

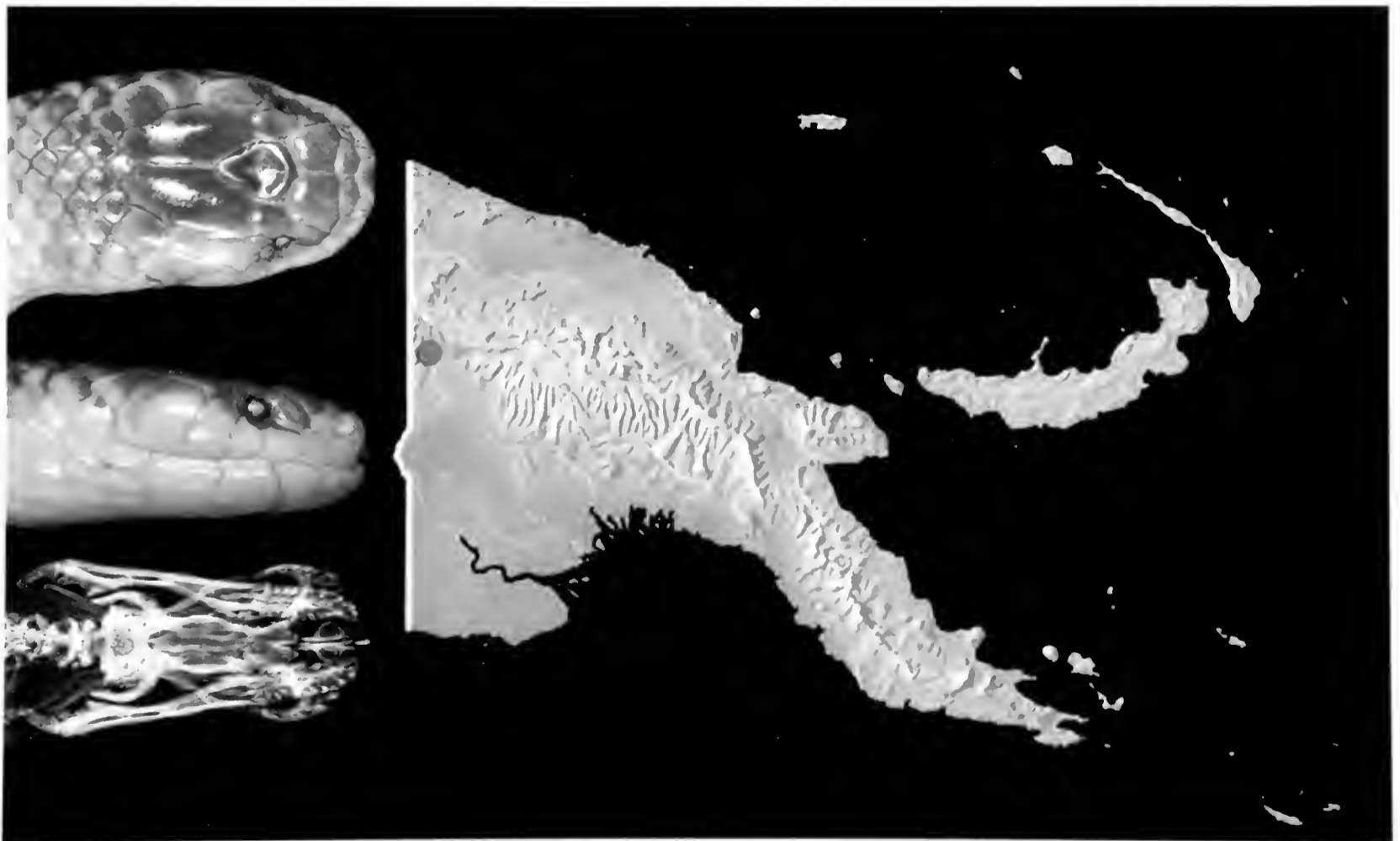
Bulletin of the Museum of Comparative Zoology

Volume 161, Number 6

23 July 2015

A New Species of New Guinea Worm-eating Snake,
Genus *Toxicocalamus* (Serpentes: Elapidae), from the
Star Mountains of Western Province, Papua New Guinea,
with a Revised Dichotomous Key to the Genus

MARK O'SHEA, FRED PARKER, AND HINRICH KAISER



BULLETIN OF THE

Museum of Comparative Zoology

BOARD OF EDITORS

Editor: Jonathan Losos

Managing Editor: Deborah Smiley

Associate Editors: Andrew Biewener, Scott Edwards,
Brian Farrell, Gonzalo Giribet, James Hanken,
Hopi Hoekstra, George Lauder, James McCarthy,
Naomi Pierce, Stephanie Pierce and Robert Woollacott

Publications Issued or Distributed by the
Museum of Comparative Zoology
Harvard University

Bulletin 1863–

Breviora 1952–

Memoirs 1865–1938

Johnsonia, Department of Mollusks, 1941–1974

Occasional Papers on Mollusks, 1945–

General queries, questions about author guidelines, or permissions for
MCZ Publications should be directed to the editorial assistant:

MCZ Publications
Museum of Comparative Zoology
Harvard University
26 Oxford Street
Cambridge, MA 02138

mczpublications@mcz.harvard.edu

EXCHANGES AND REPRINTS

All of our publications are offered for free on our website:
<http://www.mcz.harvard.edu/Publications/index.html>

To purchase individual reprints or to join our exchange program,
please contact April Mullins at the Ernst Mayr Library:
mayrlib@oeb.harvard.edu.

This publication has been printed on acid-free permanent paper stock.

A NEW SPECIES OF NEW GUINEA WORM-EATING SNAKE, GENUS *TOXICOCALAMUS* (SERPENTES: ELAPIDAE), FROM THE STAR MOUNTAINS OF WESTERN PROVINCE, PAPUA NEW GUINEA, WITH A REVISED DICHOTOMOUS KEY TO THE GENUS

MARK O'SHEA,^{1,4} FRED PARKER,² AND HINRICH KAISER³

CONTENTS

Abstract	241
Introduction	242
Materials and Methods	242
<i>Toxicocalamus ernstmayri</i> New Species	243
Holotype	243
Etymology	244
Diagnosis	244
Comparisons	248
Description of the Holotype	249
Coloration in Life	251
Coloration in Preservative	251
Tail Tip Morphology	251
Osteology	252
Natural History	252
Discussion	255
Key to the Genus <i>Toxicocalamus</i>	259
Acknowledgments	260
Appendix I. Specimens Examined	260
Literature Cited	263

ABSTRACT. We describe a new species of New Guinea vermivorous snake (*Toxicocalamus*) from a single specimen collected at Wangbin in the Star Mountains,

¹West Midland Safari Park, Bewdley, Worcestershire DY12 1LF, United Kingdom; and Australian Venom Research Unit, University of Melbourne, Victoria 3010, Australia. Author for correspondence (oshea@markoshea.info).

²P.O. Box 5623, Townsville, Queensland 4810, Australia.

³Department of Biology, Victor Valley College, 18422 Bear Valley Road, Victorville, California 92395; and Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013.

⁴Present address, Faculty of Science and Engineering, University of Wolverhampton, Wulfruna Street, Wolverhampton, West Midlands WV1 1LY, United Kingdom.

Western Province, Papua New Guinea. The new species is the largest known member of the genus and can be differentiated from all other *Toxicocalamus* by a combination of the following characters: large size (total length of the holotype 1,200 mm), dorsal head scutes in the typical “colubrid-elapid dorsal nine-scute arrangement”; separate, single preocular and paired postoculars; single anterior temporal and single or paired posterior temporals; six supralabials, with third and fourth supralabial contacting the orbit; dorsal scales in 15–15–15 rows; 203 ventral scales, 29 subcaudal scales; and a divided anal plate. Its erstwhile status, misidentified as *Micropechis ikaheka* in the collection of the Museum of Comparative Zoology, demonstrates the need for detailed examination of existing collections and is indicative of hidden diversity yet to be identified, not only in the field but also on the shelves of museum collections. We also provide a revised key to the genus *Toxicocalamus*.

ABSTRAKSI. Kami mendeskripsikan spesies baru nular pemakan eacing (*Toxicocalamus*) di Papua New Guinea dari koleksi spesimen di Wangbin, Pegunungan Bintang, Propinsi bagian Barat, Papua Nugini. Spesies baru ini merupakan anggota genus dan dapat dibedakan dari semua nular pemakan eacing tanah (*Toxicocalamus*) lainnya dengan kombinasi dari berbagai ciri-ciri sebagai berikut: berukuran besar (panjang total holotype 1200 mm), sisik di kepala bagian atas bercirikan “colubrid-elapid sembilan sisik beraturan”; terpisah, preocular tunggal and sepasang postocular; anterior temporal tunggal dan satu atau sepasang posterior temporal; enam supralabial, dengan supralabial ketiga dan keempat menghubungi orbit; sisik di bagian punggung berbaris 15–15–15; sisik di bagian perut berjumlah 203, sisik subcaudal berjumlah 29; dan piringan anal dibagi menjadi dua bagian. Status sebelumnya, salah diidentifikasi sebagai *Micropechis ikaheka* di koleksi Museum Comparative Zoology. Ini menunjukkan perlunya penyelidikan secara rinci terhadap hasil koleksi yang ada sekarang. Hal ini juga merupakan indikasi adanya keragaman tersembunyi

yang belum teridentifikasi, tidak hanya di lapangan tapi juga di rak-rak museum koleksi. Kami juga memberikan kunci revisi tentang spesies *Toxicocalamus*.

Key words: Elapidae, *Toxicocalamus*, New species, Papua New Guinea, Description, Taxonomy, Vermivory

INTRODUCTION

Toxicocalamus is a genus of enigmatic vermivorous elapid snakes with a primarily fossorial lifestyle. Although part of the very diverse Australopapuan terrestrial elapid radiation, *Toxicocalamus* is one of only six genera not represented on the Australian continent. It is endemic to the island of New Guinea, several small offshore islands, and the major island archipelagos to the south-east of the Papuan Peninsula (Fig. 1). The small offshore islands all lie along the north coast of Papua New Guinea (PNG) and include Seleo Island (Sandaun Province), Walis and Tarawai Islands (East Sepik Province), and Karkar Island (Madang Province). The southeastern archipelagos are part of Milne Bay Province and include the d'Entrecasteaux Archipelago (Goode-nough, Fergusson, and Normanby Islands), Woodlark Island, and the Louisiade Archipelago (Misima, Sudest, and Rossel Islands). *Toxicocalamus* is seemingly absent from the Bismarck, Admiralty, and Solomons Archipelagos, the great seasonally flooded Trans-Fly region of southern New Guinea, the Torres Strait Islands, the Schouten Islands, and the Vogelkop and associated Raja Ampat Archipelago of West New Guinea (Indonesia).

First described by Boulenger (1896) and later revised by McDowell (1967, 1969), the genus *Toxicocalamus* currently comprises 11 species and a single subspecies, including (in order of description): *T. longissimus* Boulenger, 1896; *T. loriae* (Boulenger, 1898); *T. stanleyanus* (Boulenger, 1903); *T. preussi* (Sternfeld, 1913); *T. buergersi* (Sternfeld, 1913); *T. grandis* (Boulenger, 1914); *T. p. angusticinctus* (Bogert & Matalas, 1945); *T. spilolepidotus* McDowell, 1969; *T. holopelturus* McDowell, 1969; *T. misimae* McDowell, 1969; *T. mintoni* Kraus, 2009; and *T. pachysomus* Kraus, 2009. Many of these taxa are poorly

represented in natural history collections, and we have so far located 475 specimens in 28 museums worldwide. Of these, 66.3% (315 specimens) are identified as *T. loriae*, but considering the great variation in habitus, patterning, and scale count we have observed among these specimens, we believe this taxon to represent a species complex. The next best-represented species are *T. preussi* and *T. stanleyanus*, with 55 and 37 specimens, respectively. Two island taxa, *T. holopelturus* and *T. longissimus*, are known from 18 and 16 specimens, respectively, whereas an anomalous “hybrid” population from Garaina (Morobe Province, PNG; McDowell, 1969) is known from 15 specimens. The remaining seven species are represented by eight or fewer specimens each, with three species, excluding the one we here describe, only known from their holotypes. The largest known species so far is *T. grandis*, at 960 mm snout–vent length (SVL) for the single known specimen (BMNH 1946.1.18.34). That species was described from the Setakwa River (southern Papua Province, West New Guinea, Indonesia), where it was collected in 1912 during the Wollaston Expedition of 1912–13 (O’Shea, 2013).

We here describe a new species, the largest of the genus, that we discovered among a series of *Micropechis ikaheka* in the collection of the Museum of Comparative Zoology, where it had languished for 45 years since its collection by one of us (FP). Its description is yet another recent example of the unrecognized diversity of natural history collections (see Kathriner et al., 2014), and it showcases their value to students of biological diversity.

MATERIALS AND METHODS

Characters used for evaluating and comparing specimens were taken from 344 museum specimens (Appendix 1). Abbreviations for measurements and scale counts used in the description include snout–vent length (SVL), tail length (TL), total length (TTL), number of subcaudal scales (SC), and number of infralabial scales (IL). Scales

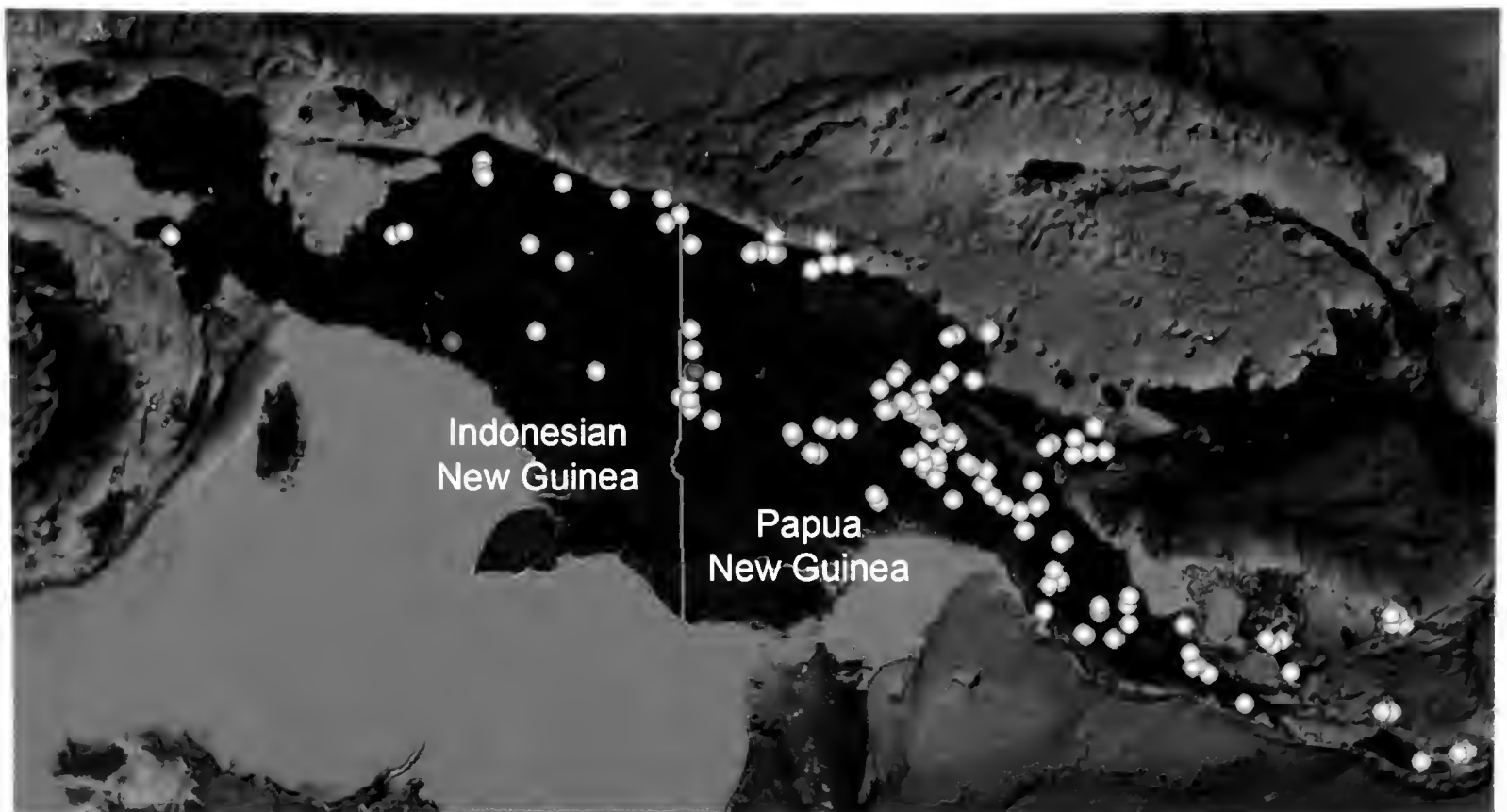


Figure 1. Satellite map showing the island of New Guinea and its surrounding islands and archipelagos. Localities for all known museum specimens of *Toxicocalamus* are marked by white dots. The red dot indicates the locality for the holotype of *T. ernstmayri* new species at Wangbin, Western Province, Papua New Guinea, whereas the yellow dot indicates the approximate type locality of *T. grandis*, “launch camp” on the Setakwa River of Papua Province, Indonesian New Guinea. The yellow line marks the international border between Papua New Guinea and Papua Province, Indonesia.

were counted as suggested by McDowell (1969). Sex was determined by examination of gonads, presence of everted hemipenes, or presence of the *retractor penis* muscle. Length measurements were taken by running a nonelastic string from the tip of the snout along the ventral medial axis of the body, under consideration of the points about measurement accuracy raised by Natusch and Shine (2012). Measurements of tail tips were taken using Mitutoyo digital calipers to the nearest 0.1 mm. X-rays of the holotype were taken using a Kevex PXS5-724EA emitter and a Varian PanScan 4030R receiver (40-kV target tube voltage) at the Museum Support Center of the U.S. National Museum of Natural History, Smithsonian Institution, Suitland, Maryland. The holotype of *T. grandis* was X-rayed using a Machlett X-ray tube in a Solus-Schall emitter (output settings: 55 kV, 15 mA) at the BMNH. Cranial characters were measured on digital X-ray images in pixels using the software AnalyzingDigitalImages (Museum of Science, Boston, Massachusetts). A list of

skull measurements (expanded from Dwyer and Kaiser, 1997) is presented in Table 1. Global positioning system coordinates were determined using individual museum records and published species accounts where available; those unavailable were obtained from Google Earth (WGS 84) to the nearest minute. Museum acronyms are taken from Sabaj Pérez (2014), with the addition of UPSZ, now the preferred acronym for the Museum of Evolution containing the Uppsala University natural history collection (Mejlon, personal communication).

TOXICOCALAMUS ERNSTMAYRI NEW SPECIES

Star Mountains Worm-Eating Snake

Figures 2–3, 5A, B, 6A, C

Holotype. MCZ R-145946, an adult female from Wangbin village (5°14'26.72"S, 141°15'31.92"E), elevation 1,468 m (4,800 ft), near the Ok Tedi River, in the Star Mountains of the North Fly District, Western Province,

TABLE 1. Cranial characters measured on the holotypes of *Toxicocalamus ernstmayri* new species (MCZ R-145946) and *T. grandis* (BMNH 1946.1.18.34). Measurements were taken on the left side of paired structures and constitute maximum measurements. All measurements were subsequently converted into ratios appropriate for comparisons (see Table 3).

Character	Abbreviation	Description
Skull length	SL	skull length from the anteriormost part of the nasal to the occipital condyle
Braincase width	BW	broadest extent of the braincase
Frontals, total width	FW _{PF}	taken at the prefrontal process
Frontals, total width	FW _{SO}	taken at the supraorbital ridge
Parietal width	ParW	greatest width
Supratemporal length	StL	measured in a straight line
Maxilla length	MxL	measured in a straight line
Atlas width	AtW	width of the first cervical vertebra, measured across the transverse processes
Axis width	AxW	width of the second cervical vertebra, measured across the transverse processes
Dentary–articular length	D–A	length of the lower jaw from the anterior tip of the dentary to the posterior end of the articular

PNG, (Fig. 2), killed by a villager and collected by FP on 23 December 1969. Originally identified and accessioned as *Micropechis ikaheka* Lesson, 1830.

Etymology. The species name *ernstmayri* is a patronym honoring the German-American ornithologist, systematist, and evolutionary thinker Ernst Mayr (1904–2005). After leaving Germany in the early 1930s Mayr took up a curatorial position at the American Museum of Natural History in New York. While there he wrote his definitive book *Systematics and the Origin of Species from the Viewpoint of a Zoologist* (Mayr, 1942), which solved one of the big questions of Darwinian evolution, that of how one species evolved into many via the mechanism of natural selection. In 1953 Mayr moved to Harvard University in Cambridge, Massachusetts, where he was Director of the MCZ from 1961–1970. He retired in 1975 as Alexander Agassiz Professor of Zoology, Emeritus (Bradt, 2005).

There are several connections linking Ernst Mayr to this new species of *Toxicocalamus*, which make him, and this snake, the ideal candidates for a patronym. First, Mayr himself visited New Guinea, and during the late 1920s he spent over 2 years conducting fieldwork in an area now part of PNG, as a member of a joint Rothschild–AMNH expedition focusing on birds of

paradise (Aves, Passeriformes, Paradisaeidae), during which he collected many new bird and orchid species. Second, the holotype of *T. ernstmayri* has been housed in the MCZ collection, mislabeled as *M. ikaheka*, after having arrived and been accessioned in June 1975, the month and year that Mayr retired. Third, the true identity of this specimen was recognized by one of us (MOS) during a visit to the MCZ in May 2014, undertaken with the financial support of an Ernst Mayr Travel Grant from Harvard University, awarded to enable examination of the *Toxicocalamus* holdings at the MCZ and the AMNH, the two U.S. institutions where Mayr worked. Finally, 2015, the publication year of this description, marks the decennial of Mayr's passing at age 100, and naming a New Guinea snake after him seems a suitable tribute.

Diagnosis. *Toxicocalamus ernstmayri* is the largest known species in the genus *Toxicocalamus* and the only one with an SVL in excess of 1.0 m. It can be distinguished from all other known *Toxicocalamus* by the following combination of characters: large size (SVL of the holotype 1,100 mm), dorsum of head exhibiting the typical “colubrid–elapid dorsal nine-scute arrangement” (*sensu* O’Shea, 2005: 12) that comprises paired internasals, paired

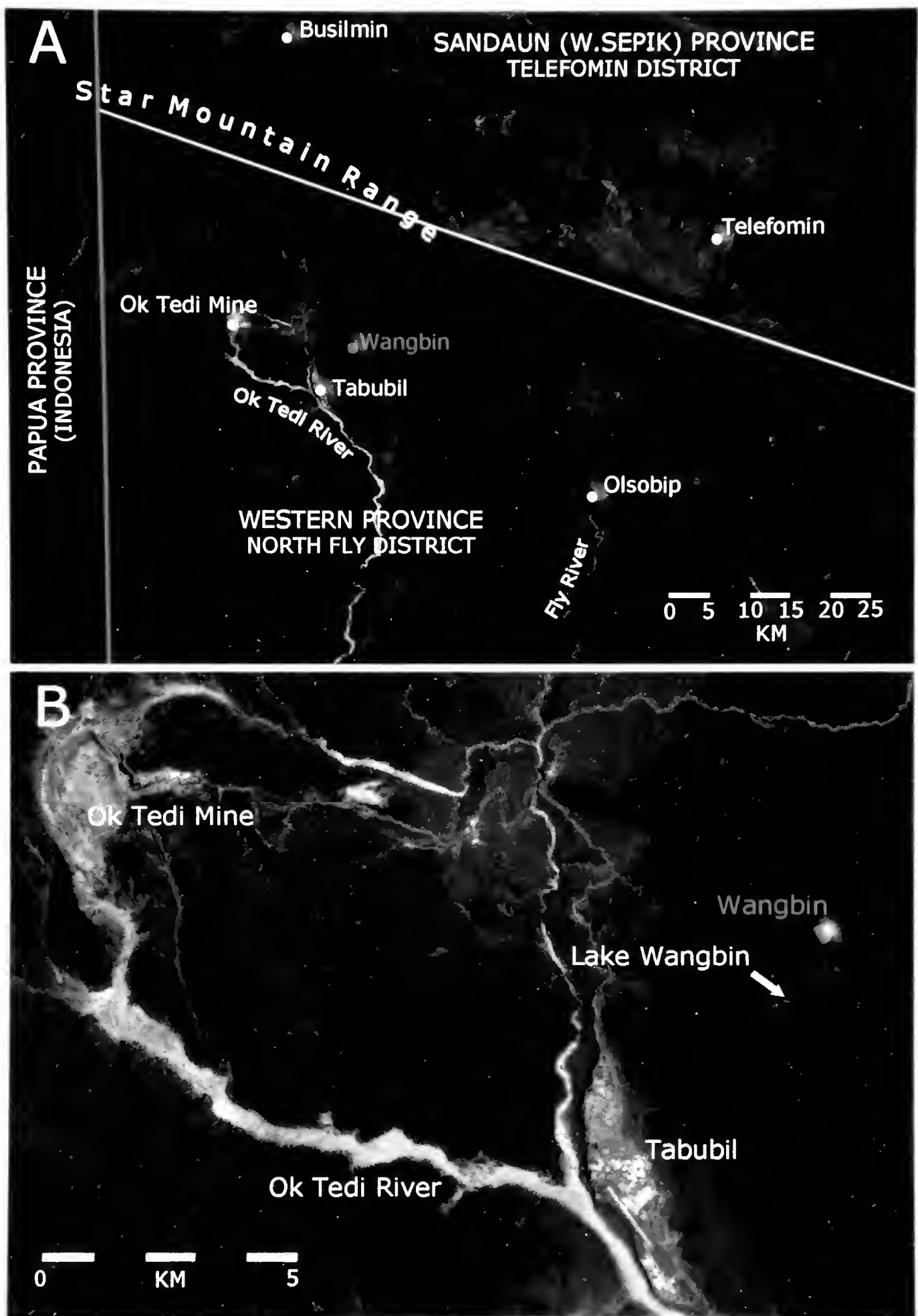


Figure 2. Satellite close-up maps of the region surrounding the Wangbin type locality, indicated by a red dot, of *Toxicocalamus ernstmayri* new species, showing (A) its position on the southern versant of the Star Mountains and proximity to the Indonesian border in relation to the Ok Tedi River and Fly River drainages, and (B) close-up view to illustrate the specific position of the locality along the Ok Tedi River.

TABLE 2. Comparative data for species in the genus *Toxicocalamus*, including *T. ernstmayri* new species. Examined characteristics include the number of specimens examined (Ne) and known (Nk), and maximum lengths for males and females. Asterisks (*) denote specimens with an incomplete tail. Abbreviations include snout-vent length (SVL), tail length (TL), total length (TTL), anal plate (AP), anterior temporals (AT), frontal (F), intermasals (IN), postoculars (PO), prefrontals (PF), preoculars (PR), posterior temporals (PT), subcaudals (SC), supralabials (SL), and supraoculars (SO), *sensu lato* (s.l.).

Character	Taxon						
	<i>ernstmayri</i> sp. nov.	<i>buergersi</i>	<i>grandis</i>	<i>holopelturus</i>	<i>longissimus</i>	<i>loriae</i> s.l.	<i>mintoni</i>
N _e (N _k)	1 (1) no data	3 (6) 330 + 35 = 365	1 (1) no data	18 (18) 665 + 122 = 787	10 (12) 590 + 75 = 665	211 (315) 610 + 83 = 693	1 (1) 500 + 111 = 611*
Length (SVL + TL = TTL)	1100 + 100 = 1200	567 + 24 = 591	960 + 80 = 1040	760 + 77 = 837	715 + 44 = 759	681 + 47 = 728	no data
Head characters							
Head scute fusion	none	PF + PR + IN	none	none	PF + PR	none	PF + PR, SO + F
PO fused SL, single, or paired	paired	fused	single	paired	usually single	usually paired	single
AT absent, single or paired	single	absent	single	single	single	single	single
PT absent, single or paired	paired	single	paired	paired	paired	single or paired	paired
SL (contact orbit)	6 (3-4)	4 (2-3)	6 (3-4)	6 (3-4)	6 (3-4)	6 (3-4)	6 (3-4)
Body characters							
Dorsals count	15-15-15	15-15-15	16-15-15	15-15-15	17-17-17	15-15-15	15-15-15
Ventrals count	no data	330	no data	226-251	244-273	150-211	194
AP entire or divided	203	313-319	207	246-256	273-304	179-227	no data
SC single or paired	paired	single	paired	paired	paired	single or paired	paired
Subcaudals count	paired	paired	paired	single	paired	paired	paired
	no data	40	no data	54-68	45-48	40-62	51+
	29	24-28	27	37-41	24-32	23-41	no data
Tail ratio to TTL (%)	no data	9.6	no data	15.0-17.5	10.4-12.1	9.9-23.1	no data
	8.3	4.1-6.3	7.7	7.9-9.2	5.3-7.7	6.5-15.6	no data
Tail shape and terminus	stout, conical	flat, rounded	stout, conical	elongate, conical	elongate, conical	elongate, conical	no data

TABLE 2. Continued

Character	Taxon					
	<i>nitimac</i>	<i>pachysomus</i>	<i>preussi</i>	<i>spilepicidotus</i>	<i>stanleyanus</i>	spp.
N_c (N_k)	2 (3)	1 (1)	42 (55)	2 (2)	31 (37)	17 (21)
Length (SVL + TL = TTL)	393 + 75 = 468 no data	500 + 46 = 546° no data	570 + 55 = 625 744 + 40 = 784	no data 770 + 80 = 850	529 + 83 = 612 667 + 38 = 705	332 + 79 = 411 667 + 38 = 705
Head characters						
Head scute fusion						none
PO fused SL, single, or paired	PF + PR	none	PF + PR + IN	none	PF + PR	usually paired
AT absent, single or paired	single or paired	single	single	paired	single	single or paired
PT absent, single or paired	single	single	absent	single	single	usually paired
SL (contact orbit)	paired	paired	single	single or paired	paired	usually paired
	6 (3-4)	6 (3-4)	5 (2-3)	6 (3-4)	5 (2-3)	6 (3-4)
Body characters						
Dorsals count	15-15-15	15-15-15	13-13-13	15-15-15	15-15-15	15-15-15
Ventrals count	227-231	171	263-295	no data	218-245	168-184
AP entire or divided	no data	no data	283-359	200-205	230-281	178-195
SC single or paired	paired	paired	single	paired	single	single or paired
Subcaudals count	paired	paired	paired	paired	paired	paired
	46-48	20+	38-42	no data	35-51	30-57
Tail ratio to TTL (%)	no data	no data	16-33	33	22-29	20-34
	13.3-16.0	no data	7.9-15.2	no data	9.0-21.1	11.1-20.8
Tail shape and terminus	no data	no data	3.5-8.4	9.4-10.7	5.1-9.7	7.3-19.7
	elongate, conical	no data	flat, rounded	elongate, conical	elongate, conical	elongate, conical

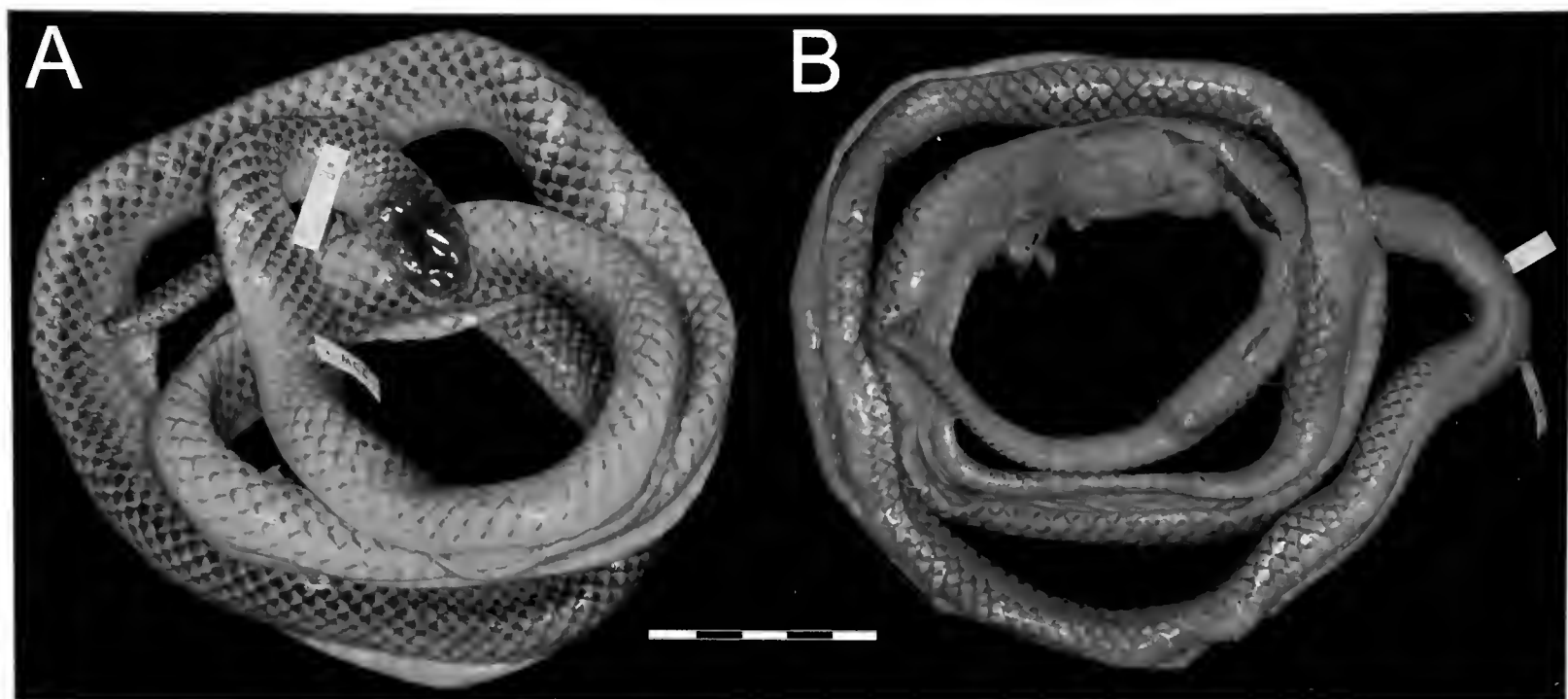


Figure 3. Holotype of *Toxicocalamus ernstmayri* new species (MCZ R-145946) in (A) dorsal and (B) ventral view. Scale = 5 cm.

prefrontals, a frontal between the supraoculars, and paired parietals (Fig. 4A'), six supralabials, with third–fourth contacting the orbit (Fig. 4C', D'); dorsal scales in 15–15–15 rows; 203 ventrals, 29 subcaudals, mostly paired, a few single; divided anal plate, short tail terminating with spinous, cone-shaped terminal scale (Fig. 4E').

Comparisons. The genus *Toxicocalamus* can be distinguished from all other New Guinea elapids, including *M. ikaheka* but excepting *Pseudonaja textilis* (Duméril et al., 1854), by the absence of a temporolabial scale between the fifth and sixth supralabials (see Discussion). From *P. textilis* it can be differentiated by its relatively small eyes (diameter two-thirds the distance from the lower edge of the orbit to the lower edge of the upper lip) and unremarkable supraoculars, whereas the highly active and visually alert *P. textilis* possesses large eyes (diameter 1.5 times the distance from the lower edge of the orbit to the lower edge of the upper lip), under strongly pronounced, shelved supraocular scales. *Toxicocalamus ernstmayri* can further be distinguished from *M. ikaheka* (characters in parentheses) by its short tail, equivalent to 8.3% TTL (11–14% TTL), its ventral scale count of 202 (174–191), and its low subcaudal count of 29 (36–49). The

holotype of *T. ernstmayri* demonstrates a complete lack of the strongly banded patterning diagnostic of Papua New Guinean *M. i. fasciatus* (Fischer, 1884). The patterning of *T. ernstmayri* is similar to that of the almost patternless “yellow phase” *M. i. ikaheka* from West Papua Province, Indonesia exemplified by the holotype of *M. i. ikaheka* (MNHN 7669). During the development of another project (O'Shea, unpublished data) we examined 132 specimens of *M. ikaheka* from across the taxon's entire range, confirming the subspecific pattern differences; 15 vouchers are included in Appendix 1 as examples for these patterns.

We here compare *T. ernstmayri* with all 12 congeners (11 species and one subspecies), with relevant characteristics for these species given in parentheses. A more expansive listing of comparative characters is provided in Table 2. *Toxicocalamus ernstmayri* exhibits the regular colubrid-elapid nine-scute dorsal arrangement (Fig. 4A') that distinguishes it from *T. mintoni* (fused, head-wide, frontal-supraocular scute), *T. buergersi*, *T. preussi preussi*, and *T. p. angusticinctus* (fused prefrontal-internasal-preocular scutes), and *T. stanleyanus*, *T. longissimus*, *T. misimae*, and *T. mintoni* (all with fused prefrontal-preocular scutes). The presence of six supralabials distinguishes

T. ernstmayri from *T. buergersi* (four), and *T. p. preussi*, *T. p. angusticinctus*, and *T. stanleyanus* (all with five). Contact between the preocular and nasal scutes separates *T. ernstmayri* from *T. pachysomus* (internasal and preocular in contact, excluding preocular contact with nasal). *Toxicocalamus ernstmayri* has a dorsal scale count of 15–15–15 that distinguishes it from *T. p. preussi*, *T. p. angusticinctus* (both 13–13–13), and *T. longissimus* (17–17–17), whereas the divided anal plate separates it from *T. buergersi*, *T. preussi*, *T. stanleyanus*, and some Oro Province *T. loriae sensu lato* (anal plates entire), and the mostly paired subcaudals separate it from *T. holopelturus* (all subcaudals single).

The ventral scale count of *T. ernstmayri* at 203 is considerably lower than that of female *T. buergersi* (313–319), *T. holopelturus* (246–256), *T. longissimus* (273–304), *T. preussi* (291–359), and *T. stanleyanus* (230–281). The subcaudal scale count of 29 is significantly lower than those of female *T. holopelturus* (37–41) and *T. spilolepidotus* (33).

Toxicocalamus ernstmayri is longer than any known *Toxicocalamus* species, with an SVL of 1,100 mm, compared with the next longest species: *T. grandis* (SVL 960 mm), *T. longissimus* (802 mm), *T. spilolepidotus* (770 mm), and *T. holopelturus* (760 mm). Males of all other *Toxicocalamus* species have shorter SVLs. *Toxicocalamus ernstmayri* has a relatively short tail (TL/TTL = 8.3%), although females of other *Toxicocalamus* species may possess shorter tails: *T. p. preussi* (3.9–6.1%), *T. p. angusticinctus* (3.5–8.4%), *T. buergersi* (4.1–6.3%), *T. longissimus* (5.3–7.7%), *T. grandis* (7.7%). Its relative tail length falls within the ranges of *T. loriae sensu lato*¹ (6.5–15.6%), *T. holopelturus* (7.9–9.2%),

and *T. stanleyanus* (5.1–9.7%), and below that of *T. spilolepidotus* (9.4–10.7%). Only males are known for *T. misimae*, *T. mintoni*, and *T. pachysomus*, and the latter two species are known only from holotypes with incomplete tails.

The general habitus is that of a stout snake with a relatively broad head, distinct from the neck, and a short tail that terminates abruptly. This build contrasts with most other *Toxicocalamus*, except *T. grandis*, and possibly *T. pachysomus*, which can be distinguished by head shape (distinctly pointed with small eyes), and most particularly with the ultraslender, elongated “bootlace” species, *T. buergersi* and *T. preussi*.

Description of the Holotype. An adult female (SVL 1,100 mm, TL 100 mm, TTL 1,200 mm), with 15–15–15 dorsal scale rows, imbricate, all smooth, 203 ventrals, a divided anal plate, 29 subcaudals, SC 1–6 paired, SC 7–14 single, and SC 15–29 paired. The head measures 21.8 mm long, from front of rostral to posterior of parietal suture, and 19.4 mm wide, across the broadest part of the head in line with the suture between the fifth and sixth supralabials. It exhibits the normal colubrid-elapid nine-scute dorsal arrangement of paired internasals, paired prefrontals, frontal between supraoculars, and paired parietals (Fig. 4A'). Rostral broad and high, almost triangular and easily visible from above. Internasals small in comparison with prefrontals (Fig. 4A'). Both internasals and prefrontals in broad contact. Frontal hexagonal, verging on triangular, longer than wide because of a backward projection into the parietals, only slightly larger than the prefrontals. Supraoculars relatively small and not projecting, shelf-like, above the eyes. Parietals angular, at least twice as long as broad. Six supralabials, the third and fourth in contact with the orbit (Fig. 4C', D'), the sixth being the largest. Nasal large and divided by a suture on either side of a relatively large naris. Loreal absent, as in all elapids; subocular absent, as in all terrestrial Papuan elapid genera except

¹Based on morphological evidence (unpubl. data) and a discordant geographic distribution of available specimens, we believe that *T. loriae*, as currently defined, is a species complex. This is a key reason why the range of relative tail length values shown here is considerably larger than for any other species in the genus. We here refer to specimens of uncertain species affinity, but currently treated as belonging to *T. loriae*, as *T. loriae sensu lato*.

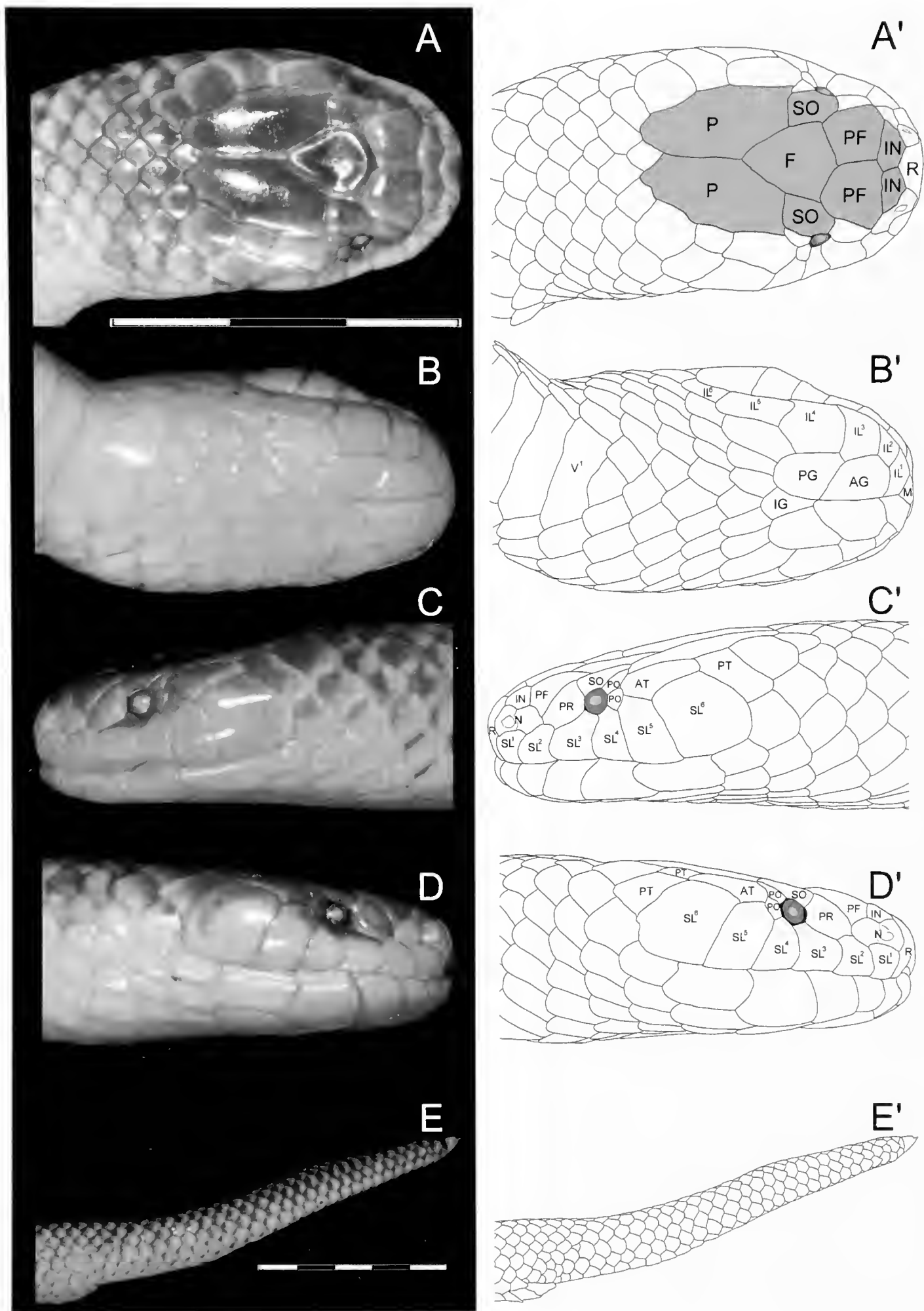


Figure 4. Detailed views of the head and tail of *Toxicocalamus ernstmayri* new species (MCZ R-145946), presented for clarity as both photographic and line-drawing illustrations. (A, A') Dorsal view of the head, showing classic colubrid-elapid nine-scutate arrangement (shaded), comprising paired internasals (IN), prefrontals (PF), supraoculars (SO), and parietals (P), and a single frontal (F). Also illustrated is the rostral (R). (B, B') Ventral view, showing the scale arrangement of six infralabials (IL¹–IL⁶), paired anterior genials (AG) and posterior genials (PG), the first intergenial (IG), the mental (M), and the first ventral scute (V¹). (C, C') Left lateral view, including a separate, single preocular (PR), paired postoculars (PO), a single anterior temporal (AT), and a single

Acanthophis; temporolabial absent, in contrast to all Papuan elapid genera except *Toxicocalamus* and *Pseudonaja*. Nasal in broad contact with a single elongate preocular, precluding contact between the second supralabial and the prefrontal. A pair of small postoculars on either side, in contact with a single elongate anterior temporal that extends backward to at least twice its width, to contact the fifth and sixth supralabials, the parietal, and the posterior temporals. Posterior temporals exist as a pair (upper small, lower large) on the right side, but as a single elongate scale on the left side. Mental small and triangular, six infralabials with IL 1–3 contacting pregenials (Fig. 4B'). Pregenials 1.5 times as long as wide, in broad contact along mental groove, posterior genials 1.5 times as long as wide, separated by an intergenial approximately 0.5 times the size of pre- and postgenials, the intergenial forming the first in a row of five gular scales before the first ventral scute.

Scales of body large, imbricate, smooth, and distinctive, arranged in 15 rows throughout without posterior reduction, and without enlargement of either the first or the midvertebral row of scales; dorsal scales of tail large and distinctive. Ventral scales broad, anal plate divided almost equally by a near-longitudinal junction, with the left half overlapping the right half, subcaudals mostly paired, except SC 7–14, which are single; tail terminating in a large, slightly upturned conical excrescence ending in a slightly damaged terminal spine (Fig. 4E').

Coloration in Life. The following description is modified from Parker (1982), where this specimen was listed as part of the *M. ikaheka* account.

Head blackish above, lips bright yellow. Dorsum and flanks bright yellow with the anterior corner of each scale gray to black,

the vertebral row with mostly black, then progressively less dark pigment on each scale row leading toward the ventrals, and with the amount of black on each scale increasing toward the tail. Venter bright yellow.

Coloration in Preservative (45 Years Post-collection). Distinctive coloration with a yellow-brown background color. The head is brown above and this pigment extends laterally to cover the rostral, preoculars, postoculars, most of the temporals, and the upper thirds of the 3rd–6th supralabials; on the remainder of the supralabials and the infralabials the dark pigment is confined to the sutures, which appear highlighted. The nasals and first two supralabials are virtually unmarked (Fig. 4A–D). On the yellow-brown body the darker brown pigment manifests as a large, dark anterior-central spot on every dorsal scale, the posterior portions of the scale remaining unmarked and pale, the whole presenting an irregular reticulated appearance (Fig. 3A). Laterally, the dark pigment weakens progressively and becomes largely confined to the anterior edge of each scale suture, although the dorsal scales of the tail are strongly marked throughout. Ventral scales are immaculate yellow-brown, without dark markings or suturing, but central sutures of the paired subcaudals are edged with brown, as a fine mid-ventral zigzag (Fig. 3B). The terminal conical excrescence is immaculate yellow, in contrast to the other adjacent dorsally visible scales of the tail (Fig. 4E).

Tail Tip Morphology. Comparisons of the distal portion of the tails of *T. ernstmayri* (Fig. 5A, B) and *T. grandis* (Fig. 5C, D) show that there is not only a difference in the structure of the keratinized terminal excrescence, but also in the dimensions of the tail. Measurements of tail width at intervals of two to five times the length of the terminal excrescence (TEL) shows that the tail of *T. ernstmayri* widens more

← posterior temporal (PT). Six supralabials (SL¹–SL⁶) are present, with SL³ and SL⁴ in contact with the orbit. The nasal scale (N) is elongate, measuring approximately twice as long as wide. (D, D') Right lateral view, differing from the left view only in the presence of two posterior temporals. (E, E') Lateral view of the tail, showing the robust, pointed terminal scale. The scale is 3 cm for the head views (A–D) and 5 cm for the image of the tail (E).

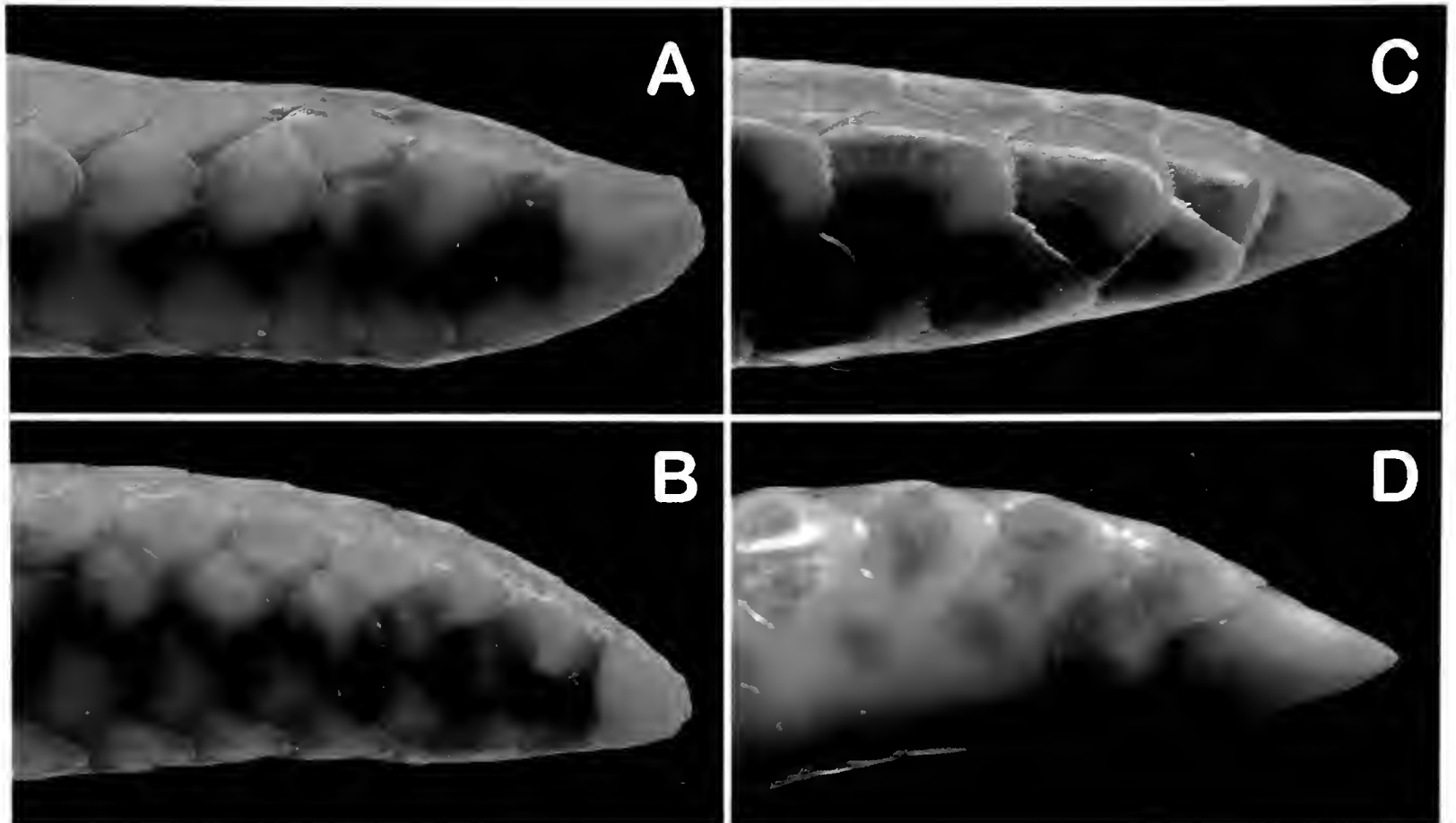


Figure 5. Tails of *Toxicocalamus ernstmayri* new species (A, B) and *T. grandis* (C, D). Tails are shown in ventral (A, C) and lateral (B, D) views. The tail tip of *T. ernstmayri* curves downward in lateral view (B) and is slightly asymmetrical in ventral view (A), with evidence of minor breakage at the tip. In contrast, the tail tip of *T. grandis* is cone-shaped in ventral view (C) and does not curve as in *T. ernstmayri*.

rapidly from the end than that of *T. grandis*. Whereas in *T. ernstmayri*, tail width doubles after 5 TEL, the tail of *T. grandis* only adds 70% in width at that length interval.

Osteology. We examined X-ray images of the skull and tail of *T. ernstmayri* (Fig. 6A, C) to determine the presence of diagnostic features and to compare these with those of *T. grandis* (Fig. 6B, D), the next largest species in the genus and the most similar in general appearance. The skull of *T. ernstmayri* (Fig. 6A) appears overall slightly more robust than that of *T. grandis* (Fig. 6B). Easily observed differences include the number of maxillary teeth (four in *T. grandis* and five in *T. ernstmayri*), the shape and dimensions of the supratemporal, the extent of the transverse processes of the atlas-axis complex (axis broader than atlas in *T. ernstmayri*, the reverse in *T. grandis*), and the extent of ossified ornamentations on the terminal vertebra.

Aside from the qualitative difference, we were also able to contrast some characteristics quantitatively (Table 3). In addition to the 16.9% difference in the transverse dimen-

sions of the atlas-axis complex, there also exists a similarly large difference in the dimension of the frontal bone (15.9% in FW_{SO}/FW_{PF}). Smaller differences can be seen in a variety of cranial elements when compared with skull length (e.g., MxL —10.8%, BW —9.7%, StL —9.7%, $ParW$ —9.1%). We recognize that none of these differences can be supported statistically because of the availability of only single specimens, and they only serve to distinguish the morphology of these bones descriptively.

Natural History. Little is known of the natural history of any members of the genus *Toxicocalamus* (O'Shea, 1996). They are believed to be fossorial, semifossorial, or terrestrial in habit, diurnal in activity, and oviparous in reproductive strategy, with clutch sizes of one to eight on record (Shine and Keogh, 1996).

Before this report, the only specimens for which gut content data had been reported were members of *T. loriae sensu lato* (McDowell, 1969; Shine and Keogh, 1996; O'Shea, personal observation). Numerous

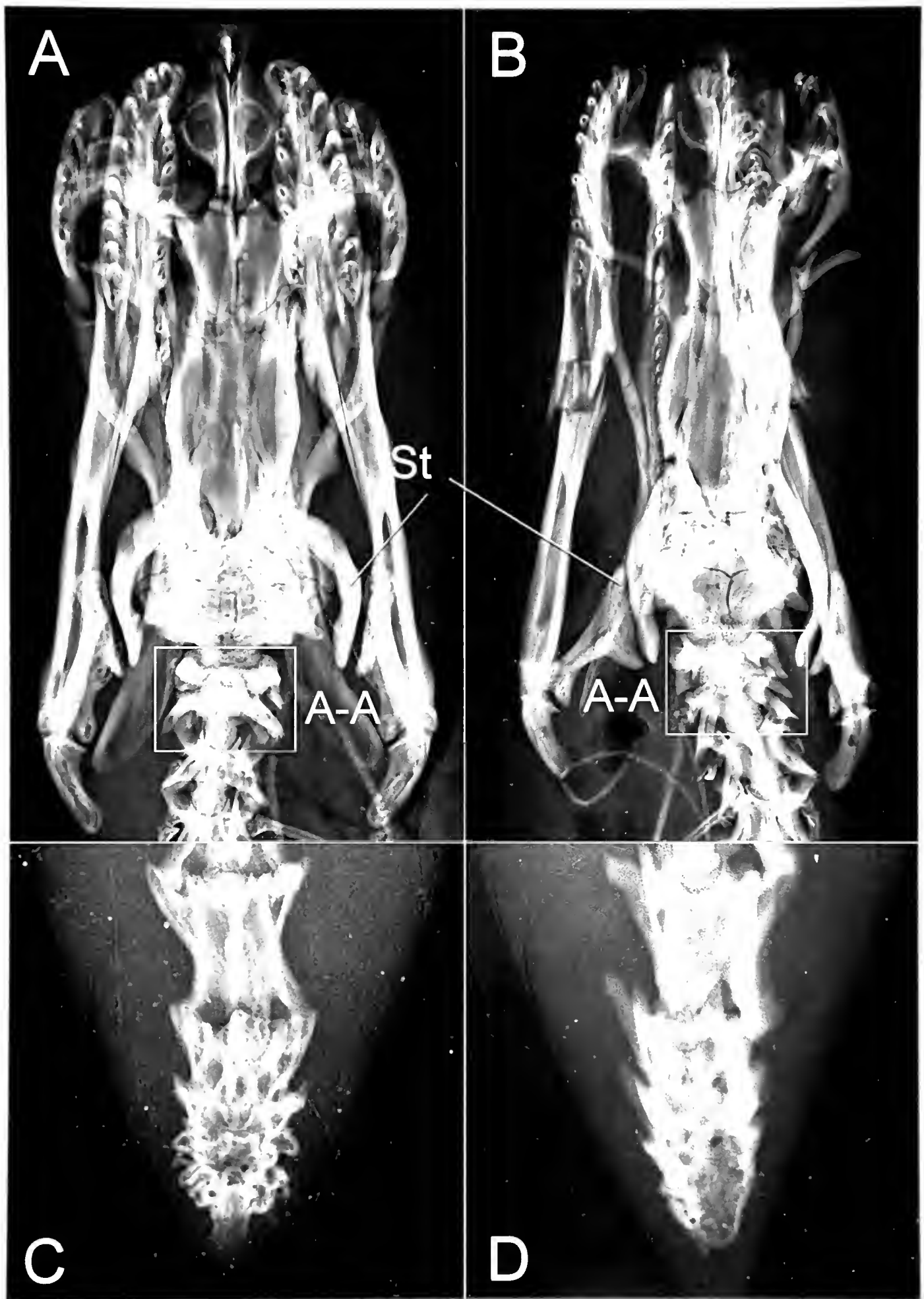


Figure 6. X-rays of the skulls (A, B) and tails (C, D) of *Toxicocalamus ernstmayri* new species (A, C) and *T. grandis* (B, D; BMNH 1946.1.18.34). Key features for comparison include the shape and length of the supratemporal bone (St) and the atlas-axis complex (A-A). The terminal vertebra of *T. ernstmayri* (C) shows a significant amount of ossified ornamentation that is all but absent in the tail of *T. grandis* (D).

TABLE 3. Comparisons between cranial characteristics of *Toxicocalamus ernstmayri* new species (MCZ R-145946) and *T. grandis* (BMNH 1946.1.18.34) using ratios of measurements taken from digital X-ray images. Abbreviations are explained in Table 1.

Ratio	<i>T. ernstmayri</i>	<i>T. grandis</i>	Difference (%)
ParW/SL	0.22	0.24	9.1
FW _{SO} /FW _{PF}	0.63	0.73	15.9
FW _{PF} /SL	0.21	0.21	0.0
MxL/SL	0.37	0.33	10.8
StL/SL	0.31	0.34	9.7

earthworms or earthworm fragments were reported from the guts of *T. loriae* specimens from the Waghi Valley, Simbu Province, including five specimens from Kondiu with earthworm fragments (AMNH R-75336–38, 75341, 75347), and a Kundiawa specimen (MCZ R-111785) with a large, complete earthworm protruding from its mouth and extending to its posterior gut. Elsewhere, a specimen of *T. loriae sensu lato* from Aguan, Milne Bay Province (BPBM 10967), and another from Maratambu in the Adelbert Mountains, Madang Province (AMNH R-82332) also contained complete earthworms, whereas the presence of soil and plant fibers in the guts of four additional Kondiu specimens (AMNH R-75340, 75343, 75345, 75348) was considered evidence of fully digested earthworms (McDowell, 1969).

Given the relative large size and lack of stomach contents for some *Toxicocalamus* species (e.g., *T. spilolepidotus* with TTL 850 mm, *T. grandis* with TTL 940 mm), it may be difficult to believe that they have adopted vermivorous lifestyles. In reference to *T. spilolepidotus*, McDowell (1969) wrote, “The only known specimen of *T. spilolepidotus*² is about the length and girth of an average mature female North American watersnake (*Natrix sipedon*) and I find it hard to believe that a snake this large

could have the burrowing and earthworm-eating habits of *T. loriae*.” And in reference to *T. grandis*, he wrote, “As in the case of *T. spilolepidotus*, it seems unlikely that so large a snake feeds primarily on earthworms, but its food preferences are quite unknown.” It is therefore interesting that the holotype of *T. ernstmayri*, now the species in the genus with the largest body size, contains a large earthworm (see below) and no other gut contents other than a parasitic nematode, demonstrating that even the larger members of the genus appear to feed on oligochaete worms.

McDowell (1969) also reported finding a small snail in the gut of one Waghi Valley specimen (AMNH R-75341), whereas a sarcophagid fly larva was retrieved from the gut of a specimen (AMNH R-59067) from Mafulu, Owen Stanley Range, Central Province (Bogert and Matalas, 1945). Sternfeld (1913) reported several peculiar “madenartige Tiere” [maggot-like animals] of length 4 cm, which he denoted as “Fliegenmaden?” [fly larvae?], in the gut of a specimen from Sattelberg, Huon Peninsula, Morobe Province. We believe it is most likely that the sarcophagid fly larvae represent postmortem artefacts, resulting from a delay between euthanasia and preservation of historical specimens in the field, and that the “small land snail” found by McDowell (1969) may have been ingested inadvertently. On the basis of the unusual size of Sternfeld’s “maggots,” we consider it possible that these were instead megascolecid earthworm cocoons. Subsequently we have also learned that a captive specimen of *T. longissimus* was induced to eat earthworms, while rejecting all other potential prey offered (Paiva, personal communication), and the holotype of *T. pachysomus* (TTL 715 mm) also contained an earthworm in its gut (Kraus, personal communication), although this fact was not reported in the original description (Kraus, 2009).

The Australasian region is inhabited by the terrestrial megadrile oligochaete family Megascolecidae, which contains the world’s largest earthworm species. Of 115 earth-

²Two female specimens of *T. spilolepidotus* (AMNH R-85745, PNGM 21332) are now known, from Purosa, near Okapa, and the Yaiya Valley in the Kratke Mountains, respectively, both localities in Eastern Highlands Province, PNG, at elevation approximately 1500–1740 m.



Figure 7. Two views of a megascolecid earthworm (likely of the genus *Pheretima* Kinberg, 1867; total length 436 mm) found in the stomach of *Toxicocalamus ernstmayri* new species. Scale = 5 cm.

worm species recorded from New Guinea, 109 belong to the Megascolecidae (Blakemore, 2006). The holotype contained a single large megascolecid earthworm (Fig. 7), likely of the genus *Pheretima* Kinberg, 1867 (Blakemore, in litteris), now accessioned in the MCZ annelid collection (MCZ 95752). The worm measured approximately 500 mm when removed upon examination of the freshly killed snake (Parker, 1982), and it is now 436 mm long after decades in preservative.

The holotype was also parasitized by a relatively large (total length 55 mm) nematode worm (Fig. 8), which has not yet been further identified.

All members of the genus *Toxicocalamus* are venomous. *Toxicocalamus buergersi* possesses extremely elongate venom glands that extend deep into the body cavity to extend posteriorly to almost midbody (McDowell, 1969; O'Shea, personal observation); McDowell (1969) remarked, "The venom gland of *T. grandis* is fully as large as that of the average New Guinea death adder (*Acanthophis*)."¹ Recent investigations into the venom composition of *T. longissimus* by Calvete et al. (2012) have demonstrated that this venom comprises primarily (92%) three-finger toxins (3FTx), combined with



Figure 8. Unidentified nematode parasite (total length = 55 mm) found loose in the body cavity of *Toxicocalamus ernstmayri* new species. We consider it likely that the parasite was dislodged when the earthworm was removed from the snake, but remained undetected inside the specimen.

smaller quantities of type-I phospholipase A₂ (PLA₂) and snake venom metalloproteinase (SVMP). 3FTxs are key components found in the neurotoxins, cardiotoxins, and platelet inhibitors of some of the world's most highly venomous snakes (e.g., Kini and Doley, 2010) and they are the main components in the venoms of elapids (Utkin, 2013). PLA₂ toxins are also common in the neurotoxins of elapid venoms that cause neuromuscular paralysis, whereas SVMPs cause hemorrhaging. Nothing is known about the venom composition or toxicity of *T. ernstmayri*, but given its large size, live specimens should be treated with respect and handled with caution.

DISCUSSION

The type locality, Wangbin (5°14'26.72"S, 141°15'31.92"E), lies in the Star Mountains, which are located in the North Fly District of Western Province, PNG, where the province borders Sandaun (formerly West Sepik) Province to the north, and Papua Province, Indonesia, to the west (Fig. 2A). The Ok Tedi River (Fig. 2) is a northern tributary of the 1,050-km-long Fly River, the second longest river in New Guinea, which flows south and southeast into the Gulf of Papua. The North Fly District is a mountainous, heavily forested region, except for the ecologically disturbed and deforested immediate vicinity of the Ok

Tedi Mine, an open-pit gold and copper mine with significant economic potential located at the site of the former Mt. Fubilan (see Jackson, 1982; Doucette 2000), 10 km NW of Tabubil on the Ok Tedi River (Fig. 2B). Olsobip (Fig. 9G) in the Star Mountains is believed to be one of the wettest places on Earth, with an annual rainfall of up to 10 m (McKinnon et al., 2008:206). Wangbin is a village located close to the northern shore of Lake Wangbin (Fig. 9C), approximately 5 km NE of Tabubil and 13 km ESE of the Ok Tedi Mine (Fig. 2B). In 1969, the year the holotype of *T. ernstmayri* was collected and before the development of the Ok Tedi Mine and Tabubil (Fig. 9H), Wangbin was a small village (Fig. 9A, B) surrounded by extensive primary mid-montane forest with some garden areas (Fig. 9D, E). At the time, gardens were established in partially cleared areas, with smaller trees and undergrowth being removed but with larger trees left standing (Fig. 9E). The presence of large trees may have reduced soil erosion in gardens established on slopes, an important factor affecting the environment in an area experiencing heavy rainfall.

The holotype of *T. ernstmayri* was collected by one of us (FP) during his employ as a kiap³ (patrol officer) while on patrol in the North Fly District (Fig. 9F). Other elapids recorded from the Ok Tedi River and Star Mountains region of Western Province include *Acanthophis laevis* Macleay, 1878, *Aspidomorphus muelleri* Schlegel, 1837, *M. ikaheka*, *T. p. angusticinctus*, and *T. stanleyanus*. A specimen of *T. loriae sensu lato* was collected at Busilmin across

the provincial border in Sandaun (West Sepik) Province, but still in the Star Mountains (Fig. 2A).

Australopapuan elapids primarily prey upon vertebrates, so *Toxicocalamus* is perhaps unique among this elapid species assemblage in its diet of earthworms. It appears to be an especially esoteric dietary choice for a snake that achieves an SVL of over 1.0 m. Although many *Toxicocalamus* exhibit a morphology that suggests a fossorial or semifossorial existence in keeping with this dietary preference, *T. ernstmayri* is morphologically similar in appearance to *M. ikaheka*, with which it was initially confused, suggesting a more active, terrestrial lifestyle.

The loss of the temporolabial scale in *Toxicocalamus*, and the subsequent reduction in the number of supralabials, is probably a derived condition within the Elapidae. Greer (1997: fig. 7.22) provided a series of head drawings that illustrate this transition, beginning with the primitive condition of seven supralabials as in *Bungarus candidus* (Linnaeus, 1758). An upward movement of the penultimate supralabial, becoming a temporolabial scale as if “squeezed” by the supralabials on either side, as seen in *Pseudechis australis* (Gray, 1842), is hypothesized to precede conditions involving the fusion of the temporolabial with the anterior temporal, a characteristic of *Vermicella annulata* (Gray, 1841), or with the last, now sixth, supralabial, such as in *Pseudonaja affinis* Günther, 1872, leading to the eventual reduction to five supralabials, as seen in *Simoselaps bimaculatus* (Duméril et al., 1854). All members of the genus *Toxicocalamus* lack a temporolabial scale and mirror the condition in *P. affinis*, with the exception of *T. preussi* and *T. stanleyanus*, which possess five supralabials and mirror the condition in *N. bimaculatus*, and *T. buergersi*, which exhibits a further reduction to four supralabials. *Toxicocalamus preussi*, *T. stanleyanus*, and *T. mintoni* demonstrate fusion of the preocular and prefrontal scutes; *T. buergersi* exhibits fusion of the preocular, prefrontal, and internasal scutes; whereas *T. mintoni* also

³Kiap is a pidgin word, derived from the German word *Kapitän*, which was applied to Australian government patrol officers in the pre-independence era. They covered considerable distances to deal with land disputes, and to apprehend murderers and cannibals to take before the courts. Fred Parker, co-author on this paper, was a *kiap* in PNG from 1960–73. His interest in herpetology caused him to make extensive collections wherever he patrolled. He deposited many specimens in MCZ, AMNH, and CAS, including the holotype of *T. ernstmayri*.

exhibits fusion of the frontal scute with the supraoculars on either side, resulting in a single head-wide scute. Bogert and Porter (1966) suggested that fusion of head scutes might be associated with a fossorial existence, whereby a reduction in the number of sutures between head scutes reduces the degree of friction for the burrowing snake. In obligatorily fossorial species fusion of scutes may also mirror underlying skull bone development, resulting in an overall strengthening of the skull. These further-derived characters are not present in *T. ernstmayri*, which belongs to an advanced elapid genus but might be considered relatively basal within that genus (Metzger et al., 2010; Pyron et al., 2013). Unfortunately, the age of the specimens available to us for this comprehensive study preclude their inclusion in molecular data sets to further elucidate the position of individual species within *Toxicocalamus*. As it stands, however, even the few studies available to include *Toxicocalamus* in a molecular framework (e.g., Keogh, 1998; Seanlon and Lee, 2004; Sanders et al., 2008; Metzger et al., 2010; Pyron et al., 2013) show that the position of the genus within the Elapidae, and even its monophyly, is still inconclusive.

On the basis of overall cranial morphology, the skulls of both *T. ernstmayri* and *T. grandis* are fairly kinetic with a relatively solid, elongated core. This morphology is perhaps ideally suited to a terrestrial or semifossorial lifestyle, and to capture earthworms with the necessary jaw pressure to subdue them. In the absence of X-rays for the other species of *Toxicocalamus*, there is unfortunately very limited utility in our data set for broader comparisons. McDowell (1969) did include some skull characteristics in generic and subgeneric definitions, but absent a more comprehensive data set and a description of assessment methods, we are unable to expand on our osteological comparisons at this time.

The ornamentation on the terminal vertebra was an unexpected feature we discovered when trying to determine whether the tail

was truncated or entire. Given the much lesser degree of ornamentation in *T. grandis*, we wish to point out the potential diagnostic value in the morphology of the terminal caudal vertebra. External aspects of tail termination have been used traditionally as stand-out features to define unusual taxa, including some uropeltids with keratinized tail plates such as *Uropeltis melanogaster* (Gray, 1858), or the “spider tail” of *Pseudocerastes urarachnoides* Bostanchi et al., 2006; these do not reflect the internal construction of the tail terminus. X-rays allow a detailed structural analysis of the terminal vertebra, and perhaps this is a useful, heretofore overlooked source of taxonomic information.

Ornamentation of the terminal vertebra brought into our focus the detailed external morphology of *Toxicocalamus* tails. In this genus, the tail tip consists not of scales as in most other snakes of this size, but of a terminal excrescence in the form of a keratinized spine or nub. The shape and dimensions of this structure appear to be useful as an additional character for distinguishing species, in addition to providing a tool for comparative measurements of the expansion of the tail thickness forward from its end. The morphometric approach to this character allowed us to quantify the statement that *T. ernstmayri* has a tail that remains relatively thick all the way toward its end, whereas by comparison *T. grandis* has a more slender tail. cursory inspection of the tail of a specimen of *T. loriae sensu lato* (AM R9351, the holotype of *Apisthocalamus lamingtoni* Kinghorn, 1928) shows a very thin tail, in which the width remains very narrow, at only 50% greater than at the beginning of the sharply pointed excrescence. The tails of *T. buergersi* (AM R120360), *T. misimae* (AM R7614), and *T. longissimus* (AM R124904) are essentially nubs. As we continue our investigations into the taxonomy of the genus *Toxicocalamus*, we intend to pay close attention to the dimensions of tails to determine whether they prove useful in field identification.

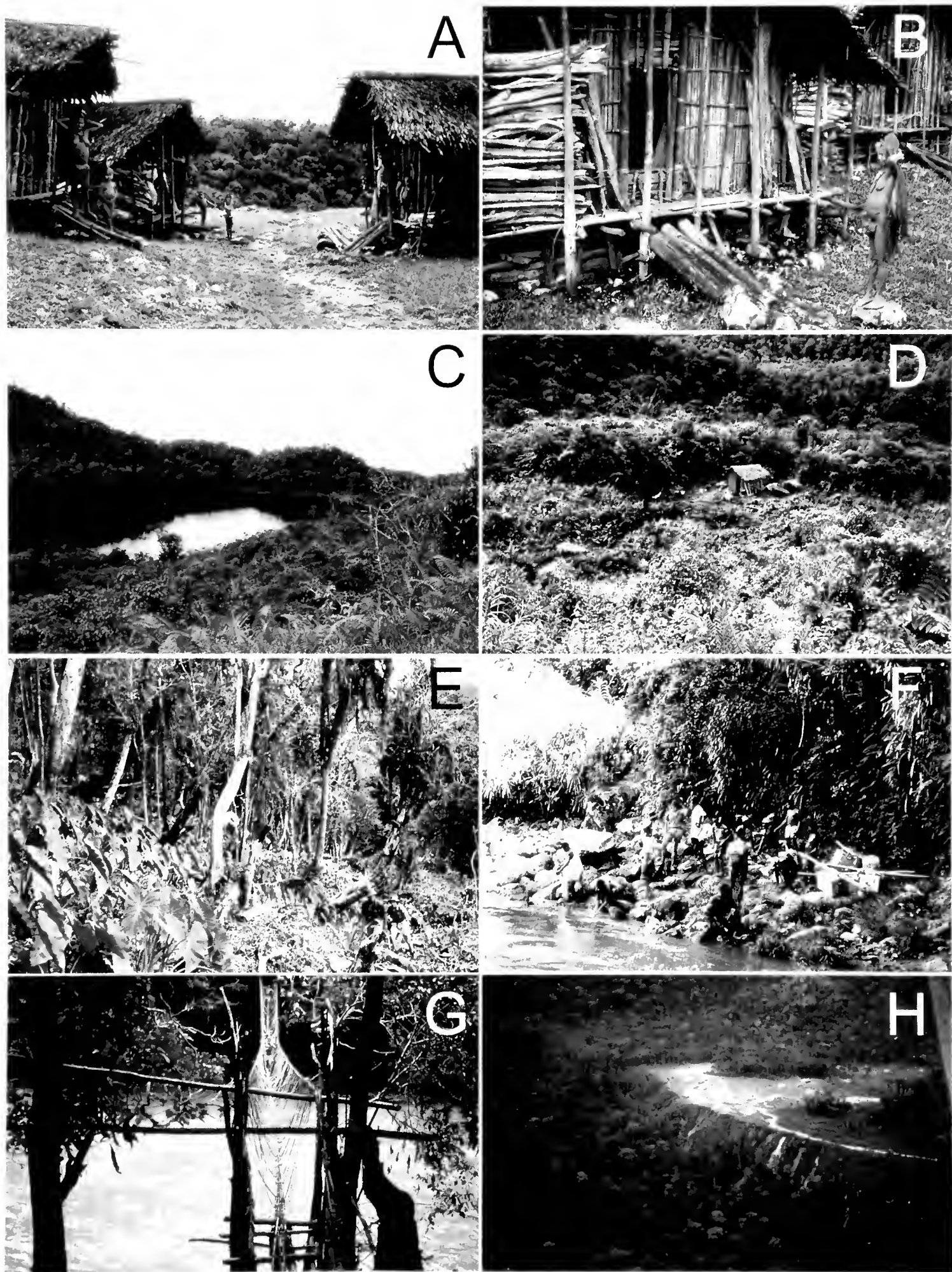


Figure 9. Photographs of Wangbin and Star Mountains environs, all taken on 24 December 1969, the day after the holotype of *Toxicocalamus ernstmayri* new species was collected, unless otherwise stated. We are presenting these images not only to illustrate the natural environment of *T. ernstmayri*, but also to provide a historical and social context for potential human-snake interactions. (A) The main path through Wangbin Village, which in 1969 was merely a hamlet. (B) Close-up of one of Wangbin's residences, showing details of access, construction, and wood storage. (C) Wangbin Lake, a small catchment surrounded by pristine rainforest. (D) The Wangbin guesthouse built by villagers in a clearing away from the main village in otherwise pristine rainforest. (E) Dense forest with large plants. (F) A rocky stream with people. (G) A net or structure in a forest. (H) A view of a lake or stream in a forest.

- 11a 13 scale rows at midbody; five supralabials; postocular present *T. preussi*
 11b 15 scale rows at midbody; four supralabials; postocular fused with supraocular *T. buergersi*

ACKNOWLEDGMENTS

The authors thank José Rosado and Joe Martinez for their generous assistance while working at the MCZ. We are very grateful to Patrick Campbell (BMNH) for providing us with the first set of X-rays for *T. grandis*, Adam Baldinger (MCZ), for locating and photographing the megascolecid earthworm predated by *T. ernstmayri*, Nicholas Griffiths and Pumehana Imada (both BPBM) for extricating and photographing the earthworm in the holotype of *T. pachysomus*, Allen Allison (BPBM) for granting permission to dissect the specimen, and Robert Blakemore (College of Natural Science, Hanyang University, Seoul, South Korea) for identifying the earthworms found in guts of *Toxicocalamus* specimens. MOS also acknowledges with thanks the hospitality of Van Wallach and Roxane Coombs during his stay in Cambridge, and Christine, Lucas, Max, and Isabel Kaiser during his stay in the Washington, DC area. Finally, thanks to the following collection managers and museum curators, in addition to those already named, for permitting access to their collections or arranging loans: Ross Sadlier (AM), David Dickey and David Kizirian (AMNH), Pumehana Imada (BPBM), Alan Resetar (FMNH), Ivan Ineich (MNHN), Irvan Sidik (MZB), Heinz Grillitsch (NMW), Bulisa Iova (PNGM), Esther Dondorp (RMNH), Carolyn Kovach (SAMA), Emily Braker (UCM), Paulus Keip (UPNG), Hans Mejlou (UPSZ), Jeremy Jacobs (USNM), and Frank Tillack (ZMB). Our thanks also go to colleagues who have assisted with the documenting, scale counting, and measuring of specimens: Lukas Hartmann, Julious Jacobs, Christine Kaiser, Max Kieckbusch, Keliopas Krey, Sven Mecke, and Øyvind Syrrist. We are also

grateful to Venancio Lopes Carvalho for preparing the Bahasa Indonesian abstract. Finally, the authors thank the five (!) anonymous reviewers whose extremely helpful and constructive comments undoubtedly improved the quality of this manuscript. Funding for the visit by MOS to the MCZ, AMNH, and USNM was provided by an Ernst Mayr Travel Grant from Harvard University.

APPENDIX 1. SPECIMENS EXAMINED

Micropechis ikaheka ($N = 15$).

Indonesia: *West Papua Province:* Doréy (= Manokwari), E Vogelkop Peninsula, elev. 70 m [00°52'S, 134°05'E], MNHN 7669 (holotype). Manokwari, E Vogelkop Peninsula, elev. 70 m [02°55'S, 132°17'E], RMNH.RENA 5585, 47926. Andai, E Vogelkop Peninsula, elev. 35 m [00°55'S, 134°00'E], BMNH 1878.2.11.48A–B. Aitinjo, W Vogelkop Peninsula, elev. 208 m [01°25'S, 132°03'E], RMNH.RENA 45779. Fak Fak Regency, Bomberai Peninsula, elev. 380–520 m [02°55'S, 132°17'E], BMNH 1909.4.30.12. Misool Is., Raja Ampat Islands, elev. 200 m [01°55'S, 130°05'E], RMNH.RENA 5585, 47926 (ex 5585). *Papua Province:* Mimika River, south coast, elev. 30 m [04°34'S, 136°40'E], BMNH 1913.10.31.220. Biak Island, Schouten Islands, Cenderawasih Bay, elev. 100 m [00°58'S, 135°57'E], RMNH.RENA 45799. Hollandia (= Jayapura) northeast coast, elev. 175 m [02°32'S, 140°42'E], AMNH 62480. **Papua New Guinea:** *Sandaun Province:* Aitape, elev. 40 m [03°08'S, 142°20'E], MCZ 48624. *Madang Province:* Kaviak Plantation, Karkar Island, elev. 30 m [04°35'S, 145°55'E], NHMUK 2013.283. *Oro Province:* Itokama, elev. 800 m [09°12'S, 148°15'E], BPBM 36148.

Toxicocalamus buergersi ($N = 4$). **Papua New Guinea:** *East Sepik Province:* Wewak, elev. 200 m [03°40'S, 143°05'E], AMNH R-75001, 75236. “Deutsch Neuguinea” [German New Guinea], ZMB 25232 (Holotype). Maprik [03°39'S, 143°02'E], AM R120360.

Toxicocalamus ernstmayri ($N = 1$). **Papua New Guinea:** *Western Province:* Wangbin, elev. 1468 m [5°14'S, 141°16'E], MCZ R-145946 (holotype).

Toxicocalamus grandis ($N = 1$). **Indonesia:** *Papua Province:* Launch camp, Setakwa River, elev. 25 m [04°45'S, 137°20'E], BMNH 1946.1.16.34 (holotype).

Toxicocalamus holopelturus ($N = 18$). **Papua New Guinea:** *Milne Bay Province:* Mt. Rossel, Rossel Is., Louisiade Archipelago, elev. 205–700 m [11°20'S, 154°13'E], AMNH R-76660 (holotype); BPBM 20823–33; PNGM 25194. Cheme, Rossel Is., Louisiade Archipelago, elev. 55 m [11°19'S, 154°14'E], BPBM 20835–36. Mt. Yuvu, Rossel Is., Louisiade Archipelago, elev. 450 m [11°22'S, 154°06'E], MCZ R-156548. Gobubob, Rossel Is., Louisiade Archipelago, elev. 336 m [11°21'S, 154°09'E], PNGM 25193.

Toxicocalamus longissimus ($N = 11$). **Papua New Guinea:** *Milne Bay Province:* Woodlark Is. [09°13'S, 152°56'E], BMNH 1946.1.18.92–93 (holotype, paratype). Guasopa, Woodlark Is., elev. 12 m [09°13'S, 152°56'E], AM R124904, BPBM 17885–87. Kulumandau, Woodlark Is., elev. 53 m [09°05'S, 152°43'E], AMNH R-76619, 76629–30, BPBM 42185. Suloga Harbour, Woodlark Is., elev. 80 m [09°12'S, 152°44'E], BPBM 17888. Waimunon Bay, Woodlark Is., elev. 72 m [09°04'S, 152°50'E], BPBM 39702. Dikoias, Woodlark Is., elev. 73 m [09°02'S, 152°45'E], BPBM 42183–84. "Fergusson Is." (possibly in error) BMNH 1904.11.1.60.

Toxicocalamus loriae ($N = 212$). **Papua New Guinea:** *Central Province:* Dinawa, Owen Stanley Range, elev. 1,220 m [08°35'S, 145°55'E], BMNH 1946.1.14.53 (holotype of *Apistocalamus pratti*). Mafulu, Owen Stanley Range, elev. 1,270 m [08°30'S, 147°04'E], AMNH R-59067; BMNH 1935.5.10.174. Fane to Bellavista road, Owen Stanley Range, elev. 1,065 m [08°32'S, 147°05'E], PNGM 23158. Tapini, Owen Stanley Range, elev. 950 m [08°21'S, 146°59'E], USNM 195619. Overs Corner, Owen Stanley Range, elev. 620 m [09°21'S, 147°29'E], MCZ R-150803. Siruohu, Mt. Obree, elev. 1,550 m [09°26'S, 140°00'E], BPBM 19603–04. Larom, elev. 900 m [09°26'S, 147°59'E], BPBM 19502, 19505–06. *Milne Bay Province:* Bunisi, Mt. Simpson, elev. 1,490 m [10°01'S, 149°36'E], BPBM 17989, 18164, 18166. Siyomu, Mt. Simpson, elev. 1,300 m [10°01'S, 149°35'E], BPBM 17987–88, 18165, 30638. Agam, Mt. Dayman, elev. 1,014 m [09°55'S, 149°20'E], PNGM 24649A–B; UPNG 4840. Dumae Creek, W. Agaun, Mt. Dayman, elev. 1,200 m [09°53'S, 149°19'E], BPBM 10966–67. Bonenau, elev. 1,340 m [09°53'S, 149°24'E], UPNG 7105, 7107–08. Mai-iu River, elev. 428 m [09°41'S, 149°16'E], UPNG 3526. Basima, Fergusson Is., d'Entrecasteaux Archipelago, elev. 10 m [09°28'S, 150°50'E], BPBM 16544. Oya Waka,

Fergusson Is., d'Entrecasteaux Archipelago, elev. 990 m [09°27'S, 150°33'E], BPBM 16545. *Oro Province:* Umwate, Itokama, elev. 943 m [09°16'S, 148°16'E], BPBM 43028–29, 43032. Akupe camp, Itokama, elev. 723 m [09°17'S, 148°16'E], BPBM 43027. Mt. Trafalgar, Cape Nelson, elev. 187 m [09°13'S, 149°09'E], BPBM 39813. Ismava, Kokoda Track, elev. 1,260 m [08°59'S, 147°44'E], BPBM 44892. Eora Creek, Kokoda Track, elev. 1,800 m [00°02'S, 147°44'E], BPBM 44892. Kokoda Track [n/a] PNGM 22762. 'Popondetta' (dubious), elev. 106 m [08°46'S, 148°14'E], AMNH R-111810, MCZ R-141009. Mt. Lamington [08°56'S, 148°10'E], AM R9351 (holotype of *Apisthocalamus lamingtoni*). *Morobe Province:* Garaina, elev. 770 m [07°53'S, 147°08'E], MCZ R-152432. Saurere, W. Garaina, elev. 1,440 m [07°55'S, 147°05'E], PNGM 22767. Saiko, elev. 1,870 m [07°57'S, 147°03'E], BPBM 41381, 41390. Amu Creek, elev. 1,660 m [07°55'S, 147°02'E], BPBM 41391. Wau and environs, elev. 1,220–2,000 m [07°20'S, 146°43'E], BPBM 17173, 17417, 17451–52, 18217, 23669, PNGM 24716. Kalolo Creek, elev. 965 m [07°18'S, 146°43'E], AMNH R-1422887, BPBM 5440, 5442. Hewieni, Kariba River, elev. 1,050 m [07°25'S, 146°25'E], BPBM 17423. Aseki, Watut Valley, elev. 1,640 m [07°20'S, 146°10'E], BPBM 6497. Kwaplalim, W. Menyamya, Tauri River, elev. 1,500 m [07°11'S, 145°58'E], UCM 51552–53, NMW 37670. Zenag, Markham Valley, elev. 940 m [06°57'S, 146°37'E], AMNH R-85744. Sattelberg, Huon Peninsula, elev. 800 m [06°29'S, 147°47'E], BMNH 1946.1.17.57 (cotype of *Pseudapistocalamus nymani*), MCZ R-76627–28, UPS 2387 (cotype of *P. nymani*). Masba Creek, Huon Peninsula, elev. 760 m [06°29'S, 147°31'E], AMNH R-95579–80. Mt. Rawlinson, Huon Peninsula, elev. 1,340 m [06°31'S, 147°16'E], AMNH R-95581. Pindui and environs, Huon Peninsula, elev. 790 m [06°17'S, 147°18'E], AMNH R-95578, 95582. Tuwop, Saravaget Range, Huon Peninsula, elev. 1,350 m [06°21'S, 146°55'E], BPBM 3397, 3399. Liahm, Huon Peninsula, elev. 116 m [06°06'S, 147°36'E], ZMB 24343–44, 78770–71. *Madang Province:* Astrolabe Bay, elev. 116 m [05°22'S, 145°39'E], NMW 27383.1–2. Wanang, elev. 120 m [05°15'S, 145°16'E], BPBM 31257. Kalne River, Bismarck Range, elev. 1,200 m [05°31'S, 144°49'E], UPNG 8695. Kaironk, Schrader Valley, elev. 1,200 m [05°14'S, 144°29'E], UPNG 963–67, 3353, 5012. Matatambu, Adelbert Range, elev. 1,140 m [04°36'S, 145°54'E],

UPNG 8695. *E. Highlands Province*: Wonenara, Yaiya Valley, elev. 1,650 m [06°48'S, 145°53'E], UPNG 1213–18. Agakamatasa, elev. 1,720 m [06°43'S, 145°37'E], MCZ R-121545. Nivi Unggai, elev. 2,030 m [06°13'S, 145°18'E], MCZ R-84142, 116791–92. Lufa, Mt. Michael, elev. 1,120 m [06°20'S, 145°15'E], MCZ R-121546. *Simbu Province*: Igindi, Suai Mts., elev. 1,630 m [06°11'S, 144°58'E], AMNH R-98134. Kebil, Wahgi Valley, elev. 1,944 m [06°10'S, 145°01'E], MCZ R-85050. Kundiawa, Wahgi Valley, elev. 1,585 m [06°01'S, 144°58'E], AMNH R-98495–98; MCZ R-83218, 84026, 84143–44, 111764–90, 115586, 116774–88, 123883–86, 140818–19, 145923; PNGM 864, 882, 24585–86; SAMA R9526; USNM 166280. Mintima, Wahgi Valley, elev. 1,830 m [05°58'S, 144°55'E], MCZ R-116789–90. Poral Ras, Wahgi Valley, elev. 1,770 m [05°59'S, 144°55'E], MCZ R-121547–48. Kondiu, Wahgi Valley, elev. 1,600 m [05°58'S, 144°52'E], AMNH R-75336–57. Kup, Wahgi Valley, elev. 1,500 m [05°57'S, 144°48'E], AMNH R-72780–81. *Jiwaka Province*: Minj, Wahgi Valley, elev. 1,560 m [05°52'S, 144°40'E], MCZ R-141849. Banz, Wahgi Valley, elev. 1,650 m [05°47'S, 144°37'E], AMNH R-85743, 88060. *W. Highlands Province*: Dobel, Mt. Hagen, elev. 1,705 m [05°51'S, 144°14'E], PNGM 22160; UPNG 3992. *S. Highlands Province*: Mendi, elev. 1,750 m [06°08'S, 143°39'E], MCZ R-121543–44. Halalinja, Waga River, elev. 2,140 m [06°09'S, 143°22'E], BMNH 1976.92. Nipa, elev. 2,070 m [06°06'S, 143°15'E], UPNG 5811. *Sandaun Province*: Busilmin, Star Mts., elev. 1,880 m [04°55'S, 141°12'E], SAMA R6275. “Neuguinea” NMW 27382.1–2. “Deutsch Neuguinea” [German New Guinea], ZMB 23533. **Indonesia**: *W. Papua Province*: Fak Fak Peninsula, elev. 518 m [02°57'S, 132°35'E], BMNH 1946.1.18.24–26; MCZ R-76634 (holotype and paratypes of *Apistocalamus loennbergii*). “New Guinea” (no further locality data), MZB 361.

Toxicocalamus mintoni ($N = 1$). **Papua New Guinea**: *Milne Bay Province*: Mt. Riu, Sudest Is., Louisiade Archipelago, elev. 410 m [11°29'S, 153°25'E], BPBM 20822 (holotype).

Toxicocalamus misimae ($N = 3$). **Papua New Guinea**: *Central Province*: Mekeo region [09°00'S, 146°50'E], AM R7614. *Milne Bay Province*: Mararoa, Mt. Sisa, Misima Is., Louisiade Archipelago, elev. 350 m [10°39'S, 152°48'E], AMNH R-76684 (holotype). Bagi-

lina, Misima Is., Louisiade Archipelago, elev. 128 m [10°39'S, 152°48'E], BPBM 17231.

Toxicocalamus pachysomus ($N = 1$). **Papua New Guinea**: *Milne Bay Province*: Gadowalai, Cloudy Mts., elev. 715 m [10°29'S, 150°14'E], BPBM 15771 (holotype).

Toxicocalamus preussi ($N = 42$). **Papua New Guinea**: *Simbu Province*: Crater Mt., elev. 2,325 m [06°35'S, 145°05'E], BPBM 17449. Haia, elev. 908 m [06°43'S, 145°05'E], USNM 562943–44. *Gulf Province*: Wabo, elev. 400 m [06°54'S, 145°03'E], USNM 562942. Koni, Purari River, elev. 76 m [07°15'S, 145°20'E], MCZ R-102176. Middletown, Kikori River, elev. 63 m [07°16'S, 144°09'E], MCZ R-59090. NW Kikori, Kikori River, elev. 37 m [07°10'S, 144°05'E], MCZ R-150804. *Western Province*: S. Palmer Junction, Strickland River, elev. 65 m [05°54'S, 141°32'E], AMNH R-57511–12 (holotype and paratype of *Ultrocalamus preussi angusticinctus*). Matkomrae, Ok Tedi River, elev. 82 m [05°49'S, 141°09'E], MCZ R-121551, 141008. Ningerum, Ok Tedi River, elev. 86 m [05°41'S, 141°08'E], MCZ R-140989, 141001; USNM 217500. Tabubil, Ok Tedi River, elev. 828 m [05°15'S, 141°12'E], UPNG 5665. Olsobip, Fly River, elev. 612 m [05°23'S, 141°31'E], PNGM 24584; UPNG 1613. *Sandaun Province*: Berlinhafen, Seleo Is., elev. 7 m [03°08'S, 142°29'E], ZMB 23948 (holotype *Ultrocalamus preussi*). Mt. Sapau, Torricelli Range, elev. 1,300 m [03°22'S, 142°31'E], BPBM 23456. Njao, Tjano River, elev. 450 m [02°48'S, 141°00'E], ZMA 17733. **Indonesia**: *Papua Province*: Arso, Tami River, elev. 53 m [02°56'S, 140°47'E], ZMA 17734B. Hollandia (= Jayapura), elev. 100 m [02°532'S, 140°42'E], FMNH 43030; ZMA 17735. Upper Sermowai River, elev. 95 m [02°29'S, 139°50'E], UIMNH 19199; ZMA 17736A–C. Etik, Biri River, elev. 140 m [02°17'S, 139°08'E], MZB 5090; ZMA 17734A. SW Bernard Camp, Idenberg River, elev. 800–850 m [03°30'S, 139°09'E], AMNH R-62469–72. Prauwenbivak, Idenberg River, elev. 40 m [02°25'S, 139°10'E], MZB 354, 5089, ZMA 17731. Albatrosbivak, Mamberamo River, elev. 40 m [02°09'S, 137°52'E], MZB 356, 5054–56. Pionierbivak, Mamberamo River, elev. 10 m [02°04'S, 137°50'E], ZMA 17732. Mamberamo River, elev. 20 m [01°55'S, 137°50'E], MZB 353.

Toxicocalamus spilolepidotus ($N = 2$). **Papua New Guinea**: *E. Highlands Province*: Purosa, Okapa, elev. 1,740 m [06°40'S, 145°33'E], AMNH R-85745 (holotype). Yaiya Valley, Kratke

Mts., elev. 1,500 m [07°00'S, 145°49'E], PNGM 21332.

Toxicocalamus stanleyanus ($N = 31$). **Papua New Guinea:** *Central Province:* Dinawa, Owen Stanley Range, elev. 840 m [08°35'S, 146°55'E], BMNH 1946.1.7.55 (holotype), 1904.3.17.13. Madew, St. Joseph River, Owen Stanley Range, elev. 1,200 m [08°36'S, 146°55'E], BMNH 1908.10.14.10–12. Mafulu, Owen Stanley Range, elev. 1,270 m [08°30'S, 147°04'E], AMNH R-59063; BMNH 1935.5.10.171–173. *Gulf Province:* Teduku, Eloa River, elev. 178 m [07°43'S, 146°29'E], USNM 562945. Middletown, Kikori River, elev. 63 m [07°16'S, 144°09'E], MCZ R-59059–60; USNM 217499. Unknown locality, UPNG 8737A–B. *Simbu Province:* Camp II, Pio River, elev. 300 m [06°44'S, 144°52'E], MCZ R-121549. Haia, elev. 640 m [06°43'S, 145°05'E], USNM 562941. *Western Province:* Matkomrae, Ok Tedi River, elev. 82 m [05°49'S, 141°09'E], MCZ R-121550. Ningerum, Ok Tedi River, elev. 86 m [05°41'S, 141°08'E], MCZ R-140988; PNGM 22159. *Madang Province:* Hinihon to Reinduk, Adelbert Range, elev. 1,000 m [04°40'S, 145°22'E], BPBM 5711. *E. Sepik Province:* Arin, elev. 560 m [03°33'S, 143°20'E], UPNG 7171. *Sandann Province:* Mt. Nibo, S. Aitape, elev. 208 m [03°23'S, 142°09'E], AMNH R-100047. Parkop, Mt. Sapau, Torricelli Range, elev. 526 m [03°25'S, 142°31'E], BPBM 223455. **Indonesia:** *Papua Province:* Ingembit, Ok Walimkan River, elev. 117 m [05°38'S, 141°00'E], MZB 1464. Canobivak, Eilanden River, elev. 37 m [05°14'S, 139°40'E], ZMA 17682. Beaufort River camp, Baliem Valley, elev. 64 m [03°27'S, 139°10'E], RMNH.RENA 4988, 47753–54. Siewa, elev. 80 m [03°03'S, 136°22'E], MZB 2784. *W. Papua Province:* Fak Fak Regency, Bomberai Peninsula, elev. 380–520 m [02°57'S, 132°35'E], ZMA 17683.

Toxicocalamus sp. ($N = 17$). **Papua New Guinea:** *Morobe Province:* Garaina, elev. 770 m [07°53'S, 147°08'E], AMNH R-95624, 101100–03, 103681, 104084–85, 107203–05; MCZ R-152428–31. *Oro Province:* Itokama 820 m [09°12'S, 148°14'E], BPBM 36185. *W. Highlands Province:* Jimi River, elev. 960 m [n/a], UPNG 962.

LITERATURE CITED

- BLAKEMORE, R. J. 2006. Checklist of New Guinea Earthworms (*Oligochaeta: Clitellata*) Available from: <http://www.annelida.net/earthworm/AustralasianEarthworms/NewGuinea.pdf> Accessed: 20 November 2014.
- BOGERT, C. M., AND B. L. MATALAS. 1945. Results of the Archbold Expeditions. No. 53. A review of the elapid genus *Urocalamus* of New Guinea. *American Museum Novitates* **1284**: 1–7.
- BOGERT, C. M., AND A. P. PORTER. 1966. A new species of *Geophis* (Serpentes, Colubridae) from the State of Colima, Mexico. *American Museum Novitates* **2260**: 1–10.
- BOULENGER, G. A. 1896. Description of a new genus of elapine snakes from Woodlark Island, British New Guinea. *Annals and Magazine of Natural History* **6(18)**: 152.
- BRADT, S. 2005. Ernst Mayr, giant among evolutionary biologists, dies at 100. *Harvard University Gazette*.
- CALVETE, J. J., P. GHEZZELOU, O. PAIVA, T. MATAINHO, A. GHASSEMPOUR, H. GOUDARZI, F. KRAUS, L. SANZ, AND D. J. WILLIAMS. 2012. Snake venomomics of two poorly known Hydrophiinae: comparative proteomics of the venoms of terrestrial *Toxicocalamus longissimus* and marine *Hydrophis cyanocinctus*. *Journal of Proteomics* **75**: 4091–4101.
- DOUCETTE, J. 2000. A petrochemical study of the Mount Fubilan intrusion and associated ore bodies, Papua New Guinea. Unpublished Ph.D. thesis. Corvallis: Oregon State University.
- DWYER, C. M., AND H. KAISER. 1997. Relationship between skull form and prey selection in the thamnophiine snake genera *Nerodia* and *Regina*. *Journal of Herpetology* **31(4)**: 463–475.
- GREER, A. E. 1997. *The Biology and Evolution of Australian Snakes*. Chipping Norton, New South Wales, Australia: Surrey Beatty & Sons.
- JACKSON, R. 1982. *Ok Tedi: The Pot of Gold*. Port Moresby, Papua New Guinea: University of Papua New Guinea Press.
- KATHIRINER, A., A. M. BAUER, M. O'SHEA, C. SANCHEZ, AND H. KAISER. 2014. Hiding in plain sight: a new species of bent-toed gecko (Squamata: Gekkonidae: *Cyrtodactylus*) from West Timor, collected by Malcolm Smith in 1924. *Zootaxa* **3900(4)**: 555–568.
- KEOGH, J. S. 1998. Molecular phylogeny of elapid snakes and a consideration of their biogeographic history. *Biological Journal of the Linnean Society* **63**: 177–203.
- KINI, R. M., AND R. DOLEY. 2010. Structure, function and evolution of three-finger toxins: mini proteins with multiple targets. *Toxicon* **56**: 855–867.
- KRAUS, F. 2009. New species of *Toxicocalamus* (Squamata: Elapidae) from Papua New Guinea. *Journal of Herpetology* **65(4)**: 460–467.
- MAYR, E. 1942. *Systematics and the Origin of Species, from the Viewpoint of a Zoologist*. Cambridge, Massachusetts: Harvard University Press.
- MCDOWELL, S. B. 1967. *Aspidomorphus*, a genus of New Guinea snakes of the family Elapidae, with notes on related genera. *Journal of Zoology, London* **151(4)**: 497–543.

- . 1969. *Toxicocalamus*, a New Guinea genus of snakes of the family Elapidae. *Journal of Zoology, London* **159**(4): 443–511.
- MCKINNON, R., J.-B. CARILLET, AND D. STARNES. 2008. *Papua New Guinea and the Solomon Islands*. Lonely Planet.
- METZGER, G. A., F. KRAUS, A. ALLISON, AND C. L. PARKINSON. 2010. Uncovering cryptic diversity in *Aspidomorplius* (Serpentes: Elapidae): evidence from mitochondrial and nuclear markers. *Molecular Phylogenetics and Evolution* **54**: 405–416.
- NATUSCH, D. J. D., AND R. SHINE. 2012. Measuring body lengths of preserved snakes. *Herpetological Review* **43**(1): 34–35.
- O'SHEA, M. 1996. *A Guide to the Snakes of Papua New Guinea*. Port Moresby, Papua New Guinea: Independent Publishing.
- . 2005. *Venomous Snakes of the World*. London: New Holland.
- . 2013. Sandy Wollaston and the Setakwa River snake. *The Herptile* **38**(4): 130–141.
- PARKER, F. 1982. *Snakes of Western Province*. Vol. 82/1. Port Moresby, Papua New Guinea: Division of Wildlife, Department of Lands and Environment.
- PYRON, R. A., F. T. BURBRINK, AND J. J. WIENS. 2013. A phylogeny and updated classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology* **13**: 93.
- SABAJ PÉREZ, M. H. 2014. Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 5.0 (22 September 2014). In Washington, DC: American Society of Ichthyologists and Herpetologists.
- SANDERS, K. L., M. S. Y. LEE, R. LEYS, R. FOSTER, AND J. S. KEOGH. 2008. Molecular phylogeny and divergence dates for Australasian elapids and sea snakes (Hydrophiinae): evidence from seven genes for rapid evolution. *Journal of Evolutionary Biology* **21**(3): 682–695.
- SCANLON, J. D., AND M. S. Y. LEE. 2004. Phylogeny of Australasian venomous snakes (Colubroidea, Elapidae, Hydrophiinae) based on phenotypic and molecular evidence. *Zoologica Scripta* **33**: 335–366.
- SHINE, R., AND J. S. KEOGH. 1996. Food habits and reproductive biology of the endemic Melanesian elapids: are tropical snakes really different? *Journal of Herpetology* **30**(2): 238–247.
- STERNFELD, R. 1913. Beiträge zur Schlangenfauna Neuguineas und der benachbarten Inselgruppen. *Sitzungsberichte der Gesellschaft Naturforschender Freunde, Berlin* **1913**: 384–389.
- UTKIN, Y. N. 2013. Three-finger toxins, a deadly weapon of elapid venom—milestones of discovery. *Toxicon* **62**: 50–55.

Photo on the front cover:

The cover image is a media collage pertaining to the description of a new species of New Guinea worm-eating snake, genus *Toxicocalamus*, by Mark O'Shea, Fred Parker, and Hinrich Kaiser. The head of new species is shown in dorsal, right lateral, and x-ray views, placed next to a topographic map of Papua New Guinea and selected surrounding islands with the type locality in the Star Mountains marked by a red circle.

US ISSN 0027-4100

MCZ Publications
Museum of Comparative Zoology
Harvard University
26 Oxford Street
Cambridge, MA 02138

mczpublications@mcz.harvard.edu