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# Taxonomic Composition of the *Oligodon arnensis* (Shaw 1802) Species Complex (Squamata: Colubridae) with the Description of a New Species from India

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Abstract: We review the taxonomic status of *Oligodon arnensis* (Shaw 1802) after examining all the name-bearing types of its synonyms, and evaluating morphological and biogeographic evidence. *Oligodon arnensis* sensu lato is widely distributed throughout Peninsular India, Sri Lanka, Pakistan, Nepal, Bhutan, and Bangladesh. We demonstrate that southern, eastern, and western populations in India represent three distinct species. *Oligodon arnensis* sensu stricto described from Arnee (now Arani), Tamil Nadu, southern India, is distributed in southern India up to 1500 m above sea level. *Oligodon albiventer* Günther 1864 and *Simotes russellii* var. *ceylonensis* Müller 1887 described from Sri Lanka closely match *O. arnensis* sensu stricto, and hence we treat them as junior synonyms. We resurrect *Coluber russelius* Daudin 1803 from the synonymy of *O. arnensis*, designate a lectotype, and restrict its type locality to Vizagapatam (now Visakhapatnam), Andhra Pradesh, eastern Peninsular India. Based on morphological differences we describe a new species from Kurduvadi, in the Deccan plateau of western India representing the western Indian population of *O. arnensis* sensu lato. We provide redescriptions for *O. arnensis* sensu stricto and *O. russelius* comb. nov. based on museum specimens, as both were named based on illustrations (iconotypes). Based on our update of the currently confirmed localities for *O. arnensis*, *O. russelius* comb. nov. and the new species, we discuss their biogeography and conservation status.

**Key words:** Asia; Distribution; Kukri snake; Lectotype; Morphology; Synonym

The Banded Kukri, *Oligodon arnensis* (Shaw 1802), a widespread colubrid snake species, is found in India, Sri Lanka, Pakistan, Nepal, and Bangladesh (Whitaker and Captain 2004; Wallach et al. 2014). Although the distribution of *O. arnensis* sensu lato in Bangladesh is based only on a few records (IUCN 2015), it is widely distributed throughout mainland India including the Himalayan foothills. Based on citizen science georeferenced photographic records, we noticed that *O. arnensis*, as it is recognized today, is likely to comprise several distinct species, limited to distinct geographical parts of India. The morphological variability of this complex has been identified since the early 19th century (e.g., Daudin 1803; Duméril et al. 1854) and geographically correlated morphological variations of the complex were explicitly provided by Wall (1921, 1923), Deraniyagala (1936, 1955), and Smith (1943).

The first illustration of Banded Kukri Snakes appeared nearly three centuries ago in the second volume of Albertus Seba's *Thesaurus* published in 1735 (Seba 1735). Although the distribution was erroneously indicated as "Africana," Fig. 4 in its Plate 62 (Supplemental Fig. S1, available online) undoubtedly represents an individual of *O. arnensis* due to its dorsal cross bands and unique head marking. In the same century, the British naturalist, Patrick Russell (1727–1805) illustrated two snakes, in his first volume of *An Account of Indian Serpents* published in 1796. The first illustration (on Plate 35) depicted was based on an 8-in (~203-mm) specimen. In his description, Russell (1796: 41) stated the specimen was found from Vizagapatam (now Visakhapatnam), Andhra Pradesh, India, and had 188 ventrals and 55 subcaudals.

The second illustration (on Plate 38) depicted was based on a 21.5-in (~546-mm) specimen. In his description, Russell (1796: 43–44) stated the specimen was found from Arnee (now Arani), Tamil Nadu, India, and had 169 ventrals and 50 subcaudals. Later, when Shaw (1802) was naming the snake depicted (Plate 38) by Russell as *Coluber arnensis*, he did not provide any clue for the species identity of the similar-looking snake on Russell's Plate 35, hence a holotype by monotypy.

A year after the description of *C. arnensis* by Shaw (1802), when naming *C. russelius*—see the English translation of the original French description in Supplemental Material I—Daudin (1803) referred his nomen to both of Russell's plates (Plates 35 and 38) in addition to his own illustration on Plate 76 in the same work, hence syntypes. He considered there to be two varieties of *C. russelius*: the first variety with 34 dorsal cross bands and referred to Russell's Plate 35. The second variety had 22 dorsal cross bands and referred to Russell's Plate 38 (the same plate used to name *C. arnensis* by Shaw 1802). Merrem (1820) and several authors subsequently, including Schlegel (1837), Duméril et al. (1854), Günther (1858, 1864), and Müller (1887), used the spelling of species epithet as "*russelii*" or "*russellii*" instead of "*russelius*" as published originally by Daudin (1803) in the genus *Coluber*. Corresponding to Daudin (1803), Jan and Sordelli (1882) also recognized two varieties in *Simotes russelii* (sic), and

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noticed one with and the other without a loreal plate (see Figs. 1A and 1B in their Plate VI of Livraison 11).

Later, Cantor (1839) described another, similar, banded species, *C. monticolus* from Nepal, but without precise type material and without any indication of an illustration. It has long been considered a junior synonym of *S. russelii* (sic; fide Günther 1864), and later of *Oligodon arnensis* (fide Smith 1943 with a question mark). The original description given by Cantor (1839) was brief and not detailed enough in diagnostic characters. A colored sketch accompanying this species description is deposited in the Bodleian Library, Oxford (Green 2010). Tillack et al. (2021) removed *C. monticolus* from the synonymy of *O. arnensis* and regarded it as a *nomen oblitum* of *Boiga multifasciata* (Blyth 1861), resolving the centuries-old nomenclatural issue of *C. monticolus*. Günther (1864) described *S. albiventer* from a single specimen (Natural History Museum, London, UK [NHMUK] 1946.1.4.36) which was collected from Sri Lanka also mentioning the type locality "Near Kandy" on the label. In the same publication, he synonymized Shaw's (1802) species with *S. russellii* (sic) misspelled Daudin's (1803) species, and considered that the species *S. russellii* was comprised of four varieties including "variety δ" from Ceylon (now Sri Lanka). Müller (1887) named Günther's "variety δ" as *S. russellii* var. *ceylonensis* originating from northwestern Sri Lanka. Based on scale differences with forma typica, Deraniyagala (1936) considered *S. albiventer* a subspecies of *O. arnensis* that is endemic to Sri Lanka. Later, this taxon was also synonymized with *O. arnensis* by Smith (1943) and subsequent authors considered *O. arnensis* a monotypic species. Recently Mirza et al. (2021) described *O. churahensis*, the western Himalayan population of *O. arnensis* sensu lato which had been recognized (Wall 1921; Deraniyagala 1936, 1955; Constable 1949) due to its higher numbers of cross bands on the body.

Although there were several attempts—see Supplemental Material II for the composition of *O. arnensis* sensu lato listed in the historical literature—to understand the morphological variations using the number of body bands/stripes and body scales, as well as the head scales, e.g., loreal (e.g., Daudin 1803; Duméril et al. 1854; Günther 1864; Wall 1921, 1923; Deraniyagala 1936, 1955; Smith 1943), *O. arnensis* has long been considered a single species widely distributed in South Asia. Therefore, based on type material and additional voucher specimens from India and Sri Lanka, we revisited the taxonomic status of *O. arnensis* sensu lato which involves the examination of the said type material of all of its synonyms. After taking morphological and morphometric characters into consideration with geographical distribution of examined specimens, we concluded that *O. arnensis* is actually a species complex. In this work, we redefine *O. arnensis*, resurrect one of its junior synonyms, and describe a new species.

## Materials and Methods

We compared the type specimens (and iconotypes) of all the described species (including synonyms) of the *Oligodon arnensis* species complex. We examined specimens and descriptions of the other known superficially similar congeners (Appendix). We examined specimens from the following collections: Chennai Snake Park Trust/Snakes collection (CSPT/S); Muséum National d'Histoire Naturelle, Paris, France (MNHN); The Natural History Museum, London, UK, (NHMUK); National Museum of Sri Lanka, Colombo, Sri Lanka (NMSL); Wildlife Heritage Trust, Sri Lanka (WHT, currently deposited at NMSL; Naturhistorisches Museum, Wien, Austria (NMW); Museum für Naturkunde, Berlin, Germany (ZMB); Zoological Survey of India, Kolkata, India (ZSI). Museum abbreviations mostly follow Uetz et al. (2019). We obtained morphological, morphometric, and meristic data for species comparisons, and distribution data from examined specimens and published literature. We also examined georeferenced photographic vouchers from the iNaturalist Citizen Science Platform. We examined the skull features and counted the number of maxillary, palatine, pterygoid, and mandible teeth of *Oligodon arnensis* sensu lato based on MicroCT scans of museum specimens. MicroCT scans were generated using a Nikon XT H 225 ST (Nikon Metrology NV Company, Tring, UK) scanner. The head of the specimen was scanned for 15–25 min at a resolution of 5–10 μm and data were recorded for every 0.09°–0.14° rotation for 360° with 0.5-mm filter. The source voltage for the scan was 110–130 kV and source current was 82–91 μA. Volume rendering was performed with Avizo v2020.3 (Thermo Fisher Scientific) and images were edited in Adobe Photoshop CS6. Osteological description is based on volume renders retrieved from Avizo following terminology of the skull described by Heatwole (2009).

We measured the following characters with a Mitutoyo digital caliper and Leica M50 (Leica Microsystems Inc.) and AmScope SM-1BZ-RL (×10–90; United Scope LLC) and Carl Zeiss DRC 475003-9902 (Carl Zeiss AG) dissecting microscopes: eye diameter (ED, horizontal diameter of eye); eye–nostril length (distance between anterior-most point of eye and middle of nostril); snout length (ES, distance between anterior-most point of eye and snout); internarial distance (IN, least distance between nostrils); interorbital width (IO, least distance between upper margins of orbits); head length (HL, distance between posterior edge of mandible and tip of snout); head width (HW, maximum width of head); snout–vent length (SVL, measured from tip of snout to anterior margin of vent); and tail length (TL, measured from anterior margin of vent to tail tip). Meristic characters were taken as follows: supralabials and infralabials (first labial scale to last labial scale bordering gape); dorsal scale rows (DSRs, counted around the body from one side of ventrals to the other in three positions, on one head length behind neck, at midbody and at one head length prior to cloacal plate); when counting the number of ventral scales, we scored values according to the method described by Dowling (1951). We counted subcaudal scales from the first subcaudal scale meeting its opposite to the scale before the tip of the tail. Sex of the specimens was identified by examining everted hemipenes or by ventral tail dissection. We evaluated the relative size of the dorsal cross markings (either bands or stripes), shape, and the number of the black cross bands/stripes of each individual. The number of cross bands/stripes on the body counted from the first band posterior to the marking on the nape up to the level of cloaca, and the count on the tail from the level of cloaca to the tip of tail. Body color pattern is considered a reliable character only when a drawing/description/photograph of a

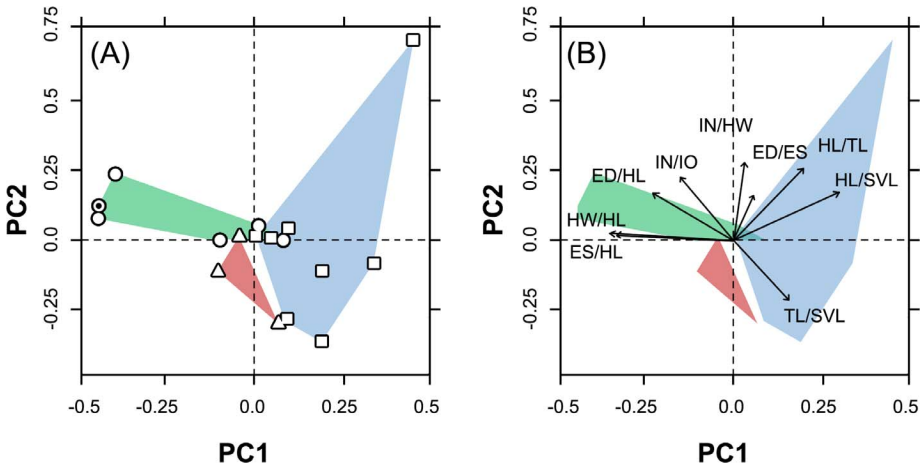


FIG. 1.—(A) Principal component analysis biplot of morphometric variation in western (triangles), southern (circles, with dot in the middle represents the examined holotype of the Sri Lankan synonym, *Simotes albiventer*), and eastern (squares) Indian populations of *Oligodon arnensis* sensu lato clearly shows the morphological distinctiveness of each population. Each point represents an individual specimen, and the relative distance between two points is equivalent to the amount of dissimilarity; (B) the same base biplot with vectors associated with population clusters. PC = principal component; TL = tail length; SVL = snout–vent length; HW = head width; HL = head length; IN = internarial distance; IO = interorbital width; ED = eye diameter; ES = snout length; PC = principal component. A color version of this figure is available online.

live or dead (freshly killed) specimen are available. Number of vertebral scales covering the cross bands/stripes at midbody and number of vertebral scales in-between cross bands/stripes at midbody are considered a reliable character for species diagnosis. In addition, the interband/stripe width between the first two cross bands/stripes (either broader or narrower) compared to the width of first two cross bands/stripes is also considered a reliable character for adult individuals.

Statistically informative tests could not be performed on separate sexes except for the Sri Lankan population of *Oligodon arnensis* sensu lato, because the smaller sample sizes representing the other regions (e.g., southern, western, eastern regions) of India would have rendered them insufficient for this purpose. Therefore, 25 adult voucher specimens from Sri Lanka for different sexes (males and females) and 17 adult voucher specimens (both males and females together) from India for different biogeographic regions (southern, western, and eastern) were used in the statistical analysis. Juveniles were excluded to avoid the bias of allometry for the statistical analysis. Univariate and multivariate analyses were conducted on nine morphometric ratios (TL/SVL, HW/HL, IN/HW, IN/IO, ED/ES, ED/HL, HL/SVL, HL/TL, and ES/HL), including the holotype of *Simotes albiventer* (a synonym of *O. arnensis* from Sri Lanka), and voucher specimens of *O. arnensis* sensu lato from India to assess the morphometric variation and taxonomic differentiation. We performed separate Kruskal–Wallis one-way analysis of variance tests on each morphometric ratio to detect any differences between populations (western India = 3, eastern Peninsular India = 8, and southern India = 5). We used this test due to the small sample size (Zar 2010). Each morphometric ratio was treated as the dependent variable and the population as the predictor variable. Multivariate analysis was conducted using principal component analysis to reduce the highly correlated multidimensional data matrix into a few uncorrelated variables (i.e., principal components [PCs]). We used the princomp function in the R statistical software program (v4.0.4; R Core Team 2021) based on a correlation matrix of nine morphometric ratios. A biplot of the first two principal component scores was used to examine the morphometric differentiation between the populations. All statistical analyses were conducted using the R statistical software program (v4.0.4; R Core Team 2021).

## RESULTS

Two out of nine morphometric ratio mean comparisons showed significant differences among southern Indian plus Sri Lankan populations (*O. arnensis* sensu stricto), the western Indian populations (described as a new species herein), and the eastern Peninsular Indian populations (resurrected as *O. russelius* comb. nov.): HW/HL ($\chi^2$ = 12.98, $P$ = 0.00) and ES/HL ($\chi^2$ = 8.16, $P$ = 0.02). Higher HW/HL and ES/HL ratios of *O. arnensis* sensu stricto and the new species indicated a relatively shorter and wider head, and longer snout than that of *O. russelius* comb. nov. Multivariate analysis by principal component analysis also showed distinct overall differences in morphometric characters among three populations with a distinct nonoverlapping cluster for the populations of the new species (Fig. 1A). PCs 1 and 2 collectively explained 63.2% of variation in the morphometric data matrix (Supplemental Table S1; Fig. 1). Morphometric ratios TL/SVL, IN/HW, ED/ES, HL/SVL, and HL/TL loaded positively with PC 1 while HW/HL, IN/IO, ED/HL, and ES/HL loaded negatively with PC 1. Additionally, morphometric ratios TL/SVL loaded negatively with PC 2 (Supplemental Table S1). Overall, morphometric ratios ED/ES, HL/SVL, and HL/TL were positively associated with the eastern population, while they showed no negative associations (Fig. 1B).

The univariate analysis on separate sexes of *O. arnensis* sensu stricto in Sri Lanka ($n$ = 25) showed significant differences in three morphometric ratios: TL/SVL ($\chi^2$ = 11.04, $P$ = 0.00), HL/TL ($\chi^2$ = 10.7, $P$ = 0.00), and ES/HL ($\chi^2$ = 7.45, $P$ = 0.00). The principal component analysis also showed distinct overall differences in morphometric char-

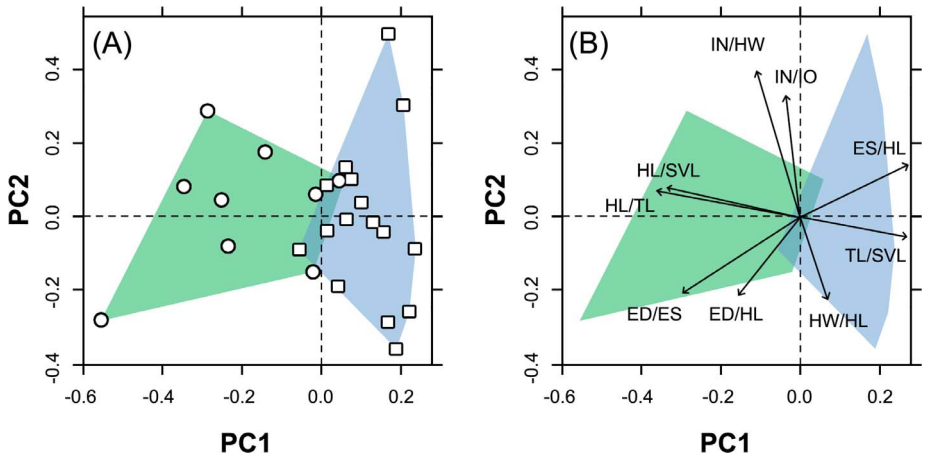


FIG. 2.—(A) Principal component analysis biplot of sexual dimorphism in *Oligodon arnensis* based on the Sri Lankan population ($n = 25$) clearly shows the morphometric distinctiveness of males (squares) and females (circles). Each point represents an individual specimen, and the relative distance between two points is equivalent to amount of dissimilarity; (B) the same base biplot with vectors associated with population clusters. PC = principal component; TL = tail length; SVL = snout–vent length; HW = head width; HL = head length; IN = internarial distance; IO = interorbital width; ED = eye diameter; ES = snout length; PC = principal component. A color version of this figure is available online.

acters between males and females within the Sri Lankan population of *O. arnensis* (Fig. 2A) indicating sexual dimorphism of the members of the *O. arnensis* species complex. Therefore, we assessed the morphometric character ratios (e.g., TL/total length), and meristic characters (e.g., ventrals) for each of the separate sexes of each species. The new species had a longer tail, TL 17.0–17.4% of total length in males compared to *O. arnensis* sensu stricto (13.5–17.1%) and shorter tail than *O. russelius* comb. nov. (17.0–18.9%). PCs 1 and 2 collectively explained 62.0% of the variation in the morphometric data matrix (Supplemental Table S2; Fig. 2). Morphometric ratios TL/SVL, HW/HL, and ES/HL were loaded positively with PC 1 while other character ratios loaded negatively with PC 1. Additionally, morphometric ratios TL/SVL, HW/HL, ED/ES, and ED/HL were loaded negatively with PC 2 (Supplemental Table S2). Overall, morphometric ratio ES/HL was positively associated with the males while ED/ES and ED/HL showed negative associations (Fig. 2B).

We present diagnostic morphological, morphometric, and meristic data taken for each of our identified species in this species complex (Table 1). The examined specimens of *O. arnensis* sensu lato from western and eastern Peninsular India are morphologically distinguishable from each other and also from *O. arnensis* sensu stricto from southern India plus Sri Lanka. Hence, we regard them as three distinct species. Currently, there are two junior synonyms under *O. arnensis* sensu lato: *C. russelius* and *S. albiventer*.

Our attempt to trace type specimens of *C. arnensis* in NHMUK was unsuccessful. Therefore, the only available original material for this nomen is the original description written by Shaw (1802) and the illustration referred to in the description, which was depicted by Russell (1796: Plate 38 [see Fig. 3A]). The species depicted on Plate 38 of Russell (1796), i.e., the iconotype of *C. arnensis*, is well standing as a distinct species, *Oligodon arnensis*. We also consider this iconotype as the illustration depicted its holotype (by monotypy), and the holotype of the *C. arnensis* is probably lost. The current status of the specimens illustrated by Russell (1796; Plate 38) and preliminary assigned dry skin from Russell's collection (fide Bauer et al. 2015) summarized in Table 2.

Our attempt to trace any type specimens of *C. russelius* at MNHN and in other possible depositories (e.g., NHMUK) was unsuccessful. Therefore, the only available original material for this nomen is the original description written by Daudin (1803) and the illustrations referred to in the description which were depicted by Russell (1796: Plate 35 [see Fig. 3B] and Plate 38 [see Fig. 3A]) and Daudin (1803: Plate 76 [see Fig. 3C]). Among these illustrations, Daudin (1803) assigned Plate 35 of Russell to his first variety of *C. russelius*, and Plate 38 to his second variety. It is probable that Daudin's Plate 76 also refers to the second variety—see Discussion. Therefore, we consider the specimens depicted in these three iconotypes as syntypes, and here designate the specimen depicted on the illustration of Russell (1796: Plate 35), which represents Daudin's first variety of *C. russelius*, as the lectotype of *C. russelius* sensu Article 74.1 and 74.4 of the Code (ICZN 1999). The lectotype of *C. russelius* is probably lost. We thus restrict the type locality of *C. russelius* to Visakhapatnam, Andhra Pradesh, India, based on its illustration of the lectotype designated herein (fide Russell 1796; Daudin 1803). However, based on the description and the illustration of lectotype, we resurrect and assign the nomen *C. russelius* to the genus *Oligodon* Boie in Fitzinger 1826 based on morphology (fide Wallach and Bauer 1996) and redescribe the species herein. The current status of the specimens illustrated by Russell (1796), Daudin (1803), and preliminary assigned dry skin from Russell's collection (fide Bauer et al. 2015) is summarized in Table 2.

Daudin (1803) considered that *C. russelius* has two varieties, and he assigned the referred illustrations (in this case iconotypes) to each of the variety. He clearly indicated that the first variety has 34 cross bands on the dorsum, and the second has 22. Among the three illustrations, i.e., original syntypes: (1) Russell's Plate 35 has 34 cross stripes (Fig. 3A), which belongs to the first variety; (2) Russell's Plate 38 has 22 cross bands (Fig. 3D), which belongs to the second variety; and (3) the third illustration made by Daudin has

TABLE 1.—Morphological, morphometric, and meristic characters of *Oligodon tillacki* sp. nov., *O. russelius* comb. nov., and *O. arnensis* sensu stricto (southern India plus Sri Lanka) including types and synonym types (see Appendix for accession data). Dash (—) = not measured.

| | *O. tillacki* sp. nov. | | | | | *O. russelius* comb. nov. | | *O. arnensis* sensu stricto | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | Southern India | | Sri Lanka | | |
| | Females | | | Males | | | | | | Males | | |
| | Holotype | Paratypes | | Paratypes | | | | | | | | |
| Character | MNHN-RA 1946.0058 | NHMUK 1860.3.19.1317 | MNHN-RA 1946.0057 | NMW 24546:4 | NMW 24545:1 | Males ($n$ = 8) | Females ($n$ = 3) | Males ($n$ = 3) | Females ($n$ = 3) | Holotype of *S. albiventer* NHMUK 1946.1.4.36 | Other ($n$ = 16) | Females ($n$ = 9) |
| Snout–vent length | 424.0 | 530.0 | 293.0 | 458.0 | 369.0 | 326.0–468.0 | 318.0–320.0 | 342.0–350.0 | 343.0–350.0 | 495.0 | 254.0–483.0 | 250.0–485.0 |
| Tail length | 78.0 | 93.2 | 51.0 | 94.0 | 78.0 | 70.0–98.7 | 59.5–72.0 | 54.7–71.0 | 60.0–68.8 | 81.0 | 58.0–106.0 | 45–78 |
| Tail length/total length (%) | 15.5 | 15.0 | 14.8 | 17.0 | 17.4 | 17.0–18.9 | 15.7–18.5 | 13.5–17.1 | 14.6–16.7 | 14.1 | 15.2–20.3 | 13.9–15.3 |
| Head length | 13.2 | 16.2 | 9.7 | 17.2 | 12.6 | 12.8–16.0 | 14.0–14.8 | 15.2–15.3 | 10.9–13.1 | 15.7 | 12.0–17.9 | 12.6–17.5 |
| Head width | 8.0 | 9.9 | 5.8 | 10.8 | 8.0 | 7.6–9.6 | 7.2–8.7 | 9.5–10.2 | 8.6–8.9 | 12.8 | 7.3–11.0 | 7.3–11.0 |
| Internarial distance | 3.0 | 3.3 | 2.4 | 3.4 | 3.0 | 2.4–3.7 | 2.5–2.8 | 3.4–3.6 | 2.9–3.4 | 4.6 | 2.5–4.4 | 2.5–3.9 |
| Interorbital width | 5.2 | 6.0 | 3.3 | 5.7 | 4.3 | 4.5–5.5 | 4.2–4.3 | 4.7–5.1 | 4.5–5.4 | 6.5 | 3.7–6.3 | 4.4–6.0 |
| Snout length | 4.4 | 5.4 | 3.5 | 5.3 | 3.9 | 3.9–4.9 | 4.7–4.8 | 4.8–4.9 | 3.8–4.5 | 6.2 | 3.8–5.9 | 3.6–5.6 |
| Eye–mandible distance | 5.2 | — | 4.8 | 9.8 | 6.7 | —[a] | — | 8.1–8.3 | — | — | 6.5–10.0 | 7.1–9.6 |
| Eye diameter | 2.1 | 2.7 | 1.9 | 2.2 | 2.0 | 1.9–2.5 | 1.8–1.9 | 2.0–2.3 | 2.1–2.3 | 2.6 | 1.6–2.7 | 1.9–2.4 |
| Ventrals | 199 | 201 | 198 | 190 | 180 | 169–180 | 183–207 | 164–175 | 181–188 | 179 | 166–180 | 169–188 |
| Subcaudals | 48 | 46 | 47 | 52 | 50 | 46–54 | 49–51 | 47–48 | 46–51 | 42 | 40–52 | 41–47 |
| Loreal | Present | Present | Present | Absent | Present | Present | | | | Absent | | |
| Postocular | 2 | 2 | 2 | 2 | 1 | 2 | | | | 2 | | |
| Preocular | Single | | | | | Single | | | | Single | | |
| Cloacal plate | Divided | | | | | Divided | | | | Divided | | |
| Nasal scale | Completely divided | | | | | Completely divided | | | | Entire; rarely divided partially | | |
| Temporals | 1 + 2 | | | | | 1 + 2 | | | | 1 + 2 | | |
| Supralabials | 7 | | | | | 7 | | | | 7 | | |
| Infralabials | 7 | | | | | 7 | | | | 7 | | |
| Nature of cross markings on body | Bands; anteriorly blotched | | | | | Stripes | | | | Bands | | |
| No. of cross markings on body + tail | (25–35) + (4–9) | | | | | (30–45) + (6–10) | | | | (15–20) + (3–6) | | |
| Anterior bands/stripes relatively | Extremely enlarged | | | | | Subequal / slightly enlarged | | | | Subequal | | |
| Thickness of the band (midbody) | 4–6 vertebral scales | | | | | 1–2 vertebral scales | | | | 2–3 vertebral scales | | |
| Distance between bands (midbody) | 2–4 vertebral scales | | | | | 4–6 vertebral scales | | | | 7–12 vertebral scales | | |
| Shape of marking on nape | Triangular | | | | | Inverted Y | | | | Inverted V | | |

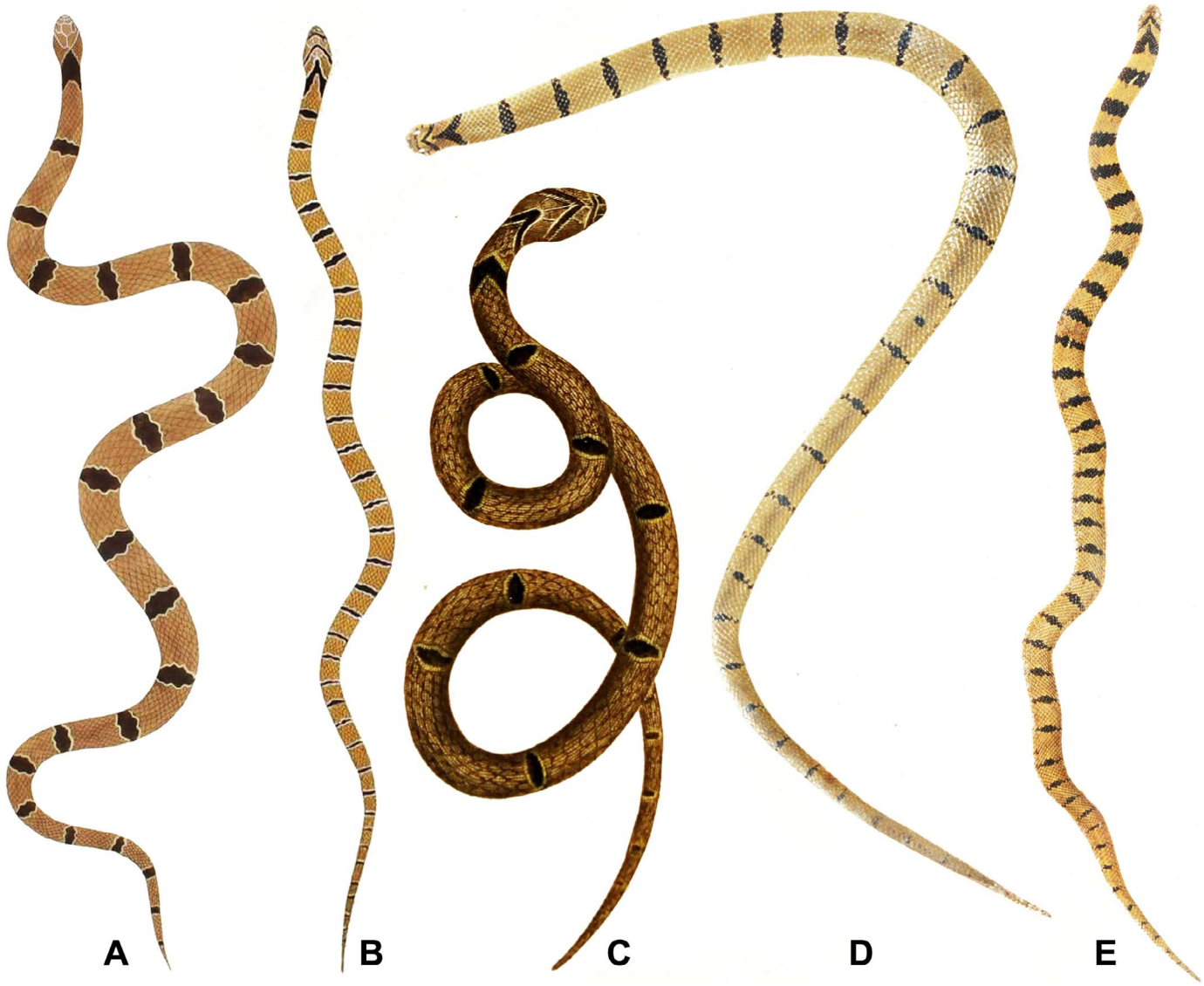


FIG. 3.—(A) Illustration (depicted by Russell 1796:Plate 38, resized) of the holotype of *Coluber arnensis* Shaw 1802; (B) the illustration (depicted by Russell 1796:Plate 35, resized) of the lectotype (designated here) of *C. russelius* Daudin 1803; (C) the illustration (depicted by Daudin 1803:Plate 76, resized) of the paralectotype of *C. russelius* here identified as an individual of *Oligodon arnensis*; (D) a dry skin from Russell's collection (fide Bauer et al. 2015; NHMUK 1837.9.26.33) preliminarily assigned as the dry skin of Russell's Plate 35 (note that the arrangement of dorsal cross stripes exactly matches with Plate 35, but there is a length mismatch); (E) a dry skin from Russell's collection (fide Bauer et al. 2015; NHMUK 1837.9.26.32) preliminarily assigned as the dry skin of Russell's Plate 38 (note the arrangement of dorsal cross bands clearly mismatch with Plate 38). A color version of this figure is available online.

only around 16 to 20 cross bands (Fig. 3B); he probably wanted to assign it also to the second variety. The first paralectotype of *O. russelius*, i.e., the specimen depicted on Russell's Plate 38 (Fig. 3D) is in fact the holotype of *C. arnensis* whereas the second paralectotype, i.e., the specimen depicted on Daudin's Plate 76 (Fig. 3B) also agrees well with *C. arnensis*, hence we assign them to *O. arnensis* sensu stricto. We did locate several individuals (not collected; Fig. 6B) from the vicinity of type locality of *O. arnensis*, Arani in southern India. Also, several other specimens (including museum specimens) from South India, in the same biogeographic region of the type locality (Appendix) matched well with the snake illustrated on Russell's Plate 38, i.e., the holotype.

We examined two assigned dry skins from Russell's collection (fide Bauer et al. 2015), deposited at NHMUK (NHMUK 1837.9.26.33 [Fig. 3D] and 1837.9.26.32 [Fig. 3E]) which were preliminary assigned to Russell's (1796) illustrations in Plate 35 and Plate 38 respectively. The snake depicted in Plate 35 (now *O. russelius*) has 34 cross bands (Fig. 3B) as well as in the assigned dry skin at the NHMUK (Fig. 3D). However, on Page 41 of Russell (1796), he clearly stated that this illustration was based on an 8-in (~203-mm) snake (clearly a juvenile), but the dry skin measures 21.5 in (~546 mm). Although the shape and the number of cross bands are clearly matched, the gross mismatch of the lengths lead us to reject it being as labelled the original dry skin of Russell's Plate 35. Interestingly, the length of this skin (NHMUK 1837.9.26.33; Fig. 3D) exactly matches the length

TABLE 2.—The current status of the referred materials by Russell (1796), Shaw (1802), and Daudin (1803). Dash (—) = not applicable.

| Russell (1796) | Shaw (1802) | Daudin (1803) | Current status (this work) |
|---|---|---|---|
| Plate 35: based on an 8-in specimen with 34 cross stripes | — | Referred to name *C. russelius* first variety | Recognized as one of the original syntypes of *C. russelius* and designated as the lectotype of *O. russelius* comb. nov. |
| Plate 38: based on a 21-in specimen with 22 cross bands | Referred to name *C. arnensis* | Referred to name *C. russelius* second variety | Recognized as the holotype (by monotypy) of *O. arnensis* (also the first paralectotype of *O. russelius* comb. nov. as one of the original syntypes of *C. russelius*). |
| — | — | Plate 76: an unknown specimen with ~20 cross bands, referred to name *C. russelius* second variety | Recognized as one of the original syntypes of *C. russelius* (now the second paralectotype of *O. russelius* comb. nov.). Here identified as an individual of *O. arnensis*. |
| Dry skin (NHMUK 1837.9.26.33) fide Bauer et al. (2015): a 21.5-in specimen with 34 cross stripes | — | — | The label referred to Russell's Plate 35, but the size is a mismatch. Therefore, rejected as the original dry skin of lectotype of *O. russelius*; here identified as just a dry skin of an individual of *O. russelius* comb. nov. |
| Dry skin (NHMUK 1837.9.26.32) fide Bauer et al. (2015): a 19-in specimen with 39 cross bands | — | — | The label referred to Russell's Plate 38, but the size and bands mismatch. Therefore, rejected as the original dry skin of holotype of *O. arnensis*; here identified as just a dry skin of an individual of *O. russelius* comb. nov.; probably this is the second specimen that Russell mentioned from Masulipatam (now Machilipatnam). |

of the snake used to illustrate Plate 38 of *O. arnensis* (Fig. 3A), which is a coincidence, but the shape and number of cross bands of this skin do not match the Plate 38 of *O. arnensis*.

The snake depicted in Plate 38 (now *O. arnensis*) has 22 cross bands (Fig. 3A), but the assigned dry skin at the NHMUK has 39 (Fig. 3E), and such an immense dissimilarity is beyond a simple counting mistake explanation. Furthermore, on Page 43 of Russell (1796), he clearly stated that illustration was based on a 21.5-in (~546-mm) snake, but the assigned dry skin measures only 19 in (~483 mm). Although the difference of 2.5 in can be considered as an artefact of the skinning process, the mismatch of the shape and the number of cross bands lead us to reject it being as stated, the original dry skin of Russell's Plate 38.

Furthermore, we identified that both dry skins are of individuals of *O. russelius* comb. nov. In the description of "Katla Tutta" (now *O. russelius* comb. nov.), Russell (1796) mentioned that he received another individual (preserved in alcohol) from Masulipatam (now Machilipatnam), Andhra Pradesh, India, which he called "cobra-monil." Perhaps Russell skinned that specimen and added it to his skin collection; if so NHMUK 1837.9.26.32 would be the second individual he mentioned from Machilipatnam which represents the central Indian morph. Also, we identified that the other dry skin, NHMUK 1837.9.26.33, is an adult individual of the northern Indian morph, but the origin is unknown. See the species account of *O. russelius* comb. nov. for further details on color morphs.

Here we compared the voucher specimens and illustration of the lectotype (Plate 35 of Russell 1796; Fig. 3B) of *Oligodon russelius* comb. nov. with the voucher specimens and illustration of the holotype (Plate 38 of Russell 1796; Fig. 3A) of *O. arnensis* sensu stricto. Based on our comparison in the morphometric analysis (Fig. 1), the holotype specimen (NHMUK 1946.1.4.36) of *S. albiventer* was well placed in the cluster of the other *O. arnensis* voucher specimens from southern India. *Simotes albiventer*, which was collected from Kandy, Sri Lanka, morphologically matches the topotypical *O. arnensis* from southern India, hence we confirm Smith's (1943) view as regarding *S. albiventer* a junior synonym of *O. arnensis*. Therefore, we first restrict the distribution of *O. arnensis* to both southern India and Sri Lanka, and describe it based on six specimens from southern India.

The populations of the western India are morphologically distinct enough to be considered an undescribed species requiring a new name; hence we describe it below as a new species. We assign both the new species and *C. russelius* to the genus *Oligodon* based on the following combination of characters: head not distinct from neck, large rostral shield, visible from above, eye small, pupil rounded, one large preocular, internasals present, ventrals rounded, tail short, 17-17-15 smooth DSRs throughout the body, paired cloacal plate, and subcaudal plates divided (Wallach and Bauer 1996).

## SYSTEMATICS

### *Oligodon* ***arnensis*** (Shaw 1802) sensu stricto
(Tables 1–3; Figs. 3A, 3C, 4–7, 9)

*Coluber arnensis* Shaw 1802 (based on specimen depicted on Russell's [1796] Plate 38).

*Coluber russelius* Daudin 1803 (partim: second variety [Plate 76]).

*Lycodon russelius*—Wagler 1830.

*Coronella russelii*—Schlegel 1837 (partim).

*Simotes russellii* (sic)—Merrem 1820 (partim); Duméril et al. 1854 (partim); Günther 1858 (partim); Jan 1865 (partim); Theobald 1868 (partim); Nicholson 1874 (partim; their Fig. 2 [below] in Plate 11); Jan and Sordelli 1882 (partim; their Fig. 1A in Livraison 11); Ferguson 1887.

*Oligodon purpurascens* var. A Günther 1858.

TABLE 3.—Main characters of the *Oligodon* species with 17 dorsal scale rows at midbody. Exceptional values are placed in parentheses. Sup = supralabials; e = entire; d = divided; p = present; a = absent; ? = unknown.

| Species | Hemipenes | Maxillary teeth | Sup | Nasal | Anal | Loreal | Ventrals | Subcaudals | Dorsal coloration |
|---|---|---|---|---|---|---|---|---|---|
| *O. affinis* | Not forked | 7 | 7 | d | d | a, p | 129–145 | 23–36 | Uniform; 33–38 indistinct stripes |
| *O. ancorus* | Not forked | 7–9 | 7, 8 | ? | e | p | 147– 173 | 32–46 | 14–22 dark cross bands; red vertebral line |
| *O. arenarius* | ? | 6–8 | 7, 8 | d | e | a | 131–144 | 36–60 | Uniform; indistinct dark speckling |
| *O. arnensis* sensu stricto | Not forked | 14–16 | 7 | e | d | a | 164–188 | 40–52 | 15–20 equal sized, black cross bands |
| *O. barroni* | Forked | 10–13 | 7, 8 | d | e | p | 136–160 | 28–48 | 10–14 dark blotches |
| *O. booliati* | ? | ? | 6, 7 | d | e | p | 143–153 | 54–60 | 19–22 faint brown cross bands |
| *O. cattienensis* | Forked | 8–10 | 8 | e | e | p | 167–178 | 31–35 | 24–35 blotches; pale vertebral line |
| *O. chinensis* | Forked | 9, 10 | 7, 8 | d | e | p | 170–206 | 31–65 | 10–15 black cross bands |
| *O. churahensis* | Forked | 8–10 | 7 | d | d | p | 170–175 | 46–48 | 54–62 equal sized, black cross stripes |
| *O. cinereus* | Not forked | 10–14 | 7, 8 | d | e | p | 155–180 | 32–43 | Reticulations |
| *O. condaoensis* | Forked | 11–13 | 8 | d | e | p | 168–176 | 33–37 | Uniform; indistinct body stripes |
| *O. cruentatus* | Not forked | 14–16 | 8 | d | d | a, p | 148–173 | 27–40 | Light brown; dark longitudinal lines |
| *O. culaochamensis* | Forked | 9, 10 | 8 | d | e | p | 167–182 | 51–66 | 13 dark blotches |
| *O. deuvei* | Forked | 12–15 | 7, 8 | d | e | p | 140–163 | 31–47 | 1 longitudinal stripe |
| *O. erythrogaster* | Not forked | 7, 8 | 7 | e | d | a | 163–186 | 42–59 | Longitudinal stripes |
| *O. forbesi* | ? | 8–12 | 7 | d | e | p | 150–170 | 43–51 | Longitudinal stripes |
| *O. joynsoni* | Not forked | 11, 12 | 7–8 | d | e | p | 186–200 | 32–50 | Reticulations |
| *O. macrurus* | Forked | 13 | 7, 8 | d | e | a, p | 139–162 | 45–94 | Uniform; indistinct cross bands |
| *O. maculatus* | Not forked | 9 | 7 | d | e | a, p | 156–164 | 52–55 | Up to 24 broad, saddle-shaped crossbars |
| *O. melanozonatus* | ? | 8 | 6, 7 | e | d | a | 171–173 | 42–45 | Black mottles, 24 indistinct dark bands |
| *O. meyerinkii* | Not forked | 9 | 6, 7 | d | e | p | 154–169 | 38–57 | Light brown with longitudinal stripes |
| *O. moricei* | Forked | 12 | 8 | d | e | p | 175 | 41 | Broad, pale vertebral line |
| *O. mouhoti* | Forked | 14–16 | 7, 8 | d | e | p | 143–169 | 29–43 | Pale vertebral line |
| *O. nagao* | Forked | 9, 10 | 7, 8 | e | e | p | 184–193 | 43–47 | 27–37 dark blotches |
| *O. octolineatus* | Not forked | 9, 10 | 6 ,7 | d | e | p | 155–197 | 42–63 | Longitudinal stripes |
| *O. perkinsi* | ? | 8 | 7 | d | e | p | 183–188 | 34–52 | Blotches forming poorly defined cross bands |
| *O. phangan* | ? | 12 | 8 | d | e | P | 163–166 | 33–42 | Pale vertebral lines |
| *O. promsombuti* | Forked | 12 | 8 | d | e | P | 177 | 40 | 2 pale paravertebral stripes |
| *O. pseudotaeniatus* | Forked | 15 | 8 | d | e | p | 137–156 | 44–46 | 2 dark paravertebral stripes |
| *O. pulcherrimus* | ? | 8, 9 | 7 | d | d | p | 152–179 | 38–53 | 28–38 oval blotches |
| *O. russelius* comb. nov. | Forked | 8–10 | 7 | d | d | p | 169–207 | 46–54 | 30–45 equal sized, black cross stripes |
| *O. saintgironsi* | Forked | 10–12 | 8 | d | e | p | 166–184 | 53–59 | 10–13 dark blotches |
| *O. saiyok* | ? | 13 | 8 | d | e | p | 181–187 | 38–43 | 21 or 22 dark blotches / white rings |
| *O. signatus* | ? | 7, 8 | 7 | d | e | p | 141–160 | 43–59 | Broad orange bands with thin light bands in between |
| *O. theobaldi* | Not forked | 15, 16 | 8 | d | d | a | 164–180 | 27–49 | Longitudinal vertebral stripe |
| *O. tillacki* sp. nov. | Forked | 12 | 7 | d | d | a, p | 180–201 | 46–52 | 25–35 black cross bands with 5–8 bands enlarged anteriorly |
| *O. travancoricus* | Not forked | 7 | 7 | d | d | a | 145–155 | 34–37 | 29–33 dark cross stripes |
| *O. trilineatus* | ? | 7–8 | 7 | d | e | p | 145–162 | 39–62 | Tri–colored dorsum; vertebral stripe |
| *O. unicolor* | ? | ? | 6 | d | e | p | 162 | 41 | Uniform |
| *O. venustus* | Not forked | 7–8 | 7 | d | d | a | 138–165 | 27–36 | Triple spots |
| *O. woodmasoni* | Not forked | 8–10 | 6 | d | e | a, p | 180–190 | 46–57 | Dark and pale longitudinal stripes |

*Simotes russellii* var. α Günther 1864 (partim).
*Simotes russellii* var. δ Günther 1864.
*Simotes albiventer* Günther 1864.
*Simotes albiventer*—Theobald 1876.
*Simotes russellii* var. *ceylonensis* Müller 1887.
*Simotes arnensis*—Boulenger 1890 (partim), 1894 (partim); Abercromby 1910 (partim).
*Oligodon arnensis*—Wall 1921 (partim); Smith 1943 (partim); Taylor 1950; De Silva 1980 (partim); Somaweera 2006; Karunarathna and Amarasinghe 2010, 2011, 2012; Karunarathna et al. 2010, 2013; Gayathri et al. 2016; Jayaneththi 2016; Karthik et al. 2018; Ganesh et al. 2018, 2020; Samarawickrama et al. 2019; Tillack et al. 2021.
*Oligodon arnensis albiventer*—Deraniyagala 1936, 1955.

**Holotype (by monotypy).**—An adult specimen of 457.2 mm SVL (probably a male due to low ventrals count, 169 fide Russell [1796:43]) collected from Arnee (now Arani; 12°40′16.81″N, 79°16′54.33″E, datum = WGS84; 145 m above sea level [a.s.l.]), Tamil Nadu, India, by Major Bonnivaeux (received by P. Russell in October 1788). Specimen was depicted by Russell (1796) in Plate 38 (see Fig. 3A).

**Diagnosis (redefined herein).**—*Oligodon arnensis* sensu stricto is distributed in southern India and Sri Lanka, and is distinguished from other congeners by having the following combination of characters: adults reach maximum SVL 550 mm, a single preocular, two postoculars, no loreal scale, divided cloacal plate, entire nasal scale or partially divided in some populations, ventrals 164–175 in males and 181–188 in females, subcaudals 46–52 in both males and females combined, temporals 1 + 2, seven supralabials with third and fourth in contact with eye, DSRs 17-17-15, TL 13.5–17.1% of total length in males, olive brownish dorsum with 15–20 more or less equal sized black cross bands (with thickness of 3–4 vertebral scales and 7–12 scales in between cross bands at midbody position) along the body and 3–6 on the tail, two V-shaped black markings on interorbital and parietal–frontal regions, another inverted V-shaped black marking on the nape. *Oligodon arnensis* is most similar to *O. russelius* comb. nov., *O. churahensis*, and the new species, but differs by having several diagnostic characters—see Table 1.

**Redescription.**—Based on examined preserved materials (Appendix, $n = 6$ from southern India) adults with SVL 147–350 mm, TL 23.0–71.0 mm; head elongate (HL 3.2–4.5% of

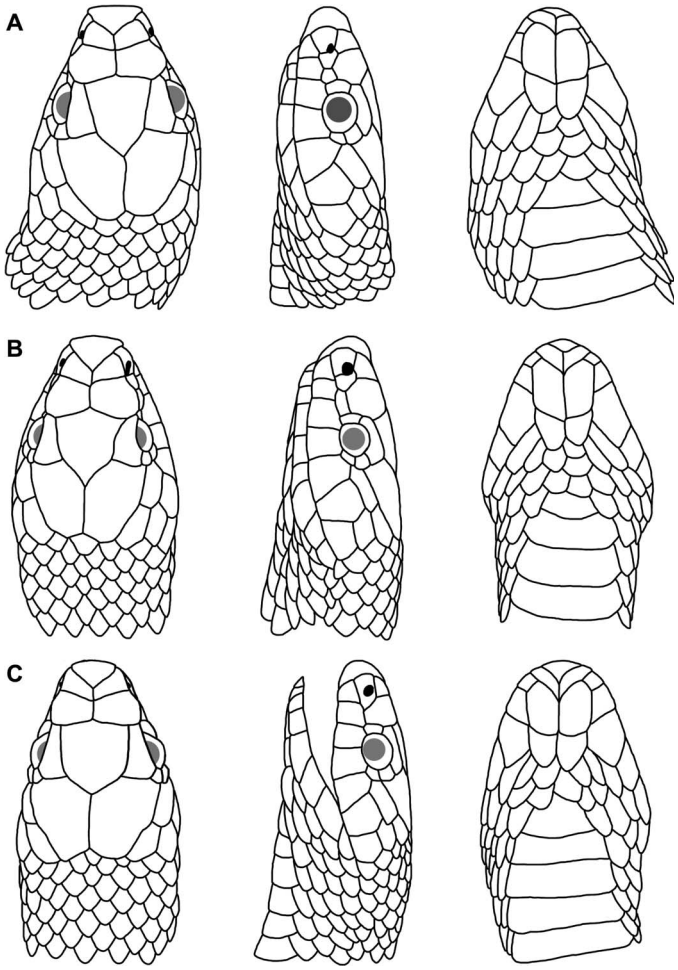


FIG. 4.—Dorsal, lateral, and ventral head views of (A) holotype of *Oligodon tillacki* sp. nov. (MNHN-RA 1946.0058), (B) a voucher of *O. russelius* comb. nov. (NHMUK 1907.2.14.30), and (C) a voucher of *O. arnensis* (NHMUK 1964). Illustrations by AATA (not to scale).

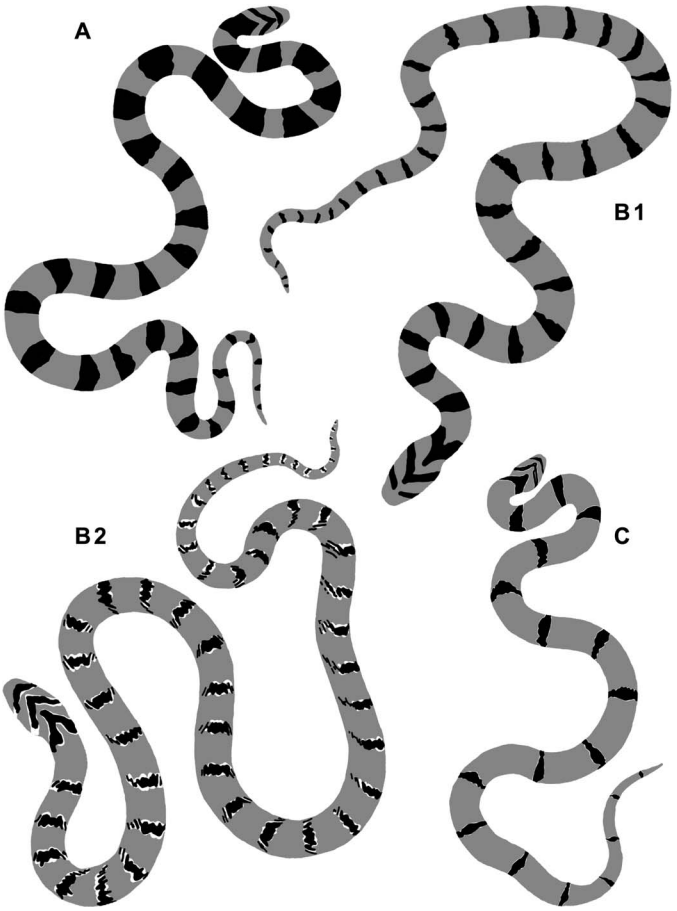


FIG. 5.—Arrangement of dorsal cross stripes and cross bands of (A) *Oligodon tillacki* sp. nov., (B) *O. russelius* comb. nov. (B1) central Indian morph and (B2) northern Indian morph, and (C) *O. arnensis* sensu stricto. Illustrations by AATA (not to scale).

SVL), wide (HW 62.2–81.7% of HL), slightly flattened, indistinct from neck; snout elongate (ES 32.1–35.3% of HL), moderate, flat in dorsal view, pointed in lateral profile, rather depressed.

Rostral shield large, flat, distinctly visible from above, pointed posteriorly; interorbital width broad (IO 49.6–62.2% of HW); internasals subtriangular; nostrils rather large, nasals large and elongated, in anterior contact with rostral, and internasal and prefrontal dorsally, first and second supralabials ventrally, prefrontal posteriorly; no loreal; prefrontal rather large, broader than long, and subhexagonal; frontal large, pentagonal, short, length same as width; supraoculars narrow, short, subrectangular, posteriorly wider; parietals large, elongate, butterfly-wing-like in shape, bordered by supraoculars, frontal, upper or both postocular anteriorly, anterior and upper posterior temporals, and five or six nuchal scales posteriorly; one preocular, vertically elongated, subrectangular, in contact with prefrontal anteriorly, supraocular dorsally, and third supralabial ventrally; eye moderate (ED 13.2–19.9% of HL), round, nearly half of the size of snout length (ED 41.0–56.3% of ES), pupil rounded; two postoculars, subequal or sometimes upper one larger, rounded or subquadrangular, upper postocular in broad contact with supraocular and parietal, lower postocular in contact with anterior temporal and fourth and fifth supralabials; temporals 1 + 2, elongated, subrectangular; anterior temporal almost the same size as upper posterior temporal, in contact with parietal and both postoculars dorsally, and fifth and sixth supralabials ventrally; lower posterior temporal in contact with sixth and seventh supralabials ventrally. Supralabials seven (on both sides), 5th–7th largest in size; first supralabial in contact with rostral anteriorly, nasal dorsally, second with nasal and prefrontal dorsally, third with preocular and orbit dorsally, fourth with orbit and the lower postocular dorsally, fifth with lower postocular and anterior temporal dorsally, and sixth with anterior and lower posterior temporals dorsally, seventh with lower posterior temporal dorsally and scales of the neck posteriorly.

Mental of smaller size, triangular; first infralabial pair larger than mental plate and in broad contact with each other, in contact with anterior chin shields posteriorly; seven infralabials, 1st–3rd in contact with anterior chin shields, fourth infralabial largest in size in contact with both anterior and posterior chin shields; 4th–7th infralabials in contact with gular scales; two larger anterior chin shields, and two smaller posterior chin shields; anterior chin shields in broad


FIG. 6.—Live photographs of (A) *Oligodon tillacki* sp. nov. from Pune, Maharashtra, India, (B) *O. arnensis* from Cheyyar near Arani (type locality), Tamil Nadu, India, (C) *O. russelius* comb. nov. central Indian morph from Jabalpur, Madhya Pradesh, India, and (D) *O. russelius* comb. nov. northern Indian morph from Dhanbad, Jharkhand, India. Photographs by VRKS and SRG.

contact between them; posterior chin shields bordered posteriorly by six gular scales.

Body robust, elongate and subcylindrical; dorsal scales in 17-17-15 rows, all smooth and pointed posteriorly; 164–175 ventrals in males and 181–188 in females; cloacal plate divided. Tail comparatively short (TL 13.5–17.1% of total length in males), robust and thick; subcaudals 47–48 in males and 46–51 in females, divided.

**Coloration.**—In preservative, dorsum light olive brown, lateral surface paler and yellowish; 15–20 black cross bands along the body and 3–6 on the tail; cross bands complete laterally, and almost reaching the ventrals; the markings on the tail distinct; two inverted V-shaped black markings on the head, (1) the first one on the interorbital region, starting from anterior edge of supraoculars, pointing forward to prefrontal–internasal region; in some individuals the V-shaped marking almost C-shaped; (2) the second one on the parietal–frontal region, starting from the gape of the mouth, pointing forward to frontal region, and complete the V shape at the interorbital position; another thick, inverted V-shaped black marking on the nape, starting from the lateral neck, pointing forward to the level of the interparietal region; dark blotches below the eye on each side, usually on the second, fourth, and fifth supralabials; all the dark markings are colored in a range of dark brown, from chocolate brown to black; venter uniform yellow or cream.

In life (Fig. 6B), same color as in preservative, but all the dark markings may be visible in a range of grey, from dark grey to black; venter uniform cream. Cross bands of juveniles are faintly margined with white and absent in adults.

**Skull and dentition.**—A complete and robust skull displays a generalized colubrid pattern (Fig. 9A); premaxilla

single, flat anteriorly, with a broad ascending process, a prominent nasal crest, and a relatively short transverse process; nasals elongate, triangular, lateral processes tapering anteriorly to form a pointed process, but bifurcating largely at the point of articulation with the ascending process; parietals smooth, anterior process curved and pointed forward in between frontals; maxilla with 14–16 functional teeth, gradually increasing in size posteriorly; palatine with 8 or 9 teeth; pterygoid and mandible with 14 or 15 teeth on each.

**Distribution.**—*Oligodon arnensis* sensu stricto is known from 33 localities in southern India and 76 localities in Sri Lanka (Fig. 10). Based on the reliable localities for this species (at least with photographic evidence), it occurs only in deciduous forests below 1500 m a.s.l. This is a common, widespread, and human commensally species in southern India (partly in Daniel 2002; Das 2002, 2010; Whitaker and Captain 2004) and Sri Lanka (Deraniyagala 1955; Das and de Silva 2005; Somaweera 2006). Our observations revealed low altitudinal areas in southern India and Sri Lanka as a potential distribution envelope for *Oligodon arnensis*. It is evident that these areas have low to moderate rainfall conditions. Most of the specimens were recorded from the lower peneplain between the southern parts of the Coromandel Coast and the Eastern Ghats across the Kaveri River tracts and delta. The northernmost recorded locality is Bellary, Karnataka (northern edge of Mysore plateau), while the westernmost record was from Davengere/Shivamogga regions, and all the known distribution points of *O. arnensis* are present only south of the Thungabadhra-Krishna river stretches, which probably acted as a biogeographic barrier for this taxon.

It seems that Palk Strait separating the Indian peninsula and Sri Lanka are not barriers as this is a species widely distributed on the island, except in the highlands. In Sri Lanka, most of the specimens reported from the southwestern lowland, and less in the lowland dry zone. The montane regions of the Western Ghats in India and the highlands of Sri Lanka were recognized as totally unsuitable areas for *O. arnensis*. Therefore, compared to the others, *O. arnensis* is actually the least spread member of this *O. arnensis* species complex in India.

**Natural history.**—Although *Oligodon arnensis* sensu stricto is an arrhythmic and nonvenomous species, active in both day and night, depending on the prevailing weather, it is mostly found in twilight or at the onset of the night. During the hot midday, it is often hidden under leaf litter, fallen logs, loose soil mounds, wall crevices, and piles of rubble. Although it is terrestrial, we found that it also has subfossorial habits, especially foraging among the vegetation roots in loose soil. This species is found in various habitats including agricultural areas, grasslands, scrub forests, secondary rain forests, and especially in anthropogenic habitats where it is most abundant due to the availability of prey. It has been known to feed on mice pups, litter skinks (*Riopa* sp., *Lankascincus* sp.), and smaller geckos (*Hemidactylus* sp.) as well as on a variety of small reptile eggs (oophagy). This species is sexually dimorphic where adult males (average SVL = 327.1 mm; $n = 22$) are larger than adult females (average SVL = 271.9; $n = 11$). During the mating season, adult males perform territorial combat. It is oviparous. The clutch contains 3–5 elongate eggs usually laid inside termitaria, holes, and crevices. Egg dimension was measured as $30 \times 10$ mm and the SVL of the hatchlings are around 168.0 mm (Deraniyagala 1955). Hatchlings are light greenish in color with faded and less prominent cross bands in the southern India and Sri Lankan dry zones, but they are much darker in the populations of the Sri Lankan wet zone. Occasionally, neonates have faded and have incomplete cross stripes in between regular cross bands. The juveniles have been mostly observed in March and during the monsoon (June–September). It is not very defensive and can be quite shy, but bites occasionally. The bite cuts the skin due to the long kukri-knife-shaped teeth. Karunarathna et al. (2017) reported this species as a prey of Bengal Monitors, *Varanus bengalensis* (Daudin 1803).

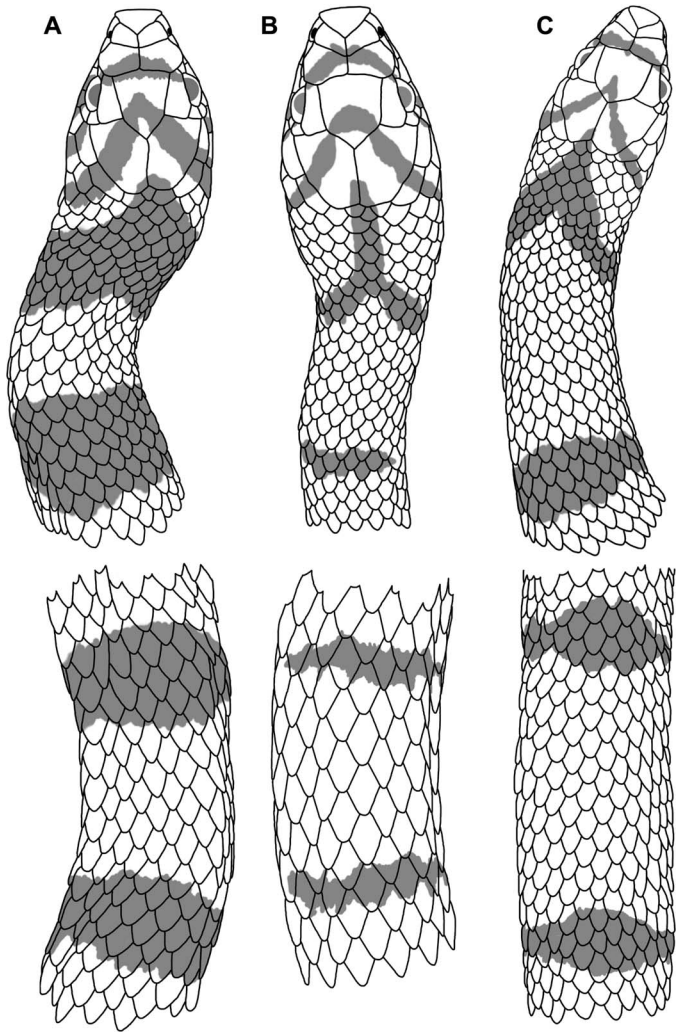


Fig. 7.—Anterior and midbody dorsal scales, and body color pattern of (A) holotype of *Oligodon tillacki* sp. nov. (MNHN-RA 1946.0058), (B) a voucher of *O. russelius* comb. nov. (ZSI 26047), and (C) a voucher of *O. arnensis* (NHMUK 1964). Illustrations by AATA (not to scale)

**Conservation status.**—The application of the Red List Criteria (IUCN 2019) with the updated distribution data shows that *Oligodon arnensis* is restricted to an area of occupancy of 463 $km^2$ recorded from 33 localities within a 124,508-$km^2$ extent of occurrence in India. Given the wider area of occurrence, here we suggest classifying it as a "Least Concern" species for India. Due to its higher abundance

around human settlements, domestic cats have been identified as the major threat for this species. In addition, the data collected from social media platforms reveal that it is in the top five lists of species often getting killed by humans due to misidentification. The presence of cross bands is frequently the reason this harmless colubrid gets misidentified as a venomous elapid, *Bungarus* sp. In both South India and Sri Lanka, this species has been regularly listed in snake rescue projects and in vehicular traffic mortalities. Also, this species is widely distributed in protected areas in South India such as Guindy National Park, Vedanthangal Bird Sanctuary, Point Calimere Sanctuary, and also those near the Western Ghats, where they occur in low, leeward slopes—in Kalakkad-Mundanthurai Tiger Reserve, Anamalai Tiger Reserve, Sathyamangalam Tiger Reserve, and Mudumalai Tiger Reserve. The application of the Red List Criteria (IUCN 2019) with the updated distribution data shows that *O. arnensis* is restricted to an area of occupancy of 792 $km^2$ recorded from 76 localities within a 38,374-$km^2$ extent of occurrence in Sri Lanka. Given the wider area of occurrence, here we suggest classifying it as a Least Concern species for Sri Lanka.

*Oligodon* ***russelius*** (Daudin 1803) comb. nov.
(Tables 1–3; Figs. 3B, 3D, 3E, 4–7, 9)

*Coluber russelius* Daudin 1803 (partim: based on specimen depicted on Russell's [1796] Plate 35).
*Simotes russelii* (sic)—Merrem 1820 (partim); Duméril et al. 1854 (partim); Günther 1858 (partim); Jan 1865 (partim); Theobald 1868 (partim); Anderson 1871; Jan and Sordelli 1882 (partim; their Fig. 1B in Livraison 11).
*Coronella russelii*—Schlegel 1837 (partim).
*Lycodon russellii* (sic)—Jerdon 1853 (partim).
*Simotes russellii* var. α Günther 1864 (partim).
*Simotes arnensis*—Boulenger 1890 (partim); Abercromby 1910 (partim).
*Oligodon arnensi*—Wall 1921 (partim); Smith 1943 (partim); De Silva 1980 (partim); Dutta et al. 2009; Ingle 2011; Nitin et al. 2012; Chettri and Chhetry 2013; Jadhav et al. 2014, 2018; Pandirkar et al. 2015; Bhattarai et al. 2017; Gayen et al. 2017; Shrestha 2017; De et al. 2018; Manhas et al. 2018; Sheikh et al. 2018; Das et al. 2019; Masroor et al. 2019; Deshmukh et al. 2020a,b; Devkota et al. 2020; Mahajan and Murugesan 2020; Rawat et al. 2020; Barhadiya and Ghosh 2021; Bhandarkar and Paliwal 2021.

**Lectotype (designated herein).**—A juvenile specimen of 171.4 mm SVL (probably a female due to high ventral count, 188 [fide Russell 1796:41]) collected from Vizagapatam (now Visakhapatnam; 17°41′12.54″N, 83°13′06.53″E, datum = WGS84; 169 m a.s.l.), Andhra Pradesh, India. Specimen was depicted by Russell (1796) in Plate 35 (see Fig. 3B).

**Diagnosis.**—*Oligodon russelius* comb. nov. is distributed in central, east and northern India, and is distinguished from other congeners by having the following combination of characters: adults reach maximum SVL 650 mm, a single preocular, two postoculars, a single loreal, divided cloacal plate, completely divided nasal, ventrals 169–180 in males and 183–207 in females, subcaudals 46–54 in both males and females combined, temporals 1 + 2, seven supralabials with third and fourth in contact with eye, DSRs 17-17-15, TL 17.0–18.9% of total length in males, olive brownish dorsum with 30–45 more or less equal in size, pale-edged black cross stripes (with thickness of 1–2 vertebral scales and 4–6 scales in between cross stripes at midbody position) along the body and 6–10 on the tail, two V-shaped black markings on interorbital and parietal–frontal regions, another inverted Y-shaped black marking on the nape. *Oligodon russelius* comb. nov. is most similar to *O. arnensis* and the new species, but differs by having several diagnostic characters—see Table 1. *Oligodon russelius* comb. nov. is also similar to *O. churahensis*, but differs by having 30–45 (vs. 48–56) cross stripes with 4–6 (vs. 2–4) vertebral scales in-between cross stripes at midbody position along the body and 6–10 (vs. 10–12) on the tail, inverted Y-shaped black marking (vs. elongated heart symbol) on the nape.


FIG. 8.—(A) Adult female holotype of *Oligodon tillacki* sp. nov. (MNHN-RA 1946.0058) collected from Kurduvadi, Solapur, Maharashtra, India. (B) The first illustration known to be depicted an individual of *Oligodon tillacki* sp. nov. Illustrated by Nicholson (1874:Fig. 2 above in Plate 11; resized), but formerly identified as *Simotes russellii* (sic). A color version of this figure is available online.

**Redescription.**—Based on examined materials (Appendix, $n = 11$). Adults with SVL 318–468 mm, TL 59.5–98.7 mm; head elongate (HL 3.1–4.7% of SVL), wide (HW 58.2–71.4% of HL), slightly flattened, indistinct from neck; snout elongate (ES 27.2–34.3% of HL), moderate, flat in dorsal view, rounded in lateral profile, rather depressed.

Rostral shield large, flat, distinctly visible from above, pointed posteriorly; interorbital width broad (IO 49.3–60.2% of HW); internasals subtriangular; nostrils rather large, nasals large and elongated, divided by the nostril, in anterior contact with rostral, internasal and prefrontal dorsally, first and second supralabial ventrally, loreal posteriorly; loreal single, elongate horizontally; prefrontal rather large, broader than long, and subhexagonal; frontal large, pentagonal, elongate, shortened posteriorly and longer than wide; supraoculars narrow, short, subrectangular, posteriorly wider; parietals large, short, butterfly-wing-like in shape, bordered by supraoculars, frontal, upper postocular anteriorly, anterior and upper posterior temporals, and three or four nuchal scales posteriorly; one preocular, vertically elongated, pentagonal, in contact with prefrontal and loreal

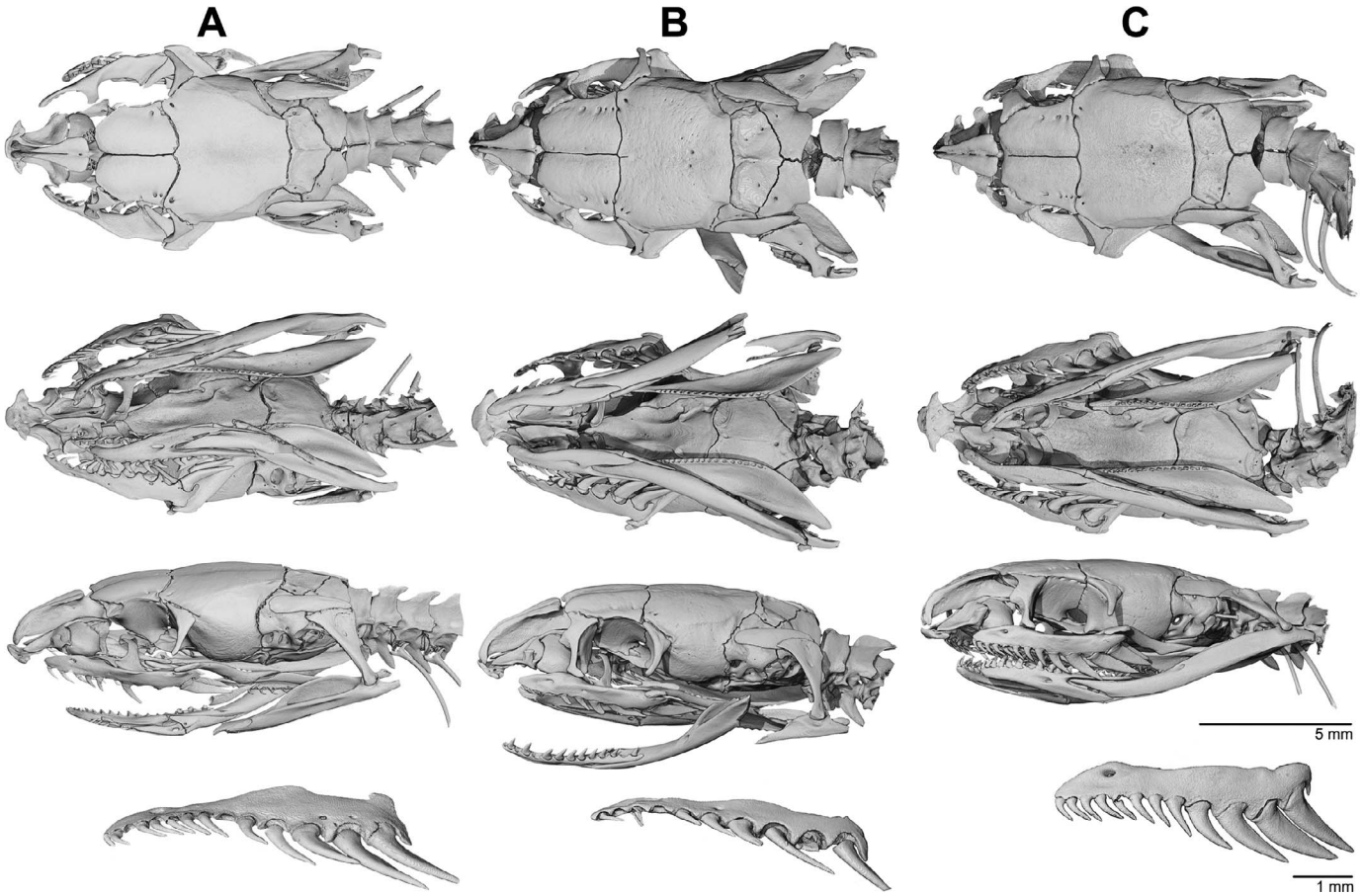


FIG. 9.—Dorsal, lateral, and ventral skull views (scale = 5 mm) and the maxilla (scale = 1 mm; note that scanning angles are slightly different) of (A) a voucher of *O. arnensis* (NHMUK 1964), (B) a voucher of *O. russelius* comb. nov. (NHMUK 1907.2.14.30), and (C) holotype of *Oligodon tillacki* sp. nov. (MNHN-RA 1946.0058). For (A), some of the maxillary teeth on the left side of the lateral view are not visible, due to the old age of the specimen or an artefact of the scan.

anteriorly, supraocular dorsally, and third supralabial ventrally; eye moderate (ED 12.2–18.9% of HL), round, nearly half of the size of snout length (ED 38.5–58.0% of ES), pupil rounded; two postoculars, subequal or sometimes upper one larger, rounded or subquadrangular, upper postocular in broad contact with supraocular and parietal, lower postocular in contact with anterior temporal and fourth and fifth supralabials; temporals 1 + 2, elongated, subrectangular; anterior temporal almost the same size as lower posterior temporal, in contact with parietal and both postoculars dorsally, and fifth and sixth supralabial ventrally; lower posterior temporal in contact with sixth and seventh supralabials ventrally. Supralabials seven (on both sides), 5th–7th largest in size; first supralabial in contact with rostral anteriorly, anterior and posterior nasals dorsally, second with posterior nasal and loreal dorsally, third with loreal, preocular and orbit dorsally, fourth with orbit and the lower postocular dorsally, fifth with lower postocular and anterior temporal dorsally, and sixth with anterior and lower posterior temporals dorsally, seventh with lower posterior temporal dorsally and scales of the neck posteriorly.

Mental of smaller size, triangular; first infralabial pair larger than mental plate and in broad contact with each other, in contact with anterior chin shields posteriorly; seven infralabials, 1st–3rd in contact with anterior chin shields, fourth infralabial largest in size in contact with both anterior and posterior chin shields; 4th–7th infralabials in contact with gular scales; two larger anterior chin shields, and two smaller posterior chin shields; anterior chin shields in broad contact between them; posterior chin shields bordered posteriorly by six gular scales.

Body robust, elongate and subcylindrical; dorsal scales in 17-17-15 rows, all smooth and pointed posteriorly; 169–180 ventrals in males, 183–207 in females; cloacal plate divided. Tail comparatively long (TL 17.0–18.9% of total length in males), robust and thick; subcaudals 46–54, divided.

**Coloration.**—In preservative, dorsum dark olive brown, lateral surface paler and yellowish; 30–45 black cross stripes along the body and 6–10 on the tail; the markings on the tail are rudimentary; two inverted V-shaped black markings on the head, (1) the first one on the interorbital region, starting from anterior edge of supraoculars, pointing forward to prefrontal–internasal region; in some individuals the V-shaped marking not complete; (2) the second one on the parietal–frontal region, starting from the gape of the mouth, pointing forward to frontal region, and complete the V shape at the interorbital position; another inverted Y-shaped black marking on the nape, starting from the lateral side of the neck, pointing forward to the level of the interparietal region; dark markings below the eye, usually on the posterior

border of fourth and fifth supralabials; all the dark markings are in a range of brown, from chestnut to chocolate brown; venter uniform yellow or cream.

In life, same as in preservative, but all the dark markings vary in a range of grey, from olive grey to black; venter uniform cream. Although the juveniles are alike, the adults of this species have two morphs of coloration: (1) the central Indian morph (Fig. 6B) has cross stripes which are comparatively complete laterally; the anterior cross stripes are comparatively wider (prominent in juveniles and subadults) than the rest of the cross stripes; the cross stripes are without distinct white margins in adults. Therefore, we will report this morph of coloration as the "central Indian morph" throughout this study. (2) The northern Indian morph (Fig. 6C) has cross stripes which are comparatively broken and variegated with streaks before disappearing laterally; all the cross stripes are comparatively more or less subequal and thinner than the central Indian morph; the cross stripes are with distinct white margins in adults. Therefore, we will report the morph of coloration as the "northern Indian morph" throughout this study.

The central Indian morph of *O. russelius* has been observed from the lower (southern) portions of the known distribution range (Figs. 6 and 9) of the species. Aside from that, the central Indian morph is parapatric to the northern Indian morph which has a wider distribution in the northern and northeastern Peninsular India. The central Indian morph has been observed from the southern parts of Andhra Pradesh, western parts of Chhattisgarh, eastern parts of Maharashtra, Madhya Pradesh, western parts of Jharkhand, and the southern parts of Uttar Pradesh, while the northern Indian morph has been observed from the northern parts of Andhra Pradesh, eastern parts of Chhattisgarh, West Bengal, eastern parts of Jharkhand, Bihar, northern parts of Uttar Pradesh, Haryana, and Punjab states).

The juveniles of all members of this species complex have distinct white margins which gradually disappear during development, but this has an exception in the northern Indian morph of *O. russelius* (Fig. 5). The lectotype of *O. russelius* is a juvenile; hence it could be either of the central Indian morph or northern Indian morph as juveniles are alike in both morphs. Andhra Pradesh seems to be an area inhabited by both morphs sympatricly and shares similar suitable habitats where both morphs can inhabit. Also, the type locality, Visakhapatnam, placed in Andhra Pradesh and the area in the year 1796 at the time of Russell, could also have been a much wider area than is recognized nowadays. Therefore, it is possible that the individual (now lectotype) collected by Russell belongs to one or the other of these morphs, and here we do not intend to assign the lectotype of *O. russelius* to one of them. However, we could locate several adult individuals (not collected) from the vicinity of type locality of *O. russelius*, Visakhapatnam, in eastern Peninsular India, and they were more similar to the central Indian morph in body coloration.

Therefore, with our current understanding, here we treat these two populations as color morphs of *O. russelius* and we leave it to future taxonomic workers to reevaluate the interpopulation distinctions with integrative taxonomic approaches. Until then these populations will remain named *O. russelius*.

**Skull and dentition.**—A complete and robust skull displays a generalized colubrid pattern (Fig. 9B); premaxilla single, blunt anteriorly, with a broad ascending process, a prominent nasal crest, and a relatively short transverse process; nasals elongate, triangular, lateral processes tapering anteriorly to form a pointed process at the point of articulation with the ascending process; parietals rough, anterior process flat behind frontals; maxilla with 8–10 functional teeth, gradually increasing in size posteriorly; palatine with 4 or 5 teeth; pterygoid with 16 or 17 teeth; and mandible with 15 or 16 teeth.

**Distribution.**—*Oligodon russelius* comb. nov. has been reported to be common and widespread (partly in Daniel 2002; Das 2002, 2010; Whitaker and Captain 2004 as *O. arnensis*) and is known from 47 localities (Fig. 10). Based on the reliable localities for this species (at least with photographic evidence), it occurs only in deciduous forests below 1400 m a.s.l. Our observations revealed an extensive area in eastern Peninsular India covering the north Eastern Ghats, parts of the Chota Nagpur Plateau, Brahmaputra Basin, and Indo Gangetic Plateau as the distribution envelope of *O. russelius* comb. nov. The species is also known from the foothills of western Himalaya to the mangrove swamps of Circar Coast and the Sal Forests of Chota Nagpur Plateau. It is also widespread and scattered across (1) the Terai landscape covering northern Uttar Pradesh, (2) Nagpur-Seoni Hills (in eastern Maharashtra/ southern Madhya Pradesh) and (3) Chota Nagpur Plateau (in western Orissa, southern Jharkhand and Chattisgarh). The range of this species is from the western Himalayan foothills near Ludhiana until Visakhapatnam (restricted type locality) of the Circar Coast, in the southeast. Within its biogeographic range, we haven't observed this species from Kanpur in Terai and near the Maredumilli hills in the Eastern Ghats. Also, there are no reports from a few outlying areas such as Bangladesh, the region south of Khasi hills (Shillong) and that east of Manipur, Chindwin River of Myanmar.

**Natural history.**—*Oligodon russelius* comb. nov. is known from low, deciduous, and scrub jungle terrains, including areas close to human settlements. This kukri snake species is also active in twilight and slightly beyond, but during monsoon (August–October) and the colder months (October–March) it is observed active in the daylight hours. When threatened it flattens its posterior head to intimidate its predator (Wall 1921). This species is sexually dimorphic where adult females are larger than adult males (Wall 1921). It is oviparous. The clutch contains four or five remarkably elongate eggs with measured dimensions 36 × 10 mm and the SVLs of the hatchlings are around 181.0–193.0 mm (Wall 1921). Usually, hatchlings are brighter in colors with faded and less prominent cross stripes, but with distinct white margins. The juveniles have been mostly observed in April to July and during the winter. A scavenging behavior of this species was observed by Pandirkar et al. (2015), where the snake fed on a dead garden lizard (*Calotes versicolor*).

**Conservation status.**—The application of the Red List Criteria (IUCN 2019) with the updated distribution data shows that *Oligodon russelius* comb. nov. is restricted to an area of occupancy of 246 $km^2$ recorded from 53 localities within a 888,932-$km^2$ extent of occurrence. Although the species often gets killed by humans, given the wider area of

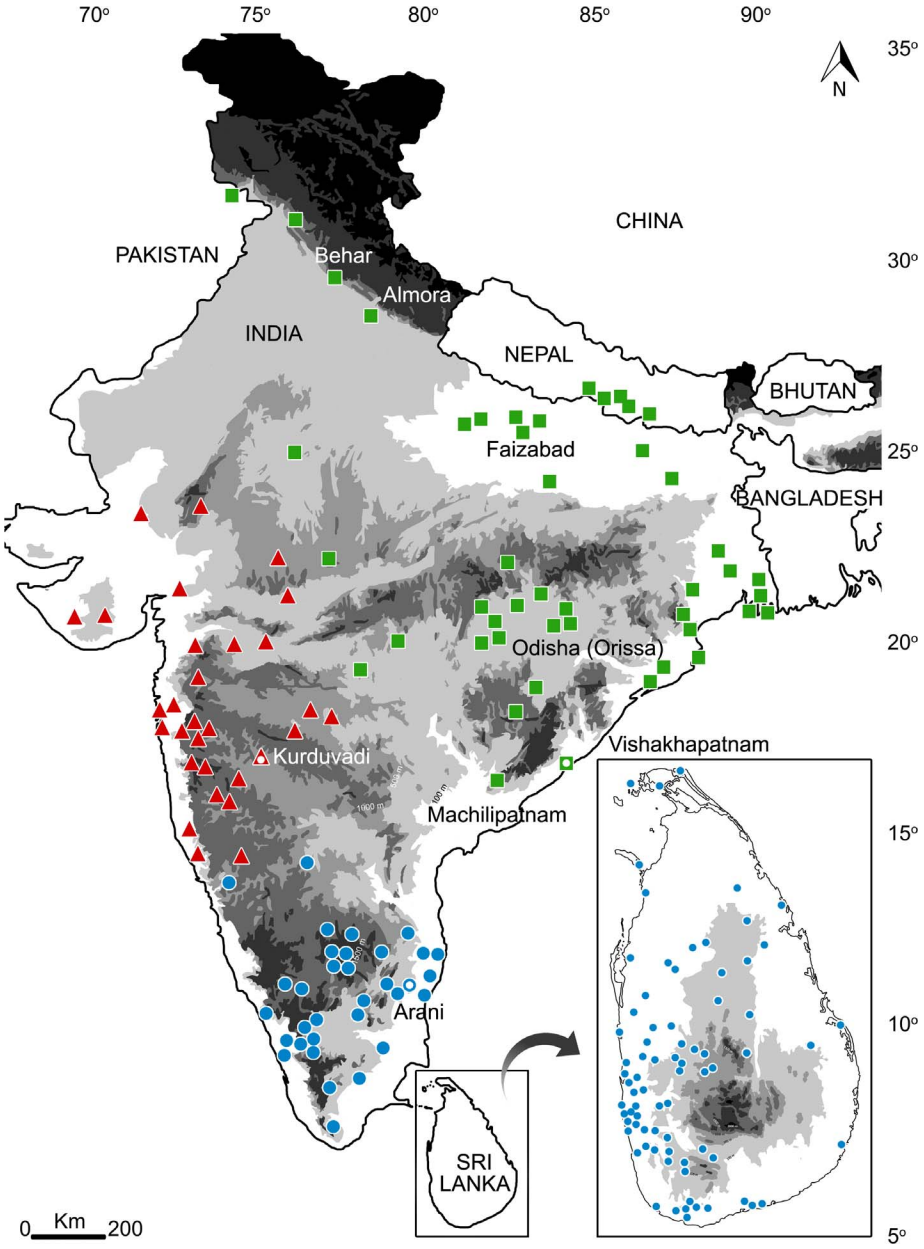


FIG. 10.—Current distribution map showing the collection/observation localities of the (A) *Oligodon tillacki* sp. nov. (red triangles), (B) *O. russelius* comb. nov. (green squares), and (C) *O. arnensis* (blue circles) in India and Sri Lanka. The symbols with dot in the middle represent the type locality of respective species. A color version of this figure is available online.

occurrence, here we suggest classifying it as a Least Concern species. This species is also often reported as road kills (Dutta et al. 2016, Bhandarkar and Paliwal 2021).

*Oligodon* ***tillacki*** sp. nov.
(Tables 1–3; Figs. 4–9)

*Simotes russellii*—Günther 1858 (partim); Nicholson 1874 (partim; their Fig. 2 [above] in Plate 11).
*Simotes russellii* var. γ Günther 1864.
*Simotes arnensis*—Boulenger 1894 (partim).
*Oligodon arnensis*—Lindberg 1932; Chikane and Bhosle 2012; Ardesana et al. 2018; Patel et al. 2019; Pawar et al. 2020.

**Holotype.**—MNHN-RA 1946.0058, adult female from Kurduvadi (18°05′50.94″N, 75°25′29.65″E, datum = WGS84; 518 m a.s.l.), Solapur, Maharashtra, India, donated by Dr. K. Lindberg on 2 April 1946.

**Paratypes (*n* = 4).**—NHMUK 1860.3.19.1317, adult female from Deccan (no precise locality, probably western India), India, collected by Colonel W.H. Sykes; MNHN 1946.0057, subadult female, other details same as holotype; NMW 24546:4 and 24545:1, adult males from India (no precise locality, probably somewhere from western India).

**Diagnosis.**—*Oligodon tillacki* sp. nov. is distributed in western India, and is distinguished from other congeners by having the following combination of characters: adults reach maximum SVL 650 mm, a single preocular, two postoculars (rarely one), a single loreal scale (rarely absent), divided cloacal plate, nasal scale completely divided by the nostril,

ventrals 180–190 in males and 198–201 in females, subcaudals 46–52 in males and females combined, temporals 1 + 2, seven supralabials with third and fourth in contact with eye, DSRs 17-17-15, TL 17.0–17.4% of total length in males, olive brownish dorsum with 25–35 black cross bands (with thickness of 4–6 vertebral scales and 2–4 scales in between cross bands at midbody position) along the body and 4–9 on the tail, anterior cross bands (5–8) wider than the rest of cross bands and visible as large blotches, first two anterior cross bands wider than the ground body color in between, two V-shaped black markings on interorbital and parietal–frontal regions, another large triangular black marking on the nape. The new species is also genetically divergent from *O. arnensis* sensu stricto with *p*-distances of 3% in the mitochondrial cytochrome b gene (fide Mirza et al. 2021)—see Discussion.

**Comparison.**—*Oligodon tillacki* sp. nov. is most similar to *O. russelius* comb. nov. and *O. arnensis* (characters in parentheses), but differs by having a longer body of maximum 650 mm SVL in adults (shorter body of 550 mm SVL in *O. arnensis*), completely divided nasal (entire or partially divided in *O. arnensis*), usually a single loreal scale (absent in *O. arnensis*), 180–190 ventrals in males (169–180 in *O. russelius* comb. nov. and 164–175 in *O. arnensis*), 198–201 ventrals in females (181–188 in *O. arnensis*), longer tail, TL 17.0–17.4% of total length in males (shorter, 13.5–17.1% in *O. arnensis*), dorsum with 25–35 black cross bands along the body and tail (30–45 cross stripes in *O. russelius* comb. nov. and 15–20 cross bands in *O. arnensis*), thickness of cross bands at midbody position 4–6 vertebral scales (2–3 in *O. arnensis* and 1–2 in *O. russelius* comb. nov.), 2–4 vertebral scales in between cross bands at midbody position (7–12 in *O. arnensis* and 4–6 in *O. russelius* comb. nov.), dorsal cross bands unequal in size, distinctly broad anteriorly (subequal in *O. arnensis* and *O. russelius* comb. nov.), dorsal cross bands not white-margined in adults (white-margined cross stripes in northern Indian morph of *O. russelius* comb. nov.), a large triangular blotch on the nape (inverted Y-shaped thin marking in *O. russelius* comb. nov. and inverted V-shaped thick marking in *O. arnensis*)—see Table 1.

The new species differs from its recently described congener, *O. churahensis*, by having a longer body of maximum 650 mm SVL in adults (vs. shorter body of 275 mm SVL), 198–201 ventrals in females (vs. 170–175), shorter tail, TL 14.8–15.5% of total length in females (vs. longer, 18.0%), dorsum with 25–35 black cross bands along the body and tail (vs. 54–62 cross stripes), dorsal cross bands unequal in size, distinctly broad anteriorly (vs. subequal), dorsal cross bands not white-margined in adults (vs. white-margined), a large triangular blotch on the nape (vs. inverted V-shaped marking), 6 and 15 teeth on palatine and pterygoid respectively (vs. no teeth), 12 maxillary teeth (vs. 8–10) and also genetically divergent with *p*-distances of 6% in the mitochondrial cytochrome b gene (fide Mirza et al. 2021)—see Discussion.

Furthermore, the new species is compared with other closely related *Oligodon* species from South and Southeast Asia based on data in Günther (1864), Boulenger (1894), de Rooij (1917), Wall (1921), Taylor (1922), Smith (1943), Leviton (1963), Manthey and Grossmann (1997), Pauwels et al. (2002), David et al. (2008a,b, 2011, 2012), Nguyen et al. (2009), Das (2010), Green (2010), Teynié and David (2010), Tillack and Günther (2010), Geissler et al. (2011), Jiang et al. (2012), Neang et al. (2012), de Lang (2013), Vassilieva et al. (2013), Weinell et al. (2019), and Amarasinghe et al. (2021) as well as on specimens deposited in collections that we examined (see Appendix).

The number of DSRs around the neck (one head length behind the head) and at midbody is a major diagnostic specific character in the genus *Oligodon* (see David et al. 2008b). This number is usually constant within a given species. This character is only variable in some exceptional species complexes such as *O. purpurascens* (Schlegel 1837), which has 19 or 21 scale rows at midbody. There are 86 species recognized in the genus *Oligodon*, of which only 41 species have 17 DSRs at midbody (see Table 3). All other species of the genus have 13, 15, 19, 21, or rarely 23 rows at midbody.

Among the 41 species that have 17 DSRs at midbody, all species display the condition consistently 17 DSRs at midbody and 15 DSRs at one head length prior to cloacal plate, including the new species here described (Table 3). The structure and length of the hemipenes are also major diagnostic characters in the genus *Oligodon* (Smith 1943). *Oligodon tillacki* sp. nov. differs from *O. affinis* Günther 1862, *O. ancorus* (Girard 1858), *O. arenarius* Vassilieva 2015, *O. cinereus* (Günther 1864), *O. cruentatus* (Günther 1868), *O. erythrogaster* Boulenger 1907, *O. joynsoni* (Smith 1917), *O. maculatus* (Taylor 1918), *O. meyerinkii* (Steindachner 1891), *O. octolineatus* (Schneider 1801), *O. theobaldi* (Günther 1868), *O. travancoricus* Beddome 1877, *O. venustus* (Jerdon 1853), and *O. woodmasoni* (Sclater 1891) by its forked hemipenes (vs. unforked).

The new species has divided nasal scale and cloacal plate, and thus differs from *O. cattienensis* Vassilieva, Geissler, Galoyan et al. 2013, *O. erythrogaster*, *O. melanozonatus* Wall 1922, and *O. nagao* David, Nguyen, Nguyen et al. 2012, which all have an entire nasal scale, and from *O. ancorus*, *O. arenarius*, *O. barroni* (Smith 1916), *O. booliati* Leong and Grismer 2004, *O. cattienensis*, *O. chinensis* (Günther 1888), *O. cinereus*, *O. condaoensis* Nguyen, Nguyen, Le et al. 2016, *O. culaochamensis* Nguyen, Nguyen, Nguyen et al. 2017, *O. deuvei* David, Vogel and van Rooijen 2008b, *O. forbesi* (Boulenger 1883), *O. joynsoni*, *O. macrurus* (Angel 1927), *O. maculatus*, *O. meyerinkii*, *O. moricei* David, Vogel and van Rooijen 2008b, *O. mouhoti* (Boulenger 1914), *O. nagao*, *O. octolineatus*, *O. perkinsi* (Taylor 1925), *O. phangan* Pauwels, Thongyai, Chantong and Sumontha 2021, *O. promsombuti* Pauwels, Thongyai, Chantong and Sumontha 2021, *O. pseudotaeniatus* David, Vogel and van Rooijen 2008b, *O. saintgironsi* David, Vogel and Pauwels 2008a, *O. saiyok* Sumontha, Kunya, Dangsri and Pauwels 2017, *O. signatus* (Günther 1864), *O. trilineatus* (Duméril, Bibron and Duméril 1854), *O. unicolor* (Kopstein 1926), *O. woodmasoni* which have an entire cloacal plate.

*Oligodon tillacki* sp. nov. has 46–52 subcaudals which is more than in *O. affinis* (23–36), *O. cruentatus* (27–40), *O. melanozonatus* (42–45), *O. travancoricus* (34–37), and *O. venustus* (27–36), and 180–201 ventrals, which is more than in *O. pulcherrimus* Werner 1909 (152–179) and *O. melanozonatus* (171–173). Finally, the new species differs from *O. theobaldi* by having 25–35 black cross bands on dorsum (vs. longitudinal vertebral stripe).

**Description of holotype.**—Adult female, SVL 424 mm; TL 78.0 mm; head elongate, HL 3.1% of SVL, twice as long as wide, HW 60.6% of HL, slightly flattened, indistinct from neck; snout elongated, ES 33.3% of HL, moderate, flat in dorsal view, rounded in lateral profile, rather depressed.

Rostral shield large, flat, distinctly visible from above, pointed posteriorly; interorbital width broad, IO 65.0% of HW; internasals subtriangular; nostrils rather large, nasals large and elongated, divided by the nostril, in anterior contact with rostral, and internasal and prefrontal dorsally, first and second supralabial ventrally, loreal posteriorly; loreal single; prefrontal rather large, broader than long, and subhexagonal; frontal large, pentagonal, shortened posteriorly and slightly longer than wide; supraoculars narrow, short, subrectangular, posteriorly wider; parietals large, elongate, butterfly-wing-like in shape, bordered by supraoculars, frontal, upper postocular anteriorly, anterior and upper posterior temporals, and three nuchal scales posteriorly; one preocular, vertically elongated, pentagonal, in contact with prefrontal and loreal anteriorly, supraocular dorsally, and third supralabial ventrally; eye moderate, ED 15.9% of HL, round, less than half of the size of snout length, ED 47.7% of ES, pupil rounded; two postoculars, upper one larger, rounded, upper postocular in broad contact with supraocular and parietal, lower postocular in contact with anterior temporal and fourth and fifth supralabials; temporals 1 + 2, elongated, subrectangular; anterior temporal almost the same size as upper posterior temporal, in contact with parietal and both postoculars dorsally, and fifth and sixth supralabial ventrally; lower posterior temporal in contact with sixth and seventh supralabials ventrally. Supralabials seven on both sides, 5th–7th largest in size; first supralabial in contact with rostral anteriorly, anterior and posterior nasals dorsally, second with posterior nasal and loreal dorsally, third with loreal, preocular and orbit dorsally, fourth with orbit and the lower postocular dorsally, fifth with lower postocular and anterior temporal dorsally, and sixth with anterior and lower posterior temporals dorsally, seventh with lower posterior temporal dorsally and scales of the neck posteriorly.

Mental of smaller size, triangular; first infralabial pair larger than mental plate and in broad contact with each other, in contact with anterior chin shields posteriorly; seven infralabials, 1st–3rd in contact with anterior chin shields, fourth infralabial largest in size in contact with both anterior and posterior chin shields; 4th–7th infralabials in contact with gular scales; two larger anterior chin shields, and two smaller posterior chin shields; anterior chin shields in broad contact between them; posterior chin shields bordered posteriorly by six gular scales.

Body robust, elongate, and subcylindrical; dorsal scales in 17-17-15 rows, all smooth and pointed posteriorly; 199 ventrals; cloacal plate divided. Tail comparatively long, TL 15.5% of total length, robust and thick; subcaudals 48, divided.

**Coloration of holotype.**—In preservative, dorsum light olive brown, lateral surface paler and yellowish; 25 black cross bands along the body and 9 on the tail; cross bands complete laterally, and almost reaching the ventrals; the markings on the tail are distinct; 5–6 anterior cross bands visible as large blotches and wider than the rest of cross bands on the body; two inverted V-shaped black markings on the head, (1) the first one on the interorbital region, starting from the anterior edge of supraoculars, pointing forward to the prefrontal–internasal region; in some individuals the V-shaped marking is almost C-shaped; (2) the second one on the parietal–frontal region, starting from the gape of the mouth, pointing forward to the frontal region, and completing the V shape at the interorbital position; another thick triangular black blotch on the nape, starting from the lateral neck, pointing forward to the level of the interparietal region; dark blotches below the eye on the fourth, and fifth supralabials each side; all the dark markings are visible in a range of dark brown, from chocolate brown to black; venter uniform cream.

Based on live individuals (Fig. 6A) the coloration is the same as in preservative, but all the dark markings are in a range of grey, from dark grey to black; venter uniform cream.

**Skull and dentition of holotype.**—A complete and robust skull display a generalized colubrid pattern (Fig. 9C); premaxilla single, pointed anteriorly, with a broad ascending process, a prominent nasal crest, and a relatively long transverse process; nasals elongate, triangular, lateral processes tapering anteriorly to form a pointed process at the point of articulation with the ascending process; parietals rough, anterior process flat behind frontals; maxilla with 12 functional teeth, gradually increasing in size posteriorly; palatine with 6 teeth; pterygoid with 15 teeth; and mandible with 18 teeth.

**Variation.**—The holotype and three paratypes (Table 1) are adults, except MNHN-RA 1946.0057. The coloration and the morphology are more or less unique for all the individuals of the type series: 25–35 black cross bands along the body and 4–9 on the tail; 5–8 anterior cross bands visible as large blotches and wider than the rest of cross bands on the body. This species is sexually dimorphic (see Table 1) as the females have 198 and 201 ventrals and the male paratypes have 180 and 190 ventrals. The smaller paratype is paler in color, and the cross bands are chestnut-brown in preservative, while the holotype and the largest paratype have black cross bands. The paratype, NMW 24546:4, has no loreal and NMW 24545:1 has one post ocular (on both sides), probably an aberrant specimen, a condition that is common in snakes. All the paratypes have five (three in holotype) nuchal scales.

**Etymology.**—The specific epithet is a noun in the singular genitive case, honoring Dr. Frank Tillack, a renowned herpetologist and the Collection Manager (Herpetofauna) of ZMB for his enormous contribution to the herpetological research, especially on the systematic research on snake fauna. We use the modern name "Tillack" formed in case of singular masculine adding the suffix (*-i*). English name: Tillack's Kukri Snakes. German: Tillaks Kukrinatter.

**Distribution.**—*Oligodon tillacki* sp. nov. is known from 30 localities (Fig. 10). Based on the reliable localities for this species (at least with photographic evidence), it occurs only in deciduous forests below 1400 m a.s.l and on lateritic plateaus. Our observations revealed an extensive area in western India covering the northern Western Ghats and upper parts of the Deccan Plateau, as the distribution envelope of *O. tillacki* sp. nov. A large linear stretch of area extending parallel to the leeward slopes of the Western Ghats, approximately between Pune and Sivamogga was

discovered to be the largest expanse region. The area between Indore and Gwalior was also identified as another distribution patch of this species. We also observed this species within a wider area on the west part of the Gujarat Bay, including Ahmedabad, Vadodara, Udaipur, Indore, Nashik, and southwards on to Pune and Satara. While Nagpur more or less marks the eastern edge of *O. tillacki* sp. nov., there appears to be a narrow geographic sympatric zone of *O. tillacki* sp. nov. and *O. arnensis* sensu stricto near the Thungabadra River in the west. While a few points of the new species are actually from areas south of the river, a few *O. arnensis* records approach more or less the same region. Thus, it is possible that *O. arnensis* and *O. tillacki* sp. nov. are parapatric (if not sympatric) in areas abutting the Thungabadra River.

**Natural history.**—*Oligodon tillacki* sp. nov. is found in moist and dry deciduous forests and scrublands. We observed it in urban ecosystems and agricultural lands too. The new species is also active in twilight and later on during the early part of the night. During the monsoon (August–October) it is not rare to observe this species active in daylight. We have seen photographic evidence of their feeding on frogs (*Euphlyctis* sp.) in Gujarat.

**Conservation status.**—The application of the Red List Criteria (IUCN 2019) with the updated distribution data shows that *Oligodon tillacki* sp. nov. is restricted to an area of occupancy of 219 $km^2$ recorded from 30 localities within a 483,421-$km^2$ extent of occurrence. Within the known distribution range of *O. tillacki* sp. nov., there are many protected areas such as the Chandoli National Park (Maharashtra), Raigad Fort Nature Reserve (Maharashtra), Koyna Wildlife (Maharashtra), Shri Bhimashankar Jyotirlinga Wildlife (Maharashtra), Gautala Autramghat Wildlife (Maharashtra), Kalsubai Harishchandragad Wildlife (Maharashtra), Tipeshwar Wildlife (Maharashtra), Bhimgad Wildlife (Karnataka) Sanctuaries, Bandipur (Karnataka), Melghat (Maharashtra), and the Tadoba-Andheri (Karnataka) Tiger Reserves. Habitat in the forests of the Northern Western Ghats has become degraded, but not to a large extent, and the recent increase in the number of protected areas has alleviated the issue to a certain extent (Panigrahy et al. 2010). Given the wider area of occurrence, here we suggest classifying this species as a species of Least Concern. Similar to other members of this complex, *O. tillacki* sp. nov. is threatened by the wanton killing by people due to misidentified body coloration. Mortalities due to vehicular traffic are also observed frequently.

## Discussion

Daudin (1803) probably had a specimen of *O. arnensis* or similar species upon which to base his illustration of *Coluber russelius* in Plate 76. After examining the *Oligodon* collection at the MNHN, we found only five specimens that are currently labelled as "*O. arnensis*," and all of them arrived in Paris after 1854, except for one specimen that was available prior to 1854 and originally labelled as *Simotes russelii* (sic) fide Duméril et al. (1854). This specimen has a very similar pattern and a similar number of cross bands to the illustration depicted by Daudin (1803: Plate 76). This was probably the specimen on which Daudin based his illustration as the third syntype of *C. russelius*. However, we have identified this as an individual of *O. ancorus*. From the remaining four specimens at MNHN, one is identified as *O. albocinctus* (Cantor 1839), and two were designated as the types of *O. tillacki* sp. nov. in this work.

We here clarify that the subsequent usage of the different spelling of species epithet as "*russelii*" or "*russellii*" instead of "*russelius*," as published originally by Daudin (1803), does not demonstrate any intention of correcting its original spelling given by Daudin, and it is rather just an incorrect spelling. Evidently, Günther (1858, 1864) listed chresonym of Daudin (1803) also incorrectly as "*russellii*." Therefore, here we retain its original spelling "*russelius*" which was an eponym after Patrick Russell given as an adjective in the masculine singular, in accordance with the genus "*Coluber*," a masculine generic epithet. As the generic epithet "*Oligodon*" is also in the masculine gender, here we assigned the species epithet in the same declension with its new combination as "*Oligodon russelius*." Interestingly, the Russell's Viper, *Daboia russelii* (Shaw and Nodder 1797) had the original description of "*Coluber russelii*" (sic), also an eponym after Patrick Russell, but with a noun in genitive case. Although both epithets might erroneously be considered primary homonyms, as named after the same person and published originally in the same genus, sensu Articles 57 and 58 of ICZN (1999), as these epithets were not spelled identically, the principle of homonymy does not apply here.

With the resurrection of *O. russelius*, the most appropriate English vernacular name for this species is "Russell's Kukri" ("Russell ka kukri saamp," in Hindi) since Daudin (1803) intended the nomen to honor Patrick Russell. However, currently, the common name Russell's Kukri is widely used for *Oligodon taeniolatus* Jerdon 1853, another species originated from Russell (1796). As there are few other alternative common names for this species, here we propose the common name "Variegated Kukri" for *O. taeniolatus* and "Russell's Kukri" for *O. russelius* comb. nov. The whole Indian populations of *O. arnensis* sensu lato have long been commonly identified as "Common Kukri" or "Common Banded-Kukri." After restricting the species to southern India and Sri Lanka, here we propose "Arani Kukri," "Arani pul uruvi pambu," and "Arani dath-katiya" as the vernacular names for *O. arnensis* in English, Tamil, and Sinhalese respectively.

Wall (1913) also illustrated a specimen of *O. arnensis* sensu lato collected from Almora, Uttarakhand, India, which has black spots at the edges of its ventrals, and mentioned another specimen from the same locality having 6–11 maxillary teeth (vs. 15–18 of a specimen from Fyzabad). Currently, there are two skulls and a skeleton deposited at NHMUK (NHMUK 1930.5.8.572–574) collected from Almora. It is probable that Wall (1913) counted the maxillary teeth from these skulls, but the species identity remains doubtful. There is another skull (NHMUK 1930.5.8.571) collected from Fyzabad, Uttar Pradesh, India, with the same collection series of Almora, which most probably refers to the species, *O. russelius*. We examined another three specimens (NHMUK 1906.5.23.11, 1907.2.14.30–31) collected from Fyzabad, and clearly identified them as *O. russelius*. *Oligodon churahensis* in the Western Himalayas, which has a similar color pattern to the north Indian morph of *O. russelius* and *Contia transcapica* Nikolsky 1903, occurs above 1400 m elevation, and presents higher numbers of

dorsal cross stripes (54–62) than *O. russelius* sensu stricto (30–45) in total. Deraniyagala (1936, 1955) also noticed a population in Behar, Haryana (the foothills of Western Himalaya), with 62 dorsal cross stripes, while the population in Orissa (East India) had 43 (now the northern Indian morph of *O. russelius* comb. nov.) and in Arni, South India, had 22 (now *O. arnensis* sensu stricto).

Despite the phenomenon of aberrant specimens, which is common among the genus *Oligodon*, such color variations can occur because of clinal change. Therefore, the identities of the outranging populations (with 54–62 cross stripes, looking similar to *O. russelius*) have been reassessed with integrative systematic approaches by Mirza et al. (2021), and these populations in the western Himalaya are considered as *O. churahensis*. The higher level of morphological variation of the *O. arnensis* species complex highlights the need for further exploration with more sampling efforts from the Western Ghats and the northern Pakistan Regions where, for now, not many data are available on this species complex. The number of cross bands of this species complex seems to show a clear pattern from South to North India. As an example, the South Indian species, *O. arnensis*, has 20+ total cross bands on the dorsum. The central to western Indian populations of *O. tillacki* sp. nov. and *O. russelius* have 25+ and 35+ total cross bands respectively. The eastern Peninsular Indian populations of *O. russelius* have around 45+ total cross bands and, the northern populations of *O.* cf. *russelius* have around 55+ total cross bands. Similarly, we also observed that the thickness of the body bands increases from east to west across Peninsular India. Within *O. arnensis* sensu stricto in southern India, the populations towards the east coast (including type locality) have thinner cross bands compared to the populations in the foothills of southern Western Ghats. Similarly, in central parts of India, the western species, *O. tillacki* sp. nov. has the widest cross bands, unlike *O. russelius* on the eastern part which has cross stripes. Interestingly, based on the data of climate, vegetation, and altitude, it seems the species in this species complex are temperature-dependent species rather than elevation-dependent.

A specimen of *Oligodon tillacki* sp. nov. was first indicated in text by Günther (1858:25) "Adult. India. (Cross bands very large and broad, lozenge-shaped: fine specimen.)." Unfortunately, though a clear diagnostic feature, no data on its provenance were given. He was probably referring to the specimen NHMUK 1860.3.19.1317 in this work, which is one of the paratypes we selected and is currently labelled as from Deccan. Boulenger (1894) also mentioned this specimen from Deccan collected by Col. Sykes. The first illustration of *Oligodon tillacki* sp. nov. seems to be depicted by Nicholson (1874; Fig. 8B); however, it is identified as an individual of *S. russellii* (sic). Günther (1864) also mentioned another individual with broad cross bands from "Dukhun," probably referred to Dakhun, Pakistan, but neither specimen has any data or precise geographical information accompanying them. There was another very old specimen, NMW 24546:1, labelled as from "Dukkun, Asian." However, we identified this specimen as an individual of *O. arnensis* sensu stricto, probably a mislabeled specimen from southern India or Sri Lanka. Although many historical workers such as Daudin (1803) and Duméril et al. (1854) recognized the difference between *O. arnensis* sensu stricto and *O. russelius* comb. nov., there was no evidence of recognition of the difference between western populations (now *Oligodon tillacki* sp. nov.) and rest of the population of *O. arnensis* sensu lato, except by Günther (1858, 1864). In the recent phylogeny of *O. arnensis* species complex (Mirza et al. 2021), the sequence of mitochondrial cytochrome b gene from *O. arnensis* sensu lato (GenBank reference no. MZ675819) from Maharshtra, India, might be referred to as *Oligodon tillacki* sp. nov. Therefore, the new species is genetically divergent from *O. arnensis* sensu stricto (GenBank reference no. KC347464 from Sri Lanka) with *p*-distances of 3% in the mitochondrial cytochrome b gene (see Table 2 in Mirza et al. 2021).

Among the three species of this species complex, *O. arnensis* is distributed in both southern India and Sri Lanka. Günther (1858, 1864) mistakenly prioritized *Simotes russellii* (sic) over *S. arnensis* which was described earlier, and included the Sri Lankan and South Indian *O. arnensis* as varieties of *S. russellii*. Therefore, the subsequent authors considered Visakhapatnam as the type locality of the Indian taxon. Following Günther (1864), Ferguson (1877: 18) considered the Sri Lankan population of *O. arnensis* as *Simotes russellii* (sic) and mentioned "Two specimens. A beautiful light olive-coloured snake with a series of black rings around its body. Not uncommon." He also listed Günther's (1864) other species, *S. albiventer*, but mentioned that he had not seen any specimens, stating, "Peculiar to Ceylon, but I have not as yet seen a specimen of it." Actually, Günther's (1864) description would not imply that *S. albiventer* is the same species he listed as *S. russellii* var. δ, unless Ferguson had seen the type specimen of *S. albiventer*. Therefore, Ferguson's (1877) reasoning makes sense, of not seeing any specimens of *S. albiventer*. Later, Müller (1887) also considered the Sri Lankan population as a variation of *S. russellii*. Therefore, Günther's species had not been recognized until Deraniyagala (1936) considered *S. albiventer* a subspecies of *O. arnensis*. However, Deraniyagala (1936, 1955) compared the Sri Lankan subspecies with forma typica of Visakhapatnam (now *O. russelius*). Therefore, it is obvious that the Sri Lankan population, i.e., *O. arnensis*, differs from the eastern Peninsular Indian population *O. russelius*.

Deraniyagala (1955) further compared the specimens from Sri Lanka and India with respect to the presence and absence of loreals, and he considered it variable within a population as he kept North and South Indian populations together. However, here we show that presence and absence of a loreal scale is a diagnostic character separating South Indian plus Sri Lankan populations (i.e., *O. arnensis*) from the North Indian species (i.e., *O. russelius* and *O. tillacki* sp. nov.). Although our study revealed that there is no such real morphological distinctiveness between South Indian and Sri Lankan *O. arnensis*, which is a single species distributed widely throughout Sri Lanka (Fig. 10), isolated or cryptic populations (island radiation) may still exist, but this requires additional field explorations on the island to uncover them.

As this species complex is sexually dimorphic, some of the meristic characters (e.g., ventrals, subcaudals) have to be assessed separately for each sex. It is evident that another Sri Lankan species, *O. sublineatus* Duméril, Bibron, and Duméril 1854 shows a nonoverlapping distinct range of subcaudals between males and females (Amarasinghe et al. 2015). However, *O. arnensis* does not show such variation in

subcaudals, but indicates dimorphism in ventral count and morphometrics, and it may be the case that it is the same for the other two members of this complex (*O. russelius* and *O. tillacki* sp. nov.). For such species complexes that involve sexual dimorphism, larger samples sizes are needed to fully investigate morphological variations for each sex. Although there were several attempts to understand the taxonomy of this species group (e.g., Daudin 1803; Duméril et al. 1854; Günther 1864; Wall 1921, 1923; Deraniyagala 1936, 1955; Smith 1943), it has proved to be so difficult to delimit, probably due to ignorance of sexual dimorphism of this group and the lack of understanding of the biogeography within the Indian subcontinent. Also, this species group in recent times appears to have been neglected, probably due to the absence of modern samples and lack of observations of geographically correlated morphological characters. Therefore, studies enhanced with integrative systematic approaches on the *O. arnensis* species complex in both Sri Lanka and India will be useful to understand not only the morphological variation, but also their biogeography, phylogeny, and evolutionary dispersal and speciation within the species complex.

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## Supplemental Material

Supplemental material associated with this article can be found online at https://doi.org/10.1655/Herpetologica-D-21-00026.1.S1.

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## APPENDIX

### Other Specimens Examined

*Contia transcaspica*.—Iran: Kopet Dag: ZISP 9869 (holotype).

*Oligodon affinis*.—India: Kerala: NHMUK 1946.1.5.52 (holotype).

*O. arnensis*.—India: ZMB 50533; Tamil Nadu: NHMUK 1964, NMW 24545.3–4, ZMB 8059, CSPT/S 31a–b; Karnataka: NHMUK 1921.6.15.19. Sri Lanka: NHMUK 1946.1.4.36 (holotype of *Simotes albiventer*), 1894.9.11.21–22, 1897.10.20.13, 1920.5.6.2, 1933.12.6.14, 1972.2188, NMW 24544.1–8, 24546.1–3, ZMB 2089, 12030, NMSL uncat 7C-12, 25a–b, 26a–b, 27a–b (9 specimens), WHT 0626, 2166.

*O. barroni*.—Thailand: NHMUK 1946.1.3.21–22, 1946.1.3.26 (syntypes), 1921.4.1.16–17, 1946.1.1.20, 1946.1.1.93, 1946.1.3.36–37, 1969.1778–1785, 1969.1786. Vietnam: MNHN 1938.0134 (syntype of *Holarchus taeniatus caudaensis*), 1938.0134, 1958.0458, 1973.0143. Laos: MNHN 2003.3329–3330.

*O. chinensis*.—Vietnam: MNHN 1896.0041–0042, 1911.0043, 1928.0014, 1935.0008, 1935.0420, 1938.0139. China: NHMUK 1946.1.3.28 (holotype), 1946.1.23.69 (holotype of *Simotes longicauda*), MNHN 7453, 1999.7952–53.

*O. cinereus*.—Cambodia: NHMUK 1946.1.1.25 (holotype); MNHN 1970.0437–0440. India: Nagaland: ZSI 7167–8 (syntypes of *Simotes semifasciatus*), NMBA 13540; Assam: NHMUK 1908.6.23.45, NMBA 13622; Bihar: ZSI 12356. Laos: MNHN 1897.0425, 1928.0070, 1999.8150–8151, ZMA 19170. Myanmar: NHMUK 845–848, 84.5.8.11, 91.11.26.32–33, 1900.9.20.14, 1908.6.23.43–44, 1940.6.5.2, MNHN 1893.0387–0388, NMBA 1564–1565. Thailand: NHMUK 1921.4.1.19, 1921.4.1.20. Vietnam: MNHN 1938.0135 (holotype of *Simotes violaceus pallidocinctus*), 1938.0136 (syntype of *Holarchus violaceus tamdaoensis*), 1948.0086 (holotype of *H. v. poilani*), 1948.0088 (holotype of *H. v. plurimaculatus*), 1892.0264, 1897.0407–0408, 1900.0330, 1901.0373, 1901.0507, 1908.0203, 1911.0040, 1937.0022, 1948.0087, 1958.0465–0466, 1996.7436, 1997.4359–4360, NHMUK 1938.8.7.33–34, ZFMK 81475–476, NMW 24533.1. China: NHMUK 62.12.6.88 (syntype of *Simotes swinhonis*), 1946.1.4.14, 1946.1.4.35 (syntypes of *Simotes swinhonis*), 82.11.25.2, 1931.8.4.9, 1969.1843–44, NMBA 1566–7, NMW 24537.1–2, 39275.

*O. deuvei*.—Vietnam: MNHN-RA 1974.1366 (holotype), 1974.1266–1267, 1974.1367 (paratype), NHMUK 1938.8.7.35–36, 1969.1810, 1696.1817, 1969.1831. Laos: NHMUK 1912.5.11.1, MNHN 1985.0395.

*O. forbesi*.—Indonesia: Timor: NHMUK 1946.1.3.98–99 (syntypes).

*O. joynsoni*.—Thailand: NHMUK 1946.1.4.23 (holotype), 1969.1809, 1938.8.7.40, 1969.1808. Laos: MNHN 1896.0633.

*O. moricei*.—Vietnam: MNHN-RA 1919.0137 (holotype).

*O. mouhoti*.—Cambodia: NHMUK 1946.1.3.32 (holotype), 1946.1.3.30–31. Thailand: NHMUK 63.9.29.12, 78.2.14.11, 97.10.8.27, 1914.5.11.7, 1969.1822, 1969.1827, 1969.1829–1830, 1969.1832–1837, 1969.1839–1840, MNHN 1991.1817–1818, 1998.0572, 1999.7635.

*O. nagao*.—Vietnam: MNHN-RA 2012.0216 (paratype).

*O. octolineatus*.—Indonesia: 1975.0104, MZB 1689; Sumatra: MNHN 0825, 5798, 1999.1704, 1999.8204, SMF 19214–15, RMNH 18140, ZFMK 33556, MZB 0787, 2002, NMW 19215, 25838; Java: MNHN 3540, 5891, MZB 1175, 2608, 2673, 3093, 5242. Malaysia: MNHN 1884.0083, 1889.0198. Singapore: MNHN 0192, 4987, 1990.4981.

*O. pseudotaeniatus*.—Thailand: NHMUK 1938.8.7.37 (holotype), 1938.8.7.38, 1969.1838, 1969.1828 (paratypes).

*O. pulcherrimus*.—Indonesia: MNHN 1912.0049 (holotype of *Simotes annulifer* var. *bipartita*); Sumatra: NMBA 1017619 (holotype of *Oligodon durheimi*).

*O. russelius*.—India: Tamil Nadu: NHMUK 1861.12.30.2, 1861.12.30.15; Andhra Pradesh: NHMUK 1837.9.26.32–33 (dry skins); Madhya Pradesh: NHMUK 1911.5.9.4–5; Uttar Pradesh: NHMUK 1907.2.14.30–31, 1906.5.23.11; Bihar: ZMB 9003; West Bengal: ZSI 26047, NMW 24545.2, ZMB 2091.

*O. saintgironsi*.—Vietnam: MNHN-RA 1974.1264 (holotype), 1974.1272. Cambodia: MNHN-RA 1877.0050.

*O. signatus*.—Singapore: NHMUK 1946.1.3.25 (syntypes of *Simotes signatus*), 1946.1.3.20. Indonesia: Sumatra: RMNH 4690 (holotype of *Simotes annulifer* var. *annulata*), ZMA 17437, 17472.1–2, MNHN 1891.0233. Malaysia: NHMUK 1946.1.4.24 (holotype of *Simotes subcarinatus*).

*O. theobaldi*.—Myanmar: NHMUK 1946.1.4.9 (holotype).

*O. travancoricus*.—India: Kerala: NHMUK 1946.1.5.53 (holotype).

*O. trilineatus*.—Indonesia: Sumatra: MNHN-RA 3541 (holotype), RMNH 468, MZB 0797.

*O. woodmasoni*.—India: Andaman: ZSI 8459 (syntype); Nicobar: ZSI 12547 (syntype).