



## A taxonomic revision of *Boiga multomaculata* (Boie, 1827) and *B. ochracea* (Theobald, 1868), with the description of a new subspecies (Squamata, Serpentes, Colubridae)

GUNTHER KÖHLER<sup>1\*</sup>, PANUPONG THAMMACHOTI CHARUNROCHANA<sup>2</sup>, LINDA MOGK<sup>1,9</sup>, NILAR THAN<sup>3</sup>, NIA KURNIAWAN<sup>4</sup>, AHMAD MUAMMAR KADAFI<sup>5</sup>, ABHIJIT DAS<sup>6</sup>, FRANK TILLACK<sup>7#</sup> & MARK O'SHEA<sup>8#</sup>

<sup>1</sup>Senckenberg Forschungsinstitut und Naturmuseum, Senckenberganlage 25, 60325 Frankfurt a.M., Germany.

<sup>2</sup>Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand 10330.

✉ [panupong.th@chula.ac.th](mailto:panupong.th@chula.ac.th); <https://orcid.org/0000-0003-3477-8964>

<sup>3</sup>Patheingyi University, Patheingyi, Myanmar. ✉ [nilarthan65@gmail.com](mailto:nilarthan65@gmail.com); <https://orcid.org/0000-0002-1098-7406>

<sup>4</sup>Department of Biology, Universitas Brawijaya, Malang, Indonesia. ✉ [wawan@ub.ac.id](mailto:wawan@ub.ac.id); <https://orcid.org/0000-0001-7383-8742>

<sup>5</sup>Department of Biology, Faculty of Mathematics and Science, University of Palangka Raya, Indonesia.

✉ [amuammarkadafi@mipa.upr.ac.id](mailto:amuammarkadafi@mipa.upr.ac.id); <https://orcid.org/0000-0003-4646-687X>

<sup>6</sup>Wildlife Institute of India, Chandrabani, Dehradun 248001 Uttarakhand, India.

✉ [protobothrops80@gmail.com](mailto:protobothrops80@gmail.com); <https://orcid.org/0000-0002-5851-8457>

<sup>7</sup>Museum für Naturkunde, Leibniz Institut für Evolutions- und Biodiversitätsforschung, Invalidenstrasse 43, 10115 Berlin, Germany.

✉ [frank.tillack@mfn.berlin](mailto:frank.tillack@mfn.berlin); <https://orcid.org/0000-0003-1418-6531>

<sup>8</sup>Faculty of Science and Engineering, University of Wolverhampton, Wulfruna Street, Wolverhampton, West Midlands, WV1 1LY, England. ✉ [m.oshea@wlv.ac.uk](mailto:m.oshea@wlv.ac.uk); <https://orcid.org/0000-0002-1566-7460>

<sup>9</sup>✉ [lmogk@senckenberg.de](mailto:lmogk@senckenberg.de); <https://orcid.org/0000-0003-2700-6675>

<sup>#</sup>these authors contributed equally

\*Corresponding author. ✉ [gkoehler@senckenberg.de](mailto:gkoehler@senckenberg.de); <https://orcid.org/0000-0002-2563-5331>

### Abstract

The analyses of molecular genetic data (mtDNA markers 16S, ND4, CYTB, and the nuclear marker c-mos) provided evidence that the Asian cat snake taxa *Boiga multomaculata* and *B. ochracea* actually represent a single species. They form mixed clades of low intraclade genetic differentiation. This evidence for conspecificity is supported by the lack of differentiation in all examined pholidotic and morphometric characters. Therefore, we formally place *Dipsas ochracea* Theobald, 1868 in the synonymy of *Dipsas multomaculata* Boie, 1827. We provide a summary of the tangled taxonomic history of the taxa involved in this study. Also, we resurrect *Dipsadomorphus stoliczkae* Wall, 1909 from synonymy of *B. ochracea*, for specimens exhibiting 21 midbody dorsal scale rows. *Boiga stoliczkae* is found in the Himalayas north and west of the Brahmaputra valley. Finally, based on the detection of historical genetic lineages within the newly defined species *Boiga multomaculata* we recognize three subspecies: *Boiga multomaculata multomaculata* (Boie, 1827), *Boiga multomaculata ochracea* (Theobald, 1868), and *Boiga multomaculata septentrionalis* n. ssp. which is distributed in northern Myanmar and Assam and Nagaland, India. We designate BMNH 1946.1.2.60 (1) as neotype of *Dipsas ochracea* Theobald, (2) as lectotype of *D. ochraceus* Günther, and (3) as lectotype of *Boiga ochracea walli* Smith, thereby making these names objective synonyms. Finally, we designate BMNH 94.12.31.55 as lectotype of *Dipsadomorphus stoliczkae* Wall.

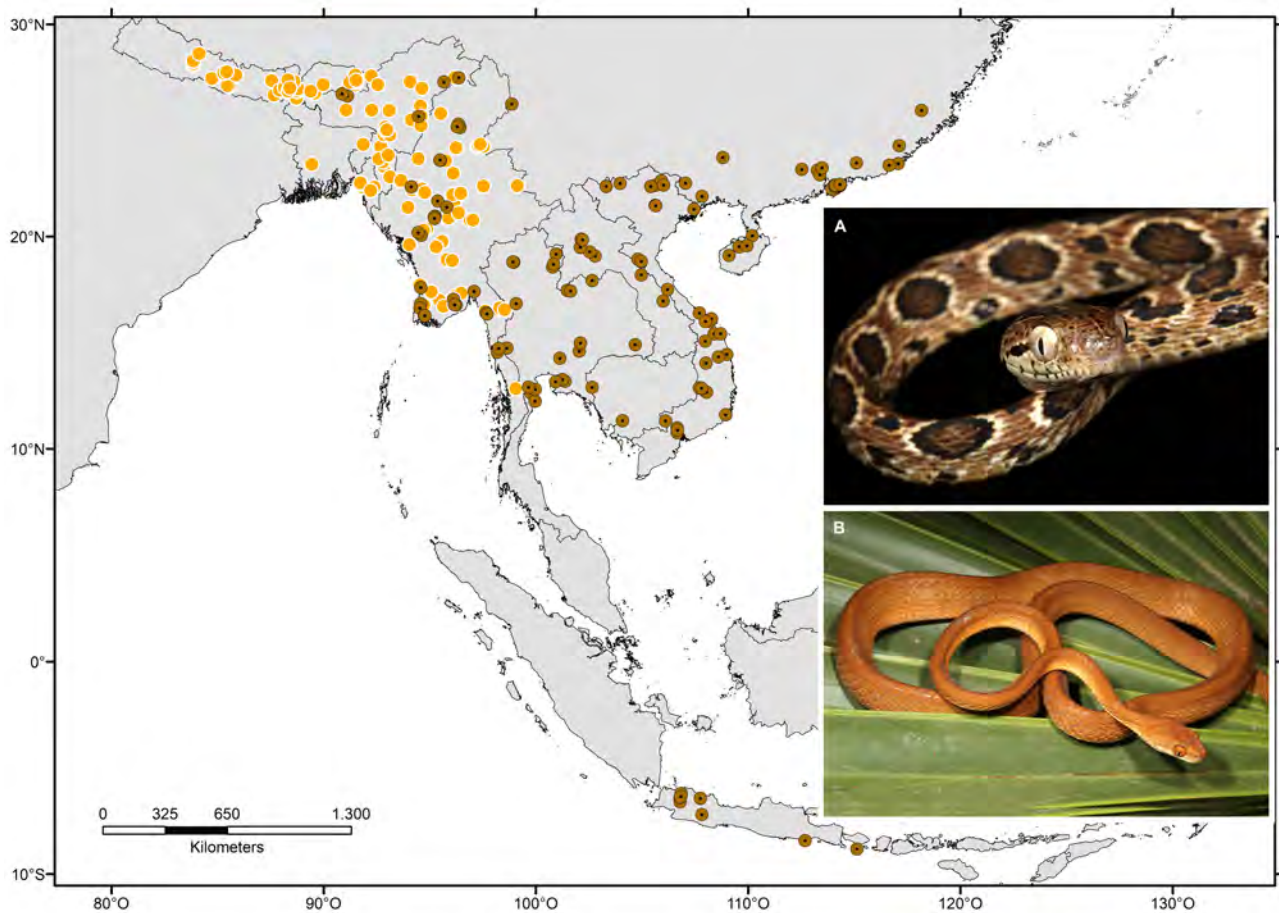
**Key words:** Asian cat snakes, *Boiga stoliczkae*, *Boiga ochracea walli*, color morphs, mimicry, Himalayas, Southeast Asia

### Introduction

Coloration and pattern are considered reliable characters that aid in the differentiation and identification of snake species of many genera (i.e., *Tantilla*, *Geophis*, *Rhadinaea*, *Lampropeltis*; Wilson 1999; Köhler 2008). In the Asian cat snakes of the genus *Boiga* Fitzinger 1826, characters of coloration and patterning are also utilized in the available

dichotomous keys to the genus (e.g., Taylor 1965; Schleich & Kästle 2002; Giri *et al.* 2019; Ganesh *et al.* 2020). During several field trips in Myanmar (2017–2019) we collected six specimens of *Boiga*, which we identified as *B. ochracea* or *B. multomaculata*, based on their color pattern. However, when we generated and analyzed mtDNA barcode sequences (16S rRNA), we were surprised to detect virtually no genetic differentiation among specimens referred to these two taxa. However, before we could publish these findings, other authors (Weinell *et al.* 2021; Ganesh *et al.* 2021) already reported their observation that *B. ochracea* and *B. multomaculata* are very close genetically and questioned the heterospecificity of these two nominal taxa.

Based on our initial findings we initiated an integrative taxonomic study to clarify the taxonomy of the populations currently referred to as *B. ochracea* and *B. multomaculata*. See Fig. 1 for the geographic distribution of the phenotypes associated with these two taxa.



**FIGURE 1.** Map showing collecting localities of *Boiga* specimens identified as *B. multomaculata* (brown circles with central black dot) and *B. ochracea* (orange circles). Each symbol can represent one or more adjacent localities. Source: Specimens examined by authors and data downloaded from GBIF as well as literature records. Insert: *Boiga* specimens in life. A. *Boiga multomaculata* phenotype (SMF 104138); B. *B. ochracea* phenotype (SMF 103827). Photographs by G.K.

To set the stage, it seems appropriate to investigate the taxonomic history and geographic distribution of the taxa involved in this study. This is not a simple process and does involve some sleuthing to determine collection and publication dates and collector’s and collection localities, factors affecting priority, authorship and synonymy, a process termed “forensic historical herpetology” (O’Shea & Kaiser 2018).

### ***Boiga multomaculata***

*Dipsas multomaculata* was described by Heinrich Boie’s elder brother Friedrich (1789–1870), in Latin and German (Boie 1827), and published in the year of Heinrich’s death. It has been suggested that Friedrich Boie attributed his description to H. Boie’s (1823–1825) “Erpétologie de Java” (Wallach *et al.* 2014). The latter work was never published and names proposed therein are considered unavailable for the purposes of nomenclature, according to the International Code of Zoological Nomenclature (ICZN 1999; ICZN 2012), hereafter referred to

as “the Code”. However, F. Boie does not actually cite his brother’s unpublished work in his *D. multomaculata* species account. Rather he cites the Prussian-born Dutch pharmacist and botanist Caspar Georg Carl Reinwardt (1773–1854), yet no Reinwardt 1825 paper describing this taxon exists and it must be assumed that F. Boie was the person who introduced this binomen. Since Boie does attribute the taxon name to Reinwardt the degree of his involvement must therefore be determined. If Reinwardt just contributed the name with the specimen the citation would be *Dipsas multomaculata* F. Boie, 1827, but if he contributed both the name and a description of sorts, then the citation should be *Dipsas multomaculata* Reinwardt in F. Boie, 1827 (Aaron Bauer, pers. comm.). It would appear that the first scenario is correct (see also David & Vogel 1996:21). Thus, the author citation is F. Boie, 1827 not Reinwardt in F. Boie, 1827 because F. Boie attributes the name to Reinwardt but not the description. Schlegel (1826:238) also attributes the description of *Dipsas multomaculata* to Reinwardt when he writes „Gen. DIPSAS Laur. Cuo, Esp. . . . . *Col. multimaculatus* (sic) Reinw. N. esp. . . .”

There is nothing in F. Boie’s account to suggest he referred to his brother’s unpublished manuscript for his description of *D. multomaculata*. However, the comparison of H. Boie’s manuscript part for “*Dipsas multimaculata*” and Friedrich Boie’s (1827) text on “[*Dipsas*] *multomaculata*”, which we regard as the original description, shows, that the latter is a verbatim copy of H. Boie’s manuscript with the exception of the different spelling of the species name and the reference to images which depict this species in earlier classical works.

The primary types of this taxon have been stated to be unlocated (Nguyen *et al.* 2009; Uetz *et al.* 2019), as deposited in “RMNH” (Iskandar & Colijn 2002) or listed with incorrect quantity, syntype composition, and collectors (Wallach *et al.* 2014). They are actually present in the collection of the Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Histoire, Leiden, Netherlands) and have been examined by one of the authors (FT).

The enquiries in Leiden by FT and MOS revealed that H. Boie wrote his manuscript between 1823 and 1825, i.e., before his departure for Java. However, this also means that the material he and Macklot collected on Java between June 1826 and September 1827 (= RMNH 978a+b) was not available to him when he wrote his manuscript. Thus, material used for the description must have already been in the Leiden collection. Therefore, only material that was previously collected by Kuhl and van Hasselt or Reinwardt would have been available to him and are very likely the specimens listed under RMNH 979. The material collected by H. Boie and Macklot (RMNH 978a+b) could never have been part of the type series of *D. multomaculata* because F. Boie (1827) added nothing new to his brother’s text. It has to be noted that the order of the inventory numbers does not relate to the order of accession into the Leiden collection. A specimen (i.e., ZMB 2642) in the collection of the Museum für Naturkunde Berlin very likely also belonged to the original type series of *D. multomaculata*. According to a letter dated “Leyden, 2<sup>nd</sup> April 1825” (preserved in the Dept. of Historical Research of Berlin Museum, Acta Sign. ZM, Dr. Temminck, Leyden, 1818), Heinrich Boie wrote to Martin Hinrich Carl Lichtenstein (1780–1857, Director of the ZMB at that time) and offered him beside many other specimens from Java under list number “38” a specimen of “*Dipsas multimaculata*” for the price of 1 [Reichsthaler]. The same specimen appeared with the same number and same price in a list written by Lichtenstein documenting the arrival of the objects with the following title [translation by us]: „List of the objects sent by Mr. Temminck from Leyden and arrived at the Museum [Berlin] on 9 March 1826“. These hitherto unnoticed documents suggest that the specimen of *D. multomaculata* offered by H. Boie to the Berlin Museum in April 1825 must have belonged to the original type series and was probably collected by Kuhl and Van Hasselt and available to H. Boie when he worked on his manuscript. In addition, the scalation values of ZMB 2642 are within the variation given by H. Boie in his manuscript. The main reason why this specimen has not been considered as a type specimen so far is probably the fact that it is linked only to Coenraad Jacob Temminck (director of the Rijksmuseum van Natuurlijke Historie, Leiden and treasurer of the Dutch East India Company) who is cited as the donor in the Berlin Museum inventory catalogue and no one had previously evaluated the associated correspondence.

Only RMNH 979 (a jar which contains six specimens) and the specimen later sent to the Zoologisches Museum Berlin were available for H. Boie’s manuscript. Of the six specimens under RMNH 979 only specimen b, d, e and f (all females) fit the scalation data of H. Boie (manuscript) and F. Boie (1827). Thus, in our opinion, the extant syntype series of *D. multomaculata* F. Boie 1827 consists of ZMB 2642 and four out of the six specimens listed under RMNH 979.

The German naturalists Heinrich Boie (1794–1827) and Heinrich Christian Macklot (1799–1832) visited Java between December 1825 and September 1827. Esther Dondorp (Senior Collection Manager) and Karien Lahaise (Naturalis archivist) informed MOS that according to an unpublished manuscript by Marinus Hoogmoed “H. Boie and Macklot arrived in Java on 6 June 1826. On December 28, 1826 they travelled to Krawang (Tjikao) [now



Karawang, a town in West Java regency, Tjikao, now Ci Kao, is a watercourse south of Karawang]. H. Boie died on 4 September 1827". Thus, the dates that both were working in Java together and collected these specimens may therefore be defined more accurately as 6 June 1826 to 4 September 1827. The two were in the employ of the Rijksmuseum voor Natuurlijke Historie (RMNH), as part of the Natuurkundige Commissie voor Nederlandsche Indie (Commission for Natural Sciences of the East Indies).

In all documents (letters and manuscript) from H. Boie's hand and publications based on H. Boie's manuscript or written notifications by him (e.g., Schlegel 1826 and 1827) the spelling "*multimaculata*" is used exclusively. This also applies to the Leiden catalogue entries. Although this is to be taken as a clear expression of his will, we have to accept Friedrich Boie's (1827) "*multomaculata*", since the latter is responsible for the valid introduction of the name in the sense of the Code, Art. 50.1. This is also in line with the statements of David & Vogel (1996:21).

Numerous authors erroneously referred to this species as *Dipsas multimaculatus* or *D. multimaculata* (e.g., Duméril *et al.* 1854b; Duméril *et al.* 1854a; Theobald 1868b; Boulenger 1890), and this misspelling of *multomaculata* as *multimaculatus* would continue when Boulenger (1896) placed the rear-fanged Asian cat snakes into the resurrected *Dipsadomorphus*, and even when they were transferred to *Boiga* by Smith (1923). In recent years most authors have been careful to use F. Boie's correct spelling *Boiga multomaculata*.

A number of obscure names have been proposed as synonyms of *B. multomaculata*. Wallach *et al.* (2014) suggested *Coluber aldrovandi* Merrem, 1820, to be a synonym of this taxon. However, reading Merrem's description (1820:125) it becomes obvious that it is not even a *Boiga* because some of the main characters noted by Merrem, e.g., keeled scales, head pointedly rounded, and the absence of a loreal scale are not characteristic for this genus. Also the values for ventrals (121) and subcaudals (49) of Merrem's *aldrovandi* are far outside the range of *B. multomaculata* (see Table 1). Their action to declare *Dipsas multomaculata* a *nomen protectum* with priority over "*Coluber aldrovandi*" is therefore obsolete. Furthermore, Merrem's taxon was not described in the combination with the genus name *Coluber* but with „*Natrix*“. The name "*Natrix sturmii*" is based on an unpublished manuscript dated around 1825 by Johann Georg Wagler (1800–1832) (pers. comm. Van Wallach 17 March 2022) and is considered *nomen ineditum* because it was not been properly published according to the Code.

Rudolf Emil Mell (1878–1970) was a German school-teacher and amateur naturalist collector working in China in the early 20<sup>th</sup> Century. He returned to Germany in May 1921 and later proposed several subspecies of *B. multomaculatus* (Mell 1931), i.e., *B. m. hainanensis*, *B. m. indica*, and *B. m. sikiangensis* but these taxa have been considered synonyms of *B. multomaculata* since their inception (e.g., Pope 1935; Bourret 1936; Smith 1943). Whereas the syntypes of *B. m. sikiangensis* are known (i.e. ZMB 49427, 50879, 52642), no type material is known to exist for *B. m. hainanensis* or *B. m. indica*. The type localities of *B. m. hainanensis* ("Hainan") and *B. m. sikiangensis* ("Kwangtung (Hongkong)") are more precise than the one given for *B. m. indica* ("continental India"), especially since continental India at that time included Sikkim, Assam, Bengal (including today's Bangladesh), Burma (Myanmar), and Pakistan.

The various author's copies of this publication that Mell distributed, including the one in the departmental herpetological library at Senckenberg Forschungsinstitut, contain a handwritten correction of *B. m. hainanensis* to "*sikiangensis* Mell". Presumably, the author had a change of mind regarding his taxon name, but this has no nomenclatorial relevance. As far as we know, Mell never corrected it formally in a subsequent publication and the introduction of the name *hainanensis* must be regarded as valid published in the sense of the Code. At the time of writing Mell's subspecies were not listed in the Reptile Database (Uetz *et al.* 2022).

### ***Boiga ochracea***

In 1868 the description of *Dipsas ochraceus* was published by the German zoologist Albert Karl Ludwig Gotthilf Günther (1830–1914), then an assistant at the British Museum (Natural History) tasked with identifying 2,000 snake specimens in the collection. In his brief description of this species Günther (1868: 425), wrote: "We have received this new snake from Mr. Theobald, who named it ", thereby attributing the authorship to William Theobald (1829–1908), a naturalist attached to the British Geological Survey of India. To complicate matters, Theobald (1868:53) also published a description of *Dipsas ochracea*, in Latin and English, in the same year.

The Reptile Database (Uetz *et al.* 2022) suggested that Theobald's paper was published prior to Günther's paper, pointing out that Günther referred to Theobald in his paper, but without providing a published source. The editors may have assumed that Günther had access to Theobald's already published paper, thereby attributing authorship to Theobald, 1868. Wallach *et al.* (2014) were of the contrary opinion and proposed that the first description of *D. ochraceus* appeared in the Günther paper, and the authorship should therefore read "Theobald *in* Günther, 1868".

**TABLE 1.** Selected measurements and proportions of the taxa of *Boiga* related to *B. multomaculata*. Range is followed by mean value and standard deviation in parentheses. Abbreviations: *m.* = *multomaculata*; *multom.* = *multomaculata*; *ochr.* = *ochracea*; *sept.* = *septentrionalis*.

	<i>m. multom.</i> ♂	<i>m. multom.</i> ♀	<i>m. ochr.</i> ♂	<i>m. ochr.</i> ♀	<i>m. sept.</i> ♂	<i>m. sept.</i> ♀	<i>stoliczkae</i> ♂	<i>stoliczkae</i> ♀
n	13	26	13	27	7	4	14	28
SVL	351–689 (495.2±99.85)	346–695 (558.4±91.81)	376–700 (544.7±94.17)	402–958 (664.6±126.80)	439–665 (585.8±80.87)	661–785 (727.8±64.01)	486–840 (695.2±98.63)	379–940 (719.5±158.30)
TL/SVL	0.243–0.291 (0.263±0.0142)	0.232–0.269 (0.249±0.0010)	0.222–0.288 (0.267±0.0169)	0.214–0.282 (0.244±0.0156)	0.235–0.280 (0.260±0.0152)	0.246–0.256 (0.252±0.0049)	0.247–0.305 (0.276±0.0158)	0.236–0.302 (0.264±0.0165)
ventrals	209–239 (214.4±8.06)	198–237 (217.1±9.50)	225–242 (231.3±5.15)	228–258 (238.9±6.30)	220–235 (227.7±5.18)	227–231 (228.8±1.71)	222–238 (229.2±5.49)	224–247 (236.2±5.81)
subcaudals	87–104 (94.5±5.33)	81–101 (89.8±4.13)	93–108 (102.8±4.72)	87–112 (99.6±5.05)	90–105 (99.1±5.82)	95–100 (97.3±2.06)	102–120 (111.2±5.62)	93–116 (106.0±5.82)
SPL	8–9 (8.1±0.30)	8–8.5 (8.1±0.18)	8–8 (8.0±0)	8–9 (8.04±0.13)	8–8 (8.0±0)	8–8 (8.0±0)	8–8 (8.0±0.00)	8–9 (8.1±0.18)
IFL	10–13 (10.7±0.81)	10–12 (10.9±0.39)	10–12 (11.1±0.34)	9–12 (11.1±0.61)	10–11 (10.9±0.19)	10–11 (10.7±0.58)	11–13 (11.4±0.59)	10–14 (11.7±0.91)
postocs	2–3 (2.0±0.14)	2–3 (2.1±0.25)	2–2 (2.0±0)	1–3 (2.0±0.14)	1–2 (1.9±0.38)	2–2 (2.0±0)	2–2 (2.0±0)	2–2 (2.0±0)
TempAnt	1–2 (1.8±0.38)	1–2 (1.8±0.38)	1–3 (2.0±0.20)	1–2 (1.8±0.34)	2–2 (2.0±0)	1–2 (1.9±0.25)	1–2 (1.8±0.32)	1–3 (2.0±0.18)
TempPos	2–3 (2.3±0.33)	1–3 (2.1±0.36)	1–3 (2.1±0.55)	2–4 (2.3±0.42)	2–3 (2.4±0.48)	2–3 (2.13±0.25)	2–4 (2.5±0.54)	2–4 (2.5±0.48)
MBS	19 (19±0.0)	19 (19±0.0)	19 (19±0.0)	19 (19±0.0)	19 (19±0.0)	19 (19±0.0)	21 (2±0.0)	21 (21±0.0)
PSR	13–15 (13.9±1.04)	13–15 (14.5±0.90)	13–15 (13.9±1.04)	13–15 (14.5±0.89)	13–15 (14.7±0.76)	15–15 (15.0±0)	15–17 (15.1±0.53)	15–17 (15.2±0.54)

This question over the priority of authorship can only be resolved by determining which of these two papers was published first. Günther published his description in the *Annals and Magazine of Natural History*, series 4, volume 1, number 6, which was published on 1st June 1868 (Evenhuis 2003; F. Tillack unpubl. obs.). Theobald published his account in the *Journal of the Linnean Society of London (Zoology)*, volume 10, number 41. The year of publication is often given as 1868 (Smith 1943; Wallach *et al.* 2014; Uetz *et al.* 2022) but the situation is somewhat unclear. Following its title, Theobald's paper reads "By W. Theobald, Jun., Geological Survey of India. Communicated by G. Busk, Esq., Sec. L.S. [Read November 7, 1867.]". The paper was therefore presented orally at a meeting of the Linnean Society of London in late 1867, but that does not constitute "published" according to the Code. According to the title page of the journal, volume 10 was not published until 1870 (Theobald 1868b) which would seem to give priority to Günther's 1868 paper, but this was not the actual date of publication of Theobald's paper. According to the archives of the Linnean Society of London "pages 4–67 of Volume 10 of the *Journal of the Linnean Society of London (Zoology)* were issued on 30 May 1868. The reason the front page is dated 1870 (May 20th) is because that is when the title and contents page were finished, ready for the rest of the journal to be bound" (Vida Milovanovic, Linnean Society of London, pers. comm.; F. Tillack unpubl. obs.). Therefore, Theobald's description takes precedence over Günther's paper, by two days, and the correct citation should be Theobald (1868).

Amongst the distinguishing characteristics of *D. ochraceus*, Günther documented 19 dorsal scale rows, 239–242 ventral scales, and 100 subcaudal scales. His description was based on the two specimens obtained from Theobald, the largest of which he measured at 44 inches (1.12 m), and both of which, he reports, were collected at Pegu (now Bago, 17°19' N, 96°28' E), central Myanmar. Theobald's description differs in a number of respects from that of Günther. He states that he personally collected the first specimen at Rangoon (now Yangon, 16°48' N, 96°09' E), and that his second specimen was collected by Colonel David Browne, at Maulmain (=Moulmein, now Mawlamyine, 16°29' N, 97°38' E) in the Tenasserim Region (now Tanintharyi Region, southern Myanmar). He also measured the first specimen at fully nine inches (229 mm) shorter than the measurement provided by Günther, and finally, Theobald reports that both specimens exhibited dorsal scale counts of 19 on the neck, 17 on the body, and 15 near the tail, in contrast to the dorsal count of 19 provided by Günther, presumably taken at midbody, and a count supported by Boulenger (1896) and Stimson (see later). Given the reported differences in localities, collectors and description, there is no doubt that the two authors described their species using different specimens. However, regarding the reported differences in the number of dorsal scale rows at midbody, it has to be noted that many *Boiga* have a rather chaotic dorsal scale row reduction which can go up and down more than three times within a range of only 10 corresponding ventral scales "at midbody". Furthermore, the measured midbody can be different from the midbody position determined by counting half the number of ventrals.

Both Günther's syntypes, an adult female with an SVL 889 + 212 TL = 1101 mm total length and an adult male with an SVL 611 + TL 149 = 760 mm total length, are housed in the collection of the Natural History Museum, London (BMNH 1946.1.2.60–61).

As far as we are aware, the two types of *D. ochracea* Theobald are unlocated. They were not listed by Theobald (1868a), nor in Sclater (1891) or in Das *et al.* (1998). Some time ago one of us (AD) checked the collection in ZSI, Kolkata, but found no specimens marked as type for Theobald's *ochracea* and none of the specimens examined by him agreed with Theobald's description or locality.

During the late 19th Century the British Museum (Natural History) received five further specimens of *D. ochracea* from Myanmar, i.e., two specimens (BMNH 74.4.29.1193–1194) from Myanmar, reportedly collected by the British army officer and naturalist Richard Henry Beddome (1830–1911), and three specimens (BMNH 89.2.25.37–39) from Bhamo, in Kachin State, northern Myanmar, collected by the Italian naturalist Leonardo Fea (1852–1903).

Ferdinand Stoliczka (1838–1874) was an Austrian paleontologist and naturalist who worked in India during the mid 19th Century, but died of altitude sickness during a Himalayan expedition. He exhibited a considerable interest in snakes and in 1870 he reported on five specimens from the Andaman Islands which he attributed to the taxon *Dipsas hexagonotus* Blyth, 1855 (Stoliczka 1870).

In the late 19th Century the Anglo-Belgian zoologist George Albert Boulenger (1858–1937), was Günther's assistant at the British Museum (Natural History) and the person now tasked with the continued cataloguing of the herpetological collection. In 1890 he resurrected the genus *Dipsadomorphus* Fitzinger, 1843, for the African, Asian, and Australasian cat snakes previously included in the genus *Dipsas* (Boulenger 1890; Boulenger 1896) and he synonymised Günther's *Dipsas ochraceus* with Blyth's older *Dipsadomorphus hexagonatus*.

Adopting this new classification, the British physician and herpetologist Major Frank Wall (1868–1950) examined Blyth's *Dipsas hexagonotus* type specimen (ZSIK 8048), from “Cherrapunji, Khasi Hills, Assam” [= Sohra, East Khasi Hills district, Meghalaya state, India] and reidentified it as a juvenile *Dipsadomorphus cyaneus*, now *Boiga cyanea* (Duméril, Bibron and Duméril, 1854) (Wall 1909). He also examined the four adult specimens in Stoliczka's Andaman *Dipsas hexagonotus*, which exhibited a dorsal scale count of 21, and included them in the syntype series of his new species *Dispadomorphus andamanensis*, now *Boiga andamanensis*. The remaining specimen from Stoliczka's Andaman series reportedly possessed 19 dorsal scale rows, but Wall commented that its description was imperfect and the specimen itself appeared to be lost.

Further, Wall (1909) recognized that the mainland *D. hexagonotus* material he had available appeared to represent two different taxa. Five of the BMNH specimens (BMNH 1946.1.2.60–61, 89.2.25.37–39) from Myanmar, and a further nine specimens he had personally collected, all possessed 19 dorsal scale rows, 221–245 ventrals and 89–107 subcaudals which complied with the description of *D. hexagonotus*, and to which he applied that name, citing Stoliczka's missing Andaman specimen as the holotype. It is curious that he sought to conserve the name “*hexagonotus*”, as *Dipsadomorphus hexagonotus*, by transferring it from Blyth's holotype, now known to be a juvenile *D. cyaneus*, to Stoliczka's missing and incompletely described juvenile. Fortunately, this move is illegal according to the Code (Smith 1943), meaning the name is unavailable and *D. hexagonotus* remains synonymized with *D. cyaneus*. The Myanmar population with 19 dorsal scale rows should therefore be known as *D. ochracea*.

Two further Myanmar specimens available to Wall (BMNH 74.4.19.1193–94) exhibited a dorsal count of 21, which was more akin to that obtained from Himalayan specimens. These two specimens were reportedly collected in Myanmar, well within the range of those specimens attributed by Wall to *D. hexagonotus*. However, they were collected by Beddome, and Wall had already voiced criticism regarding the accuracy of Beddome's record keeping. In the case of these two specimens he suggested that they could have easily come from “the hills to the west or north of Burma, the fauna of which closely agrees with that of the Eastern Himalayas”. Furthermore, Smith (1943) stated that Beddome never visited Burma, and therefore the long-accepted collection locality for these two specimens must be treated as extremely suspect. Similarly, a specimen of “*Boiga ochracea*” donated by Beddome to the Museum of Comparative Zoology (i.e., MCZ R-3886) is said to come from “Madras” [Chennai] at the southeast coast on India. However, the given locality is far outside the distribution limits of this group and our reexamination revealed that this specimen is a *B. stoliczkae* which very likely originated from the eastern Himalayas.

Wall (1909) also examined 39 specimens from the Darjeeling area of West Bengal, India, which exhibited 21 dorsal scale rows, 218–252 ventrals, and 100–119 subcaudals. To this series he added a further three Darjeeling specimens in the British Museum (Natural History). Two of these (BMNH 72.4.17.119, 72.4.17.386) were collected by the British naturalist and physician Thomas Caverhill Jerdon (1811–1872), while the third specimen (BMNH 94.12.31.55) was collected by the British geologist and naturalist William Thomas Blanford (1832–1905). Finding this Eastern Himalayan taxon without a name, Wall (1909) proposed *Dipsadomorphus stoliczkae*, “the first reference of it having been made by Stoliczka”.

Annandale (1909) discussed Wall's (1909) paper on the forms of *Dipsadomorphus*, and criticizes the, in his opinion, difficult delimitation of the species introduced by Wall, particular with regard to *Boiga ceylonensis*, but also to other species of this genus, and considered Wall's new species merely as forms of one species, i.e., of *B. ceylonensis*.

Cope (1860) resurrected the name *Boiga* Fitzinger, 1826 and designated *Coluber irregularis* as type species. In 1902 the Norwegian-American zoologist Leonard Hess Stejneger (1851–1943) described a new species of rear-fanged snake from Taiwan (then Formosa), and in so doing also resurrected the genus *Boiga* Fitzinger, 1826 from obscurity as a senior synonym for *Dipsadomorphus*, the generic name it would replace for the remainder of the 20th Century. The two taxa under discussion here would therefore become *Boiga ochracea* (Theobald, 1868), with 19 dorsal scale rows, from NE India south and east of the Brahmaputra valley across Bangladesh to Myanmar, and *B. stoliczkae* (Wall, 1909), with 21 dorsal scale rows, from the Eastern Himalayas, but including Beddome's two “Burmese” specimens.

From all that we now know and have examined, *B. ochracea* does not occur on the Andaman or Nicobar Islands, that material being referred to *Boiga andamanensis* (Wall, 1909). This assumption is also confirmed by the recent studies of Chandramouli (2022: 321), who removes *B. ochracea* from the list of snake species occurring on the Andaman Islands. It has to be noted that *B. andamanensis* usually has 21 midbody DSR, rarely 19, but in preservation the coloration looks like “*ochracea*”, particular in the red color morph, a possible reason for the confusion.



The next author to take a look at this group of snakes was the British physician and herpetologist Malcolm Arthur Smith (1875–1958). In 1941 he used for the first time the combination *Boiga ochracea walli* (as a *nomen nudum*) and applied this name to populations from the Andaman and Nicobar islands, and Burma. A few years later Smith (1943) synonymized *B. stoliczkae* with *B. ochracea*, stating: “The name *hexagonatus* must become a synonym of *cyanea*, and the next one available is Günther’s *ochracea*. The type has 21 scale rows and is therefore the Himalayan form, and the locality (Pegu) from which it is said to have come is in no doubt an error. Beddome, from whom the specimen came, was never in Burma, and his localities have been shown to be incorrect on many occasions.” Smith (1943) defined his eastern Himalayan *B. ochracea ochracea* as exhibiting 21–21–17 dorsal rows, 223–252 ventrals, and 100–119 subcaudals, and described the populations of *B. ochracea* from “Burma, south of lat. 25°; Tenasserim; the Andaman and Nicobar Islands.”, with 19–19–15 dorsal rows, 221–246 ventrals, and 89–107 subcaudals, as a new subspecies, formally named *B. ochracea walli*. On the BMNH ledger and on the jar labels, the BMNH specimens collected by Leonardo Fea at Bhamo, Myanmar, (i.e., BMNH 89.3.25.37–39) are declared as syntypes. However, this does not constitute a type selection according to the Code and is therefore not a valid syntype designation because it is not following the principles of typification. Smith (1943) did not cite any type material from his *B. ochracea walli* in its original description. Therefore, all specimens available to Smith at the time of the description of *B. ochracea walli* constitute the syntypes, not just the three specimens subsequently labeled as “syntypes” in the BMNH collection. The list of potential syntypes of Smith’s *B. ochracea walli* obviously includes specimens present at BMNH at the time but it is known that Smith travelled in South and Southeast Asia and visited all the main collections there in the preparation of his “Fauna of British India” series, the third, Serpentes, volume of which was ready to go to print in 1938 (delayed until 1943 due to WWII). He examined material from the collections in Bombay, Calcutta, Paris (Smith 1943:v–vi), Vienna (Smith 1928) and Berlin (pers. data FT, he was in contact with Mell and arranged specimen loans with ZMB), and also loans from different US museums and from Leiden and Colombo (Smith 1943). So it cannot be ruled out that specimens from these collections are also putative syntypes of Smith’s *B. o. walli*. Wallach *et al.* (2014) treated *walli* as full species and mentioned that this taxon is based on a single name-bearing type specimen, but they provided no inventory number for that specimen. According to Art. 72.4.1 of the Code (“The type series of a nominal species-group taxon consists of all the specimens included by the author in the new nominal taxon (whether directly or by bibliographic reference) ...”), we suggest that in the case of *B. ochracea walli* at least the following specimens belong to the original syntype series: BMNH 1946.1.2.60–61 from Pegu (at the same time syntypes of *Dipsas ochraceus* Günther), BMNH 89.3.25.37–39 from Bhamo, and specimens from the Andamans and Nicobars, at least from the BMNH collection which were available to Smith.

Smith appears to have made a number of errors that had a considerably impact on the nomenclature and proposed distributions of these taxa. 1) It was Theobald, not Günther, who first described *ochracea* in 1868. 2) The *ochracea* type specimens (plural not singular) were recorded by Günther, as having come from Pegu (=Bago), but Theobald’s syntypes were collected from Rangoon (=Yangon) and Maulmain (=Mawlamyine). Regardless of any confusion over precise localities, the two syntypes described by Theobald and the two other described by Günther were collected in southern Myanmar, not the eastern Himalayas or northern Myanmar. 3) Günther recorded the dorsal scale rows of these two specimens as 19, while Theobald reports 19–17–15 rows, but neither author reported a count of 21 for these specimens. 4) Beddome was responsible for collecting the two specimens reported as from “Burma”, not the two specimens from Pegu, and it is this locality that is now doubted by most authors, and it was these two specimens that exhibited 21 dorsal scale rows at midbody.

Not all authors accepted Smith’s synonymy of *stoliczkae* with *B. ochracea*, i.e., Kramer (1977) who reported that Andrew Stimson (BMNH) had checked the syntypes of Günther’s *D. ochraceus* (BMNH 1946.1.2.60–61) and confirmed their dorsal scale counts as 19, and that they were collected in southern Myanmar and therefore he did not synonymise *stoliczkae* with *ochracea*, but rather recognized it as the eastern Himalayan-northern Burmese subspecies *B. ochracea stoliczkae*. It has to be noted here that all material examined by Kramer and determined by himself as *B. o. stoliczkae* was misidentified. Our re-examination (by FT) revealed that FMNH 131957 is *Boiga multifasciata* and FMNH 152584 is *Boiga trigonata*. Gruber in Schleich & Kästle (2002) recognized all three subspecies: *B. o. ochracea* from Darjeeling, Sikkim, Assam, Bhutan and Bangladesh; *B. o. stoliczkae* from Nepal, and *B. o. walli* as characterized by Smith (1943) from southern Myanmar and the Andaman and Nicobar Islands, but they did not provide any characteristics to distinguish between the three taxa.

Therefore, there appears to be a great deal of confusion over the nomenclature and distribution of the various



populations of *B. ochracea*, largely caused by Smith's misinterpretation of the data and some recent authors (e.g., Das 2010; Wallach *et al.* 2014) largely followed Smith's (1943) erroneous concept of this group.

As a consequence of what is stated above, we consider *Boiga walli* to be a synonym of *B. ochracea*, and we elevate *B. stoliczkae* again to species level, distinct from *B. ochracea*. To summarize the current situation, *Boiga ochracea* should be the taxon with 19-19-15 or 13 dorsal scale rows, cream to beige color without any pattern, from NE India south and east of the Brahmaputra valley across Bangladesh to Myanmar. *Boiga multomaculata* should be the taxon with 19-19-15 or 13 dorsal scale rows and a bold pattern of ocellated dark blotches, definitely known from Myanmar and southern China across Thailand, Laos, Vietnam, and the Sunda Archipelago. *Boiga stoliczkae* should be the taxon with 19 or 21-21-15 or 17 dorsal rows that has been reported from Nepal, northeast India north and west of the Brahmaputra valley, and Bhutan.

In this work, we evaluate the genetic variation in the populations related to *Boiga multomaculata*, *B. ochracea*, and *B. stoliczkae*, respectively, based on the mtDNA markers 16S, ND4, and CYTB as well as the nuclear marker *c-mos*. We also analyze the variation in external morphology of these three taxa. Finally, we designate lectotypes for *Boiga multomaculata*, *B. ochracea walli*, and *B. stoliczkae*, and a neotype for *Boiga ochracea* respectively, and provide redescriptions of the primary types from these taxa.

## Materials and methods

Specimens examined for this study include all available type material of relevant taxa and were either personally collected or received on loan from various museums (see Appendix 1 for specimens examined). Specimens labeled with GK numbers were deposited in the collections of the Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany (SMF) or at East Yangon University Thanlyin, Myanmar (EYU), those with PaPa field numbers deposited at EYU, those with PT field numbers are in the collection of the Chulalongkorn University Museum of Natural History, Bangkok (CUMZ), and those with NK field numbers are in the collection of the Universitas Brawijaya, Indonesia. Other institutional abbreviations used mainly following Sabaj (2020): BMNH (Natural History Museum, London, U.K.), BNHS (Bombay Natural History Society, Mumbai, India), CAS (California Academy of Sciences, San Francisco, USA), CUZ (University of Chittagong, Chittagong, Bangladesh), FMNH (Field Museum of Natural History, Chicago, USA), MCZ (Museum of Comparative Zoology, Harvard University, Cambridge, USA), MNHN (Muséum national d'Histoire naturelle, Paris, France), NHMK (Natural History Museum, Kathmandu, Nepal), NMBA (Naturhistorisches Museum Basel, Switzerland), NME (Naturkundemuseum, Erfurt, Germany), RMNH (Naturalis Biodiversity Center, Leiden, The Netherlands), ZMB (Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany), ZMH (Centrum für Naturkunde (CeNak), Zoologisches Museum, Universität Hamburg, Germany), and ZSIK (National Zoological Collections (NZC) of the Zoological Survey of India (ZSI), Kolkata, India); WIIADR is the acronym for the Wildlife Institute of India, Abhijit Das Reptile Collection.

In evaluating species boundaries within populations, we follow the unified species concept (de Queiroz 2007). For the usage of the subspecies category we apply the Frost & Hillis (1990) concept as modified and discussed by Hillis (2020) and Köhler (2021). As lines of evidence for species and subspecies delimitation, we apply a phenotypic criterion (external morphology) and a criterion for genetic divergence (genetic distinctness of the gene fragments 16S rRNA (16S), NADH dehydrogenase subunit 4 (ND4), and Cytochrome *b* (CYTB)).

Prior to preservation of collected specimens in the field, we took color photographs of each individual in life. We euthanized the snakes with a pericardial injection of T61. We cut tissue samples from the tongue and preserved these in 98% non-denatured ethanol for DNA extraction. The tissue samples were deposited in the collection of SMF. Whenever possible, we everted the hemipenes of male specimens by injecting 70% ethanol into the hemipenial pockets after manually pre-everting the hemipenes. Specimens were then preserved by injecting a solution of 5 mL absolute (i.e., 36%) formalin in 1 L of 96% ethanol into the body cavity, and stored in 70% ethanol. Coordinates and elevation were recorded using a Garmin GPSMAP 64s. All coordinates are in decimal degrees, WGS 1984 datum. The capitalized colors and color codes (the latter in parentheses) are those of Köhler (2012) in the color descriptions. Abbreviations used are ASR (number of dorsal scale rows one head length behind head); IFL (infralabial scales); MBS (number of dorsal scale rows at midbody); PSR (number of dorsal scale rows one head length before cloaca); SPL (supralabial scales); SVL (snout-vent length); TL (tail length). The number of ventral scales was counted according to Dowling (1951a). Dorsal scale row reduction formulae were based on Dowling (1951b). The terminal

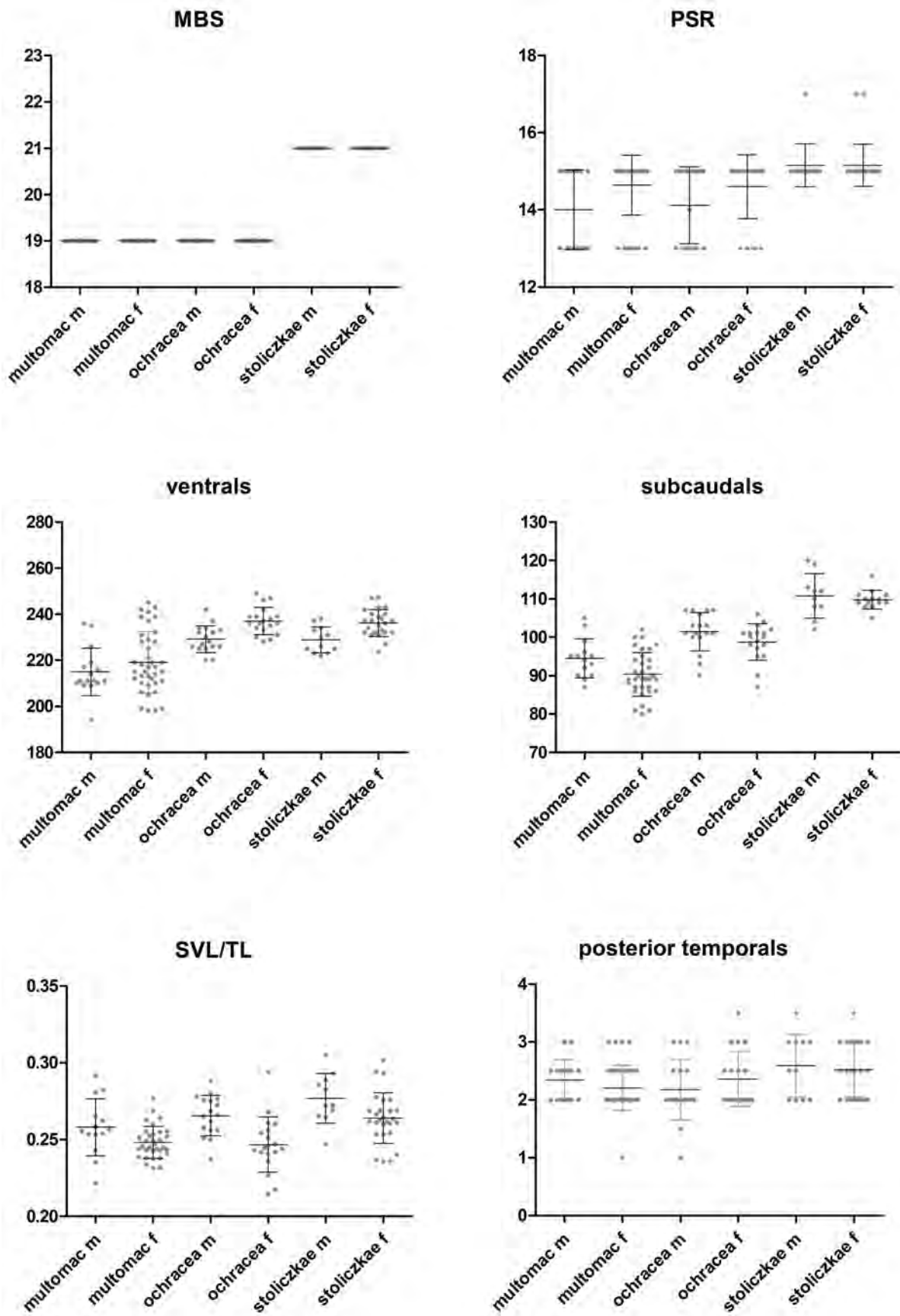
scale was not included in the subcaudal count. Values for symmetric characters are provided in left/right order. Dentition data were analyzed from 49 individuals of the larger *B. multomaculata/ochracea* clade and *B. stoliczkae* and taken either directly from the specimen or were obtained through X-ray computed tomography and visualised.

DNA extraction, PCR, and sequencing were done at SMF for the samples from Myanmar, at Chulalongkorn University for the samples from Thailand, at the Universitas Brawijaya for the sample from Indonesia, and at the Forensic Science Lab of Wildlife Institute of India, Dehradun, India, for the samples from India. See Appendix 2 for the sequences used in this study. We extracted DNA following the protocol of Ivanova *et al.* (2006). To eliminate potential PCR-inhibiting contaminants, the tissue samples were incubated overnight at 4°C in 100 µL 1x PBS buffer before overnight digestion with the vertebrate lysis buffer at 56°C. After extraction, the DNA was eluted in 50 µL TE buffer. We amplified the mitochondrial gene fragments 16S rRNA (16S), NADH dehydrogenase subunit 4 (ND4), Cytochrome *b* (CYTB), as well as the nuclear marker Oocyte maturation factor Mos (*c-mos*) in an Eppendorf Mastercycler® pro using the following protocol: initial denaturation for 1 min at 94°C; followed by 5 cycles with denaturation for 15 s at 94°C, hybridization for 45 s at 45°C and elongation for 1:30 min at 72°C; followed by 30 cycles 15 s at 94°C, 45 s at 48°C and 1 min at 72°C; final elongation for 7 min at 72°C. The reaction mix for each sample contained 1 µL DNA template, 14 µL water, 4 µL 2.5 mM dNTPs (Invitrogen), 2.5 µL PCR-buffer, 1 µL 25 mM MgCl<sub>2</sub>, 0.5 µL (containing 5 units) Taq Polymerase (PeqLab), and 1 µL of each primer. We used the following primers: 16S: forward: L2510, 5'–CGCCTGTTTATCAAAAACAT–3'; reverse: H3056, 5'–CCGGTCTGAACTCAGATCACGT–3'; ND4: forward: 12931L, 5'–CTACCAAAGCTCATGTAGAAGC–3'; reverse: Leu, 5'–CATTACTTTTACTTGGATTTGCACCA–3'; CYTB: forward: H14910 5'–GACCTGTGATMTGAAAACCAAYC–3'; reverse: THRSV2 5'–CTTTGGTTTACAAGAACAATGCT–3'; *c-mos*: forward: 5'–TTTGGTTCKGTCTACAAGGCTAC–3'; reverse: 5'–AGGGAACATCCAAAGTCTCCAAT–3'; all from Eurofins MWG Operon.

We analyzed the mtDNA dataset separate from the *c-mos* one. In all analyses, we used *Telescopus tripolitanus* (BEV 9377) as outgroup (Ganesh *et al.* 2021). For the newly generated sequences in this study and those downloaded from Genbank see Appendix 2. We aligned the sequences with MUSCLE (Edgar 2004) using the default settings in Geneious 6.1.2. (Kearse *et al.* 2012). For software applications, sequence data formatting was converted using the online server Alter (Glez-Peña *et al.* 2010). The best substitution model for each gene was identified using PartitionFinder2 (Lanfear *et al.* 2017), with linked branch lengths via PhyML 3.0 (Guindon *et al.* 2010). Model selection used the corrected (for finite sample size) Akaike Information Criterion (AICc) (Burnham & Anderson 2002). We estimated evolutionary genetic divergence, computing uncorrected pairwise distances with MEGA 7.0.26 (Kumar *et al.* 2016) to assess the degree of intra- and interspecific differences, using a Bootstrap estimation method of 10,000 replications.

We used the IQTree webserver (Trifinopoulos *et al.* 2016) to run a Maximum Likelihood (ML) analysis using 10,000 ultrafast Bootstrap approximation (UFBoot) replicates with 10,000 maximum iterations and minimum correlation coefficient of 0.99 (Minh *et al.* 2013).

Bayesian Inference analyses (BI) used MrBayes 3.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003; Ronquist *et al.* 2012) with five runs and eight chains. The first 25% of trees were discarded as burn-in. MCMC runs used an initial set of 1,000,000 generations with sampling every 500 generations, and adding 500,000 generations until chains reached convergence. Convergence was considered achieved when the standard deviation of split frequencies was 0.015 or less. Additionally, convergence was diagnosed by PRSF (Potential Scale Reduction Factor), which should approach 1.0 as runs converge (Gelman & Rubin 1992). We used FigTree 1.3.1 for tree viewing (<http://tree.bio.ed.ac.uk/software/figtree/>). We designed a species tree based on the three mtDNA gene sequences concatenated, using \*BEAST (Drummond *et al.* 2012) in BEAST 2.4.7 (Ogilvie *et al.* 2017) under 1,000,000 generations for the mcmc model, visualized in DensiTree 2.2.6 (Bouckaert & Heled 2014). We generated the xml file needed for BEAST in the BEAUti application of BEAST 2.4.7. with the following set of parameters: template StarBeast, site model GTR, and clock model strict clock with a clock rate of 1.0. We performed a species delimitation analysis by visualizing barcode gaps in the pairwise distribution of each mtDNA gene separately (excluding the outgroup), using the automatic barcode gap discovery (ABGD) approach (Puillandre *et al.* 2012) through its webserver (<http://www.wabi.snv.jussieu.fr/public/abgd/abgdweb.html>), setting the use of Simple Distance, default values for Prior Intraspecific divergence, except for relative gap width (1.5) which does not work for some Genes, as also noted by Kekkonen *et al.* (2015). Because high values in relative gap width tend to overly split species (Yang *et al.* 2016), we used an intermediate value of 1.0.



**FIGURE 2.** Scatter plots illustrating morphological variation in specimens identified as *B. multomaculata*, *B. ochracea* and *B. stoliczkae*. Abbreviations: multomac = *multomaculata*; m = males; f = females. For abbreviations of morphological characters see text.

**TABLE 2.** Mean genetic distances (in %) of the taxa of *Boiga* based on the 16S dataset. Abbreviations: *ceylon.* = *ceylonensis*; *multo* = *multomaculata*; *quincun.* = *quincunciata*; *siam.* = *siamensis*. Outgroup: *Telescopus tripoltitanus*.

	<i>ceylon.</i>	<i>nuchalis</i>	<i>whitakeri</i>	<i>barnesii</i>	<i>beddomei</i>	<i>multo2</i>	<i>cyanea</i>	<i>drapiezii</i>
<i>ceylon.</i>								
<i>nuchalis</i>	1.4							
<i>whitakeri</i>	0.8	1.0						
<i>barnesii</i>	5.0	4.2	3.9					
<i>beddomei</i>	5.2	3.4	3.7	5.4				
<i>multo3</i>	4.4	2.8	2.4	4.0	5.4			
<i>cyanea</i>	7.2	4.3	4.0	6.6	8.7	6.3		
<i>drapiezii</i>	6.4	4.1	4.2	7.0	6.8	6.2	5.9	
<i>multo2</i>	4.3	2.7	2.3	3.8	5.4	0.6	6.2	6.1
<i>multo1</i>	5.2	3.7	3.8	4.1	5.8	1.8	6.8	6.3
<i>Telescopus</i>	9.1	7.1	6.6	8.6	9.7	8.8	8.1	7.2
<i>nigriceps</i>	6.6	4.7	4.5	7.7	8.9	6.8	5.2	4.5
<i>stoliczkae</i>	4.4	1.9	1.5	5.0	4.8	3.6	7.1	6.6
<i>quincun.</i>	4.3	2.5	1.8	4.5	5.9	1.5	6.8	6.5
<i>siam.</i>	7.0	5.1	4.5	6.5	7.9	6.8	5.5	5.0
<i>trigonata</i>	5.6	3.3	3.2	4.7	6.3	1.1	6.6	6.2

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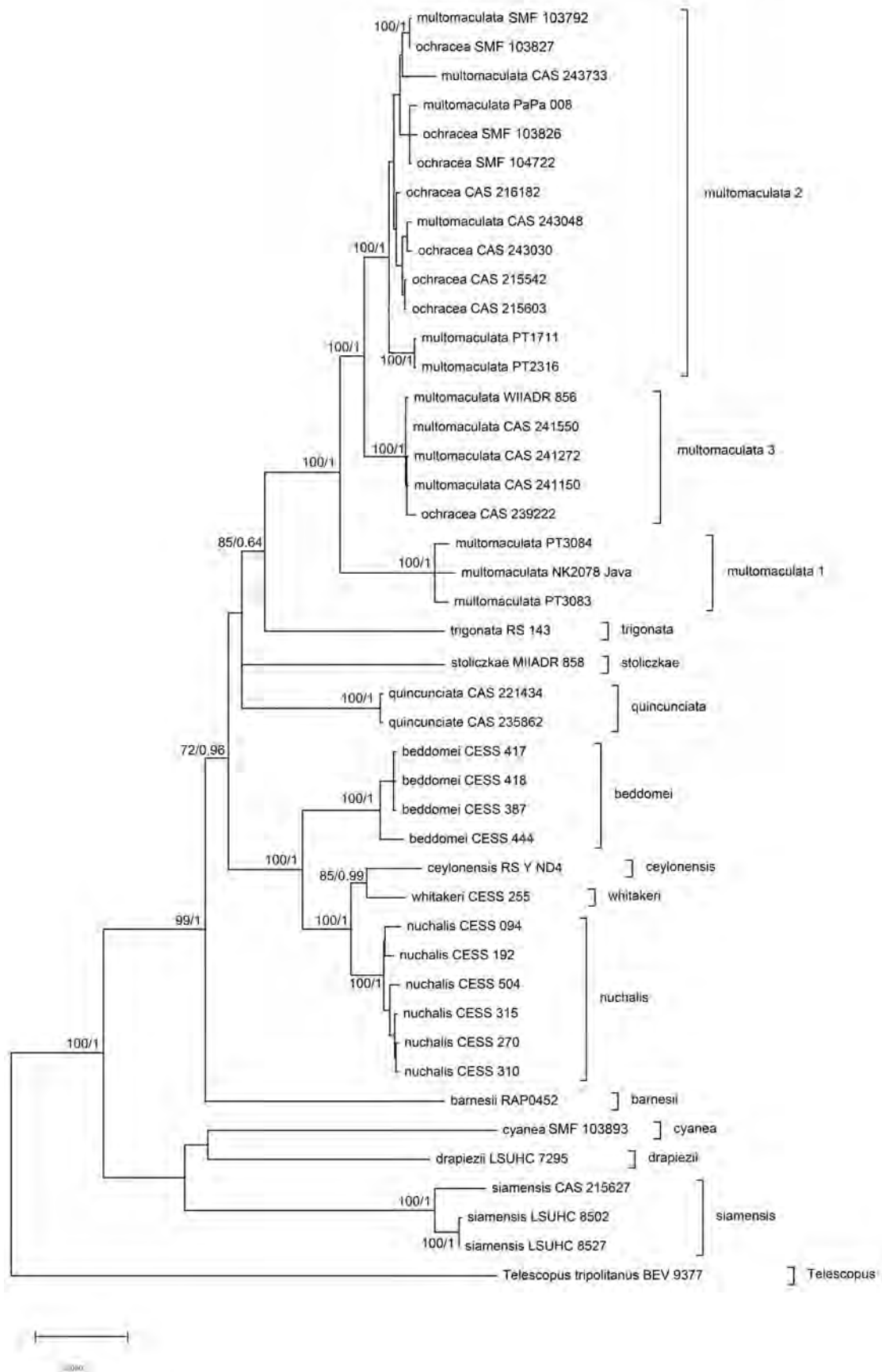


TABLE 2. (Continued)

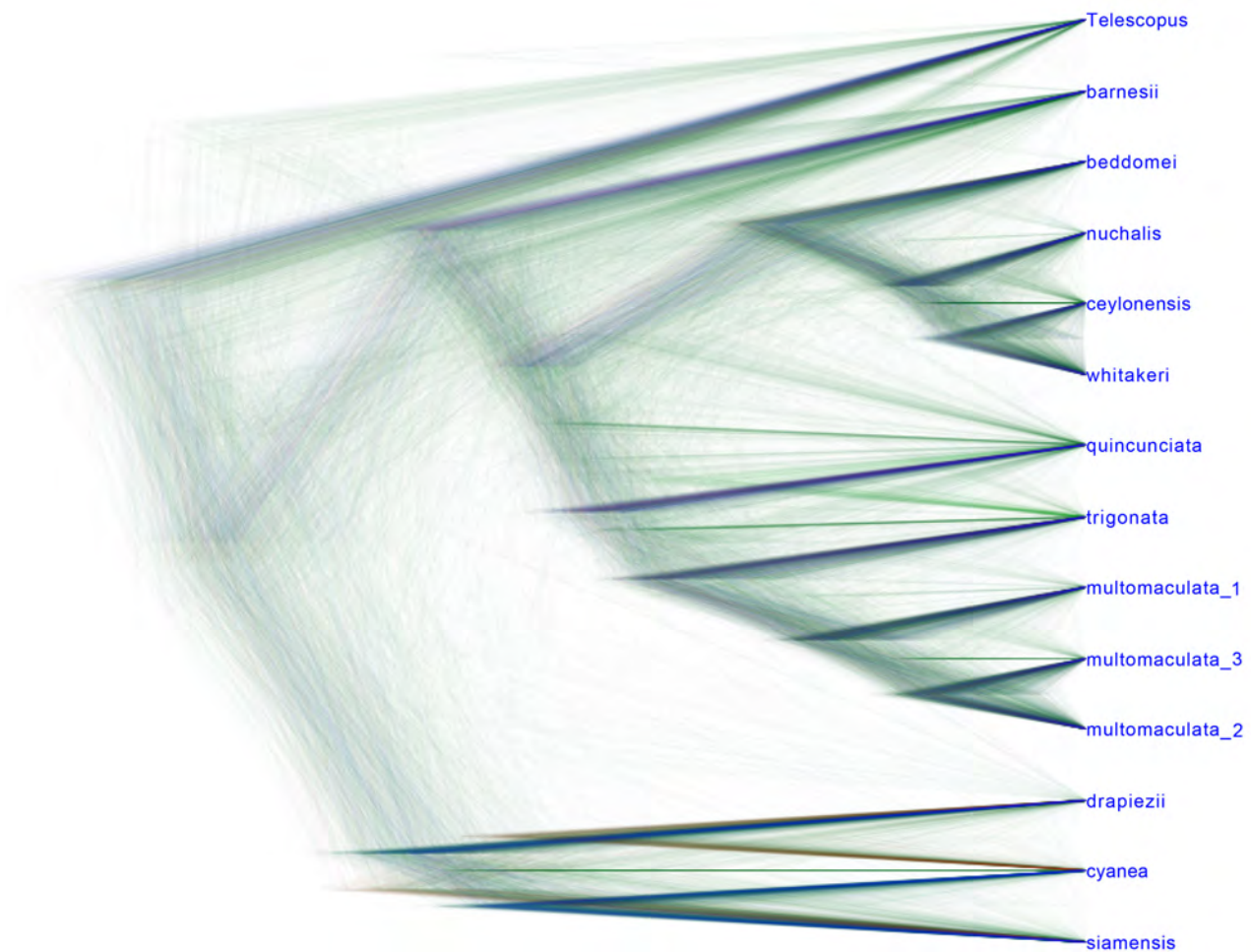
	<i>multo1</i>	<i>multo3</i>	<i>Telescopus</i>	<i>nigriceps</i>	<i>stoliczkae</i>	<i>quincun.</i>	<i>siam.</i>
<i>ceylon.</i>							
<i>muchalis</i>							
<i>whitakeri</i>							
<i>barnesii</i>							
<i>beddomei</i>							
<i>multo3</i>							
<i>cyanea</i>							
<i>drapiezii</i>							
<i>multo2</i>							
<i>multo1</i>	1.7						
<i>Telescopus</i>	8.6	9.6					
<i>nigriceps</i>	6.7	7.3	8.7				
<i>stoliczkae</i>	3.4	4.9	9.1	7.6			
<i>quincun.</i>	2.0	2.9	8.2	7.0	3.6		
<i>siam.</i>	6.7	7.1	7.6	6.1	7.3	6.4	
<i>trigonata</i>	1.5	2.0	8.9	7.4	4.5	2.5	6.6

**TABLE 3.** Mean genetic distances (in %) of the taxa of *Boiga* based on the CYTB dataset. Abbreviations: *ceylon.* = *ceylonensis*; *multo* = *multomaculata*; *quincun.* = *quincunciata*; *siam.* = *stamensis*. Outgroup: *Telescopus tripolitanus*.

	<i>schultzei</i>	<i>ceylon.</i>	<i>barnesii</i>	<i>beddomei</i>	<i>cyanea</i>	<i>drapiezii</i>	<i>multo2</i>	<i>multo1</i>	<i>multo3</i>	<i>michalis</i>	<i>quincun.</i>	<i>siam.</i>	<i>Telescopus</i>	<i>trigonata</i>
<i>schultzei</i>														
<i>ceylon.</i>	16.7													
<i>barnesii</i>	17.2	13.3												
<i>beddomei</i>	17.1	8.5	12.9											
<i>cyanea</i>	15.0	17.5	16.5	16.6										
<i>drapiezii</i>	5.2	17.0	16.2	15.6	14.9									
<i>multo3</i>	15.9	11.5	13.4	10.3	16.1	16.1								
<i>multo2</i>	16.4	12.0	13.6	10.9	16.1	16.0	3.7							
<i>multo1</i>	15.9	12.1	13.6	10.7	15.8	16.7	6.3	6.5						
<i>michalis</i>	17.1	5.6	12.4	7.2	17.1	16.6	11.1	11.2	11.5					
<i>quincun.</i>	15.4	11.5	13.1	11.0	17.3	16.0	10.4	10.9	11.3	10.8				
<i>siam.</i>	15.7	16.5	18.5	15.8	15.0	16.5	15.6	16.3	15.6	16.3	17.7			
<i>Telescopus</i>	20.9	20.5	20.7	19.5	20.4	19.7	18.6	19.0	19.8	18.8	18.7	23.0		
<i>trigonata</i>	17.6	12.4	12.6	11.5	16.6	17.0	11.4	11.4	11.6	10.7	11.7	17.1	19.6	
<i>whitakeri</i>	17.7	4.5	12.5	8.3	17.1	17.4	11.4	11.5	12.0	4.7	11.7	16.9	19.1	11.8



**FIGURE 3.** Phylogenetic tree of *Boiga* species from a maximum-likelihood analysis of three mitochondrial genes (16S, ND4, and CYTB). A scale bar is indicated. The numbers at nodes are bootstrap values (left) and Bayesian posterior probabilities (right), but only bootstrap values higher than 70 are noted. The tree is rooted with the species *Telescopus tripolitanus*.



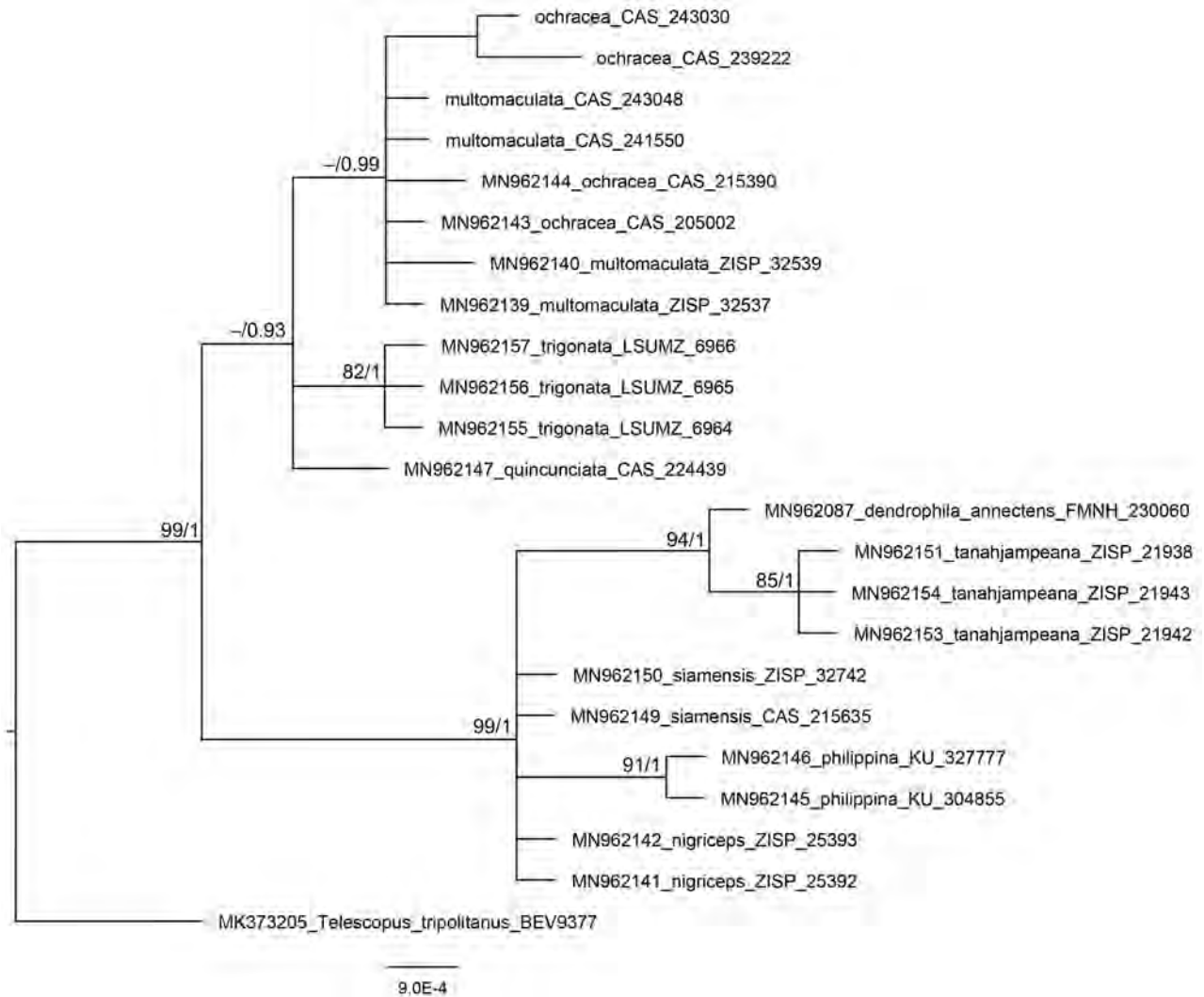
**FIGURE 4.** Species tree inferred with \*BEAST showing density of trees proportional to frequency of occurrence drawn in DensiTree.

## Results

The two color morphs (i.e., blotched versus immaculate color patterns) show completely overlapping ranges in all studied morphological characters (Fig. 2). The final concatenated alignment of 16S, ND4, and *CYTB* was of 2,220 nucleotide positions for 43 *Boiga* samples plus *Telescopus tripolitanus* as an outgroup whereas the c-mos alignment was of 544 nucleotide positions for 22 *Boiga* samples plus the same voucher specimen as outgroup (Appendix 2). Partition schemes were as follows: ND4 (1st codon position GTR+I+G; 2nd and 3rd TVM+I+G; *CYTB* (1st codon position GTR+I+G; 2nd TVM+I+G; and 3rd GTR+G); 16S GTR+I+G. c-mos (1st codon position TRN; 2nd HKY; and 3rd JCG). All trees, both for single markers and for the final concatenated alignment of the mtDNA markers, generated through ML, Bayes, BEAST, and ABGD analyses show a high degree of congruence (Figs. 3, 4 and 5). In all trees, both based on mtDNA and on nuclear DNA markers, the snakes identified as *Boiga multomaculata* and *B. ochracea* form mixed clades. Some of the specimens with a blotched body pattern are virtually identical with unblotched specimens in the analyzed mtDNA sequences. Furthermore representatives of both color morphs had been collected at the same locality (e.g., SMF 103792 and SMF 103827), providing convincing evidence that the blotched versus immaculate color patterns are of no taxonomic or diagnostic value. Rather, these have to be interpreted as intraspecific variation. Therefore, we formally place *Dipsas ochracea* Theobald, 1868 in the synonymy of *Dipsas multomaculatus* Boie, 1827. We here designate BMNH 1946.1.2.60 as the neotype of *Dipsas ochracea* Theobald. Furthermore, we here designate the same specimen, BMNH 1946.1.2.60, as the lectotype of *D. ochraceus* Günther, thereby making these names objective synonyms. However, we did find evidence for genetic divergence



among the populations formerly referred to as *Boiga multomaculata* or *B. ochracea*, with three subclades within the larger *multomaculata/ochracea* clade (Figs. 3 and 4), whereas these clades were not recovered in an analysis based on the nuclear marker c-mos (Fig. 5). However, these three clades do not correlate with the color pattern phenotype but are highly correlated geographically (i.e., are distributed allopatrically; see Fig. 6). In the ABGD analysis, these three subclades are recovered as distinct groups (prior maximal distance  $P = 0.007743$ ; barcode gap distance = 0.030). However, the mean genetic distances among them is rather low: 16S 0.3–1.0%; ND4 3.3–5.8%; CYTB 3.7–6.5% compared to 2.1–4.3% (16S), 8.5–14.9% (ND4), and 11.3–18.6% (CYTB) among most other species of *Boiga* included in our analyses (Tables 2 and 3). Similar low mean genetic distances are found among *B. whitakeri*, *B. ceylonensis* and *B. nuchalis* (16S 0.8–1.4%; ND4 3.3–3.7%; CYTB 4.5–5.6%).



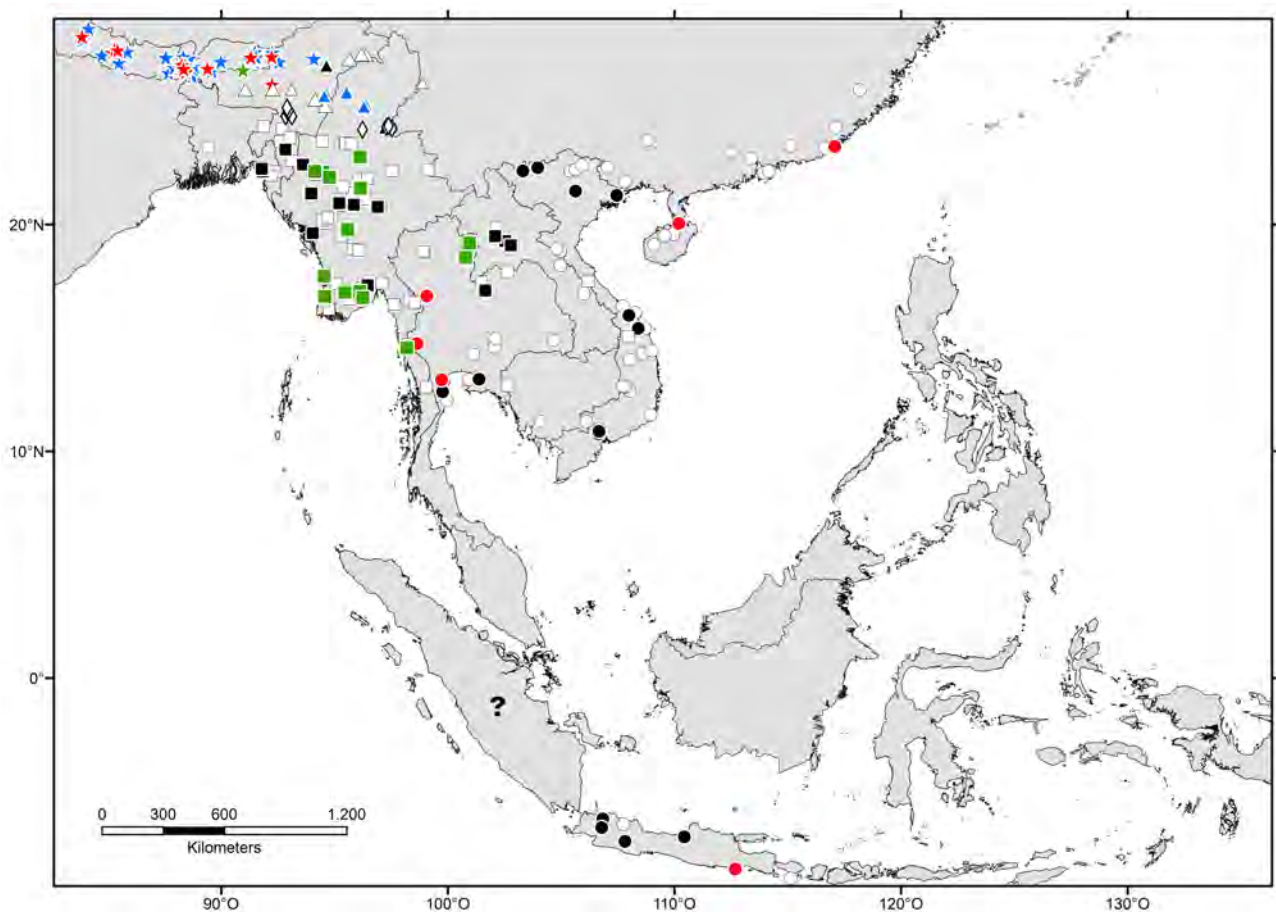
**FIGURE 5.** Phylogenetic tree of *Boiga* species from a maximum-likelihood analysis of the nuclear DNA marker c-mos. A scale bar is indicated. The numbers at nodes are bootstrap values (left) and Bayesian posterior probabilities (right), but only bootstrap values higher than 70 are noted. The tree is rooted with the species *Telescopus tripolitanus*.

In external morphology the ranges of the examined characters mostly broadly overlap among the three subclades within the larger *multomaculata/ochracea* clade. The most pronounced differences are evident in the number of ventral scales (Fig. 7): Clade 1 males 225–242 ( $231.3 \pm 5.42$ ), females 231–258 ( $240.8 \pm 6.63$ ); Clade 2 males 220–234 ( $228.3 \pm 5.06$ ), females 228–239 ( $231.5 \pm 3.74$ ); Clade 3 males 194–236 ( $214.8 \pm 11.39$ ), females 198–242 ( $216.5 \pm 12.13$ ). In the 16S fragment *Boiga stoliczkae* has a genetic distance of 3.4–4.9% from the three *multomaculata/ochracea* clades. Furthermore, the former differs from the snakes in the *multomaculata/ochracea* clades in several characters of external morphology, most pronounced in the number of dorsal scale rows at midbody (consistently 21 in *B. stoliczkae* versus 19 in the specimens of the *multomaculata/ochracea* clades). Furthermore, *B. stoliczkae* tends to have more subcaudal scales in both sexes than *multomaculata/ochracea* (see also Fig. 7).

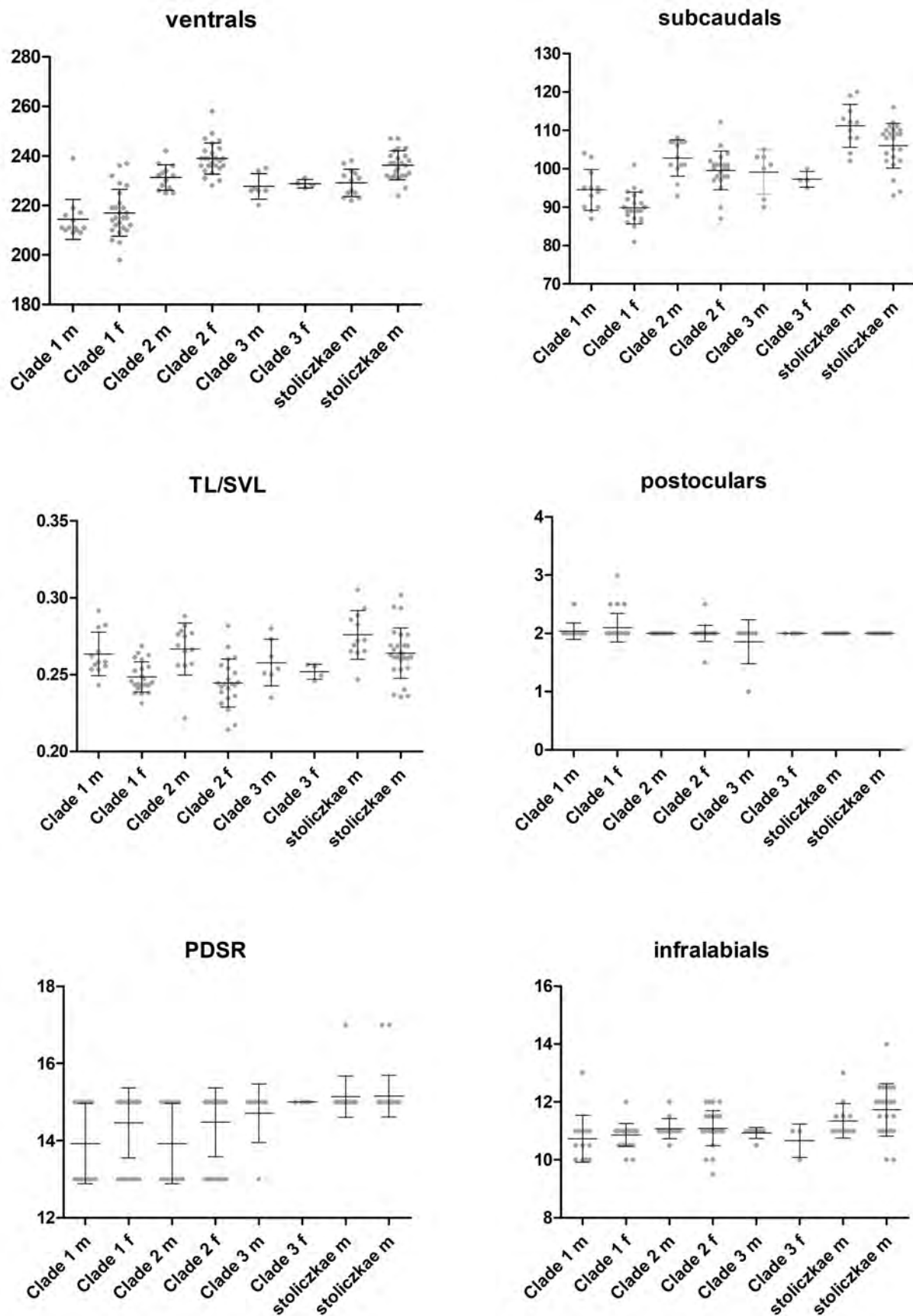
Thus, according to the Frost & Hillis (1990) concept as put into practice by Köhler (2021), we recognize those taxa with low genetic divergence (i.e., pairwise genetic distances <7% in the mtDNA markers ND4 and CYTB) as subspecies (versus mostly well above 10% among most other species of *Boiga* included in our analyses). Thus, we consider the three subclades within the larger *multomaculata/ochracea* clade to represent subspecies level units.

Based on the differences in mtDNA data and external morphology, we recognize *Boiga stoliczkae* as a valid species and formally resurrect it from synonymy with *B. ochracea*.

In order to evaluate the names to be applied to our subclades within the larger *multomaculata/ochracea* clade we need to consider the respective type localities of the available names. Our Clade 1 contains a specimen from the type locality of *B. multomaculata* (Boie 1827), and thus this name applies to Clade 1. Our Clade 2 contains a specimen from the type locality of *B. ochracea* (Theobald 1868b), and we therefore assign Clade 2 to this name. The type locality of *B. ochracea walli* Smith, 1943 (i.e., “Burma, south of lat. 25°; Tenasserim; the Andaman and Nicobar Islands.”) is—except for the islands—mostly within the geographic range represented by the samples of our Clade 2. The northernmost syntypes of *B. ochracea walli* (i.e., BMNH 89.3.25.37–39) originated at Bhamo, Myanmar, which is still south of the genetically verified southernmost sample of our Clade 3. In agreement with Art. 74.7 of the Code, we here designate BMNH 1946.1.2.60 as the lectotype of *Boiga ochracea walli* Smith to introduce a standard of application for the species group name *stoliczkae* Wall by a single name-bearer, thereby making it an objective synonym of *Dipsas ochracea* Theobald and *D. ochraceus* Günther (see above).



**FIGURE 6.** Map showing distributional records of *Boiga* specimens of the three clades recovered in our phylogenetic analyses. Circles = Clade 1 specimens; squares = Clade 2 specimens; triangles = Clade 3 specimens; stars = *B. stoliczkae*; white symbols = records, not genetically confirmed, obtained from GBIF and literature; black symbols = specimens examined for external morphology, not genetically confirmed; red circles = genetically confirmed records of our Clade 1 specimens; green squares = genetically confirmed records of our Clade 2 specimens; blue triangles = genetically confirmed records of our Clade 3 specimens; red stars = *B. stoliczkae*, specimens examined for external morphology, not genetically confirmed; blue stars = *B. stoliczkae*, records, not genetically confirmed, not examined, obtained from GBIF and literature; green star = genetically confirmed record of *B. stoliczkae*; diamonds = specimens of *B. multomaculata* that are not assigned to subspecies because no genetic samples had been analyzed. Each symbol can represent one or more adjacent localities.



**FIGURE 7.** Scatter plots illustrating morphological variation among specimens of the three clades recovered in our phylogenetic analyses. Abbreviations: m = males; f = females. For abbreviations of morphological characters see text.

Two of Mell's (1931) *B. multomaculata* subspecies are within the geographic range represented by the samples of our Clade 1 (i.e., *B. multomaculata hainanensis*, type locality "Hainan" and *B. m. sikiangensis*, type locality "Kwangtung (Hongkong)") and thus remain in the synonymy of *B. multomaculata*. The type locality of Mell's (1931) *B. m. indica* ("continental India") coincides with the area represented by the samples of our Clade 2 and 3 and thus remain in the synonymy of *B. ochracea*. Mell's *indica* has no type material therefore, the assignment to either Clade is not justified by any data and would be completely arbitrarily no matter which clade we would chose. In our opinion, *Boiga multomaculata indica* Mell, 1931 is a *nomen dubium* that cannot be applied to any of the taxa as defined by us. Consequently, there is no name available for our Clade 3 and we describe it as a new subspecies of *Boiga multomaculata* below. As stated above, we consider the three subclades within the larger *multomaculata/ochracea* clade to represent subspecies level units and provide the following synonymies:

***Boiga multomaculata* (Boie, 1827)**

Polymorphic Asian Cat Snake

1827 *Dipsas multomaculata* Boie: 549.

Content: Three subspecies: *Boiga multomaculata multomaculata*, *Boiga multomaculata ochracea*, and a new subspecies (our Clade 3) described below.

***Boiga multomaculata multomaculata* (Boie, 1827)**

Ocellated Asian Cat snake

1931 *B. multomaculata hainanensis* Mell: 213.

1931 *B. multomaculata sikiangensis* Mell: 213.

**Geographic distribution.** As currently known, *B. m. multomaculata* is distributed across Thailand south of 17° N latitude, central and southern Laos, Cambodia, Vietnam, southern China (including Hainan) and on the Indonesian islands of Java, Bali, and probably Sumatra (Zhao & Adler 1993; David & Vogel 1996; Nguyen *et al.* 2009; Das 2010; Chan-ard *et al.* 2015).

There are a number of incorrect listings of this taxon. An erroneous Singapore record goes back to Cantor and led to *B. multomaculata* being listed for West Malaysia, too. The absence of *B. multomaculata* on Malayan Peninsula was already clarified by Smith (1930:63–64). For Sulawesi, Borneo, Singapore (West Malaysia) no reliable records are available or no vouchers are preserved in any collection. However, various authors still listed some of these implausible localities in very recent literature and in databases. David & Vogel (1996) report the presence of *B. multomaculata* on Sumatra but there are no references that provide a reliable record for the taxon from this island. Most probably the inclusion of Sumatra is based on a misinterpretation of a paper from Franz Werner (1900) about a collection from Sumatra purchased by Schneider. This paper includes a table with species that occur on Sumatra set against adjacent regions/islands. In this table *B. multomaculata* is listed, but not for Sumatra! It is possible someone reading the title of Werner's paper and seeing *B. multomaculata* listed, came to the incorrect conclusion that it was present.

**Type material.** The description of *Dipsas multomaculata* is based on an unknown number of specimens. Our research has revealed that specimens from the collections in Leiden and Berlin can be attributed to the original syntype series (see Introduction). In agreement with Art. 74.7 of the Code, we here designate RMNH.RENA 979b (Figs. 8 and 9) as lectotype of *Dipsas multomaculata* Boie, 1827 to introduce a standard of application for the species group name *multomaculata* Boie with a single name-bearer.

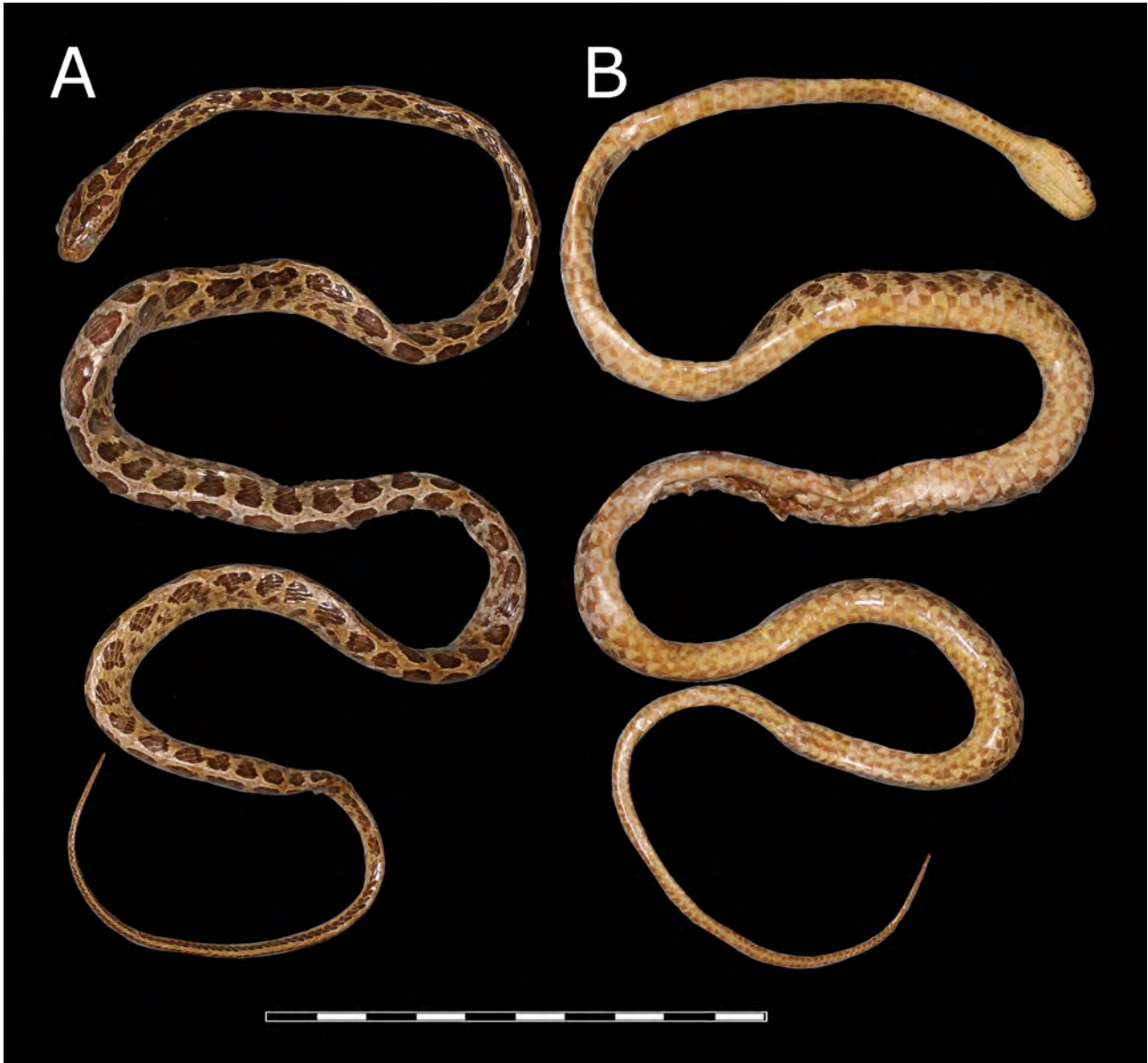
**Lectotype.** RMNH.RENA 979b, an adult female from Java, collector and date of collection not stated in RMNH inventory catalogue.

**Paralectotypes.** RMNH.RENA 979d an adult female, RMNH.RENA 979e a subadult female, RMNH 979f a juvenile female, and ZMB 50879 an adult female, same collecting data as for the lectotype.

**Description of the lectotype.** Adult female, indicated by the absence of hemipenes; 1/1 loreal, wider than high; nasal scale completely divided; 1/1 preocular; 1/1 supraocular; 2/2 postoculars, upper not reaching onto top of head;



2 prefrontals; 2/1 anterior and 2/2 posterior temporals; supralabials 8/8, 3<sup>rd</sup>–5<sup>th</sup> supralabials entering eye; 11/11 infralabials, first four in contact with anterior chin shields; dorsal scales in 19-19-15 rows, smooth with single tiny apical pits on body and single or paired apical pits on dorsocaudal scales; vertebral scale row significantly enlarged; no preventral; 214 ventrals; cloacal plate entire; 89 paired subcaudal scales. Body slender; tail long (TL/SVL 0.243); SVL 592 mm; TL 144 mm, head length measured from tip of snout to posterior border of parietals 14.2 mm, head length measured from tip of snout to posterior edge of mandible 18.8 mm, head width 11.1 mm; diameter eye 3.3 mm; distance anterior border eye to tip of snout 5.2 mm.



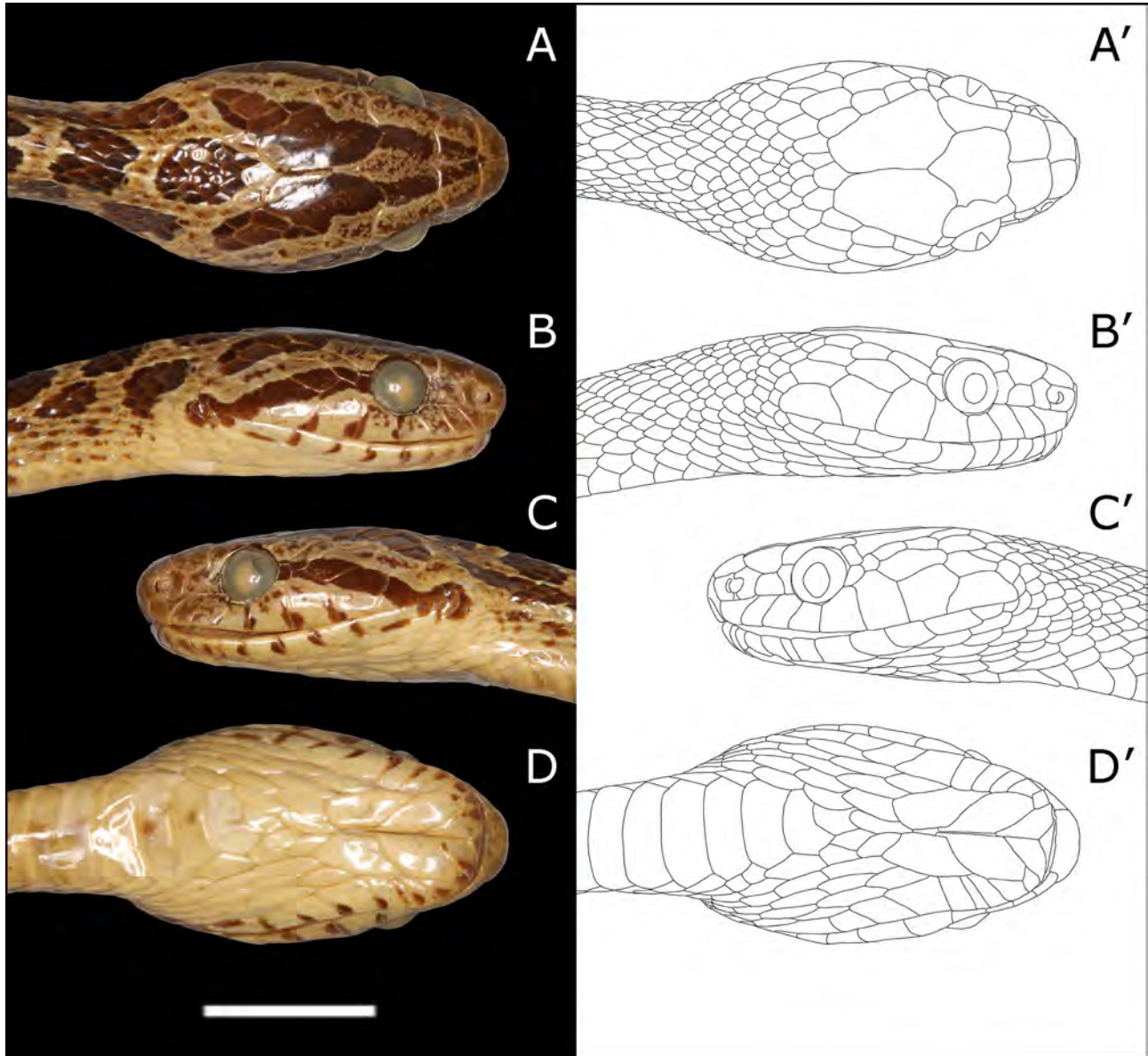
**FIGURE 8.** Lectotype of *Dipsas multomaculata* Boie (RMNH.RENA 979b). A. dorsal view; B. ventral view. See text for details. Scale bar = 10 cm. Photo by FT.

**Dentition.** Maxillary bone with 11/11 prediastemal teeth, followed by a distinct diastema which is 65% longer than the socket of the last prediastemal tooth and followed by two distinctly enlarged, grooved and posteriorly bent postdiastemal teeth. Prediastemal teeth slightly decrease in size posteriorly, the anterior two distinctly posteriorly hooked, the following with less pronounced curvature. On the left side, prediastemal teeth number five, seven, nine, 11, and second postdiastemal loose. On the right side, prediastemal teeth two, four, five, and second postdiastemal tooth loose. Medial to each maxillary tooth is a single replacement tooth at different growth stages.

Palatine bone with 6/6 posteriorly curved teeth, shorter than the prediastemal teeth and slightly decreasing in size posteriorly. Tooth one broken, teeth two, four and six loose on left side. Tooth three broken, teeth two, four and

six loose on the right side. Lateral to each palatine tooth is a single replacement tooth at different growth stages. Pterygoid bone with 12/12 posteriorly curved teeth, shorter than the palatine tooth, gradually decreasing in size posteriorly. Teeth one, three, four, five and 12 loose on left side. Teeth three, four, five and nine loose on right side. The posterior 60% of the pterygoid bone are without teeth.

Mandibular bone with 17/17 posteriorly curved teeth, shorter than maxillary teeth, gradually decreasing in size posteriorly. Medial to each mandibular tooth is a single replacement tooth in different growth stages. Teeth two, four and six loose on left side. Teeth two, four, six, eight and 10 loose on right side.



**FIGURE 9.** Lectotype of *Dipsas multomaculata* Boie (RMNH.RENA 979b). A. dorsal view of head; B. right lateral view of head; C. left lateral view of head; D. ventral view of head. Scale bar = 1 cm. Photos by FT, line drawings by MOS.

Coloration after approximately 200 years preservation in ca. 70% ethanol was recorded as follows: Dorsal ground color Tawny Olive (Color 17) with Natal Brown (49) mottling on scales and with 62 dorsolateral pairs of Sepia (279) colored blotches on body that have a paler (Amber 51 suffused with Smoke Gray 266) center and a white to Pale Buff (1) border; dorsolateral body blotches separated by a Pale Buff (1) vertebral interspace; below the dorsolateral row of blotches an alternating row of smaller, irregularly shaped blotches with the same coloration; dorsal head with same ground color as dorsal body and a V-shaped Sepia (279) marking open towards the neck, starting from the inner posterior edges of the internasals and ending at the level of the last third of the last supralabial; an oval marking on the neck partly inside the bifurcation of the V-shaped element and with the same coloration as



described for the body blotches; a Sepia (279) colored postocular stripe ending at the angle of the mouth; edges of posterior upper labials and edges of infralabials Sepia (279). Venter Cream Color (12) with Tawny Olive (17) colored alternating irregular shaped spots; ventral head Cream Color (12) without prominent markings.

Dorsal scale reduction formula.

5+6(6)	4+5(8)	8+9(142)	2+3(154)	
(5)23 -----	21 -----	19 -----	17 -----	15(214).
4+5(7)	4+5(11)	8+9(145)	2+3(151)	

**Variation.** Paralectotypes and additional examined material agree well with the lectotype in general appearance, morphometrics and scalation (Table 1).

Variation in dentition. Nine to 13 prediastemal teeth followed by a distinct diastema and two enlarged grooved postdiastemal teeth; six to seven palatine, eight to 12 pterygoid, and 17 to 19 dental teeth.

Variation in live coloration and pattern. Only a blotched morph is known (Fig. 10). The dorsal ground color can vary from Pale Neutral Gray (color 296) to True Cinnamon (260), blotches on body Dark Grayish Brown (284) to Sepia (286), edged Smoky White (261) or Cream White (52). Iris may vary, in accordance with the dorsal ground color, from Pale Neutral Gray (color 296) to Medium Neutral Grey (299) or from Orange-Rufous (56) to True Cinnamon (260), with black Sepia (286) pupil. Ventral head and throat Smoky White (261), rest of venter can vary from Pale Neutral Gray (296) to Cream White (52) with small Pale Neutral Grey (296) or Cinnamon (255) spots.



**FIGURE 10.** *Boiga m. multomaculata* from Java in life (NK 2078). Photo by Luhur Septiadi.

**Natural History.** *Boiga m. multomaculata* is arboreal and nocturnal and known to inhabit different forest types, agricultural land and gardens from near sea level up to 1600 m above sea level (a.s.l.), where it is found in bushes, bamboo groves and trees. It is reported to feed on birds and lizards. The reproduction is oviparous with clutch sizes of four to eight eggs. The total length of hatchlings vary from 195 to 200 mm (Mell 1922; Pope 1935; Manthey & Grossmann 1997; McKay 2006; Das 2010; Chan-ard *et al.* 2015). Kopstein (1938) reported *amphigonia retardata* for populations from Java with additional ovipositions of uniquely fertilized females after two and eight months, respectively.

***Boiga multomaculata ochracea* (Theobald, 1868), comb. nov.**

Tawny Asian Cat Snake

1868 *Dipsas ochracea* Theobald: 53.

1868 *Dipsas ochraceus* Günther: 425.

1931 *Boiga multomaculata indica* Mell: 213 [partim].

1943 *Boiga ochracea walli* Smith: 349 [partim].

**Geographic distribution:** Most of Myanmar (except for the northern portion of the country), northeastern India (Mizoram), Bangladesh, Thailand north of 18° N latitude, and northern Laos (own observation; Smith 1943; Whitaker & Captain 2004; Ahmed *et al.* 2009; Das 2010; Hasan *et al.* 2014; Wallach *et al.* 2014; Chan-ard *et al.* 2015; Lalremsanga & Lalronunga 2017; Lalremsanga *et al.* 2018; Hmar *et al.* 2020).

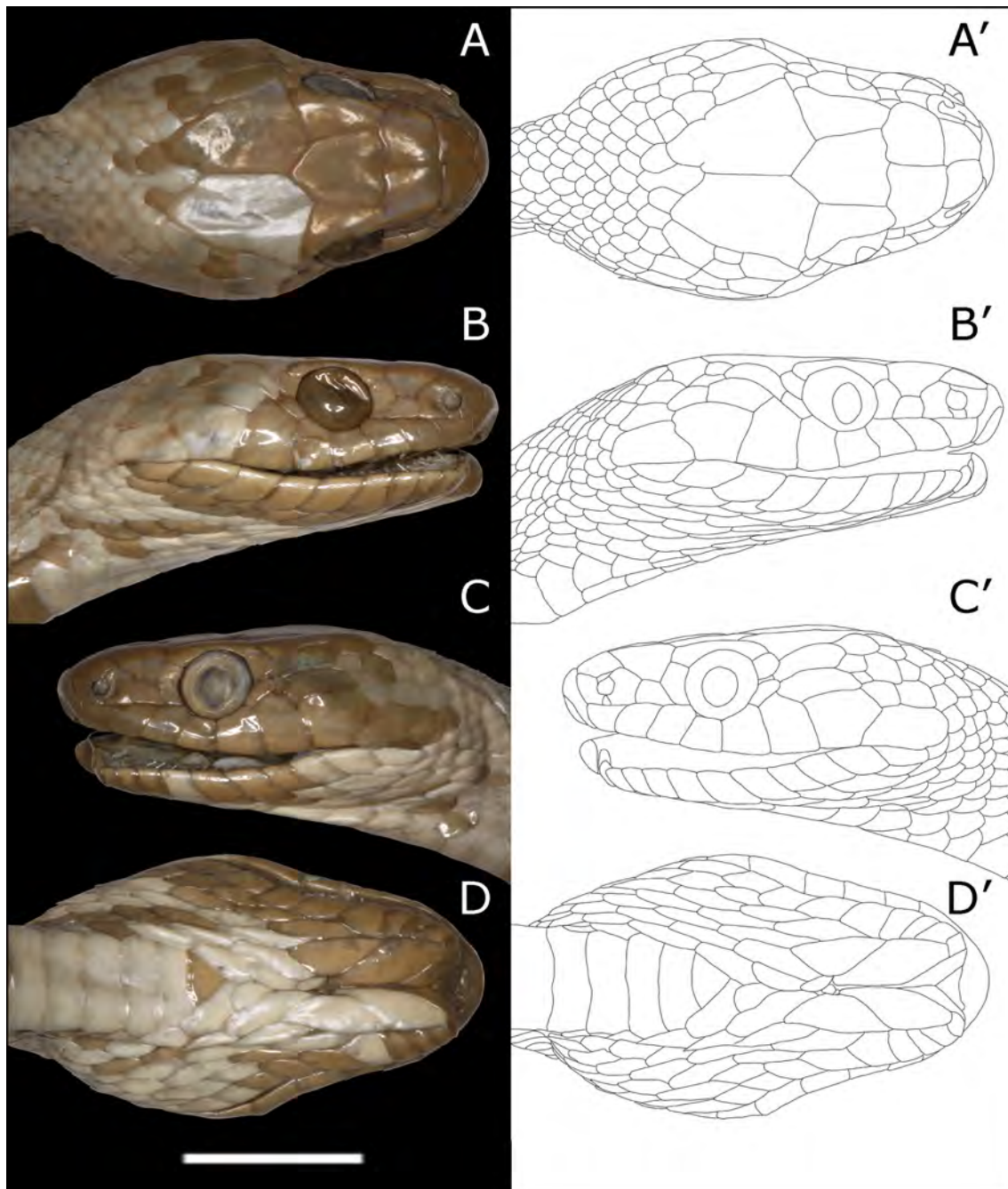
**Type material.** The description of *Dipsas ochracea* is based on two specimens from “Rangoon” and “Maulmain”, but the two syntypes are not located and must be regarded as lost (see Introduction). In agreement with Art. 72.2 and Art. 75 of the Code, we here designate BMNH 1946.1.2.60 (formerly BMNH 68.4.3.16) (Figs. 11 and 12) as neotype of *Dipsas ochracea* Theobald, 1868 to ensure stability and universality by specifying a single name-bearer for this nominal taxon. With the selected specimen, which at the same time represents one of the syntypes of *Dipsas ochraceus* Günther, 1868, we preserve the original connection and exchange between Günther and Theobald with respect to the nearly simultaneous description and naming of an ochraceous colored Asian cat snake taxon from southern Burma. By selection of the neotype and in accordance with Art. 76.3 of the Code, the type locality is “Pegu”, replacing the ‘corrected’ type locality by Wallach *et al.* (2014:106), which includes two different divisions in southern Myanmar.



**FIGURE 11.** Neotype of *Dipsas ochracea* Theobald (BMNH 1946.1.2.60); also, this specimen is the lectotype of *Dipsas ochraceus* Günther and the lectotype of *Boiga ochracea walli* Smith. Dorsal view. See text for details. Scale bar = 10 cm. Photo by FT.

**Neotype.** BMNH 1946.1.2.60 (formerly BMNH 68.4.3.16), an adult female from “Pegu” [Bago, Bago Region, Myanmar, approx. 17.32°N, 96.47°E], collected by William Theobald and donated to the BMNH collection in spring 1868.





**FIGURE 12.** Neotype of *Dipsas ochracea* Theobald (BMNH 1946.1.2.60). A. dorsal view of head; B. right lateral view of head; C. left lateral view of head; D. ventral view of head. Scale bar = 1 cm. Photos by FT, line drawings by MOS.

**Description of the neotype.** Adult female, indicated by the absence of hemipenes; 1/1 loreal, wider than high; nasal scale completely divided; 1/1 preocular; 1/1 supraocular; 2/2 postoculars, upper not reaching onto top of head; 2 prefrontals; 2/2 anterior and 4/3 posterior temporals; supralabials 8/8, 3<sup>rd</sup>–5<sup>th</sup> supralabials entering eye; 12/11 infralabials, first five in contact with anterior chin shields; dorsal scales in 19-19-15 rows, smooth with paired tiny apical pits on body and paired or triple apical pits on dorsocaudal scales; vertebral scale row significantly enlarged; one preventral and 237 ventrals; cloacal plate entire; 98 paired subcaudal scales. Body slender; tail long (TL/SVL 0.239); SVL 889 mm; TL 212 mm; head length measured from tip of snout to posterior border of parietals 18.3 mm, head length measured from tip of snout to posterior edge of mandible 23.8 mm, head width 15.5 mm; diameter eye 4.2 mm; distance anterior border eye to tip of snout 7.3 mm.

**Dentition.** Maxillary bone with 11/10 prediastemal teeth, followed by a distinct diastema which is 68% longer than the socket of the last prediastemal tooth and followed by two distinctly enlarged, grooved and posteriorly bent

postdiastemal teeth. Prediastemal teeth slightly decrease in size posteriorly, the anterior three distinctly posteriorly hooked, the following with less pronounced curvature. On the left side, prediastemal teeth number one, three, five, seven, nine, 11, and second postdiastemal loose. On the right side, prediastemal tooth six broken, teeth one, three, five, and seven and second postdiastemal tooth loose. Medial to each maxillary tooth is a single replacement tooth at different growth stages.

Palatine bone with 6/6 posteriorly curved teeth, shorter than the prediastemal teeth and slightly decreasing in size posteriorly. Second tooth on left side broken. Teeth one, three and five loose on right side. Lateral to each palatine tooth is a single replacement tooth at different growth stages. Pterygoid bone with 10/9 posteriorly curved teeth, shorter than the palatine tooth, gradually decreasing in size posteriorly. Teeth one, three, five, seven and nine loose on left side. Teeth one, three, five, seven and eight loose on right side. The posterior 58% of the pterygoid bone are without teeth.

Mandibular bone with 18/17 posteriorly curved teeth, shorter than maxillary teeth, gradually decreasing in size posteriorly. Medial to each mandibular tooth is a single replacement tooth in different growth stages. Tooth two broken, teeth one, three, four, 15 and 17 loose on left side. Teeth one, three, nine, 12 and 14 loose on right side.

The neotype of *B. m. ochracea* coloration after approximately 150 years preservation in ca. 70% ethanol was recorded as follows: Dorsal ground color of head body and tail with intact “Oberhäutchen” uniform Drab (Color 19), body parts without “Oberhäutchen” uniform Light Lavender (201); interstitial skin Fawn Color (258); venter of head, body and tail same color as described for dorsal body.

Dorsal scale reduction formula.

-	8+9(157)	2+3(160)	-	-	6+V(218)	
(10)19	----- 18	----- 17	----- 16	----- 15	----- 14	----- 13(237).
	2+3(156)	-	-	2+3(163)	7+V(212)	-

**Variation.** Individuals of this subspecies are either blotched or immaculate whereas specimens with an intermediate color pattern have not been reported yet (Fig. 13). For variation in morphometrics and scalation see Table 1.



**FIGURE 13.** *Boiga multomaculata ochracea* in life. A. SMF 104138; B. SMF 103792; C. SMF 103826; D. WIIADR 1156. Photos by GK (A–C), AD (D).

Variation in dentition. Ten to 13 prediastemal teeth followed by a distinct diastema and two enlarged grooved postdiastemal teeth; six palatine, eight to 13 pterygoid, and 15 to 18 dental teeth.

Variation in live coloration and pattern. Two color morphs, blotched and unicolored are known. The blotched morph resembles the color and pattern of brownish individuals of the nominate subspecies. Dorsal ground color of the unicolored morph Pale Cinnamon (Color 55) to Dark Salmon Color (59), interstitial skin Pale Neutral Grey (296), posterior supralabials and infralabials Chamois (84) with Dark Salmon Color (59) edges. Venter of head, body and tail Pale Buff (1). Iris Light Chrome Orange (76) or Dark Salmon Color (59), pupil Sepia (286).

**Natural History.** *Boiga m. ochracea* is mostly arboreal, crepuscular and nocturnal. It is known to inhabit different forest types, parks and gardens and agricultural land like banana plantations in lowlands, mid hills and submontane regions, from around 10 m up to 1884 m a.s.l. It is reported to feed on birds and their eggs, and lizards (our observations; Whitaker & Captain 2004; Mahony *et al.* 2009; Das 2010; Hasan *et al.* 2014).

### ***Boiga multomaculata septentrionalis* ssp. nov.**

Northern Polymorphic Asian Cat Snake

urn:lsid:zoobank.org: act:439A42EE-0B42-4063-B04A-E18B14FA6023

1931 *Boiga multomaculata indica* Mell: 213 [partim].

1943 *Boiga ochracea walli* Smith: 349 [partim].

**Geographic Distribution.** As currently known, *B. m. septentrionalis* is distributed in northern Myanmar (Kachin state and Sagaing Region) and NE India (Assam and Nagaland), but is probably more widespread and based on the documented pattern of geographic distribution we have referred an adult male specimen from southern China (CAS 242550 from Yunnan Province) tentatively to this subspecies, pending genetic confirmation.

**Holotype.** CAS 241272, an adult male from Indawgyi Lake Wildlife Sanctuary (25.30347, 96.35417; 235 m a.s.l.), vicinity Kyang Kyar village, Moenyin Township, Myitkyina District, Kachin State, Myanmar, collected on 20 July 2008 by J.A. Wilkinson, J.V. Vindum, S.L. Oo, K.T. Kyaw, and M. Win. Original field tag MHS 25921.

**Paratypes (3).** CAS 241150, an adult female from Indawgyi Lake Wildlife Sanctuary (25.30347, 96.35417; 235 m a.s.l.), E of Nat Mouk Kan village, Moenyin Township, Myitkyina District, Kachin State, Myanmar, collected on 14 July 2008 by G.O.U. Wogan, J.A. Wilkinson, J.V. Vindum, A.K. Shein. CAS 241550, an adult female from Indawgyi Lake Wildlife Sanctuary (25.17869, 96.29156; 270 m a.s.l.), vicinity of Lwe Mon village, Moenyin Township, Myitkyina District, Kachin State, Myanmar, collected on 26 July 2008 by J.A. Wilkinson, K.T. Kyaw, and J.V. Vindum. SMF 106288 (formerly CAS 239222), an adult male from Linpha village (25,80489, 95,52667; 140 m a.s.l.), Hkanti Township, Hkanti District, Sagaing Region, Myanmar, collected on 10 September 2006 by K.S. Lwin, S.L. Oo, and A.K. Shein.

**Diagnosis.** A subspecies of *Boiga multomaculata* that differs from the other two subspecies (i.e., *B. m. multomaculata* and *B. m. ochracea*) by mean pairwise genetic distances of 3.3–5.8% (ND4) and 3.7–6.5% (CYTB), respectively. It further differs from *B. m. multomaculata* by having on average more ventral scales in both sexes (males 227.7±5.19, females 228.8±1.71 in *B. m. septentrionalis* versus males 214.4±8.06, females 217.1±9.50 in *B. m. multomaculata*), by having on average more subcaudal scales in both sexes (males 99.1±5.82, females 97.3±2.06 in *B. m. septentrionalis* versus males 94.5±5.33, females 89.8±4.13 in *B. m. multomaculata*), and by having both blotched and patternless individuals (versus only blotched specimens in *Boiga m. multomaculata*). It further differs from *B. m. ochracea* by having on average fewer ventral scales in females (228.8±1.71 in *B. m. septentrionalis* versus 238.9±6.30 in *B. m. ochracea*).

**Description of the holotype** (Figs. 14 and 15). Adult male, indicated by fully developed everted hemipenes; 1/1 loreal, wider than high; nasal scale partly divided below the naris; 1/1 preocular; 1/1 supraocular; 2/2 postoculars; 2 prefrontals; 2/2 anterior and 3/2 posterior temporals; supralabials 8/8, 3<sup>rd</sup>–5<sup>th</sup> supralabials entering eye; 11/11 infralabials, first five in contact with anterior chin shields; dorsal scales in 19-19-15 rows, smooth with single or paired apical pits on body and single to triple apical pits on dorsocaudal scales; vertebral scale row distinctly enlarged; two preventrals and 226 ventrals; cloacal plate entire; subcaudal scales 92, paired. Body slender; tail long (TL/SVL 0.235); SVL 578 mm; TL 136 mm; head length measured from tip of snout to posterior edge of mandible 18.1 mm, head width 10.5 mm; diameter eye 3.4 mm; distance anterior border eye to tip of snout 4.9 mm.





**FIGURE 14.** Holotype of *Boiga multomaculata septentrionalis* ssp. nov. (CAS 241272). A. dorsal view; B. ventral view. See text for details. Scale bar = 10 cm. Photos by FT.

**Dentition.** Maxillary bone with 11/11 prediastemal teeth, followed by a distinct diastema which is 40% longer than the socket of the last prediastemal tooth and followed by two distinctly enlarged, grooved and posteriorly bent postdiastemal teeth. Prediastemal teeth slightly decrease in size posteriorly, the anterior three distinctly posteriorly hooked, the following with less pronounced curvature. On the left side, prediastemal teeth number two, four, six, eight and ten, and first postdiastemal loose. On the right side, prediastemal teeth one, three, five, seven and nine, and first postdiastemal tooth loose. Medial to each maxillary tooth is a single replacement tooth at different growth stages.

Palatine bone with 6/6 posteriorly strongly curved teeth, shorter than the prediastemal teeth and slightly decreasing in size posteriorly. Tooth three six loose on left side. Teeth two, four and six loose on the right side. Lateral to each palatine tooth is a single replacement tooth at different growth stages.

Pterygoid bone with 11/12 posteriorly curved teeth, shorter than the palatine tooth, gradually decreasing in size posteriorly. Teeth two, five, seven and 10 loose on left side. Teeth one, three, five, 10 and 12 loose on right side. The posterior 63% of the pterygoid bone are without teeth.

Mandibular bone with 18/17 posteriorly curved teeth, shorter than maxillary teeth, gradually decreasing in size posteriorly. Medial to each mandibular tooth is a single replacement tooth in different growth stages. Teeth one, three, five, seven, nine, 11, 13 and 15 loose on left and right side. Tooth 17 missing on right side.

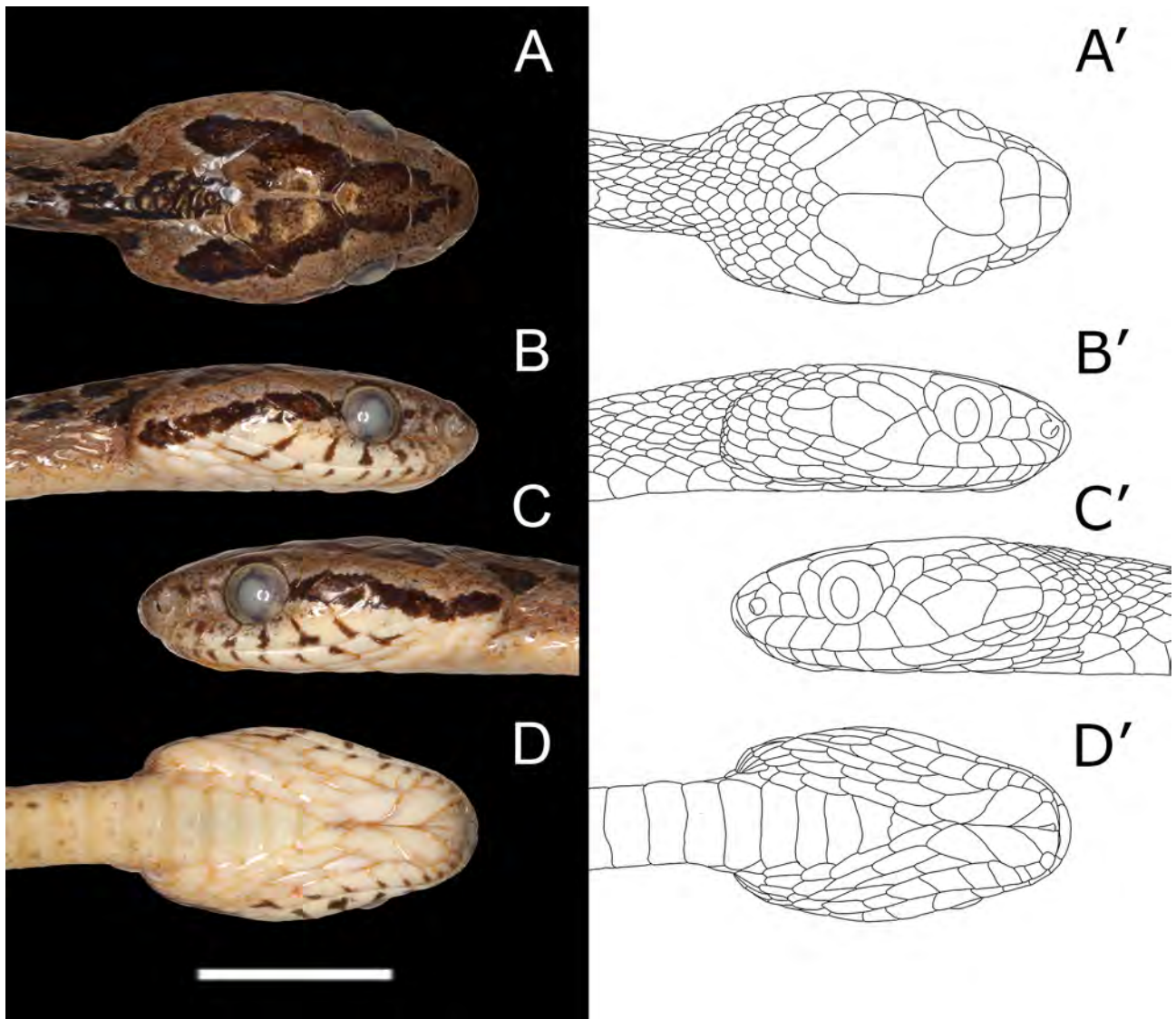
Coloration after about 13 years preservation in 70% ethanol was recorded as follows: Dorsal ground color Smoke Gray (Color 266) with Natal Brown (49) mottling on scales and with 62 Sepia (286) blotches that have a paler (Grayish Olive 274 suffused with Smoke Gray 266) center and a white to Pale Buff (1) border.

Dorsal scale reduction formula.

$$\begin{array}{r}
 4+5(10) \quad -9(150) \quad 2+3(158) \\
 (5)21 \text{ -----} 19 \text{ -----} 17 \text{ -----} 115(226). \\
 4+5(10) \quad -9(152) \quad 3+4(159)
 \end{array}$$

**Variation.** Paratypes agree well with the holotype in general appearance, morphometrics and scalation (Table 1). Most paratypes are blotched as is the holotype. An exception is SMF 106288 (formerly CAS 239222) that has no blotches but exhibits 58 indistinct transverse dark bars composed of dark edges of adjacent dorsal scales.





**FIGURE 15.** Holotype of *Boiga multomaculata septentrionalis* ssp. nov. (CAS 241272). A. dorsal view of head; B. right lateral view of head; C. left lateral view of head; D. ventral view of head. Scale bar = 1 cm. Photos by FT, line drawings by MOS.

Variation in dentition. Ten to 12 prediastemal teeth followed by a distinct diastema and two enlarged grooved postdiastemal teeth; five to six palatine, seven to 12 pterygoid, and 16 to 19 dental teeth.

Variation in live coloration and pattern. Two color morphs, blotched and unicolored are known. The blotched morph resembles the color and pattern of brownish individuals of the nominate subspecies. The unicolored morph (Fig. 16) resembles the unpatterned morph of *B. m. ochracea*.

An intermediate color variation is known from Nagaland, NE India (WII-AD 856), which resembles the ground coloration of the unicolored morph but shows a Raw Umber (280) postocular stripe, faint dark dorsal had pattern similar to that of the nominate subspecies and an irregular strippled Raw Umber (280) pattern forming broken bands along dorsal body and tail.

**Etymology.** The species epithet is formed from the Latin words *septentrio* (= “north”) and the suffix *-alis* (to form an adjective) and refers to the geographic distribution of this taxon. *Boiga m. septentrionalis* has the most northern distribution of the subspecies of *B. multomaculata*.

**Natural History.** The holotype of *B. m. septentrionalis* was collected at 19:30 hrs. in bamboo, about 2 m above ground. The paratypes were all collected at night when *Boiga* is active. At the time of capture, the air temperature was 26.1–28.2°C and the relative air humidity was recorded as 81–96%.



**FIGURE 16.** *Boiga m. septentrionalis* from Nagaland, India, in life (WIIADR 856). Photo by AD.

***Boiga stoliczkae* (Wall, 1909)**

Stoliczka's Asian Cat Snake

1909 [*Dipsadomorphus*] *stoliczkae* Wall: 155.

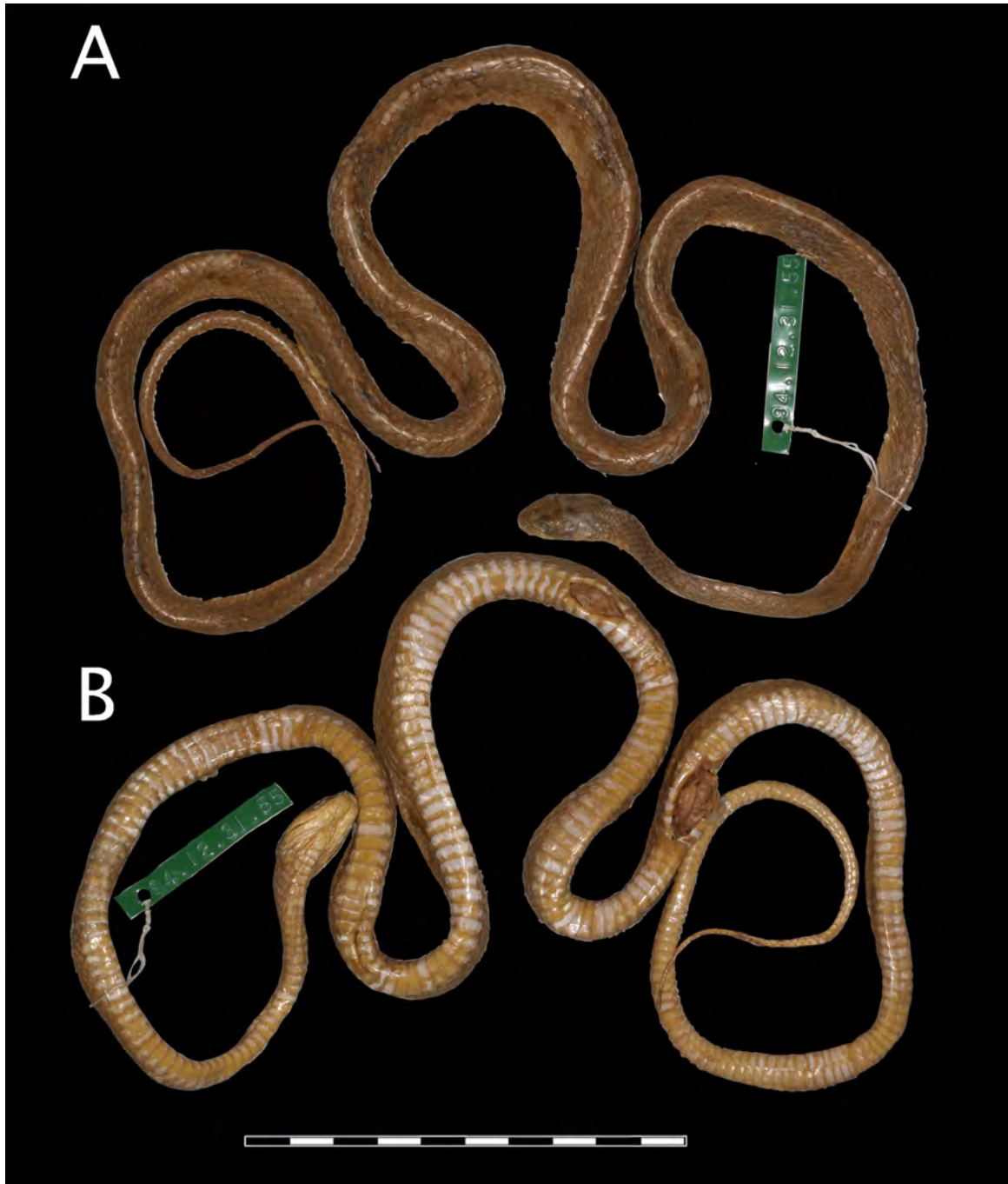
**Geographic distribution.** In the west from central Nepal (ca. 83°51'E) through Darjeeling, Sikkim and Bhutan to Arunachal Pradesh and Assam in northeastern India (north and west of the Brahmaputra valley) (own observation; Wall 1909; Smith 1943; Fleming, JR. & Fleming, SR. 1974; Kramer 1977; Ahmed & Dasgupta 1992; Bauer & Günther 1992; Gruber 2002; Shah & Tiwari 2004; Whitaker & Captain 2004; Sanyal & Gayen 2006; Agarwal *et al.* 2010; Purkayastha 2013; Wallach *et al.* 2014; Das *et al.* 2016; Wangyal & Das 2021).

**Type material.** Wall (1909:155) mentioned that he has examined 39 specimens of this new species from the “neighbourhood of Darjiling” (Darjeeling, West Bengal state, India), which is characterised by having 21 [midbody] scale rows, 218–252 ventrals and 100–119 subcaudals. He did not specify particular specimens by inventory number and with the exception of the British Museum (Natural History) he does not mention any other collection in which the type material could be deposited. However, it is documented through his publications (e.g., Wall 1909; 1921) that he examined for his studies not only his own material but beside specimens from the British Museum also material from various collections in India (e.g., BNHS Mumbai, ZSI Kolkata, and St. Joseph's College in Darjeeling). After his retirement in 1925 he presented parts his own collection, including type specimens, to the British Museum (Natural History) in London (Smith 1951). Based on information provided by Andrew Stimson, Curator of Herpetology at the BMNH, Kramer (1977:735) was the first to mention inventory numbers for the type material of *D. stoliczkae* and regarded a series of eight specimens, i.e., BMNH 72.4.17.119, 72.4.17.386, BMNH 74.4.1193–94, BMNH 94.12.31.55, and 1909.3.13–15 as syntypes. The two specimens mentioned by Wall (1909) and already considered by him as doubtful with respect to the locality “Burma”, refer to BMNH 74.4.1193–1194 and were presented by R.H. Beddome (see also Introduction, and Wall 1908:714 footnote; Wall 1910:791 footnote). All aforementioned specimens are also marked as syntypes in the inventory ledger of the herpetological collection of

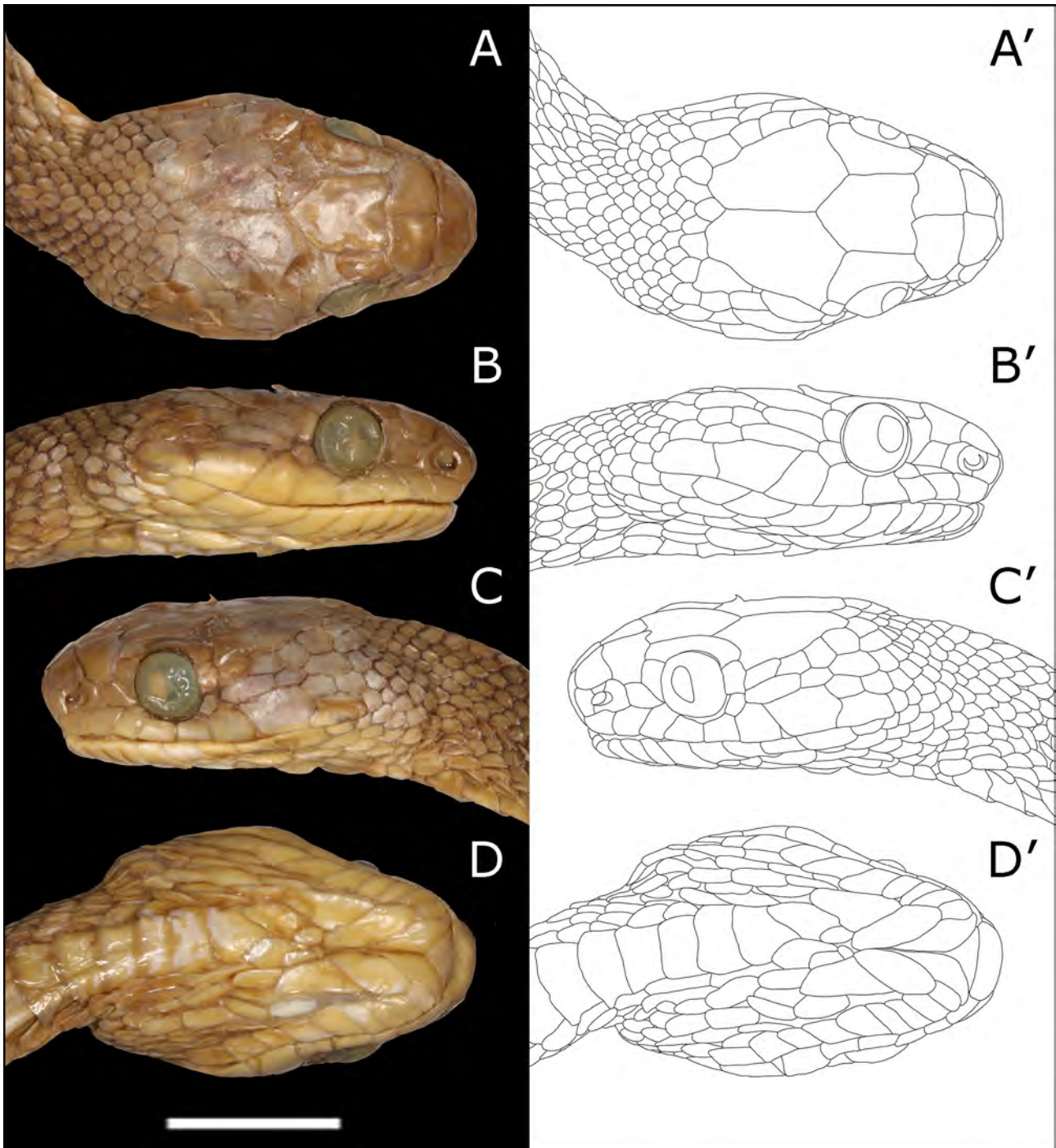


the BMNH, now NHM London. However, some other specimens must also be regarded as part of the original series of *D. stoliczkae*, since they came from “Darjeeling” and were part of Wall’s donation to the collection in London, registered in 1930, viz. BMNH 1930.5.8.648–649, 1930.5.8.650, and 1930.5.5.651. Thus, the material in the NHM London alone represents only a portion of the original specimens examined by Wall. Therefore, we also consider specimens in Indian collections as potential type material of *D. stoliczkae* that could have been available to Wall if the temporal context, locality, and morphological characters are consistent with those in his original description. Putative syntypes that fit Wall’s diagnosis, were collected in the “neighbourhood of Darjiling”, and which were already in the respective collection prior to 1909 include BNHS 1772 from “Tindharia” (~20 km southeast of Darjeeling), and ZSIK 7869, 7873, 7878, 8476 and 11367 all from “Darjeeling”.

In agreement with Art. 74.7 of the Code, we here designate BMNH 94.12.31.55 (Figs. 17 and 18) as lectotype of *Dipsadomorphus stoliczkae* Wall, 1909 to introduce a standard of application for the species group name *stoliczkae* Wall by a single name-bearer.



**FIGURE 17.** Lectotype of *Dipsadomorphus stoliczkae* Wall (BMNH 94.12.31.55). A. dorsal view; B. ventral view. See text for details. Scale bar = 10 cm. Photos by FT.



**FIGURE 18.** Lectotype of *Dipsadomorphus stoliczkae* Wall (BMNH 94.12.31.55). A. dorsal view of head; B. right lateral view of head; C. left lateral view of head; D. ventral view of head. Scale bar = 1 cm. Photos by FT, line drawings by MOS.

**Lectotype.** BMNH 94.12.31.55 (Figs. 17 and 18), an adult male from “Darjeeling” (West Bengal state, India), presented by William Thomas Blanford.

**Paralectotypes.** BMNH 72.4.17.119 and 72.4.17.386, both females from „Darjeeling“, presented by T.C. Jerdon; BMNH 74.4.1193–1194, both females from „Burma“ [in error, most probably from the Eastern Himalayas], presented by R.H. Beddome; BMNH 1909.3.13–15, halfgrown, one female and two with unknown sex; BMNH 1930.5.8.648–649, two skulls, 1930.5.8.650, genitals, and 1930.5.5.651, three vertebrae, all from „Darjeeling“ collected and presented by F. Wall; BNHS 1772, a female from „Tindharia, Darjeeling“, collector unknown; ZSIK 7869, male, 7873, 7878, 8476 and 11367 all females from „Darjeeling“ collected and presented by British botanist George Alexander Gammie (1864–1935).



**Description of the lectotype.** Adult male, indicated by the presence of hemipenes; 1/1 loreal, wider than high; nasal scale completely divided; 1/1 preocular; 1/1 supraocular; 2/2 postoculars, upper not reaching onto top of head; 2 prefrontals; 2/2 anterior and 2/3 posterior temporals; supralabials 8/8, 3<sup>rd</sup>–5<sup>th</sup> supralabials entering eye; 11/11 infralabials, first four in contact with anterior chin shields; 21 dorsal scales in 19-19-15 rows, smooth with single tiny apical pits on body and single or paired apical pits on dorsocaudal scales; vertebral scale row significantly enlarged; no preventral; 235 ventrals; cloacal plate entire; 111 paired subcaudal scales. Body slender; tail long (TL/SVL 0.282); SVL 740 mm; TL 209 mm; head length measured from tip of snout to posterior border of parietals 16.5 mm, head length measured from tip of snout to posterior edge of mandible 21.8 mm, head width 13.0 mm; diameter eye 3.9 mm; distance anterior border eye to tip of snout 5.2 mm.

Maxillary bone with 10/11 prediastemal teeth, followed by a very distinct diastema which is 125% longer than the socket of the last prediastemal tooth and followed by two distinctly enlarged, grooved and posteriorly bent postdiastemal teeth. Prediastemal teeth slightly decrease in size posteriorly, the anterior two distinctly posteriorly hooked, the following with less pronounced curvature. On the left side, prediastemal teeth number one, three, five and seven missing, teeth six and eight broken, tooth nine and first postdiastemal tooth loose. On the right side, prediastemal teeth two, four, six, eight, 10 and first postdiastemal tooth loose. Medial to each maxillary tooth is a single replacement tooth at different growth stages.

Palatine bone with 6/6 posteriorly curved teeth, shorter than the prediastemal teeth and slightly decreasing in size posteriorly. Anterior two teeth missing on left side. Tooth two missing on the right side. Lateral to each palatine tooth is a single replacement tooth at different growth stages.

Pterygoid bone with 10/10 posteriorly curved teeth, shorter than the palatine tooth, gradually decreasing in size posteriorly. Teeth two, four, six and eight loose on left side. Teeth two, four, six, seven and nine loose on right side. The posterior 49% of the pterygoid bone are without teeth.

Mandibular bone with 17/17 posteriorly curved teeth, shorter than maxillary teeth, gradually decreasing in size posteriorly. Medial to each mandibular tooth is a single replacement tooth in different growth stages. Teeth one and two broken, teeth two, four, six, seven, nine, 11, 13 and 15 loose, and tooth 16 missing on left side. Teeth two, four, six, eight and nine loose, teeth 11, 13, and 15 missing on right side.

Coloration after about 130 years preservation in ca. 70% ethanol was recorded as follows: Dorsal ground color Cinnamon-Drab (Color 50) with Sepia (286) interstitial skin; dorsal head with same ground color as dorsal body, upper and lower labials Light Buff (2). Venter of head, body and tail Light Buff (2) without markings.

Dorsal scale reduction formula.

–	10+V(147)	3+4(152)	–	8+V(192)
(10)21	----- 20	----- 19	----- 17	----- 16
	----- 15(235).			
	3+4(142)	–	3+4(152)	8+V(187)
		–		–

**Variation.** Paralectotypes and additional examined material agree well with the lectotype in general appearance, morphometrics and scalation (Table 1).

Variation in dentition. Nine to 14 prediastemal teeth followed by a distinct diastema and two enlarged grooved postdiastemal teeth; five to eight palatine, nine to 15 pterygoid, and 15 to 21 dental teeth.

Variation in live coloration and pattern. Only a unicolored morph is known (Fig. 19). The dorsal ground color may vary from Cinnamon (255) or Cinnamon-Rufous (31) to Tawny (60) in adults or Gem Ruby (65) in young individuals. Rarely a faint Cinnamon Brown (43) streak is running from the posterior border of the eye to the angle of the mouth. In some individuals a small faint banded dorsal body pattern is visible, which is caused by the Medium Neutral Grey (298) interstitial skin. Lower half of supralabials, infralabials, throat and first third of ventral body Pale Buff (1) or Chamois (84), rest of venter and tail Yellow Ocher (14) or Tawny Olive (17). Iris resembling the dorsal ground color of body and can vary from Cinnamon (255) to Gem Ruby (65); pupil Sepia (286).

**Natural History.** *Boiga stoliczkae* is mostly semiariboreal, crepuscular and nocturnal. It is known to inhabit open forest types, agricultural land, human habitations, and gardens, where it is found on low vegetation, bushes and walls. The altitudinal distribution ranges from lowlands, mid hills and submontane regions, from around 85 m up to 2000 m a.s.l. It is reported to feed on birds, their eggs, lizards, snakes (*Trachischium fuscum*), and small rodents (our observations; Shaw *et al.* 1941; Greene 1989; Tillack 1999; Gruber 2002; Jha & Thapa K. 2002; Shah & Tiwari 2004; Nepali & Singh 2020; Pradhan 2021).



**FIGURE 19.** *Boiga stoliczkae* in life. A. WIIAD 858, unsexed specimen from Royal Manas NP, Bhutan; B. ZMB 73660, a female from Naudanda, Kaski, Nepal, 1300 m a.s.l. Photo by AD (A) and FT (B).

## Discussion

The recognition of subspecies has become an unpopular measure among herpetologists during the past 50 years or so, with some researchers completely ignoring subspecies (e.g., Burbrink *et al.* 2000; Manier 2004). This was mostly due to an over-use and abuse of this category during the first half of the 20<sup>th</sup> century with recognizing subspecies based on arbitrary divisions of gradual variation, individual variation, and geographic variation based on single characters as well as for almost every allopatric population. However, recently the species versus subspecies issue has received increased attention (e.g., Hawlitschek *et al.* 2012; Hillis 2020) and we do see merit in the use of the subspecies category for incompletely separated lineages. de Queiroz (2020: 460) suggested „to conceptualize subspecies as incompletely separated species (lineages) within a more inclusive species (lineage).“ Thus, subspecies are subsets of a species and all subspecies together constitute the species, and are distributed allopatrically (Köhler 2021). It has been argued that trinomials should be “used to indicate the nesting of incompletely separated lineages within a more inclusive lineage” (de Queiroz 2020: 461). It has been emphasized that the recognition of subspecies as defined above “requires that any hypothesized subspecies be supported by the same kinds of evidence that would be required to infer that an entity is a species, as well as evidence that its separation from one or more other species is incomplete” (de Queiroz 2020: 461).

As presented in this present study, the evaluation of genetic distance of various mtDNA markers, or even complete mt genomes among the studied organisms, has been used as a proxy for distinguishing between completely and incompletely separated lineages with a low level of mitochondrial divergences interpreted as evidence for incompletely separated lineages (e.g., Hawlitschek *et al.* 2012; Köhler 2021; Kehlmaier *et al.* 2021).

Reproductive isolation by intrinsic isolation mechanisms has been proposed as a property of species level units whereas subspecies differ from other subspecies of the same species but are still capable of interbreeding with them (Mayr 1942; Patten 2010). Thus, subspecies of the same species always exist in allo- or parapatry but by definition never coexist in sympatry.

Patterns in ecological and genetic variation among species and communities have been often attributed to the geographic barriers such as rivers. In case of less vagile species such as amphibians, allopatric occurrence and absence of gene flow across the Red River valley in China and Vietnam was shown in taxa such as *Microhyla fissipes*, *Nanorana yunnanensis*, *Leptobranchium ailaonicum*, and *Ichthyophis bannanicus* (Zhang *et al.* 2010a; Zhang *et al.* 2010b; Wang *et al.* 2015).

The Brahmaputra river is considered a major biogeographic barrier for vertebrates in northeast India (Mani 1974; Ripley & Beehler 1990; Pawar *et al.* 2007; Lehman, S.M. & Fleagle, J.G. 2006; Sengupta *et al.* 2009; Deepak & Karanth 2018). However, whether it is the Brahmaputra River or the Brahmaputra valley that is acting as a barrier, remains to be tested in a phylogenetic framework. Similarly, the role of Brahmaputra as a barrier or faunal filter (*sensu* Das 1996) also needs further research. Das *et al.* (2021) indicated that the Brahmaputra may not be a strong barrier for some semiaquatic snake species such as *Rhabdophis himalayanus* which showed very low genetic

differences among population of both side of the River. In contrast, the present study rather provides evidence that the Brahmaputra might be acting as a barrier for typical Himalayan species such as *Boiga stoliczkae* and widespread Southeast Asian species such as *B. multomaculata* that meets its northwestern distributional limit in northeast India. However, among the material we examined is a single individual of *B. stoliczkae* (ZSIK 8476), supposedly from Goalpara (Assam, India), directly from the south bank of the Brahmaputra. In this area the river is interspersed by many small islands and sandbanks and it cannot be ruled out that this specimen drifted from the north bank of the Brahmaputra to the south, e.g., during high water. The role of the Brahmaputra as a barrier and a prerequisite for allopatric speciation in the region, should be further investigated by intensive sampling in a larger geographic area along the river and extended to several other taxa

It seems possible that the blotched color morph of *Boiga multomaculata* is involved in a mimicry system with the sympatrically distributed *Daboia siamensis* and *D. russelii*, respectively. The similarity in pattern and coloration in the three taxa is astonishing and for a potential visually oriented predator (e.g., a bird) that would avoid such a patterned snake it is not relevant whether it encounters the snake on the ground or in a tree. Müllerian mimicry between Asian cat snakes and vipers in South Asia is discussed by Kroon (1975) between *Boiga trigonata melanocephala* and *Echis carinatus*. However, although a mimicry system seems plausible, *Boiga multomaculata* and *Daboia siamensis*, vs. *D. russelii*, differ in so many ways (e.g., arboreal vs. terrestrial; slender vs. stout; silent vs. noisy) that alternative hypotheses need to be considered. The large-spotted dorsal pattern might simply function as a disruptive patterning whereas the unicolor morph may benefit from being better camouflaged. If clutches of eggs contain hatchlings demonstrating both color patterns it might improve the chances for survival of one or the other pattern in any given habitat type.

Not all subspecies of *B. multomaculata* exhibit polymorphism, the nominate form only appearing in the blotched livery while *B. m. ochracea* and *B. m. septentrionalis* both exhibit non-sexual, non-ontogenetic dichromatism. There would seem to be a trend with the eastern and southern populations (*B. m. multomaculata*: southern China [including Hainan], Thailand, Laos, Vietnam, Cambodia, Indonesia [Sunda Islands]) exhibiting only the grey blotched livery; the western and northern forms (*B. m. ochracea*: northern Thailand, northern Laos, Myanmar, Bangladesh and northeastern India [Mizoram], and *B. m. septentrionalis* (northeastern India [Assam, Nagaland], peninsular India and possible southwestern China [Yunnan]) are represented by specimens with both patterns, whereas the extreme western populations of *B. m. ochracea* (Bangladesh and northeastern India [Mizoram]) as well as all known populations of *B. stoliczkae* appear to exhibit the immaculate ocher phenotype (see also Fig. 1). Individuals that show an intermediate color pattern are mostly unknown. See Fig. 16 for a specimen of *B. m. septentrionalis* that exhibits a kind of intermediate color pattern having transverse series of dark dashes on a cream-colored background.

Such polymorphism is also seen in the highly arboreal Neotropical boid genus *Corallus*, especially in Caribbean *C. grenadensis* and Amazonian *C. hortulanus* (Henderson 2015; MOS pers. obs.) which not only exhibit color patterns similar to those observed in the *B. multomaculata* group, but other patterns comprised of reds or greens that do not occur in these cat snakes. This may be a case of convergence based on some benefits received by polymorphic *Boiga* or *Corallus*. However, the absence of *Daboia* from the Neotropics does not fully undermine the mimicry argument since *Corallus hortulanus* exists in sympatry with a number of stocky-bodied, terrestrial *Bothrops*, with patterning similar to the blotched morph, and also the arboreal pitviper, *Bothrops taeniatus*, which exhibits a similar patterning.

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## References

- Agarwal, I., Mistry, V.K. & Athreya, R. (2010) A preliminary checklist of the reptiles of Eaglenest Wildlife Sanctuary, West Kameng District, Arunachal Pradesh, India. *Russian Journal of Herpetology*, 17, 81–93.
- Ahmed, M.F., Das, A. & Dutta S.K. (2009) *Amphibians and Reptiles of Northeast India. A photographic Guide*. Aaranyak, Guwahati, India.
- Ahmed, S. & Dasgupta, G. (1992) Reptilia. In: Gosh, A.K. (Ed.), *Zoological Survey of India, State Fauna Series 3, Fauna of West Bengal. Part 2*, Calcutta, pp. 1–65.
- Annandale, N. (1909) Major Wall on some forms of *Dipsadomorphus*. *Records of the Indian Museum*, 3, 281–282.  
<https://doi.org/10.26515/rzsi/v3/i3/1909/163284>
- Bauer, A.M. & Günther, R. (1992) A preliminary report on the reptile fauna of the Kingdom of Bhutan with the description of a new species of scincid lizard. *Asian Herpetological Research*, 4, 23–36.  
<https://doi.org/10.5962/bhl.part.6178>
- Boie, F. (1827) Bemerkungen über Merrem's Versuch eines Systems der Amphibien. Marburg, 1820 1te Lieferung, Ophidier. *Isis von Oken, Jena*, 20, 508–566.
- Boie, H. (1823–1825) *Erpétologie de Java*. (unpublished manuscript deposited in Naturalis, Leiden, the Netherlands, snake section contains 30 pages).
- Bouckaert, R. & Heled, J. (2014) *DensiTree 2: Seeing trees through the forest*.  
<https://doi.org/10.1101/012401>
- Boulenger, G.A. (1890) *The Fauna of British India, including Ceylon and Burma. Reptilia and Batrachia*. Taylor and Francis, London, United Kingdom, xviii+541.  
<https://doi.org/10.5962/bhl.title.100797>
- Boulenger, G.A. (1896) *Catalogue of the Snakes in the British Museum (Natural History). Vol.III*. Trustees of the British Museum (Natural History), London, United Kingdom, xiv+727.
- Bourret, R. (1936) Les Serpents de l'Indochine. *Imprimerie Henri Basuyau & Cie., Toulouse*.
- Burbrink, F.T., Lawson, R. & Slowinski, J.B. (2000) Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): a critique of the subspecies concept. *Evolution*, 54, 2107–2118.



<https://doi.org/10.1111/j.0014-3820.2000.tb01253.x>

- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach*. Springer-Verlag New York Inc, New York, NY.
- Chan-ard, T., Parr, J. & Nabhitabhata, J. (2015) *A field guide to the reptiles of Thailand*. Oxford University Press, Oxford, New York, xxix+314.
- Chandramouli, R.S. (2022) Snake fauna of the Andaman Islands, Bay of Bengal - A review of species richness, taxonomy, distribution, natural history and conservation status. *Zootaxa*, 5209 (3), 301–331.  
<https://doi.org/10.11646/zootaxa.5209.3.1>
- Cope, E.D. (1860) Catalogue of the Colubridae in the Museum of the Academy of Natural Sciences of Philadelphia, with notes and descriptions of new species. Part 2. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 12, 241–266.
- Das, A., Sharma, P., Surendran, H., Nath, A., Gosh, S., Dutta, D., Mondol, J. & Wangdi, Y. (2016) Additions to the herpetofauna of Royal Manas National Park, Bhutan, with six new country records. *Herpetology Notes*, 9, 261–278.
- Das, A., Smith, E.N., Sidik, I., Sarker, G.C., Boruah, B., Patel, N., Murthy, B. H. C. K. & Deepak, V. (2021) Hidden in the plain sight: a new species of *Rhabdophis* (Serpentes: Natricinae) from the *Rhabdophis himalayanus* complex. *Zootaxa*, 5020 (3), 401–433.  
<https://doi.org/10.11646/zootaxa.5020.3.1>
- Das, I. (1996) *Biogeography of the reptiles of South Asia*. Krieger Publishing Co, Malabar FL, vii + 87.
- Das, I. (2010) *A field guide to the reptiles of South-East Asia*. New Holland Publishers (UK) Ltd., London, 376 pp.
- Das, I., Dattagupta, B. & Gayen, N.C. (1998) History and catalogue of reptile types in the collection of the Zoological Survey of India. *Journal of South Asian Natural History*, 3, 121–172.
- David, P. & Vogel, G. (1996) *The Snakes of Sumatra: An Annotated Checklist and Key with Natural History Notes*. Eidtion Chimaira, Frankfurt, 259 pp.
- Deepak, V. & Karanth, P. (2018) Aridification driven diversification of fan-throated lizards from the Indian subcontinent. *Molecular phylogenetics and evolution*, 120, 53–62.  
<https://doi.org/10.1016/j.ympev.2017.11.016>
- de Queiroz, K. (2007) Species concepts and species delimitation. *Systematic biology*, 56, 879–886.  
<https://doi.org/10.1080/10635150701701083>
- de Queiroz, K. (2020) An updated concept of subspecies resolves a dispute about the taxonomy of incompletely separated lineages. *Herpetological Review*, 51, 459–461.
- Dowling, H.G. (1951a) A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology*, 1, 5, 97–99.
- Dowling, H.G. (1951b) A proposed method of expressing scale reductions in snakes. *Copeia* 1951, 2, 131–134.
- Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, 29, 1969–1973.  
<https://doi.org/10.1093/molbev/mss075>
- Duméril, A., Bibron, G. & Duméril, A. (1854a) *Erpétologie Générale on Histoire Naturelle Complète des Reptiles. Tome 7*. Roret/Fain et Thunot, Paris, xvi + 780.  
<https://doi.org/10.5962/bhl.title.118797>
- Duméril, A., Bibron, G. & Duméril, A. (1854b) *Erpétologie Générale on Histoire Naturelle Complète des Reptiles. Tome 9*. Roret/Fain et Thunot, Paris.  
<https://doi.org/10.5962/bhl.title.118797>
- Edgar, R.C. (2004) MUSCLE: a multiple sequence alignment method with reduced time and space complexity. *BMC bioinformatics*, 5, 1–19.  
<https://doi.org/10.1186/1471-2105-5-113>
- Evenhuis, N.L. (2003) Publication and dating of the journals forming the Annals and Magazine of Natural History and the Journal of Natural History. *Zootaxa*, 385, 1–68.  
<https://doi.org/10.11646/zootaxa.385.1.1>
- Fitzinger, L.I. (1826) *Neue Classification der Reptilien nach ihren Natürlichen Verwandtschaften. Nebst einer Verwandtschafts-Tafel und einem Verzeichnisse der Reptilien-Sammlung des K. K. Zoologischen Museum's zu Wien*. J.G. Heubner, Wien, 66 pp.  
<https://doi.org/10.5962/bhl.title.4683>
- Fleming, R.L., JR. & Fleming, R.L., SR. (1974) Some snakes of Nepal. *Journal of the Bombay Natural History Society*, 70, 426–437.
- Frost, D.R. & Hillis, D.M. (1990) Species in concept and practice: Herpetological applications. *Herpetologica*, 46, 87–104.
- Ganesh, S.R., Achyuthan, N.S., Chandramouli, S.R. & Vogel, G. (2020) Taxonomic revision of the *Boiga ceylonensis* group (Serpentes: Colubridae): re-examination of type specimens, redefinition of nominate taxa and an updated key. *Zootaxa*, 4779 (3), 301–322.  
<https://doi.org/10.11646/zootaxa.4779.3.1>
- Ganesh, S.R., Mallik, A.K., Achyuthan, N.S., Shanker, K. & Vogel, G. (2021) A new species of *Boiga* (Serpentes: Colubridae) from the Southern Western Ghats of India with a molecular phylogeny and expanded characterisation of related species. *Zootaxa*, 4981 (3), 449–468.

<https://doi.org/10.11646/zootaxa.4981.3.2>

- Gelman, A. & Rubin, D.B. (1992) Inference from iterative simulation using multiple sequences. *Statistical Science*, 7, 457–472.  
<https://doi.org/10.1214/ss/1177011136>
- Giri, V.B., Deepak, V., Captain, A., Pawar, S. & Tillack, F. (2019) A new species of *Boiga* Fitzinger, 1826 (Serpentes: Colubridae) from the northern Western Ghats of India. *Journal of Bombay Natural History Society*, 116, 71–81.
- Glez-Peña, D., Gómez-Blanco, D., Reboiro-Jato, M., Fdez-Riverola, F. & Posada, D. (2010) ALTER: program-oriented conversion of DNA and protein alignments. *Nucleic Acids Research*, 38, 14–18.  
<https://doi.org/10.1093/nar/gkq321>
- Greene, H.W. (1989) Ecological, evolutionary, and conservation implications of feeding biology in old world cat snakes, genus *Boiga* (Colubridae). *Proceedings of the California Academy of Science*, 46, 193–207.
- Gruber, U. (2002) Family Colubridae (colubrid snakes). In: Schleich, H.H. & Kästle, W. (Eds.). *Amphibians and Reptiles of Nepal*. A.R.G. Gantner Verlag, Ruggell, pp. 803–950.
- Guindon, S., Dufayard, J.-F., Lefort, V., Anisimova, M., Hordijk, W. & Gascuel, O. (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic biology*, 59, 307–321.  
<https://doi.org/10.1093/sysbio/syq010>
- Günther, A. (1868) Sixth account of new species of snakes in the British Museum. *Annals and Magazine of Natural History*, (4) 1, 425.  
<https://doi.org/10.1080/00222936808695725>
- Hasan, M., Islam, M.M., Kuramoto, M., Kurabayashi, A. & Sumida, M. (2014) Description of two new species of *Microhylla* (Anura: Microhylidae) from Bangladesh. *Zootaxa*, 3755 (5), 401–418.  
<https://doi.org/10.11646/zootaxa.3755.5.1>
- Hawlitshchek, O., Nagy, Z.T. & Glaw, F. (2012) Island evolution and systematic revision of Comoran snakes: why and when subspecies still make sense. *PLoS ONE*, 7, e42970.  
<https://doi.org/10.1371/journal.pone.0042970>
- Henderson, R.W. (2015) *Natural History of Neotropical Treeboas (genus Corallus)*. Edition Chimaira, Frankfurt, 338 pp.
- Hillis, D.M. (2020) The detection and naming of geographic variation within species. *Herpetological Review*, 51, 52–56.
- Hmar, G.Z., Muansanga, L., Biakzuala, L., Lalrinsanga, R. & Lalremsanga, H.T. (2020) Inventory survey on the ophidian fauna of Reiek Community Reserved Forest, Mamit district, Mizoram, India. *Journal of Environmental Biology*, 41, 821–826.  
[https://doi.org/10.22438/jeb/41/4\(SI\)/MS\\_1906](https://doi.org/10.22438/jeb/41/4(SI)/MS_1906)
- Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* (Oxford, England), 17, 754–755.  
<https://doi.org/10.1093/bioinformatics/17.8.754>
- ICZN (1999) International Code of Zoological Nomenclature. Available from <http://www.nhm.ac.uk/hosted-sites/iczn/code>.
- ICZN (2012) Amendment of Articles 8, 9, 10, 21 and 78 of the International Code of Zoological Nomenclature to expand and refine methods of publication. *ZooKeys*, 219, 1–10.  
<https://doi.org/10.3897/zookeys.219.3994>
- Iskandar, D.T. & Colijn, E. (2002) *A checklist of Southeast Asian and New Guinean reptiles I. Serpentes*. Biodiversity Conservation Project, Indonesian Institute of Sciences, Bandung.
- Ivanova, N.V., Waard, J. de & Hebert, P.D. (2006) An inexpensive, automation-friendly protocol for recovering high-quality DNA. *Molecular Ecology Notes*, 6, 998–1002.  
<https://doi.org/10.1111/j.1471-8286.2006.01428.x>
- Jha, A. & Thapa K. (2002) *Reptiles and Amphibians of Sikkim*. Mrs. S. Jha Publ, Raipur.
- Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P. & Drummond, A. (2012) Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, 28, 1647–1649.  
<https://doi.org/10.1093/bioinformatics/bts199>
- Kehlmaier, C., Albury, N.A., Steadman, D.W., Graciá, E., Franz, R. & Fritz, U. (2021) Ancient mitogenomics elucidates diversity of extinct West Indian tortoises. *Scientific Reports*, 11, 3224.  
<https://doi.org/10.1038/s41598-021-82299-w>
- Kekkonen, M., Mutanen, M., Kaila, L., Nieminen, M. & Hebert, P.D.N. (2015) Delineating species with DNA Barcodes: A case of taxon dependent method performance in moths. *PLoS one*, Article ID e0122481.  
<https://doi.org/10.1371/journal.pone.0122481>
- Köhler, G. (2008) *Reptiles of Central America. Second edition*. Herpeton, Offenbach [Germany], 400 pp.
- Köhler, G. (2012) *Color Catalogue for Field Biologists*. Herpeton, Offenbach.
- Köhler, G. (2021) Taxonomy of horned lizards, genus *Phrynosoma* (Squamata, Phrynosomatidae). *Taxonomy*, 1, 83–115.  
<https://doi.org/10.3390/taxonomy1020009>
- Kopstein, F. (1938) Ein Beitrag zur Eierkunde und zur Fortpflanzung der Malaiischen Reptilien. *Bulletin of the Raffles Museum*, 14, 81–167, pl. vi–xxvii.
- Kramer, E. (1977) Zur Schlangenfauna Nepals. *Review Suisse de Zoologie*, 84, 721–761.  
<https://doi.org/10.5962/bhl.part.91420>

- Kroon, C. (1975) A possible Müllerian mimetic complex among snakes. *Copeia*, 75, 425–428.  
<https://doi.org/10.2307/1443639>
- Kumar, S., Stecher, G. & Tamura, K. (2016) MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. *Molecular Biology and Evolution*, 33, 1870–1874.  
<https://doi.org/10.1093/molbev/msw054>
- Lalremsanga, H.T. & Lalronunga, S. (2017) *Mizoram Rul Chanchin [Snakes of Mizoram] [in Mizo]*. Biodiversity and Nature Conservation Network (BIOCON), Aizwal, 132 pp.
- Lalremsanga, H.T., Sailo, S. & Chinliansiam, H. (2018) Diversity of snakes (Reptilia: Squamata) and role of environmental factors in their distribution in Mizoram, Northeast India. *Advances in Environmental Chemistry*, 265–268.
- Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B. (2017) PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*, 34, 772–773.  
<https://doi.org/10.1093/molbev/msw260>
- Lehman, S.M. & Fleagle, J.G. (Ed.) (2006) *Primate biogeography: progress and prospects*. Springer Science & Business Media.  
<https://doi.org/10.1007/0-387-31710-4>
- Mahony, S., Hasan, K., Kabir, M. & Ahmed, M., & Hossain, K. (2009) A catalogue of amphibians and reptiles in the collection of Jahangirnagar University, Dhaka, Bangladesh. *Hamadryad*, 34, 80–94.
- Mani, M.S. (1974) *Ecology and biogeography in India*. Dr. W. Junk b.v. Publishers, The Hague, The Netherlands.  
<https://doi.org/10.1007/978-94-010-2331-3>
- Manier, M.K. (2004) Geographic variation in the long-nosed snake, *Rhinocheilus lecontei* (Colubridae): beyond the subspecies debate. *Biological Journal of the Linnean Society*, 83, 65–85.  
<https://doi.org/10.1111/j.1095-8312.2004.00373.x>
- Manthey, U. & Grossmann, W. (1997) *Amphibien und Reptilien Südostasiens*. Natur und Tier Verlag, Münster, 512 pp.
- Mayr, E. (1942) *Systematics and the origin of species*, New York, 334 pp.
- McKay, J.L. (2006) *A field guide to the amphibians and reptiles of Bali*. Krieger Publishing Co, Malabar FL, vii+138.
- Mell, R. (1922) Beiträge zur Fauna sinica I. Die Vertebraten Südchinas, Feldlisten und Feldnoten der Säuger, Vögel, Reptilien, Batrachier. *Archiv für Naturgeschichte A*, 88, 1–134.
- Mell, R. (1931) List of Chinese snakes. *Lingnan Science Journal*, 8, 199–219.
- Minh, B.Q., Nguyen, M.A.T. & Haeseler, A. von (2013) Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution*, 30, 1188–1195.  
<https://doi.org/10.1093/molbev/mst024>
- Nepali, P.B. & Singh, N.B. (2020) Documentation of herpetofaunal diversity in Nawalparasi district, Nepal. *Uttar Pradesh Journal of Zoology*, 41, 56–70.
- Nguyen, V.S., Ho, T.C. & Nguyen, Q.T. (2009) *Herpetofauna of Vietnam*. Edition Chimaira, Frankfurt, 768 pp.
- Ogilvie, H.A., Bouckaert, R.R. & Drummond, A.J. (2017) StarBEAST2 brings faster species tree inference and accurate estimates of substitution rates. *Molecular Biology and Evolution*, 34, 2101–2114.  
<https://doi.org/10.1093/molbev/msx126>
- O’Shea, M. & Kaiser, H. (2018) Erroneous Environs or Aberrant Activities? Using Historical Accounts to Resolve Unexpected Collection localities for specimens of New Guinea Worm-eating Snakes (*Toxicocalamus*, Serpentes, Elapidae). *Herpetological Review*, 49, 189–207.
- Patten, M.A. (2010) Chapter 3: Null Expectations in Subspecies Diagnosis. *Ornithological Monographs*, 67, 35–41.  
<https://doi.org/10.1525/om.2010.67.1.35>
- Pawar, S.S., Birand, A.C., Ahmed, M.F. & Sengupta, S. & Raman, T. R. (2007) Conservation biogeography in north-east India: hierarchical analysis of cross-taxon distributional congruence. *Diversity and Distributions*, 13, 53–65.
- Pope, C.H. (1935) *The reptiles of China. Turtles, crocodilians, snakes and lizards. Natural History of Central Asia Vol. 10*, New York, 604 pp.  
<https://doi.org/10.5962/bhl.title.12104>
- Pradhan, A. (2021) *Boiga ochracea*, Tawny Cat Snake, Diet. *Herpetological Review*, 52, 147.
- Puillandre, N., Lambert, A., Brouillet, S. & Achaz, G. (2012) ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular ecology*, 21, 1864–1877.  
<https://doi.org/10.1111/j.1365-294X.2011.05239.x>
- Purkayastha, J. (2013) *An amateur’s guide to reptiles of Assam*. EBH Publishers, Guwahati, 146 pp.
- Ripley, S.D. & Beehler, B.M. (1990) Patterns of speciation in Indian birds. *Journal of Biogeography*, 17, 639–648.  
<https://doi.org/10.2307/2845145>
- Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics (Oxford, England)*, 19, 1572–1574.  
<https://doi.org/10.1093/bioinformatics/btg180>
- Ronquist, F., Teslenko, M., Mark, P., Ayres, D., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. & Huelsenbeck, J. (2012) MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. *Systematic biology*, 61, 539–542.



- <https://doi.org/10.1093/sysbio/sys029>
- Sabaj, M.H. (2020) Codes for natural history collections in ichthyology and herpetology. *Copeia*, 108, 593–669.  
<https://doi.org/10.1643/ASIHCODONS2020>
- Sanyal, D.P. & Gayen, N.C. (2006) Reptilia. In: Alfred, J. (Ed.). *Zoological Survey of India. State Fauna Series 13. Part 1. Fauna of Arunachal Pradesh.*, Kolkata, pp. 247–284.
- Schlegel, H. (1826) Notice sur l'erpétologie de l'île de Java; par M Boié (ouvrage manuscrit). *Bulletin des Sciences Naturelles et de Géologie*, 9, 233–240.
- Schleich, H.H. & Kästle, W. (Eds.) (2002) *Amphibians and Reptiles of Nepal*. A.R.G. Gantner Verlag, Ruggell, 1201 pp.
- Sclater, W.L. (1891) *List of snakes in the Indian Museum*. Trustees of the Indian Museum, Calcutta, 79 pp.  
<https://doi.org/10.5962/bhl.title.8746>
- Sengupta, S., Das, A., Das, S., Hussain, B., Choudhury, N.K. & Dutta, S.K. (2009) Taxonomy and biogeography of *Kaloula* Species of Eastern India. *The Natural History Journal of Chulalongkorn University*, 9, 2, 209–222.
- Shah, K.B. & Tiwari, S. (2004) *Herpetofauna of Nepal: A conservation companion*. IUCN Nepal, Kathmandu, viii+237.
- Shaw, G.E., Shebbeare, E.O. & Barker, P.E. (1941) The snakes of northern Bengal and Sikkim, Part IX. *Journal of the Darjeeling Natural History Society*, 15, 60–68.
- Smith, M.A. (1923) On a collection of reptiles and batrachians from the island of Hainan. *The Journal of the Natural History Society of Siam*, 6.
- Smith, M.A. (1928) The status of some recently described genera and species of snakes. *Annals and Magazine of Natural History*, 1, 494–497.  
<https://doi.org/10.1080/00222932808672813>
- Smith, M.A. (1930) The Reptilia and Amphibia of the Malay Peninsula from the Isthmus of Kra to Singapore including the adjacent islands (A supplement to Dr. G. A. Boulenger's Reptilia and Batrachia, 1912). *Bulletin of the Raffles Museum*, 3, i–xviii + 1–149.
- Smith, M.A. (1941) The herpetology of the Andaman and Nicobar Islands. *Proceedings of the Linnean Society of London*, 153, 152–158.  
<https://doi.org/10.1111/j.1095-8312.1941.tb00277.x>
- Smith, M.A. (1943) *The Fauna of British India, Ceylon and Burma, including the whole of the Indo-Chinese Subregion. Reptilia and Amphibia. Vol. III. - Serpentes*. Taylor & Francis, London, 583 pp.
- Smith, M.A. (1951) Frank Wall, 1868–1950. *Copeia*, 1951, 113–114.  
<https://doi.org/10.2307/1437539>
- Stejneger, L.H. (1902) A new opisthoglyph snake from Formosa. *Proceedings of the Biological Society of Washington*, 15, 15–17.
- Stoliczka, F. (1870) Observations on some Indian and Malayan Amphibia and Reptilia. *Annals and Magazine of Natural History*, Ser. 4. 6, 105–109.  
<https://doi.org/10.1080/00222937008696209>
- Taylor, E.H. (1965) The serpents of Thailand and adjacent waters. *The University of Kansas Science Bulletin*, 45, 609–1096.
- Theobald, W. (1868a) Catalogue of reptiles in the Museum of the Asiatic Society of Bengal. *Journal of the Asiatic Society of Bengal*, Extra Number, vi+82 pp., Appendix i–iii.  
<https://doi.org/10.5962/bhl.title.5477>
- Theobald, W. (1868b) Catalogue of the reptiles of British Birma, embracing the provinces of Pegu, Martaban, and Tenasserim; with descriptions of new or little-known species. *Journal of the Linnean Society (Zoology)*, 10, 4–67.  
<https://doi.org/10.1111/j.1096-3642.1868.tb02007.x>
- Tillack, F. (1999) Das Portrait: *Boiga ochracea stoliczkae*. *Sauria*, 21, 1–2.
- Trifinopoulos, J., Nguyen, L.-T., Haeseler, A. von & Minh, B.Q. (2016) W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research*, 44, W232–W235.  
<https://doi.org/10.1093/nar/gkw256>
- Uetz, P., Cherikh, S., Shea, G., Ineich, I., Campbell, P.D., Doronin, I.V., Rosado, J., Wynn, A., Tighe, K.A., McDiarmid, R., Lee, J.L., Köhler, G., Ellis, R., Doughty, P., Raxworthy, C.J., Scheinberg, L., Resetar, A., Sabaj, M., Schneider, G., Franzen, M., Glaw, F., Böhme, W., Schweiger, S., Gemel, R., Couper, P., Amey, A., Dondorp, E., Ofer, G., Meiri, S. & van Wallach (2019) A global catalog of primary reptile type specimens. *Zootaxa*, 4695 (5), 438–450.  
<https://doi.org/10.11646/zootaxa.4695.5.2>
- Uetz, P., Freed, P. & Hošek, J. (2022) The Reptile Database. Available from <http://www.reptile-database.org> (accessed 6 February 2022)
- Wall, F. (1908) A popular treatise on the common Indian snakes, Part VIII. *Journal of the Bombay Natural History Society*, 18, 711–735.
- Wall, F. (1909) Remarks on some forms of *Dipsadomorphus*. *Records of the Indian Museum*, 3, 151–155.  
<https://doi.org/10.26515/rzsi/v3/i2/1909/163268>
- Wall, F. (1910) A popular treatise on the common Indian snakes, Part XII. *Journal of the Bombay Natural History Society*, 19, 775–792.
- Wall, F. (1921) *Ophidia Taprobanica or the snakes of Ceylon*. H. R. Cottle, Government Printer, Colombo, 581 pp.  
<https://doi.org/10.5962/bhl.title.53694>

- Wallach, V., Williams, K.L. & Boundy, J. (2014) *Snakes of the World: a Catalogue of Living and Extinct Species*. Taylor and Francis, CRC Press, Boca Raton, Florida, USA, xxvii+1237.
- Wang, H., Luo, X., Meng, S., Bei, Y., Song, T., Meng, T., Li, G. & Zhang, B. (2015) The phylogeography and population demography of the Yunnan caecilian (*Ichthyophis bannanicus*): massive rivers as barriers to gene flow. *PloS ONE*, 10, e0125770.  
<https://doi.org/10.1371/journal.pone.0125770>
- Wangyal, J.T. & Das, I. (2021) *A guide to the reptiles of Bhutan*. Bhutan Ecological Society, Thimphu, 109 pp.
- Weinell, J.L., Barley, A.J., Siler, C.D., Orlov, N.L., Ananjeva, N.B., Oaks, J.R., Burbrink, F.T. & Brown, R.M. (2021) Phylogenetic relationships and biogeographic range evolution in cat-eyed snakes, *Boiga* (Serpentes: Colubridae). *Zoological Journal of the Linnean Society*, 192, 169–184.  
<https://doi.org/10.1093/zoolinnean/zlaa090>
- Werner, F. (1900) Reptilien und Batrachier aus Sumatra, gesammelt Herrn Gustav Schneider jr. im Jahre 1897-98. *Zoologische Jahrbücher. Abtheilung für Systematik, Geographie und Biologie der Thiere*, 13, 479–508, pl. 31–35.
- Whitaker, R. & Captain, A. (2004) *Snakes of India. The field guide*. Draco Books, Chennai, 479 pp.
- Wilson, L.D. (1999) Checklist and key to the species of the genus *Tantilla* (Serpentes: Colubridae), with some commentary on distribution. *Smithsonian Herpetological Information Service*, 1–36.  
<https://doi.org/10.5479/si.23317515.122.1>
- Yang, Z., Landry, J.-F. & Hebert, P.D.N. (2016) A DNA barcode library for North American Pyraustinae (Lepidoptera: Pyraloidea: Crambidae). *PloS one*, 11, e0161449.  
<https://doi.org/10.1371/journal.pone.0161449>
- Zhang, D.R., Chen, M.Y., Murphy, R.W., Che, J., Pang, J.F., Hu, J.S., Luo, J., Wu, S.J., Ye, H. & Zhang, Y.P. (2010a) Genealogy and palaeodrainage basins in Yunnan Province: phylogeography of the Yunnan spiny frog, *Nanorana yunnanensis* (Dicroglossidae). *Molecular ecology*, 19, 3406–3420.  
<https://doi.org/10.1111/j.1365-294X.2010.04747.x>
- Zhang, M., Rao, D., Yang, J., Yu, G. & Wilkinson, J.A. (2010b) Molecular phylogeography and population structure of a mid-elevation montane frog *Leptobrachium ailaonicum* in a fragmented habitat of southwest China. *Molecular phylogenetics and evolution*, 54, 47–58.  
<https://doi.org/10.1016/j.ympev.2009.10.019>
- Zhao, E.-M. & Adler, K. (1993) *Herpetology of China*. Society for the Study of Amphibians and Reptiles (Contributions to Herpetology, 10), Oxford, OH, 522 pp.

## APPENDIX 1. Specimens Examined.

*Boiga multomaculata multomaculata*—**China**: Guangdong: no specific locality: CHS760; Nan'aodao: CHS580; Hainan: Haikou: CHS112. **Indonesia**: “N. Celebes” [in error]: ZMB 7470; Java: no specific locality: NK 2078, RMNH 978(2), 979(1–6), SMF 19672, ZMB 2640–44, 4851, 7149, 75944; Djakarta: MNHN 0974, 3881, 1864.0050; Provinz Jawa Barat, Bogor: SMF 19670–71; Samarang: RMNH 978(1), ZMB 14348, 90183. **Thailand**: Kanchanburi: Thong Pha Phum: PT3083; Petchaburi: near Nong Ya Plong: PT3484–85; Ban Thung Kham: MNHN 1998.0519; Tak: near Tak: PT3084; between Bangkok and Chanthaburi: MNHN 1985.392. **Vietnam**: no specific locality: MNHN 1911.102; Đà Nẵng: Bana Nature Reserve: MNHN 1997.4368; Hồ Chí Minh: Hồ Chí Minh: MNHN 1974.1363; vicinity of Hồ Chí Minh: MNHN 1974.1327; Lai Châu: no specific locality: MNHN 1935.95; Lào Cay: Haut Tonkin: MNHN 1902.83; Quảng Nam: Bông-Miêu: MNHN 97-428-4551/2526-6/3; Tonkin: Pointe Pagode: MNHN 1911.46; Tam Dao: MNHN 1935.96.

*Boiga multomaculata ochracea*—**Bangladesh**: Chittagong: Chittagong: CAS 95252; Chittagong Uni Campus: CUZ 31, 37. **India**: Mizoram: no specific locality: HT R 190, 224, 230–31; Dampa Tiger Reserve, 414 m: WIIADR 1156; Nagaland: Kohima–Meluri road, 650 m: WIIADR 856. **Laos**: Louangphrabang: Ban Nammadao: NME R 499/06; Pak Gaeng Noi, Louang Prabang, 1200 m: NME R 0733/12, 0948/13; Vientiane: Phon Khoun, ca. 40 km SE of Ban Nammadao, 1100 m: NME R 0499/06. **Myanmar**: Ayeyarwady: near Kan Ywa: SMF 103792, 103827; outskirts of Pantanaw: SMF 103826; Bago: Bago: BMNH 1946.1.12.60–61; Chin: Min Dat Township, Nat Ma Taung National Park: CAS 220037; Kayin: Hakha, Chin hill: BNHS 1780; Magwe: Gangaw Township, Mauk village: CAS 243048, 243030; near Taungdwingyi: SMF 104722; Mandalay: Kyaukpadaung Township, near Myauk Taw Village: CAS 210680; Kyaukse: CAS 205049; Meiktila: ZSIK 13250; Tha Baik Kyin Township, Shwe U Daung Wildlife Sanctuary, Kyauk Kyi Village, 22 59 06.8 N, 96 06 40.3 E: CAS 216182; Mon: Kawkareik: BNHS 1778; Rakhine: An Township, Singaung village: CAS 240123; Pleasant Beach Resort: CAS 205002; Sagaing: no specific locality: CAS 215542; Alaungdaw Kathapa National Park, Thaipetsae (Log Cabin Camp: CAS 215603; Yin Ma Bin Township, Yinpaungtaing Village: CAS 215390; Tanguyi: no specific locality: BNHS 1781; Tanintharyi: Yebyu Township, Yepon village: CAS 243733; Yangon: Mingalardon Township, Hlawga Wildlife Park: CAS 213324; Yangon: CAS 210834; Thanlyin: SMF

104138; Thanlyin, near East Yangon University: PaPa 008. **Thailand:** Loei: Phu Luang: ZMB 55191; Nan: near Ban Khueng: PT1711; near Ban Mon: PT2316.

*Boiga multomaculata septentrionalis*—**India:** Nagaland: Kohima–Meluri Road: WIIADR 856; Sivasagar: ZSIK 7933. **Myanmar:** Kachin: Bhamo: BMNH 1889.3.25.37–39, MNHN 1893.0412, ZMH R09334; Moenyin Township, Indawgyi Lake Wildlife Sanctuary, E of Nat Mouk Kan village: CAS 241150, 241272, 241550; Sagaing: Khandi Township, Linpha village: SMF 106288.

*Boiga stoliczkae*—**Bhutan:** Chukha: Phuntsholing: NMB 22730; Zhemgang: near Manas: WIIADR 858. **India:** Arunachal Pradesh: Dirang: no reg. no.; N.E. Bengal: no specific locality: ZSIK 12565; India: West Bengal: Darjeeling: BMNH 72.4.17.119, 72.4.17.386, 94.12.31.55, ZMB 10335, ZSIK 7869, 7873, 7878, 8476, 11367; Goalpara: ZSIK 7932; Kurseong: BNHS 1781, 2745 (1–2); Mal Dist. Doars, N. Bengal: BMNH 1936.7.6.16–19; near Darjeeling: BMNH 1909.3.9.13; Sureil (near Mirik) Darjeeling: ZSIK 15207, 17297; Tindharia: BNHS 1772–73, 1780; Phubeseng, Darjeeling district: BNHS 1774, 1778. **Nepal:** Bagmati: Bhadgaon: CAS 90726; Ichangu, Kathmandu: NHMK 3 (unregistered); Kulekhani, Makwanpur District: NHMK 1–2 (unregistered); Swoyambhu, Kathmandu: NHMK 17B-0119; Naudanda-Serachaur, District Kaski, Zone Gandaki: ZMB 73660; Pyaudi, District Kaski, Zone Gandaki: ZMB 73661; Serachaur, District Kaski, Zone Gandaki: ZMB 73662.

**APPENDIX 2.** GenBank accession numbers of specimens included in the molecular analyses. Sequences generated in this study are marked with an asterisk (Genbank accession number to be included).

Species	Voucher	CYTB	ND4	16S	c-mos
<i>Boiga barnesii</i>	RAP 0452	KC347469	KC347499	KC347345	-
<i>Boiga beddomei</i>	CESS 387	MT733290	MT733317	MT734904	-
<i>Boiga beddomei</i>	CESS 417	MT733291	MT733318	MT734905	-
<i>Boiga beddomei</i>	CESS 418	MT733292	MT733319	MT734906	-
<i>Boiga beddomei</i>	CESS 444	MT733294	MT733321	MT734908	-
<i>Boiga cyanea</i>	SMF 103893	ON932767*	ON932766*	ON782358*	-
<i>Boiga dendrophila annectens</i>	FMNH 230060	-	-	-	MN962087
<i>Boiga drapiezii</i>	LSUHC 7295	KX660482	KX660608	KX660210	-
<i>Boiga multomaculata</i>	CAS 205002	-	-	-	MN962143
<i>Boiga multomaculata</i>	CAS 215390	-	-	-	MN962144
<i>Boiga multomaculata</i>	CAS 215542	ON932768*	ON932753*	ON782359*	-
<i>Boiga multomaculata</i>	CAS 215603	ON932769*	ON932752*	ON782360*	-
<i>Boiga multomaculata</i>	CAS 216182	ON932770*	ON932751*	ON782361*	-
<i>Boiga multomaculata</i>	CAS 241150	ON932772*	ON932765*	ON782359*	-
<i>Boiga multomaculata</i>	CAS 241272	ON932773*	ON932764*	ON782360*	-
<i>Boiga multomaculata</i>	CAS 241550	ON932774*	ON932763*	ON782361*	ON805810*
<i>Boiga multomaculata</i>	CAS 243030	ON932775*	ON932749*	ON782362*	ON805809*
<i>Boiga multomaculata</i>	CAS 243048	ON932776*	ON932762*	ON782363*	ON805808*
<i>Boiga multomaculata</i>	CAS 243733	ON932777*	ON932761*	ON782364*	-
<i>Boiga multomaculata</i>	NK2078	ON932778*	ON932759*	ON782365*	-
<i>Boiga multomaculata</i>	PaPa 008	ON932779*	ON932757*	ON782366*	-
<i>Boiga multomaculata</i>	PT1711	ON932780*	ON932758*	ON782367*	-
<i>Boiga multomaculata</i>	PT2316	ON932781*	ON932756*	ON782368*	-
<i>Boiga multomaculata</i>	PT3083	ON932782*	ON932755*	ON782369*	-
<i>Boiga multomaculata</i>	PT3084	ON932783*	ON932754*	ON782370*	-
<i>Boiga multomaculata</i>	SMF 103792	ON932784*	ON932760*	ON782371*	-
<i>Boiga multomaculata</i>	SMF 103826	ON932785*	ON932748*	ON782372*	-

.....continued on the next page



**APPENDIX 2. (Continued)**

Species	Voucher	CYTB	ND4	16S	c-mos
<i>Boiga multomaculata</i>	SMF 103827	ON932786*	ON932747*	ON782373*	-
<i>Boiga multomaculata</i>	SMF 104722	ON932787*	ON932746*	ON782374*	-
<i>Boiga multomaculata</i>	SMF 106288	ON932771*	ON932750*	ON782362*	ON805811*
<i>Boiga multomaculata</i>	WIIADR 856	ON932788*	-	ON782379*	-
<i>Boiga multomaculata</i>	ZISP 32537	-	-	-	MN962139
<i>Boiga multomaculata</i>	ZISP 32539	-	-	-	MN962140
<i>Boiga nigriceps</i>	ZISP 25392	-	-	-	MN962141
<i>Boiga nigriceps</i>	ZISP 25393	-	-	-	MN962142
<i>Boiga nuchalis</i>	CESS 094	MT733277	MT733304	MT734890	-
<i>Boiga nuchalis</i>	CESS 192	MT733282	MT733308	MT734895	-
<i>Boiga nuchalis</i>	CESS 270	MT733285	MT733311	MT734898	-
<i>Boiga nuchalis</i>	CESS 310	MT733288	MT733314	MT734901	-
<i>Boiga nuchalis</i>	CESS 315	MT733289	MT733316	MT734903	-
<i>Boiga nuchalis</i>	CESS 504	MT733295	MT733322	MT734909	-
<i>Boiga philippina</i>	KU 304855	-	-	-	MN962145
<i>Boiga philippina</i>	KU 327777	-	-	-	MN962146
<i>Boiga quincunciata</i>	CAS 221434	KX660451	KX660579	KX660177	-
<i>Boiga quincunciata</i>	CAS 224439	-	-	-	MN962147
<i>Boiga quincunciata</i>	CAS 235862	KX660450	KX660578	KX660176	-
<i>Boiga siamensis</i>	CAS 215627	KX660449	KX660577	KX660175	-
<i>Boiga siamensis</i>	CAS 215635	-	-	-	MN962149
<i>Boiga siamensis</i>	LSUHC 8502	KX660487	KX660612	KX660215	-
<i>Boiga siamensis</i>	LSUHC 8527	KX660488	KX660613	KX660216	-
<i>Boiga siamensis</i>	ZISP 32742	-	-	-	MN962150
<i>Boiga stoliczkae</i>	WIIADR 858	OQ079990*	OQ079991*	OQ078743*	-
<i>Boiga tanahjampeana</i>	ZISP 21938	-	-	-	MN962151
<i>Boiga tanahjampeana</i>	ZISP 21942	-	-	-	MN962153
<i>Boiga tanahjampeana</i>	ZISP 21943	-	-	-	MN962154
<i>Boiga trigonata</i>	LSUMZ 6964	-	-	-	MN962155
<i>Boiga trigonata</i>	LSUMZ 6965	-	-	-	MN962156
<i>Boiga trigonata</i>	LSUMZ 6966	-	-	-	MN962157
<i>Boiga trigonata</i>	RS 143	KC347475	KC347515	KC347349	-
<i>Boiga whitakeri</i>	CESS 255	MT733284	MT733310	MT734897	-
<i>Telescopus tripolitanus</i>	BEV 9377	JX315531	MK373166	MK372141	MK373205