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Hidden diversity in semi-fossorial Melanesian forest snakes: A revision of the *Toxicocalamus loriae* complex (Squamata, Elapidae) from New Guinea

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Abstract

With its conservative set of scalation characters, *Toxicocalamus loriae* is a morphologically confusing species to which a wide array of phenotypes has been assigned. Careful analysis of 224 museum specimens reveals that multiple distinct species remain hidden under the name *T. loriae* and that diagnostic, species-level differences are more nuanced in this group of snakes than among other members of the genus. Our taxonomic reassessment leads us to resurrect the species *T. lamingtoni* **comb. nov.**, *T. loennbergii* **comb. nov.**, and *T. nymani* **comb. nov.** from synonymy with *T. loriae*, retain only *T. pratti* as a synonym, and describe three new species. As a consequence, *T. loriae* is no longer recognized as ranging throughout the entire island of New Guinea but is instead restricted to the southern versant of the Papuan Peninsula, and *T. lamingtoni* and *T. spilorhynchus* **sp. nov.** are species restricted to that same peninsula's northern versant. *Toxicocalamus loennbergii* is known only from the type series taken on the Onin Peninsula in West Papua, Indonesia, *Toxicocalamus atratus* **sp. nov.** is a high-elevation (800–2200 m) Central Highlands endemic, and *T. vertebralis* **sp. nov.** ranges from the Central Highlands of Papua New Guinea eastward into the Wau area of Morobe Province. *Toxicocalamus nymani* inhabits a geologically more heterogenous region, occurring from the Central Highlands eastward to the Huon Peninsula, including Karkar Island, and adjacent areas of Madang Province as well as the northernmost reaches of the Papuan Peninsula. We expect that denser geographic sampling across New Guinea and focussed specimen collection of a few known populations will result in the recognition of additional species in this complex.

Keywords

Biogeography, Hydrophiinae, morphology, new species, New Guinea, snake, taxonomy

Introduction

Toxicocalamus Boulenger, 1896 is the most speciose genus of terrestrial snakes in Melanesia, with 17 species currently recognized (O'Shea et al. 2018; Kraus 2020; Roberts and Austin 2020). These snakes are terrestrial, fossorial, or semi-fossorial, and they are so infrequently collected that a common scenario in museum collections is to find only single specimens from a specific locality. Even modest series of specimens from a given locality are rare, and only two large series from single locations are known – both of the same species. The genus and first species were described by Boulenger (1896), and only six species were known by the time of McDowell's (1969) revision, in which he described three additional species. Before then, a measure of taxonomic uncertainty had descended over these six species, which had first been assembled into the genera *Toxicocalamus*, *Apistocalamus* Boulenger, 1898, *Pseudapistocalamus* Lönnberg, 1900, and *Ultrocalamus* Sternfeld, 1913, with the validity of *Apistocalamus* and *Pseudapistocalamus* questioned by Boulenger (1908), who used the incorrect subsequent spellings *Apisthocalamus* and *Pseudapisthocalamus*. McDowell (1969) then placed those six species along with the three he described into the single taxon *Toxicocalamus* but also designated *Apistocalamus*, *Toxicocalamus*, and *Ultrocalamus* as subgenera to preserve the historical taxonomic distinctions between these groups.

Toxicocalamus is a morphologically unusual lineage on account of diverse scale fusions and divisions and differences in body habitus, the combination of which might be used to characterize distinct genera in other snake clades. However, phylogenetic analysis has shown that *Toxicocalamus* is indeed monophyletic and that McDowell's recognition of generic or subgeneric divisions would render each of those purported genera or subgenera polyphyletic (Strickland et al. 2016). We therefore follow Strickland et al. (2016) in recognizing *Toxicocalamus* as a well-defined clade with the other genus-level nomina relegated to its synonymy.

The aforementioned distinctive scale patterns and body morphologies allow ready distinction of many *Toxicocalamus* species. Among the exceptions are species related to *T. loriae* (Boulenger, 1898), which were informally called the "*T. loriae* group" by Kraus (2017). Based on the phylogenetic work of Strickland et al. (2016) and the species descriptions of Kraus (2009, 2017, 2020), we here formally adopt the classification *T. loriae* Group to identify the species under investigation. These species are morphologically similar in having divided subcaudals, the prefrontal fused to neither the preocular nor the internasal, the internasal and preocular almost always separated from each other by the intervening prefrontal, and a uniformly dark grey or brown dorsum (Kraus 2009, 2020). Included in the *T. loriae* Group are the nominate species *T. loriae* and four taxa synonymized with it by McDowell (1969): *Pseudapistocalamus nymani* Lönnberg, 1900, *Apistocalamus loennbergii* Boulenger, 1908, *A. pratti* Boulenger, 1908, and *A. lamingtoni* Kinghorn, 1928. Also included are a set of six clades identified in the phylogenetic study of Strickland et al. (2016), of which two were subsequently described as new species (*T. nigrescens* Kraus, 2017 and *T. mattisoni* Kraus, 2020), with another identified as true *T. loriae* (Kraus, 2020). More recently, Roberts and Austin (2020) described *T. goodenoughensis* from Goodenough Island and provided genetic data for that species using the same loci as Strickland et al. (2016), which placed their species as sister to *T. nigrescens* from adjacent Fergusson Island.

The *T. loriae* Group is not morphologically cohesive, however, because the somewhat divergent *T. mintoni* Kraus, 2009 and *T. pachysomus* Kraus, 2009 cluster with members of this group in the molecular analysis, whereas true *T. loriae* may be more closely related to other species of *Toxicocalamus* (based on relatively low branch support that could easily be overturned with study of additional loci; Strickland et al. 2016). Further phylogenetic investigation and the inclusion of *T. mintoni* and *T. pachysomus* may prove the *T. loriae* Group to be monophyletic, though its morphological diagnosis would be complicated because of the disparate scale patterns that characterize these last two species.

Among *Toxicocalamus*, the *T. loriae* Group is rather unusual in being moderately well collected overall, and two of the sampled localities have produced large specimen series that allow for a better assessment of intraspecific morphological variation than for other species in the genus. Nonetheless, the taxonomy of this group has not been addressed in comprehensive fashion since McDowell (1969), even though recognition that some of the taxa McDowell synonymized are valid has been mentioned before (Kraus 2009, 2017, 2020; O'Shea et al. 2018). Within the *T. loriae* Group, it remains uncertain what to do with the hundreds of museum specimens not partitioned into the recently described *T. goodenoughensis*, *T. mattisoni*, *T. mintoni*, *T. nigrescens*, and *T. pachysomus*. Following McDowell (1969), almost all of these specimens have remained lumped into a heterogeneous *T.* "*loriae*" that shows a broad range of scale counts and colour-pattern features. Both morphological heterogeneity and molecular evidence make clear that multiple species are agglomerated under this name, but sorting them out has been hindered by a bewildering array of unique character combinations and a paucity of specimens with these unique character combinations. Furthermore, as noted above, scalational differences among many of these groups are not nearly as definitive as in other species of the genus.

McDowell (1969) based his understanding of *T. loriae* on the examination of a limited sample of this group, consisting of only 51 specimens. It is the purpose of the present study to reassess the snakes currently assigned to *T.* "*loriae*," resolve the status of the nomina synonymized by McDowell (1969), and describe additional species as necessary. Although we are still unable to resolve all taxonomic questions surrounding the *T. loriae* Group with the currently available pool of specimens, we were able to resolve several key issues and deliver several taxonomic decisions, while pointing to additional areas requiring

research once new specimens, tissues, and photographs in life become available.

Materials and methods

Specimens

We examined 224 specimens, including all known specimens of *T.* "*loriae*" from all localities where members of this complex have been collected. We made one exception for the largest, single-locality sample for one new species we describe and recognize below as a member of this group (Kundiawa, Chimbu Province, Papua New Guinea; $n = 118$), of which we included only 21 specimens to avoid overwhelming trends within and between populations represented by far fewer specimens with the sheer quantity of data from a single locality. GPS coordinates for localities use the Australian Geodetic Datum (AGD66), and specimen numbers are listed with institutional abbreviations as follows: American Museum of Natural History, New York, USA (AMNH), Australian Museum, Sydney, Australia (AMS), Bernice P. Bishop Museum, Honolulu, Hawaii, USA (BPBM), The Natural History Museum, London, United Kingdom (BMNH), California Academy of Sciences, San Francisco, California, USA (CAS), Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (IRSNB), University of Kansas Biodiversity Institute, Lawrence, Kansas, USA (KU), Louisiana State University Museum of Zoology, Baton Rouge, Louisiana, USA (LSUMZ), Museum of Comparative Zoology, Cambridge, Massachusetts, USA (MCZ), Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy (MSNG), Museums Victoria, Melbourne, Australia (NMV), Naturhistorisches Museum Wien, Vienna, Austria (NMW), Papua New Guinea National Museum and Art Gallery, Port Moresby, Papua New Guinea (PNGM), South Australian Museum, Adelaide, Australia (SAMA), University of Colorado Museum of Natural History, Boulder, Colorado, USA (UCM), University of Papua New Guinea, Natural Sciences Resource Centre, Port Moresby, Papua New Guinea (UPNG), United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM), and Uppsala Universitet, Evolutionsmuseet, Uppsala, Sweden (UUMZ), with the addition of those identified as FK (Fred Kraus field series).

Characteristics

We measured snout–vent length (SVL) and tail length (TL) to the nearest mm with a plastic ruler on freshly euthanized specimens and by laying a non-elastic string along preserved specimens and measuring the length of string against a tape measure. We acknowledge that measurements of coiled snakes have inherent inaccuracies due to the twisting of specimens (such as dorsiflexion and ventriflexion or sideways coiling instead of regular, dorsoventral coiling), and our measurements may therefore differ from actual measurements by several millimetres. Our main use of these measurements is in the calculation of ratios, which makes potential measurement errors less impactful since numerator and denominator share these errors. We calculated the tail-length ratio (TL_R) as TL / (SVL + TL). We found relative snout width to be important in diagnosing some of the species, and we quantified this character by taking the ratio (to two decimal places) of snout length (SNL, measured from the posterior point of the frontal scale to the tip of the snout) to snout width (SNW, measured across the head at the anterior margin of the eyes) from photographs of each specimen. We found relative eye diameter to be useful for discriminating among these same species, and we quantified that character by taking the ratio (to two decimal places) of eye diameter (EY) to SNL. We also used the subcaudal ratio (SC_R, the number of subcaudal scales divided by the number of ventral + subcaudal scales; Kaiser et al. 2021) to contrast some species pairs. We followed the method of McDowell (1969) to count scales and determined sex by examination for hemipenes, eggs, or by assessing the numbers of subcaudals in a sample, which in this genus invariably allows distinction between longer-tailed males and shorter-tailed females. We obtained colour-pattern details from photographs of dorsum, venter, and tail, as well as from dorsal, ventral, and both lateral views of the heads of all specimens.

Comparisons

Diagnostic features and comparisons to other species are based on our own data as well as those from Boulenger (1898, 1904, 1908), Lönnberg (1900), Kinghorn (1928), McDowell (1969), Kraus (2009, 2017, 2020), O'Shea et al. (2015, 2018), and Roberts and Austin (2020), with reference to specimens housed in publicly accessible natural-history collections (Appendix). Based on the phylogenetic tree presented by Strickland et al. (2016), *T. mintoni* and *T. pachysomus* lie within the set of lineages comprising the *T. loriae* Group even though they are morphologically divergent and easily distinguished from the other members of that group. The same is true for the recently described *T. goodenoughensis* (Roberts and Austin 2020). Within this set of lineages, *T. mintoni* is unique in having the preocular fused to the prefrontal and the frontal fused to the supraoculars, and *T. pachysomus* is unique in its robust habitus and uniformly pale-brown venter. Neither can be confused with the other members of the group treated in this report. *Toxicocalamus pachysomus* and *T. goodenoughensis* are also distinguished by having the preocular in contact with the internasal, a feature occurring rarely among other members of the *T. loriae* Group but never diagnostic of them. Because these three species are easily distinguished from all other members of the *T. loriae* Group, we omit them from the comparison sections below. Additionally,

all other *Toxicocalamus* species outside of this group are easily distinguished (see key in Kraus 2020). Consequently, for simplicity, we restrict comparisons herein to close relatives discussed below and to *T. mattisoni* and *T. nigrescens*, retrieved as members of the *T. loriae* Group by Strickland et al. (2016). This admittedly paraphyletic assemblage of species (paraphyletic due to the deliberate omission of the morphologically distinctive *T. goodenoughensis*, *T. mintoni*, and *T. pachysomus*) is united by its combination of (1) paired subcaudals; (2) prefrontal not fused to internasal; (3) preocular not fused to prefrontal or internasal and typically in contact with nasal but not internasal; and (4) dorsum uniformly grey or brown and unspotted.

During the final preparations of our revision of this manuscript, the description of *T. longhagen* was published by Roberts et al. (2022). The authors based this taxon on a single specimen (PNGM 22160) collected at Dobel, close to Mt. Hagen, Western Highlands Province, PNG. This is a specimen we also examined and photographed, and we can confirm that it is undoubtedly a member of the *T. loriae* Group. However, we decided to list it as *Toxicocalamus* sp. in the Appendix (see below) and excluded it from our analysis, because its colour pattern is clearly aberrant – an artifact of its long period of preservation in various liquids and differential exposure to light – and because its scale characteristics do not permit assignment to any already defined or otherwise cohesive group within the *T. loriae* Group. Furthermore, PNGM 22160 is actually one of a series of specimens, all of which display similar characteristics, and a second specimen from the same locality (UPNG 3992) also exists. Among all these specimens, the "diagnostic" features relied upon by Roberts et al. (2022) are widely variable. Hence, *T. longhagen* may or may not represent a distinct taxon – as we advised the authors of Roberts et al. (2022) in earlier correspondence. Given the poor colour preservation of PNGM 22160 and the absence in Roberts et al. (2022) of comparisons using data from more than three of the over 300 available specimens of *T.* "*loriae*", the description of *T. longhagen* provides no distinctive characteristics by which to define that species' boundaries relative to other members of the *T. loriae* Group. For these reasons, we consider the name *longhagen* a *nomen dubium* [doubtful name] following the definitions of this term in the Glossary of the International Code of Zoological Nomenclature (ICZN 1999; see Granzow 2000) and the discussion by Mones (1989). We have begun writing a more detailed comment on the taxonomic status of *T. longhagen* and limit our discussion of this nomen relative to the *T. loriae* Group to this paragraph.

Statistical analyses

When applying statistical methods to a group like *Toxicocalamus*, in which sample sizes are generally small, care must be taken to ensure statistical procedures follow best practices. We therefore report the results of our tests with a suitable degree of confidence (using significance levels of at least $p < 0.01$) but with the caveat that additional sampling may shift the significance level of inference (Bryhn and Dimberg 2011), even if it does not shift the inference itself. We first subjected the largest specimen series in our data, separated into females and males, to Kolmogorov-Smirnov Tests to ensure normality of the data, followed by Levene's Tests to ascertain homogeneity of variance (homoscedasticity). Because any natural snake population generally satisfies these conditions (Boback and Guyer 2002), we used unpaired Student's *t*-tests to determine whether differences in length and scale count distributions were statistically significant. Such tests cannot be applied when a ratio includes a value in both numerator and denominator. This is the case for TL_R and SC_R, and those values were not subjected to *t*-tests. We report ranges for SVL, ventrals, subcaudals, and subcaudal ratios including means ± standard deviations ($\bar{x} \pm SD$). For scales counts, figures are rounded to the nearest whole scale. We considered specimens with an SVL ≥ 300 mm to be adults (see Shine and Keogh 1996) and included only those in our overall length comparisons.

We initially considered comparing the morphology of some *T. loriae* Group populations on a finer scale based on geography and colouration, and this appeared especially relevant to the diagnosis of populations in the Central Highlands, the Huon Peninsula, the Adelbert Range, and the Wau–Garaina Region of Morobe Province in Papua New Guinea. However, due to the small sample sizes for some of these localities, we could not use an analysis of variance at this stage and worked instead using *t*-tests in pairwise sample comparisons. When no statistically significant differences could be identified between samples in one or more of these comparisons, we combined those samples and conducted successively more inclusive comparisons until only samples with significant differences remained. We then tested the hypotheses represented by these operational taxonomic units (OTUs) against morphological characteristics to reach well-founded taxonomic decisions. Values for the results of our *t*-tests include the *t*-values with subscripted degrees of freedom as well as the *p*-value. Once species boundaries could be confirmed independently by gross morphological characteristics and tests of basic measurements, we conducted an ANOVA, with post-hoc Tukey pairwise comparisons.

Results

Basic statistics

The outcome of our Kolmogorov-Smirnov and Levene's Tests showed that the *T. loriae* Group populations for which more than five specimens were available showed no significant difference from what would be expected in normally distributed populations and there was no indication of heteroscedasticity. We extrapolated these

Table 1. Basic statistics for certain length and scale characteristics of *Toxicocalamus loriae* Group species discussed herein.

Character	Sex	Taxon						
		***atratus* sp. nov.**	***lamingtoni***	***loennbergi***	***loriae***	***nymani***	***spilorhynchus* sp. nov.**	***vertebralis* sp. nov.**
n		43♀, 49♂	9♀, 9♂	4♀	4♀, 15♂	21♀, 18♂	6♀, 8♂	10♀, 9♂
Maximum known length (mm) SVL + TL = TTL	♀	682 + 49 731	500 + 57 = 557	565 + 55 = 620	440 + 93 = 533	540 + 68 = 608	600 + 67 = 667	685 + 82 = 767
	♂	655 + 117 = 772	420 + 110 = 530	none	490 + 90 + = 580	422 + 84 = 506	332 + 79 = 411	565 + 103 = 668
TL_R, mean ± SD (Range)	♀	9.9 ± 1.7 (6.7–14.9)	10.3 ± 0.9 (9.0–11.6)	10.2 ± 0.9 (8.9–11.2)	14.1 ± 3.3 (10.8–17.5)	10.5 ± 1.0 (9.2–12.9)	9.6 ± 0.6 (8.9–10.2)	9.4 ± 1.4 (6.5–10.7)
	♂	15.6 ± 1.7 (12.9–19.4)	18.8 ± 1.4 (16.7–20.8)	none	16.6 ± 1.7 (13.4–19.1)	16.1 ± 1.3 (13.3–17.9)	18.4 ± 0.5 (17.9–19.2)	14.7 ± 1.3 (13.3–17.1)
Ventrals, mean ± SD (Range)	♀	206 ± 7 (187–218)	190 ± 3 (186–195)	216 ± 2 (214–220)	179 ± 7 (175–190)	198 ± 5 (191–210)	190 ± 7 (178–197)	218 ± 9 (203–232)
	♂	196 ± 5 (177–206)	170 ± 5 (160–178)	none	184 ± 10 (162–197)	187 ± 7 (178–198)	178 ± 4 (172–184)	201 ± 5 (194–210)
Subcaudals, mean ± SD (Range)	♀	31 ± 3 (26–41)	29 ± 2 (26–34)	28 ± 3 (23–32)	31 ± 2 (28–33)	30 ± 3 (26–37)	26 ± 3 (20–29)	35 ± 2 (31–38)
	♂	44 ± 2 (40–47)	46 ± 4 (41–53)	none	44 ± 3 (40–50)	44 ± 2 (39–48)	51 ± 4 (43–57)	45 ± 4 (39–52)
SC_R, mean ± SD (Range)	♀	12.9 ± 1.3 (11.2–17.8)	13.2 ± 0.8 (12.2–14.9)	11.3 ± 1.1 (9.7–12.7)	14.6 ± 1.0 (13.5–16.1)	13.1 ± 1.1 (11.6–15.8)	11.9 ± 1.1 (10.0–13.1)	13.7 ± 0.7 (12.8–14.8)
	♂	18.3 ± 0.8 (16.9–21.0)	21.4 ± 1.2 (19.3–23.0)	none	19.4 ± 1.4 (17.1–21.5)	19.1 ± 0.9 (17.5–20.7)	22.1 ± 1.2 (20.0–24.0)	18.4 ± 1.0 (16.7–20.5)

findings to propose that smaller samples were also derived from normally distributed, homoscedastic populations, and we used *t*-tests with the caveat that additional samples of smaller populations may indeed shift the statistical inference for those comparisons. However, in a testament to the distinctiveness of these groups, levels of significance in analyses with $p << 0.01$ would most likely remain significant at $p < 0.01$ even if sample sizes were expanded. Based on maximum female size there appear to be three divisions in body size among members of the *T. loriae* Group, which we consider modest (maximum female SVL < 575 mm), moderate (SVL between 575 and 650 mm), and large (SVL > 650 mm). Furthermore, as with all species of *Toxicocalamus*, members of the *T. loriae* Group display a strong, statistically highly significant ($p < 0.00001$ for six tested OTUs; $n = 90$ females, 105 males) sexual dimorphism in the number of subcaudal scales, with females invariably possessing a much lower number of subcaudals than males (nearly 40% fewer on average in the data set for the species discussed herein). The ANOVA confirmed that the variation in ventral and subcaudal scales between the analysed OTUs identified significant differences, all at $p < 0.00001$ (ventral scales in males: $f = 58.5312$; ventral scales in females: $f = 24.6121$; subcaudal scales in males: $f = 8.8254$; subcaudal scales in females: $f = 9.3021$). A summary of several relevant characteristics is provided in Table 1 to facilitate comparisons between species.

Characters

Intergenials. The posterior genials may be separated by one or two intergenials. Presence of two intergenials invariably results in the complete separation of the posterior genials, but when only a single intergenial is present anterior contact between the posterior genials may or may not occur and can extend for up to half their length. In the sole species characterized by two intergenials (*T. loriae*), these occur one behind the other with the widest point of each scale at its anterior end. The three new species described below predominantly possess a single intergenial, but specimens may rarely have two intergenials in a slightly anomalous arrangement, which may include (1) side-by-side instead of midline positioning, or (2) the presence of a tiny intercalary scale at the anterior end of a normal-sized intergenial. In all species with single intergenials, their widest portion is usually at the posterior end but may occasionally occur at the centre or, in very few specimens, at the anterior portion of the scale.

Vent covering. The vent is covered by a single scale in one species (*T. lamingtoni*) and by two scales in all others. The traditional way of handling this character in snake taxonomy has been to misname this covering as the "anal scale" (anus = opening for solid waste excretion, vent = cloacal opening for urinary, faecal, and reproductive excretion) and/or to use the character state "single" for a covering made up by one scale and "divided" when two scales are present. Describing a scale as "divided" implies a process: at some point the scale was whole. The development of scales begins with "nuclei" of scale formation (i.e., tissue sections before there is a scale; Alibardi 2002, Klein and Gorb 2012), and dual nuclei produce "paired" scales (e.g., subcaudals that lie next to each other in an offset, "zig-zag" format). The plate covering the vent is developmentally neither a gastrostege

nor a urostege but a third type of ventrally positioned scale. Its position and shape are influenced by the development of the cloacal orifice, and in some snakes, twin scale nuclei produce this covering: two scales that overlap to varying degrees in different groups of snakes, which are morphologically and developmentally distinct from gastrosteges and urosteges. Furthermore, the process of splitting a single scale into two scales could not produce the type of overlap observed. Thus, the use of "divided" related to such a structure would be incorrect because the scale does not divide. We here use the terminology of the vent being covered by one scale vs. two scales.

Contact between preocular and nasal. In most species of this group the preocular and nasal are in contact with each other. The recently described *T. mattisoni* is characterized by lacking this contact due to intervening contact between the prefrontal and second supralabial. Most species considered herein show rare variation in this feature, though they usually exhibit contact between preocular and nasal. In cases where the prefrontal does contact the second supralabial, it is usually only a point contact and rarely exhibits the broad contact between those scales seen in *T. mattisoni*.

Postoculars. The number of postoculars can be one or two and shows no variation in some species. In others, this character may vary intraspecifically but within such variation manifests strong tendencies (> 90%) to favour one state over the other.

Posterior temporals. The number of posterior temporals (scales between the parietals and supralabials that are not also in contact with the postoculars) varies between one and five, but the vast majority of specimens have two (55.5%) or three (43.2%). One specimen has a single posterior temporal on one side (two on the other), three specimens have four on one side (three on the other), and one specimen has five on one side (three on the other). Some species show no variation in temporal number, but usually there is intraspecific variation though showing a strong central tendency toward either two or three posterior temporals. Specimens with one, four, or five temporals invariably have two or three on the other side, which indicates that posterior temporal combinations other than two or three are aberrations.

Ventral colour pattern. Ventral colour pattern is a key distinguishing feature for species in this complex. In adults, venters are uniformly pale yellow in four species, yellow with or without a central row of brown spots or bars in another species, and black in two. Species with black venters (brown in preservative) may have the posterior area of each ventral scale appear paler than its anterior area, creating a banded appearance. This banding becomes more pronounced in specimens after an extended time in preservative, presumably due to melanin degradation in ethanol or via light exposure, with melanin apparently lost first in the thinner tissues along the posterior end of each scale. For some specimens, this feature may become difficult to observe when severe bleaching has occurred, in which case it is also difficult to determine whether a yellowish or pale-brown venter was the natural state for a particular specimen or an artifact of preservation. It is often possible to infer the natural state by consulting the dorsal side, where an unnaturally pale colour would indicate that bleaching has occurred. Furthermore, in one black-ventered species, small juveniles have a uniformly yellow venter that soon becomes clouded with melanin as the animal grows; in the second black-ventered species, the venter is black throughout life. All other species for which information is available have yellow venters as juveniles.

Juvenile head pattern. Members of the *T. loriae* Group are well known for having yellow markings on the nape and often on the head. The exact patterning of these pale elements on the heads of juveniles and their ontogenetic change is diagnostic for several of the species of this group. Of specific diagnostic utility are the completeness and width of the pale nuchal collar and the presence of pale blotches on the prefrontals.

Tail spine. The tail spine is usually paler than the remainder of the tail in most species but is uniformly dark in others.

Taxonomic accounts

Toxicocalamus loriae (Boulenger, 1898)

Figs 1A, A', 2A, A', B, B', 3A, A', 4A, B, 5

Apistocalamus loriae Boulenger, 1898: 705.
Apistocalamus Pratti Boulenger, 1904: 451.
Apisthocalamus loriae – Boulenger, 1908: 249.
Apisthocalamus pratti – Boulenger, 1908: 249.
Apisthocalamus prattii – Barbour, 1912: 201.
Apistocalamus pratti – McDowell, 1967: 537.
Toxicocalamus (*Apistocalamus*) *loriae* – McDowell, 1969: 455.
Toxicocalamus loriae Clade 1 – Strickland et al., 2016: 671.

Holotype and collection. MSNG 29141, an adult male from Haveri, British New Guinea (vicinity of 9.40°S, 147.60°E). The specimen was collected by the Italian anthropologist, ethnographer, explorer, and naturalist Lamberto Loria (1855–1913), who travelled in British New Guinea from 1889–1897 and sent a series of zoological specimens to the Museo Civico di Storia Naturale in Genoa, Italy. Based on Loria's diary accounts of his travels (see Dimpflmeier 2014, 2019), the specimen was most likely collected during an excursion on 28 June 1893 to the southern versant of the Owen Stanley Range a point-to-point distance of 50 km east of Port Moresby. Thus, Boulenger's (1898) estimate of 1889–1892 for the collection he described appears to have been at least a year short. The species was described in Series 2, Volume

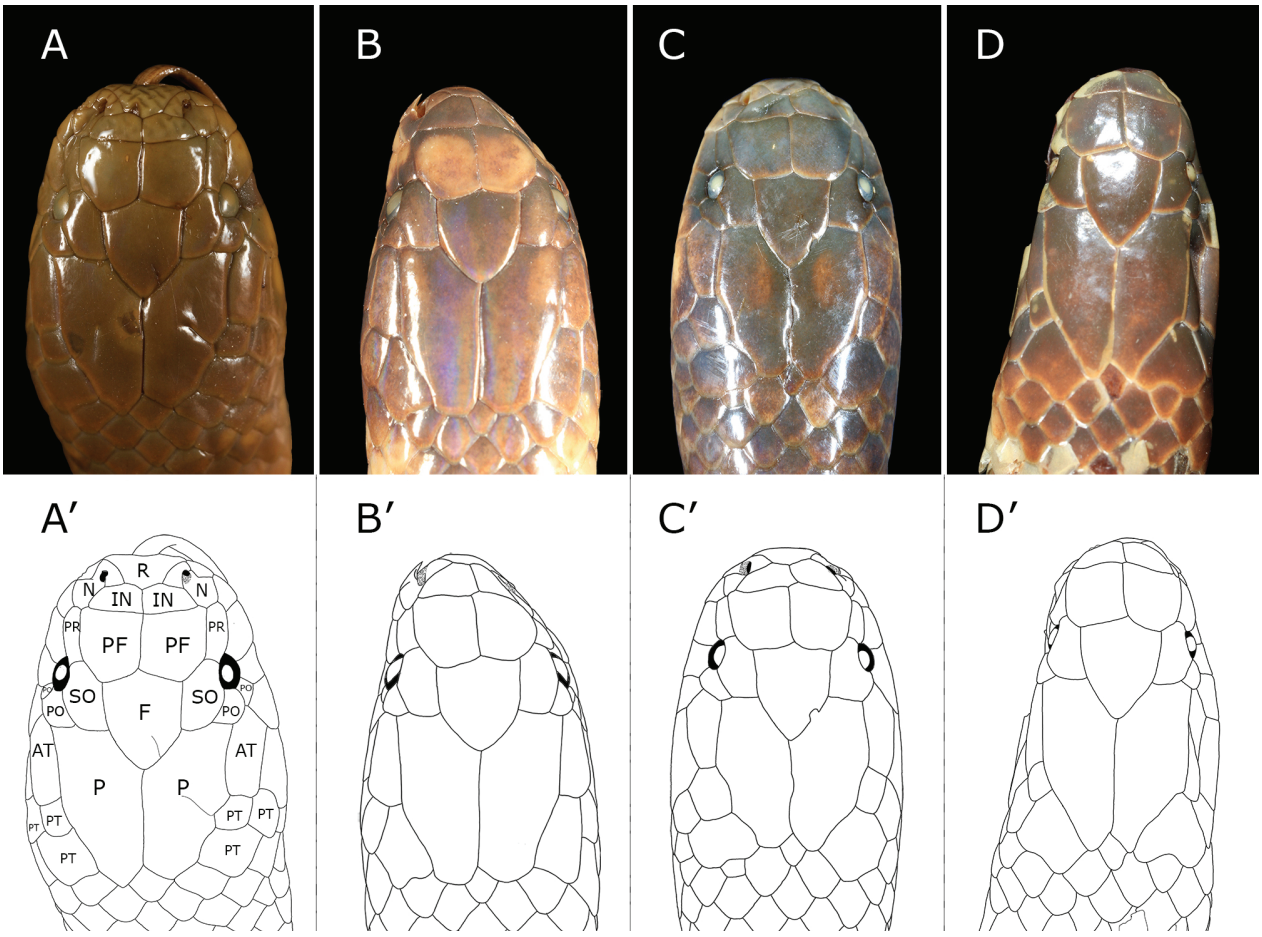

Figure 1. Dorsal views of heads of *Toxicocalamus loriae* Group snakes, presented as both photographic and line-drawing illustrations. **A**, **A'** holotype of *T. loriae* (MSNG 29141), Haveri, Bartholomew Range, Central Province, PNG. **B**, **B'** lectotype of *T. nymani* **comb. nov.** (UUMZ 290/2387), Sattelberg, Huon Peninsula, Morobe Province, PNG. **C**, **C'** lectotype of *T. loennbergii* **comb. nov.** (BMNH 1946.1.18.24), Fakfak, Onin Peninsula, West Papua Province, Indonesia. **D**, **D'** holotype of *T. lamingtoni* **comb. nov.** (AMS R9351), Mount Lamington, Oro Province, PNG. Images not to scale. Scale abbreviations: anterior temporals (AT), frontal (F), internasals (IN), nasals (N), parietals (P), prefrontals (PF), postoculars (PO), preoculars (PR), posterior temporals (PT), rostral (R), supraoculars (SO).

18 of the Annali del Museo Civico di Storia Naturale di Genova, which is an 1897 volume that was published in March 1898 (Poggi 2010).

Etymology. Named by Boulenger (1898) for the collector of the holotype. The description was published in English.

Diagnosis. A modestly sized member of the *T. loriae* Group (maximum SVL in males 490 mm, in females 440 mm) with the following unique combination of characters: two scales covering vent; three infralabials contacting anterior genial; posterior genials separated by two intergenials, one in front of the other; intergenials widest anteriorly. Elongate preocular, at least twice as long as wide, contacting nasal but not internasal; one (in 58% of specimens) or two (42%) postoculars; two (55%) or three (45%) posterior temporals; ventral scale count not sexually dimorphic, 162–197 ventrals in 15 males, 172–190 in four females; subcaudal scale count sexually dimorphic without overlap, 40–50 in males, 28–33 in females; SC_R 17.1–21.5% in males, 12.5–16.1% in females; pale markings on prefrontals absent (67%), small or vaguely developed (28%), or present (5%), not obviously correlated with body size; tail spine white, paler than the rest of the tail; venter uniformly yellow, yellow with a mid-ventral row of brown spots on each ventral, with a few brown spots scattered down the venter, or with each spot expanded into a brown bar across the anterior of each ventral.

Comparisons with other species. *Toxicocalamus loriae* is distinguished from all other members of the *T. loriae* Group in having the posterior genials separated by two intergenials that are aligned in the midline, one in front of the other, with each scale widest anteriorly. All other species are characterized by having the posterior genials separated by only a single intergenial that is widest posteriorly (typically) or centrally (occasionally). As noted above, in the other species there will rarely be two (or three in AMS R23069) intergenials, but the anterior one is either tiny or the two scales occur side-by-side at the posterior portion of the posterior genials; the rarity of these anomalous features suggests they are developmental oddities. *Toxicocalamus loriae* may be

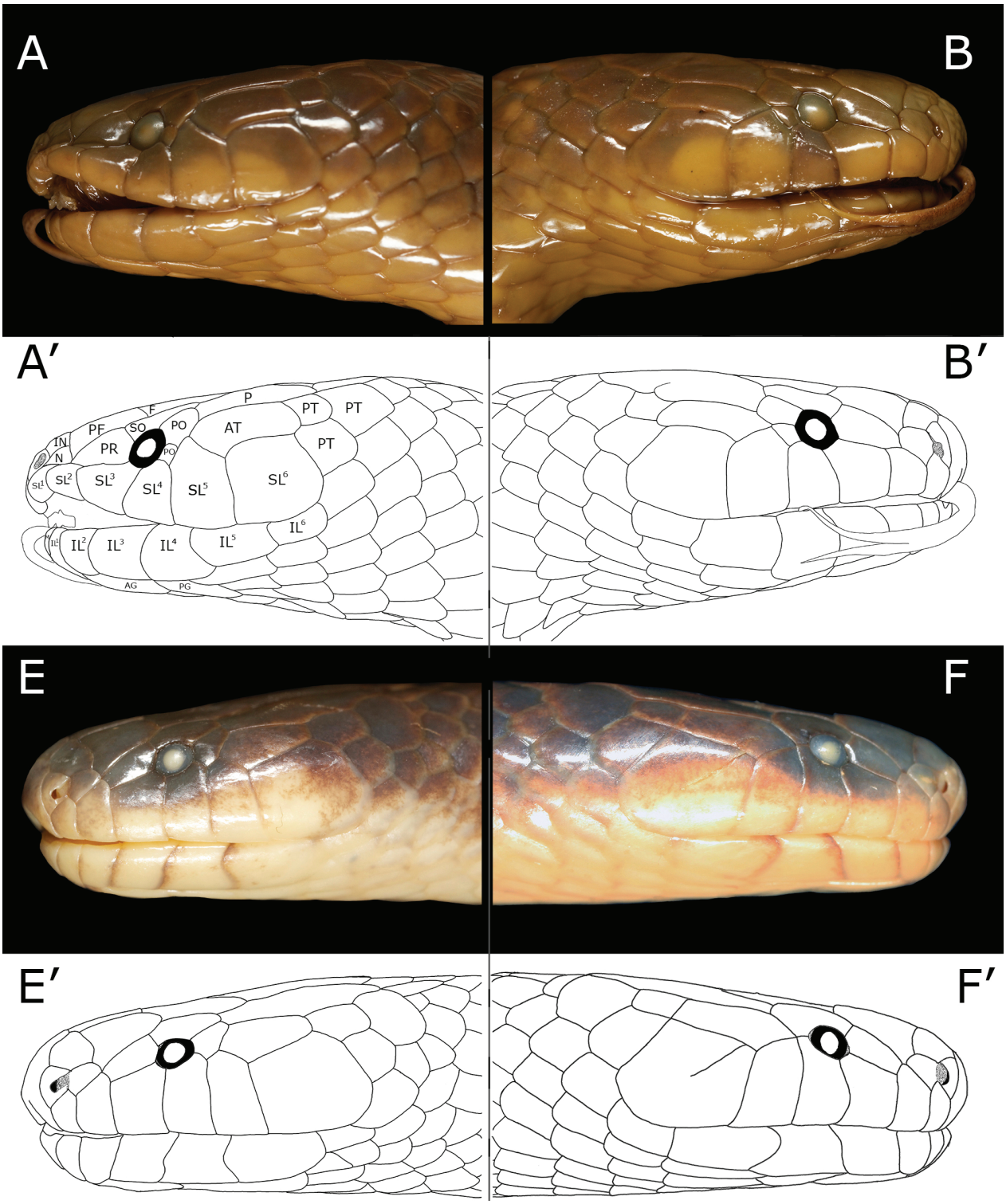

Figure 2 – part one. Right and left lateral views of heads of *Toxicocalamus loriae* Group snakes, presented as both photographic and line-drawing illustrations. **A**, **A'**, **B**, **B'** holotype of *T. loriae* (MSNG 29141). **C**, **C'**, **D**, **D'** lectotype of *T. nymani* **comb. nov.** (UUMZ 290/2387). **E**, **E'**, **F**, **F'** lectotype of *T. loennbergii* **comb. nov.** (BMNH 1946.1.18.24). and **G**, **G'**, **H**, **H'** holotype of *T. lamingtoni* **comb. nov.** (AMS R9351). Images not to scale. Scale abbreviations: anterior genial (AG), anterior temporal (AT), frontal (F), numbered infralabials ($IN^{1–6}$), internasal (IN), mental (M), nasal (N), parietal (P), posterior genial (PG), postocular (PO), preocular (PR), posterior temporals (PT), numbered supralabials ($SL^{1–6}$), supraocular (SO).

further distinguished from *T. nigrescens* by its smaller body size (maximum SVL in males 490 mm vs. 635 mm in *T. nigrescens*), and yellow ventral colouration (grey in *T. nigrescens*). It can be distinguished from *T. mattisoni* by preoculars that are in contact with the nasals (separated by prefrontal contact with second supralabial in *T. mattisoni*) and its venter that is uniformly yellow or yellow with a mid-ventral row of brown spots or short bars (venter grey or yellow with each ventral scale barred anteriorly with darker grey in *T. mattisoni*).

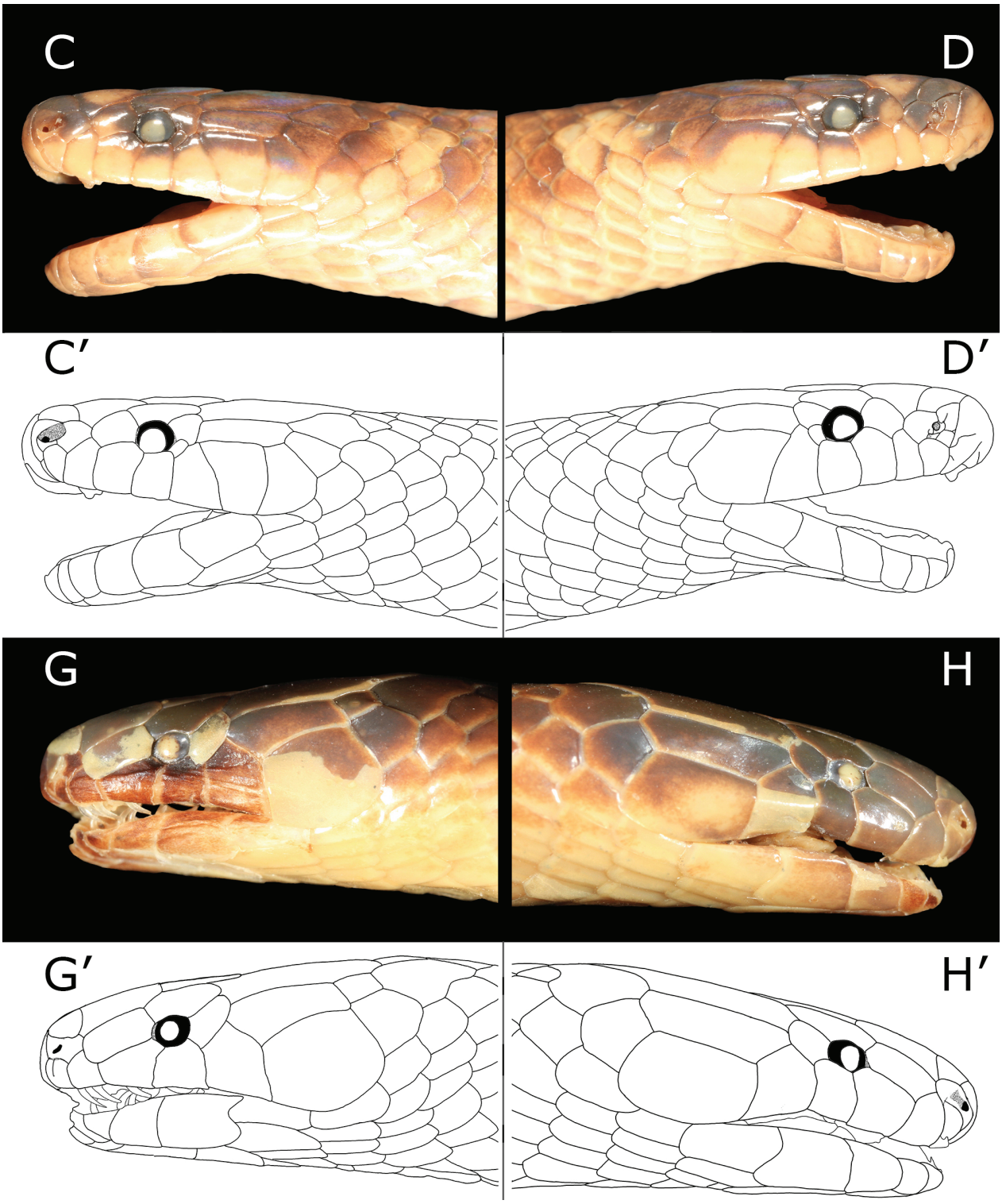

Figure 2 – part two.

Redescription of the holotype. An adult male, with tongue extending from right side of mouth; 490 mm SVL, tail tip missing but TL > 90 mm. Rostral, internasals, and anterior portions of nasals crossed by series of linear impressions, as if the snout had been pressed against a screen during preservation. Rostral wider than tall, notched ventromedially; internasals angulate, semi-triangular, wider than long. Prefrontals distinct from preoculars, approximately square but angled laterally and posteriorly, slightly longer than wide (Fig. 1A, A'), bordered below by preocular and nasal; preoculars elongate, narrower anteriorly, approximately twice as long as tall, bordered anteriorly by nasal, below by second and third supralabials (Fig. 2A, A', B, B'). Nasal divided by large naris, with distinct groove above and below centre of naris on right side (region damaged on left side). Postoculars two, irregularly shaped, upper approximately four times larger than lower, combined they occupy approximately same area as eye. Frontal shield-shaped, not fused with supraoculars, its anterior

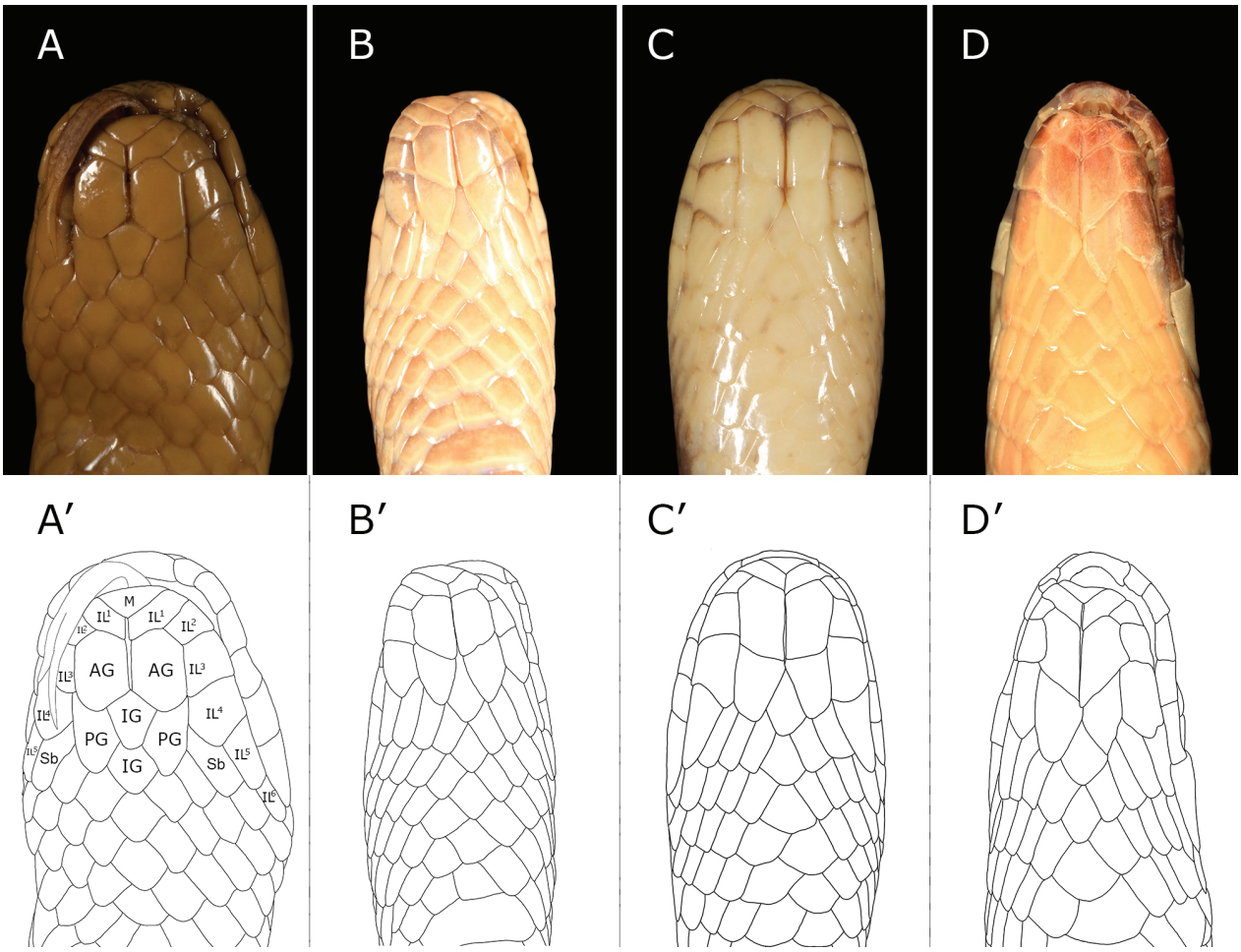

Figure 3. Ventral views of heads of *Toxicocalamus loriae* Group snakes, presented as both photographic and line-drawing illustrations. **A**, **A'** holotype of *T. loriae* (MSNG 29141). **B**, **B'** lectotype of *T. nymani* **comb. nov.** (UUMZ 290/2387). **C**, **C'** lectotype of *T. loennbergii* **comb. nov.** (BMNH 1946.1.18.24). **D**, **D'** holotype of *T. lamingtoni* **comb. nov.** (AMS R9351). Images not to scale. Scale abbreviations: anterior genials (AG), intergenials (IG), numbered infralabials ($IL^{1–6}$), mental (M), posterior genials (PG), sublabials (Sb).

margin may extend slightly forward medially from rest of scale; parietals approximately twice as long as wide. One elongate anterior temporal above fifth and sixth supralabials, separating latter from parietal; three posterior temporals, anteriormost smallest, followed posteriorly by a larger upper temporal and below it a smaller lower temporal, ventralmost temporal abutting posterodorsal margin of sixth supralabial. Supralabials six, third and fourth contacting eye; infralabials six, first three in contact with anterior genial. Mental small, shallow, triangular, wider than long, bordered posteriorly by first supralabials; anterior genials wider than posterior genials, in broad medial contact; posterior genials completely separated by two diamond-shaped intergenials, anterior of which is widest anteriorly, posterior of which is widest centrally; four gulars separate intergenials from first ventral in the midline; an elongate sublabial of a length equal to anterior genial separates posterior genial from fifth infralabial (Fig. 3A, A'). Eye relatively small; pupil round.

Dorsal scales smooth, not notched posteriorly, without apical pits, in 15-15-15 rows; ventrals 189, each approximately four times as wide as long, tail tip incomplete; two scales covering vent; subcaudals 44+, paired.

In preservative (122 years after collection), dorsum uniformly medium brown; venter yellow with a mid-ventral row of brown spots. Supralabials pale yellow ventrally, suffused with brown on upper portions of Supralabials 2–5 and on posterior portion of Supralabial 6; small amount of yellow colouration also present on the lower parts of the nasals. Chin and throat yellow, with small area of brown suffusion on posterior portions of infralabials, genials, intergenials, and gulars. Iris black.

Variation. The anterior margin of the frontal may be almost straight but usually extends slightly forward of the rest of the scale in the midline of the head. The nasals usually have a distinct groove above and below the posterior margin of each naris; a sample from Mt. Obree has either very shallow grooves or lacks them entirely. One (58%) or two (42%) postoculars, both smaller than or occupying approximately the same area as an eye; two (55%) or three (45%) posterior temporals, positioned either as one larger scale above a smaller one, or with the smallest of three scales positioned anterior

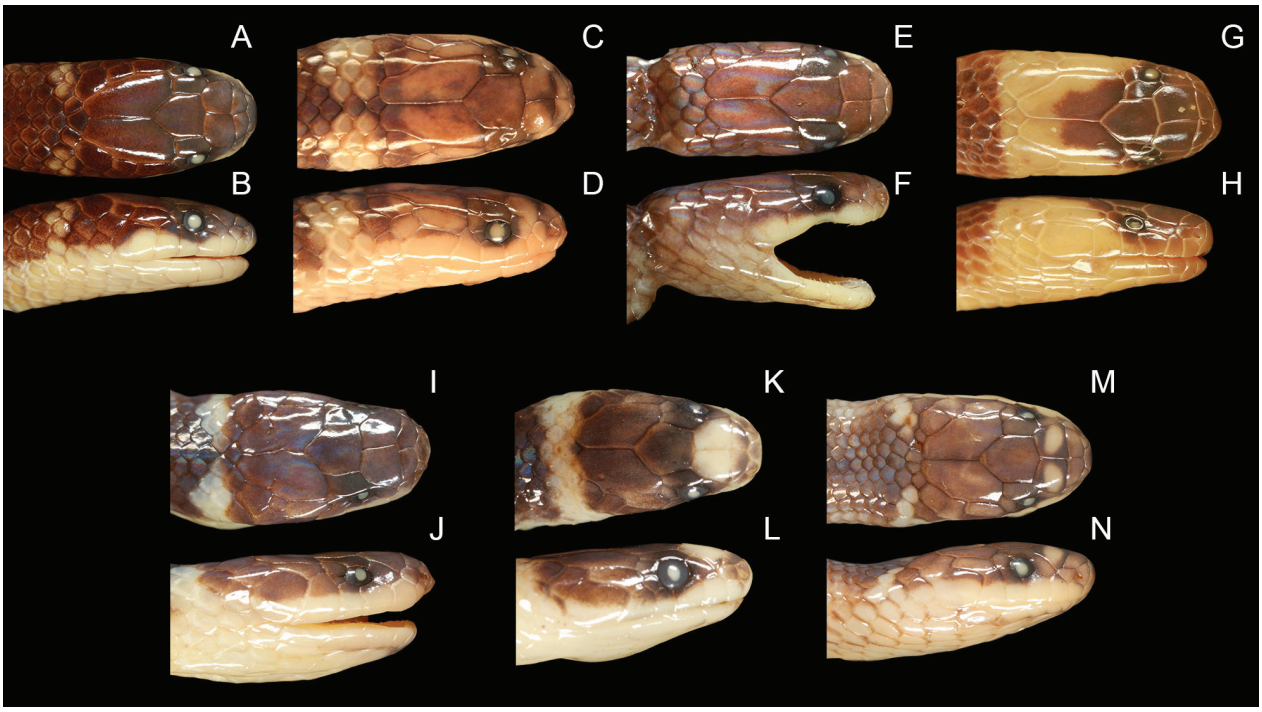

Figure 4. Dorsal and right lateral views of heads of juveniles of *Toxicocalamus loriae* Group snakes. **A**, **B** *T. loriae* (BPBM 10966), Agaun, Milne Bay Province, PNG. **C**, **D** *T. nymani* **comb. nov.**, spotted form (BPBM 5442), Kalolo, Morobe Province, PNG. **E**, **F** *T. nymani*, dark form (BPBM 23699), Wau, Morobe Province, PNG. **G**, **H** *T. lamingtoni* **comb. nov.** (AMS R9352), Mt. Lamington, Oro Province, PNG. **I**, **J** *T. vertebralis* **sp. nov.** (KU 129086), Wau, Morobe Province, PNG. **K**, **L** *T. spilorhynchus* **sp. nov.** (AMNH R-107204), Garaina, Morobe Province, PNG. **M**, **N** *T. atratus* **sp. nov.** (CAS 118958), Mintima, Chimbu Province, PNG.

to the other two, followed posteriorly by a larger upper and a smaller lower temporal; in either configuration, the lowest temporal scale is abutting the posterodorsal margin of the sixth supralabial. Six (97.4%) or seven (2.6%) supralabials, the third and fourth (97.4%) or the third to fifth (2.6%) supralabials contacting eye; five (2.6%) or six (97.4%) infralabials, the first three (22%) or four (78%) in contact with the anterior genial. The anterior genials are wider than the posterior genials and approximately the same length or slightly longer; anterior genials in broad medial contact except in NMW 23783.1 and USNM 195619, where they are separated along most or all their length by an intergenial; posterior genials invariably separated by two diamond-shaped intergenials, whose anterior width is greatest.

Dorsal scales invariably in 15-15-15 rows. Ventrals not sexually dimorphic ($t_{14} = -0.2688$, $p = 0.3958$), 162–197 (184 ± 10) in 15 males, 172–190 (179 ± 7) in four females; subcaudals sexually dimorphic without overlap, 40–50 in males, 28–33 in females; SC_R sexually dimorphic without overlap, 17.1–21.5% (19.4 ± 1.4%) in males, 12.5–16.1% (14.6 ± 1.0%) in females. Tail tipped by a blunt to pointed conical spine. Maximum SVL 490 mm in males and 440 mm in females, adult TL_R = 13.4–19.1% (16.6 ± 1.7%) and 10.8–17.5% (14.1 ± 3.3%), in males and females, respectively. The current dataset, with only two adult females, indicates that there is no statistically significant male-female difference in SVL ($t = 0.3034$, $p = 0.3832$). TL_R in the two juvenile males (PNGM 23158, 24649b) is smaller (12.6% and 13.9%, respectively) than in adults, indicating that in this species, there may be an ontogenetic lengthening of the tail relative to SVL in males. In the four females, this trend appears to be reversed. Even though the sample size is very small, the two subadult females (BPBM 10966, 44892) display TL_R values of 12.0% and 11.8%, respectively, with the adult individuals displaying slightly shorter tails relative to their SVLs.

In preservative, the dorsal colouration is uniformly medium brown (84%) or dark brown (11%) except that one specimen (BPBM 10967) is grey-brown mid-dorsally and laterally and has a dorsolateral stripe of medium brown extending the length of the body. The ventral colouration is uniformly pale yellow (37%), yellow with a mid-ventral row of brown spots (32%), yellow with some mid-ventral brown spots that are not present on each scale (11%), or yellow with a brown bar across the anterior portion of each ventral (16%) and with the brown colour more concentrated mid-ventrally into semi-circular spots; one specimen (NMW 27383.2) is uniformly pale brown ventrally, but this may be a discolouration artifact of an originally yellow venter inasmuch as the specimen was preserved in 1904–1906). Lower portions of the supralabials pale yellow, some or all suffused with brown on their upper portions. Yellow markings variably present on nasals, prefrontals, temporals, parietals, and in the nuchal area, virtually absent in the holotype and the sample from Mt. Obree; pale, invariably incomplete nuchal collar, usually limited to lateral markings but in some specimens with small, mid-dorsal yellow spots. Chin and throat pale yellow, usually with a small amount of brown suffusion on portions of the mental, the infralabials, and sometimes on the genials or the

Figure 5. Portraits in life **A**, **B** and perimortem ventral views **C**, **D** of *Toxicocalamus loriae* BPBM 19503 **A**, **B**, **C** and BPBM 19502 **D** from NW side Mt. Obree, Central Province, PNG.

anterior intergenial. Conical tail spine with a white (95%) or brown or pale brown (5%) tip. Iris black. Juveniles (n = 4) have a brown head with a broken yellow nuchal band and yellow supralabials (Fig. 4A, B). They may or may not have a small yellow spot on each prefrontal.

In life, field notes described BPBM 19502 as: "Dorsum dark slate-gray, changing to gray-brown laterally. No nuchal collar." BPBM 19503 was dark olive brown dorsally and slightly lighter dorsolaterally (Fig. 5A, B), its venter and supralabials were bright lemon yellow, and its subcaudals were bright lemon yellow with grey margins (Fig. 5C). The venter of BPBM 19502 was uniform yellow with a more orange cast than BPBM 19503 and featuring grey mid-ventral spots at the centre of ventrals in the posterior third of body; the subcaudals were lemon yellow, with dark grey margins (Fig. 5D).

Range. Known almost exclusively from the southern versant of the Owen Stanley Range of Papua New Guinea, from Tapini, Central Province, in the north to Mt. Dayman, Milne Bay Province, in the south, at elevations from 620–1530 m (Fig. 6B). A single specimen (BPBM 44892) is known from Isurava, along the Kokoda Track, on the north side of the Owen Stanley Mountains in Oro Province.

Ecological notes. Three individuals from Mt. Obree (elevation ca. 880 m) were obtained from local villagers, who presumably discovered the snakes while gardening. One specimen came from near a stream in primary rainforest (1570 m), and one more was found on the forest floor in primary rainforest on a ridge top (1680 m). At the time of collection, the understory on this ridge was not dense and contained a thick duff layer with a tight root network at the surface; the canopy was 25–30 m above the forest floor, with large emergent araucarians (*Araucaria* sp., Araucariaceae) reaching heights of 50 m. Farther downslope, near the stream, the forest had a much denser understory. These specimens were found active on the forest floor at 12:00 h and in mid-afternoon (~16:00 h), respectively.

Remarks. We retain *Apistocalamus pratti* (BMNH 1946.1.17.53, Fig. 7) in the synonymy of *Toxicocalamus loriae* because the sole specimen shares with the holotype of the latter the two diagnostic features of having two intergenials separating the posterior genials and a yellow venter with a mid-ventral row of brown spots. It differs from the holotype of *T. loriae* in being smaller (330 vs. 490 mm SVL), having slightly fewer ventrals (186 vs. 189) and subcaudals (40 vs. 46), having a single postocular (vs. 2), and having a small, indistinctly defined yellow spot on each prefrontal. The last feature merely reflects variation seen in some of the smaller specimens of *T. loriae.* The other differences are trivial and not diagnostic.

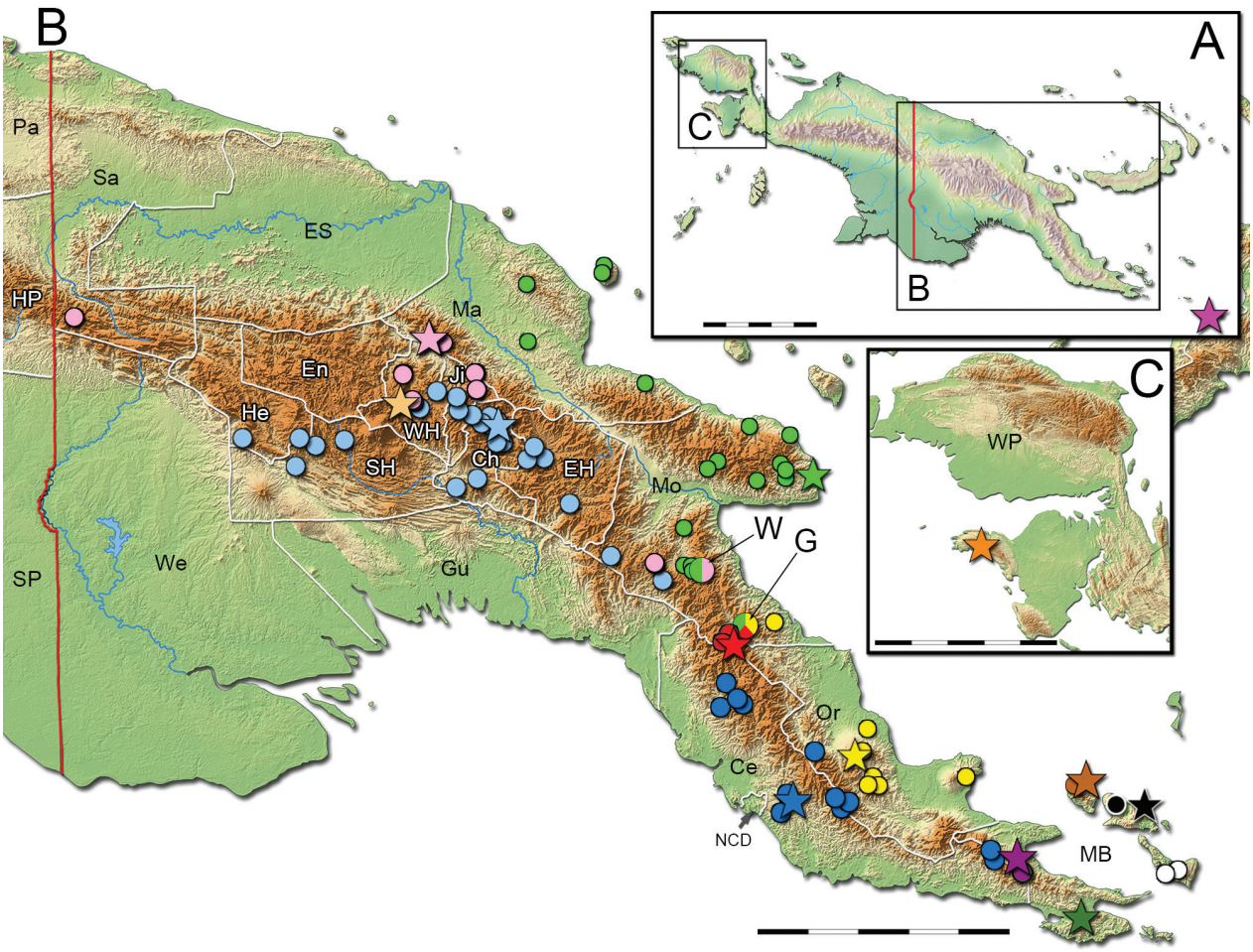

Figure 6. Type localities (stars) and other collection sites (circles) of *Toxicocalamus loriae* Group species. **A** Map of New Guinea and its satellite islands, showing the positions of the inset maps and the type locality of *T. mintoni* (magenta), an endemic of Sudest Island, Milne Bay Province, PNG. Scale = 500 km. **B** Papua New Guinea and adjacent areas of West New Guinea, Indonesia, with white lines demarcating provincial boundaries. Scale = 250 km. **C** West Papua Province, Indonesia (WP), showing the type locality of *T. loennbergii* **comb. nov.** (orange). Other species treated in this report are *T. loriae* (dark blue), *T. lamingtoni* **comb. nov.** (yellow), *T. spilorhynchus* **sp. nov.** (red), *T. nymani* **comb. nov.** (neon green), *T. vertebralis* **sp. nov.** (pink), and *T. atratus* **sp. nov.** (light blue). Additional related species in the *T. loriae* clade are *T. goodenoughensis* (brown), *T. mattisoni* (violet), *T. nigrescens* (black), *T. pachysomus* (dark green), and *T.* "*loriae*" Clade 4 (white). The type locality of the recently described dubious taxon *T. longhagen* (tan) is also indicated. Scale = 250 km. Provinces of PNG are Central (Ce), Chimbu (Ch; also spelled Simbu), Gulf (Gu), Hela (He; created in 2012), Eastern Highlands (EH), East Sepik (ES), Enga (En), Jiwaka (Ji; created in 2012), Madang (Ma), Milne Bay (MB), Morobe (Mo), National Capital District (NCD), Oro (Or; also known as Northern Province); Sandaun (Sa; formerly West Sepik), Southern Highlands (SH), Western (We), and Western Highlands (WH). Provinces of West New Guinea are Highland Papua (HP; created in 2022), Papua (Pa), and South Papua (SP; created in 2022). Sites of sympatry are Wau (W; neon green + pink) with two species and Garaina (G; neon green + red + yellow) with three species.

Toxicocalamus loriae is unique among members of the *T. loriae* Group in having the posterior genials completely separated from contact with each other by two intervening intergenials aligned in the midline of the chin. This character state is among the more distinctive features that diagnose any of the *T. loriae* Group species. Furthermore, this feature occurs in only a small, contiguous portion of the entire geographical range occupied by the group. In our view, it provides compelling evidence for the unity of this species. However, we note that the sample size for this species is small (n = 19) and almost one-third of those specimens come from a single area (on the NW slope of Mt. Obree); all other localities are represented by only 1–3 specimens. Consequently, it is difficult to assess the importance of some of the morphological and geographic variation seen in this sample. We here consider four points in question that deserve further assessment once sufficiently large specimen series become available.

Ventral colour pattern. This character is variable. Three specimens (AMNH R-59067, BMNH 1935.5.10.174, PNGM 23158) from Mafulu and from near Fane (9 km apart) show an expansion of brown pigment on each ventral that is not seen in any other specimens. In particular, the anterior edge of each ventral is adorned with a narrow bar of brown. Other specimens are either uniformly yellow ventrally (37%) or yellow with a row or scattering of brown dots mid-ventrally (42%); one

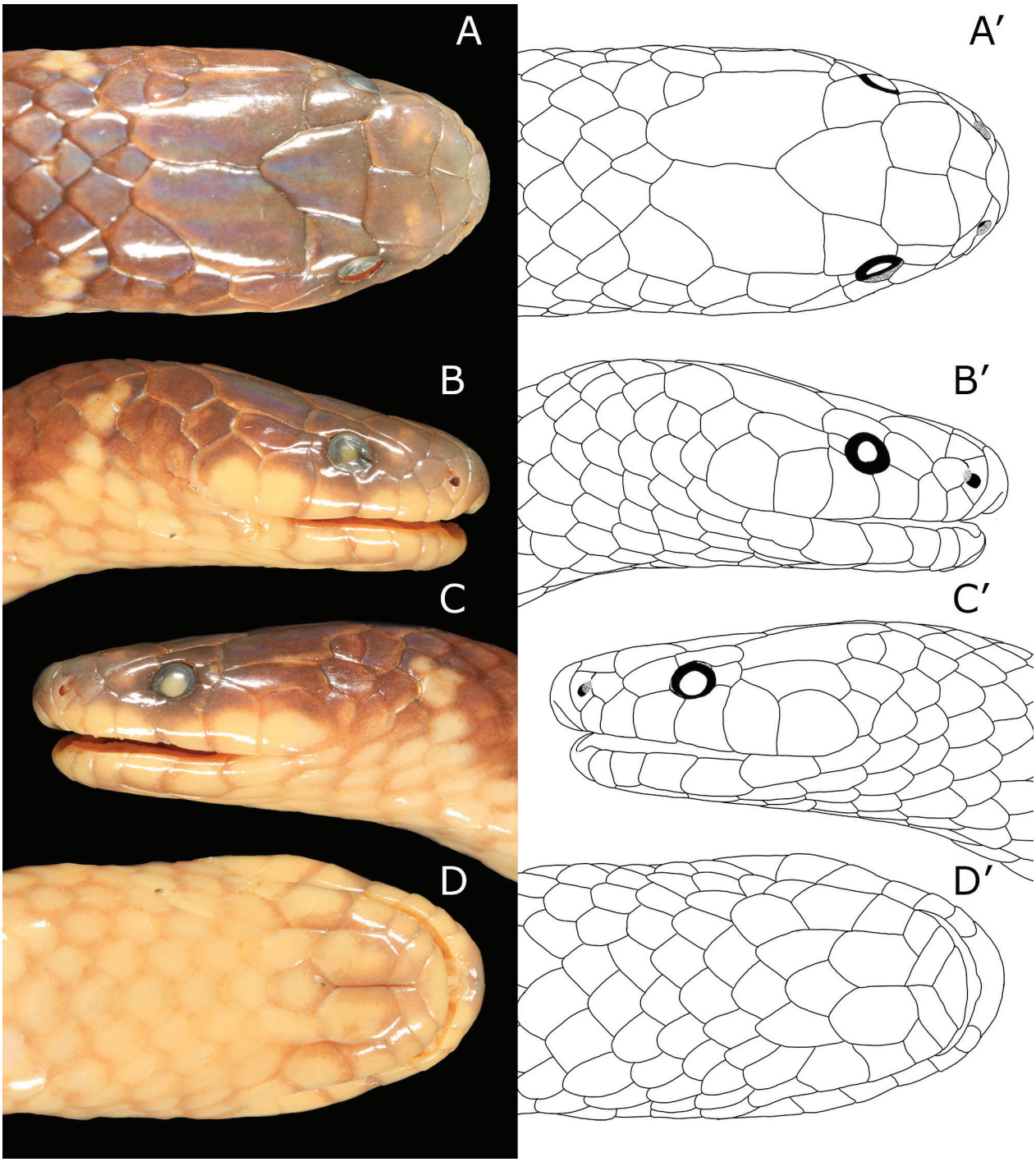

Figure 7. Head of holotype of *Apistocalamus pratti* (BMNH 1946.1.17.53) from Dinawa, Central Province, PNG, in both photographic and line-drawing illustrations. **A**, **A'** dorsal, **B**, **B'** right lateral, **C**, **C'** left lateral, and **D**, **D'** ventral views.

specimen (NMW 27383.2) is uniformly pale brown ventrally, though we suspect this may be an artifact of preservation or storage. Of the three specimens from Mafulu and Fane, two still retain the central row of brown dots but the brown colouration extends laterally to these dots. Assuming these specimens are true *T. loriae*, this extends the range of colour-pattern variation seen in the species. We believe these are true *T. loriae*, both because they have the characteristic medial separation of the posterior genials by two intergenials as well as the fact that the medial brown dots are still evident in two of these three specimens. Furthermore, the sample of six specimens from Mt. Obree also makes clear that the degree of brown markings on the venter is variable within this species: one of these specimens has a yellow venter with a complete row of mid-ventral brown spots, two have yellow venters with some mid-ventral brown spotting, and three have uniformly yellow venters. Variation in degree of brown ventral spotting does not appear to be ontogenetic since the largest adults can be either uniformly yellow or have a complete series of brown spots.

Ventral counts. Male ventral counts in our sample cover an unusually wide range (162–197) and might be

thought to possibly reflect the presence of more than one species in our sample. However, these values seem to vary geographically, with two of the three highest counts (193, 194, 197) seen in the two northernmost samples (Fane, Mafulu) and the two lowest counts in the southernmost samples from Agaun, Milne Bay Province (162) and nearby Mt. Obree (169). Furthermore, the six males from Mt. Obree, Central Province, themselves show a range of variation (169–189) that encompasses 55% of the total variation seen in the entire sample of *T. loriae*, suggesting that considerable variation in male ventral counts does indeed characterize this species and may not in itself be evidence of multiple species. This interpretation could possibly change when larger sample sizes become available, but the overlap in counts seen in the Agaun and Mt. Obree samples, coupled with the broad variation seen in the latter, makes this seem unlikely.

Geography. The large majority of specimens was collected on the southern versant of the central Owen Stanley Range. However, one specimen (BPBM 44892) came from the northern versant of these mountains in Oro Province. This is an unexpected locality for what appears to be a southern-versant species, for two reasons. Firstly, two other species of the *T. loriae* Group also occur in this general area of Oro Province (see below), and one of those is restricted to the northern versant. However, current evidence suggests that these species are segregated elevationally in this area, with the sole *T. loriae* specimen having been collected at an elevation of 1260 m, the second species occurring in hill forest from 100–940 m, and the third appearing to be a high-elevation form found at 1660–1850 m. Secondly, even if these species all segregate along elevational gradients, it remains uncertain how *T. loriae* would have crossed the formidable barrier presented by the Owen Stanley Range (elevation > 2000 m in this region). It could possibly have spread around these mountains from the south, through the low-elevation Musa Divide. If that is true, then additional surveys of this poorly explored region should reveal a more extensive presence of *T. loriae* at middle elevations of the Owen Stanley Range in Oro Province.

Provenance. Two specimens (NMW 27383.1–2) are of ambiguous provenance. These were sent to Vienna by the anthropologist and explorer Rudolf Pöch (1870–1921), who worked in German New Guinea from 1904–06 (Pöch 1907). The locality for these specimens ("Astrolabe Gebirge") can be interpreted as referring to the mountains visible from Astrolabe Bay (potentially either the Finisterre or Adelbert Mts.) in Madang Province, or to the Astrolabe Range south of the Owen Stanley Range in Central Province. The former interpretation is consistent with the fact that most of Pöch's work was done in German New Guinea, including the area now contained within Madang Province. Against this is the fact that all *Toxicocalamus* in the *T. loriae* Group otherwise collected from this region are not *T. loriae* and do not match the NMW specimens. Contrarily, if the locality is interpreted to refer to the Astrolabe Range in Central Province, this would make geographical and morphological sense, because these specimens would then be from within 25 km of the type locality of *T. loriae* and are morphologically unremarkable *T. loriae* specimens. Pöch is known to have visited nearby Port Moresby for a few days before his departure from New Guinea, and it is possible that the specimens were on hand and given to him there by his hosts. In any event, these two specimens are morphologically and geographically consistent with their provenance being from the Astrolabe Range, Central Province. If they truly did come from somewhere in Madang Province, then they are morphologically unique for that region and would suggest that either *T. loriae* has a much wider range than currently evident (> 350 km from the nearest known locality for the species) or that a morphologically similar species occurs in the Madang region that has not been collected since Pöch's time. Some specimens were indeed sent to Vienna from Port Moresby in the time frame under consideration, but there is no further information in the records of the Vienna Museum to determine what the shipment may have included. We tentatively adopt the position that these specimens came from Central Province, and we have included them in the diagnosis of *T. loriae*.

Toxicocalamus nymani (Lönnberg, 1900) comb. nov.

Figs 1B, B', 2C, C', D, D', 3B, B', 4C, D

Pseudapistocalamus Nymani Lönnberg, 1900: 578.
Pseudapisthocalamus nymani – Boulenger, 1908: 249.
Pseudapistocalamus nymani – de Rooij, 1917: 263.
Pseudapistocalamus nymanni – Klemmer, 1963: 328.
Apistocalamus pratti (part) – McDowell, 1967: 537.
Toxicocalamus (*Apistocalamus*) *loriae* (part) – McDowell, 1969: 456.

Types and collection. The Swedish zoologist Einar Lönnberg (1865–1942) described this species on the basis of three specimens from Sattelberg, German New Guinea, at the eastern end of the Huon Peninsula (now in Morobe Province, PNG). These were collected by the Swedish botanist Erik Nyman (1866–1900), who visited the area from June–November 1899 (Nordstedt 1899, 1900; Svedmark 1900). Whereas Lönnberg (1900) did not designate a holotype, he provided a little more information for the largest specimen, a female with approximate measurements of SVL = 445 mm and TL = 47 mm, and which contained eggs of about 13 mm length. De Rooij (1917) examined what she called the "type-specimen [...] from the Upsala Museum" and confirmed the size of the eggs. The measurements of SVL = 398 mm and TL = 47 mm she provided for the species just before her discussion of the "type-specimen" do not correlate with the Uppsala specimen and may refer to one of the

other specimens from "New Guinea" she examined. We have examined the sole specimen of this series remaining at the Uppsala Museum, an untagged specimen that was loaned to FK as UUZM 290 in 2003 and to MOS as UUZM 2387 in 2013. Our measurements of this female specimen are SVL = 435 mm and TL = 42 mm, which is very close to the size reported by Lönnberg for his largest specimen, given more than a century of possible shrinkage in ethanol. Of the other two specimens referred to in the original description, one is now deposited as BMNH 1946.1.17.57 (originally catalogued as BMNH 1900.9.21.6) and is noted in their catalogue and on their jar label to be "one of the types." It is also a female, and its measurements are SVL = 325 mm and TL = 43 mm, so it is clearly too small to be the large specimen noted by Lönnberg (1900). We are unable to locate the third specimen or any other museum specimen from Sattelberg, so we presume the third syntype is lost. As the larger specimen of the two extant syntypes and as the one with nearly the same measurements as those provided in the original description, we designate UUZM 290/2387 as the lectotype of *Pseudapistocalamus Nymani* Lönnberg, 1900. This renders the second remaining specimen from the type series (BMNH 1946.1.17.57) a paralectotype.

Etymology. The species was named for Erik Nyman, the collector of the type series. It also serves as a tribute to a remarkable scientist, who died in 1900 on the journey home to Europe. The description was published in English.

Diagnosis. A modestly sized member of the *T. loriae* Group (maximum SVL in males 422 mm, in females 540 mm) with the following unique combination of characters: two scales covering vent; three infralabials contacting anterior genial; posterior genials entirely separated (45%) by a single intergenial or in anterior (53%) or entire (2%) contact with each other; intergenial usually widest posteriorly or centrally. Preocular approximately as long as wide and never twice as long as wide, usually contacting nasal (94%), not contacting internasal; one (4%) or two (96%) postoculars; one (1%), two (69%), three (27%), four (1%), or five (1%) posterior temporals; 178–198 ventrals in 18 males, 191–210 in 22 females, sexually dimorphic with overlap ($t_{37} = 4.9581$, $p < 0.00001$); 39–48 subcaudals in males, 26–37 in females, sexually dimorphic without overlap; SC_R 17.5–20.7% in males, 11.6–15.8% in females, sexually dimorphic without overlap; yellow nuchal collar and yellow markings on prefrontals absent (48%), small or vaguely developed (7%), or present (45%); tail spine paler than remainder of tail; venter uniformly dark brown or dark brown with the posterior of each ventral paler brown or yellowish brown, giving a banded appearance (reported as "blackish brown, edged with light grey" within one year of preservation; Lönnberg 1900).

Comparisons with other species. *Toxicocalamus nymani* is distinguished from *T. loriae* in having a single intergenial (two in *T. loriae*) that is widest posteriorly or centrally (widest anteriorly in *T. loriae*), by its short, squarish preocular (elongate, more than twice as long as high, in *T. loriae*), and by its dark brown or black venter (yellow with or without mid-ventral series of brown spots in *T. loriae*); from *T. nigrescens* by its smaller size (maximum SVL = 540 mm vs. 635 mm in *T. nigrescens*), short preocular (elongate, more than three times as long as high, in *T. nigrescens*), and in having two postoculars (one in *T. nigrescens*) and a dark brown or black venter (grey in *T. nigrescens*); and from *T. mattisoni* in having the prefrontal usually (93%) excluded from contacting the second supralabial (prefrontal and second supralabial in contact in *T. mattisoni*), short preocular (elongate, more than twice as long as high, in *T. mattisoni*), and in having two postoculars (one in *T. mattisoni*) and a dark brown or black venter (yellow or pale grey with grey bands across each ventral in *T. mattisoni*).

Description of the lectotype. An adult female, 435 mm SVL + 42 mm TL = 477 mm TTL. Rostral wider than tall, notched ventromedially; internasals angulate, semi-triangular, wider than long. Prefrontals distinct from preoculars, approximately square but angled posteriorly, slightly longer than wide (Fig. 1B, B'), bordered below by preocular and nasal; preoculars angulate but approximately as high as long, bordered anteriorly by nasal, below by second and third supralabials (Fig. 2C, C', D, D'). Nasals divided by large nares, with two grooves below and partial groove above naris on right, no grooves on left, both nasals damaged. Postoculars two, irregularly pentagonal in shape, upper larger, slightly smaller than eye. Frontal shield-shaped, not fused with supraoculars, anterior margin extending slightly anterior to remainder of scale medially, lateral margins curved posteriorly; parietals approximately twice as long as wide. One elongate anterior temporal above fifth and sixth supralabials, separating latter from parietal; two posterior temporals, upper twice size of lower, with lower abutting posterodorsal margin of sixth supralabial. Supralabials six on right, seven on left due to division of sixth, third and fourth contacting eye; infralabials six, first three in contact with anterior genial. Mental small, shallow, triangular, wider than long, bordered posteriorly by first supralabials; anterior genials slightly larger than posterior genials but of approximately same length, in medial contact along their entire length; posterior genials completely separated by single elongate intergenial that is widest posteriorly; five gulars separate intergenials from first ventral in the midline; first sublabial separates posterior genial from fifth infralabial (Fig. 3B, B'). Eye relatively small; pupil round.

Dorsal scales smooth, not notched posteriorly, without apical pits, in 15-15-15 rows; ventrals 202, each approximately four times as wide as long; two scales covering vent; subcaudals 28, paired. Tail tipped by a pointed conical spine.

In preservative (114 years after collection), dorsum dark brown dorsally, paler laterally, with brown centre of each scale becoming paler yellow brown at posterior edges. Each ventral scale, including subcaudals, dark

brown with paler yellow brown along posterior edges, imparting an overall impression of a dark venter banded with dark brown. Supralabials and rostral largely yellow, all with dark-brown upper margins. Head dark brown with large yellow blotch on each prefrontal and small yellow blotch in anterior part of each preocular. Incomplete yellow nuchal collar, interrupted mid-dorsally by three rows of brown dorsal scales. Chin and throat pale yellow, suffused with brown on mental and anterior portions of anterior gulars and first five infralabials. Tail spine brown, paler than remainder of dorsum. Iris black.

Variation. Preoculars are not in contact with the nasals in three specimens from Madang Province (AMS R25304, R25752, IRSNB 733678), in which they are separated by contact between prefrontal and second supralabial; in contact with internasals only in MCZ R-76627. Two postoculars, except one on both sides of BPBM 3397 and one on the left side of the paralectotype. Posterior temporals two (in 69% of sides), one (1%), three (27%), four (1%), or five (1%). Six supralabials, except seven on left sides of lectotype and AMS R25608, seven on both sides of BPBM 17173, and five on right side of BPBM 31257 and left side of PNGM 24716; third and fourth supralabials invariably contacting eye. Six infralabials, except five on left side of BPBM 17451 and seven on right side of BPBM 30638. Posterior genials partially (53%) or entirely (45%) separated by single intergenial, except in BPBM 30638, which lacks an intergenial and has irregular scales behind the genials. Intergenials usually widest posteriorly (68%) but may be widest centrally (26%) or occasionally anteriorly (5%).

Dorsal scales invariably in 15-15-15 rows. Ventrals 178–198 (187 ± 7) in 18 males, 191–210 (198 ± 5) in 21 females; subcaudals 39–48 (44 ± 2) in 18 males, 26–37 (30 ± 3) in 20 females; SC_R 17.5–20.7% (19.1 ± 0.9%) in males, 11.6–15.8% (13.1 ± 1.1%) in females. Tail tipped by a blunt to pointed conical spine. Maximum SVL in males 422 mm, 540 mm in females, not sexually dimorphic ($t_{31} = -1.4431$, $p = 0.0795$); TL_R sexually dimorphic without overlap, in males 13.3–17.9% (16.1 ± 1.3%), in females 9.2–12.9% (10.5 ± 1.0%).

Variation in head colouration is largely geographical, with yellow-spotted heads largely confined to the Huon Peninsula; the specimen from Garaina (MCZ R-152432) also has some vague pale markings on the head, which are difficult to characterize. All specimens from other areas have uniformly dark heads without yellow markings, as do six specimens from the Huon Peninsula. The Huon populations with spotted heads have a large yellow blotch on each prefrontal, a smaller one on the preocular, and a partial or complete yellow nuchal collar; they may also have yellow marks on the internasals, rostral, posterior portion of the nasal, and anterolateral portion of the parietals. Juveniles of the spotted morph (e.g., BPBM 5442, SVL = 184 mm) also have yellow colouration widely distributed on the parietals, temporals, and frontals (Fig. 4C, D). These seem to darken and disappear with age in larger animals. In contrast, both adults and the smallest specimens of the dark-headed phenotype (BPBM 23669, SVL = 185 mm; PNGM 24716, SVL = 197 mm) have uniformly dark heads (Fig. 4E, F), suggesting there is no ontogenetic variation in that morph.

Range. Known from the Huon Peninsula, Morobe Province, to Karkar Island, Madang Province, in northeastern PNG to the general vicinity of Wau and Garaina in the northern Owen Stanley Range at elevations from 120–1470 m (Fig. 6B).

Ecological notes. We have no particular ecological information for this species but assume its habits are similar to the other species in this complex based on similar morphology and ecological conservatism in the genus.

Remarks. Subsequent to the original description of *T. nymani*, the German anthropologist and scientific photographer Richard Gustav Neuhauss (1855–1915) collected an additional six specimens at Lialun – 50 km NNW of Sattelberg along the coast – that were shipped to the ZMB as part of three consignments between July 1909 and August 1910. Only the first shipment was large enough to contain these six specimens, so they must have been collected during 1909. These specimens were briefly listed by Vogt (1911), who provided locality data, and then examined by Sternfeld (1913), who provided ventral and subcaudal counts for each but erroneously referred to them as originating from Sattelberg, whence most of Neuhauss's specimens came (Vogt 1911). The first person to examine these specimens was certainly Vogt, who would have had the benefit of field labels in the collection jars sent by Neuhauss. It would appear that Vogt dissociated jars and labels while preparing his manuscript, and we conclude that Vogt examined Neuhauss's six specimens with the benefit of exact locality data but leaving Sternfeld to erroneously infer that they came from Neuhauss's main reptile collecting site. We consider all six specimens to have originated at Lialun.

These six Lialun specimens are now catalogued as ZMB 24343–44, 78770–71, and MCZ R-76627–28. In the Berlin collection, multiple specimens with the same data were chronologically assigned to numbered lots up until the Second World War. Beginning in 1991, the museum started to divide these early lots and inventory the included specimens individually. As part of this process, one specimen retained the original number and additional specimens were given a number current for that time. Thus, ZMB 24343 was originally a lot with two specimens, one of which retained the original number and the second of which was re-catalogued in April 2013 as ZMB 78770; hence, collection data for ZMB 24343 and ZMB 78770 are identical. Likewise, ZMB 24344 was a lot of two and the second specimen became ZMB 78771. Lastly, there is a note hand-written by Günther Peters from 1963 in the Berlin specimen catalogue explaining that two additional specimens (it is not clear whether both came from lot ZMB 24343, both from lot ZMB 24344, or one came from each) were exchanged in August 1963 with Ernest Williams at

the MCZ. These two specimens were catalogued at the MCZ on 24 June 1964 as *Pseudapistocalamus nymani* (MCZ R-76627–28). The information for these two specimens in the MCZ catalogue is erroneous, however, and the locality is noted as "New Guinea: Neuhauss" with no collector given. McDowell (1969) listed these same specimens as coming from Sattelberg. Both are incorrect listings. It is clear that "Neuhauss" in this case is not a locality but refers to the collector of these specimens, and the locality is Lialun, now Morobe Province, PNG.

This species is unusual within the *T. loriae* Group for the presence of a distinct head colour-pattern dimorphism, with the heads of most adults from the Huon Peninsula boldly spotted with yellow in both juveniles and adults, whereas a few specimens from the Huon Peninsula and all specimens from other localities have uniformly dark heads as adults and only sparse spotting in some juveniles. Given our observations in other *T. loriae* Group species, we would expect these variants to represent different species, but we have found no other characters that support such a conclusion. Both morphotypes appear sympatric in at least one location (Masba Creek, Morobe Province), and although the microhabitat of these collection sites differed by 60 m in elevation, we do not consider this to be meaningful. Nonetheless, our hypothesis of conspecificity should be tested with molecular and updated morphological data when additional specimens of both forms become available.

Toxicocalamus loennbergii (Boulenger, 1908) comb. nov.

Figs 1C, C', 2E, E', F, F', 3C, C'

Apisthocalamus loennbergii Boulenger, 1908: 248.
Apistocalamus loennbergi – Sternfeld, 1913: 387.
Apistocalamus lönnbergi – de Rooij, 1917: 260.
Apistocalamus loriae (part) – McDowell, 1967: 537.
Toxicocalamus (*Apistocalamus*) *loriae* (part) – McDowell, 1969: 456.

Types and collection. As reported by Boulenger (1908) in the original description, four specimens were collected by the British naturalist and explorer Antwerp Edgar Pratt (1852–1924) during his sojourns in New Guinea with his collector sons Charles Henry Pratt (1886–1936) and Felix Thomas Biet Pratt (1891–1955). Pratt spent the months of May–June 1905 and December 1907–January 1908 near Fakfak on the Onin Peninsula (formerly Fakfak Peninsula), an extension of the Bomberai Peninsula in Dutch New Guinea (Papua Insects Foundation 2015). The specimens on which Boulenger based his description (four females, BMNH 1946.1.18.24–26, MCZ R-76634) were originally accessioned as BMNH 1908.6.30.7–10 with one of them (BMNH 1908.6.30.10) exchanged with the MCZ in 1963. These would have been collected on Pratt's earlier voyage, given that specimens collected in January 1908 could not have reached Boulenger in time for a March 1908 publication date, because delivery of passengers (or specimens) from New Guinea to London on the prevalent early 20th Century steamship route via Australia and the Suez Canal would have taken at least 75 days (Phillips 2002). Thus, we presume the type material of *T. loennbergii* was collected in May or June 1905.

Because Boulenger (1908) did not designate a holotype, McDowell (1969: 456) designated BMNH 1946.1.18.24 as the "holotype" of *A. loennbergii*. This designation is invalid because a holotype cannot be designated from among syntypes after the original description. We nevertheless follow McDowell and designate BMNH 1946.1.18.24 as the lectotype of *A. loennbergii*. This is the largest specimen (SVL = 565 mm). The remaining syntypes (BMNH 1946.1.18.25–26 and MCZ R-76634) become paralectotypes.

Etymology. Named by Boulenger (1908) for Professor Einar Lönnberg (1865–1942), the Swedish zoologist who described *Pseudapistocalamus nymani*. The description was published in English.

Diagnosis. A modestly sized member of the *T. loriae* Group (maximum SVL 565 mm, only females known) with the following unique combination of characters: two scales covering vent; four infralabials contacting anterior genial; a single intergenial separating posterior genials, widest posteriorly. Preocular elongate, approximately twice as long as wide, contacting nasal (62%) or not (38%), not contacting internasal; relatively short snout (SNL/SNW $\bar{x}$ = 0.95, range = 0.93–0.99); relatively small eye (EY/SNL $\bar{x}$ = 0.16, range = 0.15–0.18); one postocular (fused to supraocular on one side of one specimen); three posterior temporals; 214–220 ventrals in four females; 23–32 subcaudals; SC_R 9.7–12.7%; dark vertebral stripe; large pale blotch on parietal; pale markings on prefrontals absent (50%), small or vaguely developed (25%), or well developed (25%), best developed in the smallest specimen; tail spine white, paler than remainder of tail; and venter uniformly yellow.

Comparisons with other species. *Toxicocalamus loennbergii* can be distinguished from all other members of the *T. loriae* Group except some *T. loriae* and juvenile *T. nymani* by its uniformly yellow venter. It can be distinguished from *T. loriae* in having only a single intergenial (two in *T. loriae*) and from juvenile *T. nymani* by having four infralabials in contact with the anterior genial (three in 87.5% of *T. nymani*), a single postocular (usually two in *T. nymani*), and a dark vertebral stripe (absent in *T. nymani*). It can further be distinguished from *T. nigrescens* by its greater number of ventrals (214–220 vs. 184–193 in female *T. nigrescens*), and dark vertebral stripe (absent in *T. nigrescens*); and from *T. mattisoni* in having the preocular contact the nasal (separated by prefrontal contact with the second supralabial in *T. mattisoni*), its greater number of ventrals (214–220 vs. 170–181 in female *T. mattisoni*), and dark vertebral stripe (absent in *T. mattisoni*).

Description of the lectotype. An adult female, 565 mm SVL + 55 mm TL = 620 mm TTL. Rostral wider than tall, notched ventromedially; internasals angulate, semi-triangular, wider than long. Prefrontals distinct from preoculars, approximately square, rounded posterolaterally, bordered below by preocular and nasal, in point contact with second supralabial on right side; preoculars elongate, narrower anteriorly, approximately twice as long as tall (Fig. 1C, C'), bordered anteriorly by nasal, below by second and third supralabials (Fig. 2E, E', F, F'). Nasal divided by large naris, without grooves above or below naris. Postoculars one on left, fused to supraocular on right; irregularly hexagonal in shape, longer than tall, occupying approximately same area as eye. Frontal shield-shaped, lateral margins angled obliquely, not fused with supraoculars, anterior margin extending slightly anterior to remainder of scale medially; parietals approximately twice as long as wide; one elongate anterior temporal above fifth and sixth supralabials, separating sixth from parietal; three posterior temporals, lowest abutting posterodorsal margin of sixth supralabial. Supralabials six, third and fourth contacting eye; infralabials six, first four in contact with anterior genial. Mental small, shallow, triangular, wider than long, bordered posteriorly by first supralabials; anterior genials slightly larger than posterior genials, in medial contact along their entire length; posterior genials in medial contact for first 20% of their length; intergenial single, diamond-shaped, widest posteriorly; five gulars separate intergenials from first ventral in the midline; first sublabial separates posterior genial from fifth infralabial on right but not on left (Fig. 3C, C'). Eye relatively small; pupil round.

Dorsal scales smooth, not notched posteriorly, without apical pits, in 15-15-15 rows; Ventrals 214, each approximately four times wider than long; two scales covering vent; subcaudals 23, paired. Tail tipped by a blunt conical spine.

In preservative (108 years after collection), dorsum reddish brown, darker mid-dorsally, with darker-brown vertebral stripe one scale wide; each dorsal scale with darker brown edges, imparting a reticulated appearance to dorsum, especially laterally. Venter uniformly pale yellow; subcaudals lightly edged in brown at their medial junctures. Supralabials pale yellow ventrally, suffused with brown dorsally. Top of head with vague traces of yellow blotches on parietals and anterior temporals; no pale nuchal collar. Chin and throat pale yellow, with small amount of brown suffusion on mental, sutures between infralabials, and anterior suture of anterior genial. Tail spine brown above and white below. Iris black.

Variation. All specimens are female. Prefrontals are bordered below by the preocular and the nasal, but they are in point contact with the second supralabial on one side in two specimens; preoculars are bordered below by the second and third supralabials, except by only the third supralabial on the right side of BMNH 1946.1.18.25. One postocular, except when it is fused to the supraocular on the right side of BMNH 1946.1.18.24, smaller than or occupying approximately same area as the eye. Six supralabials, except seven on the right side of MCZ R-76634; third and fourth supralabials contact the eye, except when Supralabial 2 also contacts it, as on the right side of MCZ R-76634. The posterior genials are entirely separated by a single elongate intergenial in MCZ R-76634, in point contact anteriorly in BMNH 1946.1.18.26, and in medial contact for the first 20–35% of length in the remaining two specimens.

Dorsal scales invariably in 15-15-15 rows. Ventrals 214–220 (216 ± 2); subcaudals 23–32 (28 ± 3); SC_R 9.7–12.7% (11.3 ± 1.1%). Tail tipped by a blunt to pointed conical spine. Maximum SVL 565 mm, TL_R 8.9–11.2% (10.2 ± 0.9%).

In preservative, all specimens are coloured as the holotype dorsally and ventrally. Subcaudals are lightly edged in brown at their medial junctures but dusted with brown posteriorly in MCZ R-76634. Supralabials are pale yellow ventrally, variably suffused with brown on dorsal portions of some or all supralabials (absent on second supralabial in two specimens). In the smallest specimen (BMNH 1946.1.18.25, SVL = 373 mm), yellow markings occupy a band across the prefrontals and the anterior portion of the frontal, there is a large yellow blotch on each parietal and a complete yellow collar. In BMNH 1946.1.18.26, there is a yellow blotch on each anterior temporal in addition to these other markings. In larger specimens, these markings become suffused with brown and may disappear, with the markings on the prefrontals disappearing first. Conical tail spine white or brown above and white below (BMNH 1946.1.18.24).

Range. Known only from the type locality, north of Fakfak town on the Onin Peninsula, West Papua Province, Indonesia, at an elevation of 520 m (Fig. 6C).

Toxicocalamus lamingtoni (Kinghorn, 1928) comb. nov.

Figs 1D, D', 2G, G', H, H', 3D, D', 4G, H

Apisthocalamus lamingtoni Kinghorn, 1928: 290.
Apistocalamus lamingtoni – Roux, 1934: 79.
Toxicocalamus (*Apistocalamus*) *loriae* (part) – McDowell, 1969: 456.
Toxicocalamus loriae X *T. stanleyanus* (part) – McDowell, 1969: 485.
Toxicocalamus loriae Clade 3 – Strickland et al., 2016: 671.

Types and collection. The specimens on which Kinghorn (1928) based his description of *T. lamingtoni* (an adult male, AMS R9351; two juveniles, AMS R9352 and R61072) were obtained by C. Terence McNamara (born ca. 1900), the Resident Magistrate (later referred to as District Commissioner) of Mount Lamington District, Northern Division, Papua (Troughton 1946), during August and September 1927. Of these, Kinghorn designated the male as the holotype and commented on the two juveniles, which we therefore consider to be paratypes. Our examination shows that both juveniles are immature females. The collector appears to have sent one

additional specimen from the same locality in the same time frame (AMS R9851), but this has no type status.

Etymology. Kinghorn (1928: 291) stated that the specimens on which his description was based were all collected in "Mount Lamington district, Northern Division, Papua." It is possible that the author chose the name of the district, which itself takes its name from Mt. Lamington (8.94°S, 148.16°E, elevation 1680 m), a stratovolcano in Oro Province, Papua New Guinea, as the name for the new species. However, this would ordinarily be indicated by the adjectival suffix *-ensis*, which Kinghorn did not use. He may have been unaware of proper Latinized name formation, as he incorrectly named other species for localities using the genitive case (*-i* or *-ae*). Regardless, the person after whom these localities were named is Lord Lamington, Charles Wallace Alexander Napier Cochrane-Baillie (1860–1940), was the 2nd Baron Lamington and a British colonial administrator, who served as the 8th Governor of Queensland (1896–1901) and the 14th Governor of Bombay (1903–1907). The description was published in English.

Diagnosis. A modestly sized member of the *T. loriae* Group (male SVL up to 428 mm, female SVL up to 500 mm), with the following unique combination of characters: cloacal plate single; a single intergenial separating posterior genials, widest posteriorly. Preocular elongate, approximately twice as long as high, contacting nasal but not internasal; one postocular; two (92%) or three (8%) posterior temporals; 160–178 ventrals in nine males, 186–195 in nine females, sexually dimorphic without overlap; 41–53 subcaudals in males, 26–34 in females, sexually dimorphic without overlap; SC_R 19.3–23.0% in males, 12.2–14.9% in females, sexually dimorphic without overlap; females with very short tails relative to males (TL_R sexually dimorphic without overlap, 16.7–20.8% in adult males, 9.0–11.6% in adult females); pale markings on prefrontals absent, even in juveniles; tail spine brown, same colour as remainder of tail; venter uniformly yellow; juveniles with brown anterior supralabials; and head pattern in juveniles typically consisting of a complete, broad, pale band across the nape, parietals, temporals, and last two supralabials, with remainder of head anterior to that lacking pale markings.

Comparisons with other species. *Toxicocalamus lamingtoni* is unique within the *T. loriae* Group and distinguished from all other members of the genus except *T. buergersi*, *T. cratermontanus*, and *T. stanleyanus* in having a single cloacal plate; from these last three species *T. lamingtoni* is easily distinguished by having the preocular and prefrontal distinct (vs. fused). It is further distinguished from *T. loriae* in having only a single intergenial (vs. two in *T. loriae*), a dark-brown (vs. white in *T. loriae*) tail spine, brown anterior supralabials in juveniles (vs. yellow in *T. loriae*), and the broad yellow nuchal collar in juveniles (vs. narrow and incomplete in *T. loriae*); from *T. nymani* by its uniformly yellow venter in adults (vs. black or very dark brown in adult *T. nymani*), single postocular (usually two in *T. nymani*), dark-brown (vs. white in *T. nymani*) tail spine, brown anterior supralabials in juveniles (vs. yellow in *T. nymani*) , and the broad yellow nuchal collar in juveniles (vs. narrow and incomplete in *T. nymani*); from *T. loennbergii* by having two (vs. three in *T. loennbergii*) posterior temporals, lacking (vs. possessing) a dark vertebral stripe, and having a dark-brown (vs. white in *T. loennbergii*) tail spine; from *T. nigrescens* by its smaller size (SVL up to 500 mm in *T. lamingtoni* and 635 mm in *T. nigrescens*) and in having a uniformly yellow (vs. grey) venter; and from *T. mattisoni* in having the preocular contact the nasal (vs. separated by prefrontal contact with the second supralabial in *T. mattisoni*) and its uniformly yellow venter (vs. pale grey or yellow with grey band in *T. mattisoni*).

Redescription of the holotype. Adult male, 342 mm SVL + 78 mm TL = 420 mm TTL. Rostral broader than high, notched ventromedially; internasals angulate, semi-triangular, wider than long; prefrontals distinct from preoculars, approximately square but angled posteriorly, slightly longer than wide (Fig. 1D, D'), bordered below by preocular and nasal; preoculars elongate, narrower anteriorly, approximately 2.0–2.5 times as long as deep (Fig. 2G, G', H, H'), bordered anteriorly by nasal, below by second and third supralabials; frontal shield-shaped, lateral margins angled obliquely, not fused with supraoculars, anterior margin extending slightly anterior to remainder of scale medially; parietals approximately twice as long as wide. Nasals divided by large nares, without grooves above or below naris, though this area dimpled or creased. Postoculars one, irregularly hexagonal in shape, approximately same size as eye; one elongate anterior temporal above fifth and sixth supralabials, separating latter from parietal; two posterior temporals on right (one above the other, with upper larger), three on left (anteriormost smallest followed posteriorly by a larger upper and smaller lower temporal), in either configuration lowest abutting posterodorsal margin of sixth supralabial. Supralabials six, third and fourth entering eye; infralabials six, first four in contact with anterior genial. Mental small, shallow, triangular, wider than deep, bordered behind by first supralabials; anterior genials larger and longer than posterior genials, in medial contact along entire length; posterior genials in narrow anterior contact, otherwise separated by single elongate intergenial, which is widest posteriorly; three gulars separate intergenial from first ventral in the midline; first sublabial separates posterior genial from fifth infralabial (Fig. 3D, D'). Eye relatively small; pupil round.

Dorsal scale rows 15-15-15, smooth, not notched posteriorly, without apical pits. Ventrals 173, each approximately four times wider than long; vent covered by single scale; subcaudals 46, paired. Tail tipped by a pointed conical spine.

In preservative (88 years after collection), dorsum uniformly brown-grey, paler laterally. Venter uniformly pale yellow; medial brown markings scattered on several anterior subcaudals, posterior subcaudals largely brown. Anterior five supralabials and rostral uniformly dark

brown, last supralabial brown with large yellow blotch. Head otherwise uniformly dark brown. Chin and throat pale yellow suffused with brown on mental, anterior gulars, and first four supralabials. Tail spine brown, not distinct in colour from remainder of tail but slightly paler at tip. Iris black.

Variation. Nasals divided by large nares, without grooves above or below naris, though these areas often dimpled or creased. Postoculars one, except two in AMNH R-101103, irregularly hexagonal in shape, smaller than or occupying approximately same area as eye; two (63%) or three (37%) posterior temporals, either one above the other, with upper larger, or with anteriormost smallest followed posteriorly by a larger upper and smaller lower temporal, in either configuration lowest abutting posterodorsal margin of sixth supralabial. Supralabials six, except two specimens with five on one side; third and fourth supralabials contacting eye, except third or second and third in specimens with five supralabials. Anterior genials usually larger and longer than posterior genials but may be subequal; posterior genials entirely separated by single elongate intergenial (n = 5) or in medial contact for first quarter to first three-quarters of length (n = 12); intergenial one (except AMNH R-101103, which has an additional tiny intercalary scale anteriorly), widest posteriorly.

Dorsal scale rows invariably 15-15-15. Ventrals 160–178 (170 ± 5) in nine males, 186–195 (190 ± 3) in nine females; subcaudals 41–53 (46 ± 4) in nine males, 26–34 (29 ± 2) in nine females; SCR 19.3–23.0% (21.4 ± 1.2%) in males and 12.2–14.9% (13.2 ± 0.8%) in females. Tail tipped by a blunt to pointed conical spine. Maximum male SVL 428 mm, TL_R = 16.7–20.8% (18.8 ± 1.4%); maximum female SVL 500 mm, TL_R = 9.0–11.6% (10.3 ± 0.9%).

In preservative, dorsum uniformly grey or brown-grey in recent specimens, fading to uniform medium brown in specimens retained longer in alcohol. Venter uniformly pale yellow; most larger specimens and one neonate have some brown markings on the posterior subcaudals or midventrally on more anterior subcaudals, but these are never densely arrayed. In the Garaina sample, all supralabials and rostral pale yellow ventrally; in samples from south of there supralabials and rostral often densely suffused with brown or grey; in populations from Mt. Lamington and Cape Nelson, anterior 4–5 supralabials and rostral uniform black or dark brown, posterior supralabials mostly yellow. Yellow markings typically absent on nasals and prefrontals, though vaguely developed on prefrontals in two specimens. Nuchal collar evident in specimens < 260 mm SVL but absent or very obscure in specimens > 330 mm SVL, better developed in southern samples; collar narrow in AMNH R-101100 (SVL = 160 mm) but very wide in AMS R9352 (SVL = 163 mm), AMS R61027 (SVL = 167 mm), and BPBM 36171 (SVL = 190 mm), extending from behind head anteriorly across most of parietals, anterior temporals, and supralabials 5 and 6 (Fig. 4G, H). AMS R61027 also has a yellow blotch centrally located on the anterior frontal and posterior prefrontals. Chin and throat uniformly pale yellow in Garaina samples, with brown suffusion on anterior of chin in all other specimens. Conical tail spine invariably brown, not distinct in colour from remainder of tail.

In life, field notes described BPBM 39813 (a juvenile) as "Slate gray above with yellow nuchal collar. Venter pale gray, with each scale darker anteriorly and lighter posteriorly".

Range. Restricted to the northern versant of the Owen Stanley Mts. in Oro Province and southern Morobe Province, Papua New Guinea, at elevations from 100–940 m (Fig. 6B).

Ecological notes. AMNH R-101100 was ploughed out of an old clump of sugar cane in a field being cleared for a new tea plantation. BPBM 43032 (SVL = 480 mm) contains four shelled eggs.

Toxicocalamus vertebralis sp. nov.

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Figs 4I, J, 8–10, 11A, B

Toxicocalamus (*Apistocalamus*) *loriae* (part) – McDowell, 1969: 485.

Holotype. AMS R23072, an adult female collected by Harold G. Cogger at Fungoi, Kaironk Valley, 5.33°S, 144.42°E, elevation 1800 m, Schrader Range, Madang Province, Papua New Guinea in December 1964.

Paratypes (n = 18). Papua New Guinea: Madang Province: same locality as holotype, AMS R23068–69, R23071, R23073; Kaironk Valley, 5.23°S, 144.48°E, elev. 1850 m, UPNG 963–67, 3353, 5012; Kalne River, 5.53°S, 144.82°E, elev. 1200 m, UPNG 8695; Morobe Province: Wau, 7.33°S, 146.71°E, elev. 1070 m, KU 129086; ridge between Aseki and No. 1 Watut Valley, ca. 30 km W Wau, 7.33°S, 146.17°E, elev. ca. 2000 m, BPBM 6497; Western Highlands Province: Kol, Jimi Valley, 5.70°S, 144.84°E, elev. 1500 m, CAS 140042; Baiyer River, 5.53°S, 144.16°E, elev. 1170 m, AMS R16575, R16581; Sandaun Province: Busilmin, 4.92°S, 141.14°E, elev. 1880 m, SAMA 6275.

Etymology. The species epithet is a Latin masculine adjective in recognition of the vertebral stripe that distinguishes this species from most other *Toxicocalamus*.

Diagnosis. A large member of the *T. loriae* Group (known male SVL up to 565 mm, known female SVL up to 685 mm) with the following unique combination of characters: body length sexually dimorphic (t_{10} = 2.3826, p = 0.0192); two scales covering vent; three infralabials contacting first genial; a single intergenial between posterior genials, widest

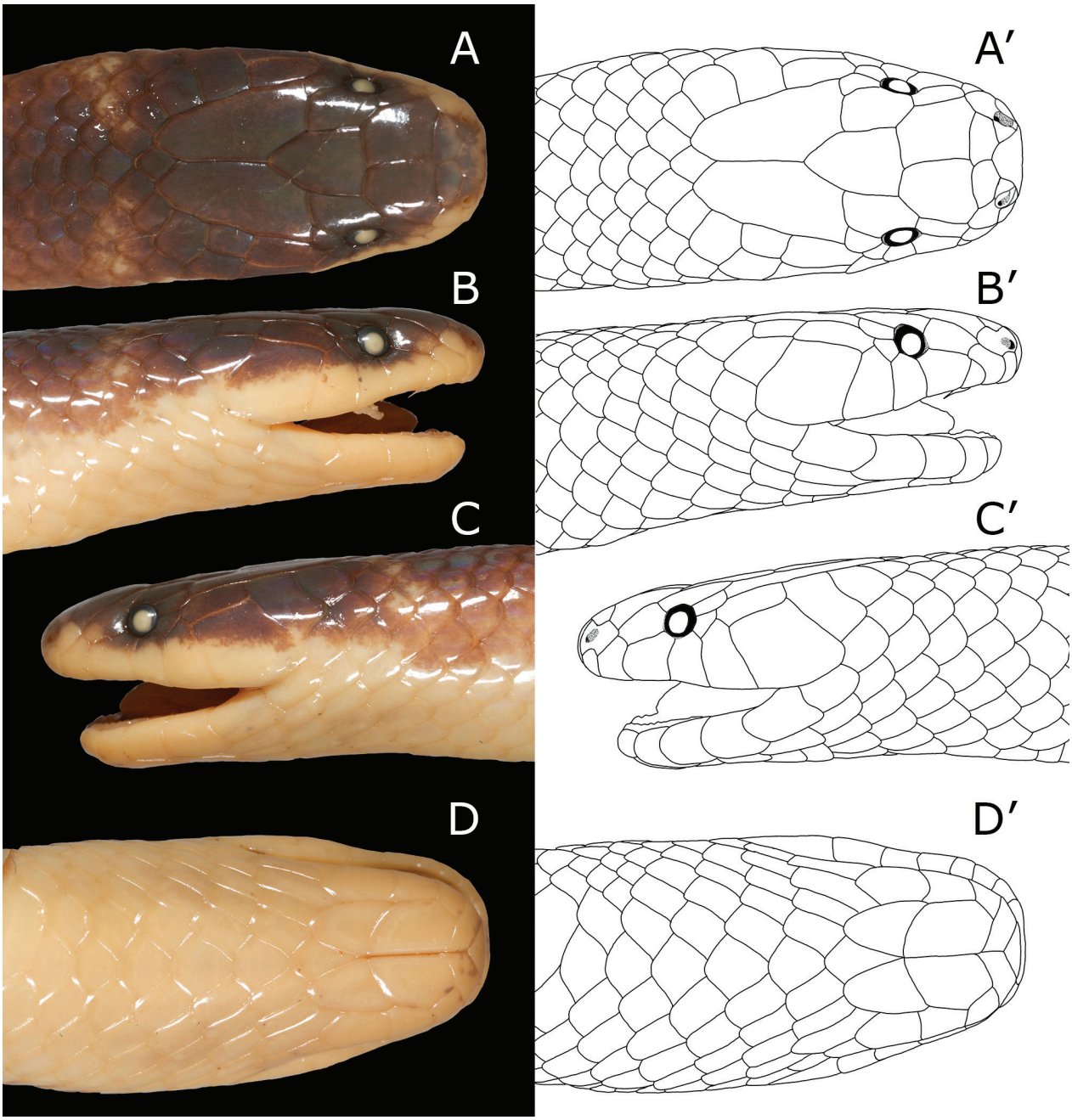

Figure 8. Head of holotype of *Toxicocalamus vertebralis* **sp. nov.** (AMS R23072) from Fungoi, Kaironk Valley, Madang Province, PNG, in both photographic and line-drawing illustrations. **A**, **A'** dorsal, **B**, **B'** right lateral, **C**, **C'** left lateral, and **D**, **D'** ventral views.

posteriorly; preocular contacting nasal (81%) or not (19%), not contacting internasal; relatively long snout (SNL/SNW mean = 1.07, range = 0.95–1.18); relatively large eye (EY/SNL mean = 0.21, range = 0.16–0.28); two postoculars; usually three (74%) posterior temporals; ventral scale count sexually dimorphic with overlap ($t_{17} = 4.7511$, $p < 0.0001$), 194–210 in nine males, 203–232 in nine females and a female embryo; subcaudals 39–52 in males, 31–38 in females, sexually dimorphic without overlap; SC_R sexually dimorphic without overlap, 16.7–20.5% in males, 12.8–14.8% in females; adult females with much shorter tails than adult males, TL_R 13.3–17.1% in adult males, 6.5–10.7% in adult females; pale parietal blotch absent; pale markings on prefrontals absent (95%) or vague (5%); tail spine white, paler than remainder of tail; and venter uniformly yellow.

Comparisons with other species. *Toxicocalamus vertebralis* can be distinguished from all other members of the *T. loriae* Group except *T. loennbergii* by its dark vertebral line. It is further distinguished from *T. mattisoni* and *T. nigrescens* by its greater number of ventrals (198–228 vs. 170–181 and 184–193 in *T. mattisoni* and *T. nigrescens*, respectively) and yellow venter (grey or yellow barred with grey in *T. mattisoni* and *T. nigrescens*); from *T. loriae* in having only a single intergenial (vs. two in *T. loriae*); from juvenile *T. nymani* by lacking a pale blotch on the prefrontals (vs. present in 80% of *T. nymani*) and from all *T. nymani*

Figure 9. A Right, and **B** left sides of holotype of *Toxicocalamus vertebralis* **sp. nov.** (AMS R23072), from Fungoi, Kaironk Valley, Madang Province, PNG. The distinctive vertebral stripe of this taxon is difficult to discern due to the position in which the holotype was fixed during preservation.

by significant differences in ventral scale counts for both sexes (males: 194–210 vs. 178–198 in *T. nymani*, $t_{24} = 5.2049$, $p = 0.000012$; females: 203–232 vs. 182–210 in *T. nymani*, $t_{30} = 7.3288$, $p < 0.00001$) and subcaudal scale counts in females (31–38 vs. 26–39 in *T. nymani*, $t_{29} = –3.5633$, $p = 0.000645$); and from *T. lamingtoni* in having two scales covering the vent (vs. one scale in *T. lamingtoni*), non-overlapping ventral scale counts in both sexes (males: 194–210 vs. 160–178 in *T. lamingtoni*; females: 203–232 vs. 189–194 in *T. lamingtoni*) and subcaudal scale counts in females (31–38 vs. 26–34 in *T. lamingtoni*; $t_{17} = –4.9232$, $p = 0.000064$), and a white (vs. dark brown in *T. lamingtoni*) tail spine. The uniformly yellow venter and dark vertebral stripe make *T. vertebralis* most similar to *T. loennbergii*, but it can be distinguished from that species in having two postoculars (vs. one in *T. loennbergii*), a significantly greater number of subcaudals in females (31–38 vs. 23–32 in *T. loennbergii*; $t_{12} = –4.3818$, $p = 0.000447$), three (vs. four) infralabials contacting the anterior pair of genials, a longer snout (SNL/SNW mean = 1.07, range = 0.95–1.18 vs. 0.95 and 0.93–0.99 in *T. loennbergii*), larger eye (EY/SNL mean = 0.21, range = 0.16–0.28 vs. 0.16 and 0.15–0.18 in *T. loennbergii*), and lacking a pale blotch on the parietals (present in *T. loennbergii*).

Description of the holotype. Adult female with mid-ventral slit extending through 47 ventrals anterior to vent; 666 mm SVL + 69 mm TL = 735 TTL. Rostral broader than high, notched ventromedially, extending dorsoposteriorly behind nares; internasals angulate, semi-triangular, wider than long (Fig. 8A, A'); prefrontals distinct from preoculars, approximately square, wider anteriorly than posteriorly, rounded posterolaterally, bordered below by preocular and nasal; preoculars elongate, narrower anteriorly, approximately twice as long as deep, bordered anteriorly by nasal, bordered below by second and fourth supralabials on right (Fig. 8B, B') and by second and third supralabials on left (Fig. 8C, C'); frontal shield-shaped, lateral margins angled obliquely, not fused with supraoculars, anterior margin extending slightly anterior to remainder of scale medially; parietals approximately twice as long as wide. Nasals divided by large nares, without grooves above or below naris. Postoculars two, upper longer and larger than lower, both smaller than eye; one elongate anterior temporal above fifth and sixth supralabials on left, sixth and seventh supralabials on right, separating supralabials from parietal; two posterior temporals on left, three on right, lowest abutting posterodorsal margin of sixth supralabial. Supralabials six on left, seven on right; third and fourth supralabials contacting eye on left, fourth and fifth supralabials contacting eye on right; infralabials six, first three in contact with anterior genial, third and fourth in contact with posterior genials. Mental small, shallow, triangular, wider than deep, bordered behind by first supralabials; anterior genials slightly larger than posterior genials, in medial contact along entire length; posterior genials in point contact anteriorly; intergenial single, widest posteriorly; five gulars separate intergenial from first ventral in the midline; first sublabial separates posterior genial from fifth infralabial (Fig. 8D, D'). Eye relatively small; pupil round.

Dorsal scale rows 15-15-15, smooth, not notched posteriorly, without apical pits. Ventrals 220, each approximately four times wider than long; two scales covering vent; subcaudals 33, paired. Tail tipped by a pointed conical spine.

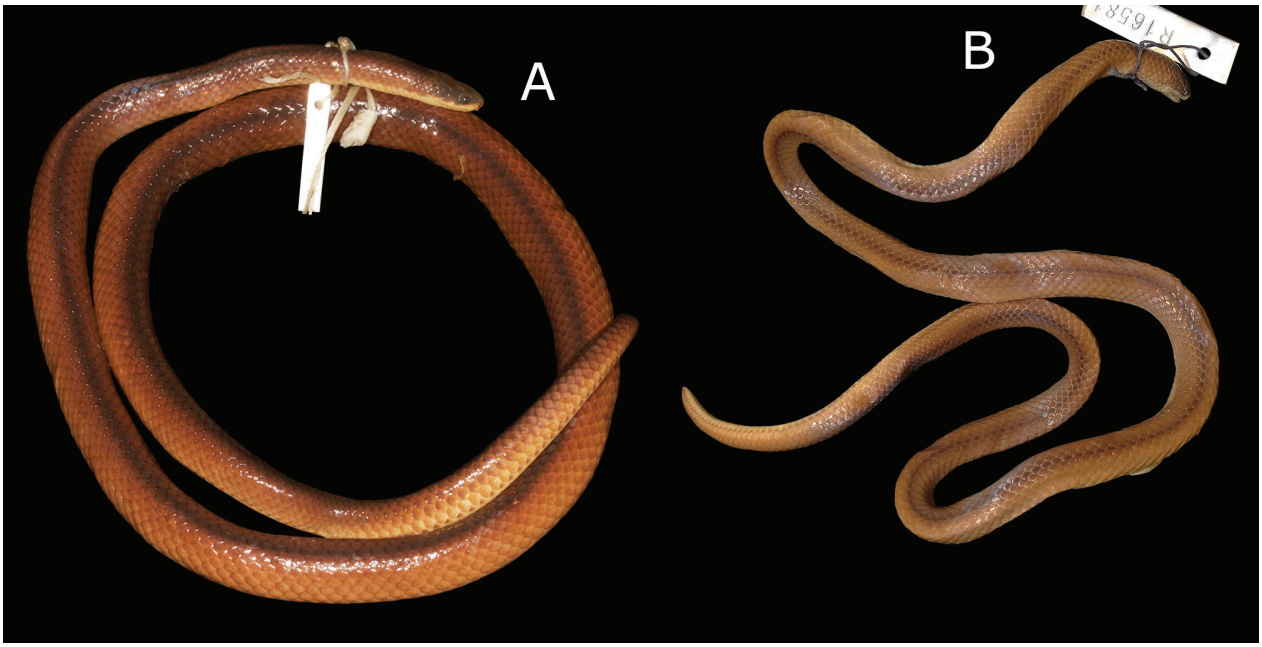

Figure 10. Paratypes of *Toxicocalamus vertebralis* **sp. nov.** to illustrate the black vertebral stripe in this species. **A** AMS R23068, from Fungoi, Kaironk Valley, Madang Province, PNG. **B** AMS R16581, from Baiyer River, Western Highlands Province, PNG.

In preservative (52 years after collection), dorsum pale brown (Fig. 9A), with darker brown vertebral stripe one scale wide; lowest one and one-half dorsal scale rows yellow, with brown spots on ventral margin of each scale on approximately posterior three-fourths of body, giving this ventrolateral region the appearance of being striped. Venter and subcaudals uniformly pale yellow (Fig. 9B). Supralabials pale yellow ventrally, brown dorsally on supralabials 3–6 on left, 4–7 on right. Remnants of a yellow nuchal collar present but widely infused with brown, not meeting mid-dorsally. Nasals largely yellow; yellow mottling on rostral, internasals, dorsal portions of nasals, and anterior portions of preoculars. Chin and throat pale yellow, with few small brown flecks along sutures joining mental, first two infralabials, and anterior genials. Conical tail spine white with brown tip. Iris black.

Variation. Ventrals 194–210 (201 ± 5) in nine males and 203–232 (218 ± 9) in ten females; subcaudals 39–52 (45 ± 4) in nine males and 31–38 (35 ± 2) in ten females; SCR 16.7–20.5% (18.4 ± 1.0%) in males, 12.8–14.8% (13.7 ± 0.7%) in females. The lowest male ventral and subcaudal counts are in SAMA 6275 from Busilmin (194 and 39, respectively) but these are not strong outliers. Numbers of postoculars are two, except on the left side of AMS R16581, which has one. TL_R 13.3–17.1% (14.7 ± 1.3%) in six adult males, 6.5–10.7% (9.4 ± 1.4%) in six adult females, sexually dimorphic without overlap. Numbers of posterior temporals are usually three (74%) but sometimes two (24%) or four (3%). Preoculars typically broadly contact the nasals, except for two specimens that have the two scales separated by point contact between the prefrontal and second supralabial; a third specimen (UPNG 8695) has the two scales separated by broad contact between the prefrontal and second supralabial. Typically, only a single intergenial separates the posterior genials; however, two specimens also have a small intercalary scale anterior to the intergenial and between the posterior genials, and a third specimen has three small intergenials: one anterior and two posterior. Posterior genials are entirely separated by the intergenial(s) in ten specimens and in anterior contact for ¼–½ their length in eight.

Specimens are red brown (Fig. 10A) or medium brown (Fig. 10B) dorsally with a dark-brown vertebral stripe. Venters are uniformly yellow at all sizes. Heads are dark above in all specimens except in the one from Busilmin (SAMA 6275), which is vaguely mottled with dark yellow on several scales. All supralabials are yellow, except for the upper portions of the larger scales; the nasal and ventral portion of the rostral are also typically coloured with yellow. Chin and throat typically uniformly yellow, but a few brown flecks may occur anteriorly, and the specimen from Busilmin has the junctions between the infralabials narrowly margined in brown. In neonates and small juveniles (153–213 mm) the nuchal collar consists of a lateral yellow crescent on each side of the neck, each of which narrows medially and almost meets its opposite member (Fig. 4I, J). In larger animals, these yellow blotches are invaded with brown and become obscure.

Colour in life. A photo of CAS 140042, a large (685 mm SVL) male, shows a dark-brown animal with a darker-brown vertebral region and yellow venter, lips, and tail spine (Fig. 11A, B).

Range. Known from the Schrader and Bismarck Ranges at the eastern end of the Central Highlands of Papua New Guinea, the vicinity of Wau (Morobe Province), and the Star Mountains near the Indonesian border, at elevations from 1170–1880 m (Fig. 6B).

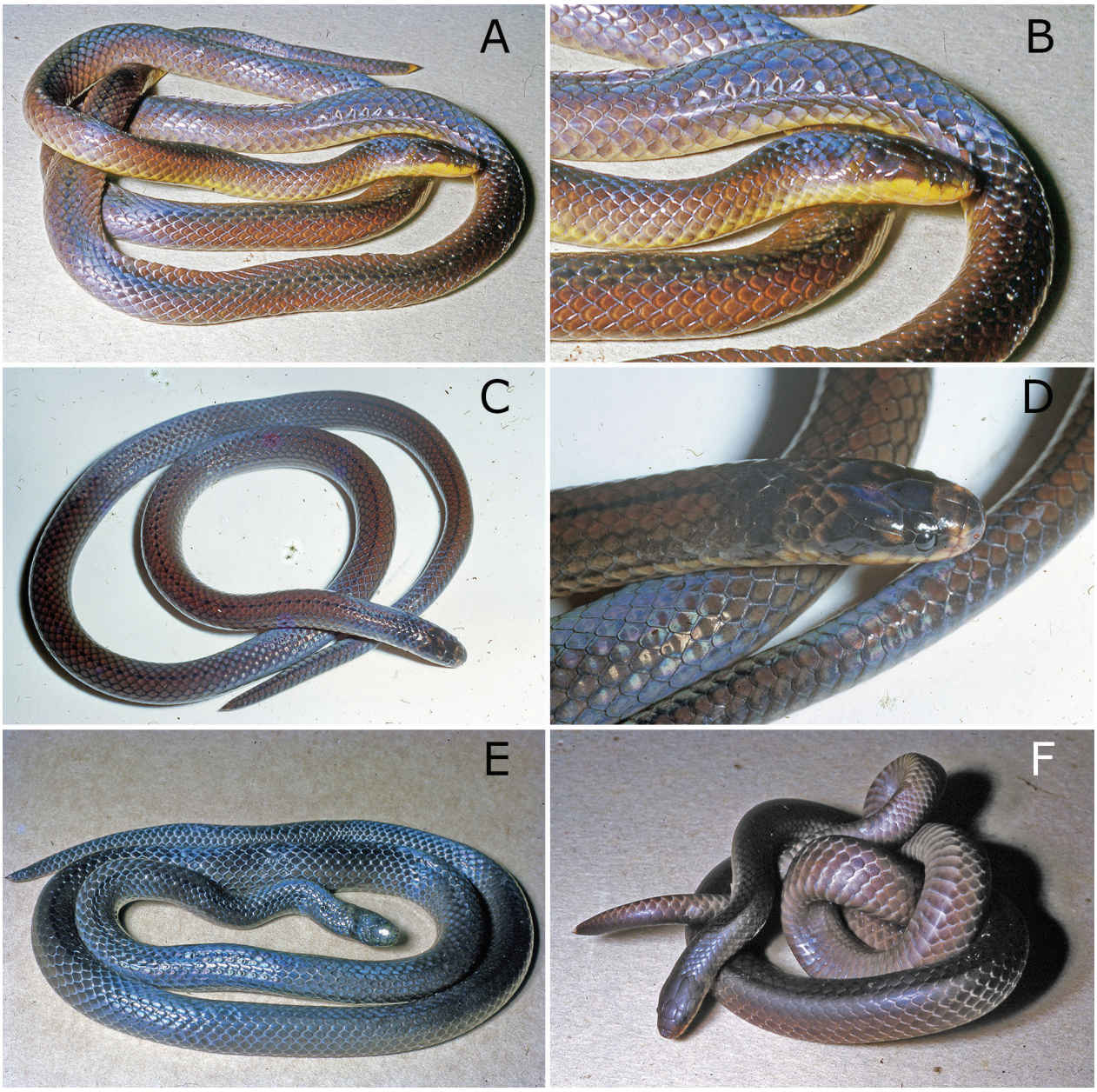

Figure 11. *Toxicocalamus loriae* Group species in live and perimortem photographs to show colour in life. **A**, **B** *T. vertebralis* **sp. nov.** (CAS 140042) from Kol, Jimi Valley, Jiwaka Province, PNG. **C**, **D** *T. spilorhynchus* **sp. nov.** (MCZ R-152431) from Garaina, Morobe Province, PNG. **E** *T. atratus* **sp. nov.** (MCZ R-84026) from Kundiawa, Wahgi Valley, Chimbu Province, PNG. **F** *T. atratus* (MCZ R-111767) from Kundiawa, Wahgi Valley, Chimbu Province, PNG. Photographs by Fred Parker.

Toxicocalamus spilorhynchus sp. nov.

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Figs 4K, L, 11C, D, 12, 13

Toxicocalamus loriae X *T. stanleyanus* (part) – McDowell, 1969: 485.
Toxicocalamus loriae Clade 2 – Strickland et al., 2016: 671.

Holotype. BPBM 41381, an adult female collected by Allen Allison at Saiko, 11 km SW Garaina, 7.9538°S, 147.0567°E, elevation 1856 m, Morobe Province, Papua New Guinea on 15 February 2012.

Paratypes (*n* = 12). Papua New Guinea: Morobe Province: same locality as holotype, BPBM 41390; Amu Creek, near Garaina, 7.9555°S, 147.0569°E, elev. 1660 m, BPBM 41391; Garaina, 7.89°S, 147.14°E, elev. 770 m, AMNH R-95624, R-101101, R-101103, R-103681, R-107203–04, MCZ R-152428–29, R-152431; Saurere, 7 km W Garaina, 7.9222°S, 147.0878°E, elev. 1440 m, PNGM 22767.

Referred specimen. Papua New Guinea: Morobe Province: Garaina, 7.89°S, 147.14°E, elev. 770 m, AMNH R-107205.

Etymology. The species epithet is a Latinized masculine adjective formed by combining the Greek σπίλος (*spilos*, meaning *spot*) and ῥύγχος (*rhynchos*, meaning *snout*), in recognition of the distinctive prefrontal blotch that typifies the species.

Diagnosis. A moderately sized member of the *T. loriae* Group (SVL up to 600 mm) with the following unique combination of characters: two scales covering vent; three infralabials contacting first genial; a single intergenial between posterior genials, widest posteriorly; preocular contacting nasal (87%) or not (13%), not contacting internasal (93.3%); relatively long snout (SNL/SNW mean = 1.16, range = 0.99–1.40); relatively large eye (EY/SNL mean = 0.22, range = 0.17–0.24); two postoculars (93%); usually three (67%) posterior temporals; ventral scale count sexually dimorphic with overlap ($t_{12} = 3.7381$, $p = 0.001416$), 172–184 ventrals in eight males, 178–197 in six females; subcaudals sexually dimorphic without overlap, 43–57 in males, 20–29 in females; SC_R strongly sexually dimorphic, with the relative contribution of subcaudal scale number in males twice what it is in females (20.0–24.0 in males, 10.0–13.1 in females); pale parietal blotch usually absent (present in four small specimens); pale markings on prefrontals present; and venter uniformly yellow.

Comparisons with other species. *Toxicocalamus spilorhynchus* can be distinguished from all other members of the *T. loriae* Group except *T. loennbergii* and *T. vertebralis* by its dark vertebral stripe. It is further distinguished from *T. mattisoni*, *T. nigrescens*, and adult *T. nymani* by its yellow venter (vs. grey, yellow barred with grey, or dark brown in those other species); from *T. loriae* in having only a single intergenial (vs. two in *T. loriae*); and from *T. lamingtoni* in overlapping but significantly different ventral and subcaudal counts in males (ventrals: 172–184 vs. 160–178 in *T. lamingtoni*, $t_{15} = -3.0499$, $p = 0.004053$; subcaudals: 43–57 vs. 41–53 in *T. lamingtoni*, $t_{15} = -1.8533$, $p = 0.041808$), by having two scales covering the vent (vs. one scale in *T. lamingtoni*), and a white (vs. dark-brown in *T. lamingtoni*) tail spine. It can be distinguished from juvenile *T. nymani* by details of head patterning: in *T. spilorhynchus* the pale blotches on the prefrontals are typically fused into a continuous chevron or blotch across the snout (vs. one discrete small spot on each prefrontal in *T. nymani*), the pale nuchal collar is continuous and includes the posterior portion of the parietals (vs. the band is replaced by a single elongate spot on each side of the nape in *T. nymani*), and there is often a pale blotch on the anterior temporal and anterolateral portion of the parietal (vs. absent in *T. nymani*). The yellow venter and dark vertebral stripe make *T. vertebralis* most similar to *T. loennbergii* and *T. vertebralis*. It can be distinguished from *T. loennbergii* by having two postoculars (vs. one in *T. loennbergii*), three (vs. four) infralabials contacting the anterior pair of genials, a longer snout (SNL/SNW mean = 1.16, range = 0.99–1.40 vs. 0.95 and 0.93–0.99 in *T. loennbergii*), larger eye (EY/SNL mean = 0.22, range = 0.17–0.24 vs. 0.16 and 0.15–0.18 in *T. loennbergii*), and lacking a pale blotch on the parietals (present in *T. loennbergii*) except in four small specimens. *Toxicocalamus spilorhynchus* can be distinguished from *T. vertebralis* by both sexes having significantly fewer ventrals (172–184 in males vs. 194–210 in *T. vertebralis*, $t_{15} = -10.1025$, $p < 0.00001$; 178–197 in females vs. 203–232 in *T. vertebralis*, $t_{14} = 6.0435$; $p < 0.000015$) and more subcaudals (43–57 in males vs. 39–52 in *T. vertebralis*, $t_{15} = 2.4970$, $p = 0.012326$; 20–29 in females vs. 31–38 in *T. vertebralis*, $t_{14} = -5.8962$, $p = 0.000019$); a pale blotch on each prefrontal (vs. absent in [or vague in one] *T. vertebralis*); and having the yellow venter become dusted with brown on the anterior of each ventral scale in large adults (vs. uniformly yellow throughout life in *T. vertebralis*).

Description of the holotype. Adult female with mid-ventral slit extending through seven ventrals at midbody; 600 mm SVL + 65 mm, TL = 665 mm TTL. Rostral broader than high, notched ventromedially, not extending dorsoposteriorly as far as nares; internasals angulate, semi-triangular, wider than long; prefrontals distinct from preoculars, approximately square, wider anteriorly than posteriorly, angled posterolaterally (Fig. 12A, A'), bordered below by preocular and nasal; preoculars elongate, narrower anteriorly, approximately twice as long as deep, bordered anteriorly by nasal, below by second and third supralabials (Fig. 12B, B', C, C'); frontal shield-shaped, lateral margins roundly angled obliquely, not fused with supraoculars, anterior margin extending slightly anterior to remainder of scale medially; parietals approximately twice as long as wide on right, shorter and wider on left. Nasals divided by large nares, with grooves above and below naris. Postoculars two, lower larger on right, subequal on left, both smaller than eye; one elongate anterior temporal above fifth and sixth supralabials, separating latter from parietal; two posterior temporals, lower abutting posterodorsal margin of sixth supralabial. Supralabials six, third and fourth contacting eye; infralabials six, first three in contact with anterior genial, third and fourth in contact with posterior genials. Mental small, shallow, triangular, wider than deep, bordered behind by first supralabials; anterior genials subequal to posterior genials, in medial contact along entire length; posterior genials separated along entire length; intergenial single, widest posteriorly; four gulars separate intergenial from first ventral in the midline; first sublabial separates posterior genial from fifth infralabial (Fig. 12D, D'). Eye relatively small; pupil round.

Dorsal scale rows 14-15-15, smooth, not notched posteriorly, without apical pits; on approximately posterior third of body vertebral scale row and sixth row on right composed of scales larger than adjacent rows. Ventrals 193, each approximately four times wider than long; two scales covering vent; subcaudals 29, paired. Tail tipped by a pointed conical spine.

In preservative (nine years after collection), dorsum pale brown, with poorly defined darker-brown vertebral stripe (Fig. 13A); each dorsal scale margined posteriorly in darker brown, giving the appearance of a reticulated

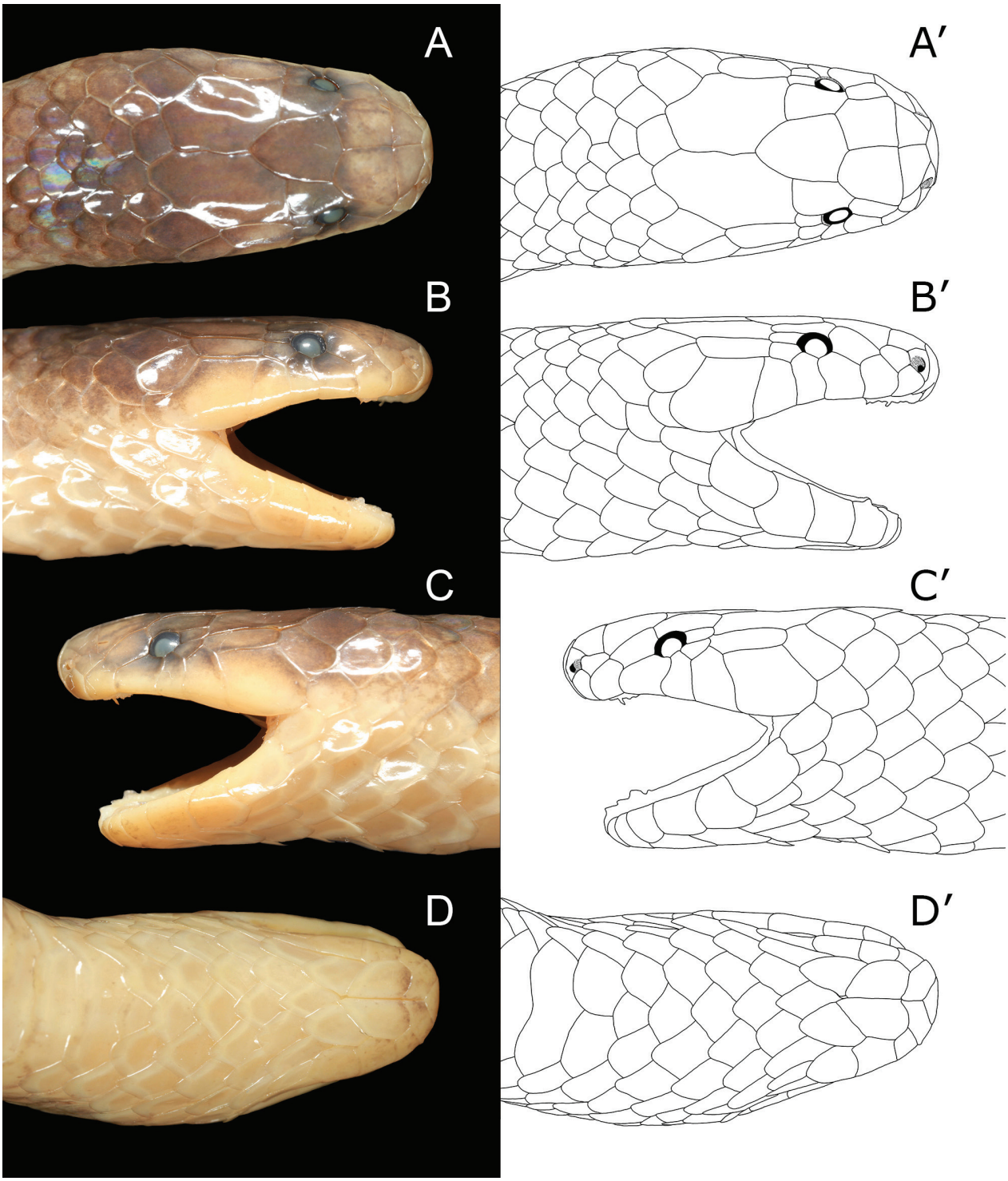

Figure 12. Head of holotype of *Toxicocalamus spilorhynchus* **sp. nov.** (BPBM 41381) from Saiko, Morobe Province, PNG, in both photographic and line-drawing illustrations. **A**, **A'** dorsal, **B**, **B'** right lateral, **C**, **C'** left lateral, and **D**, **D'** ventral views.

dorsum. Venter and subcaudals dark yellow dusted with pale brown on anterior of each scale, imparting a clouded yellow appearance to venter (Fig. 13B). Supralabials pale yellow ventrally, suffused with brown dorsally as well as anteriorly on first supralabial. Yellow nuchal collar absent. Supraoculars, frontal, and posterior margin of prefrontals dark brown; scales anterior to this on snout light brown clouded with dark brown; posterior of parietals and scales behind them dark brown; anterior temporals and anterior portion of parietals lighter brown clouded with dark brown. Chin and throat dark yellow, dusted with small brown flecks on mental, first four infralabials, and anterior genials. Conical tail spine white, finely dusted with brown mid-dorsally. Iris black.

Variation. Ventrals 172–184 (178 ± 4) in eight males and 178–197 (190 ± 7) in six females; subcaudals 43–57 (51 ± 4) in eight males and 20–29 (26 ± 3) in six females. Tails in females are much shorter than in males, both in terms of adult tail length and relative subcaudal number.

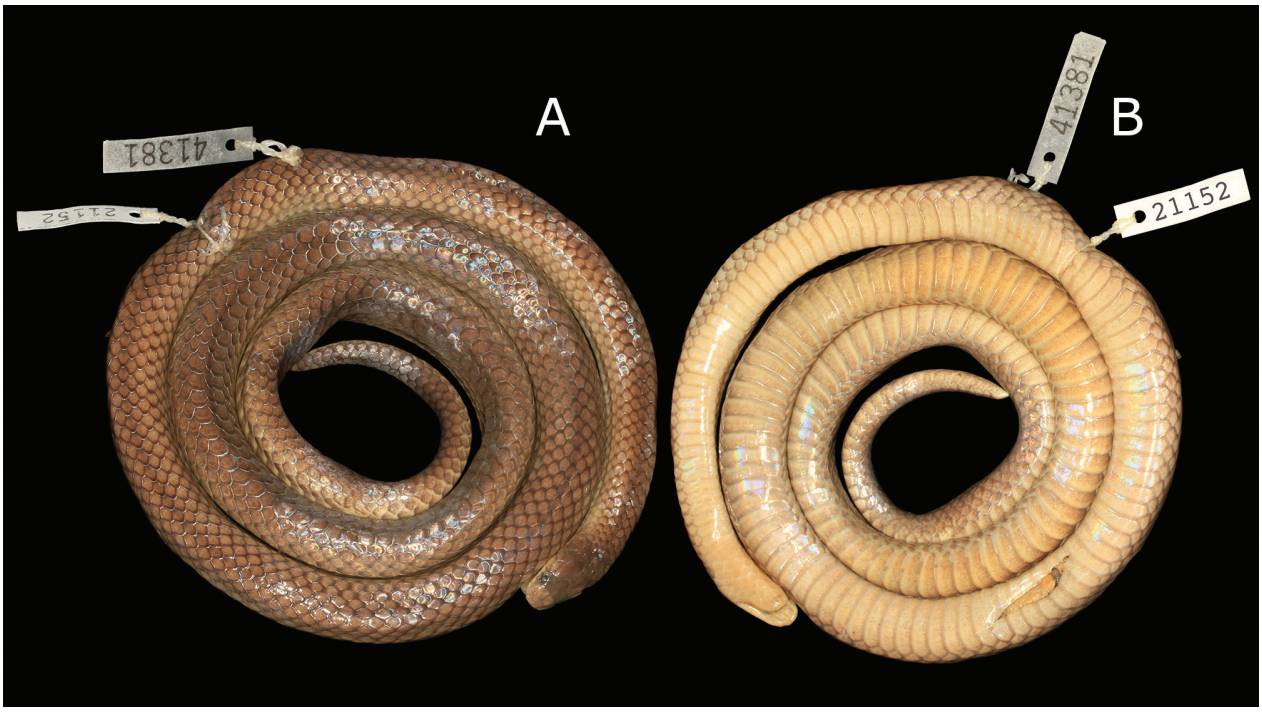

Figure 13. A Dorsum and **B** venter of the *Toxicocalamus spilorhynchus* **sp. nov.** holotype (BPBM 41381), Saiko, Morobe Province, PNG.

TL_R is 17.9–19.2% (18.4 ± 0.5%) in four adult males and 8.9–10.2% (9.6 ± 0.6%) in two adult females, whereas SC_R is 20.0–24.0% (22.1 ± 1.2%) in eight males and 10.0–13.1% (11.9 ± 1.1%) in six females. Numbers of postoculars are two, except on the right side of BPBM 41391, which has one. Numbers of posterior temporals are usually three (67%) but sometimes two (29%) or four (4%). Preoculars typically broadly contact the nasals, except for two specimens (BPBM 41390–91) that have the two scales separated by broad contact between the prefrontal and second supralabial. Preoculars do not contact the internasals, being separated by the intervening prefrontal, except on the right side of MCZ R-152431, in which there is point contact between the two. Typically, only a single intergenial separates the posterior genials; however, smaller intercalary scales occur in five specimens, usually anterior to the intergenial, though lateral to it in one specimen. Posterior genials are entirely separated by the intergenial(s) in ten specimens, in minimal anterior contact in two, and in broad contact along ⅓ their length in one.

Specimens are brown dorsally with a dark-brown vertebral stripe and with each scale narrowly margined in dark brown posteriorly. The first rows of scales in small specimens are yellow, so that the dark-brown margining of each scale imparts the appearance of narrow brown stripes on the lower sides. Venters are uniformly yellow in smaller specimens (153–336 mm SVL) but each scale is clouded with pale brown anteriorly in the only large specimen (the holotype, 600 mm SVL). Juveniles are boldly patterned with yellow blotches on a black ground that typically involves a yellow chevron across the prefrontals, a yellow nuchal collar, and yellow blotches on the parietals and anterior temporals (Fig. 4K, L). These become obscured in larger specimens, and the sole adult has very vague remnants of these markings on a brown ground and no nuchal collar. All specimens have yellow on the supralabials, ventral portion of the rostral, and usually on the posterior portion of the nasal. Chin and throat are typically uniformly yellow but may be dusted with brown along the margins of the anterior scales and are more heavily flecked with brown anteriorly in BPBM 41390–91.

Colour in life. A photo of MCZ R-152431, a small (225 mm SVL) male, shows a medium-brown animal with a narrow, black vertebral stripe that is typically strongest on the anterior of each scale and often disappears on the posterior portion, imparting a somewhat spotted appearance to the stripe (Fig. 11C). The lower sides are narrowly striped with black anteriorly, becoming more continuously dark posteriorly, and most dorsal scales appear narrowly margined in black posteriorly, imparting a reticulate appearance to the dorsum. Top of the head is black, with yellow mottling on the snout, parietals, anterior temporal, and nuchal region. The region immediately behind the nuchal region is black, but this abruptly changes to the brown dorsal colouration of the body. Supralabials, anterior preocular, and posterior nuchal yellow (Fig. 11D).

Range. Known from the uplands of the Owen Stanley Range from the vicinity of Garaina, Morobe Province, PNG, at elevations from 770–1850 m (Fig. 6B).

Ecological notes. AMNH R-95624 was caught among tree roots in a garden, and AMNH R-101101 was found in an office filing cabinet. AMNH R-101103 was caught

together with AMNH R-101102 (*T. lamingtoni*), showing that these two species occur syntopically; the habitat in which they were collected was not noted.

Remarks. McDowell (1969) referred to a sample of six snakes from Garaina as "*T. loriae* X *T. stanleyanus*". Four of the AMNH paratypes of *T. spilorhynchus* were included in that sample. This odd designation of an entire sample of six snakes as hybrids resulted, in part, because McDowell was unable to make sense of the morphological variation he observed and, in part, because he cited other instances of hybridization among taxa from that region of New Guinea. This was an error, at least in part because two of these six snakes are, in fact, *T. lamingtoni*, a taxon he had already synonymized with *T. loriae*. This may perhaps have precluded him from noticing that his sample involved two species, neither of which is similar to *T. stanleyanus*, a species with five (not six) supralabials and the preocular fused to the prefrontal. Furthermore, it is worth noting that for a hybridization event to take place, both implicated species must occur in sympatry. The nearest *T. stanleyanus* specimens to Garaina were collected 76 km west of Garaina at Tekadu, Eloa River, Gulf Province (USNM 562945) and 68 km south of Garaina at Mafulu, Central Province (AMNH R-59063, BMNH 1935.10.171–73). It is possible that both spatial and elevational geography could preclude sympatry of these species.

We refer AMNH R-107205 to this species but do not include it among the paratypes because its state of preservation is too poor to allow confident determination of head-scale characters. Nonetheless, its dorsal and ventral colour and ventral and subcaudal counts allow it to be confidently assigned to this species.

Toxicocalamus atratus sp. nov.

https://zoobank.org/2DED0238-6F17-414E-BEF3-801E852AB976

Figs 4M, N, 11E, F, 14, 15

Toxicocalamus (*Apistocalamus*) *loriae* (part) – McDowell, 1969: 485.

Holotype. MCZ R-84144, an adult female collected by Fred Parker at Kundiawa, 6.02°S, 144.97°E, elevation 1585 m, Chimbu Province, Papua New Guinea on 25 May 1964.

Paratypes (*n* = 90). Papua New Guinea: Chimbu Province: along Wahgi River, 5.94°S, 144.80°E, elev. 1470 m, CAS 113665, 139564; Karimui, 6.50°S, 144.83°E, elev. 1170 m, CAS 118961–62; Kondiu, 5.98°S, 144.87°E, elev. 1600 m, AMNH R-75336–57; Kundiawa, 6.02°S, 144.97°E, elev. 1585 m, AMNH R-98495, R-98497, CAS 99916, 100069, 113670, 115986, 118948, 118960, 139584, 140043, MCZ R-83218, R-84026, R-111767, R-111788, R-115586, R-116774, R-116788, R-140818, R-145923, NMV 13421, USNM 166280; Kup, 5.95°S, 144.80°E, elev. 1500 m, AMNH R-72780–81; Mintima, 5.98°S, 144.91°E, elev. 1770 m, CAS 103374–75, 113663, 118957–59, MCZ R-116789–90, R-121547–48; Noru, 6.60°S, 144.63°E, elev. 1770 m, AMS R115365; Eastern Highlands Province: Agakamatasa, 6.72°S, 145.62°E, elev. 1720 m, MCZ R-121545; Lida Patrol Post, 6.32°S, 145.40°E, elev. 1800 m, CAS 139575; Lufa, Mt. Michael, 6.33°S, 145.25°E, elev. 1120 m, CAS 113666–67, MCZ R-121546; Nivi Unggai, 6.21°S, 145.31°E, elev. 2030 m, MCZ R-84142, R-116791–92; Hela Province: Bobole, 6.23°S, 142.77°E, elev. 1145 m, AMS R122803, R122806; Halalinja, 6.15°S, 143.37°E, elev. 2140 m, BMNH 1976.92; Nipa, 6.10°S, 143.25°E, elev. 2070 m, UPNG 5811; Jiwaka Province: Banz, 5.78°S, 144.62°E, elev. 1650 m, AMNH R-85743, R-88060; Minj, 5.86°S, 144.87°E, elev. 1560 m, MCZ R-141849; Morobe Province: Kwaplalim, 12–13 km W Menyamya, 7.19°S, 145.97°E, elev. 1490 m, NMW 37670, UCM 51552–53; Southern Highlands Province: Mendi, 6.14°S, 143.66°E, elev. 1750 m, CAS 113664, MCZ R-121543–44; Moro Camp, Lake Kutubu, 6.36°S, 143.23°E, elev. 840 m, SAMA R69950; Western Highlands Province: Igindi, 6.19°S, 144.98°E, elev. 1630 m, AMNH R-98134; Kimil, 5.72°S, 144.53°E, elev. 1700 m, AMNH R-14783; Korn, Mt. Hagen, 5.84°S, 144.31°E, elev. 1630 m, AMNH R-14771, R-14773, R-14785–88.

Referred specimen. Papua New Guinea: Morobe Province: S side Ekuti Divide, 7.42°S, 146.43°E, elev. 1050 m, BPBM 17423.

Etymology. The species epithet is a masculine Latin adjective meaning "dressed in black," in recognition of the dark dorsal and ventral colouration of adults of this species.

Diagnosis. A large member of the *T. loriae* Group (male SVL up to 655 mm, female SVL up to 682 mm) with the following unique combination of characters: sexual size dimorphism in SVL present ($t_{71} = 2.5689$, $p = 0.0062$); two scales covering vent; posterior genials usually entirely separated (80%) but may be in anterior contact (20%) with each other; intergenial usually widest posteriorly (89%) or centrally (11%); preocular usually contacting nasal (77%), not contacting internasal; preocular rather short, less than twice as long as deep; postoculars two (one in 26%); posterior temporals two (58%) or three (42%); ventrals sexually dimorphic ($t_{85} = 7.400$, $p < 0.00001$), 177–206 in males, 187–218 in females; subcaudals sexually dimorphic with overlap ($t_{87} = –24.8814$, $p < 0.00001$), 40–47 in males, 26–41 in females; two scales covering vent; yellow nuchal collar and yellow markings on prefrontals present in juveniles, usually absent (but sometimes merely faded) in adults; tail spine paler than remainder of tail; and venter uniformly dark brown or dark brown with the posterior of each ventral paler brown or yellowish brown in adults, giving a banded appearance, black in life; venter yellow with a black spot on lateral margins of each ventral in juveniles.

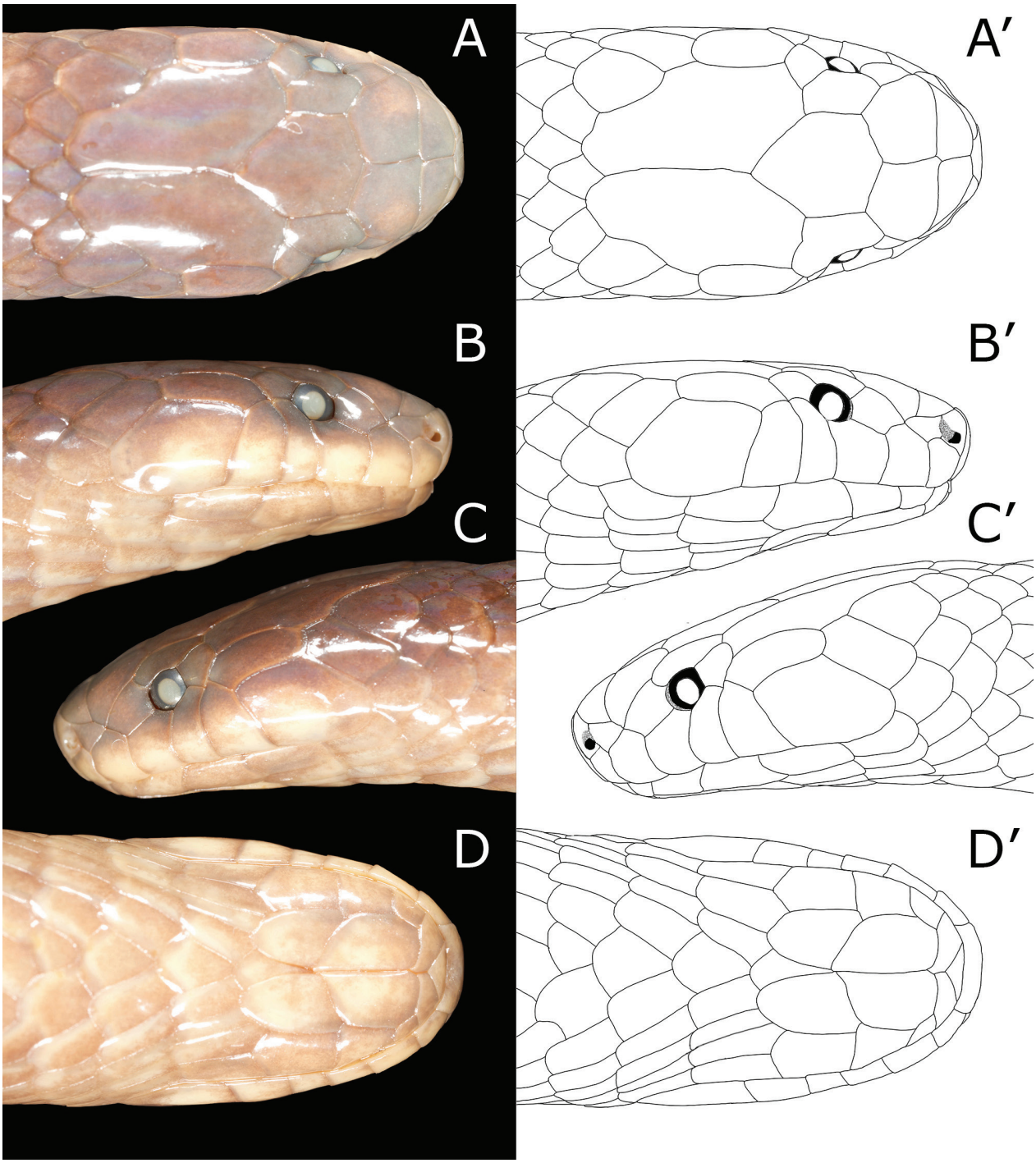

Figure 14. Head of the *Toxicocalamus atratus* **sp. nov.** holotype (MCZ R-84144) from Kundiawa, Chimbu Province, PNG, in both photographic and line-drawing illustrations. **A**, **A'** dorsal, **B**, **B'** right lateral, **C**, **C'** left lateral, and **D, D'** ventral views.

Comparisons with other species. Adult *Toxicocalamus atratus* is easily distinguished from all other members of the *T. loriae* species group except *T. nymani* in having a dark venter that is black or very dark brown in life and either uniformly brown or with each ventral banded dark brown in preservative. Other members of this complex have venters that are yellow (*T. lamingtoni*, *T. loennbergii*, *T. loriae*, *T. spilorhynchus*, *T. vertebralis*), grey (*T. nigrescens*), or yellow or pale grey with grey bands across each ventral (*T. mattisoni*). *Toxicocalamus atratus* can be distinguished from *T. nymani* by its juvenile ventral colour pattern (pale yellow with a black spot on the lateral edges of each ventral vs. uniformly black or dark brown but banded with dark brown in preservative in *T. nymani*), larger size (males to 655 mm SVL, females to 682 mm SVL vs. 422 mm and 540 mm, respectively, in *T. nymani*), and the greater number of ventrals with overlap in both sexes (males 177–206 vs. 178–198 in *T. nymani*; $t_{65} = 5.0261$, $p < 0.00001$; females: 187–218 vs. 191–210 in *T. nymani*, $t_{62} = 4.3472$, $p = 0.000026$). Although the venter of *T. atratus* is much darker, its banded pattern in most preserved specimens could perhaps be mistaken for the paler banded pattern seen in preserved *T. nigrescens* and *T. mattisoni*. *Toxicocalamus*

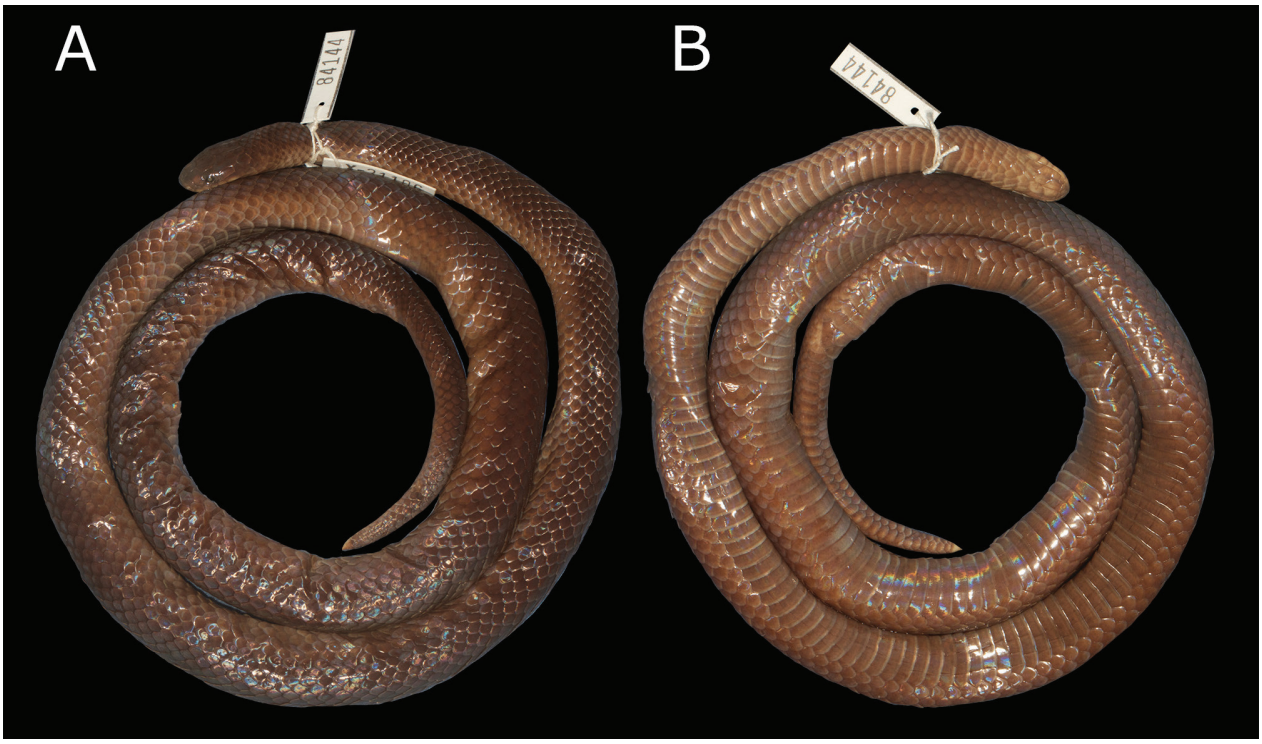

Figure 15. A Dorsum and **B** venter of the *Toxicocalamus atratus* **sp. nov.** holotype (MCZ R-84144) from Kundiawa, Chimbu Province, PNG.

atratus can be further distinguished from *T. nigrescens* in having a shorter preocular (preocular approximately squarish, slightly longer than tall in *T. atratus* vs. more than twice as long as tall in *T. nigrescens*), and from *T. mattisoni* in having the preocular usually contacting nasal (vs. never in *T. mattisoni*) and usually two postoculars (vs. one in *T. mattisoni*).

Description of the holotype. Adult female, 590 mm SVL + 72 mm TL = 662 mm TTL. Rostral broader than high, notched ventromedially; internasals angulate, semi-triangular, wider than long; prefrontals distinct from preoculars, approximately square but angled laterally and posteriorly, slightly wider than long (Fig. 14A, A'), bordered below by preocular and nasal; preoculars angulate, slightly longer than high, bordered anteriorly by nasal, below by second and third supralabials (Fig. 14B, B', C, C'); frontal shield-shaped, lateral margins straight, not fused with supraoculars, anterior margin extending slightly anterior to remainder of scale medially; parietals approximately twice as long as wide. Nasals divided by large nares, with a short groove above and below along the posterior of naris. Postoculars single on each side, irregularly pentagonal in shape; one elongate anterior temporal above fifth and sixth supralabials, separating latter from parietal; two posterior temporals, subequal in size, lower abutting posterodorsal margin of sixth supralabial. Supralabials six on each side, third and fourth entering eye; infralabials six, first three in contact with anterior genial. Mental small, shallow, triangular, wider than deep, bordered behind by first supralabials; anterior genials slightly larger than posterior genials, in medial contact along entire length; posterior genials longer on left than right, completely separated by single elongate intergenial, which is widest posteriorly; seven gulars separate intergenial from first ventral in the midline; first sublabial separates posterior genial from fifth infralabial (Fig. 14D, D'). Eye relatively small; pupil round.

Dorsal scale rows 15-15-15, smooth, not notched posteriorly, without apical pits. Ventrals 207, each approximately four times wider than long; two scales covering vent; subcaudals 30, paired. Tail tipped by a pointed conical spine.

In preservative (50 years after collection), dorsum dark brown dorsally, slightly paler laterally (Fig. 15A). Venter dark brown, anterior ventrals dark brown, narrowly margined with paler brown posteriorly (Fig. 15B), subcaudals dark brown. Supralabials yellow, dark brown on approximately dorsal half of each scale. Head dark brown with vague yellow blotch on each prefrontal just extending onto posterolateral corner of each internasal. No pale nuchal collar present. Chin and throat with pale straw yellow ground heavily suffused with brown throughout, imparting a largely brown impression overall. Tail spine white. Iris black.

Variation. Preoculars contact nasals in most specimens but are separated by prefrontal contact with the second supralabial on both sides in 17 specimens and on one side in nine specimens; preoculars are invariably separated from contact with internasals. Postoculars one (25.5%) or two (74%), absent on left side of MCZ R-141849. Posterior temporals two (58%) or three (42%). Supralabials six, except five on right side of AMS R14788, CAS 118948, and MCZ R-84142, the left side of MCZ R-116790, and both sides of CAS 115986, 118962, and

Figure 16. Uncollected juvenile *Toxicocalamus atratus* **sp. nov.** from Kutubu area, 1760 m elevation, Southern Highlands Province, PNG, to show the colouration in life. Photographs by Nick Baker.

MCZ R-141849; third and fourth supralabials contacting eye, except third through fifth on right side of AMNH R-75344, and only third supralabial on right side of AMS R14788, CAS 118962, and MCZ R-84142. Infralabials invariably six. Posterior genials in small anterior contact (20% of specimens) or entirely separated (80%) by single intergenial (two small intergenials in AMNH R-72780–81 from Kup). Intergenials widest posteriorly (89% of specimens) but widest centrally in ten (11%).

Dorsal scale rows invariably 15-15-15. Ventrals 177–206 (196 ± 5) in 49 males, 187–218 (206 ± 7) in 43 females; subcaudals 40–47 (44 ± 2) in 48 males, 26–41 (31 ± 3) in 41 females. SC_R 16.9–21.0% (18.3 ± 0.8%) in 48 males, 11.2–17.8% (12.9 ± 1.3%) in 41 females. Tail tipped by a blunt to pointed conical spine. Maximum male SVL = 655 mm, TL_R in 38 adult males 12.9–19.4% (15.5 ± 1.7%); maximum female SVL = 682 mm, TL_R in 33 adult females 6.7–18.7% (10.2 ± 2.2%); sexual size dimorphism present ($t_{71} = 2.5689$, $p = 0.0062$). There appears to be an ontogenetic effect of tail length in juvenile males, whose tails are relatively shorter (mean TL_R 12.5 ± 0.6; $n = 10$) than those of adult males (mean TL_R 15.6 ± 1.7; $n = 39$). This difference is not present in females (mean TL_R in eight juveniles 10.4 ± 1.4, in 32 adults 9.9 ± 1.7). The vent is typically covered by two scales, but this covering is incompletely formed in AMNH R-75355 and covered by a single scale in CAS 103774–75 and 139584.

Variation in colouration is largely ontogenetic, with adults being black or dark brown above and below, although these colours fade to brown in preservative, and often with each ventral appearing banded with dark and light brown as colouration fades in preservative. Small juveniles (SVL = 161–262 mm) are often paler than this, with a dark vertebral stripe often being present, but this seems to be lost as animals darken ontogenetically. Small juveniles also have a large yellow blotch on each prefrontal and an incomplete yellow nuchal collar whose sides are separated by two to four brown dorsal scale rows (Fig. 4M, N, 16). These markings usually disappear in adults but may be retained as vague markings. Furthermore, small juveniles have a yellow venter with each ventral marked on each lateral extremity with a black spot. Because the first row of dorsal scales is also yellow or pale brown, this imparts the impression of the venter having a row of black spots along each side. In a few small specimens (CAS 103374, 113666, MCZ R-116774), these yellow venters also have a few small brown flecks. The tail spine is white in most specimens but pale brown in two.

Colour in life. Photographs of MCZ R-84026 (540 mm SVL) and R-111767 (480 mm SVL), both adult males, show uniformly black animals, with the venter of the latter also being black (Fig. 11E, F). Photographs provided to us by Nick Baker of an uncollected juvenile from Southern Highlands Province, PNG, show an animal with a black dorsum (Fig. 16A), yellow venter having a mid-ventral row of brown spots (Fig. 16B, C), and yellow supralabials, a yellow spot on each prefrontal, and a very

incomplete nuchal collar consisting of only two small yellow lateral spots (Fig. 16C, D).

Fred Parker, the collector, took numerous field notes on this species in life. Colour patterns for adults were described by him as follows: "Black with pair of yellow spots on the snout, partial bars laterally on back of head." (MCZ R-121547, SVL = 360 mm); "Part grown, black above and below." (CAS 139564, SVL = 455 mm); "Olive-black above, a narrow darker vertebral line from behind head to tip of tail. Lips translucent pinkish marked grey. Ventrals greyish, paler than dorsum." (MCZ R-84142, SVL = 470 mm); "Uniform iridescent black on dorsal surfaces. Ventrally and laterally uniform black with no markings. Lips faintly yellowish. Spike on tail yellow with black tip." (MCZ R-84026, SVL = 540 mm). "Black above, brown laterally. Grey-brown underneath. Lips paler." (CAS 99916, SVL = 610 mm). "Black above and below. Head slightly paler with olive tinge. Highly iridescent." (AMNH R-98495, SVL = 515 mm).

He described the colour pattern for two juveniles as follows: "A juvenile with bright yellow bar across snout and short similar bars laterally on back of head from behind corner of jaw to posterior corners of large head shields but not meeting dorsally. Ventrally, translucent yellow, with a black spot at side of each ventral [scale]. Tail with yellow spike at tip, the spike with small brown tip. Whole of upper lips yellow. Some greyish markings under the head. A narrow dark vertebral stripe. Flanks paler than dorsum. Pair of anals marked grey." (MCZ R-83218, SVL = 211 mm); "Grey-brown above, whitish below, yellow bar on snout, lips yellow, part bars laterally at back of head." (AMNH R-98498, SVL = 299 mm). Finally, a neonate that hatched on 23 December 1964 was recorded as black above, translucent below, and with paler lips; we have been unable to locate this specimen in any museum catalogue.

Range. Known from the Central Highlands of Papua New Guinea and extending as far east as the southern side of the Ekuti Dividing Range, Morobe Province, at elevations of 840–2140 m (Fig. 6B).

Ecological notes. Considered common at Kundiawa, Chimbu Province, PNG (Fred Parker, pers. comm.). For example, 88 animals were obtained in gardens on 3 December 1967. In general, most individuals of this species were collected during the day from under piles of vegetation in sweet potato gardens. In forested situations, only the occasional animal would be collected in or under logs during the day. Parker never observed the species active at night, which is consistent with the first author's experience with other *Toxicocalamus* species. One specimen (MCZ R-111769, SVL = 437 mm) contained a large earthworm in its stomach.

Parker's field notes also recorded that MCZ R-84144 (SVL = 590 mm) laid two eggs on 25 May 1964 and one on the following day; one of these hatched on 23 December, indicating a 7-month incubation period. MCZ R-111790 (SVL = 440 mm) was captured on 3 December 1967 and "laid four eggs after capture," CAS 115987 (SVL = 375 mm) was captured on 29 February 1969 when gravid with three eggs, CAS 115992 (SVL = 435 mm) and CAS 115996 (SVL = 625 mm) were captured on 11 March 1968 and noted to be gravid, and CAS 115997 (SVL = 480 mm) was captured on 19 April 1968 gravid with six eggs. All of these snakes were from Kundiawa, Chimbu Province. Thus, gravid females were captured during the months of February to April and eggs were laid in May and December, suggesting that reproduction in this species occurs year-round. The observed eggs were cylindrical, bluntly rounded at each end, and measured 35 × 12 mm, 35 × 12.5 mm, and 39 × 14 mm.

Remarks. The primary feature distinguishing *T. atratus* from the very similar *T. nymani* is the ontogenetic change in ventral colour pattern, which is dramatic in *T. atratus* but absent in *T. nymani*. Some populations of *T. nymani* also retain the yellow nuchal collar and prefrontal spots into adulthood, which individuals of *T. atratus* never do. Furthermore, Lönnberg (1900: 579) described the dorsal colour of his freshly preserved specimens of *T. nymani* as "bronzy brown (almost blackish in the largest specimen)", whereas notes by Fred Parker recorded that a neonate and small juvenile of *T. atratus* were black above (see also Fig. 16). As noted in the Comparisons section above, *T. atratus* also differs from *T. nymani* by its larger maximum size and, statistically, by its greater mean count of ventral scales in both males and females. These differences are confirmed by post-hoc Tukey Tests in an ANOVA ($p = 0.00551$ and $p = 0.04195$ for males and females, respectively). Its lesser mean SC_R in males also differs significantly from that seen in *T. nymani*. Each of these differences suggests that *T. nymani* and *T. atratus* are separate species, but scalational differences that would be useful to field observation are not obvious at this point. It will be useful to investigate this issue in greater detail once fresh specimens with tissues and colour notes become available for both species.

We refer the sole specimen from south of the Ekuti Divide (BPBM 17423) to this species on the basis of its ventral colour pattern, which indicates the lateral rows of brown spots on each ventral. However, the venter of this specimen is somewhat discoloured, and its collection locality is close to Wau, where *T. nymani* primarily resides, so confirmation of this assignment to *T. atratus* would be desirable once further specimens become available. This uncertainty leads us to exclude this specimen from the series of paratypes.

Discussion

The species that appear closely related to *Toxicocalamus loriae* – based on the phylogeny of Strickland et al. (2016) with the addition of *T. goodenoughensis* (Roberts & Austin, 2020) – seem to break down into three groups based on ventral colour pattern. The first of these comprises those species with yellow venters as adults and includes *T. loriae*, *T. lamingtoni*, *T. loennbergii*, *T.*

spilorhynchus, and *T. vertebralis*. The second group comprises those with black venters (appearing brown or brown banded in preservative) and includes *T. nymani* and *T. atratus*. The last group is somewhat intermediate between these, comprising species having venters with varying degrees of grey or brown pigmentation in life, and includes *T. goodenoughensis*, *T. mattisoni*, *T. mintoni*, *T. nigrescens*, and *T. pachysomus*. The first group occurs along the mountainous spine of New Guinea from the far west of the island to the southeastern end of the island; the second group occupies the Central Highlands of Papua New Guinea and areas adjacent to the east and northeast; the third is restricted to Milne Bay Province, which comprises the southeastern tip of New Guinea and adjacent islands. More comprehensive phylogenetic assessment is required to determine whether any of these colour-pattern groups is monophyletic, but it seems likely that the black-ventered species are and that the third group likely is not, based on the results obtained by Strickland et al. (2016).

This study increases the number of known *Toxicocalamus* species from 17 to 23. It seems likely that additional species exist in this species complex for at least two reasons. First, with the exception of the four *T. loennbergii* specimens from Fakfak in far western New Guinea and one specimen from Angguruk (4.20°S, 139.43°E; ZSM 54/2015), collected in 1979, the western half of the island is completely lacking in specimens of these snakes. This cannot be a true range disjunction and no doubt stems from a lack of reptile surveys over the past century in that large region. Second, we have examined several small snake samples that we cannot assuredly assign to any of the species treated herein. These comprise a total of 19 specimens from nine localities, with samples consisting of merely 1, 1, 1, 1, 2, 2, 2, 3, and 6 specimens/locality, and we include them as *Toxicocalamus* sp. in the Appendix (including the holotype of the purported taxon *T. longhagen*). One or two of them may belong to species discussed herein, but at this time we cannot confirm this with confidence. Meanwhile, others show character combinations that are inconsistent with an assignment to the *T. loriae* Group species as defined herein. Additional material of good preservation quality, combined with good photographs, will be needed to resolve the status of the populations represented in these specimens. Related to this, it will also be of interest to determine whether *T. nymani* truly contains the two dramatically different colour patterns referred here to that species or whether they in fact represent distinct species that exhibit range overlap on the Huon Peninsula.

These few specimens point to a larger limitation in further resolving species in this taxonomic complex: the need to obtain ontogenetic series for samples from single locations so as to better understand the variation among samples seen among localities with few specimens. We have shown that *T. atratus* and *T. spilorhynchus* exhibit ontogenesis in ventral colour pattern, and the same has been demonstrated for *T. nigrescens*. Ventral colour-pattern ontogenesis may also occur in *T. mattisoni* and *T. goodenoughensis* – given the variation described in those species – though sample sizes are too small to be certain. The critical value of ventral colour pattern for identifying species in this complex requires a broader understanding of the degree to which these and other species – both described and undiscovered – vary ontogenetically and among adults. These details need to be documented prior to long-term storage because of the relatively rapid alteration of some colour-pattern details in preservation.

In combination with the work of Kraus (2017, 2020), this report now allows us to assign species names to most of the numbered clades of Strickland et al. (2016). To wit, Clade 1 = *T. loriae*, Clade 2 = *T. spilorhynchus*, Clade 3 = *T. lamingtoni*, Clade 5 = *T. nigrescens*, and Clade 6 = *T. mattisoni*. Clade 4 of Strickland et al. (2016) is still of uncertain taxonomic resolution. That lineage is from Normanby Island in the d'Entrecasteaux Archipelago, and it is morphologically very similar to *T. nigrescens* from immediately adjacent Fergusson Island. There are only two specimens each for these two lineages, and only one of each is an adult. Hence, insufficient material is available to find compelling diagnostic morphological differences between the two. In the phylogeny of Strickland et al. (2016), Clade 4 was joined as sister to the morphologically divergent *T. pachysomus*, but the branch connecting those two lineages with *T. nigrescens* was very short and with low support values; hence, it is reasonable to view the relationships among these three lineages to be an unresolved polytomy requiring further investigation. This result was not changed by the later addition of *T. goodenoughensis* to this tree (Roberts and Austin 2020). It will be instructive to determine whether additional loci can resolve these relationships and whether such resolution places Clade 4 with *T. nigrescens* or confirms its recognition as an independent lineage.

Of the 23 species of *Toxicocalamus*, 12 are restricted to the Papuan Peninsula or its offshore islands, a geological region referred to as the East Papuan Composite Terrane (EPCT, Pigram and Davies 1987; Pigram and Symonds 1991). Six species are restricted to the Central Highlands ($n = 4$) or barely extend beyond that region to the mountains just east of there ($n = 2$), one is restricted to the Onin Peninsula in far western New Guinea, one is found in two of the north-coast ranges in Papua New Guinea, and three are more widespread within Papua New Guinea. One additional candidate species lacking sufficient specimen numbers to resolve its taxonomic status also occurs in the EPCT (Strickland et al. 2016). Clearly, the EPCT has been a centre of diversification for this genus, and eight of the 12 species found there are endemic to the small Milne Bay Region, as are numerous other endemic reptiles and amphibians (Kraus 2021). It might be thought that this diversity signifies a centre of origin for the genus, but the phylogenetic relationships retrieved by Strickland et al. (2016) were ambiguous on this point, placing a clade comprised of two of the widespread species (*T. preussi* and *T. stanleyanus*) as sister to all other members of the genus. We note, however, that the genus is estimated to have originated approximately 20 million years or so ago and that the two widespread *Toxicocalamus* species retrieved as basal in the phylogeny of Strickland et al.

(2016) occupy regions of New Guinea that formed much more recently than that time (Cloos et al. 2005). It makes more geological sense that the genus arose on the EPCT, a region that has been subaerial since the origin of *Toxicocalamus*. Consequently, we suggest that the rooting of the *Toxicocalamus* phylogeny obtained by Strickland et al. (2016) merits further testing to confirm the likely geological origin of the genus.

Since publication of the key to *Toxicocalamus* in Kraus (2020) seven additional species have now been added to the genus, requiring a revised key, which we provide here.

Key to *Toxicocalamus*

1a Subcaudals entire ..... *T. holopelturus*
1b Subcaudals divided 2
2a Preocular fused to prefrontal 3
2b Preocular distinct from prefrontal 9
3a Frontal fused to supraoculars; ventrals wide, 5–6 times wider than first row of dorsal scales ..... *T. mintoni*
3b Frontal distinct from supraoculars; ventrals narrow, 3–4 times wider than first row of dorsal scales 4
4a Internasal distinct from prefrontal; temporal scale separates last supralabial from parietal 5
4b Internasal fused with prefrontal; temporal fused with last supralabial, allowing supralabial contact with parietal 8
5a Vent covered by a single scale; 5 supralabials; venter without dark stripes 6
5b Vent covered by two scales; 6 (rarely 7) supralabials; venter with a pair of longitudinal dark stripes 7
6a Ventrals 281; last supralabial broader than tall; chin and throat brown; ventrals and subcaudals brown, barred with darker brown; pale nuchal collar absent ..... *T. cratermontanus*
6b Ventrals 227–255; last supralabial taller than broad; chin and throat white; ventrals and subcaudals white, with or without small brown spots; pale nuchal collar present ..... *T. stanleyanus*
7a 15 dorsal scale rows at midbody ..... *T. misimae*
7b 17 dorsal scale rows at midbody ..... *T. longissimus*
8a Four supralabials; postocular fused with supraocular; 15 dorsal scale rows at midbody ..... *T. buergersi*
8b Five supralabials; postocular usually distinct from supraocular; usually 13 (rarely alternating between 13 and 15) dorsal scale rows at midbody ..... *T. preussi*
9a Prefrontal fused to internasal ..... *T. pumehanae*
9b Prefrontal distinct from internasal 10
10a Dorsum spotted 11
10b Dorsum uniformly dark grey or brown, without pale spots 13
11a Dorsum yellow with a brown spot on posterior of every scale ..... *T. ernstmayri*
11b Dorsum dark grey or brown with pale spots 12
12a Pale dorsal scales sparsely scattered across dorsum; venter white ..... *T. grandis*
12b Almost all dorsal scales except vertebral row with pale yellow spot; ventrals with broad black spot on each ..... *T. spilolepidotus*
13a Internasal and preocular in contact, separating nasal from prefrontal 14
13b Internasal and preocular not in contact, separated by prefrontal 15
14a Habitus robust; nasal divided by large naris; no yellow on prefrontals; venter uniformly brown in life ..... *T. pachysomus*
14b Habitus slender; nasal entirely surrounds naris; yellow markings on prefrontals; venter dark yellow heavily mottled with dark brown posteriorly ..... *T. goodenoughensis*
15a Venter uniformly yellow or yellow with mid-ventral row of brown spots 16
15b Venter brown, grey, black, or yellow barred with grey or brown 20
16a Two in-line intergenials between posterior genials ..... *T. loriae*
16b Single intergenial between posterior genials 17
17a Vent covered by a single scale; dark vertebral line absent ..... *T. lamingtoni*
17b Vent covered by two scales; dark vertebral line present 18
18a Single postocular; four infralabials in contact with each posterior genial; snout short (SNL/SNW = 0.93–0.99); pale blotch on each parietal in adults ..... *T. loennbergii*
18b Two postoculars; three infralabials in contact with each posterior genial; snout long (SNL/SNW = 0.95–1.40); pale blotch absent on parietals in adults 19
19a Ventrals 172–184 in males, 178–193 in females; subcaudals 20–29 in females; pale blotch on each prefrontal; venter yellow dusted with brown in adults ..... *T. spilorhynchus*
19b Ventrals 194–210 in males, 203–232 in females; subcaudals 31–38 in females; pale blotches absent on prefrontals; venter uniformly yellow in adults ..... *T. vertebralis*
20a Venter black in life, banded with brown in preservative; preocular short, slightly longer than diameter of eye, approximately same width as second supralabial 21

20b Venter grey or yellow in life, banded with grey or brown; preocular long, significantly longer than diameter of eye, longer than second supralabial 22
21a Juvenile venter black, banded with brown in preservative; body size smaller (male SVL to 422 mm, female SVL to 540 mm) ..... *T. nymani*
21b Juvenile venter yellow with row of black spots down each side; body size larger (male SVL to 655 mm, female SVL to 682 mm) ..... *T. atratus*
22a Prefrontal and second supralabial in contact, separating preocular from nasal; venter yellow or grey, banded with brown or grey ..... *T. mattisoni*
22b Prefrontal separated from second supralabial by contact between preocular and nasal; ventrals grey, banded with darker grey or blackish brown ..... *T. nigrescens*

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Appendix 1

Examined specimens are listed using their respective museum abbreviations, with the addition of FK (Fred Kraus Field Series numbers). Species are listed alphabetically. Locality names include the country in capital letters, lesser administrative units (e.g., provinces) in small capitals, and specific information (e.g., islands, regions) in regular font.

***Toxicocalamus goodenoughensis* (*n* = 2).** PAPUA NEW GUINEA, Milne Bay Province: Goodenough Island, Moniu River, LSUMZ 89042 (paratype); Blawin River, LSUMZ 89043 (holotype).

***Toxicocalamus lamingtoni* (*n* = 18).** PAPUA NEW GUINEA, Morobe Province: Garaina, AMNH 101100, 101102, 104084–85, 111810. — Oro Province: Mt. Lamington, AMS R9351 (holotype), R9352, 61027 (paratypes), R9851; Popondetta, 8.76°S, 148.24°E, elev. 100 m, AMNH R-111810, MCZ R-141009; Itokama, 9.1200°S, 148.2646°E, elev. 780 m, BPBM 36169, 36171; Waria Valley, 7.8055°S, 147.3986°E, elev. 485 m, BPBM 38855; Mt. Trafalgar, 9.2238°S, 149.1561°E, elev. 187 m, BPBM 39813; Akupe Camp, 9.286°S, 148.2727°E, elev. 700 m, BPBM 43027; Umwate, 9.2673°S, 148.2399°E, elev. 800 m, BPBM 43028–29, 43032.

***Toxicocalamus loennbergii* (*n* = 4).** INDONESIA, West Papua Province: Onin Peninsula, north of Fakfak town, elevation 520 m, BMNH 1946.1.18.24 (lectotype of *Aposthocalamus loennbergii* Boulenger, 1898), 1946.1.18.25–26 (paralectotypes of *A. loennbergi*), MCZ R-76634 (paralectotype of *A. loennbergii*).

***Toxicocalamus loriae* (*n* = 19).** PAPUA NEW GUINEA, Central Province: Haveri, 9.40°S, 147.60°E, MSNG 29141 (holotype of *Toxicocalamus loriae*); Dinawa, 8.60°S, 146.90°E, BMNH 1946.1.17.53 (holotype of *Apistocalamus pratti*); near Fane, 8.45°S, 147.10°E, PNGM 23158; Mafulu, 8.55°S, 147.00°E, elev. 1100 m, AMNH R-59067, BMNH 1935.5.10.174; Laronu, 9.44°S, 147.98°E, elev. 880 m, BPBM 19502, 19505–06, FK 9260; W slope Mt. Obree, 9.44°S, 148.01°E, elev. 1570–1640 m; BPBM 19503–04; Ower's Corner, 9.36°S, 147.49°E, elev. 660 m, MCZ R-150803; Tapini, 8.36°S, 146.99°E, elev. 960 m, USNM 195619; "Astrolabe Mountains," no specific locality, NMW 27383.1–2. — Milne Bay Province: Agaun, 9.93°S, 149.39°E, elev. 1000 m, BPBM 10966–67, PNGM 24649b. — Oro Province: Isurava, 8.99°S, 147.74°E, elev. 1260 m, BPBM 44892.

***Toxicocalamus mattisoni* (*n* = 7).** PAPUA NEW GUINEA, Milne Bay Province: Mt. Simpson, BPBM 17987 (paratype), 17988 (holotype), 17989 (paratype), 181164–66 (paratypes), PNGM 25152.

***Toxicocalamus mintoni* (*n* = 1).** PAPUA NEW GUINEA, Milne Bay Province: Sudest Is., Mt. Riu, BPBM 20822 (holotype).

***Toxicocalamus nigrescens* (*n* = 2).** PAPUA NEW GUINEA, Milne Bay Province: Fergusson Is., Basima, BPBM 16544 (paratype); Fergusson Is., Oya Waka, BPBM 16565 (holotype).

***Toxicocalamus nymani* (*n* = 39).** PAPUA NEW GUINEA, Madang Province: Maratambu, Adelbert Mts., 5.06°S, 145.47°E, elev. 700 m, AMNH R-82332; Maibang, 5.63°S, 146.30°E, elev. 450 m, IRSNB 733678; Karkar Is., Miak, 4.59°S, 145.90°E, elev. 20 m, AMS R25236, R25752, R25304; Karkar Is., Mom, 4.61°S, 145.92°E, elev. 280 m, AMS R25608; Wanang, 4.90°S, 145.32°E, elev. 120 m, BPBM 31257. — Morobe Province: Boana, 6.43°S, 146.82°E, elev. 1020 m, CAS 113668; Garaina, 7.89°S, 147.14°E, elev. 770 m, MCZ R-152432; Kalolo, 6.03°S, 147.14°E, elev. 750 m, AMNH R-142887, BPBM 5440, 5442; Lialun, 6.08°S, 147.58°E, elev. 120 m, MCZ R-76627–28, ZMB 24343–44, 78770–71; Masba Creek, 6.49°S, 147.52°E, elev. 700 m, AMNH R-95579–80; Pindiu, 6.50°S, 147.50°E, elev. 790 m, AMNH R-95578, R-95582; Mt. Rawlinson, 6.50°S, 147.25°E, elev. 1340 m, AMNH R-95581; Sattelberg, 6.50°S, 147.75°E, elev. 800 m, BMNH 1946.1.17.57 (paralectotype of *Pseudapistocalamus nymani*), UUZM 290/2387 (lectotype of *P. nymani*); Tewep, 6.36°S, 146.92°E, elev. 1350 m, BPBM 3397, 3399; Wau area, 7.34°S, 146.72°E, elev. 1070–2000 m, BPBM 17173, 17417, 17451–52, 18217, 23669, 30638, CAS 198320–22, PNGM 24716; Zenag, 6.95°S, 146.58°E, elev. 1470 m, AMNH R-85744.

***Toxicocalamus pachysomus* (*n* = 1).** PAPUA NEW GUINEA, Milne Bay Province: Cloudy Mts., BPBM 15571 (holotype).

***Toxicocalamus* sp. (*n* = 19).** INDONESIA, Highland Papua Province: Angguruk, Jahûli River, ZSM 54-2015. — PAPUA NEW GUINEA, Eastern Highlands Province: Wonenara, Yaiya Valley, elev. 1650 m, UPNG 1213–18. — Madang Province: Bundi, elev. 1150 m, AMS R124482. — Milne Bay Province: Agaun, elev. 1010 m, PNGM R24649a, UPNG 4840, Bonenau, elev. 1340 m, UPNG 7105, 7107–08, Mai-U River, elev. 430 m, UPNG 3536. — Morobe Province: Garaina, 7.89°S, 147.14°E, elev. 770 m, MCZ R-152430. — Oro Province: Kokoda Track, PNGM R22762, Eora Creek, elev. 1800 m, BPBM 44893. — Western Highlands Province: Dobel, Mt. Hagen, elev. 1700 m, UPNG 3992, PNGM R22160 (holotype of *T. longhagen*).