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Systematics of the Sri Lankan Water Snakes of the Genus *Fowlea* Theobald 1868 (Reptilia: Natricidae)

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Abstract: Based on phylogenetic and morphological characters, we revise the systematics of the natricid genus *Fowlea* in Sri Lanka, comprising two morphospecies. The taxonomy of the Sri Lankan populations has long been controversial, and one of the species has, for more than a decade, been listed as *Xenochrophis* cf. *piscator*. Although the Sri Lankan populations are morphologically allied to *Fowlea piscator* in India, they are genetically highly divergent from the eastern Indian *F. piscator* sensu lato with a *p*-distance of 9.9–12.3%, and from southwestern Indian *Fowlea* species with a *p*-distance of 4.9–11.1% in the mitochondrial cytochrome b gene. Here, we resurrect Müller's (1887) variety, *Tropidonotus quincunciatus* var. *unicolor*, as a distinct taxon, elevate it to the species level, and assign it to the genus *Fowlea*. Therefore, the population so far recognized as *X.* cf. *piscator* will be treated hereafter as *F. unicolor* and we redescribe it and its holotype (by monotypy). We tentatively restrict this species to Sri Lanka and state the possibility of a population in southern India too. The second distinct species, *Fowlea asperrima*, which is endemic to Sri Lanka, has long been confused with its sympatric congener, *F. unicolor* comb. nov., and we designate a lectotype and redescribe it herein. Currently, nine species of the genus *Fowlea* are now recognized, but it is likely that further species (including those regarded as subjective synonyms) remain unrecognized.

Key words: Asia; Distribution; Lectotype; Keelback snake; Morphology; Synonym

The Asiatic water snakes of the genus *Xenochrophis* Günther 1864 have long been taxonomically indefinite until its largest species group, the *Xenochrophis piscator* group, was extensively reviewed by Vogel and David (2006, 2012) based on their morphological traits across the entire geographic range in Asia. Later, Purkayastha et al. (2018) proposed the assigning of this species group to the resurrected genus *Fowlea* Theobald 1868 based on phylogenetic, morphological, and osteological evidence. Recently, Cheng et al. (2021) reviewed the systematic position of one of the little-known taxa, *Atretium schistosum yunnanensis* (sic) Anderson 1879, and elevated the subspecies to species level and combined it with the genus *Fowlea* based on integrative taxonomic evidence. Although some species of the genus *Fowlea* were allocated without any systematic definitions, currently nine species are recognized (Cheng et al. 2021): *Fowlea melanzosta* (Gravenhorst 1807), *F. punctulata* (Günther 1858), *F. flavipunctata* (Hallowell 1860), *F. tytleri* (Blyth 1863), *F. yunnanensis* (Anderson 1879), *F. asperrima* (Boulenger 1891), *F. piscator* (Schneider 1799), *F. schnurrenbergeri* (Kramer 1977), and *F. sanctijohannis* (Boulenger 1890)—the last of which has not been systematically resurrected yet—while having the remaining five water snake species in the genus *Xenochrophis*. Among the nine species of the genus *Fowlea* listed above, the latter three are distributed in Peninsular India, while the Sri Lankan member, *X.* cf. *piscator* has yet been assessed in recent systematic revisions (e.g., Purkayastha et al. 2018; Cheng et al. 2021; Deepak et al. 2021).

Hydrus piscator was described by Schneider (1799) based on an illustration made by Russell (1796: 38, pl. 33, "Neeli Koea"), but without providing a precise locality, the locality only being stated as "Indiae orientalis" (eastern India). Vogel and David (2012) examined the dry skin (holotype; Natural History Museum, London, UK [NHMUK] 1904.7.27.32) of *Hydrus piscator* deposited at the Natural History Museum, London, and redefined the taxon, evaluating all the synonyms associated with that nomen. In their review, Vogel and David (2012) restricted the type locality of *F. piscator* to the northern coastal areas of Andhra Pradesh. Among the long list of synonyms of *F. piscator*, Daudin's (1803) three species (*Coluber umbratus*, *C. mortuarius*, and *C. dora*) and *C. bengalensis* Gray 1834 described from the surroundings of "Bengal"—the northeastern part of the Indian subcontinent—were synonymized with *F. piscator*. Among these four subjective synonyms, *C. umbratus* has been considered a typically patterned *X. piscator* (fide Vogel and David 2012). Daudin's other two species were considered to represent a single taxon and the authors selected *C. mortuarius* as having priority over *C. dora*. Furthermore, this taxon is considered a possible distinct species inhabiting northeastern India. Vogel and David (2012) considered that *C. bengalensis* most probably stems from an area close to Vishakhapatnam (northern Andhra Pradesh) and they suspect that it should have a distinct taxonomic status due to the presence of a straight collar streak (vs. the indistinct collar streak, if present, inverted V-shaped in *F. piscator* sensu stricto).

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Gray's (1834) other species, C. *rectangulus* from an unknown locality, has been considered as conspecific with *C. mortuarius* (fide Vogel and David 2012).

Günther (1864) considered the populations of *F. piscator* sensu lato as *Tropidonotus quincunciatus* Schlegel 1837—currently a junior objective synonym of *F. piscator*—composed of four varieties. Among them, varieties α and β referred to the Mainland Indian species and varieties γ and δ referred to the populations in Ceylon (Sri Lanka). Müller (1887) also followed the species nomen *T. quincunciatus* but defined different varieties from Sri Lanka, namely (1) Günther's (1864) variety γ, assumed to be distinct species with distinct color pattern, and two more varieties based on specimens collected by Sarasin and Sarasin; (2) a new variety as "var. *unicolor*" based on a single individual (Naturhistorisches Museum Basel [NMB] 723) with a uniform pale coloration; and (3) a banded variety (NMB 721–722; conspecific with Günther's 1864 variety δ). However, subsequent authors neglected Müller's nomen, which might be a subjective senior synonym for the Sri Lankan populations of *F. piscator* sensu lato. Although two distinct species of these water snakes were recognized by several subsequent authors (e.g., Wall 1921; Smith 1943; Deraniyagala 1955; etc.), they considered them to be either two color morphs or varieties or just subspecific entities; see Discussion.

Another subjective synonym of *F. piscator* sensu lato, *Tropidonotus sanctijohannis* Boulenger 1890, from Kashmir, northwest India, was considered an available name for some patternless specimens inhabiting northern India, Nepal, and northern Pakistan, if proved to be distinct from *F. piscator*. Wall's (1907) varieties, *T. piscator* var. *unicolor* (note: *T. quincunciatus* var. *unicolor* Müller 1887 has no relation to this taxon; see Discussion) and *T. p.* var. *obscurus* were suspected as being the same taxon as *T. sanctijohannis* (fide Vogel and David 2012).

In addition, two varieties of the species, *T. piscator* var. *lateralis* and *punctatus*, described by Wall (1907), respectively from central and southern parts of India, have also been considered to be junior subjective synonyms of *F. piscator*. However, Vogel and David (2012) claimed, in the case of *F. piscator* populations from the southern tip of Peninsular India, that they would deserve a distinct taxonomic status, and that the name *X. punctatus* (Wall 1907) might be assigned. In the same publication, they further identified the *F. piscator* population in Sri Lanka as likely deserving a distinct specific status also, and treated it as "*X.* cf. *piscator*." Here, we compare the Sri Lankan population of *F. piscator* sensu lato with the eastern Indian population, including populations from northern Andhra Pradesh and Bengal, based on morphological characters and phylogenetic data with further taxonomic actions on the subjective synonyms of *F. piscator*. Additionally, we provide a redescription for *F. asperrima* based on its lectotype from Sri Lanka designated herein.

Materials and Methods

We compared the type specimens (and iconotypes) of all the described species (including synonyms) of the *F. piscator* species group. We examined specimens and descriptions of the other known superficially similar congeners (see Appendix). We examined specimens from the following collections: Field Museum of Natural History, Chicago, USA (FMNH); Muséum d'histoire naturelle, Genève (Geneva), Switzerland (MHNG); Muséum national d'Histoire naturelle, Paris, France (MNHN-RA); NHMUK; NMB; National Museum of Sri Lanka, Colombo, Sri Lanka (NMSL), and Wildlife Heritage Trust, Sri Lanka (WHT, currently deposited at NMSL but retaining their former WHT registration identity); Smithsonian Institution National Museum of Natural History, Washington, DC, USA (USNM); Museum für Naturkunde, Berlin, Germany (ZMB), Zoologisches Museum Hamburg, Germany (ZMH), and Zoological Survey of India, Kolkata, India (ZSI). Museum abbreviations mostly follow Uetz et al. (2019). We obtained the diagnostic morphological characters for *F. piscator* sensu stricto (see Appendix) from the holotype (dry skin, NHMUK 1904.7.27.32), the original description, redescription, and redefinition provided by Vogel and David (2012), and voucher specimens assigned therein which were collected from the restricted type locality and surrounding localities of the same biogeographic regions (e.g., northern Andhra Pradesh, Odisha, West Bengal, etc.) that were a close match to those descriptions and the holotype. We compared the voucher specimens of *F. piscator* sensu stricto to the specimens from Sri Lanka and specimens of other *Fowlea* species (including types) distributed in India and Sri Lanka. We obtained morphological, morphometric, and meristic data for species comparisons, and distribution data from examined specimens and published literature, and we also examined georeferenced photographic vouchers from the iNaturalist Citizen Science Platform (available at https://www.inaturalist.org).

We examined features of the skull and counted the number of maxillary, palatine, pterygoid, and mandible teeth of *F. piscator* sensu lato and *F. asperrima* based on MicroCT scans of museum specimens. MicroCT scans were generated using a Nikon XT H 225 ST and General Electric Phoenix Nanotom M scanners. The head of the specimen was scanned for 15–30 min at resolution of 5–20 μm and data were recorded for every 0.09–0.14° rotation for 360° with a 0.5-mm filter. The source voltage for the scans was 110–130 kV and source current was 82–91 μA. Volume rendering was performed with Avizo, v.2020.3 (Thermo Fisher Scientific), and images were edited in Adobe Photoshop CS6 (Adobe, Inc, San Jose, CA). Osteological description is based on volume renders retrieved from Avizo, following terminology of the skull described by Gans et al. (2008). We measured the following characters with a Mitutoyo digital caliper and dissecting microscopes: eye diameter (ED, horizontal diameter of eye); snout length (ES, distance between anteriormost point of eye and snout); 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 (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 prior to the 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 examined the basic structure and systematic characteristics of the hemipenes according to the method described by Dowling and Savage (1960). We evaluated the body coloration: initially checkered color pattern, shape of the collar streak, and the circular mark on the nape of each individual. This body color pattern was considered a reliable character only when a drawing, description, or photograph of a live or dead (freshly killed) specimen was available.

We performed separate Kruskal–Wallis one-way analysis of variance tests on the TL ratio to detect any significant differences between *F. piscator* sensu stricto from eastern India ($n = 10$) and *X.* cf. *piscator* from Sri Lanka ($n = 14$). We used this test due to the small sample size (Zar 2010). In addition, other statistically informative tests were performed on the same voucher specimens and *F. asperrima* ($n = 11$) specimens from Sri Lanka. Juveniles were excluded to avoid the bias of allometry for the statistical analysis, and boxplots were generated for tail ratio (TL/total length) in order to visualize the range, mean, median, and degree of difference between the above three species bearing statistically different mean values. Additionally, variation in adult size was normalized using the following equation: $\log X_{adj} = \log(X) - \beta(\log[SVL] - \log[SVL_{mean}])$, where X_{adj} = adjusted value, X = measured value, β = unstandardized regression coefficient for each population, and SVL_{mean} = overall average SVL of all populations (Lleonart et al. 2000) prior to multivariate analyses on four morphometric characters, TL, HL, ED, and ES. The scale morphometrics were treated as the dependent variable and the population as the predictor variable. Multivariate analysis was conducted using principal component analysis (PCA) to reduce the highly correlated multidimensional data matrix into a few uncorrelated variables (principal components [PC]). We used the princomp function in the R statistical software program (v4.0.4; R Core Team 2021). A biplot of the first two PC 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).

Molecular data for the mitochondrial DNA (cytochrome b; 1096 bp) were taken from published studies (Table 1). Two sequences from *X. cerasogaster* were used as outgroups in the analysis and the resultant phylogeny is congruent with results recovered in earlier studies of the "*Fowlea* clade" of water snakes (Purkayastha et al. 2018). The sequences were aligned in MEGA 7 (Kumar et al. 2016) using ClustalW with default settings. The PartitionFinder v1.1.1 (Lanfear et al. 2012) was used to determine the best nucleotide substitution model and the best partitioning scheme using the "greedy" algorithm under the Bayesian information criterion (BIC). The software selected the models HKY + I + G (Hasegawa–Kishino–Yano with invariant sites and gamma distribution), HKY + I (Hasegawa–Kishino–Yano with invariant sites), GTR + I (general time reversible with invariant sites) as the ones with the lowest BIC scores. The Bayesian inferences (BIs)– and maximum likelihood (ML)–based approaches were adopted for constructing the phylogenetic trees; MrBayes v3.2.6 (Ronquist et al. 2012) and BEAST v2.6.3 (Bouckaert et al. 2019) analysis methods was used for the BI method while RAxML GUI v1.5 incorporated in RAxML v8 (randomized accelerated ML; Stamatakis 2014) was used for the ML method. The program BEAST v2.6.3 was used to perform the coalescent-based analysis in the BI method. We carried out a log likelihood ratio test with and without enforcing the molecular clock in MEGA 7. The molecular clock test rejected the null hypothesis at a 5% significant level and hence a relaxed clock under lognormal distribution was used as the prior for the clock model. We ran the two independent runs in the Markov chain Monte Carlo (MCMC) algorithm for 100 million iterations, sampling every 1000 generations in the Yule coalescent model. The effective sample size values for the priors were checked using Tracer software v1.7.1 (Rambaut and Drummond 2009), and a value greater than 200 was used as the threshold. The initial 10% of the trees were discarded as the burn-in, which was suggested by Tracer v1.7.1 and a consensus tree was constructed by combining the two runs using Tree Annotator (Rambaut and Drummond 2009). ML analysis was performed using RAxML GUI v1.5 incorporating the RaxML-style partition defined by Partition Finder and node support was computed by rapid bootstrap method for 10,000 iterations (Wickramasinghe et al. 2017). Trees obtained from ML and BI methods were visualized using FigTree v1.4.3 (Rambaut 2014). The uncorrected p distance was calculated in Mega 7, and missing data or gaps were dealt with using the pairwise-deletion option. To distinguish them from synonyms, we place colons after chersonyms in the species accounts.

RESULTS

Morphologically, we confirm that the populations of the true *F. piscator* (based on its holotype) are distributed in the northern portion of eastern India. Therefore, following Vogel and David (2012) we accept its type locality as northern Andhra Pradesh (possibly Vishakhapatnam) and currently, we expand its distribution towards the north including Odisha and West Bengal.

The Grammatical Gender of the Genus *Fowlea*

Cheng et al. (2021) considered that the genus "*Fowlea*" was named by Mr. E. Fowle, the collector of the type specimen of *F. peguensis* (now *F. punctulata*). They also interpreted the gender of the Latinized generic epithet as masculine without providing any explanations. As a matter of fact, the genus *Fowlea* was named after Mr. E. Fowle by William Theobald (1829–1908) to place its monotypic species *F. peguensis*, which is the type species of the genus. As Theobald (1868) did not explicitly mention that the gender of the generic epithet is masculine, in accordance with Article 30.2.4 of the Code (ICZN 1999), "If no gender was specified or indicated [by the describer], the name is to be treated as masculine, except that, if the name ends in *–a* the gender is feminine, and if it ends in *–um*, *–on*, or *–u* the gender is neuter." Hence, the generic nomen, *Fowlea* is indeed feminine and the species epithets must be revised accordingly in agreement with the gender of the genus. Therefore, the following species epithets must be revised as

Table 1.—Sample of species used in the molecular study with locality information and GenBank accession numbers. Museum acronyms follow Uetz et al. (2019).

Species	Voucher no.	Locality	Cyt b	Source
Fowlea sp.	SN2019.31	Wayanad, India	OK315811	Deepak et al. 2021
F. asperrima 1	HT797	Sri Lanka	LC325346	Takeuchi et al. 2018
F. asperrima 2	RS-J	Sri Lanka	KC347480	Pyron et al. 2013
F. flavipunctata 1	CIB 116028	Hainan, China	MT199263	Cheng et al. 2021
F. flavipunctata 2	HT682	Vietnam	LC325330	Takeuchi et al. 2018
F. flavipunctata 3	CIB 116026	Hainan, China	MT199262	Cheng et al. 2021
F. flavipunctata 4	HT347	Thailand	LC325317	Takeuchi et al. 2018
F. flavipunctata 5	HT371	Vietnam	LC325318	Takeuchi et al. 2018
F. flavipunctata 6	ZMMU R-14811	Quang Binh, Vietnam	OK315808	Deepak et al. 2021
F. cf. *flavipunctata* 1	FMNH 250122	Thailand	MT587286	Conradie et al. 2020
F. cf. *flavipunctata* 2	XFL3	Bangkok, Thailand	LC105632	Laopichienpong et al. 2016
F. cf. *flavipunctata* 3	XFL2	Bangkok, Thailand	LC105631	Laopichienpong et al. 2016
F. cf. *piscator* 1	JP335	Guwahati, Assam, India	KY379915	Purkayastha et al. 2018
F. cf. *piscator* 2	JP336	Guwahati, Assam, India	KY379908	Purkayastha et al. 2018
F. cf. *piscator* 3	JP341	Guwahati, Assam, India	KY379909	Purkayastha et al. 2018
F. punctulata	CAS 201594	Ayeyarwady, Myanmar	AF471079	Lawson et al. 2005
F. schnurrenbergeri 1	JP0217	Guwahati, Assam, India	KY379924	Purkayastha et al. 2018
F. schnurrenbergeri 2	JP0337	Guwahati, Assam, India	KY379922	Purkayastha et al. 2018
F. tytleri 1	1618	Andaman	MG999966	Mohan et al. 2018
F. tytleri 2	1631	Andaman	MG999965	Mohan et al. 2018
F. cf. *tytleri*	ZMMU R-16510	Ratchaburi, Thailand	OK315810	Deepak et al. 2021
F. unicolor comb. nov.	HT796	Sri Lanka	LC325345	Takeuchi et al. 2018
F. yunnanensis 1	CIB 102884	Jingdong, China	MT199264	Cheng et al. 2021
F. yunnanensis 2	CIB 106885	Jingdong, China	MT199265	Cheng et al. 2021
F. yunnanensis 3	GP842	China	GQ281787	Guo et al. 2012
F. yunnanensis 4	CIB 102887	Cangyuan, China	MT199261	Cheng et al. 2021
F. cf. *yunnanensis*	ZMMU NAP-08416	Kachin State, Myanmar	OK315809	Deepak et al. 2021
X. cerasogaster 1	JP0346	Guwahati, India	KY379923	Purkayastha et al. 2018
X. cerasogaster 2	JP0211	Guwahati, India	KY379920	Purkayastha et al. 2018

follows: *F. asperrima*, *F. flavipunctata*, *F. melanzosta*, and *F. punctulata*. We noticed that Deepak et al. (2021) correctly used the above species epithets in their publication.

The Status of *Tropidonotus piscator punctatus* Wall 1907

Although the type locality of *T. p. punctatus*—a junior subjective synonym of *F. piscator*—was restricted to "Tranquebar" (now Tharangambadi, Tamil Nadu, India) by Vogel and David (2012), we noticed that this nomen encompasses several specimens (syntypes) that represent multiple species: fide Russell (1801: Plate 15A) from (1) Tranquebar, (2) Calcutta (now Kolkata, West Bengal, India), and (3) Bombay (now Mumbai, Maharashtra, India); and fide Günther (1864), variety δ from (1) Nepal and (2) Sri Lanka as referred by Wall (1907). Although here we apply the above nomen mainly to the specimen on the illustration on Plate 15A depicted by Russell (1801), Wall (1907: 861) stated in the original description that the species he (Wall) intended to describe was different in coloration from the depiction of Russell stating "… but I have usually seen them with the spots arranged quincuncially, and not irregularly scattered as in his [Russell's] specimen." Based on the description provided by Russell (1801), we assume that Russell considered all the specimens that he had were from the above three localities, while illustrating in his Plate 15A. However, Vogel and David (2012) restricted the type locality to "Tranquebar" (now Tharangambadi), Tamil Nadu, India, India. Furthermore, they claimed that, in the case of *F. piscator* populations from the southern tip of Peninsular India, they deserve a distinct taxonomic status, and that the name *X. punctatus* (Wall 1907) might be assigned. Therefore, to solve this taxonomic dispute involved with this nomen, following Vogel and David (2012), here we designate the specimen Russell (1801) had from Tranquebar (Tharangambadi) as the lectotype of *T. p. punctatus* and tentatively synonymize it with *F. piscator* sensu lato. We have no intention in designating a neotype for that nomen, nonetheless the designated lectotype has not been traced and could be lost (fide Vogel and David 2012). Although it is necessary to designate a neotype for this nomen, we leave it to future taxonomic workers.

The Status of Sri Lankan Populations

The molecular analysis based on the mitochondrial cytochrome b gene (total length of 1080 bp) using BI (Fig. 1) indicated that the *X.* cf. *piscator* sample from Sri Lanka is nested within the *F. piscator* group, but deeply divergent from their sampled relatives from Mainland India and other related taxa in the Clade B. The molecular analysis using ML (Fig. S1) yielded trees with similar topology. The population from Sri Lanka is most closely related to the sample assigned to the *Fowlea* species from Wayanad in the Kerala state of India. However, it differs from these samples by a minimum *p* distance of 4.9% (Table S1) in the mitochondrial cytochrome b gene. Although this *Fowlea* species might be an unnamed taxon, the taxonomic status of *T. p. punctatus* (see above) and *C. bengalensis* must be resolved before naming it; see Discussion. The eastern Indian *F. piscator* sensu lato differs from the Sri Lankan *X.* cf. *piscator* samples by a minimum *p* distance of 9.9% (Table S1). The northern most locality of *F. piscator* sensu stricto was so far evidently recorded from Darjeeling, West Bengal, India.

The TL ratio (TL/total length) comparison showed significant differences between eastern Indian (*F. piscator*

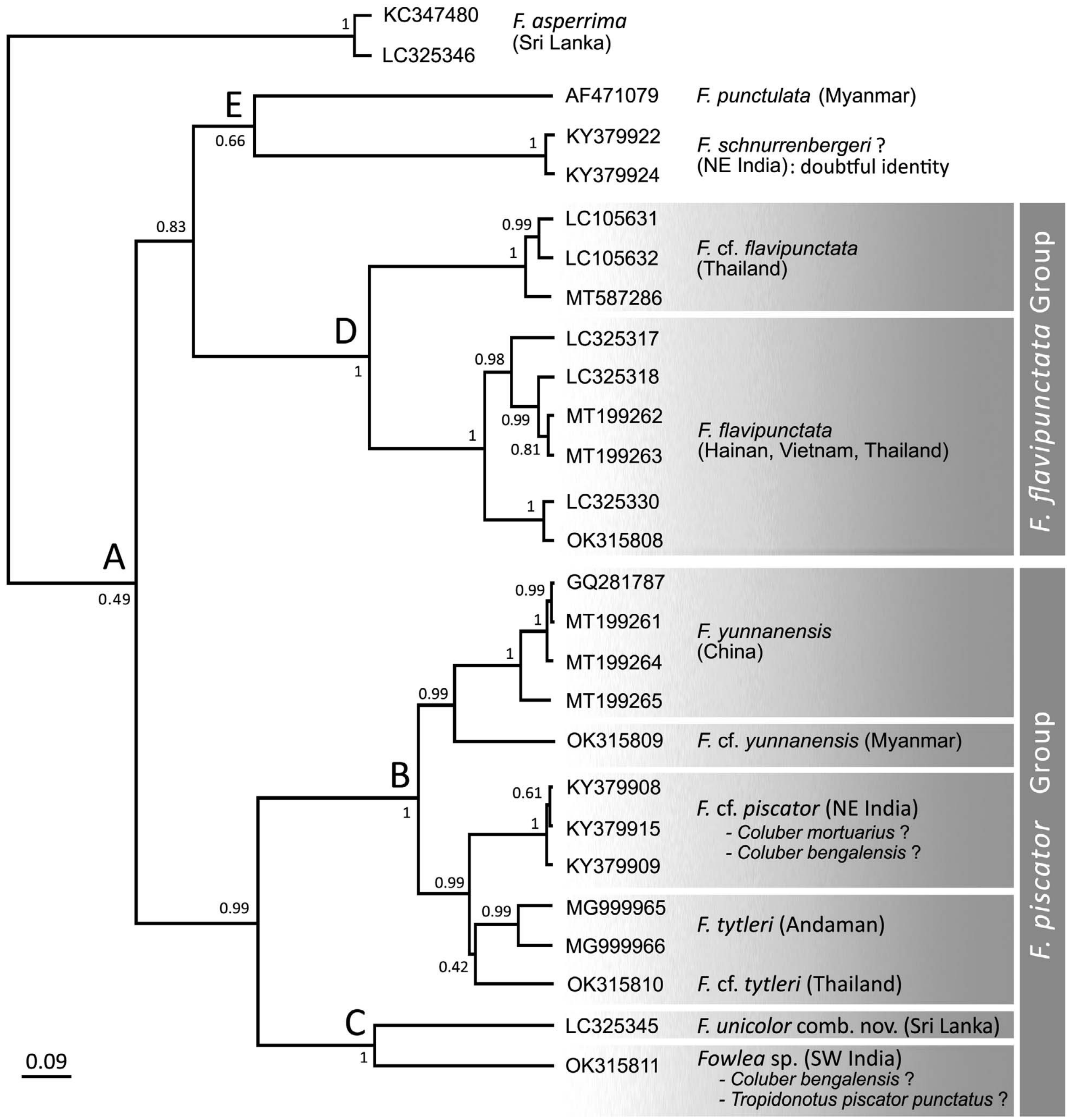

FIG. 1.—Phylogenetic affinities of the members of the genus *Fowlea* using a Bayesian Inference analysis of the cytochrome b region. ? = tentative assigning of species identity. Outgroup taxon, *Xenochrophis cerasogaster* is not shown.

sensu stricto) and Sri Lankan populations of *X.* cf. *piscator* ($\chi^2 = 6.94$, $P = 0.008$; Kruskal–Wallis test). A greater tail ratio of the Sri Lankan population indicated a relatively longer tail than that of *F. piscator* sensu stricto in eastern India (Fig. 2A). Multivariate analysis by PCA also showed other differences in morphometric characters between these two populations as well as *F. asperrima* in Sri Lanka with a distinct non-overlapping cluster for mixed sexes (Fig. 2B). PCs 1 and 2 collectively explained 90.23% of variation in the morphometric data matrix (Table S2). Scaled TL loaded positively and scaled HL loaded negatively for both PCs while scaled ED and scaled ES loaded positively only on the second PC. There was a slight difference in tail ratio between males and females within the Sri Lankan population ($\chi^2 = 3.92$, $P = 0.048$, Kruskal–Wallis test) indicating weak sexual dimorphism. Therefore, we assessed the morphometric character ratios (e.g., TL/total length), and meristic characters (e.g., ventrals, subcaudals) for each sex of each species separately.

Vogel and David (2012) recognized the populations of *X.* cf. *piscator* from Sri Lanka as morphologically distinct enough to be considered an undescribed species requiring a new name. Morphological analyses revealed a suite of characters to diagnose the population from each of our identified species in this species group (Table 2). Based on morphological and genetic differences we accept the Sri

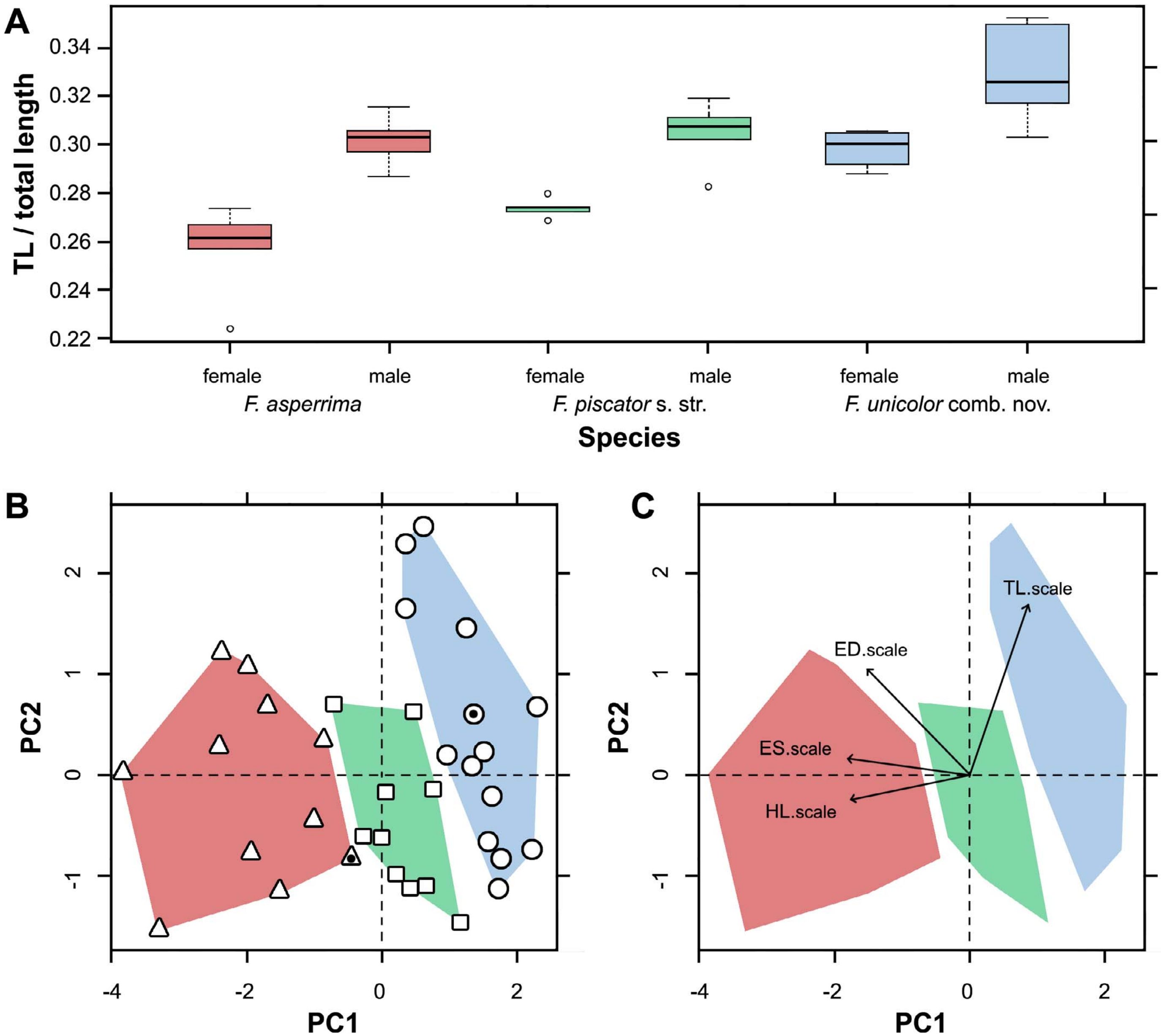

FIG. 2.—(A) Boxplots of tail ratio; top, middle and bottom lines of the boxes indicate 75th percentile, median, and 25th percentile, respectively. (B) Principal component analysis biplot of morphometric variation between *Fowlea unicolor* comb. nov. (circles) and its congeners, *F. piscator* sensu stricto from east India (squares), and *F. asperrima* (triangles). (C) The same base biplot with vectors associated with population clusters. Each point represents an individual specimen, and the relative distance between two points is equivalent to the amount of dissimilarity. The symbol with dot in the middle represents the examined type specimen; TL = tail length; HL = head length; ED = eye diameter; ES = snout length; PC = principal component. A color version of this figure is available online.

Lankan population of *X.* cf. *piscator* as a distinct species. However, the Sri Lankan population of *X.* cf. *piscator* has previously been recognized by Müller (1887) as "*Tropidonotus quincunciatus* var. *unicolor*." Therefore, we examined the holotype (by monotypy; NMB 723) collected from Sri Lanka. Interestingly, the holotype of *T. q.* var. *unicolor* clearly represents an individual of *X.* cf. *piscator* sensu Vogel and David (2012). A closer examination of the specimen reveals a slightly visible typical body coloration of the Sri Lankan population and it confirmed the resurrecting of Müller's variety as a valid nomen sensu Article 45.6.4 of the Code (ICZN 1999). Furthermore, here we combine it as a distinct species of the genus *Fowlea*. We tentatively restrict *Fowlea unicolor* comb. nov. to Sri Lanka and also include southern India as a possible additional location; see "Distribution" section and Fig. 9.

Fowlea asperrima has a unique body coloration with a banded pattern, and a lower tail ratio indicating a relatively shorter tail compared to *F. unicolor* comb. nov. (Fig. 2A). The molecular analysis also indicated that the *F. asperrima* sample from Sri Lanka is nested outside the *F. piscator* group (Fig. 1; Fig. S1) with a minimum *p* distance of 16.0% from its sympatric species of *F. unicolor* comb. nov. The Sri Lankan endemic, *F. asperrima*, is deeply divergent from their sampled relatives from Mainland India and Sundaland (Table S1; Fig. 1, Fig. S1), and is also basal to all others in

TABLE 2.—Selected morphological, morphometric and meristic characters to diagnose *Fowlea asperrima* and the species of the *F. piscator* group (including types, see Appendix for accession data).

Character		*Fowlea*							
		F. unicolor comb. nov. (*n* = 18)	*F. asperrima* (*n* = 35)	*F. flavipunctata* (*n* = 231)	*F. melanzosta* (*n* = 27)	*F. piscator* s. str. (*n* = 10)	*F. schnurrenbergeri* (*n* = 37)	*F. tytleri* (*n* = 11)	*F. yunnanensis* (*n* = 5)
Confluent blotches on the dorsum absent (0), present (1)		0	1	1	0, 1*	0	1	0, 1*	0, 1
Dorsal color pattern with regular (0), irregular (1) blotches		1	0	0	0, 1*	0	0	1	0
Dorsal color pattern obscure posteriorly (0), spread throughout body (1)		0	0, 1	1	1	1	0	1	0
Pale dots on the flank absent (0), present (1)		1	1	1	0	0	0	0, 1*	0, 1
Dorsolateral stripe absent (0), present (1)		0	0	—	0, 1	0	0	0, 1*	0
Collar streak indistinct (0), well defined (1)		1	1	1	1	0, 1*	1	1	0
Ring mark on the neck absent (0), present (1)		1	0	—	0	0	0	0	0
Subocular streaks indistinct (0), well defined (1)		1	1	1	1	1	1	1	0
Venter uniform (0), with markings or dark margins (1)		0	0	1	1	1	1	0, 1	0
Maxillary teeth		26	22	—†	—	24	—	—	21–23
Ventrals	Males	125–132	127–133	120–132	128–136	132–138	132–139	131–138	140–141
	Females	131–138	132–142	128–143	151–156	143–149	141–152	140–145	142–149
Subcaudals	Males	86–93	77–92	76–91	74–86	83–91	71–80	79–86	80–87
	Females	79–91	75–83	62–83	65–80	79–82	61–70	76–77	65–78
TL/total length%	Males	32.0–35.3	28.3–31.4	27.6–34.8	28.6–30.2	28.3–31.9	25.7–28.3	30.8–32.4	30.1–31.4
	Females	28.8–30.5	25.7–28.9	23.9–30.5	23.3–26.5	26.9–27.9	21.5–23.6	27.0–27.9	25.1–25.4
Distribution		Sri Lanka and southern India	Sri Lanka	Northeast India and Sundaland	Great Sundaic Islands	Eastern India	North and northeast India	Andaman Island	Southern China and Myanmar

* Two color variations available.

† —, not evaluated.

the genus *Fowlea*. Finally, with the morphological (including skull, dentition, and hemipenes), and genetic evidences, here we redescribe *F. asperrima* based on the lectotype (NHMUK 1946.1.7.60) designated herein; see Discussion. We also restrict the species to Sri Lanka and also restrict its type locality to Kandy, Sri Lanka.

SYSTEMATICS

Fowlea unicolor (Müller 1887) comb. nov.
(Table 2; Figs. 3B, 4AB, 5CE, 6AB, 7B, 8A, 9)

Tropidonotus quincunciatus var. γ Günther 1858, 1864.
Tropidonotus quincunciatus: Theobald 1876 [partim]; Ferguson 1877 [partim].
Tropidonotus quincunciatus var. *unicolor* Müller 1887.
Tropidonotus piscator: Boulenger 1890 [partim]; Abercromby 1910 [partim].
Nerodia (*Tropidonotus*) *piscator*: Wall 1921 [partim].
Natrix piscator asperrimus (sic): Smith 1943 [partim]; Deraniyagala 1955 [partim]; De Silva 1969 [partim].
Natrix piscator: Taylor 1950.
Fowlea piscator: Malnate 1960 [partim]; Deepak et al. 2021 [partim].
Xenochrophis piscator: Malnate and Minton 1965 [partim]; De Silva 1980; Das and de Silva 2005; Somaweera 2006; Takeuchi et al 2018 [partim].
Xenochrophis cf. *piscator*: Vogel and David 2006, 2012; Karunarathna and Amarasinghe 2010, 2011, 2012; Karunarathna et al. 2010; de Silva and Ukuwela 2017.
Fowlea cf. *piscator*: Madawala et al. 2019.

Holotype (by monotypy).—NMB 723, adult female from Peradenia (sic) (Peradeniya; 7°16′13.26″N, 80°35′54.92″E, datum = WGS84; 485 m above sea level), Kandy District, Central Province, Sri Lanka, collected by Paul Benedict Sarasin and Karl Friedrich Sarasin in 1886.

Other material (n = 17).—NMB 725–726 from Peradeniya, Kandy District; NMSL uncatalogued (hereafter, uncat) 1 from Warakawehera, Kurunegala District, Northwestern Province; NMSL uncat 2 from Kottawa, Galle District, Southern Province; NMSL uncat 3–4 from Navinna, Galle District, Southern Province; FMNH 121494–121496 from Western Province; MNHN-RA 1890.0482 from Sri Lanka; NHMUK 1905.3.25.82 from Pundaluoya, Nuwara Eliya District, Sri Lanka; NHMUK 1905.3.25.83–84, 1933.12.6.4 from Sri Lanka; ZMH R07930 from Wakwella, Galle District, Southern Province; ZMH R07935 from Sri Lanka; ZMB 2028 from Sri Lanka.

Diagnosis.—*Fowlea unicolor* comb. nov. is distributed in Sri Lanka and probably also in southern India, and it is distinguished from other congeners by having the following combination of characters: adults reaching a maximum total length 662 mm (males) and 714 mm (females), a longer tail of 32.0–35.3% of total length (in males) and 28.8–30.5% (in females), a single preocular, three postoculars (very rarely four), a single loreal scale, a divided cloacal plate, nasal scale completely divided by the nostril, smooth ventrals 125–132 in males and 131–138 in females, paired subcaudals 86–93 in males and 79–91 in females, temporals 2 + 2 (rarely 2 + 1 or 2 + 3), nine supralabials with fourth and fifth in contact with eye, 10 infralabials (rarely nine), dorsal scale rows 19-19-17, dorsals strongly keeled except the

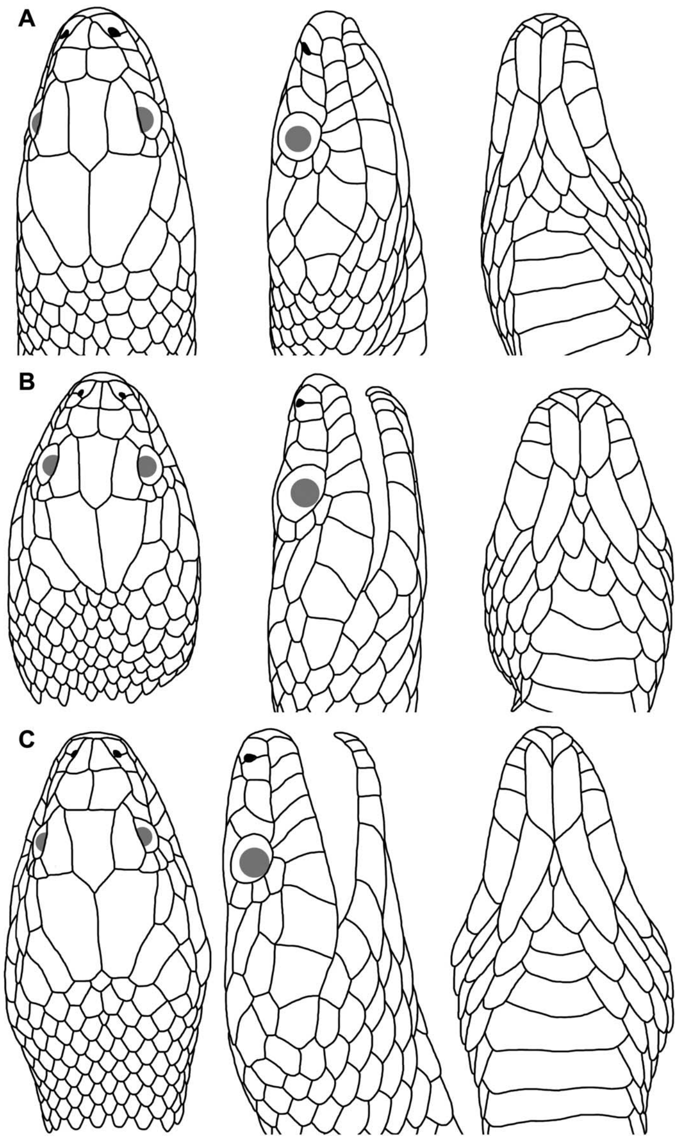

FIG. 3.—Dorsal, lateral, and ventral head views of (A) a voucher of *Fowlea piscator* sensu stricto (NHMUK 1872.4.7.393 from Darjeeling, West Bengal, India), (B) holotype of *F. unicolor* comb. nov. (NMB 723 from Peradeniya, Sri Lanka), and (C) lectotype of *F. asperrima* (NHMUK 1946.1.7.60 from Kandy, Sri Lanka). Illustrations by AATA (not to scale).

outer 2–4 rows, vertebral row not enlarged, greyish or brownish olive dorsum with 2–6 lines of irregular black blotches along the anterior body, dorsal marks become indistinct or obscure on the posterior body, small and narrow, vertical, white spots on flanks up to base of tail, two dark oblique streaks extending backwards on side of head and downwards from eye, thin or broad distinct black collar streak on the nape, collar streak mostly straight or curved forward (rarely pointed forward as an inverted V-shaped), a black thick ring mark (complete or broken) on the neck behind the collar streak, venter uniform cream or pale yellow (rarely with cloudy spots laterally). *Fowlea unicolor* comb. nov. is also genetically divergent from the eastern Indian *F. piscator* with *p* distance of 9.9% in the mitochondrial cytochrome b gene.

Comparison.—*Fowlea unicolor* comb. nov. is most similar to *F. piscator* sensu stricto (characters in parentheses), but differs by having a smaller body of maximum 413 mm SVL in adult males (larger body of 573 mm SVL), more temporals 2+2 (1+1), 125–132 ventrals in males (132–138) and 131–138 in females (143–149), a longer tail, TL 32.0–35.3% of total length in males (28.3–31.9%) and 28.8–30.5% in females (26.9–27.9%), dorsals strongly keeled (weakly keeled), dorsum with rather irregular blotches in 2–6 lines (regular blotches in 5 or 6 lines) on the anterior body, dorsal marks become indistinct (distinct) on the posterior body, vertical white spots on flanks (absent), collar streak on the nape distinct (mostly indistinct), ring mark on nape distinct (absent), maxillary teeth 26 (24), palatine teeth 16 (12–14), pterygoid teeth 31 or 32 (24), and mandible teeth 31 or 32 (26).

Fowlea unicolor comb. nov. is also compared with other congeners of the *F. piscator* species group; see Table 2, based on specimens examined (Appendix). Among the nine species known of the species group, only *F. yunnanensis* lacks subocular streaks, and *F. melanzosta* alone is missing the checkered or blotched dorsal color pattern. *Fowlea unicolor* comb. nov. has 86–93 subcaudals in males and 79–91 in females, which are more than in *F. schnurrenbergeri* (71–80 in males, 61–70 in females). *Fowlea unicolor* comb. nov. has a uniform venter without any markings, and thus differs from *F. flavipunctata, F. schnurrenbergeri*, and *F. tytleri*, which all have markings or dark margins on the ventrals. Finally, *F. unicolor* comb. nov. differs from its only sympatric congener, *F. asperrima*, by having an irregular blotch pattern on its dorsum (vs. confluent blotches creating regular cross bands) and longer tail, TL 32.0–35.3% of total length (shorter tail, 28.3–31.4) in males.

We further compare *F. unicolor* comb. nov. with the population in the southern Western Ghats, evidently from Travancore (based on NHMUK 94.3.15.2, 93.4.18.11, FMNH 217404, which were thought to be *C. bengalensis* by Vogel and David 2012, still a junior synonym of *F. piscator* sensu lato), but differs by having 131–138 ventrals in females (vs. 138–144), subcaudals 79–91 in females (vs. 68–71), longer tail, TL 28.8–30.5% of total length in females (vs. shorter, 23.5–28.5%), dorsals strongly keeled (vs. weakly keeled), vertical white spots on flanks (vs. absent), ring mark on nape distinct (vs. two separate blotches).

Description of the holotype.—Adult female, SVL 445.0 mm; TL 188.0 mm; head elongate, HL 6.0% of SVL, twice as long as wide, HW 65.2% of HL, slightly flattened, indistinct from neck; snout elongated, ES 24.7% of HL, moderate, rounded in dorsal and lateral profiles, rather depressed.

Rostral shield large, rounded, slightly visible from above, rounded posteriorly; IO width broad, IO 42.5% 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 supralabials ventrally, loreal posteriorly; loreal single; prefrontal twice large as internasal, broader than long, and pentagonal; frontal large, pentagonal, shortened posteriorly and twice longer than wide; supraoculars wide, short, subrectangular, posteriorly wider; parietals (slightly damaged) large, elongate, butterfly wing-like in shape, bordered by supraoculars, frontal, upper postocular anteriorly, upper anterior and upper posterior temporals, and six nuchal scales posteriorly; one preocular, vertically elongated, more or less pentagonal, in contact with prefrontal and loreal anteriorly,

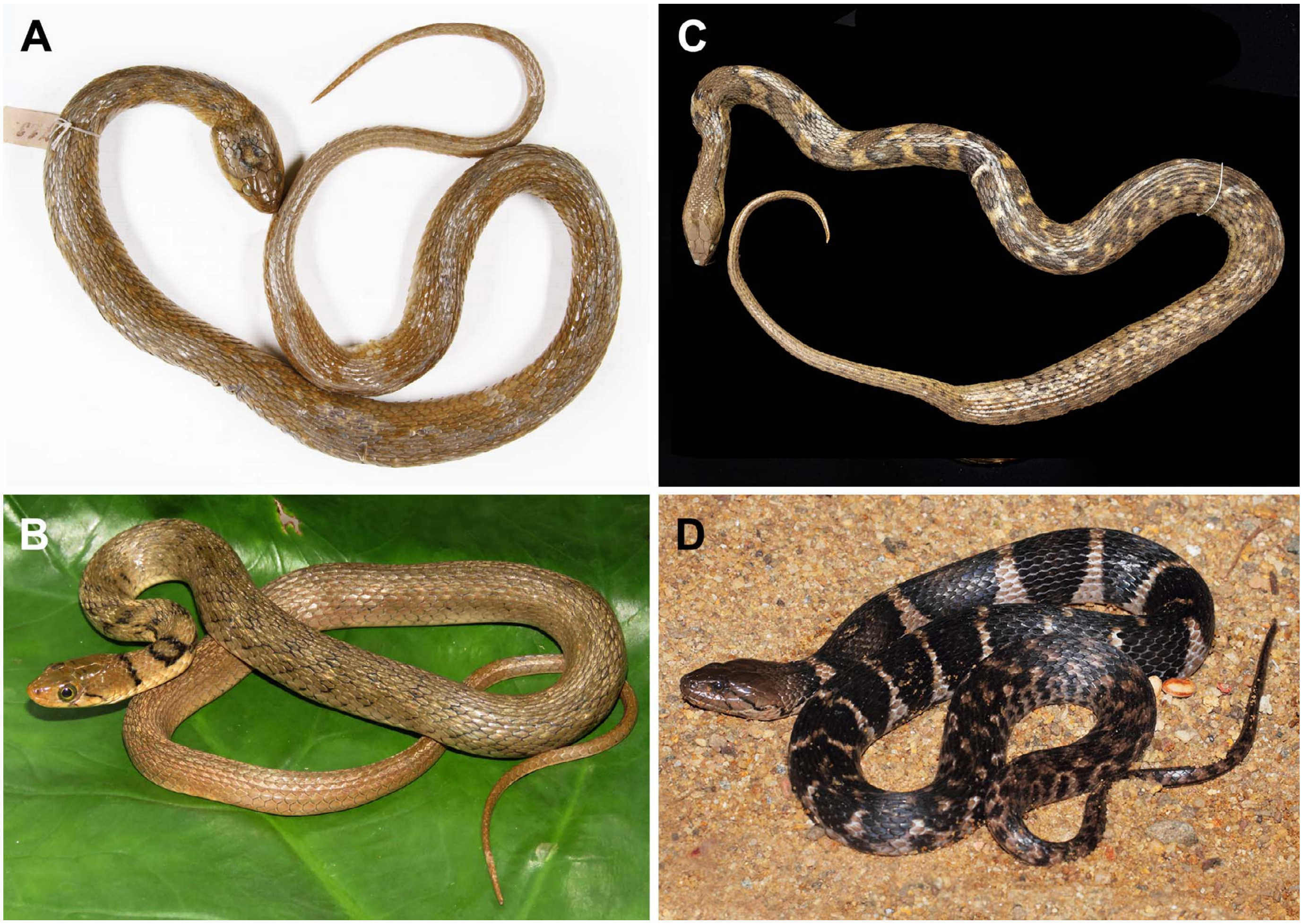

FIG. 4.—*Fowlea unicolor* comb. nov. from Peradeniya, Sri Lanka: (A) Holotype (NMB 723) and (B) subadult in life (not collected) from the type locality; Photos by DAM and SKB. *Fowlea asperrima*: (C) lectotype from Kandy (NHMUK 1946.1.7.60) and (D) adult in life (not collected) from Horana, Sri Lanka. Photos by PDC and ADD. A color version of this figure is available online.

supraocular dorsally, and fourth supralabial ventrally; eye large, ED 18.7% of HL, round, nearly half of snout length ED 75.7% of ES, pupil rounded; three postoculars, subequal, pentagonal, upper postocular in broad contact with supraocular, parietal, and upper anterior temporal, middle postocular in contact with upper and lower anterior temporals, lower postocular in contact with lower anterior temporal and fifth to seventh supralabials; temporals 2 + 2, elongated, pentagonal; lower anterior temporal almost the same size as upper posterior temporal, upper anterior temporal and lower posterior temporals smaller; upper anterior temporal in contact with parietal and upper and middle postoculars, lower anterior temporal in contact with middle and lower postoculars and seventh and eighth supralabials; lower posterior temporal in contact with eighth and ninth supralabials ventrally. Supralabials nine on both sides, seventh and eighth 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, fourth with preocular and orbit dorsally, fifth with orbit and the lower postocular dorsally, sixth with lower postocular, seventh with lower postocular and lower anterior temporal dorsally, eighth with lower anterior and lower posterior temporals dorsally, ninthwith lower posterior temporal dorsally and scales of the neck posteriorly.

Mental small, triangular; first pair of infralabials larger than mental plate and in broad contact with each other, in contact with anterior chin shields posteriorly; 10 infralabials, 1st–5th in contact with anterior chin shields, fifth infralabial largest in size in contact with both anterior and posterior chin shields; 5th–6th infralabials in contact with posterior chin shields, 6th–10th infralabials in contact with gular scales; two shorter anterior chin shields, and two longer posterior chin shields; anterior chin shields in broad contact between them; posterior chin shields bordered posteriorly by nine gular scales.

Body robust, elongate and subcylindrical; dorsal scales in 19-19-17 rows, all strongly keeled except the outer 2–4 rows, elongated, and bluntly pointed posteriorly, vertebral row not enlarged; 133 ventrals; cloacal plate divided. Tail comparatively long, TL 29.7% of total length, robust and thick; subcaudals 84, divided.

Coloration of the holotype.—In preservative, dorsum pale olive brown, lateral surface paler and yellowish; snout darker olive brown and dorsal head greyish-olive brown; almost indistinct 2–6 lines of irregular black blotches along the anterior body, but these marks become completely

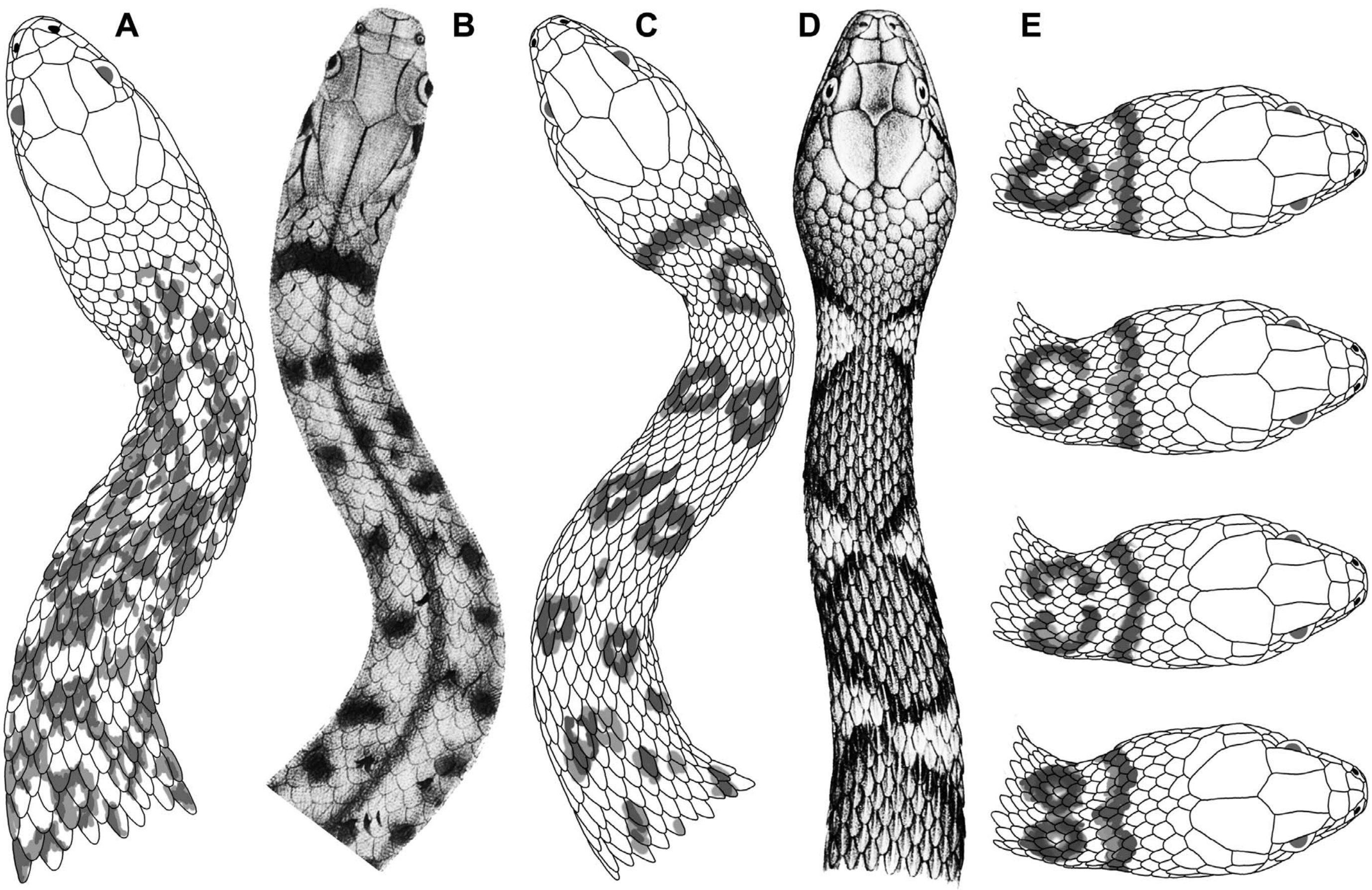

FIG. 5.—Arrangement and variation of anterior body color pattern of (A) *Fowlea piscator* sensu stricto, (B) *Coluber bengalensis* (currently a subjective synonym of *F. piscator* sensu lato; the original illustration of Gray [1834: plate 82] is resized, cropped, and grey-scaled for better comparison); (C) *F. unicolor* comb. nov., (D) *F. asperrima* (an illustration of Boulenger 1894: plate 15, fig. 2, resized), and (E) the variation of ring-mark pattern and collar on the nape of *Fowlea unicolor* comb. nov. Illustrations A, C, and E by AATA (not to scale).

indistinct or obscure on the posterior body; small and narrow vertical white spots on flanks up to base of tail; two almost indistinct greyish oblique streaks extending on side of head backwards and downwards from eye: (1) the first streak starts in between fifth supralabial and lower postocular extends along the margin between sixth and seventh supralabials up to its mid position, (2) the second streak starts in between upper and middle postocular extending up to the gape of mouth across the lower anterior temporal and eighth supralabial; almost indistinct grey collar streak on the nape, slightly curved forwards up to the nuchal behind parietal, another almost indistinct complete grey ring mark on the neck behind the collar streak with a three dorsal-scale gap; venter uniform cream or pale yellow.

Based on living individuals, the coloration is the same in preserved specimens, but the body coloration changes from yellowish-brown to dark grey; most animals from the upper peneplains (Figs. 4B and 5C) usually show a brighter coloration with less distinctive dorsal blotches, but with a very prominent collar streak and ring mark—the shape of the ring can vary slightly (Fig. 5E); the ring mark is most prominent in juveniles (Fig. 6A); the animals in the lower peneplains (especially in the coastal areas) show a red margin around black spots, sometimes these red margins spread and the animal may show as a red morph (Fig. 6B). This color might be variation may well be seasonal too, perhaps more prominent during the breeding season. Also, the snakes in lower peneplains may have an indistinct collar streak, but still the ring mark on neck is distinct.

Variation.—The holotype has a faded coloration, but on closer examination revealed a similar coloration to other examined individuals. The faded, pattern-less (unicolor) body is a common phenomenon as individuals grow into adults. This species shows little sexual dimorphism because their ventral and subcaudal scale counts overlap. The other examined specimens (all from the lower peneplain of the island) have a darker body color compared to the holotype.

Skull and dentition of holotype.—A complete and robust skull displays a general pattern of Colubroidea; premaxilla single, round anteriorly, with a broad ascending process, a prominent nasal crest, and a relatively short transverse process; nasals shorten, triangular, lateral processes tapering anteriorly to form a pointed process, but bifurcate largely at the point of articulation with the ascending process; parietals smooth, anterior process curved and slightly pointed forward in between frontals; maxilla with 26 functional teeth, gradually increasing in size posteriorly; palatine with 16 teeth; pterygoid and mandible with 31 or 32 teeth on each.

Hemipenis.—Based on NMSL uncat. 4 (Fig. 8A), the organ is bulbous in shape, relatively long, robust, non-capitate, and prominently bilobate (about 25% of the total

FIG. 6.—*Fowlea unicolor* comb. nov.: (A) a juvenile from Kandy, Sri Lanka, (B) an adult reddish color morph (mostly found in the coastal areas) from Meegoda, Sri Lanka. Photos by SKB and B. Prabashwara. A color version of this figure is available online.

length of the organ); lobes blunt; many hooks like small spines evenly distributed on the calyces body, the size of the spines increase slightly towards the base; the apical part of the hemipenis is richly ornamented with numerous small and evenly dispersed spines; when inverted, the organ extends as far as the ninth subcaudal scale; sulcus spermaticus bifurcated, deep and centripetal; the point of bifurcation of the lobes extends inwardly towards the central region; the region between the lobes spinose on both the sulcate and asulcate surfaces; sulcate and asulcate expansion pleat naked.

Distribution.—*Fowlea unicolor* comb. nov. is known from 84 localities (Fig. 9) from Sri Lanka, and probably from southern India (based on photographic evidence), e.g., Mayiladuthurai, Tamil Nadu (Figs. 38 and 39 in Vogel and David 2012) and Nagappattinam, Tamil Nadu (iNaturalist database). However, the distribution of *F. unicolor* in southern India needs further confirmation based on integrative systematic approaches. Based on reliable records for this species from Sri Lanka, it usually occurs up to 1200 m in elevation. *Fowlea unicolor* is sympatric with *F. asperrima* in most of the localities in the lowland and mid hills.

Natural history.—*Fowlea unicolor* comb. nov. is found around freshwater bodies. Fully grown adults reach more than 1 m in length, and females tend to grow longer than males. The populations found in the coastal line, especially in brackish water lagoons, need to be reassessed as to whether they are identical with the highland population that we redescribe in this paper. We observed this snake in both urban ecosystems and in agricultural lands. *Fowlea unicolor* is also active in twilight and later on during the early part of the night. Primary diet includes amphibians and fish and occasionally small mammals (Somaweera 2006). Sudasinghe and Kusuminda (2012) reported that this species feeds on amphibian eggs in the foam nest of a *Polypedates* species. We have also seen photographic evidence of their feeding on a mass of fertilized frog eggs of a *Duttaphrynus* species (Fig. S2A). Observations of individuals with broken tails, but that recovered subsequently, were commonly observed. Ananjeva and Orlov (1994) suggested possible caudal autotomy based on another species within the same species complex. When threatened, this species flattens the anterior part of the body and strikes repeatedly. It is a very defensive snake which attacks with bites when handled. Oviparous, based on our observations, usually the clutch is composed of more than 20 eggs.

Conservation status.—The application of the Red List criteria (IUCN Standards and Petitions Subcommittee 2019) with the updated distribution data shows that *Fowlea unicolor* comb. nov. is restricted to an area of occupancy of 1867 km^2 recorded from 84 aquatic localities within a 38,374 km^2 extent of occurrence. Considering the wider distribution, and its ability to survive in anthropogenic and disturbed or agricultural aquatic habitats, we suggest classifying this species as a Least Concern (LC) species. *Fowlea unicolor* is threatened by the frequent and wanton killing by people due to fear as the body coloration leads to it being misidentified as a cobra, its ring mark on the nape resembling the mark on cobra's shrunk hood, also the defensive behavior it displays of flattening the anterior body is also visibly similar to that of a cobra's hood. Mortalities due to vehicular traffic (Fig. S2B) are also observed commonly throughout the year (Karunarathna et al. 2013).

Fowlea asperrima (Boulenger 1891)
(Table 2; Figs. 3C, 4CD, 5D, 7C, 8B, 9)

Tropidonotus umbratus: Kelaart 1852 (non Daudin 1803).
Tropidonotus quincunciatus var. δ Günther 1858, 1864 [partim].
Tropidonotus quinqunciatus: Ferguson 1877 [partim]; Müller 1887.
Tropidonotus asperrimus Boulenger 1891.
Nerodia (*Tropidonotus*) *piscator*: Wall 1921 [partim].
Natrix piscator asperrimus (sic): Smith 1943 [partim]; Deraniyagala 1955 [partim]; De Silva 1969 [partim].
Natrix asperrimus (sic): Taylor 1950.
Xenochrophis asperrimus: de Silva 1990; Das and de Silva 2005; Vogel and David 2006, 2012; Somaweera 2006; Karunarathna and Amarasinghe 2010, 2011, 2012; Karunarathna et al. 2010; Pyron et al. 2013; Wallach et al. 2014; de Silva and Ukuwela 2017; Takeuchi et al. 2018; Purkayastha et al. 2018.
Fowlea asperrimus (sic): Cheng et al. 2021.

Lectotype (designated herein).—NHMUK 1946.1.7.60, adult female from near Candy (Kandy; 7°17′24.37″N, 80°38′14.77″E; datum = WGS84; 540 m above sea level), Kandy District, Central Province, Sri Lanka, presented by Captain Gascoigne (fide Boulenger 1894). Note: Only five syntypes are clearly traceable corresponding to the specimens in Boulenger (1894). Among those specimens, only a single specimen (NHMUK 1946.1.7.60) corresponds to the Specimen "*e*" in Boulenger 1894 and exactly matches the body measurement given in the original description, and furthermore the stated sex, ventrals, and subcaudals in Boulenger

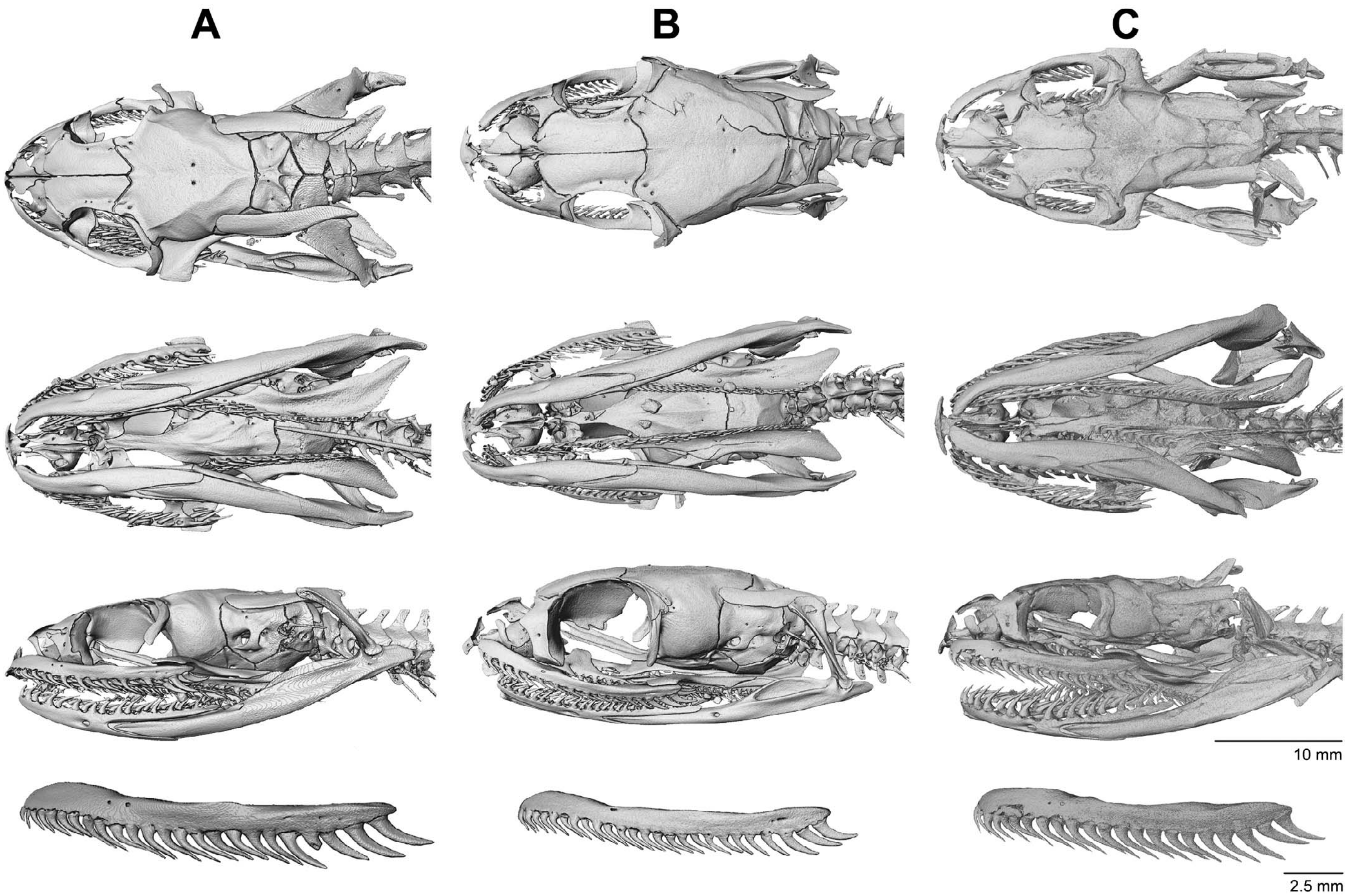

FIG. 7.—Dorsal, lateral, and ventral skull views (scale = 10 mm) and the maxilla (scale = 2.5 mm; note that scanning angles are slightly different) of (A) a voucher of *F. piscator* sensu stricto (NHMUK 1872.4.7.393), (B) a voucher of *F. unicolor* comb. nov. (NHMUK 1905.3.25.82; the skull of holotype is not in a good state), and (C) lectotype of *F. asperrima* (NHMUK 1946.1.7.60).

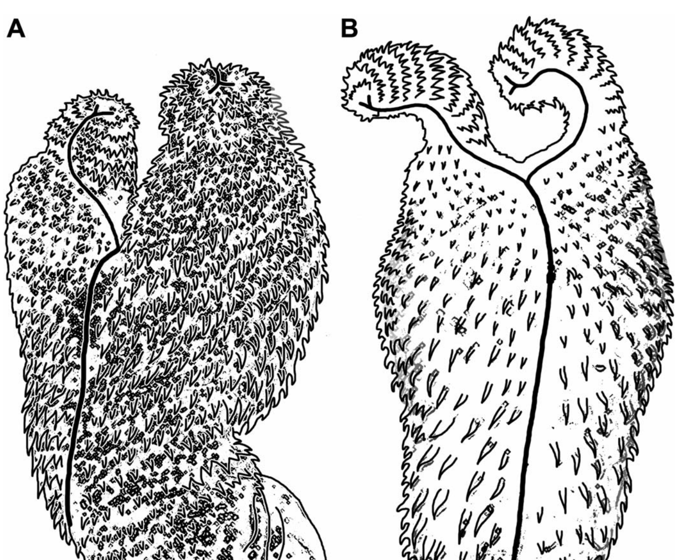

FIG. 8.—(A) Sulcate view of the right hemipenis of *Fowlea unicolor* comb. nov. (NMSL uncat. 4) from Navinna near Galle, Sri Lanka, and (B) sulcate view of the left hemipenis of *F. asperrima* (WHT 2232) from Kottawa near Galle, Sri Lanka. Illustrations by AATA (not to scale).

(1894) also match that specimen. Therefore, we have selected above this syntype, NHMUK 1946.1.7.60 as the lectotype of *T. asperrimus*.

Paralectotype.—Only 12 specimens are catalogued (out of 14 specimens available to Boulenger 1891) as "cotypes": NHMUK 1946.1.7.61, 1946.1.12.73–75, 1946.1.12.83, 1946.1.13.33–34, 1946.1.14.50, 1946.1.15.17, 1946.1.15.22–23, from Ceylon (Sri Lanka) and NHMUK 1946.1.15.30 from Pundaluoya, Nuwara Eliya District, Sri Lanka.

Other material (n = 22).—NHMUK 1982.600–601, 1946.1.13.36, 1946.1.13.39–40, ZMB 14299, NMB 721–2, from Ceylon (Sri Lanka); NHMUK 1905.3.25.85 from Pundaluon, Nuwara Eliya District; FMNH 121493 from Western Sri Lanka; ZMH R07929 from Wakwella, Southwest Sri Lanka; WHT 2232, male from Kottawa, Galle District; NHMUK 1931.5.13.35, 1931.5.13.37–38, 1931.5.13.41–42, 1946.1.12.85, ZMH R07923, R07934, R07936, from Ceylon (Sri Lanka); and NHMUK 1910.3.16.24 from Galle, Galle District, Sri Lanka.

Diagnosis.—*Fowlea asperrima* is endemic to Sri Lanka, mostly confined to the wet zone of the island, and it is distinguished from other congeners by having the following combination of characters: adults reaching a maximum SVL 582 mm (in males) and 665 mm (in females), a longer tail of 28.3–31.4% of total length (in males) and 25.7–28.9% (in females), a single preocular, three postoculars, a single loreal

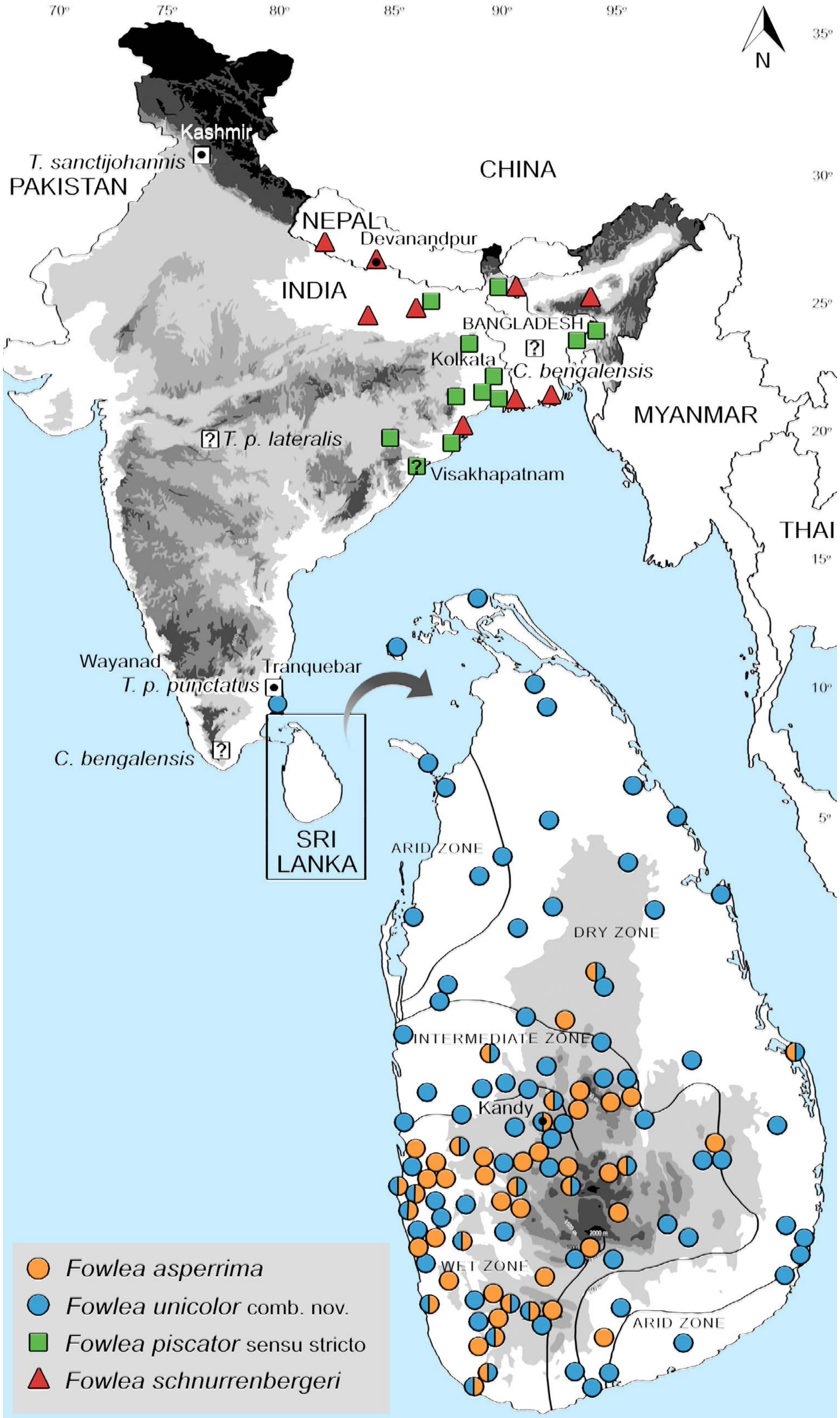

FIG. 9.—Current distribution map showing the collection/observation localities of *Fowlea unicolor* comb. nov. and *F. asperrima* in blue and orange circles, respectively (sympatric localities filled partially); *F. piscator* sensu stricto (green squares); and *F. schnurrenbergeri* (red triangles) in India and Sri Lanka. The type localities of junior synonyms are shown in open squares and the imprecise type localities are filled with question mark (?). The symbols with a dot in the middle represent the type locality of respective species. A color version of this figure is available online.

scale, a divided cloacal plate, nasal scale completely divided by the nostril, smooth ventrals 127–133 in males and 132–142 in females, paired subcaudals 77–92 in males and 75–83 in females, temporals 2 + 2 (rarely 2 + 3), nine supralabials (rarely 10) with fourth and fifth (rarely fifth and sixth) in contact with eye, 10 infralabials (rarely nine), dorsal scale rows 19-19-17, dorsal scales strongly keeled except the outer 1 or 2 rows, vertebral row not enlarged, reddish-grey or brownish-olive dorsum with two series of 22–32 more or less distinct, large, rounded or rhomboid, black-edged dark brown blotches arranged alternating or partly or fully confluent along the vertebral line and possibly forming a sinuous stripe, the blotches might be appeared as triangles laterally, posterior body usually uniform dark olive with blackish-brown spots arranged quincuncially and a series of yellow dorsolateral spots. *Fowlea asperrima* is also genetically divergent from its one and only sympatric congener, *F. unicolor* comb. nov. with *p* distance of 16.0% in the mitochondrial cytochrome b gene.

Description of the lectotype.—Adult female, SVL 610 mm; TL 210.0 mm; head elongate, HL 4.9% of SVL, more than twice as long as wide, HW 64.7% of HL, slightly flattened, indistinct from neck; snout elongated, ES 25.0% of HL, moderate, bluntly pointed in dorsal and rounded lateral profiles, rather depressed.

Rostral shield large, rounded, slightly visible from above, rounded posteriorly; IO width broad, IO 51.5% 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 supralabials ventrally, loreal posteriorly; loreal single; prefrontal twice large as internasal, broader than long, and pentagonal; frontal large, pentagonal, shortened posteriorly and nearly twice longer than wide; supraoculars wide, short, subrectangular, posteriorly wider; parietals large, elongate, butterfly wing-like in shape, bordered by supraoculars, frontal, upper postocular anteriorly, upper 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 fourth supralabial ventrally; eye large, ED 14.0% of HL, round, nearly half of snout length ED 56.0% of ES, pupil rounded; three postoculars, upper one larger, pentagonal, upper postocular in broad contact with supraocular, parietal, and in narrow contact with upper anterior temporal, middle postocular in contact with upper and lower anterior temporals, lower postocular in contact with lower anterior temporal and fifth and sixth supralabials; temporals 2 + 2, elongated, pentagonal; lower anterior temporal smaller than the upper posterior temporal, lower anterior temporal and lower posterior temporals smaller; upper anterior temporal in contact with parietal and upper and middle postoculars, lower anterior temporal in contact with middle and lower postoculars and seventh and eighth supralabials; lower posterior temporal in contact with eighth supralabial ventrally. Supralabials nine on both sides, eighth 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, fourth with preocular and orbit dorsally, fifth with orbit and the lower postocular dorsally, sixth with lower postocular, seventh with lower anterior temporal dorsally, eighth with lower anterior and lower posterior temporals dorsally, ninth with scales of the neck posteriorly.

Mental small, triangular; first pair of infralabials larger than mental plate and in broad contact with each other, in contact with anterior chin shields posteriorly; 10 infralabials, 1st–5th in contact with anterior chin shields, fifth infralabial largest in size in contact with both anterior and posterior chin shields; 5th–6th infralabials in contact with posterior chin shields, 6th–10th infralabials in contact with gular scales; two shorter anterior chin shields, and two longer posterior chin shields; anterior chin shields in broad contact between them; posterior chin shields separated and bordered posteriorly by nine gular scales.

Body robust, elongate and subcylindrical; dorsal scales in 19-19-17 rows, all strongly keeled except the outer one or two rows, elongated, and bluntly pointed posteriorly, vertebral row not enlarged; 141 ventrals; cloacal plate divided. Tail comparatively long, TL 25.6% of total length, robust and thick; subcaudals 81, divided.

Coloration of the lectotype.—In preservative, dorsum pale olive brown, lateral surface paler and yellowish; head dorsally dark olive brown; two distinct black oblique streaks extending on side of head backwards and downwards from eye: (1) the first streak starts in between middle and lower postoculars extends along the margin between sixth and seventh supralabials, (2) the second streak starts in between upper and middle postocular extending up to the gape of mouth across the lower anterior temporal and eighth supralabial; another black streak start from the gape extends posteriorly surrounding the dark blotch on the head; nuchal marking absent because first two or three blotches are merged (aberrant); dorsum with two series of more or less distinct, large, rounded or rhomboid, black-edged dark brown blotches arranged alternating or partly or fully confluent along the vertebral line and possibly forming a sinuous stripe, posterior body with blackish-brown spots arranged quincuncially and a series of yellow dorsolateral spots; venter uniform pale yellow, tip and outer quarter of each ventral clouded with black and grey.

Based on living individuals (Figs. 4D and 5D), the coloration is the same as in preservative, but the body coloration changes from yellowish-brown to dark reddish-grey.

Variation.—The lectotype has aberrant, merged blotches on the anterior body, and the number of blotches varies from 22 to 32, but anterior blotches very distinct and strongly dark margined. This species shows a little sexual dimorphism because their ventral and subcaudal scale counts are very much overlapped (Table 2).

Skull and dentition of lectotype.—A complete and robust skull displays a general pattern of Colubroidea (Fig. 7C); premaxilla single, slightly pointed anteriorly, with a broad ascending process, a prominent nasal crest, and a relatively short transverse process; nasals shorten, triangular, lateral processes tapering anteriorly to form a pointed process, but bifurcates slightly at the point of articulation with the ascending process; parietals rough, anterior process curved and pointed slightly forward in between frontals; maxilla with 22 functional teeth, gradually increasing in size posteriorly; palatine with 11 teeth; pterygoid and mandible with 26 or 23 teeth on each.

Hemipenis.—Based on WHT 2232 (Fig. 8B), the organ is bulbous in shape, relatively long, robust, noncapitate, and prominently bilobate (about 35% of the total length of the organ); lobes blunt; many hooks like small spines evenly distributed on the noncalyces body, the size of the spines increase slightly towards the base; the apical part of the hemipenis is richly ornamented with numerous small and evenly dispersed spines; when inverted, the organ extends as far as the 11th subcaudal scale; sulcus spermaticus bifurcated, deep and centripetal; the point of bifurcation of the lobes extends inwardly towards the central region; the region between the lobes spinose on both the sulcate and asulcate surfaces; sulcate and asulcate expansion pleat naked.

Distribution.—*Fowlea asperrima* is known from 48 localities (Fig. 9) in Sri Lanka. Based on the reliable records for this species from Sri Lanka, it usually occurs up to 1200 m in elevation. *Fowlea asperrima* is mostly confined to the wet zone and has a patchy distribution in the dry zone. It is sympatric with *F. unicolor* in most of the localities in the lowland and upper hills.

Natural history.—*Fowlea asperrima* is found only in freshwater bodies, especially in riverine habitats. Fully grown adults reach more than 1 m in length, and females tend to grow longer than males. We observed this snake in both urban ecosystems and in agricultural lands, but never in highly polluted waters. This species is also active in twilight and later on during the early part of the night. When threatened, it flattens the anterior part of the body and strikes repeatedly. It is a very defensive snake which readily bites when handled. Primary diet includes amphibians and fish (Somaweera 2006). We have observed this species regularly scavenging on leftover fish. Oviparous, females usually lay clutches of 4–30 eggs (Somaweera 2006).

Conservation status.—The application of the Red List criteria (IUCN Standards and Petitions Subcommittee 2019) with the updated distribution data shows that *Fowlea asperrima* is restricted to an area of occupancy of 752 km^2 recorded from 48 aquatic (freshwater) localities within a 25,487 km^2 extent of occurrence. Considering the area of occupancy, restriction to undisturbed freshwater habitats, and that most of their freshwater habitats in Sri Lanka are being degraded due to the water pollution of household waste, garbage dumping, soil erosion, eutrophication by excess use of fertilizers, and industrial or agricultural toxic waste, etc., we suggest classifying this species as a Vulnerable (VU) species. *Fowlea asperrima* is also threatened by the frequent and wanton killing by people due to fear as the body coloration leads to it being misidentified as a viper, its dark blotches sometimes resembling the marks on Russel's viper (*Daboia russelii*). Mortalities due to vehicular traffic are also observed commonly throughout the year (Karunarathna et al. 2013).

Discussion

The Status of Sri Lankan Populations

The two Sri Lankan representatives of the genus *Fowlea* have long been known, but remained taxonomically unclear until Vogel and David (2006, 2012) provided diagnostic characters to distinguish these sympatric species, *X.* cf. *piscator* and *F. asperrima*. In their revision, the Sri Lankan *X.* cf. *piscator* population was regarded as an undescribed species sharing characters of both *X. flavipunctatus* and *X. piscator*, hence it was kept as "*X.* cf. *piscator*." Their morphological understanding is clearly evident in molecular analysis too (see Clades B and D in Fig. 1). In addition to the morphological distinctiveness between Indian and Sri Lankan *F. piscator* sensu lato, the morphological variance between *X.* cf. *piscator* (now *F. unicolor*) and *F. asperrima* in Sri Lanka had already been observed by Wall (1921), but he mentioned them as three varieties of *Nerodia* (*Tropidonotus*) *piscator*, namely "variety *asperrima*," "variety *quinquunciata*," and "variety *flavipunctata*." Later, Smith (1943) stated *Natrix piscator* sensu lato comprised four varieties, but considered only *Natrix piscator asperrima* the sole variety endemic to Sri Lanka. Although Taylor (1950) believed that there were two distinct populations (*piscator* and *asperrimus*) within the island, Deraniyagala (1955: 59) followed Smith (1943) and further stated, "specimens only distinguishable apart from each other by color exist side by side in the same paddy field, clearly showing that they were only color variations of a single species." De Silva (1980) again considered *X. piscator* and *X. asperrimus* two distinct species.

Interestingly, De Silva (1980) noticed that the Sri Lankan *X. piscator* sensu lato population has a nuchal band followed by a median darker spot (in this study termed as ring mark). We also regarded this as a unique diagnostic character to distinguish *F. unicolor* comb. nov. from both the east Indian *F. piscator* sensu stricto and *F. asperrima*. The sequence of *F. asperrima* shows high intrageneric divergence of 16.0% with *F. unicolor* comb. nov. for mitochondrial cytochrome b. We noticed that the hemipenis of *F. asperrima* (Fig. 8B) has elongated lobes, and is feebly spinose compared to the hemipenis of *F. unicolor* comb. nov. Also, the hemipenis of *F. asperrima* has no calyces on the body (vs. present in *F. unicolor* comb. nov.) and when inverted, the organ extends as far as the 11th subcaudal scale (vs. ninth).

As *Fowlea unicolor* comb. nov. is commonly found in anthropogenic habitats and is generally encountered by people during their daily chores, this species has been included in the village stories and poems in Sri Lanka. One of the famous folk poems (see Document SI) mentions a girl named Tikiri who was bitten by this water snake, commonly known as "*diya-bariya*." This poem has been depicted numerous times on the cover pages of children's books (Fig. S3). Therefore, for conservation priorities we suggest the vernacular names of "Tikiri diyabariya" and Tikiri keelback in Sinhala and English languages, respectively. The other sympatric species, *Fowlea asperrima*, is already known as "Lanka diyabariya" and Sri Lankan keelback in Sinhala and English languages, respectively.

In the original description of *T. asperrimus*, Boulenger (1891) did not link the description to any specimen or mention a precise locality for the species. However, he did provide measurements (total length 810 mm) for a single specimen, and it is clear that several specimens were available to Boulenger (hence, syntypes) because he provided ranges for ventral and subcaudal scale counts. Later, Boulenger (1894), in his second volume of the *Catalogue of the Snakes in the British Museum (Natural*

History) listed 14 specimens under the species account of *T. asperrimus*, but again did not pick out specimens he considered the types, like he usually indicated for other species. Among the 14 specimens listed as examined materials, currently only 13 specimens (including the designated lectotype herein) are catalogued as "cotypes" at the NHMUK, and only five of them are clearly traceable corresponding to the specimens in Boulenger (1894). As this species has long been considered a synonym or a color morph of its sympatric congener (now *F. unicolor*), and based on the inability to identify the entire original type series (syntypes), in order to stabilize the nomen with a recognized name bearing type specimen, we believe it is essential to designate a lectotype with a precise type locality for further taxonomic clarifications of the genus. This lectotype designation qualifies with all the conditions of Article 74.7 of the Code (ICZN 1999).

The Status of Other Taxa of the *Fowlea piscator* Complex

After Vogel and David (2006, 2012) and Purkayastha et al. (2018), there are five subjective synonyms of *F. piscator* sensu lato which still need further taxonomic actions: *C. mortuarius*, *C. bengalensis*, *T. sanctijohannis*, *T. piscator lateralis*, and *T. piscator punctatus*. Following Vogel and David (2012), we also consider that *C. mortuarius* might be a distinct species restricted to northeast India. The *F. piscator* sensu lato samples from northern Assam in the phylogeny of Purkayastha et al. (2018) probably represent *C. mortuarius* or *C. bengalensis* (see Table 1; Fig. 1; and Fig. S1) or even *F. piscator* sensu stricto. Vogel and David (2012) further predicted that the distribution of *C. bengalensis* might extend towards southern India, and considered one of the specimens in particular (NHMUK 94.3.15.2) from Travancore which is similar to the depicted holotype of *C. bengalensis* in Plate 82, Fig. 1 of Gray (1834; see Fig. 5B in this work). They further argued that the number of subcaudal counts on the illustration is well within the range of *X. piscator*, and concluded the taxon as a subjective synonym of *X. piscator* sensu lato. Although in appearance it looks like an individual of *F. schnurrenbergeri*, they considered the subcaudal count in the depicted illustration out of the range for *F. schnurrenbergeri*. Such is the case, that if *C. bengalensis* turns out to be a valid species from the southern Western Ghats, it is safe to compare *F. unicolor* comb. nov. with the population of southern India—see the comparison. Thus, the populations from southern India must be compared with the iconotype (see Fig. 5B) of *C. bengalensis*, and a close match probably can be designated as a neotype in order to solve the taxonomic dispute of this nomen.

Wall (1907) described *T. piscator* var. *unicolor* from "Ajmere" (Ajmer, Rajasthan, India) based on several specimens (syntype; lost fide Vogel and David 2012), and Vogel and David (2012) concluded that its description is detailed enough to treat it as a trinomen, but synonymized with *T. sanctijohannis*, which also a junior subjective synonym of *F. piscator* sensu lato. Wall (1907) was probably unaware that the nomen "*unicolor*" had already been used by Müller (1887) to describe the Sri Lankan variety *T. quincunciatus unicolor*. These trinomens were originally established with different species epithets, although they were in combination with the same generic name, *Tropidonotus*. The nominotypical trinomen of *T. quincunciatus* is also now a junior objective synonym of "*F. piscator*," hence making Wall's nomen a primary homonym sensu Articles 52 and 53.3 of ICZN (1999). According to the Code 52.2, only the senior nomen, as determined by the Principle of Priority (sensu Article 52.3), in this case the nomen used by Müller (1887) is valid without any exception. Therefore, in applying the principle of homonymy, we reject the junior homonym, *T. p. unicolor* Wall 1907 sensu Article 60 of the Code, and following the Article 60.2, we replace Wall's nomen, *T. p. unicolor* with its potentially next available junior synonym, *T. p. obscurus* Wall 1907, with its own authorship and date (in this case, the same author and year, sensu Article 23.3.5 of the Code; ICZN 1999). As *T. sanctijohannis* is a montane species (fide Vogel and David 2012), and *T. p. obscurus* nom. nov. is from hot deserts in Rajasthan, further taxonomic works are needed to confirm the synonymy of the latter taxon.

As Vogel and David (2012) suggested, we also consider that *T. sanctijohannis* might be another distinct species restricted to northern India and northeastern Pakistan. Although, it was included in recent publications (e.g., Purkayastha et al. 2018; Singh et al. 2020; Cheng et al. 2021; Deepak et al. 2021) as a valid species, we still place it in the synonymy with *F. piscator* sensu lato (fide Vogel and David 2012) until the species is properly resurrected as a distinct species with a redescription and a diagnosis followed by combination with the genus *Fowlea*. The genetic sequences, MZ312620 and GQ225659, assigned to *F. piscator* sensu lato from Pakistan and Jabalpur (locality doubtful), India, were included in MrBayes v3.2.6 and BEAST v2.6.3– produced trees. The results showed polytomy with 29.6% genetic distance with the Sri Lankan population of *F. unicolor* comb. nov. and such high intrageneric divergence within the *Fowlea* genus is probably not reliable. Therefore, we removed these samples from our analysis, and additional molecular works are needed to confirm such a high divergence, which also could be an artifact of poor-quality sequences. *Tropidonotus piscator lateralis* might also be a distinct species (fide Vogel and David 2012), and the *F. piscator* sensu lato samples from Hyderabad in the phylogeny of Purkayastha et al. (2018) probably represent this species. However, we did not include this sequence for our analysis due to the unavailability of the cytochrome b gene in the GenBank.

Even though all the branches in the members of the *F. piscator* group have relatively high posterior probability values, the one internal and two external branches remain poorly supported. The branch supported at Node A (Fig. 1) is just 0.4981, which is considerably low. *Fowlea punctulata* and *F. schnurrenbergeri* in Clade E could be the main reason for this low value, because a tree with a higher branch supported at Node A was observed when the sample of *F. punctulata* had been removed from the analysis. Also, we have doubts about the species identity of KY379922 and KY379924, specifically, whether they were truly extracted from *F. schnurrenbergeri*, because morphologically, this species shares most of the characters of *F. piscator* group.

Recently, Köhler et al. (2021) showed that *F. tytleri* in Andaman is conspecific with *F. piscator* in the mainland.

There are no DNA samples of *F. piscator* sensu stricto from eastern India available on GenBank, therefore we have doubts with which species *F. tytleri* has been compared by Köhler et al. (2021). In the Andamans, we have noticed there are two color morphs of *F. tytleri* (see Table 2), and our molecular analysis using BI (Fig. 1), clearly indicates that *F. tytleri* is only allied to one of the mainland populations of *F.* cf. *tytleri* (or *F. piscator* sensu lato). Based on the available sequences of *F. piscator* (as *F.* cf. *piscator* in this study) from northeastern India on GenBank, both *F. tytleri* from Andaman and *F.* cf. *tytleri* from northern Thailand are genetically divergent from the northeastern Indian *F. piscator* with a *p* distance of 3.7–4.9% and 2.5%, respectively, in the mitochondrial cytochrome b gene. On the other hand, Köhler et al. (2021) did not provide any morphological comparison between *F. piscator* sensu stricto and Thailand; hence, such misleading statements in Köhler et al. (2021) threaten the taxonomic stability of the clearly distinct species of *F. tytleri*, as the nomen "*piscator*" has priority over the nomen "*tytleri*." Therefore, here we disagree with Köhler et al. (2021) that "*F. tytleri* is conspecific with *F. piscator*" and conclude that Köhler et al. (2021) just reported a range extension of *F. tytleri* (one of its color morphs) towards the mainland.

Currently, nine species of the genus *Fowlea* are now recognized, but it is likely that further species (including those regarded as subjective synonyms) remain unrecognized. In this study we mainly deal with the two Sri Lankan species (1) by resurrecting a neglected 135-yr-old nomen and assigning it to the species so far recognized as *F.* cf. *piscator*, and (2) by designating a lectotype to the endemic species, *F. asperrima*, in order to stabilize its taxonomic status. The remaining taxonomic issues of related mainland Indian species must be resolved before naming any new *Fowlea* species from the region, e.g., the genetically distinct population from Wayanad, southern India. Despite dealing with the following synonyms—*C. mortuarius*, *C. bengalensis*, *T. sanctijohannis*, and *T. piscator obscurus*—a neotype designation might also be required to stabilize the nomen *T. piscator punctatus* from Tranquebar (= Tharangambadi), Tamil Nadu. Therefore, an extensive level of integrative systematic works throughout India need to be carried out; and we leave it to future taxonomic workers.

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SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at https://doi.org/10.1655/Herpetologica-D-22-00004.1.S1.

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Appendix

Other Specimens Examined

Fowlea flavipunctata.—China: USNM 7387 (neotype), ZMH R07933, MNHN-RA 1902.0069, FMNH 24815, 6728–32, ZMB 8491; Cambodia: MNHN-RA 1970.449–59, 1988.2103; Laos: ZMH R05308, MNHN-RA 1063.0753, 1063.0758–9, 1962.0288, 1962.0290–91, 1963.0754–7, 1963.0760–61, 1985.0403, 2003.3345, FMNH 254785–6, 255241–5; Thailand: NHMUK 1977.1925, 1977.1933, 1987.1733, 1987.1736, 1977.1931–2, FMNH 142159, 169411, 169413, 178627–33, 178644–5, 178705, 180161, 180163–4, 180185–7, 191104–5, MNHN-RA 1885.0395–6, 1963.0716–9, 1998.8536, 1999.7614, ZMH R05306; Vietnam: NHMUK 1920.1.20.453a–b, 1921.4.1.10, MNHN-RA 1894.0108, 1907.0032, 1908.0038, 1908.0053, 1908.0193, 1911.0007, 1911.0032, 1911.0113, 1912.0064, 1927.0059–60, 1974.1279, 1974.1281, 1974.1284, 1974.1355–7, 1885.0293–300, 1885.0397–399, 1991.1610; West Malaysia: NHMUK 1965.974–8, 95.10.7.8, 97.2.3.4, ZMH R07943.

Fowlea melanzosta.—Indonesia: Java: MNHN-RA 0060 (neotype), 3517, 3506, 7410, 1911.0163, 1991.1602, 1991.1603, 1991.1601, 1991.1604, 1991.1600, 1991.1605, NHMUK 94.3.24.10, 49.1.12.8, 1935.11.9.1.

Fowlea piscator sensu stricto.—India: West Bengal: USNM 129715, FMNH 152348–9, 152351–2, 152363, 152393, 154592, NHMUK 72.4.7.393, ZMH R04827, ZMB 35738.

Fowlea schnurrenbergeri.—Nepal: MHNG 1377.44 (holotype), 1377.39–40, 1377.43, 1377.46–7, 1377.52, 1377.54–7, 1377.59–60, 1377.65, 1377.68, 1377.71; India: West Bengal: NHMUK 1911.9.8.1; Uttar Pradesh: ZMH R04811, R04814.

Fowlea tytleri.—India: Andaman: ZSI 7402 (holotype), NHMUK 1940.3.7.5–9, 1940.3.7.10, FMNH 134922–6.

Fowlea yunnanensis.—ZSI 4191–92 (syntypes), 4196 (syntype).