

Description of a New *Oligodon* (Squamata: Colubridae) from Sulawesi, Indonesia, Including Redescriptions of *O. waandersi* and *O. propinquus*

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ABSTRACT: We review the taxonomic status of *Oligodon waandersi* sensu lato after examining all the name-bearing types (including synonyms) and morphological evidence. *Oligodon waandersi* sensu stricto is widely distributed (up to 1200 m above sea level) throughout the southern, some parts of the central, and the northern slopes of Central Sulawesi Island, Indonesia, whereas a similar species, *O. propinquus*, is only known from its holotype and considered to have originated from Java. Here, we demonstrate that *O. propinquus* is a close match with the northern population (North and Gorontalo) of *O. waandersi* and morphologically distinct; hence, we consider the type locality of *O. propinquus* as North Sulawesi, not Java. *Oligodon taeniurus*, long considered a junior synonym of *O. waandersi*, is a distinct species, but here we synonymize it with the morphologically closely matched *O. propinquus*, which has priority over *O. taeniurus*. *Oligodon waandersi* in Southeast Sulawesi (including some populations of Buton Islet) is morphologically distinct from *O. waandersi* sensu stricto in South Sulawesi; hence, it requires a new name. The new species is distinguished from congeners by having the following combination of characters: maximum snout–vent length of 340 mm, a single postocular, a single cloacal plate, a completely divided nasal, ventrals 150–169, subcaudals 18–26, temporals 1+2, six supralabials with third and fourth in contact with eye, dorsal scale rows 15-15-15, hemipenes not forked and covered with spines, maxillary teeth 6–7, shorter tail (6.8–11.2% of total length), brownish dorsum with few dark-edged spots on the vertebral line anteriorly, reddish brown vertebral line on the posterior body and tail, mostly a blackish brown blotch below the eye, and whitish collar band interrupted middorsally. We provide a complete redescription for *O. waandersi* and *O. propinquus* based on respective holotypes deposited at the Natural History Museum London and the Zoologisches Museum Hamburg.

Key words: Celebes; Distribution; Kukri snake; Morphology; *Rabdion waandersi*; Synonym

SULAWESI is a composite island formed by the geological aggregation of several separate paleoislands, and because of this tectonic history, at least seven areas of endemism have been identified on Sulawesi: Northeast, North-central, Northwest, Southeast, Southwest, East-central, and West-central (Evans et al. 2003; Setiadi et al. 2011; Bacon et al. 2013). The genus *Rabdion* was described by Duméril et al. (1854) to accommodate two snake species originating from Sulawesi, *R. forsteni* Duméril, Bibron and Duméril 1854 and *R. torquatum* Duméril, Bibron and Duméril 1854, described in the same work. Bleeker (1860) added two more species, *R. cruciatum* and *R. waandersi* from “liet rijk van Boni” (=Boni Regency) in South Sulawesi. Jan (1862) discovered a similar species to *R. waandersi*, but placed it in the genus *Oligodon* Boie in Fitzinger 1826 as *O. propinquus*, with the type locality being “Giava” (Java). Later, *Rabdion torquatum* was removed from the genus *Rabdion* and transferred to *Pseudorabdion* by Jan (1862), who considered it a subjective synonym of *P. longiceps* (Cantor 1847). However, Vogel et al. (2016) recently resurrected *P. torquatum* as a valid species. Günther (1865) removed both *R. waandersi* and *R. cruciatum* from the genus *Rabdion* and transferred them to the genus *Oligodon*. Furthermore, *O. cruciatum* was synonymized with *O. waandersi* (fide Günther 1865). After the work of Boulenger (1894), the genus *Rabdion* remained

monotypic until Amarasinghe et al. (2015a) discovered a second species, *Rabdion grovesi*. Müller (1895) added a new species similar to *O. waandersi* from two localities—“Kema, Lilang (Südwestlich von Kema),” namely southwest of Kema, and “Pinogo im Bona-Thal” in North Sulawesi—and named it *O. taeniurus*. de Rooij (1917), synonymized *O. taeniurus* with *O. waandersi*. in den Bosch (1994) re-examined all the synonymized types and confirmed all the previous synonymies; he considered *O. waandersi* to be a single species distributed throughout Sulawesi, whereas *O. propinquus* was distributed in Java. However, despite the distribution of *O. propinquus* in Java being dubious, it is still considered a valid species (David and Vogel 2012).

Based on the type material and additional voucher specimens from Sulawesi, we revisited the taxonomic status of *O. waandersi* sensu lato, which involves several synonyms. After taking morphological and morphometric characters into consideration, we recognized that *O. waandersi* is actually a species complex. We found several specimens collected from Southeast Sulawesi in the collections of the Museum Zoologicum Bogoriense that differ from *O. waandersi* and its synonymized types in several aspects. They are here described as a new species. Furthermore, we recognize *O. propinquus* as a distinct species, and here restrict it to northern Sulawesi, providing a comprehensive redescription of its holotype.

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MATERIALS AND METHODS

We compared the type specimen of the new species, deposited at the Museum Zoologicum Bogoriense, Bogor, Indonesia (MZB), to specimens and the descriptions of the other known congeners (Appendix). We examined specimens from the following collections: the Natural History Museum, London, UK (NHMUK); MZB; Naturhistorisches Museum, Wien, Vienna (NMW); Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt-am-Main, Germany (SMF); Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK) and Zoologisches Museum Hamburg, Germany (ZMH). Museum acronyms mostly follow Uetz et al. (2019).

We obtained the diagnostic morphological characters for *O. propinquus* and *O. waandersi* sensu lato (Appendix) and compared the holotype of *O. waandersi* (NHMUK 1946.1.2.52) collected from South Sulawesi with the types of *R. cruciatum* and *O. taeniurus*, regarded as synonyms, as well as other voucher specimens ($n = 28$) of *O. waandersi* sensu lato throughout the island. We obtained morphometric and meristic data for species comparisons and distribution data from examined specimens as well as from the published literature. We measured the following characters with a Mitutoyo digital caliper and M50 (Leica Microsystems Inc.), AmScope SM-1BZ-RL (10–90×; United Scope LLC), or DRC 475003-9902 (Carl Zeiss AG) dissecting microscope: eye diameter (ED; horizontal diameter of eye); eye–nostril length (distance between anteriormost point of eye and middle of nostril), snout length (ES; distance between anteriormost point of eye and snout), internarial distance (IN; least distance between nostrils), posterior eye–mandible distance (EM; distance between posteriormost edge of eye and posterior edge of mandible), 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 (SUPs) and infralabials (first labial scale to last labial scale bordering gape), and dorsal scale rows (DSRs; counted around the body from one side of ventrals to the other in three positions: at one head length behind neck, at midbody, and at one head length before cloacal plate); when counting the number of ventral scales, we scored

specimens according to the method described by Dowling (1951). We counted subcaudal scales from the first subcaudal scale to the scale before the tip of the tail. Male specimens were identified by the presence of everted hemipenes or by ventral tail dissection.

Statistically informative tests could not be performed on separate sexes because the smaller sample sizes that represent the different geographic regions (e.g., southern, northern, and southeastern in this study) of the island would have rendered them insufficient for this purpose. Therefore, only the types and 25 adult voucher specimens were used for the statistical analysis. Juveniles were excluded to avoid the bias of allometry for the statistical analysis. Univariate and multivariate analyses were conducted on 10 morphometric ratios (TL/SVL, HW/HL, IN/HW, IN/IO, ED/ES, ED/EM, ED/HL, HL/SVL, HL/TL, and ES/HL), including the holotype of *O. propinquus* (from Java fide Jan 1862), the holotype of *O. waandersi* and all name-bearing types (onomatophores) of its synonyms (*R. cruciatum*, *O. taeniurus*) from Sulawesi, and voucher specimens of *O. waandersi* sensu lato from Sulawesi 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 (North = 7, South = 13, and Southeast = 5). We used this test because of 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). We used the princomp function in R statistical software (v.3.3.2, R Core Team 2016) based on a correlation matrix of 10 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 (v.3.3.2).

RESULTS

Three of 10 morphometric ratio mean comparisons (Table 1) showed significant differences among northern Sulawesi populations (including the holotype of *O. propinquus* and one of the syntypes of *O. taeniurus*), southern Sulawesi populations of *O. waandersi* (forma typica), and the

TABLE 1.—Average population values and statistics of Kruskal–Wallis tests on variation of morphometric ratios of northern, southern, and southeastern populations of *Oligodon waandersi* sensu lato. Statistically significant comparisons are in bold. 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; EM = eye–mandible distance.

Morphometric ratio	Avg. population value (\pm SE)			χ^2	P value
	South	North	Southeast		
TL/SVL	0.118 (\pm0.004)	0.139 (\pm0.006)	0.098 (\pm0.009)	10.51	0.005
HW/HL	0.626 (\pm0.021)	0.654 (\pm0.021)	0.559 (\pm0.013)	6.94	0.03
IN/HW	0.460 (\pm 0.017)	0.413 (\pm 0.014)	0.430 (\pm 0.007)	3.24	0.20
IN/IO	0.579 (\pm0.016)	0.529 (\pm0.006)	0.685 (\pm0.021)	13.31	0.001
ED/ES	0.492 (\pm 0.011)	0.508 (\pm 0.025)	0.585 (\pm 0.037)	4.94	0.08
ED/EM	0.370 (\pm 0.030)	0.399 (\pm 0.016)	0.378 (\pm 0.022)	0.83	0.66
ED/HL	0.177 (\pm 0.006)	0.181 (\pm 0.014)	0.197 (\pm 0.013)	1.91	0.38
HL/SVL	0.045 (\pm 0.003)	0.042 (\pm 0.002)	0.038 (\pm 0.002)	2.46	0.29
HL/TL	0.386 (\pm 0.030)	0.309 (\pm 0.025)	0.401 (\pm 0.044)	4.03	0.13
ES/HL	0.361 (\pm 0.012)	0.357 (\pm 0.021)	0.336 (\pm 0.006)	1.16	0.56

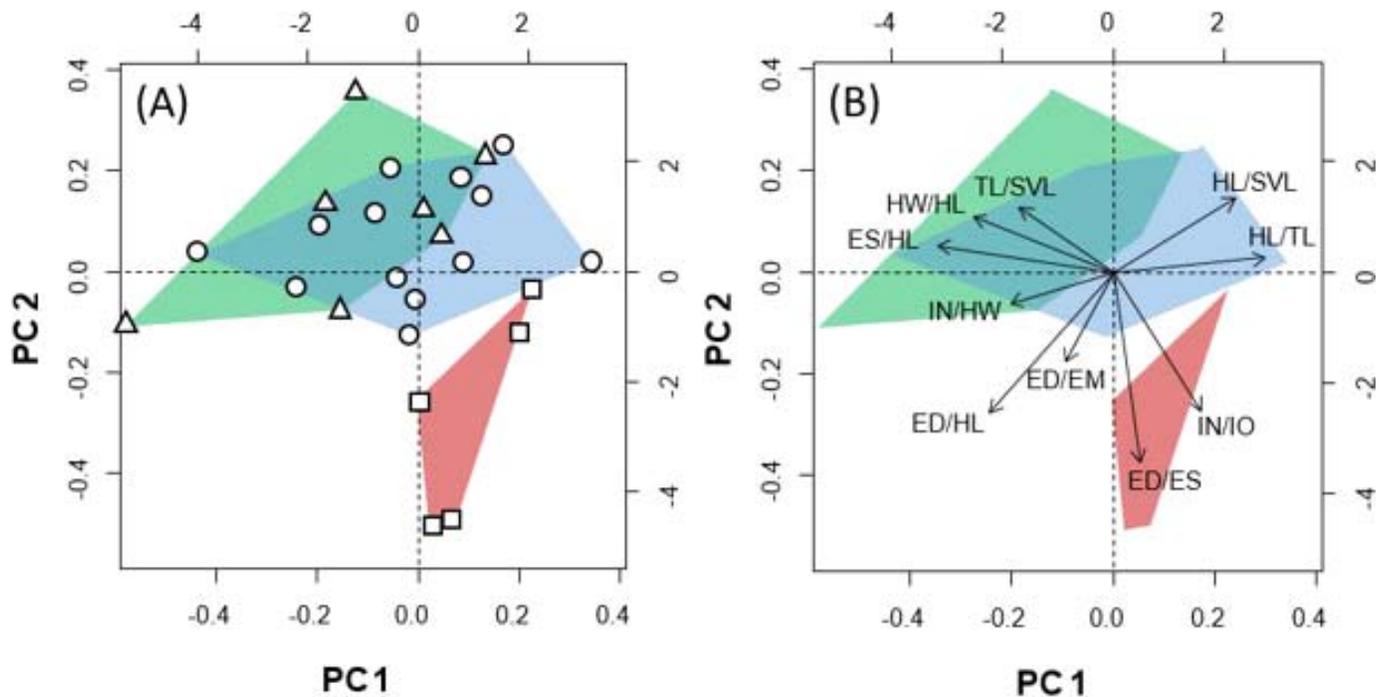


FIG. 1.—(A) Principal component analysis biplot of morphometric variation in northern (triangles), southern (circles), and southeastern (squares) populations of *Oligodon waandersi* sensu lato clearly shows the morphological distinctiveness of the southeastern population. Each point represents an individual 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. TL = tail length; SVL = snout-vent length; HW = head width; HL = head length; IN = interorbital distance; IO = interorbital width; ED = eye diameter; ES = snout length; EM = eye-mandible distance; PC = principal component. A color version of this figure is available online.

southeastern populations of *O. waandersi* (described as a new species herein). The TL/SVL of snakes in the southeastern population was significantly smaller, indicating a relatively shorter tail than that of snakes in the southern and northern populations. In addition, HW/HL of the southeastern population snakes was significantly smaller, indicating a relatively narrower head than that of southern and northern population snakes. Finally, IN/IO of the southeastern population snakes was significantly larger, indicating a more pointed snout than that of snakes of southern and northern populations.

Multivariate analysis by principal component analysis also showed distinct overall differences in morphometric characters among three populations, with a distinct nonoverlapping cluster for the southeastern population (Fig. 1A). Principal components 1 and 2 collectively explained 47.5% of the variation in the morphometric data matrix (Fig. 1A; Table 2). Morphometric ratios HL/SVL and HL/TL loaded positively with principal component 1, whereas HW/HL, ED/HL, and ES/HL loaded negatively with principal component 1. In addition, morphometric ratios IN/IO, ED/ES, and ED/HL loaded negatively with principal component 2 (Table 2). Overall, morphometric ratios IN/IO and ED/ES were positively associated with the southeastern population, whereas TL/SVL and HW/HL showed negative associations (Fig. 1B).

We present diagnostic morphological, morphometric, and meristic data taken for the type specimens in Tables 3 and 4. The examined syntype of *O. taeniurus* (NHMUK 1946.1.3.15), originating from northern Sulawesi, is morphologically distinguishable from *O. waandersi*; hence, we

regard it as a distinct species. Furthermore, *O. taeniurus* was placed well within the cluster of the northern population, and the holotype of *O. waandersi* within the southern population, in the morphometric analysis (Fig. 1). However, the other synonym, *R. cruciatum*, which was collected from the same locality as *O. waandersi*, is morphologically identical with *O. waandersi*; hence, we confirm the view of Günther (1865) to regard *R. cruciatum* as a junior synonym of *O. waandersi*. We also compared the holotype of *O. propinquus* (ZMH R04432), which was considered to be collected from Java (fide Jan 1862), with the holotype of *O. waandersi*. It was then revealed that *O. propinquus* is morphologically distinct enough to be separated from *O. waandersi*; interestingly, it is morphologically close to the syntype of *O. taeniurus*. It is also placed within the cluster of the northern population in the morphometric analysis (Fig. 1). In addition to morphological and morphometric characters, both holotypes, which are more or less equal in body size (SVL = 220 and 242 mm), are within very close range of meristic characters (e.g., ventrals 141 and 146; subcaudals 28, 29, etc.; see Table 4). Because there are no morphological, morphometric, or meristic characters to distinguish *O. taeniurus* from *O. propinquus*, we consider these two taxa to be synonyms and, in agreement with the principle of priority, Article 23 of the Code (ICZN 1999), *O. propinquus* has priority over *O. taeniurus*. Based on morphology, the population of northern Sulawesi, distributed in North Sulawesi and Gorontalo, and perhaps also those in some northern parts of Central Sulawesi, should be known as *O. propinquus* with *O. taeniurus* as a synonym, and southern populations (distributed in South Sulawesi and some western

TABLE 2.—Principal component analysis (PCA) and loadings. Principal component 1 (PC 1) and PC 2 collectively explained 47.5% of the variation. Relatively strong loadings associated with PCs 1 and 2 are indicated in bold. 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; EM = eye-mandible distance.

PCA variable	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
SD	1.65	1.42	1.32	1.18	0.92	0.79
Proportion of variance	0.27	0.20	0.17	0.14	0.08	0.06
Cumulative percentage (%)	27.40	47.50	64.90	78.90	87.30	93.50
Loadings						
TL/SVL	-0.26	0.21	0.50	-0.20		-0.60
HW/HL	-0.38	0.18	-0.28	-0.36		0.31
IN/HW	-0.28	-0.10	-0.39	0.24	-0.55	-0.34
IN/IO	0.24	-0.44	-0.18	0.30		-0.41
ED/ES		-0.61	0.13	-0.30	0.19	
ED/EM	-0.13	-0.28	0.31	-0.34	-0.69	0.13
ED/HL	-0.34	-0.45	-0.17	-0.28	0.34	
HL/SVL	0.34	0.24	-0.16	-0.54		-0.45
HL/TL	0.42		-0.45	-0.33		
ES/HL	-0.48		-0.35		0.21	-0.18

and northern parts of Central Sulawesi) should bear the name *O. waandersi* (with *R. cruciatum* as a synonym). We provide redescriptions for *O. waandersi* and *O. propinquus* based on their holotypes (NHMUK 1946.1.2.52 and ZMH R04432, respectively). The populations of southeast Sulawesi are morphologically distinct enough to be considered undescribed species, requiring a new species name; hence, we provide a description below.

SYSTEMATICS

We assign the new species 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 round, single loreal, one large preocular, internasals present, ventrals rounded, tail short, 15 smooth DSRs throughout the body without apical pits, a single or paired cloacal plate, and subcaudal plates divided (Wallach and Bauer 1996).

Oligodon tolaki sp. nov.
(Figs. 2–4; Tables 3–5)

Oligodon waandersi de Lang and Vogel 2005 [partim].

Holotype.—Adult male (MZB 4570), Gunung (=Mt.) Mekongga (3°34'49.60"S, 121°09'34.50"E; datum = WGS84; 1097 m above sea level), Tinukari, Wawo, North Kolaka Regency, Southeast Sulawesi, Indonesia, collected on 6 July 2010 by W. Trilaksana.

Paratypes (n = 5).—Adult female (MZB 2669), Amoito Village near Wolasi (near montane forest), Ranomeeto, South Konawe Regency, South East Sulawesi, Indonesia, collected on 14 July 2000 by R. de Lang; adult males (MZB 2812, 2831) and adult female (MZB 2991, 2832), Labusango, Kapontori, Buton Regency, South East Sulawesi, Indonesia, collected between 8 August 2001 and 11 July 2002 by G. Gillespie.

Diagnosis.—*Oligodon tolaki* sp. nov. is distinguished from other congeners by having the following combination of

TABLE 3.—Morphometric (in mm) and meristic characters of the holotype and paratypes of *Oligodon tolaki* sp. nov. MZB = Museum Zoologicum Bogoriense; M = male; F = female, J = juvenile; L = left; R = right; — = not applicable.

Character	<i>Oligodon tolaki</i> sp. nov.							Range (n = 6)	Mean ± SD
	Holotype MZB 4570	Paratype							
		MZB 2669	MZB 2831	MZB 2832	MZB 2991	MZB 2812			
Sex	M	M	F	M	F	F (J)			
Snout-vent length (SVL)	340	205	305	225	295	93	205–340	274 ± 50.8	
Tail length (TL)	42.8	18.8	32.2	21.4	21.5	10.1	18.8–42.8	27.3 ± 8.9	
TL/total length (%)	11.2	8.4	9.5	8.7	6.8	9.8	6.8–11.2	8.9 ± 1.4	
Head length	12.0	8.8	10.1	9.4	10.9	6.8	8.8–12.0	10.2 ± 1.1	
Head width	7.2	4.7	5.4	5.4	6.0	3.9	4.7–7.2	5.7 ± 0.8	
Internarial distance	3.3	2.0	2.3	2.3	2.5	2.1	2.0–3.3	2.5 ± 0.4	
Interorbital width	4.4	3.2	3.3	3.3	3.8	3.1	3.2–4.4	3.6 ± 0.4	
Eye-snout length	3.9	2.9	3.3	3.3	3.8	2.6	2.9–3.9	3.4 ± 0.3	
Eye-mandible distance	5.7	4.6	5.2	5.2	5.8	7.2	4.6–5.8	5.3 ± 0.4	
Eye diameter	2.2	1.6	2.2	2.2	1.8	1.2	1.6–2.2	2.0 ± 0.2	
Ventrals	169	150	160	160	153	154	150–169	—	
Subcaudals	26	20	23	18	19	21	18–26	—	
Supralabials	6	6	6	6	6	6	—	—	
Infralabials	7	7	7	7	7	7	—	—	
Preocular	1	1	1	1	1	1	—	—	
Postocular	1	1	L1, R2	1	1	1	—	—	
Temporals	1+2	1+2	1+2	1+2	1+2	1+2	—	—	
Loreal absent (0), present (1)	1	1	1	0	0	0	—	—	
Anal entire (1), divided (2)	1	1	1	1	1	1	—	—	

TABLE 4.—Morphological, morphometric, and meristic characters of *Oligodon tolaki* sp. nov., *O. waandersi*, and *O. propinquus* including types and synonym types (see Appendix for accession data). MZB = Museum Zoologicum Bogoriense; NHMUK = Natural History Museum, London, UK; ZMH = Zoologisches Museum Hamburg, Germany; — = not measured.

Character	<i>Oligodon tolaki</i> sp. nov.		<i>Oligodon waandersi</i>			<i>Oligodon propinquus</i>		
	Holotype MZB 4570	Range (n = 6)	Holotype <i>Rabdion waandersi</i> NHMUK 1946.1.2.52	Holotype <i>Rabdion cruciatum</i> NHMUK 1946.1.3.12	Range (n = 14)	Holotype <i>Oligodon propinquus</i> ZMH R 04432	Syntype <i>Oligodon taeniurus</i> NHMUK 1946.1.3.15	Range (n = 12)
Snout-vent length (SVL)	340	205–340	197	93	93–335	242	220	187–318
Tail length (TL)	42.8	18.8–42.8	24.7	10.1	10.1–38.1	37.0	36.3	23.0–42.0
TL/total length (%)	11.2	6.8–11.2	11.1	9.8	9.1–12.0	13.3	14.2	12.0–14.2
Head length	12.0	8.8–12.0	7.2	6.7	6.4–13.0	7.9	9.8	7.9–12.6
Head width	7.2	4.7–7.2	5.0	4.3	4.3–7.6	5.8	6.0	5.8–8.1
Internarial distance	3.3	2.0–3.3	2.6	1.8	1.8–3.6	2.7	2.5	2.5–3.1
Interorbital width	4.4	3.2–4.4	3.7	3.1	3.1–6.5	5.4	4.6	4.6–5.9
Eye-nostril length	—	—	1.9	1.3	1.3–2.4	2.5	1.5	1.5–2.5
Eye-snout length	3.9	2.9–3.9	3.3	2.0	2.0–3.9	3.6	3.7	3.3–4.0
Eye-mandible distance	5.7	4.6–5.8	3.8	2.4	2.4–6.9	4.5	4.3	3.9–5.6
Eye diameter	2.2	1.6–2.2	1.6	1.2	1.2–2.0	2.0	1.8	1.7–2.3
Ventrals	169	150–169	146	153	144–176	141	146	134–147
Subcaudals	26	18–26	24	25	20–25	29	29	22–29
Supralabials	6	6	6	6	6	6	7	6, 7
Infralabials	7	7	7	7	7	7	8	7, 8
Postocular	1	1	2	2	2	2	2	2
Loreal absent (0), present (1)	1	0, 1	0	0	0	1	1	0, 1
Anal entire (1), divided (2)	1	1	2	2	2	1	2	1, 2
Ventrolateral stripe	Absent		Absent or slightly visible anteriorly			Present and prominent		
Spotted line on ventrals	Absent		Present			Absent or present		
Whitish collar on the nape (in case of present)	Broad, interrupted		Broad, continuous			Narrow, continuous		
Dark-edged pale vertebral spots (in case of present)	Prominent		Prominent			Indistinct		

characters: maximum SVL 340 mm, a single postocular, a single loreal, a single cloacal plate, completely divided nasal, ventrals 150–169, subcaudals 18–26, temporals 1+2, six SUPs with third and fourth in contact with eye, DSRs 15–15–15, hemipenes not forked and covered with spines, maxillary teeth 6–7, shorter tail (TL 6.8–11.2% of total length), brownish dorsum with few dark-edged spots on the vertebral line anteriorly, reddish brown vertebral line on the posterior body and tail, mostly a blackish brown blotch below eye, and whitish collar band interrupted middorsally.

Comparison.—*Oligodon tolaki* sp. nov. is most similar to *O. waandersi* and *O. propinquus* (characters in parentheses). The new species differs from *O. waandersi* by having a single postocular (two); a single loreal (absent); a single cloacal plate (divided); completely divided nasal (undivided, rarely partially divided); a narrow, deep, and pointed rostral (broader, shallower, and rounded); and rounded snout in lateral aspect (pointed). The new species differs from *O. propinquus* by having a single postocular (two), a single cloacal plate (divided, rarely entire), ventrals 150–169 (134–147), completely divided nasal (undivided, rarely partially divided), rounded snout in lateral aspect (pointed), and shorter tail (TL 6.8–11.2% of total length; longer, 12.0–14.2%).

Furthermore, the new species is compared with other closely related *Oligodon* species from Southeast Asia based on data in de Rooij (1917), Taylor (1922), Smith (1943), Leviton (1963), Manthey and Grossmann (1997), Pauwels et al. (2002), Das (2010), and Tillack and Günther (2010) as well as on specimens deposited in collections (see Appendix). The number of DSRs around the neck (one head length behind the head) and at midbody is a major diagnostic character in the genus *Oligodon* (see David et al. 2008). This

number is usually constant within a given species. This character is only variable in some exceptional species complexes such as *Oligodon purpurascens* (Schlegel 1837), which has 19 or 21 scale rows at midbody. There are 80 species recognized in the genus *Oligodon*, of which only 31 species have 15 DSRs, either constantly along the length of body or at least at midbody (see Table 5). All other species of the genus have 13, 17, 19, 21, or rarely 23 rows at midbody or throughout the body.

Among the 31 species that have 15 DSRs at midbody, 25 species display the condition consistently (15–15–15), including the new species: *O. brevicauda* Günther 1862; *O. calamarius* (Linnaeus 1758); *O. dorsalis* (Gray 1834); *O. erythrorachis* Wall 1910; *O. everetti* Boulenger 1893; *O. hamptoni* Boulenger 1918; *O. inornatus* (Boulenger 1914); *O. jintakunei* Pauwels, Wallach, David, and Chanhom 2002; *O. kampucheaensis* Neang, Grismer, and Daltry 2012; *O. lacroixi* Angel and Bourret 1933; *O. lungshenensis* Zheng and Huang in Huang et al. 1978; *O. melaneus* Wall 1909; *O. modestus* Günther 1864; *O. nikhili* Whitaker and Dattatri 1982; *O. notospilus* Günther 1873; *O. ornatus* van Denburgh 1909; *O. petronellae* Roux in de Rooij 1917; *O. praefrontalis* Werner 1913; *O. propinquus* Jan 1862; *O. sublineatus* Duméril, Bibron, and Duméril 1854; *O. taeniolatus* (Jerdon 1853); *O. torquatus* (Boulenger 1888); *O. vertebralis* (Günther 1865); *O. waandersi* (Bleeker 1860); *O. wagneri* David and Vogel 2012; and *O. tolaki* sp. nov. The structure and length of the hemipenes are major diagnostic characters in the genus *Oligodon* (Smith 1943). *Oligodon tolaki* sp. nov. differs from *O. dorsalis*, *O. kampucheaensis*, *O. sublineatus*, and *O. taeniolatus* by its unforked hemipenes (forked). The new species has six or seven maxillary teeth; thus, a lower number than in both *O. inornatus* (11–12) and

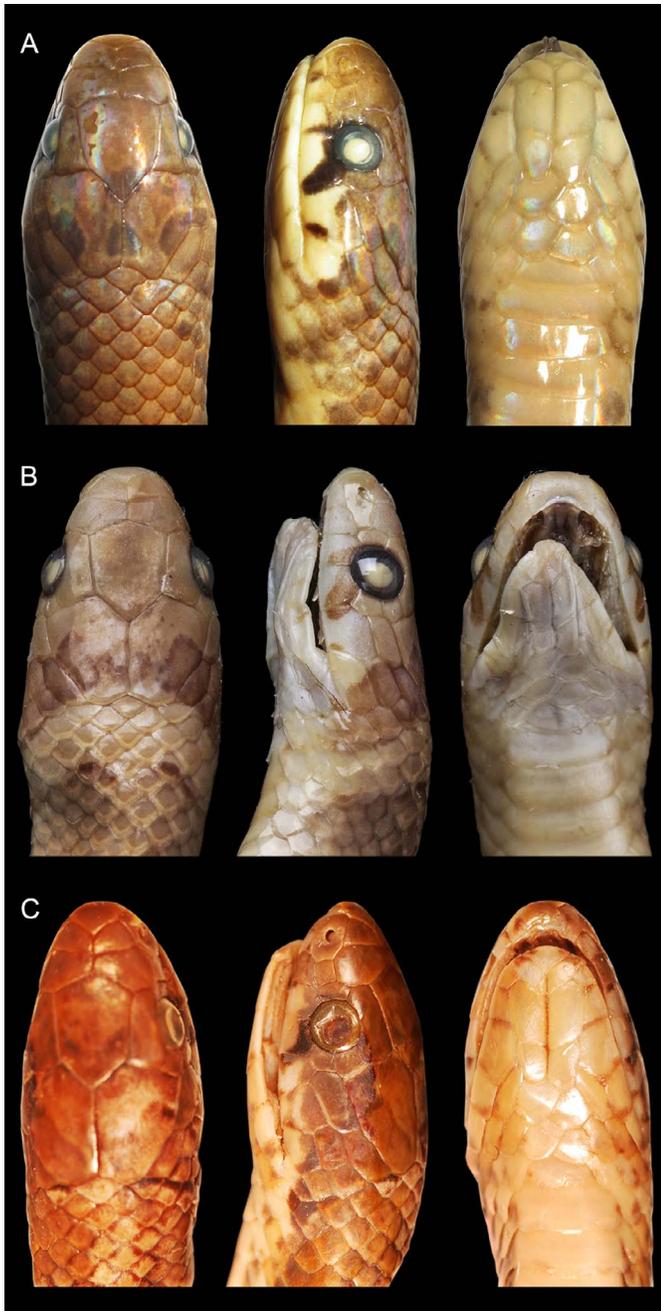


FIG. 2.—Dorsal, lateral, and ventral head views of (A) holotype of *Oligodon propinquus* (Zoologisches Museum Hamburg, Germany [ZMH] R04432), (B) holotype of *Rabdion waandersi* (Natural History Museum, London, UK [NHMUK] 1946.1.2.52), and (C) holotype of *Oligodon tolaki* sp. nov. (Museum Zoologicum Bogoriense [MZB] 4570). A color version of this figure is available online.

O. torquatus (15–16). *Oligodon tolaki* sp. nov. has a complete head scalation complement and thus differs from *O. brevicauda*, *O. hamptoni*, *O. jintakunei*, and *O. praefrontalis* that lack internasals. *Oligodon tolaki* sp. nov. has 150–169 ventrals, representing a higher number than in *O. nikhili* (144), *O. notospilus* (136–140), and *O. vertebralis* (136–143), and fewer than in *O. praefrontalis* (193). Also, the new species has 18–26 subcaudals; thus, fewer than in *O. dorsalis* (27–51), *O. erythrorachis* (46), *O. everetti* (46–72),



FIG. 3.—A live individual of *Oligodon tolaki* sp. nov. (not collected, photographed in 2004) from Lambusango Forest Reserve, Buton Island, Southeast Sulawesi, Indonesia. Photo by B. Lardner.

O. hamptoni (30–32), *O. inornatus* (31–42), *O. jintakunei* (46), *O. kampucheaensis* (39), *O. lacroixi* (29), *O. lungshe-nensis* (31–38), *O. melaneus* (39–40), *O. modestus* (27–44), *O. nikhili* (33), *O. notospilus* (35–42), *O. ornatus* (27–44), *O. petronellae* (30–42), *O. praefrontalis* (37), *O. taeniolatus* (29–59), *O. vertebralis* (35–43), and *O. wagneri* (41). *Oligodon tolaki* sp. nov. further differs by having a TL 6.8–11.2% of total length, which is shorter than in *O. bitorquatus* (17.2–19.2%), *O. everetti* (25.8–28.8%), *O. modestus* (15.0–21.1%), *O. notospilus* (19.7–21.7%), *O. petronellae* (15.0–17.8%), and *O. wagneri* (16.2%). Finally, the new species differs from *O. calamarius* by having uniform dorsum, sometimes with reddish brown longitudinal stripes and darker edged pale vertebral spots (a yellow vertebral stripe with paler edged narrow transverse stripes anteriorly).

Description of holotype.—Adult male, SVL 340 mm; TL 42.8 mm; head elongate (HL 3.5% of SVL), twice as long as wide (HW 60.0% of HL), slightly flattened, indistinct from neck; snout elongate (ES 32.5% of HL), moderate, bluntly pointed in dorsal view, rounded in lateral profile, forming an oval shape, rather depressed.

Rostral shield large, hemispherical, distinctly visible from above, pointed posteriorly; interorbital width broad (IO 61.1% of HW); internasals semicircular; nostrils rather large; nasals short, divided by nostrils, in anterior contact with rostral, and internasal and prefrontal dorsally, first and second SUPs ventrally; a single loreal present; prefrontal rather large, broader than long, and subhexagonal; frontal large, subhexagonal, elongate posteriorly and longer than wide; supraoculars narrow, elongated, subrectangular, posteriorly wider; parietals large, butterfly wing-like in shape, bordered by supraoculars, frontal, postoculars anteriorly, anterior and upper posterior temporals, and three nuchal scales posteriorly; one preocular, vertically shortened, subpentagonal, in contact with prefrontal and loreal anteriorly, supraocular dorsally, and third SUP ventrally; eye moderate (ED 18.3% of HL), round, half of the size of snout length (ED 56.4% of ES), pupil rounded; one postocular, subpentagonal, in broad contact with supraocular, parietal anterior temporal and fourth and fifth SUPs; temporals 1+2, elongated, subrectan-

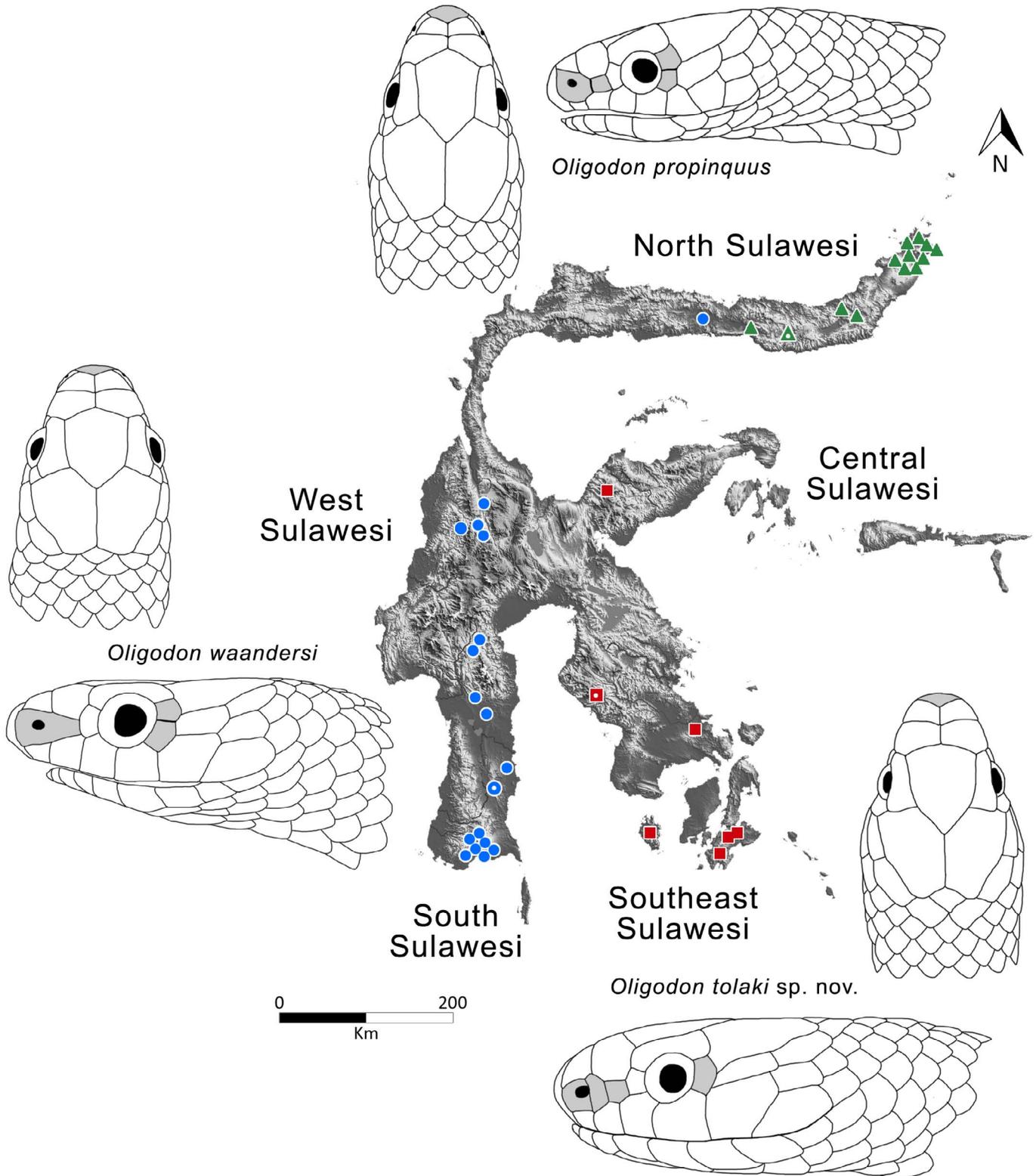


FIG. 4.—Current distribution map showing the collection/observation localities of the *Oligodon* species on Sulawesi, Indonesia: (A) *O. propinquus* (green triangles), (B) *O. waandersi* (blue circles), and (C) *O. tolaki* (red squares). The symbols with dot in the middle represent the name bearing type locality of respective species. A color version of this figure is available online.

gular; anterior temporal almost the same size of upper posterior temporal, in contact with parietal and postocular dorsally, fifth SUP ventrally; lower posterior temporal in contact with fifth and sixth SUPs ventrally. SUPs six (on both

sides), fifth largest in size; first SUP in contact with rostral anteriorly, anterior nasal dorsally, second with posterior nasal and loreal dorsally, third with loreal, preocular and orbit dorsally, fourth with orbit and the postocular dorsally, fifth

TABLE 5.—Main characters of the *Oligodon* species with 15 dorsal scale rows at midbody (modified after David and Vogel [2012]). Exceptional values are placed in parentheses. See text for explanations of the acronyms used in character. e = entire, d = divided, p = present, a = absent, ? = unknown.

Species	Hemipenes	Hemipenes length	Maxillary teeth	Anal	Ventrals	Subcaudals	Sup	Inter nasals	Loreal	Anterior temporals	TL/total length (%)
<i>O. bitorquatus</i>	Not forked	15–16	6–9	e	136–165	29–44	6, 7	p	a, p	1	17.2–19.2
<i>O. brevicauda</i>	?	?	7–8	d	158–176	25–29	7	a	a	1	?
<i>O. tolaki</i> sp. nov.	Not forked	?	6–7	e	150–169	18–26	6	p	a, p	1	6.8–11.2
<i>O. calamarius</i>	Not forked	9–10	7	d	127–152	20–34	7	p	p	1	?
<i>O. dorsalis</i>	Forked	11	6–7	d	162–188	27–51	7	p	p	1	?
<i>O. erythrorachis</i>	?	?	7–8	d	154	46	7	p	a	1	?
<i>O. everetti</i>	Not forked	35	7–8	e	132–154	46–72	7	p	p	1, 2	25.8–28.8
<i>O. hamptoni</i>	Not forked	11	7–8	d	160–175	30–32	5	a	a, p	1	?
<i>O. huahin</i>	Forked	?	6	e	166–173	35–41	7, 8	p	a		
<i>O. inornatus</i>	Not forked	10–12	11–12	e	169–174	31–42	8	p	p	1	?
<i>O. jintakunei</i>	?	?	6	d	189	46	7	a	p	1	?
<i>O. kampucheaensis</i>	Forked	11	11	e	164	39	8	p	p	1	15.1
<i>O. lacroixi</i>	?	?	8–12	d	162–178	29	5	p	a	1	?
<i>O. lungshenensis</i>	?	?	?	?	166–180	31–38	6	p	a	2	?
<i>O. melaneus</i>	Not forked	15	7	d	152–160	39–40	7	p	p	1	?
<i>O. modestus</i>	Not forked	18	7–8	e	156–176	27–44	6	p	a	1	15.0–21.1
<i>O. nagao</i>	Not forked	16	9–10	e	184–193	?	8	p	p	?	13.5–14.6
<i>O. nikhili</i>	?	?	?	d	144	33	7	p	a	1	?
<i>O. notospilus</i>	?	?	7–8	d	136–140	35–42	7	p	p	1	19.7–21.7
<i>O. ornatus</i>	Not forked	9	6–8	d	156–182	27–44	6, 7	p	a	1	?
<i>O. petronellae</i>	Not forked	?	7–8	e	144–163	30–42	7	p	p	1, 2	15.0–17.8
<i>O. praefrontalis</i>	?	?	?	d	193	37	7	a	a	1	12.9
<i>O. propinquus</i>	Not forked	5	8–9	d, e	134–147	22–29	6, 7	p	p	1	12.0–14.2
<i>O. rostralis</i>	Forked	8	6	e	167	47	6	p	a	1	19.6
<i>O. signatus</i>	Not forked	25–26	7–8	e	144–160	44–59	7	p	p	1	18.1–24.9
<i>O. sublineatus</i>	Forked	13	6–8	d	130–161	23–39	7	p	p	1	?
<i>O. taeniolatus</i>	Forked	9–11	6–7	d	158–218	29–59	7	p	p	1	?
<i>O. torquatus</i>	Not forked	8	15–16	d	114–169	25–34	7	p	p	1	?
<i>O. vertebralis</i>	Not forked	?	8–9	e	136–143	35–43	7	p	p	1	?
<i>O. waandersi</i>	Not forked	5–7	8–9	d	144–176	20–25	6	p	a, p	1	9.1–12.0
<i>O. wagneri</i>	Not forked	18	9	e	156	41	7	p	p	1	16.2

with postocular and anterior and lower posterior temporals dorsally, and sixth 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, first to fourth in contact with anterior chin shields, fourth infralabial largest in size in contact with both anterior and posterior chin shields; fourth to seventh infralabials in contact with gular scales; two larger, elongate anterior chin shields, and two smaller, short posterior chin shields all in broad contact; posterior chin shields bordered posteriorly by four gular scales.

Body robust, elongate and subcylindrical; dorsal scales in 15–15–15 rows, all smooth and bluntly pointed; 169 ventral scales; cloacal plate entire. Tail comparatively short (TL 11.2% of total length), robust and thick; subcaudals 26, divided.

Coloration.—After 10 yr in preservative, dorsum dark olive brown, lateral surface paler; faded reddish brown vertebral line on the tail; three dark brown blotches on parietals and one on frontal posteriorly; faded whitish collar mark on nape, interrupted middorsally; a blackish brown blotch below eye; venter uniform yellow.

In life (based on Fig. 3), dorsum dark olive brown, lateral surface paler; faded reddish brown vertebral line on the tail; three blackish brown blotches on parietals and one on frontal posteriorly; faded whitish, uninterrupted collar mark on nape with dark-edged posteriorly; a blackish brown blotch below eye; another black blotch above eye on the junction of

supraocular, frontal, and prefrontal; with several pale, dark-edged blotched along the vertebral line up to the tail; four to seven dorsal scale gap in between each pale spot.

Variation.—The holotype and paratypes (Table 3) are composed of adults, except for MZB 2812, which is a juvenile. The coloration and the morphology are more or less unique for all the individuals of the type series. This species is not sexually dimorphic (see Table 3). The presence or absence of loreal varies among individuals. MZB 2831 has two postoculars on the right side (single on left side), probably an aberrant.

Etymology.—The specific epithet refers to the major ethnic group in Sulawesi, “Tolaki,” and is formed here as an invariable noun in apposition. The Tolaki tribe is mostly distributed in the Southeast Sulawesi where the new species is also found. The suggested English name is Tolaki Kukri snake.

Distribution and natural history.—This species is found in primary forests, mostly in montane forests at midelevations (100–1000 m above sea level) in Southeast Sulawesi, and in eastern parts of Central Sulawesi (Fig. 4). Kopstein (1935) recorded this species for the first time from Buton Island. The female paratype (MZB 2669) collected from Amuito Village was caught during the daytime in a clove tree (de Lang and Vogel 2005). In addition, de Lang and Vogel (2005) observed a specimen from Buton Island in the morning, crawling in the leaf litter along a forest path. The specimen that de Lang and Vogel (2005) mentioned from Kabaena Island may relate to this new species.

Oligodon waandersi (Bleeker 1860)

(Figs. 2, 4; Tables 3–5)

Rabdion waandersi Bleeker 1860.*Rabdion cruciatum* Bleeker 1860.*Oligodon waandersi*—Günther 1865 [partim], de Rooij 1917 [partim], in den Bosch 1985 [partim], in den Bosch 1994 [partim], Malkmus 2000 [partim], Inger and Voris 2001 [partim], de Lang and Vogel 2005 [partim], Wagner et al. 2011, Koch 2012 [partim], et al. 2014 [partim].

Holotype.—Adult male (NHMUK 1946.1.2.52), SVL 197.0 mm, collected from “liet rijk van Boni,” i.e., the empire of Bone, Bone Regency near Makassar, Province of South Sulawesi, Indonesia, by Waanders.

Diagnosis.—*O. waandersi* is distinguished from *O. tolaki* sp. nov. (characters in parentheses) by having two postoculars (single); no loreal (present); divided cloacal plate; undivided or partially divided nasal (completely divided); a broader, shallower, and rounded rostral (narrow, deep, and pointed); pointed snout in lateral aspect (rounded); and from *O. propinquus* (characters in parentheses) by absence of loreal (present) and by having a broader, shallower, and rounded rostral (narrow, deep, and pointed); ventrals 146–176 (134–147). Furthermore *O. waandersi* is distinguished from all other congeners of the genus *Oligodon* by having the following combination of characters: maximum SVL 335 mm, two postoculars, no loreal, divided cloacal plate, single or partially divided (rarely) nasal, ventrals 146–176, subcaudals 20–27, temporals 1+2, six SUPs with third and fourth in contact with eye, DSRs 15-15-15, brownish dorsum with few dark-edged spots on the vertebral line along the body and tail, mostly a blackish brown blotch below eye, and whitish collar band middorsally.

Redescription of the holotype.—Adult male, SVL 197 mm; TL 24.7 mm; head elongate (HL 3.6% of SVL), slightly longer as wide (HW 72.2% of HL), slightly flattened, indistinct from neck; snout elongate (ES 45.8% of HL), moderate, blunt in dorsal view, pointed in lateral profile, forming an oval shape, rather depressed.

Rostral shield large, hemispherical, slightly visible from above, bluntly pointed posteriorly; interorbital width broad (IO 74.0% of HW); internasals rectangular; nostrils rather large; nasals elongate, undivided by nostrils, in anterior contact with rostral, internasal and prefrontal dorsally, first and second SUPs ventrally; loreal absent; prefrontal rather large, broader than long, and subhexagonal; frontal large, subhexagonal, shorten posteriorly and slightly longer than wide; supraoculars narrow, elongated, subrectangular, posteriorly wider; parietals large, butterfly wing-like in shape, bordered by supraoculars, frontal, upper postoculars anteriorly, anterior and upper posterior temporals, and five nuchal scales posteriorly; one preocular, vertically elongated, subrectangular, in contact with prefrontal and nasal anteriorly, supraocular dorsally, and second and third SUPs ventrally; eye large (ED 22.2% of HL), elliptical, less than half of the size of snout length (ED 48.5% of ES), pupil rounded; two postoculars, upper postocular smaller, rectangular, contact with supraocular and parietal broad, in narrow contact with anterior temporal; lower postocular crescentic in contact with fourth and fifth SUPs ventrally, anterior temporal posteriorly; temporals 1+2, elongated, hexagonal;

anterior temporal almost the same size than upper posterior temporal, in contact with parietal dorsally, fifth SUP ventrally; lower posterior temporal in contact with fifth and sixth SUPs ventrally. SUPs six, fifth largest in size; first SUP in contact with rostral anteriorly, nasal dorsally, second with nasal and preocular dorsally, third with preocular and orbit dorsally, fourth with orbit and the lower postocular dorsally, fifth with lower postocular, anterior and lower posterior temporal dorsally, sixth SUP with lower posterior temporal dorsally and scales of the neck posteriorly.

Mental of moderate size, triangular; first infralabial pair larger than mental plate and in broad contact with each other, in contact with anterior chin shield posteriorly; seven infralabials, first to fourth in contact with anterior chin shields, fourth infralabial largest in size in contact with both anterior and posterior chin shields; fourth to sixth infralabials in contact with gular scales; two larger, elongate anterior chin shields, and two smaller, short posterior chin shields all in broad contact; posterior chin shields bordered posteriorly by four gular scales.

Body robust, elongate and subcylindrical; dorsal scales in 15-15-15 rows, all smooth and bluntly pointed; 146 ventral scales; cloacal plate divided. Tail comparatively short (TL 11.1% of total length), robust and thick; subcaudals 24, divided.

Coloration.—After 160 yr in preservative, dorsum has faded to pale pinkish brown; with several pale, dark-edged blotched along the vertebral line up to the tail, and a pale blotch on the tail tip, lateral surface paler; a continuous chestnut brown transverse band on the parietals; a continuous prominent whitish collar mark on nape; a dark brown blotch below eye; venter cream, uniform; MZB 3367 from South Sulawesi (near the type locality; ~100-km direct distance) has a dark olive brown dorsum with blackish brown interrupted band on parietals, and yellowish venter with two light brown spots on each ventral scale; the color pattern of NHMUK 1946.1.3.12 (holotype of *R. cruciatum*) agrees with its senior synonym except for the whitish collar mark on nape interrupted middorsally.

Distribution.—This species is distributed mostly in the southern part of the island, but is also found on the western and northern slopes of Central Sulawesi toward the north, from sea level up to 1200 m above sea level (Fig. 4). It is found in primary as well as secondary forests and also in villages near montane forests. The highest elevation for this species was recorded by Smith (1927) from Mt. Bonthain (=Mt. Lampobatang, altitude 1200 m above sea level) in South Sulawesi.

Oligodon propinquus Jan 1862

(Figs. 2, 4; Tables 3–5)

Oligodon propinquus Jan 1862.*Oligodon taeniurus* Müller 1895.*Oligodon waandersi*—Günther 1865 [partim], de Rooij 1917 [partim], in den Bosch 1985 [partim], in den Bosch 1994 [partim], Malkmus 2000 [partim], Inger and Voris 2001 [partim], de Lang and Vogel 2005 [partim], Koch 2012 [partim], Wallach et al. 2014 [partim].*Oligodon propinquus*—Hallermann 1998.

Holotype.—Adult male (ZMH R04432), SVL 242.0 mm, allegedly collected from “Giava,” namely Java; based on our

study, this locality is obviously in error, and we here specify the type locality of *O. propinquus* as “Pinogo im Bona-Thal,” i.e., Pinogu in Bona Valley, Province of Gorontalo, Indonesia, based on the type locality of the junior synonym *O. taeniurus* Müller 1895.

Diagnosis.—*Oligodon propinquus* is distinguished from *O. tolaki* sp. nov. (characters in parentheses) by having two postoculars (single), ventrals 134–147 (150–169), undivided or partially divided nasal (completely divided), pointed snout in lateral aspect (rounded), longer tail (TL 12.0–14.2% of total length; shorter, 6.8–11.2%); from *O. waandersi* (characters in parentheses) by having a single loreal (absent), a narrow, deep, and pointed rostral (broader, shallower, and rounded), ventrals 134–147 (146–176); furthermore *O. propinquus* is distinguished from all other congeners of the genus *Oligodon* by having the following combination of characters: maximum SVL 318 mm, two postoculars, a single loreal, single or rarely divided nasal, ventrals 134–147, subcaudals 22–29, temporals 1+2, seven SUPs with third and fourth in contact with eye, DSRs 15–15–15, brownish dorsum with few dark-edged spots on the vertebral line anteriorly, reddish brown vertebral line on the posterior body and tail, mostly a blackish brown blotch below eye and blackish brown color continuous band on parietals.

Redescription of the holotype.—Adult male, SVL 242.0 mm; tail length 37.0 mm; head elongate (HL 3.3% of SVL), slightly longer as wide (HW 73.4% of HL), slightly flattened, indistinct from neck; snout elongate (ES 45.6% of HL), moderate, bluntly pointed in dorsal view, pointed in lateral profile, forming an oval shape, rather depressed.

Rostral shield large, hemispherical, distinctly visible from above, pointed posteriorly; interorbital width broad (IO 93.1% of HW); internasals rectangular; nostrils rather large; nasals short, undivided by nostrils, in anterior contact with rostral, internasal and prefrontal dorsally, first and second SUPs ventrally; a single loreal present; prefrontal rather large, broader than long, and subhexagonal; frontal large, subhexagonal, short posteriorly and longer than wide; supraoculars narrow, elongated, subrectangular, posteriorly wider; parietals large, 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, subrectangular, in contact with prefrontal and loreal anteriorly, supraocular dorsally, and third SUPs ventrally; eye large (ED 25.3% of HL), round, half of the size of snout length (ED 55.6% of ES), pupil rounded; two postoculars, upper postocular larger, rectangular, contact with supraocular, parietal, and lower postocular broad, in narrow contact with anterior temporal; lower postocular subpentagonal in contact with fourth and fifth SUPs ventrally, anterior temporal posteriorly; temporals 1+2, elongated, hexagonal; anterior temporal almost the same size of upper posterior temporal, in contact with parietal dorsally, fifth and sixth SUPs ventrally; lower posterior temporal in contact with sixth and seventh SUPs ventrally. SUPs seven, sixth largest in size; first SUP in contact with rostral anteriorly, nasal dorsally, second with nasal and loreal dorsally, third with preocular and orbit dorsally, fourth with orbit and the lower postocular dorsally, fifth with lower postocular, and anterior temporal dorsally, sixth SUP with anterior and lower posterior

temporal dorsally, seventh with lower posterior temporal dorsally and scales of the neck posteriorly.

Mental of moderate 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, first to fourth in contact with anterior chin shields, fourth infralabial largest in size in contact with both anterior and posterior chin shields; fourth to sixth infralabials in contact with gular scales; two larger, elongate anterior chin shields, and two smaller, short posterior chin shields all in broad contact; posterior chin shields bordered posteriorly by four gular scales.

Body robust, elongate and subcylindrical; dorsal scales in 15–15–15 rows, all smooth and bluntly pointed; 141 ventral scales; cloacal plate divided. Tail comparatively short (TL 13.3% of total length), robust and thick; subcaudals 29, divided.

Coloration.—After 160 yr in preservative, dorsum dark brown, lateral surface paler, the anterior part of the dorsum darker; dark blotches on the parietals completely faded, no collar marks on nape; a dark brown blotch below eye; venter cream, anterior edge of each ventral scale darker; blackish brown colored distinct ventrolateral stripe present along the body; NHMUK 1946.1.3.15 (syntype of *O. taeniurus*) also has a similar color pattern, but dark blotches on parietal prominent, not faded; the ventrolateral stripe is darker.

Distribution.—This species is distributed in the northern part of Sulawesi from sea level up to height of the mountains (Fig. 4). The records of de Rooij (1917) from Masarang, Paso, and Rurukan in North Sulawesi probably refer to this species. Also, the records of in den Bosch (1994) from Gurupahi, Kema, Lilang, Manado, Pinogo (=Pinogu), Tomohon, Tongkoko, and Batuangus in Mongondow may refer to the same species.

DISCUSSION

Although several synonyms were involved, *O. waandersi* has long been considered a single species distributed throughout the Sulawesi Island, and it was the sole member of the genus *Oligodon* recorded on Sulawesi, except for a doubtful record of *O. octolineatus* fide de Lang and Vogel (2005). The morphological variation, especially the color pattern of *O. waandersi*, was extensively discussed by in den Bosch (1994). This species has been considered a morphologically highly diverse snake with a loreal present or absent, the nasal divided or single, the cloacal plate entire or divided, the postocular single or two, as well as ventrals with a range of 134–176 (de Rooij 1917; in den Bosch 1994; de Lang and Vogel 2005). The diverse morphology suggests a species complex with several morphospecies isolated to different biogeographic regions in Sulawesi. Most divergence time estimates for the split of Sulawesi lineages from their sister groups on the island as well as to other islands postdate relevant tectonic vicariant events, suggesting that the island was predominantly colonized by dispersal (Stelbrink et al. 2012).

Bleeker (1860) discovered both *R. waandersi* and *R. cruciatum* from “liet rijk van Boni” (=empire of Bone), which is in South Sulawesi close to Makassar. In the original description, *R. cruciatum* was described on page 82 and *R. waandersi* on page 83. In this case, Günther (1865)

prioritized *O. waandersi* and synonymized *O. cruciatum* with it. When the descriptions of the two taxa are published at the same time and in the same work, the precedence of the names is fixed by the First Reviser (in this case Günther 1865) sensu principle of First Reviser Article 24.2 of the Code (ICZN 1999). Therefore, we follow Günther's (1865) act of synonymy.

The syntypes of *O. taeniurus* originated from three localities (1) "Kema," (2) "Lilang, Südwest von Kema" (Lilang, Southwest of Kema), and (3) "Pinogo im Bona-Thal" (Pinogu in the Bona Valley), which are situated in the North Sulawesi (1 and 2) and the Gorontalo (3) provinces. In this study we examined only one syntype (NHMUK 1946.1.3.15) of *O. taeniurus*. In den Bosch (1994) also examined one syntype only (the same syntype as ours). Müller (1895) clearly mentioned that he had three specimens, with 29 subcaudals, 24, 23, and 29. The syntype we examined has 29 subcaudals, which is the third syntype collected from "Pinogo im Bona-Thal." However, in the original description the ventral scale count was provided for only two type specimens, 153 and 154. The syntype we examined has 146, which must be the count that Müller (1895) did not provide. The other two syntypes (1) NMB 5218 and (2) NMB 5217 are deposited at the Naturhistorisches Museum Basel, Switzerland (E. Stöckli, personal communication). The third syntype, NMB 1606, was given to Dr. Taylor (fide Schenkel 1901:162), and this was the type currently deposited at the NHMUK with the catalog number NHMUK 1946.1.3.15. Müller (1895) probably assumed that biogeographic isolation from *O. waandersi*, which is from South Sulawesi, led to the difference seen in his species, which is from the north. However, de Rooij (1917) synonymized *O. taeniurus* with *O. waandersi* probably based on the color pattern. A litter-dwelling snake, *Rabdion forsteni*, also shows a similar wide distribution pattern from South Sulawesi toward the north, whereas the population in Southeast Sulawesi evolved as a distinct species, *Rabdion grovesi* (see Amarasinghe et al. [2015a]); this is similar to our findings for *Oligodon tolaki* sp. nov. We extensively compared the southern and northern populations of *O. waandersi* sensu lato, including the respective type specimens, and we found that the northern population (*O. taeniurus*) is morphologically distinct enough to be resurrected from its synonymy.

Species *Oligodon propinquus* of Jan (1862) has been considered a Javan species, because in the original description its locality is mentioned as "Giava," now Java. However, locality data in the old collection of ZMH often lack details. Catalogues and correspondence were destroyed during World War II, and nothing but the jar label remains. Materials from that time were often mislabeled or the lacked exact locality details. We compared the holotype of *O. propinquus* with the types of its closely related taxon *O. waandersi* as well as with *O. taeniurus*. Interestingly, the holotype of *O. propinquus* is morphologically identical to this latter taxon, and there are no diagnostic characters present to separate them (Table 4). Therefore, as *O. propinquus* Jan 1862 has priority over *O. taeniurus* fide Article 23 of the Code (ICZN 1999), *O. taeniurus* needs to be transferred from the synonymy of *O. waandersi* to the synonymy of *O. propinquus*. We therefore synonymize *O. taeniurus* with *O. propinquus*. Furthermore, we assume that the holotype of *O. propinquus* was collected from Sulawesi,

but mistakenly labeled as originating from "Java." It is significant to note that neither *O. propinquus* nor *O. taeniurus* has ever been recorded from Java, except in the original description of *O. propinquus*. In the same publication of Jan (1862), he compared his species with a Sri Lankan endemic species, *O. sublineatus* Duméril, Bibron and Duméril 1854, which has some close similarity in color pattern. Interestingly, in Jan (1862) the Sri Lankan species type locality is also listed as "Batavia, Giava" (=Jakarta, Java), in error, however, as this mistake was corrected by Amarasinghe et al. (2015b). Such locality errors between Java and Sulawesi continue to occur in the literature. Most recently, the type locality of *Mabuaya macrophthalmia* Mausfeld and Böhme 2002 was considered to be "Java" and later corrected as Sulawesi by Amarasinghe et al. (2018). Therefore, taking the above-mentioned information into consideration, the locality "Java" is probably another such error, and to stabilize the taxon with a recognized and more stable locality, we here specify the type locality of *O. propinquus* as "Pinogo im Bona-Thal," i.e., Pinogu in Bona Valley, Province of Gorontalo, Indonesia, based on the type locality of the junior synonym *O. taeniurus* Müller 1895.

The reptile fauna of Sulawesi is one of the least known in Southeast Asia (Amarasinghe et al. 2015a). According to Koch (2012) approximately 60% of the known snake fauna from Sulawesi is endemic, although this is likely to be underestimated. Given the biogeographical complexity of Sulawesi, with poorly known upland rainforests in the island's interior portion, more cryptic species of the *O. waandersi* complex may be found. Such isolated or cryptic populations have to be reinvestigated along with the support of phylogenetic studies.

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APPENDIX

Specimens Examined

- Oligodon ancorus*.—Philippines: Muséum National d'Histoire Naturelle, Paris (MNHN-RA) 0611, 3537, 5768, 1900.0381–385, 1900.0381a–b.
- Oligodon bitorquatus*.—Indonesia: Java: Naturalis Biodiversity Center, Leiden (RMNH) 10429 (syntype), 18154 (holotype of “*Simotes bitorquatus obscurus*,” nomen nudum), MNHN 1621, 1999.8147 (syntypes of *Oligodon subquadratus*), 1029a–c, 1975.0083, Museum Zoologicum Bogoriense (MZB) 0423, 0526, 0784, 0893, 0895, 0977, 1031, 1073, 1091, 1198, 1254, 1256, 1361, 2747, 0792a–b; Sumatra: MZB 3582, RMNH 54.1–2.
- Oligodon tolaki* sp. nov.—Indonesia: Southeast Sulawesi MZB 4570 (holotype), 2669 (paratype); Buton Island: MZB 2812, 2831–2, 2991 (paratypes).
- Oligodon everetti*.—Indonesia: Borneo: MZB 3023, MNHN 1975.0103.
- Oligodon octolineatus*.—Indonesia: Java: MZB 2673, MNHN 3540, 5891; Sumatra: MZB 2002, Naturhistorisches Museum, Wien (NMW) 19215, 25838.3, NMW 25838.4; MNHN 0825, 5798, 1999.1704, 1999.8204, 1975.0104, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt (SMF) 19214–15, ZSM 16/1909, Zoologisches Forschungsmuseum Alexander Koenig Bonn (ZFMK) 33556, RMNH 18140; West Malaysia: MNHN 1884.0083; Borneo: MNHN 1889.0198; Singapore: MNHN 0192, 4987, 1990.4981.
- Oligodon petronellae*.—Sumatra: Muséum d'histoire naturelle, Genève (MHNG) 767.2 (holotype of *Oligodon ornatus*), NMW 16048 (holotype of *Oligodon annulifer confluentis*), Museum für Naturkunde, Berlin (ZMB) 30586.
- Oligodon propinquus*.—Indonesia: North Sulawesi: Zoologisches Museum Hamburg (ZMH) R04432 (holotype, Java in error), Natural History Museum, London (NHMUK) 1946.1.3.15 (syntype of *Oligodon taeniurus*), 1896.12.9.55–56, NMW 23779.1, 37452, ZFMK 85276, ZMB 52081.
- Oligodon pulcherrimus*.—Sumatra: Naturhistorisches Museum Basel (NMB) 1017619 (holotype of *Oligodon durheimi*), MNHN 1912.0049 (holotype of *Simotes annulifer* var. *bipartite*).
- Oligodon purpurascens*.—Indonesia: Java: RMNH 242A–C (syntypes), MZB 3013; Kalimantan: MZB 2880; Sumatra: MZB 2171, 3789, MNHN 3539, NMW 25816:1–2, RMNH 18153, SMF 22423, Smithsonian National Museum of Natural History, Washington DC (USNM) 103580, Zoological Museum Amsterdam (ZMA.RENA) 17463–4, ZFMK 33551, ZMB 8460, 15881, 15999, 24047, 32198; West Malaysia: California Academy of Sciences, San Francisco (CAS) 16820.
- Oligodon signatus*.—Indonesia: Sumatra: RMNH 4690 (holotype of *Simotes annulifer* var. *annulata*), MZB 1840a–b. USNM 82212, ZMA.RENA 17437, 17472.1–2, MNHN 1891.0233, Borneo: NHMUK 1946.1.4.24 (holotype of *Simotes subcarinatus*); Singapore: NHMUK 1946.1.3.20, 1946.1.3.25 (syntypes of *Simotes signatus*).
- Oligodon sublineatus*.—Sri Lanka: MNHN 3238 (lectotype), 3239 (paralectotype), 1747, 4234, 4234a, NMB 21366–7, 1595–9, 10775, 21364–5, NHMUK 1841.1.7.12, 1858.10.19.29, 1858.10.19.37–38, 1852.9.13.41, 1845.8.7.6, 1846.12.2, 1853.3.30.53, 1852.2.19.90, 1852.2.19.95, 1969.2769–2771, 1890.11.8.21–22, 1895.7.23.29, 1897.10.20.14, 1915.5.3.6, 1920.5.6.3, 1951.1.8.36, 1955.1.9.81–82, 1862.8.14.31, 1968.875.
- Oligodon trilineatus*.—Indonesia: Sumatra: MNHN 3541 (holotype of *Simotes trilineatus*), MZB 0797, RMNH 468
- Oligodon vertebralis*.—Borneo: MNHN 1889.0195–0.197.
- Oligodon waandersi*.—Indonesia: South Sulawesi: NHMUK 1946.1.2.52 (holotype), 1946.1.3.12 (holotype of *Rabdion cruciatum*), 1896.4.29.40, 1896.4.29.42–43, 1926.8.20.152–154, MZB 0798, 3367, 2097; North Sulawesi: Gorontalo: MZB 5325; Central Sulawesi: NHMUK 1980.916; Sulawesi: NMW 23779.2.
- Oligodon wagneri*.—Indonesia: Nias, Sumatra: MNHN 1891.0233 (holotype).