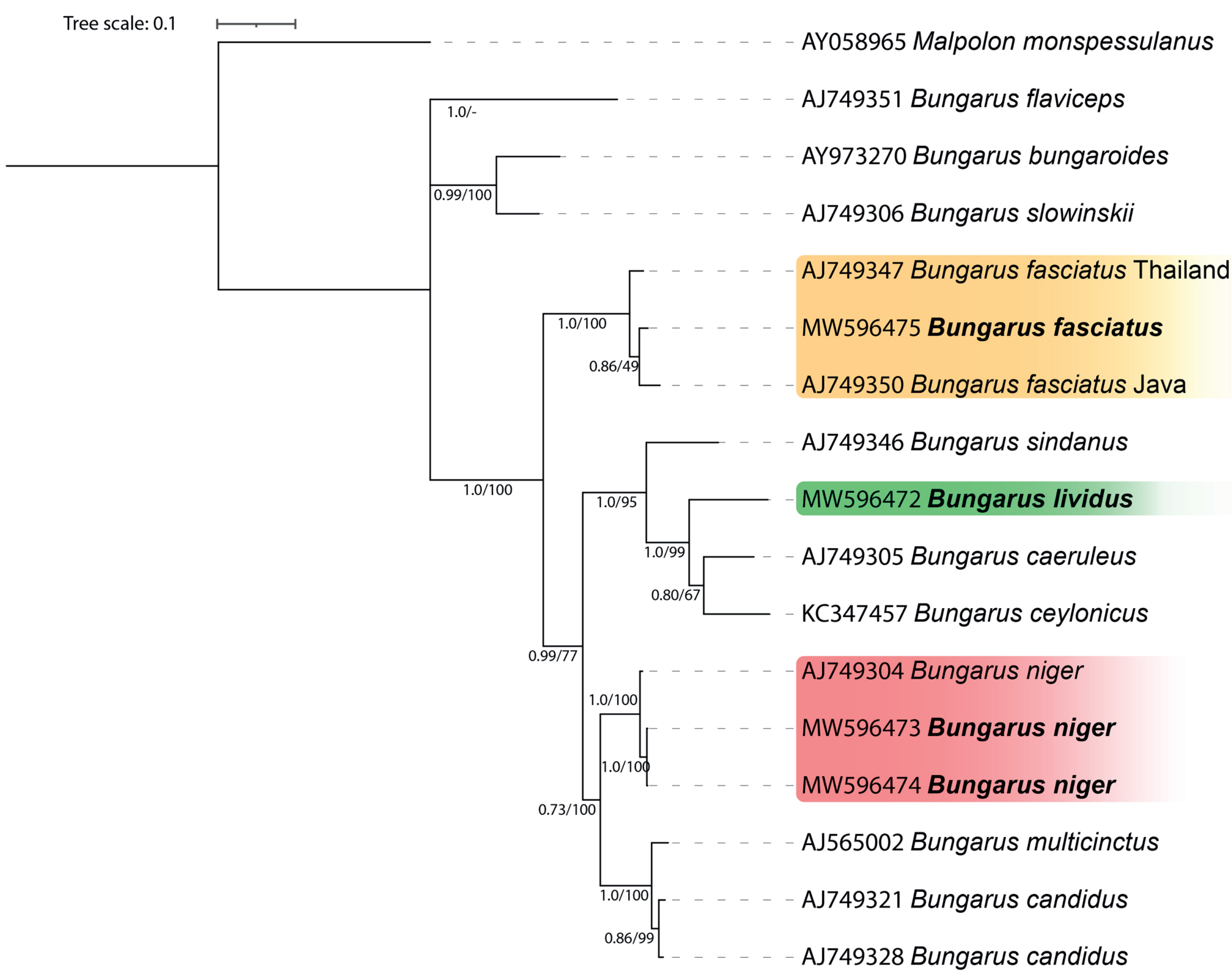

Figure 5. Bayesian inference (BA) phylogeny based on partial cyt*b* gene inferred the relationship of *Bungarus lividus* and *Bungarus niger* with other congeners. Newly generated sequences are shown in bold. Numbers along internodes represent posterior probabilities from the BA phylogeny (before slashes) and bootstrap values from the Maximum Likelihood (ML) phylogeny (after slashes). (– = node not recovered in the ML analysis).

bootstrap value=100).The clade consisting of *B. sindanus* + *B. lividus* + *B. caeruleus* + *B. ceylonicus* was also inferred as sister group to *B. niger* (BPP=0.99; bootstrap value=77). Regardless of the ML bootstrap value (100), the nodal support between *B. niger* and *B. multicinctus* + *B. candidus* is not strong in the BA analysis (BPP=0.73). Likewise, with regardless of the BPP (0.99), the relationship of *B. niger* and the group containing *B.sindanus* + *B. lividus* + *B. caeruleus* + *B. ceylonicus* is also poorly supported in the ML analysis (bootstrap value=77). We therefore hinted the possibility of *B. candidus* and *B. multicinctus* as sister to *B. caeruleus*, *B. ceylonicus*, *B. lividus* and *B. sindanus*. Also, *B. niger* and *B. lividus* differ from each other by 0.151–0.154 uncorrected p-distance; the latter species differs from its closest congeners, *B. caeruleus* by 0.117and *B. ceylonicus* by 0.120, and from its more distant congener *B. bungaroides* by 0.210 (Fig. 5, Supplementary Tables 3–4). According to the present cyt*b* based phylogenetic reconstruction and genetic divergences, we argued that the two species of black kraits (*B. niger* and *B. lividus*) are possibly not sister taxa as they constituted distinct lineages. This contradicted with the morphology based phylogeny of the genus proposed by Slowinski (1994). Yet, more comprehensive studies are necessary to clear up the genetic as well as morphological relationships between the two species.

As the members of this genus are known to be amongst medically important venomous snakes, accurate species identification is essential, considering the prevalence of variation in the composition of snake venom (Chippaux et al. 1991) and its potential effects on the efficacy of antivenoms (Harrison et al. 2003). The phylogenetic study itself does not elucidate the pattern of venom composition, but contributes to the resolution of the systematics as well as provide a framework for illustrating the causes and patterns of the evolution of snake venom composition (Daltry et al. 1996, Thorpe et al. 2007, Barlow et al. 2009).In conclusion, the present study not only contributes to the knowledge on the two krait species, but also will aid in future reference on assessing the conservation status of the species may be important for biomedical and other biological studies.

Acknowledgements

We are thankful to the Chief Wildlife Warden of Environment, Forests and Climate Change Department, Govt. of Mizoram for the herpetofaunal collection permit (Permit No.A.33011/2/99-CWLW/225), and the Chief Wildlife Warden, Forest Department of Meghalaya for the permit (Permit No. FWC/G/173/Pt-V/2377-87). We acknowledge Department of Biotechnology (DBT), New Delhi (DBT-NER/AAB/64/2017), National Mission for Himalayan Studies (NMHS), Uttarakhand (GBPNI/NMHS-2017/MG-22)and Defence Research and Development Organisation (DRDO), New Delhi (DGTM/DFTM/GIA/19-20/0422) for the financial support. We are grateful to Laltlanchhuaha Hrahsel, Samuel Lianzela, Ro Malsawma, Lal Rinsanga, Lal Muansanga, Ht. Decemson, Michael Vanlalchhuana, Gospel Zothanmawia Hmar and Roluahpuia for their help in the field surveys during this study.

References

Abtin, E. G., A. Nilson, A. Mobaraki, A. Hosseini & M. Dehgannejhad (2014): A new species of krait, *Bungarus* (Reptilia, Elapidae, Bungarinae) and the first record of that genus in Iran. – Russian Journal of Herpetology, **21**: 243–250.

Ahmed, M. F., A. Das & S. K. Dutta (2009): Amphibians and reptiles of Northeast India – a photographic guide. – Aaranyak, Guwahati, 169 pp.

Ahsan, M. F. & M. M. Rahman (2017): Status, distribution and threats of kraits (Squamata: Elapidae: Bungarus) in Bangladesh. – Journal of Threatened Taxa, **9**: 9903–9910.

Athreya, R. (2005): Herpetofauna of W. Arunachal Pradesh – checklist. – http://www.clsp.jhu.edu/people/zak/ramana/wapListHerp.htm.

Barlow, A., C. E. Pook, R. A. Harrison & W. Wüster (2009): Coevolution of diet and prey-specific venom activity supports the role of selection in snake venom evolution. – Proceedings of the Royal Society B: Biological Sciences, **276**: 2443–2449.

Bauer, A. & R. Günther (1992): A preliminary report on the reptile fauna of the Kingdom of Bhutan with the description of a new species of scincid lizard (Reptilia: Scincidae). –Asiatic Herpetological Research, **4**: 23–36.

Biswas, S. & D. P. Sanyal (1978): A new species of krait of the genus *Bungarus* Daudin, 1803 (Serpentes: Elapidae) from the Andaman Island. – Journal of the Bombay Natural History Society, **75**: 179–183.

Blyth, E. (1861): Proceedings of the Society. Report of the Curator. – Journal of the Asiatic Society of Bengal, **29**: 87–115.

Borang, A., B. B. Bhatt, S. B. Chaudhury, A. Borkotoki & P. T. Bhutia (2005): Checklist of snakes of Arunachal Pradesh, Northeast India. – Journal of the Bombay Natural History Society, **102**: 19–26.

Boulenger, G. A. (1897): A new krait from Sind (*Bungarus sindanus*). – Journal of the Bombay Natural History Society, **11**: 73–74.

Boulenger, G. A. (1896): Catalogue of the snakes in the British Museum, Vol. 3. – Taylor & Francis, London, 727 pp.

Boulenger, G. A. (1890): The Fauna of British India, Including Ceylon and Burma. Reptilia and Batrachia. – Taylor & Francis, London, xviii, 541 pp.

Burbrink, F. T. & B. I. Crother (2011): Evolution and taxonomy of snakes. – pp. 19–53 in: Idridge R. A. & D. M. Sever (eds): Reproductive biology and phylogeny of snakes. – CRC Press, Boca Raton.

Burbrink, F. T. & R. Lawson (2007): How and when did Old World ratsnakes disperse into the New World? – Molecular Phylogenetics and Evolution, **43**: 173–189.

Burbrink F. T., R. Lawson & J. B. Slowinski (2000): Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): A critique of the subspecies concept. – Evolution, **54**: 2107–2118.

Campbell, J. A. & W. W. Lamar (2004): The Venomous Reptiles of the Western Hemisphere. Volumes I–II. – Cornell University Press, Ithaca.

Cantor, T. E. (1839): Spicilegium serpentium indicorum [part 1]. – Proceedings of the Zoological Society of London, **1839**: 31–34.

Castoe, T. A., J. W. Streicher, J. M. Meik, M. J. Ingrasci, A. W. Poole, A. P. de Koning, J. A. Campbell, C. L. Parkinson, E. N. Smith & D. D. Pollock (2012): Thousands of microsatellite loci from the venomous coralsnake *Micrurus fulvius* and variability of select loci across populations and related species. – Molecular Ecology Resources, **12**:1105–1113.

Chippaux, J. P., V. Williams & J. White (1991): Snake venom variability: methods of study, results and interpretation. – Toxicon, **29**: 1279–1303.

Daltry, J. C., W. Wüster & R. S. Thorpe (1996): Diet and snake venom evolution. – Nature, **379**: 537–540.

Das, A. (2018): Notes on Snakes of the Genus *Bungarus* (Serpentes: Elapidae) from Northeast India. – pp. 23– 35 in: Sivaperuman, C. & K. Venkataraman (eds): Indian Hotspot. – Springer Nature Singapore Pvt. Ltd., Singapore.

Dasgupta, G. & S. Raha (2006): Reptilia. – pp. 433–460 in: Alfred, J. R. B. (ed.): Fauna of Nagaland. – Zoological Survey of India State Fauna Series, Calcutta.

Daudin, F. M. (1803): Histoire naturelle, générale et particulière des reptiles: ouvrage faisant suite à l'histoire naturelle générale et particulieère, composée par Leclerc de Buffon, et rédigée par CS Sonnini, membre de plusieurs sociétés savantes (Vol. 3). – F. Dufart, 365 pp.

Dowling, H. G. (1951): A proposed standard system of counting ventrals in snakes. – British Journal of Herpetology, **1**: 97–99.

Dowling, H. G. & J. M. Savage (1960): A guide to the snake hemipenis: a survey of basic structure and systematic characteristics. – Zoologica, **45**: 17.

Edgar, R. C. (2004): MUSCLE: multiple sequence alignment with high accuracy and high throughput. – Nucleic Acids Research, **32**: 1792–1797.

Faiz, M. A., A. Ghose, M. F.Ahsan, M. R. Rahman, M. R. Amin, M. M. U. Hassan, M. A. W.Chowdhury, U. Kuch, T. Rocha, J. B. Harris, R. D. G. Theakston & D. A. Warrell (2010): The greater black krait (*Bungarus niger*), a newly recognized cause of neuro-myotoxic snake bite envenoming in Bangladesh. – Brain, **133**: 3181–3193.

Grosselet, O., M. Vauché, A. Gupta & A. Susmita (2004): *Bungarus niger* Wall, 1908 (Reptilia: Serpentes: Elapidae): extension of range to Cachar District, Assam, India. – Russian Journal of Herpetology, **11**: 10–11.

Günther, A. (1864): The Reptiles of British India. – Taylor & Francis, London, 452 pp.

Harrison, R. A., W. Wüster & R. D. G. Theakston (2003): The conserved structure of snake venom toxins confers extensive immunological cross-reactivity to toxin-specific antibody. – Toxicon, **41**: 441–449.

Khan, M. A. R. (2004): Checklist of the herpetofauna of Bangladesh. – Cobra, **57**: 1–31.

Khan, M. A. R. (1992): Bangladesher Shap (Snakes of Bangladesh) (in Bengali). – Bangla Academy, Dhaka, 227 pp.

Kuch, U., B. E. Molles, T. Omori-Satoh, L. Chanhome, Y. Samejima & D. Mebs (2003): Identification of alpha-bungarotoxin (A31) as the major postsynaptic neurotoxin, and complete nucleotide identity of a genomic DNA of *Bungarus candidus* from Java with exons of the *Bungarus multicinctus* alpha-bungarotoxin (A31) gene. – Toxicon, **42**: 381–390.

Kuch, U. (2007): The effect of Cenozoic global change on the evolution of a clade of Asian front-fanged venomous snakes (Squamata: Elapidae: *Bungarus*). – Unpubl. PhD thesis.

Kuch, U., S. K. Sharma, E. Alirol & F. Chappuis (2011): Fatal neurotoxic envenomation from the bite of a Lesser Black Krait (*Bungarus lividus*) in Nepal. – The Southeast Asian Journal of Tropical Medicine and Public Health, **42**: 960–964.

Kuch, U., D. Kizirian, N. Q. Truong, R. Lawson, M. A. Donnelly & D. Mebs (2005): A new species of krait (Squamata: Elapidae) from the Red River system of northern Vietnam. – Copeia, **4**: 818–833.

Kumar, S., G. Stecher, M. Li, C. Knyaz & K. Tamura (2018): MEGA X: molecular evolutionary genetics analysis across computing platforms. – Molecular Biology and Evolution, **35**: 1547–1549.

Lalbiakzuala (2019): Study on the morphology, distribution and phylogenetic status of the genus *Bungarus* (Reptilia: Serpentes: Elapidae) in Mizoram, India. – Unpubl. MPhil thesis.

Lalbiakzuala, Lalrinsanga, H. T. Lalremsanga, Romalsawma, Vanlalhrima, V. Sailo & H. Laltlanchhuaha (2019): Natural History Notes: *Bungarus niger* (Diet and Maximum/Minimum Elevation). – Herpetological Review, **50**: 797–798.

Lalremsanga, H. T., S. Sailo & Chinliansiama(2011):Diversity of snakes (Reptilia: Squamata) and role of environmental factors in their distribution in Mizoram, Northeast India. – pp. 265–268 in: Tiwari, D. (ed.): Advances in Environmental Chemistry. – Excel India Publishers, New Delhi.

Laopichienpong, N., N. Muangmai, A. Supikamolseni, P. Twilprawat, L. Chanhome, S. Suntrarachun, S. Peyachoknagul & K. Srikulnath (2016): Assessment of snake DNA barcodes based on mitochondrial *COI* and *Cytb* genes revealed multiple putative cryptic species in Thailand. – Gene, **594**: 238–247.

Leviton, A. E., G. R. Zug, J. V. Vindum & G. O. U. Wogan (2008): Handbook to the dangerously venomous snakes of Myanmar. – California Academy of Sciences, San Francisco, 120 pp.

Linnaeus, C. (1758): Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. – Laurentii Salvii, Holmiae, 824 pp.

Nei, M. & S. Kumar (2000): Molecular Evolution and Phylogenetics. – Oxford University Press, 348 pp.

Nylander, J. (2004): Mr.Modeltest v2, program distributed by the author. – Evolutionary Biology Centre, Uppsala University, Uppsala.

Pandey, D. P., S. K. Sharma, E. Alirol, F. Chappuis & U. Kuch (2016): Fatal neurotoxic envenomation following the bite of a greater black krait (*Bungarus niger*) in Nepal: a case report. – Journal of Venomous Animals and Toxins including Tropical Diseases, **22**: 1–4.

Pawar, S. & A. Birand (2001): A survey of amphibians, reptiles, and birds in Northeast India. – CERC Technical Report 6, Centre for Ecological Research and Conservation, Mysore, 126 pp.

Purkayastha, J. (2020): *Bungarus niger* Wall, 1908. – India Biodiversity Portal. Version 3.5.7., https://indiabiodiversity.org/species/show/257456.

Pyron, R. A., F. T. Burbrink & J. J. Wiens (2013): A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. – BMC Evolutionary Biology, **13**: 1–54.

Ray, P. & S. Pandey (2020): A Leucistic Lesser Black Krait, *Bungarus lividus* (Squamata: Elapidae), from West Bengal, India. – IRCF Reptiles and Amphibians, **27**: 103–104.

Reinhardt, J. T. (1843): Beskrivelse af nogle nye Slangearter. – Kongelige Danske videnskabernes selskabs skrifter, **10**: 233–279.

Ronquist, F. & J. P. Huelsenbeck (2003): MrBayes 3: Bayesian phylogenetic inference under mixed models. – Bioinformatics, **19**: 1572–1574.

Schleich, H. H. & W. Kästle (2002): Amphibians and reptiles of Nepal. Biology, Systematics, Field Guide. – Koeltz Scientific Books, Königstein, 1201 pp.

Schneider, J. G. (1801): Historiae Amphibiorum naturalis et literariae. Fasciculus secundus continens Crocodilos, Scincos, Chamaesauras, Boas. Pseudoboas, Elapes, Angues. Amphisbaenas et Caecilias. – Frommanni, Jena, 374 pp.

Sharma, S. K., D. P. Pandey, K. B. Shah, F. Tillack, F. Chappuis, C. L. Thapa, E. Alirol & U. Kuch (2013): Venomous Snakes of Nepal – A Photographic Guide, 1st Edition. – B. P. Koirala Institute of Health Science, Dharan, 77 pp.

Slowinski, J. B. (1994): A phylogenetic analysis of *Bungarus* (Elapidae) based on morphological characters. – Journal of Herpetology, **28**: 440–446.

Smith, M. A. (1943): The Fauna of British India, Ceylon and Burma, Including the Whole of the Indo-Chinese Sub-Region. Reptilia and Amphibia. 3 (Serpentes). – Taylor and Francis, London, 583 pp.

Sunagar, K., S. Khochare, R. R. S. Laxme, S. Attarde, P. Dam, V. Suranse, A. Khaire, G. Martin & A. Captain (2021): A Wolf in Another Wolf's Clothing: Post-Genomic Regulation Dictates Venom Profiles of Medically-Important Cryptic Kraits in India. –Toxins, **13**: 69.

Theophilus, E., A. Captain, F. Tillack & U. Kuch (2008): Reptilia, Elapidae, *Bungarus niger*: Distribution extension and first record for the state of Uttarakhand, India, with notes on snakebites in the Gori River valley. – Check List, **4**: 404–409.

Thorpe, R. S., C. E. Pook & A. Malhotra (2007): Phylogeography of the Russell's viper (*Daboia russelii*) complex in relation to variation in the colour pattern and symptoms of envenoming. – Herpetological Journal, **17**: 209–218.

Tillack, F. & W. Grossmann (2001): Ein neuer Nachweis zur Schlangenfauna Nepals: *Bungarus niger* Wall, 1908 (Reptilia: Serpentes: Elapidae). – Sauria, **23**: 3–9.

Tshewang, S. & L. Letro (2018): The herpetofauna of Jigme Singye Wangchuck National Park in central Bhutan: status, distribution and new records. – Journal of Threatened Taxa, **10**: 12489–12498.

Wall, F. (1924): A hand-list of the snakes of the Indian Empire. Part IV. – Journal of the Bombay Natural History Society, **30**: 12–24.

Wall, F. (1923): A hand list of the snakes of the Indian Empire, Part II. – Journal of the Bombay Natural History Society, **29**: 598–632.

Wall, F. (1908): A popular treatise of the common Indian snakes. Part VIII. – Journal of the Bombay Natural History Society, **18**: 711– 735.

Wall, F. & G. H. Evans (1901): Notes on Ophidia collected in Burma from May to December, 1899. – Journal of the Bombay Natural History Society, **13**: 343–354.

Wallach, V., K.L. Williams & J. Boundy (2014): Snakes of the World: A Catalogue of Living and Extinct Species. – Taylor and Francis Ltd., CRC Press, New York, 1237 pp.

Warrell, D. A. (1999): WHO/SEARO guidelines for the clinical management of snake bites in the Southeast Asian region. – Southeast Asian Journal of Tropical Medicine and Public Health, **30**: 1–85.