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A new species of New Guinea Worm-Eating Snake (Serpentes, Elapidae, *Toxicocalamus* Boulenger, 1896) from Western Highlands Province, Papua New Guinea

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Abstract

We describe a new species of New Guinea Worm-Eating Snake (Elapidae: *Toxicocalamus*) from a specimen in the reptile collection of the Papua New Guinea National Museum and Art Gallery. *Toxicocalamus longhagen* **sp. nov.** can be easily distinguished from other species of this genus by the presence of paired subcaudals, a preocular scale unfused from the prefrontal scale, a prefrontal distinct from the internasal scale that contacts the supralabials, a single large posterior temporal and two postocular scales. The new taxon is currently known only from one specimen, which was collected from Mt. Hagen Town in Western Highlands Province, Papua New Guinea in 1967. The new species was originally identified as *T. loriae*, but the unique head scalation and postfrontal bone morphology revealed through micro-computed tomography scanning easily distinguish the new species from *T. loriae sensu stricto*. This is the first species of this genus described from Western Highlands Province.

Abstract in Tok Pisin

Mipela tokaut lon nupela kain sinek I save kaikai ol liklik sinek insait lon graun lon New Guinea (Elapidae: *Toxicocalamus*) blo wanpela sinek I bin stap lon ol sinek koleksen insait lon Papua New Guinea National Museum and Art Gallery. *Toxicocalamus longhagen* **sp. nov.** em u ken lukim isi tru lon ol arapela wankain poro blo em lo ol wantok blo em we u ken lukim tupela aninit lo tel, na polhet blo eye girere or sikin stap em yet lon polhet na nus girere wantem lo antap wisket, na tupela girere stap baksait lo ai blo em. Dispela nupla kain sinek em nau yet ol kisim save lon wanpla sinek ol kisim lon Mt. Hagen Taun lon Western Highlands Province, Papua New Guinea lon 1967. Dispela nupela kain sinek em pastem tru ol givim nem olsem *T. loriae* tasol em gat wanpela spesol kain girere lo polhet blo em I tok aut lon liklik masin/computa I galasim isi namel lon nupela sinek na *T. loriae* sensu stricto. Dispela em nambawan kain sinek ol kisim save lo wantok blo em na tok klia olsem em kam lo Western Highlands Province.

Key Words

Australasia, fossorial, Melanesia, micro-computed tomography, morphology

Introduction

New Guinea is an island of superlatives: the largest tropical island in the world (Pratt and Beehler 2014), richest flora in the world (Cámara-Leret et al. 2020), and both one of the most diverse terrestrial vertebrate faunas and rates of endemism of any wilderness area in the world (Mittermeier et al. 2003). Vicariant speciation on the island has been driven by significant uplift of the fold belt creating the Central Cordillera and other ranges, caused

by the northern movement of the Australian plate colliding with the Caroline plate and its associated arc terranes during the late Miocene and early Pliocene. (Allison 1996; Hall 2002; Hill and Hall 2003; van Ufford and Cloos 2005; Toussaint et al. 2014; Slavenko et al. 2020). One of the many diverse groups of vertebrates are the squamates, *i.e.*, snakes and lizards, comprising upwards of 412 species (Uetz et al. 2022). To date, the most speciose snake genus endemic to New Guinea is the New Guinea Worm-Eating Snakes, genus *Toxicocalamus* Boulenger, 1896, with 17 species. The past decade has seen increased taxonomic attention on this group, with eight species described since 2009 (Kraus 2009, 2017, 2020; O'Shea et al. 2015, 2018; Roberts and Austin 2020). Seven of the eight species described since the major revision of *Toxicocalamus* by McDowell (1969) are based on specimens collected after 1990 contributing to the construction of the first near-comprehensive molecular-based phylogeny for the genus (Kraus 2009, 2017; Strickland et al. 2016; O'Shea et al. 2018; Kraus 2020; Roberts and Austin 2020). *Toxicocalamus ernstmayri* O'Shea, Parker & Kaiser, 2015 was collected in 1969 by Fred Parker but, due to its impressive size and dorsal coloration, the holotype in the Museum of Comparative Zoology (**MCZ**) had been incorrectly identified as a New Guinea Small-eyed Snake (*Micropechis ikaheka* [Lesson, 1830]). Careful inspection of the MCZ specimen by Mark O'Shea led to its re-identification and description as a new, and the largest, species of *Toxicocalamus* (O'Shea et al. 2015). This serves as a reminder of the value of reexamination of older specimens in collections.

In 2019 we examined a jar of six snake specimens labeled as *Toxicocalamus loriae* (Boulenger, 1898) in the Papua New Guinea National Museum and Art Gallery (**PNGM**) herpetology collection. One of these snakes was not *T. loriae* and could not be identified as any known *Toxicocalamus* species. Below, we describe this new species using external and internal morphology via gross inspection and micro-computed tomography (μCT) scanning.

Materials and methods

The methodology of fixation and preservation are unspecified; however, at time of examination, the specimen was stored in 70% ethanol. Morphological comparisons comprised scalation comparison by eye and, for finer detail, a Wild A5 dissecting microscope. Internal osteology data was generated by micro-computed tomography scanning performed at the Shared Materials and Instrumentation Facility at Duke University. Prior to visualization in Avizo 9.5 (ThermoFisher Scientific, United States), we used the Contrast Limited Adaptive Histogram Equalization (CLAHE) plugin in imageJ (Schneider et al. 2012) on the reconstructed TIFF stack to limit background noise around and enhance local contrast of low-density features such as teeth. After CLAHE adjustment, we constructed three-dimensional volume renderings and surfaces following established segmentation procedures in Avizo. These scans were compared to scans of congenerics that were scanned both at Duke and at the University of Florida Research Service Center (Roberts and Austin 2020).

Morphometric data comprised traditional external morphological characters, *i.e.*, scale counts, scale patterns, and snout-vent length (**SVL**), measured from the tip of the rostrum to the vent. Head length was measured from the tip of the rostrum to the posterior margin of parietal scales, and head width was measured as the widest point anterior to quadrate bone. Ventral scales were counted according to Dowling (1951) and excluded the cloacal plate. Dorsal and subcaudal scales were counted following McDowell (1969). Temporal scale counts include those for both the anterior and posterior temporals. Anterior temporals comprise all scales posterior to and contacting postoculars. Posterior temporals comprise scales in contact with the posterior margin of the anterior temporals. All measurements were taken in millimeters and reported to the first decimal as executed previously in recent *Toxicocalamus* descriptions (Kraus 2017, 2020; O'Shea et al. 2018; Roberts and Austin 2020). Species descriptions follow the format and organization presented by Kraus (2017) where applicable. Roman numerals indicate the number of grooved maxillary fangs attached to the venom gland (McDowell 1969). We also provide an updated dichotomous key modified slightly from Kraus (2020) and Roberts and Austin (2020). Museum abbreviation codes follow those presented by Sabaj (2020).

Results

Toxicocalamus longhagen sp. nov.

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Figs 2–5

Holotype. PNGM 22160, Dobel, Mt. Hagen Town, -5.837603, 144.278022, 1,650 meters a.s.l., 25 February 1967, collector unknown.

Etymology. The specific epithet, *longhagen*, is a combination of "long" – a Tok Pisin word meaning 'from' and "hagen" that refers to the type locality of Mt. Hagen Town (Fig. 1). Tok Pisin is a uniting and official language of Papua New Guinea, the most linguistically complex region on the planet with more than 800 unique languages (Foley 2010).

Diagnosis. A medium-sized species with moderate habitus (566.0 total length, 12.8 maximum lateral width) with 15-15-15 dorsal scale rows, 200 ventral scales, 43 paired subcaudals, preocular present and not fused to prefrontal, preocular not in contact with internasal or nasal; prefrontal separating preocular from internasal and nasal by contacting second supralabial; frontal not fused with supraoculars; internasals not fused; four circumoculars – one supraocular, one preocular, two postoculars; nasals divided; one anterior temporal not fused with supralabials, one posterior temporal; six supralabials, the second in

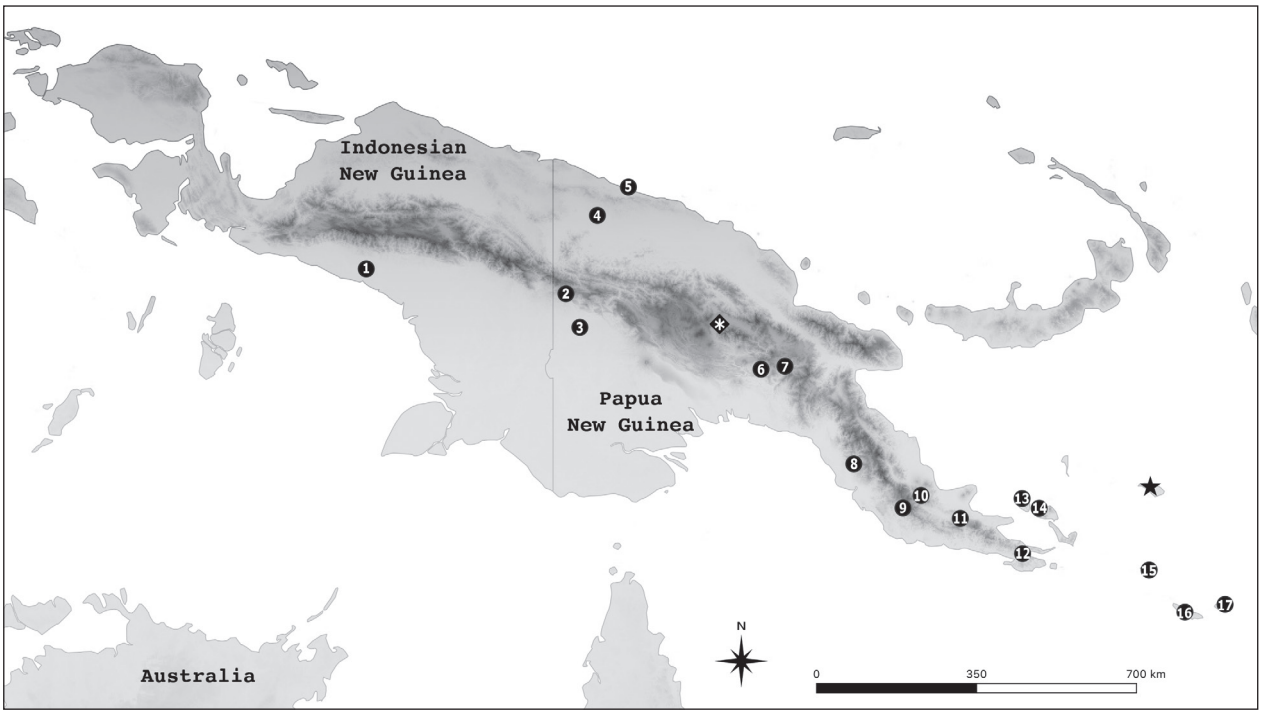

Figure 1. Map of New Guinea and its adjacent islands. Markers indicate type localities of all accepted species of *Toxicocalamus* Boulenger, 1896. The new species, *Toxicocalamus longhagen*, is marked by a diamond with inset asterisk. The type species of the genus, *T. longissimus* Boulenger, 1896, is marked by a star on Woodlark Island. Black circles with numbers represent the type localities for the remaining congenerics (numbered longitudinally west-to-east): 1) *T. grandis* (Boulenger, 1914), 2) *T. ernstmayri* O'Shea, Parker, and Kaiser 2015, 3) *T. preussi anguisinctus* Bogert & Matalas, 1945, 4) *T. buergersi* (Sternfeld, 1913) (precise locality unknown, placement based on O'Shea et al. 2018), 5) *T. preussi preussi* (Sternfeld, 1913), 6) *T. cratermontanus* Kraus 2017, 7) *T. spilolepidotus* McDowell, 1969, 8) *T. stanleyanus* Boulenger, 1903, 9) *T. loriae* (Boulenger, 1898), 10) *T. pumehanae* O'Shea, Allison & Kaiser, 2018, 11) *T. mattisoni* Kraus, 2020, 12) *T. pachysomus* Kraus, 2009, 13) *T. goodenoughensis* Roberts & Austin, 2020, 14) *T. nigrescens* Kraus, 2017, 15) *T. misimae* McDowell, 1969, 16) *T. mintoni* Kraus, 2009, and 17) *T. holopelturus* McDowell, 1969. Localities have not been indicated for current subjective synonyms of *T. loriae*. For thorough taxonomic history and localities of these taxa, please see Kraus (2017), O'Shea et al. (2018), O'Shea et al. (2021).

contact with prefrontal, preventing contact between nasal and preocular; cloacal plate divided; ventrals yellowish with light to dark brown.

Toxicocalamus longhagen can be distinguished from *T. holopelturus* McDowell, 1969 by having paired subcaudals (vs. single); from *T. mintoni* Kraus, 2009, *T. cratermontanus* Kraus, 2017, *T. stanleyanus* Boulenger, 1903, *T. misimae* McDowell, 1969, *T. longissimus* Boulenger, 1896, *T. buergersi* (Sternfeld, 1913), and *T. preussi* (Sternfeld, 1913) by having preocular not fused to prefrontal (vs. fused); from *T. pumehanae* O'Shea, Allison & Kaiser, 2018 by having prefrontal distinct from internasal (vs. fused); from *T. goodenoughensis* Roberts & Austin, 2020, and *T. pachysomus* Kraus, 2009, by lacking contact between internasal and preocular (vs. internasal and preocular in contact); from *T. nigrescens* Kraus, 2017, *T. loriae* (Boulenger, 1898), *T. spilolepidotus* McDowell, 1969, *T. grandis* (Boulenger, 1914), and *T. ernstmayri* by having preocular lacking contact with nasal (vs. preocular contacting prefrontal and nasal).

In having prefrontal in contact with second supralabial, preventing contact between preocular and either internasal or nasal, *T. longhagen* is most similar in head scalation to *T. mattisoni* Kraus, 2020. It can be further distinguished from *T. mattisoni* by presence of two postoculars (vs. one), by having one large posterior temporal (vs. two posterior temporals), and presence of more ventrals (200 vs.170–181).

Toxicocalamus longhagen has scalation similar to some specimens of *Apistocalamus loennbergii* Boulenger, 1908, a taxon currently in synonymy with *T. loriae* (Kraus 2017; Kraus 2020); specifically, in both the new species and some *A. loennbergii* specimens, the prefrontal scale contacts the second supralabial, preventing preocular and nasal scale contact. Kraus (2020) described *A. loennbergii* as having "preocular and nasal scales [that] may or may not be in contact" because they are barely separated on just the right side in the lectotype (BMNH 1946.1.18.24) but bilaterally in contact in the two paralectotypes (BMNH 1946.1.18.25–26). Disregarding this character, *T. longhagen* can still be distinguished from *A. loennbergii* by having two postoculars (vs. 1, "exceptionally two" *sensu* Boulenger 1908), fewer ventrals (200 vs. 213–218), and more subcaudals (43 vs. 22–32).

Description of the holotype. Adult male confirmed by μCT scans showing the presence of well-developed

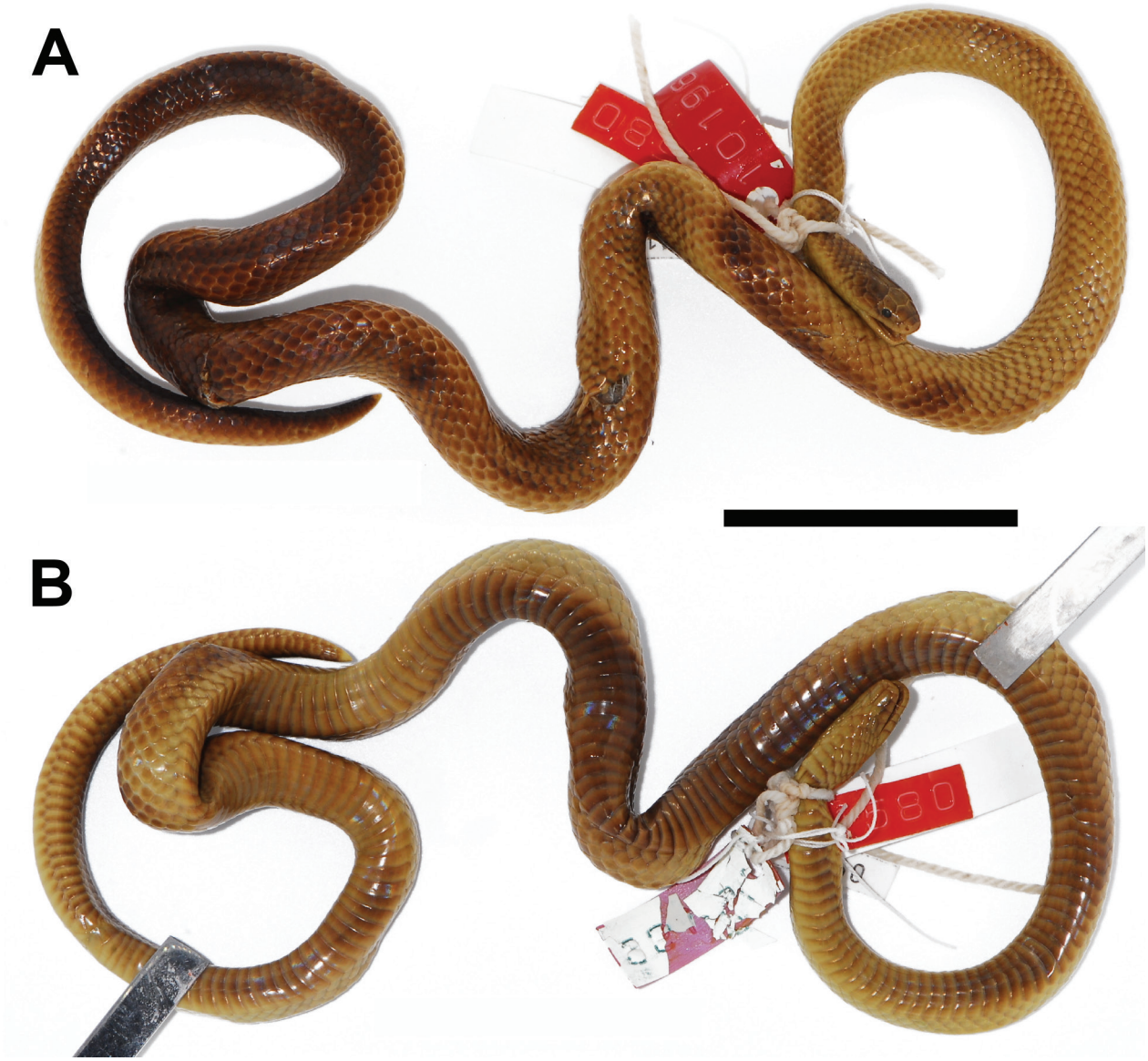

Figure 2. Photographs of **A.** Dorsal **B.** Ventral views of the holotype of *Toxicocalamus longhagen* (PNGM 22160). Metallic rectangles in image B are specimen probes used to pin specimen down for ventral scale visualization. Scale bar indicates 5 cm.

hemipenes, length 19.0, width 3.2 (1.6 each) (Fig. 3). Total length 566.0, snout-vent length 476.0, tail length 90.0, eye-naris distance 2.8, internarial distance 2.8, head length 12.7, head width 8.6.

Rostral broader (3.2) than tall (2.4); internasals near triangular, wider (2.2) than long (1.3); prefrontals pentagonal, unfused to preoculars (Fig. 4D, E), as long (2.8) as they are wide (2.8); preocular fan-shaped, not fused with supraocular and not in contact with internasal or nasal (Fig. 4A, B); parietal scales longer (5.7) than wide (each 3.5), parietal suture 4.0. Nasals divided, separated by large nares; postoculars two, top postocular 3× larger than bottom postocular; anterior temporal single, rectangular, positioned above and in contact with fifth and sixth supralabials; posterior temporal single, positioned between sixth supralabial and parietals. Supralabials six, third and fourth in contact with eye; infralabials six, first four in contact with genials (first three with anterior genials, fourth with posterior genials). Mental triangular, wider (2.0) than tall (1.3); anterior genials in contact, anterior margin bordering first infralabials; posterior genials separated from each other along entire interior margin by intergenial gular (2.7 long by 1.7 wide) and separated entirely from fifth infralabial by two lateral gulars. Eye small (diameter 1.6); pupil round.

Dorsal scale rows 15-15-15, smooth without apical pits. Ventrals 200, 5× wider than long; paired subcaudals 43. Cloacal plate divided, wider (6.3) than long (2.5). Tail with conical spine (length 3.3).

Maxilla with six (right) and five (left) teeth, both sides with maxillary positions for two grooved envenoming front fangs (II,4 / II,3; but each side appears to be missing one of the front envenomating fangs); dentary with 11 (right) and 12 (left) teeth, front three (four on right) separated from remaining posterior dentary teeth by 0.5 mm; palatine with six (right) and seven (left) teeth; pterygoid

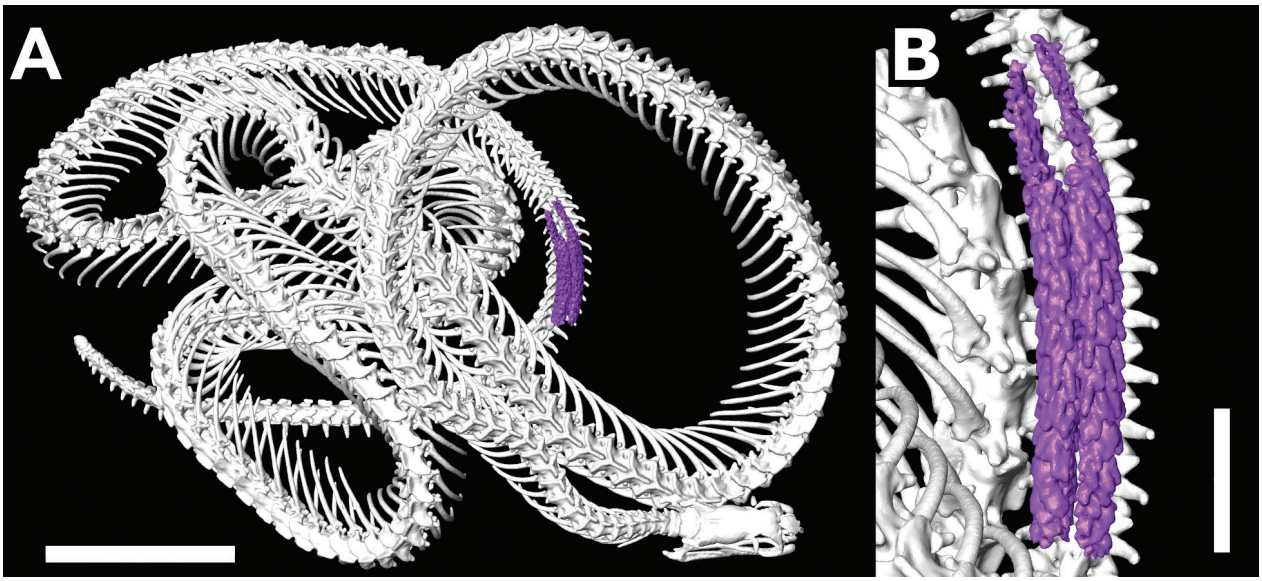

Figure 3. A μCT scan of the holotype of *T. longhagen* (PNGM 22160) showing the **A.** Whole body (scale bar 20 mm) and the **B.** Hemipenes (scale bar 5 mm) highlighted in purple.

with 15 and 16 (left) teeth that extend posteriorly past basisphenoid and basioccipital suture. Postfrontal bones present, triangular or teardrop in shape, curved and extending ventrally at roughly 45-degree angle from skull (Roberts and Austin 2020).

Color in preservative. Color in life is unknown but color in preservative is atypical for the genus. This may reflect the specimen's preservation position; rather than a coil, the specimen's resting position is that of a crumpled-up ball. This fixation position appears to have affected the coloration; at the sharpest turns in the body, the scales facing the outside of the balled-up snake are almost all uniformly pale yellow while those on the inner surfaces (presumably protected more from light damage) are variable shades of dark mousy brown depending on the position along the body (closer to the tail = darker brown). Based on these observations, we suggest that this irregular color pattern has been the product of light exposure, and the intense crumpling of the specimen has facilitated color loss differentially across the body in the specimen. Nonetheless, we describe the current color pattern of the specimen below.

Dorsal head scales almost entirely mousy brown, becoming light yellow laterally on sides of the face once reaching the middle of the supralabials. Dorsum becomes lighter beyond second dorsal scale row behind parietals. Along spine, dorsal scale rows retain small amount of brown, but brownish yellow dominates; a dark vertebral patch of brown, roughly 3 dorsal scale rows in width, present at level of 66th ventral scale. A second dark vertebral patch posterior to first patch at 76th ventral, is roughly 7 scale rows in width; these dark brown patches connect on the right side of body by light brown dorsal scales. Dorsal scales posterior to second brown patch (excluding first row), with pale-yellow background overlain by mousy brown that darkens towards tail; tail darker brown than all other dorsal surfaces.

The lightest ventral scales are on the anterior and posterior thirds of the body, with the scales near mid-body being darker brown than all other ventrals. Each ventral scale darkens anteriorly, with the posterior of each scale light yellow. The ventrals of the first and last third of the body are more contrasting, with the anterior margin of these scales obviously darker brown than the brownish yellow color of the posterior margin. In the mid-body, the darkest ventral scales are almost uniformly dark brown with no yellow posterior margin.

The subcaudals are nearly uniform in color and pattern, with the anterior margin dark brown with a yellow posterior margin. As the subcaudals approach the tail tip, the proportion of dark brown to yellow increases, with the last eight paired subcaudals almost entirely dark brown. The base of the conical tail tip is dark brown, with the rest of the tip the same yellow as that of the subcaudals.

Two red embossed dymo tags (numbers 10198 and 1580) are tied along the neck. The anteriormost tag (10198) has been tied so tightly that the dorsal and ventral scales are damaged and partially torn. The official PNGM catalog tag has its own string but is tied to this anterior 10198 tag as well. Other damages to the specimen include three lacerations to the dorsum that probably occurred during field collection.

Distribution. Currently, *T. longhagen* is only known from the holotype, collected in Dobel Village (1,650 m a.s.l., -5.837603, 144.278022), Mt. Hagen Town, Western Highlands Province, Papua New Guinea. This area now, according to satellite imagery, is within a developing portion of Mt. Hagen Town comprising small structures and small-scale tilled plots of land and gardens. We also examined vouchers of *T. loriae*

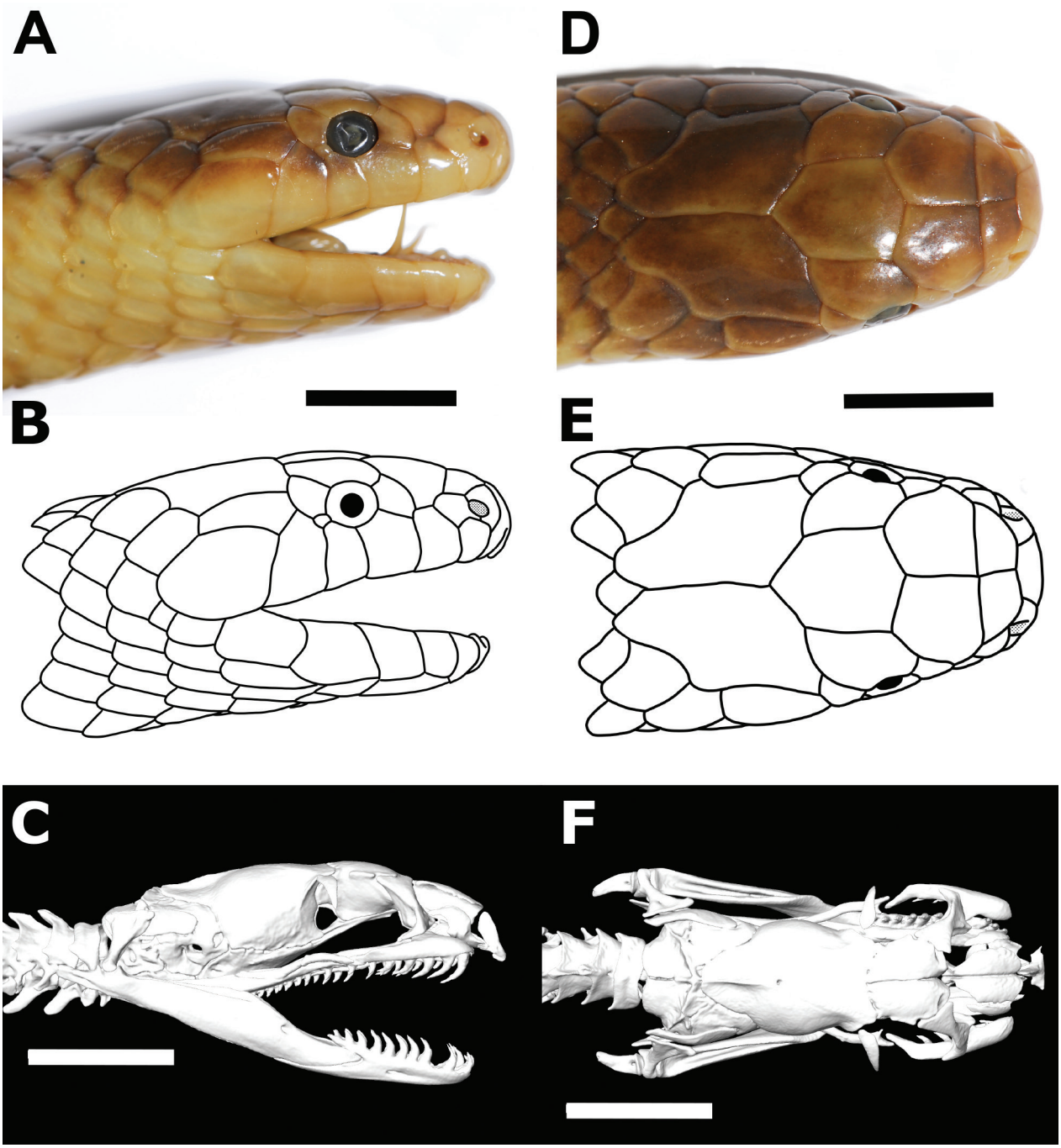

Figure 4. Photograph, line illustrations, and 3D µCT renderings of the right (**A–C**) and dorsal (**E–F**) views of the holotype of *T. longhagen* (PNGM 22160). Scale bars: 5 mm.

from three localities from Chimbu Province in the Waghi Valley east of the *T. longhagen* type locality (Dobel Village): Kup near Mt. Kubor (58 km straight-line distance from Dobel Village), Kondiu (66 km), and Kundiawa (79 km). Based on the straight-line distance from type locality and some morphological similarities, these specimens may be conspecific but we are not confident of this and do not include them as conspecific at this time.

Deposited material. µCT scans of holotype comprise scans of the body and CLAHE corrected scans of the head deposited on Morphosource (Identifier – PNGM 22160).

Discussion

Toxicocalamus longhagen comprises the 18th species of this genus and is currently known from only one specimen; however, this is not unusual for the genus. In addition to *T. longhagen*, five of the eight *Toxicocalamus* species described since 1969 have been done so based on single specimens: *T. mintoni*, *T. pachysomus*, *T. ernstmayri*, *T. cratermontanus*, and *T. pumehanae* (Kraus 2009; O'Shea et al. 2015; Kraus 2017; O'Shea et al. 2018). Orogeny of the mainland Cordillera during the Pliocene likely provided the vicariant mechanism that enabled *Toxicocalamus* diversification within the Cordillera at

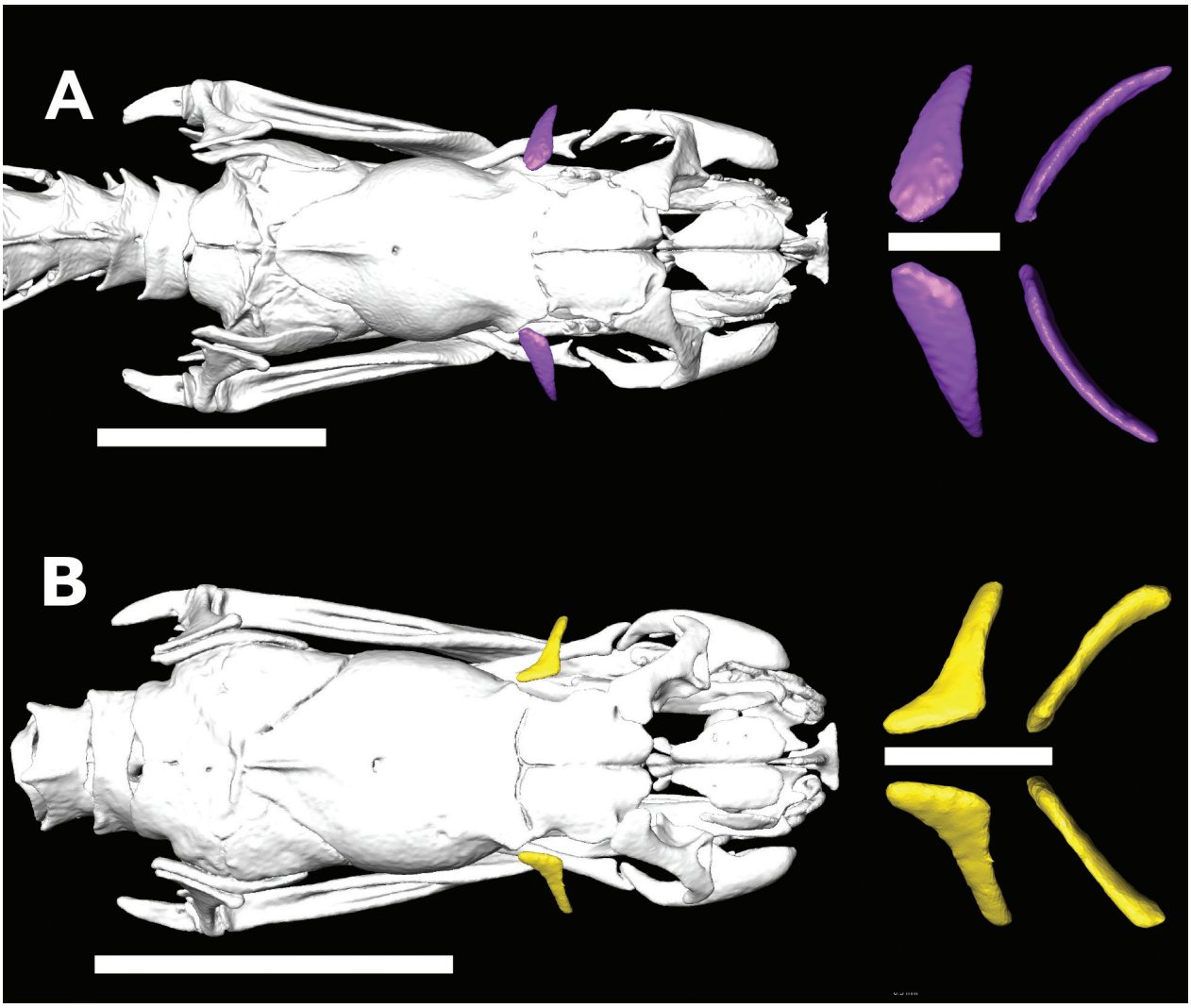

Figure 5. µCT scans of the A) holotype of *T. longhagen* (PNGM 22160) with the prefrontal bones highlighted in purple with closer dorsal and anterior views and a B) voucher from the type locality of *T. loriae* (LSUMZ 129270) with the prefrontals highlighted in yellow. Skull scale bars are 5 mm and postfrontal scale bars are 0.5 mm.

high elevations. *Toxicocalamus* has exceptional species diversity and endemism typically above 1,000 meters in the Central Cordillera of the mainland but is found at lower elevations on the islands southeast of the Papuan Peninsula. This distribution was described as "Highland or island" by O'Shea et al. (2021). Although the southeastern islands are considered low to mid-elevation now, the southeastern archipelagos, *i.e.*, D'Entrecasteaux, Louisiade, Woodlark, are subaerial remnants of a larger New Guinea mainland that sank into the Solomon Sea post-Woodlark Rift formation during the late-Miocene and early Pliocene (Baldwin et al. 2012; Toussaint et al. 2014; Roberts and Austin 2020). Therefore, it is possible that these lowland island endemics originally were high elevation adapted, but with the sinking of the eastern Papuan Peninsula as the Solomon Sea opened, the now isolated island populations became secondarily adapted to low elevation forests with the loss of montane habitat. *Toxicocalamus* species occurring below 1,000 m a.s.l. on the mainland could be secondarily lowland adapted species that dispersed from the highlands or were isolated to either the northern or southern slope of the Cordillera during Pliocene mountain building. To thoroughly investigate both macro- and microevolutionary patterns within this diverse group across the topographically complex landscape, additional field collections across large elevational transects combined with population genomics will be required.

While the natural history gaps in our knowledge of *Toxicocalamus* are still vast, it is known that a common prey item for several species of *Toxicocalamus* are earthworms (O'Shea 1996; Shine and Keogh 1996; O'Shea et al. 2015; Roberts and Austin 2020). In New Guinea, 106 of the 113 known earthworm species are contained within the Megascolecidae (Aspe 2016), a group that dominates earthworm diversity across the Pacific. In reviewing the phylogenetics and biogeography of megascolecids of Taiwan, Shen et al. (2022) classified these worm species based on elevational preference, either as "hill species" (<1,000 meters) or "mountain species" (>1,000 meters). These earthworms are quite large, with some species reaching lengths of up to 2 m (Sims and Easton 1972; Fahri et al. 2018). Megascolecids

in the Philippines are more abundant and more speciose at higher elevations (Aspe and James 2015). Although the distributions of New Guinea megascolecids are poorly known, if this positive correlation between increasing elevation and megascolecid diversity and biomass holds in New Guinea as well, then high biomass of their preferred prey-item might have been a significant factor in the maintenance and diversification of high elevation *Toxicocalamus* species in the New Guinea highlands.

Traditional morphological comparisons of head and ventral scalation of *T. longhagen* finds that the new species most closely resembles *T. mattisoni*; however, the new species can be distinguished by presence of two postoculars (vs. one), one large posterior temporal (vs. two), and a higher ventral scale count. Both *T. mattisoni* and the holotype of the new species were identified previously as *T. loriae*, a species that has been shown to be a cryptic species complex based on DNA sequence and morphological data (Kraus 2017, 2020). The postfrontal bones, referenced as postorbitals in McDowell (1969), were demonstrated by Roberts and Austin (2020) to have species-specific shapes and orientations that are diagnostic within this genus. The tear-drop shaped postfrontal bones of the new species also serve to distinguish it from *T. loriae* (L-shaped postfrontal bones) based on scans of a *T. loriae* specimen (topotypic voucher, LSUMZ 129270) that was collected near the *T. loriae* type locality in 2019 (Fig. 5; Kraus 2017, 2020; Dimpflmeier 2019). In addition to difference in shape, the postfrontal bones of *Toxicocalamus longhagen* are more curved, each individually forming a near "C" shape when viewed anteriorly, while those of *T. loriae* are nearly straight. Investigations of external and internal *Toxicocalamus* morphology continue to prove useful in the delimitation and identification of new and cryptic taxa. This is important because six species of *Toxicocalamus* have not been included in DNA-based phylogenetic analyses: *T. buergersi*, *T. cratermontanus*, *T. grandis*, *T. pumehanae*, *T. spilolepidotus*, and *T. longhagen*. With the improvements of formalin-fixed tissue DNA extraction and next-generation sequencing, work is underway to expand phylogenetic analyses to include all *Toxicocalamus* species, including those represented only by formalin fixed vouchers (Ruane and Austin 2017; McGuire et al. 2018; Hahn et al. 2021; Ruane 2021; Bernstein and Ruane 2022; Roycroft et al. 2022). Through construction of completely inclusive phylogenies, we hope to better understand the evolution of the many unique morphological and behavioral traits of New Guinea Worm-Eating snakes.

Key to species of *Toxicocalamus* Boulenger, 1896

1	Subcaudals entire	*T. holopelturus*
–	Subcaudals divided	2
2	Preocular separate from prefrontal	3
–	Preocular fused to prefrontal	12
3	Prefrontal fused to internasal	*T. pumehanae*
–	Prefrontal separate from internasal	4
4	Internasal and preocular in contact, separating nasal from prefrontal	5
–	Internasal and preocular not in contact	6
5	Nasal scales clearly divided by large nares; purple markings on supralabials; nape unbanded; medium brown dorsum; light brown ventrals (<175)	*T. pachysomus*
–	Nasal scales entire, surrounding nares; pale yellow markings on supralabials; yellow nape band; dark gray-brown dorsum; ventrals darkening anterior-to-posterior (pale yellow to dark brown) (>175)	*T. goodenoughensis*
6	Dorsum uniform dark gray or brown, without spots	9
–	Dorsum spotted	7
7	Dorsum yellow with brown spot on anterior margin of scales	*T. ernstmayri*
–	Dorsum dark gray or brown, with pale spots	8
8	Pale dorsal scales sparsely scattered across dark brown dorsum; ventrals white	*T. grandis*
–	Almost all dark brown to black dorsal scales with pale yellow spot except vertebral row; ventrals with broad black spot on each	*T. spilolepidotus*
9	Prefrontal and second supralabial in contact, separating preocular from nasal	10
–	Preocular and nasal in contact, separating prefrontal from second supralabial	11
10	One postocular, dorsum dark gray-brown	*T. mattisoni*
–	Two postoculars, dorsum yellow and brown	*T. longhagen*
11	Ventrals gray, banded with darker gray or blackish brown; dorsum dark charcoal gray; snout longer (eye-naris/internarial distance 1.8)	*T. nigrescens*
–	Ventrals yellow, may be spotted or suffused with brown; dorsum pale gray; snout shorter (eye-naris/internarial distance 1.0–1.1)	*T. loriae*
12	Frontal fused to supraoculars; ventrals wide, 5–6 times wider than first row of dorsal scales	*T. mintoni*
–	Frontal distinct from supraoculars; ventrals narrow, 3–4 times wider than first row of dorsal scales	13
13	Internasal distinct from prefrontal; temporal scale separates last supralabial from parietal	14
–	Internasal fused with prefrontal; temporal fused with last supralabial, allowing supralabial contact with parietal	17

14 Cloacal entire; 5 supralabials; venter without dark stripes 15
– Cloacal divided; 6 (rarely 7) supralabials; venter with pair of longitudinal dark stripes 16
15 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*
– 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*
16 15 dorsal rows at mid-body ..... *T. misimae*
– 17 dorsal rows at mid-body ..... *T. longissimus*
17 Four supralabials; postocular fused with supraocular; 15 dorsal scale rows at mid-body ..... *T. buergersi*
– Five supralabials; postocular usually distinct from supraocular; usually 13 (rarely alternating between 13 and 15) dorsal scale rows at mid-body ..... *T. preussi*

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Appendix 1

Specimens examined

Toxicocalamus ernstmayri – Papua New Guinea: Western Province: Wangbin: Ok Tedi, 1,463 m (MCZ R-145946).

Toxicocalamus holopelturus: Papua New Guinea: Milne Bay Province (AMNH R-76660, holotype). Morphosource identifier (AMNH R-76660).

Toxicocalamus loriae – Papua New Guinea: Chimbu Province [as Simbu in catalog]: Kundiawa (AMNH R98495, R98497, R98498); Kup, Kubor Mountains (AMNH R72781); Kondiu, near Kup (AMNH R75336, R75337, R75339, R75343, R75345).

Toxicocalamus loriae sensu Kraus (2020) – Papua New Guinea: Central Province: Laronu (LSUMZ 129270, voucher). Morphosource identifier (LSUMZ 129270).

Toxicocalamus loriae (clade 3 *sensu* Strickland et al. 2016) – Papua New Guinea: Oro Province: Mt. Trafalgar (BPBM 39813, voucher). Oro Province: Collingwood Bay (LSUMZ 93563, voucher). Morphosource identifier (LSUMZ 93563).

Toxicocalamus mintoni – Papua New Guinea: Milne Bay Province: Sudest Island: western slope Mt. Rio, 400 m (BPBM 20822, holotype). Morphosource identifier (BPBM 20822).

Toxicocalamus misimae – Papua New Guinea: Milne Bay Province: Misima Island (AMNH R-76684, holotype). Morphosource identifier (AMNH R-76684).

Toxicocalamus nigrescens – Papua New Guinea: Milne Bay Province: Fergusson Island: Oya Waka (BPBM 16545, holotype). Morphosource identifier (BPBM 16545).

Toxicocalamus pachysomus – Papua New Guinea: Milne Bay Province: along Upaelisafupi Stream, Cloudy Mountains (BPBM 15771, holotype). Morphosource identifier (BPBM 15771).

Toxicocalamus spilolepidotus – Papua New Guinea: Eastern Highlands Province (AMNH R-85745, holotype), Morphosource identifier (AMNH R-85745); Papua New Guinea: Eastern Highlands Province: Yaiya, Kratke Mountains (PNGM 22132).