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Discovery of the second specimen of *Toxicocalamus ernstmayri* O'Shea et al., 2015 (Squamata: Elapidae), the first from Papua Province, Indonesia, with comments on the type locality of *T. grandis* (Boulenger, 1914)

Mark O'Shea[1,*], Paul Blum[2] & Hinrich Kaiser[3]

[1] *Faculty of Science and Engineering, University of Wolverhampton, Wulfruna Street, Wolverhampton, WV1 1LY, UK*
[2] *Habsburgerstraße 99, D-79104 Freiburg im Breisgau, Germany*
[3] *Department of Vertebrate Zoology, Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany*
[3] *Department of Biology, Victor Valley College, 18422 Bear Valley Road, Victorville, California 92395, USA*
* *Corresponding author: Email: m.oshea@wlv.ac.uk*

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[2] urn:lsid:zoobank.org:author:D96AE0C6-E512-433A-8B60-CE6C28B13B28
[3] urn:lsid:zoobank.org:author:3283F957-6817-4C69-8C31-324D49AF735A

Abstract. Examination of historical specimens from western New Guinea in the Zoologische Staatssammlung Munich, Germany, led to the discovery of only the second specimen of the rarely encountered Star Mountains Worm-eating Snake, *Toxicocalamus ernstmayri*. This specimen is the first record of the species from the Indonesian part of New Guinea, extending its known range northwestward by 150 km. We also question the long-accepted collection locality for another poorly known species, *T. grandis* and document that it was most likely collected further up the Setekwa River at a higher elevation, in habitat more conducive to the ecology of a terrestrial to semi-fossorial genus and in keeping with the known mainland distribution of *Toxicocalamus*.

Keywords. Indonesia, Jayawijaya Range, Sudirman Range, Utekwa River, Setekwa River, rare snake.

INTRODUCTION

Toxicocalamus is an endemic New Guinea genus of secretive, semi-fossorial or terrestrial snakes that occurs throughout the island in both the sovereign state of Papua New Guinea (PNG), which occupies the eastern half of the island, and western New Guinea (WNG), the Indonesian half of New Guinea that includes the provinces Papua and West Papua. These snakes have also been recorded from a number of satellite islands off the coast of PNG, including Seleo (Sandaun Province), Walis and Tarawai (East Sepik Province), and Karkar (Madang Province). *Toxicocalamus* also has an island radiation in the archipelagos of Milne Bay Province, PNG, including six species in the d'Entrecasteaux Archipelago (Good-enough, Fergusson, and Normanby Islands), the Louisiade Archipelago (Misima, Sudest, and Rossel Islands), and on Woodlark Island. Sixteen species are currently recognised, but we expect that this figure will increase considerably due to a recent resurgence of interest in the genus that has already led to the description of seven species since 2009 (Kraus 2009, 2017, 2020; O'Shea et al. 2015, 2018a).

Toxicocalamus ernstmayri O'Shea et al., 2015 was described from a female holotype (MCZ R-145946) collected by former *kiap*[1] Fred Parker on 23 December 1969 at Wangbin (5.2408° S, 141.2589° E, elev. 1468 m; Fig. 1), a small hamlet near Tabubil in the Star Mountains, North Fly District, Western Province, PNG. It was accessioned into the collection of the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ), as a specimen of *Micropechis ikaheca*[2] Lesson, 1830, and it remained misidentified until it was examined by the first author during a research visit to the MCZ collection in 2014. With a snout-to-vent length (SVL) of 1.1 m and a total length (TTL) of 1.2 m, the holotype is the largest known specimen of *Toxicocalamus*, a genus which rarely

1 *Kiap* is a word in *tok pisin* (a Papuan creole language), derived from the German for captain and referring to a pre-Independence patrol officer in PNG.

2 The correct spelling is *ikaheca* rather than the commonly used *ikaheka*, according to Lesson's original description.

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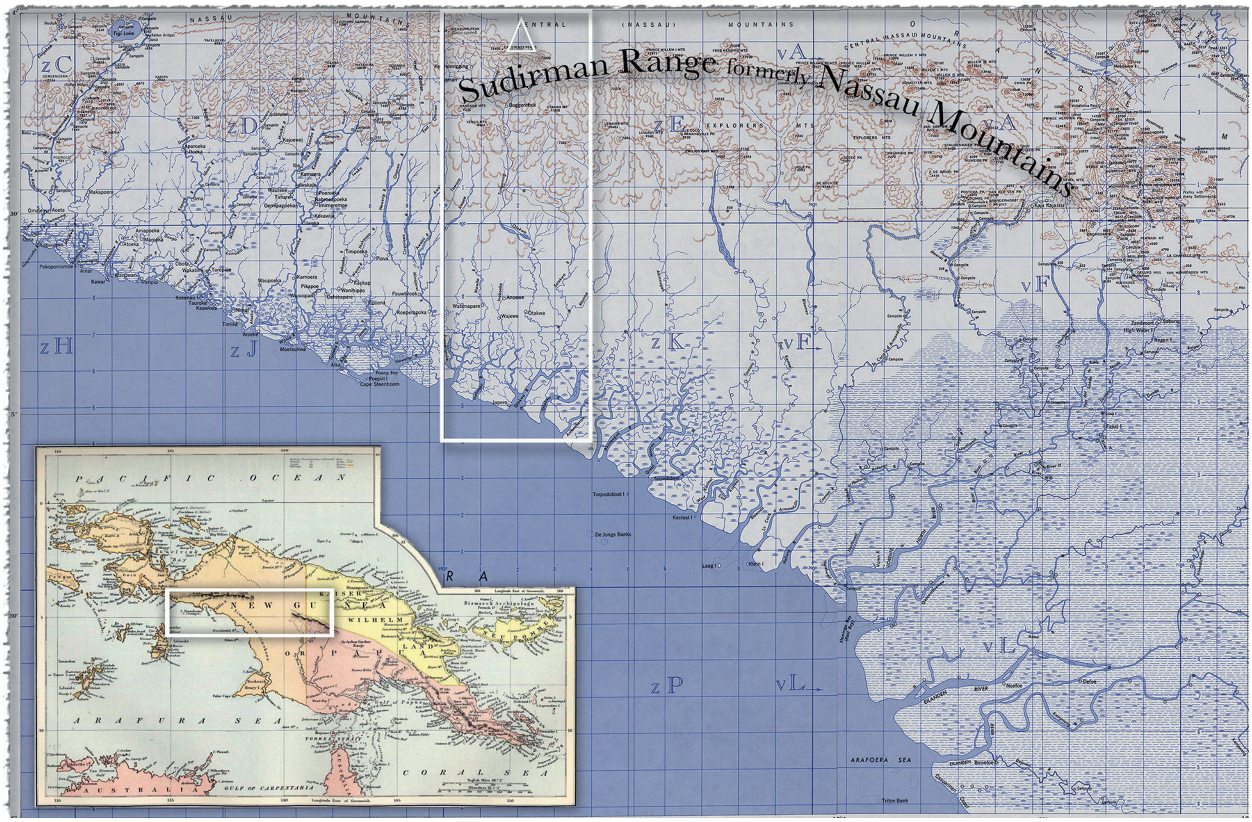

Fig. 1. Note to the reader: This figure comprises a left panel (above) and a right panel at the top of the facing page. Shown is a 1942 map of southwestern New Guinea, including the mountain ranges from which the existing records of *Toxicocalamus ernstmayri* and *T. grandis* were reported. Numbered red circles indicate localities for (**1**) the holotype of *T. ernstmayri* (MCZ R-145946), (**2**) the sighting of *T. ernstmayri* at the Ok Tedi Mine (O'Shea et al. 2018b), and (**3**) the locality where ZSM 55/2015 was collected. The vertical white frame on the main map identifies the location of the Wollaston Expedition of 1912–13, which nearly reached Carstensz Pyramid, now Puncak Jaya (white triangle). The highlighted yellow line is the border between Papua New Guinea to the east and Indonesian West New Guinea to the west. The inset is an 1884 map showing Dutch, German and British boundaries, with the position of the main map, relative to the island of New Guinea, northern Australia, and eastern Indonesia, indicated by the horizontal white frame.

exceeds 600 mm TTL. The only other species of near equal size is *T. grandis* (Boulenger, 1914), whose single specimen is housed in The Natural History Museum, London, United Kingdom (BMNH) and accessioned as BMNH 1946.1.18.34. It was ostensibly collected on the Setekwa River[3], southern Papua Province, WNG (Fig. 1) in 1912, and possesses an SVL of 960 mm and a TTL of 1040 mm. A second, live individual of *T. ernstmayri* was identified in 2018 from photographs, which are of an unsexed adult (approximate TTL 850 mm, estimated from the known size of tire tracks) as it moved slowly and unmolested across an area of active mine workings at the Ok Tedi Mine (5.2150° S, 141.1442° E, elev. 1670 m; Fig. 1) on 9 October 2015 (O'Shea et al. 2018b). The two locations, Wangbin and the Ok Tedi Mine, are only 13.2 km apart and *T. ernstmayri* was presumed to be a localised species found only in the Star Mountains of Western and Sandaun Provinces, PNG.

During a visit to the Zoologische Staatssammlung Munich, Germany (ZSM), the first author examined a small collection of snakes from the mountains of WNG made by the second author in the 1970s. This collection included two specimens of *Toxicocalamus* that had tentatively been identified as *T. grandis*. While the identity of one of these (ZSM 54/2015) still has to be determined, the other (ZSM 55/2015) represents the first known specimen of *T. ernstmayri* from the western half of the island of New Guinea, and we herein document it as such.

3 When dealing with colonial and local place names, it is common that differences in names or spelling exist. Sometimes this is because a colonial power insisted on renaming places that already had local names, as a sign of superiority, oppression, or to honor their leadership, other times honest transcription errors derived from communication problems between the local population and colonial officials crept in, especially when dealing with oral names that were never intended to be written down and which may sound different when spoken by different groups of indigenous people or even individual persons. The names of the Setekwa and Utekwa Rivers in WNG we use here are examples of the latter, and they can also be spelled as Setakwa and Oetakwa.

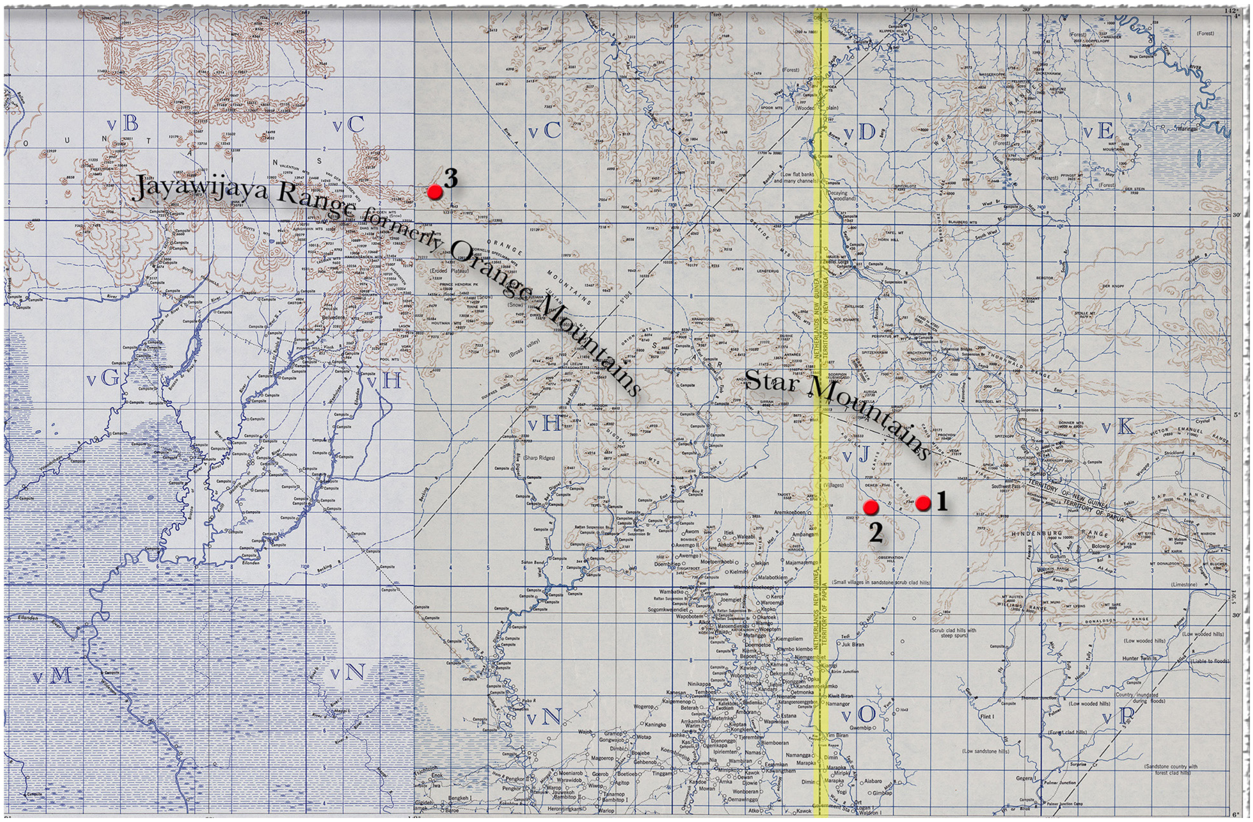

Fig. 1. Continued: right panel.

MATERIALS AND METHODS

Measurements

Our length measurements and our assessment of *Toxicocalamus* scales follow the methods described by O'Shea et al. (2018a). SVL was obtained by running a non-elastic string from the tip of the snout along the ventral medial axis of the body, the string then being placed against a cloth tape-measure taped to a workbench with attention being paid to accuracy of measurement, *fide* Natusch & Shine (2012). Tail length (TL) was easily measured by laying the tail along the tape-measure. TTL is the sum of SVL + TL, and TL as a percentage of TTL was calculated as TL/TTL × 100. Other abbreviations include V (ventrals), SC (subcaudals), SCR (subcaudal ratio, calculated as SC divided by V+SC), SL (supralabials), and IL (infralabials).

Scale counts

Scale counts recorded on the body included dorsals, ventrals, and subcaudals. The dorsal scale rows were counted transversely across the body at three points, one head length posterior to the head, at midbody, and one head length anterior to the cloaca. These counts in *Toxicocalamus* are usually 15-15-15, with the exceptions of *T. preussi* (Sternfeld, 1913) with 13-13-13 and *T. longissimus* Boulenger, 1896 with 17-17-17. Dorsal scales of *Toxicocalamus* are smooth without apical pits. Ventral scales, or gastrosteges, were counted beginning with the first broad scale on the anterior part of the body that contacts a scale of the lowest dorsal scale row on both sides, the count then continuing to the scale immediately anterior to the cloacal plate. In *T. pumehanae* O'Shea et al., 2018, this scale is divided into a pair of pre-cloacal scales. The condition of the cloacal plate, entire or paired, is also noted as this has taxonomic implications in *Toxicocalamus*. The condition of the subcaudal scales is also of taxonomic importance since all *Toxicocalamus* except for *T. holopelturus* McDowell, 1969 exhibit paired subcaudals. Subcaudal scales were counted along one side of the tail beginning with the scale immediately posterior to the vent and continuing to the scale immediately anterior to the tail tip; the tail tip was not included in the count. The subcaudal counts of specimens with truncated tails are suffixed with a plus sign (+) indicating the specimen once possessed at least the number of scales counted (e.g., 54+ indicates that the specimen's tail was truncated posterior to scale 54). If present, the shape of the tail tip is recorded as sharply pointed, rounded, or laterally compressed.

Sex and sexual dimorphism

Sex was determined by the examination of the gonads, presence of ova, the presence of everted hemipenes, or the presence of the *retractor penis magnus* muscle. In some species of *Toxicocalamus*, especially the more slender, short-tailed semi-fossorial species *T. preussi* and *T. buergersi* (Sternfeld, 1913), sex can be determined from relative tail length and subcaudal scale counts, with males exhibiting tails more than twice as long as those of females. Females also often exhibit proportionally longer bodies and higher ventral counts than conspecific males.

Head scale patterns

Head scalation provides extremely important clues for species determination in the genus *Toxicocalamus*. Eight of the 16 species, including *T. ernstmayri* and *T. grandis*, exhibit the classic colubrid-elapid dorsal nine-plate arrangement (O'Shea 2005: 12) with distinct and separate pairs of internasals (IN), prefrontals (PF), supraoculars (SO) and parietals (P) with a single central frontal (F). The other eight species exhibit some degree of head scute fusion, either of the internasal and prefrontal or of the prefrontal and preocular (PR), or possesses a pair of large anterior head scutes comprising the fused internasal, prefrontal, and preocular. One species even exhibits fusion of the supraoculars and frontal into a single broad scale across the top of the head. Other important dorsal scales on the head include nasals (N), which may be completely divided by a large naris (nostril) or almost entire with a small countersunk naris in the centre, a rostral (R), preoculars (PR, if not fused with the prefrontals), postoculars (PO) with occasional fusion of the upper PO to the supraocular or the lower PO to a supralabial (SL), and the number and status of the anterior and posterior temporals (AT and PT, respectively). Supralabial counts are provided, and we report which of them contact the orbit (eye) and which is the largest. *Toxicocalamus* is almost unique amongst terrestrial New Guinea elapids in not possessing a temporolabial scale[4], a diamond-shaped scale protruding downwards between the penultimate and ultimate supralabials. On the ventral side of the head we list the number of infralabials (IL) on either side, noting which contact the anterior and posterior genials (AG and PG, respectively), and whether these scales are themselves in contact at the mental groove or whether the posterior genials are separated by an intergenial (IG). The first pair of ILs is elongate and the only pair that meet at the mental groove, anterior to the AGs and posterior to the triangular mental (M) at the front of the lower jaw.

Specimen illustrations

Specimens were photographed using the basic methods explained in Kaiser et al. (2018), but with dual photographic set-ups and relatively high-end DSLR equipment to ensure visual clarity in photographs of specimens with very dark, shiny surfaces. All images were uploaded to Aperture 3.6[5] on a MacBook Pro (OS X Mavericks ver. 10.10). The figures used in this paper were then obtained on a MacPro desktop computer (OS X Sierra ver. 10.12), using Adobe Photoshop CC 2019 and a Wacom Cintiq 13" HD Touch.

RESULTS AND DISCUSSION

Basic morphology and pholidosis

ZSM 55/2015 (Fig. 2A, D) was collected in June 1976 at Dingerkon (4.4508°S, 140.0347°E, elev. 1600 m), Pegunungan Bintang Regency, Papua Province, WNG. This locality is on the Eipomek River in the Jayawijaya (formerly Orange) Range, the mountain range immediately to the west of the Star Mountains (Fig. 1). The specimen was accessioned into the ZSM collection in 2015. ZSM 55/2015 is a female (SVL 765 mm + TL 87 mm = TTL 851 mm). Its scale counts are identical or close to those of the holotype of *T. ernstmayri* (Fig. 2B, E; different values in the holotype provided in parentheses), including a dorsal scale count of 15-15-15; 202 ventrals; a divided cloacal plate; 30 (29) paired subcaudals; SL = 6, with SL3 and SL4 contacting the orbit (Fig. 3A, A', B, B'); IL = 6, with IL1–IL3 in contact with the anterior genials and IL3 and IL4 in contact with the posterior genials; an intergenial scale separating the posterior genials is present (Fig. 4A, A', B, B'); "colubrid-elapid dorsal nine-plate arrangement" of two internasals, two prefrontals, a frontal between two supraoculars, and two parietals on the head; single preocular, in contact with SL2 and SL3; prefrontal and supraocular have broad contact with the nasal; postocular single (paired) in contact with SL4 and SL5, supraocular, and anterior temporal (Fig. 5A, A', B, B', C, C', D, D'); temporal arrangement 1+2 (left: 1+1, right: 1+2). In this listing of scale characteristics, the only differences between ZSM 55/2015 and the holotype of *T. ernstmayri* are one subcaudal scale, the single versus paired postocular condition, and the fusion of the posterior temporals on the left side of the head in the holotype.

4 The other terrestrial New Guinea elapid lacking a temporolabial scale is *Pseudonaja*, which is unlikely to be confused with *Toxicocalamus* for numerous reasons, not least its very large eyes. All other terrestrial Papuan elapid genera (*Acanthophis, Aspidomorphus, Cryptophis, Demansia, Furina, Micropechis, Oxyuranus,* and *Pseudechis*), exhibit an obvious temporolabial scale.

5 Apple have discontinued and no longer support Aperture. It will also run on OS X High Sierra (10.13) and OS X Mojave (10.14) but not OS X Catalina (10.15). An alternative application is Adobe Lightroom.

The ZSM specimen appears to exhibit a subterminal mouth (an "underbite"), with the lower jaw appearing to extend beyond the upper jaw, combined with an apparent compression of the snout, certainly on the right side (Figs. 5A, A', B, B', 6). The latter is likely an artefact of preservation, such that the snake was stored in a container with its snout pressed against the container's inner surface. However, the front of the snout does appear to be slightly malformed as seen by the continuation of the prefrontal-internasal suture anteriorly onto the rostral to form a vertical division (Fig. 6). Whether this slight abnormality was the cause or a post-fixation contributory factor to shaping the head as we see it now is open to conjecture.

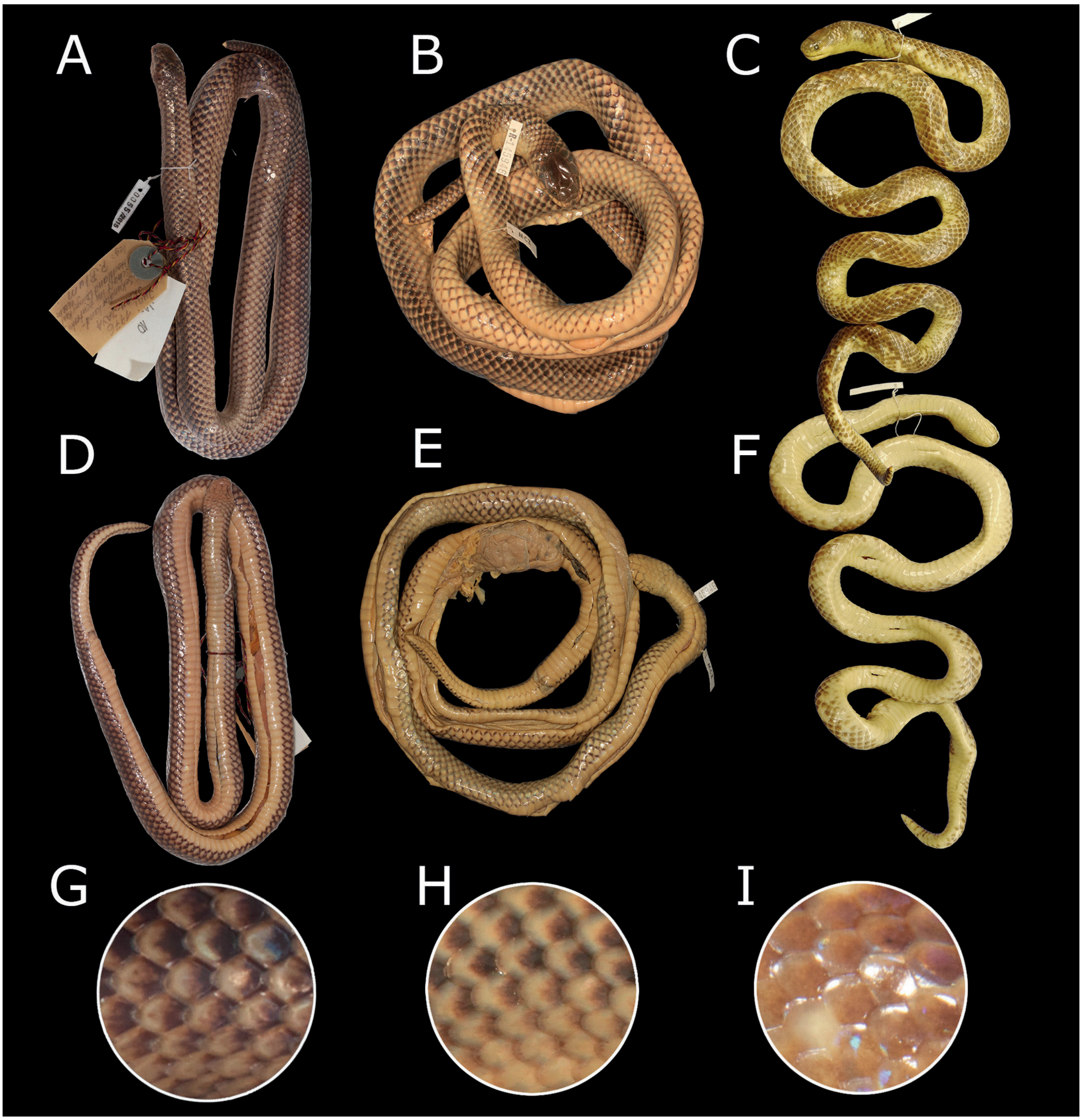

Fig. 2. Whole body views and colour patterning in three specimens of *Toxicocalamus*. Dorsal views include those of (**A**) ZSM 55/2015; (**B**) the holotype of *T. ernstmayri* (MCZ R-145946); and (**C**) the holotype of *T. grandis* (BMNH 1946.1.18.34). Ventral views (**D–E**) are listed in the same order as the dorsal views. The circular images show closeups of dorsal scale patterns and are provided to illustrate the observed pattern reversal. Whereas the pattern in ZSM 55/2015 (**G**) and *T. ernstmayri* (**H**) is characterized by dorsal scales with dark centers and light edging, there is no such prominent patterning in *T. grandis* (**I**). Images not to scale. Photos by Mark O'Shea.

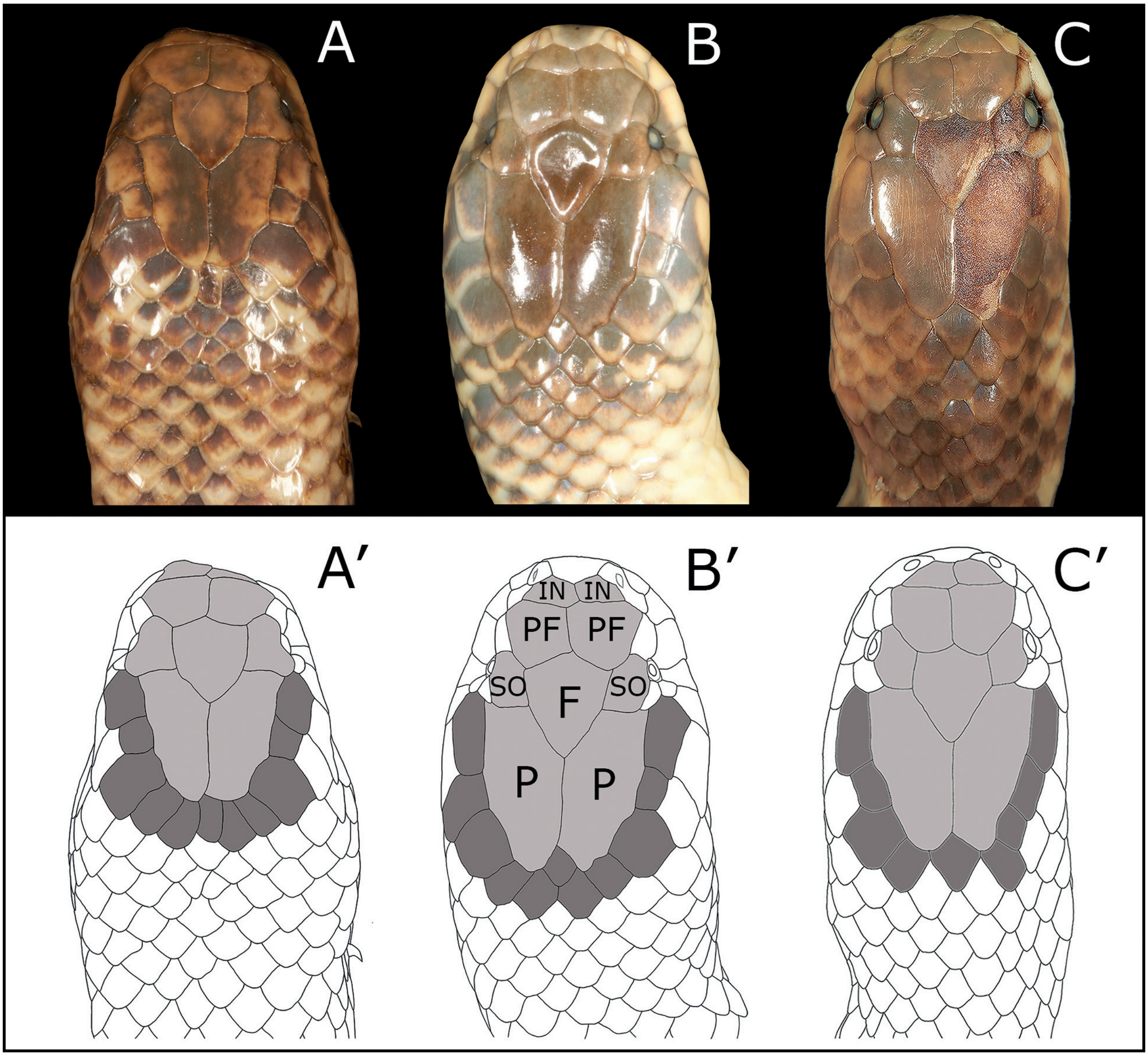

Fig. 3. Dorsal views of the heads of *Toxicocalamus* specimens from New Guinea, presented as both photographic and line-drawing illustrations. The drawing in (**B'**) features the classic colubrid-elapid nine-plate arrangement (light grey), comprising paired internasals (IN), prefrontals (PF), supraoculars (SO), and parietals (P), and single frontal (F), and eleven scales bordering the parietals (mid-grey), including anterior temporals and upper posterior temporals. The drawings in (**A'**) and (**C'**) follow the same pattern. Shown are (**A, A'**) the first West New Guinea specimen of *T. ernstmayri* (ZSM 55/2015), (**B, B'**) the holotype of *T. ernstmayri* (MCZ R-145946), and (**C, C'**) the holotype of *T. grandis* (BMNH 1946.1.18.34). Images not to scale. Photos and line drawings by Mark O'Shea.

Comparisons with *Toxicocalamus grandis*

Differences in scalation between the two extant specimens of *T. ernstmayri* (MCZ R-145946, ZSM 55/2015), and the single known specimen of *T. grandis* (BMNH 1946.1.18.34; Figs. 2C, F, 3; characteristics in parentheses) include broad contact between the preocular and the nasal scales (point contact on the left side and exclusion by contact between SL2 and the prefrontal on the right side; Fig. 5E, E', F, F'), eleven temporal and post-temporal scales bordering the parietals (nine scales), and SL6 only narrowly separated from the upper posterior temporal (SL6 widely separated by broad contact between the anterior temporal and the lower posterior temporal). The only character in which ZSM 55/2015 agrees with *T. grandis* and not *T. ernstmayri* is the presence of a single postocular where the type of *T. ernstmayri* has a pair of postoculars. Whilst this is perhaps an important difference in the grand scheme of *Toxicocalamus* taxonomy, when weighed against the number of characters in which ZSM 55/2015 agrees with

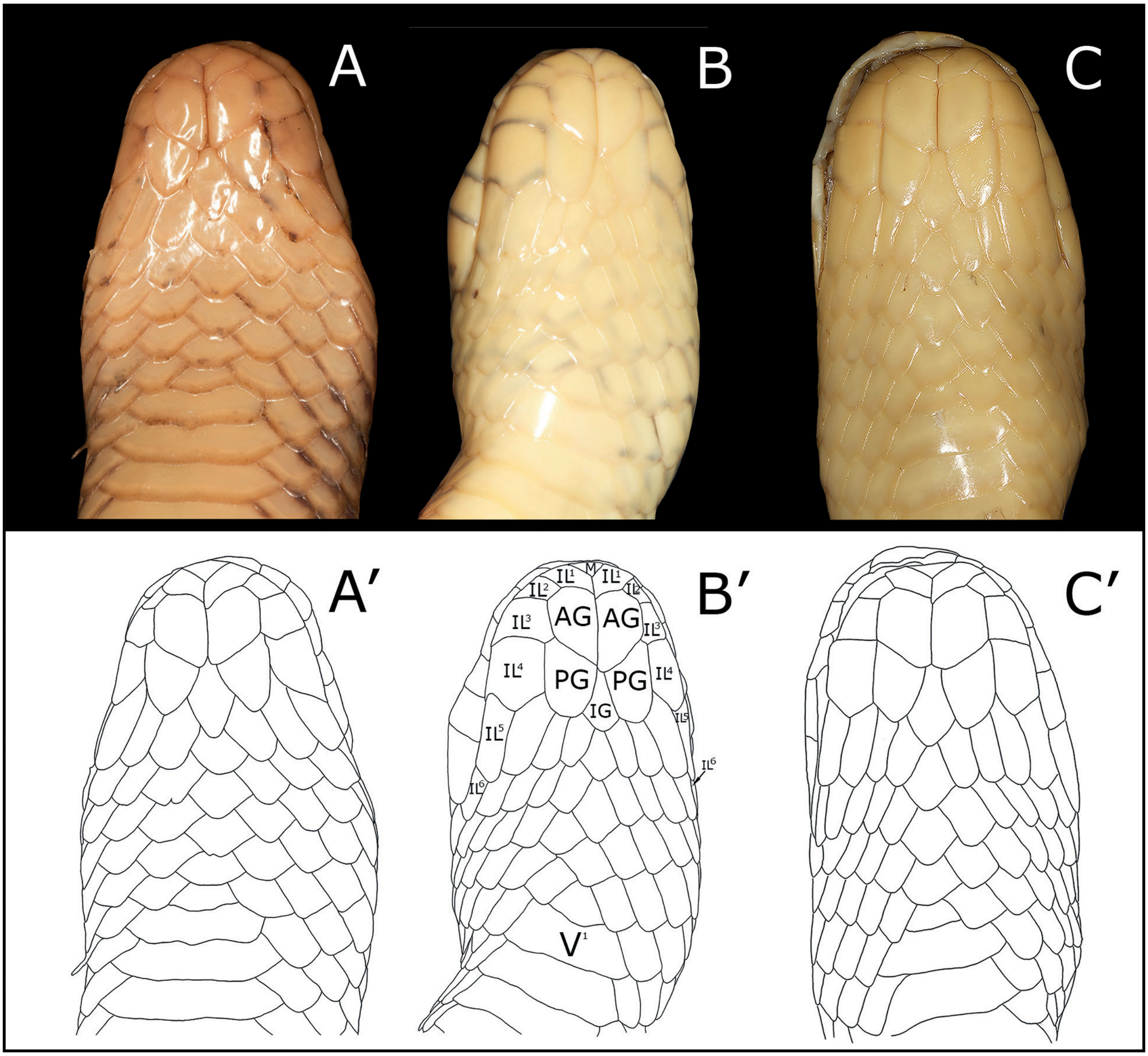

Fig. 4. Ventral views of the heads of *Toxicocalamus* specimens from New Guinea, presented as both photographic and line-drawing illustrations. The drawing in (**B'**) includes scales identified by lettering, including mental (M), numbered infralabials (IL), anterior genials (AG) in contact along the mental groove, posterior genials (PG) separated by an intergenial (IG), and the first gastrostege (V^1). The drawings in (**A'**) and (**C'**) follow the same pattern. Shown are (**A, A'**) the first West New Guinea specimen of *T. ernstmayri* (ZSM 55/2015), (**B, B'**) the holotype of *T. ernstmayri* (MCZ R-145946), and (**C, C'**) the holotype of *T. grandis* (BMNH 1946.1.18.34). Images not to scale. Photos and line drawings by Mark O'Shea.

T. ernstmayri and, given the propensity for scale fusions in the genus, its importance is diminished.

In its colouration, ZSM 55/2015 is remarkably similar to the holotype of *T. ernstmayri*. In the original list of specimens donated to the ZSM both ZSM 54/2015 and ZSM 55/2015 were classified as *T. grandis*, but in BMNH 1946.1.18.34, the only known specimen of that species, the dorsal pattern comprises fairly uniformly coloured scales (Fig. 2I), whereas in both specimens of *T. ernstmayri* (MCZ R-145946, ZSM 55/2015; Fig. 2G, H, respectively) the pattern is striking, comprising light dorsal scales edged with dark pigmentation.

Natural history and ethnology

The second author participated in a 1976 ethnological and ethnobiological expedition (Fig. 7), conducted by the Museum für Völkerkunde (Ethnological Museum) in Berlin and led by the medical anthropologist

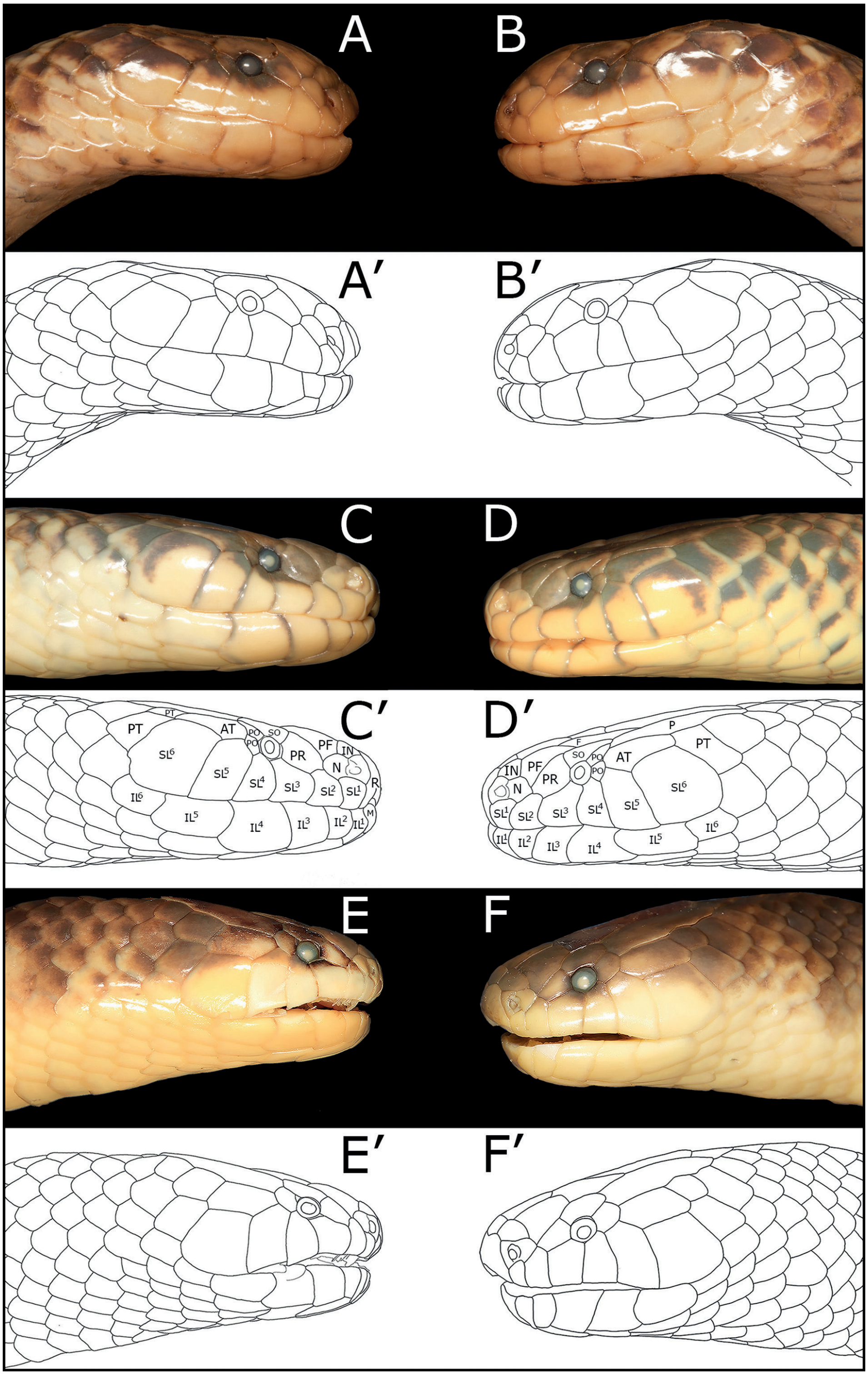

Fig. 5. Lateral views of the heads of *Toxicocalamus* specimens from New Guinea, presented as both photographic and line-drawing illustrations in right and left aspect. The drawings in (**C’**) and (**D’**) include scales identified by lettering, including rostral (R), mental (M), nasals (N), internasals (IN), prefrontals (PF), preoculars (PR), supraoculars (SO), postoculars (PO), anterior temporals (AT), posterior temporals (PT), numbered supraoculars (SL), and numbered infralabials (IL). The drawings in (**A’, B’**) and (**E’, F’**) follow the same pattern. Shown are the first West New Guinea specimen of *T. ernstmayri* (ZSM 55/2015) in right (**A, A’**) and left (**B, B’**) lateral views, the holotype of *T. ernstmayri* (MCZ R-145946) in right (**C, C’**) and left (**D, D’**) lateral views, and the holotype of *T. grandis* (BMNH 1946.1.18.34) in right (**E, E’**) and left (**F, F’**) lateral views. Images not to scale. Photos and line drawings by Mark O’Shea.

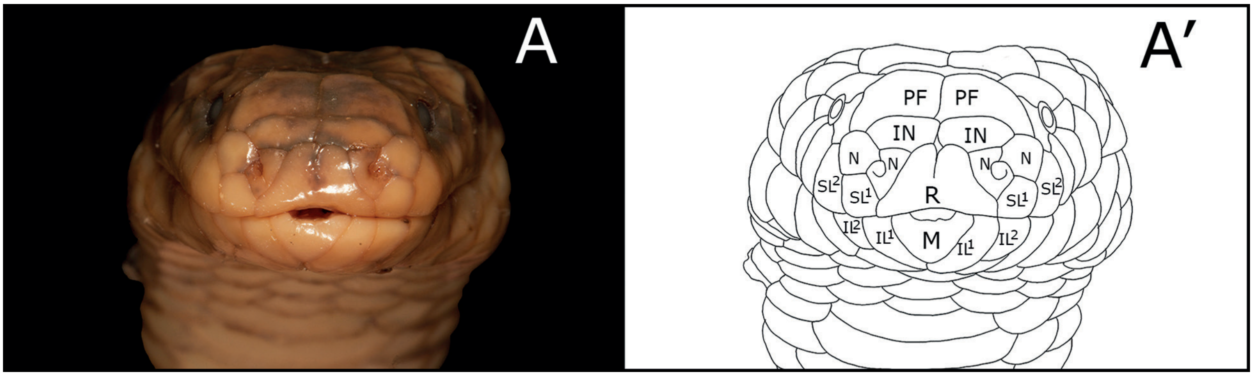

Fig. 6. Frontal view of the head of the first West New Guinea specimen of *T. ernstmayri* (ZSM 55/2015) as a photo (**A**) and a line drawing (**A'**), illustrating the deeply scored and deformed rostral (R), divided nasals (N), internasals (IN), prefrontals (PF), supralabials (SL), mental (M), and infralabials (IL). Photo and line drawing by Mark O'Shea.

Wulf Schiefenhövel[6], to study the Eipo people of the remote Eipomek Valley in central mountainous WNG (Schiefenhövel 1997). We would therefore be remiss if in our account of ZSM 55/2015 we did not include information on how a snake like *T. ernstmayri* is perceived by the indigenous human population. We therefore expand our specific report on this snake to include its relevance to the local residents, who are very much a part of the natural environment in New Guinea.

ZSM 55/2015 was discovered and killed in a village garden (Fig. 8) during daylight hours on 18 June 1976. Snakes of the genus *Toxicocalamus* are believed to be exclusively vermivorous (O'Shea et al. 2015), and they appear to be especially common in highland gardens, possibly because of the abundance of giant earthworms (Annelida: Megascolecidae) in well-turned, irrigated, and composted montane vegetable plots operating for 35,000–60,000 consecutive years (Schiefenhövel 2001). The high density of *Toxicocalamus* in these habitats is supported by the large number (165 specimens = 32% of all known specimens) collected in the heavily populated and intensively farmed Wahgi Valley (Simbu and Jiwaka Provinces, PNG) by Australian *kiap* and herpetologist Fred Parker, Divine Word missionary Father Otto (Shelly) Schellenberger (1914–2007), and other field collectors. That the snake was active during the day is also not unusual, certainly the larger and more terrestrial species (including *T. ernstmayri* and *T. pachysomus*) appear to be diurnally active, as evidenced by the observation of *T. ernstmayri* moving unhurriedly across mine-workings at Ok Tedi in broad daylight (O'Shea et al. 2018b).

6 On an earlier ethnological/zoological expedition to New Guinea, the "Papua Expedition 1966" by the Zoological Institute at Ludwigs-Maximilians-Universität Munich (Schultze-Westrum 1968), the expedition leader Thomas Schultze-Westrum was bitten by a Müller's crowned snake (*Aspidomorphus muelleri*). The symptoms and treatment of this snakebite, the only known record of a snakebite from this genus, were documented and published by Schiefenhövel (1969).

The dead snake was delivered to the second author by a Dingerkon villager named Ewinde, who carried it in secrecy and protectively wrapped in three layers of leaves so that other villagers would not see it. The Eipo are apparently frightened by snakes, which they call *kwatema*, but they were especially averse to this species which they call *amau*, considering it highly dangerous[7] and capable of causing death, and even to look upon it is considered highly undesirable. The second author was warned to be very careful with the dead snake, especially to avoid pricking himself on its sharp tail tip, the keratinized sting-like terminal scale, because that could prove fatal. Thus, the dead snake was positioned on a flat rock and photographed surreptitiously (Fig. 9).

Where is the type locality of *Toxicocalamus grandis*?

The Jayawijaya Range, where ZSM 55/2015 was collected, is adjacent to the Star Mountains of Western Province, where the holotype of *T. ernstmayri* was collected in 1969 and from where the 2018 sighting was documented (Fig. 1). The elevation for these observations ranges from 1468 m at Wangbin, the type locality of *T. ernstmayri*, to 1600 m at Dingerkon, the collection locality of ZSM 55/2015, and to as high as 1670 m at the Ok Tedi Mine. Whereas these specimens and sightings are accurately pinpointed localities, "Launch Camp" on the Setekwa River, where the holotype of *T. grandis* was supposedly collected, has not previously been located with any certainty.

The *T. grandis* holotype (BMNH 1946.1.18.34) was collected by the British explorer Alexander Frederick

7 The only toxinological study of *Toxicocalamus* venom was conducted on *T. longissimus* from Woodlark Island, Milne Bay Province, PNG (Calvete et al. 2012). Its venom was found to contain high levels of potentially dangerous 3-finger toxins (3FTx). However, there are no human snakebites due to *Toxicocalamus* on record and the reasons why a vermivorous snake should possess relatively toxic venom are unknown.

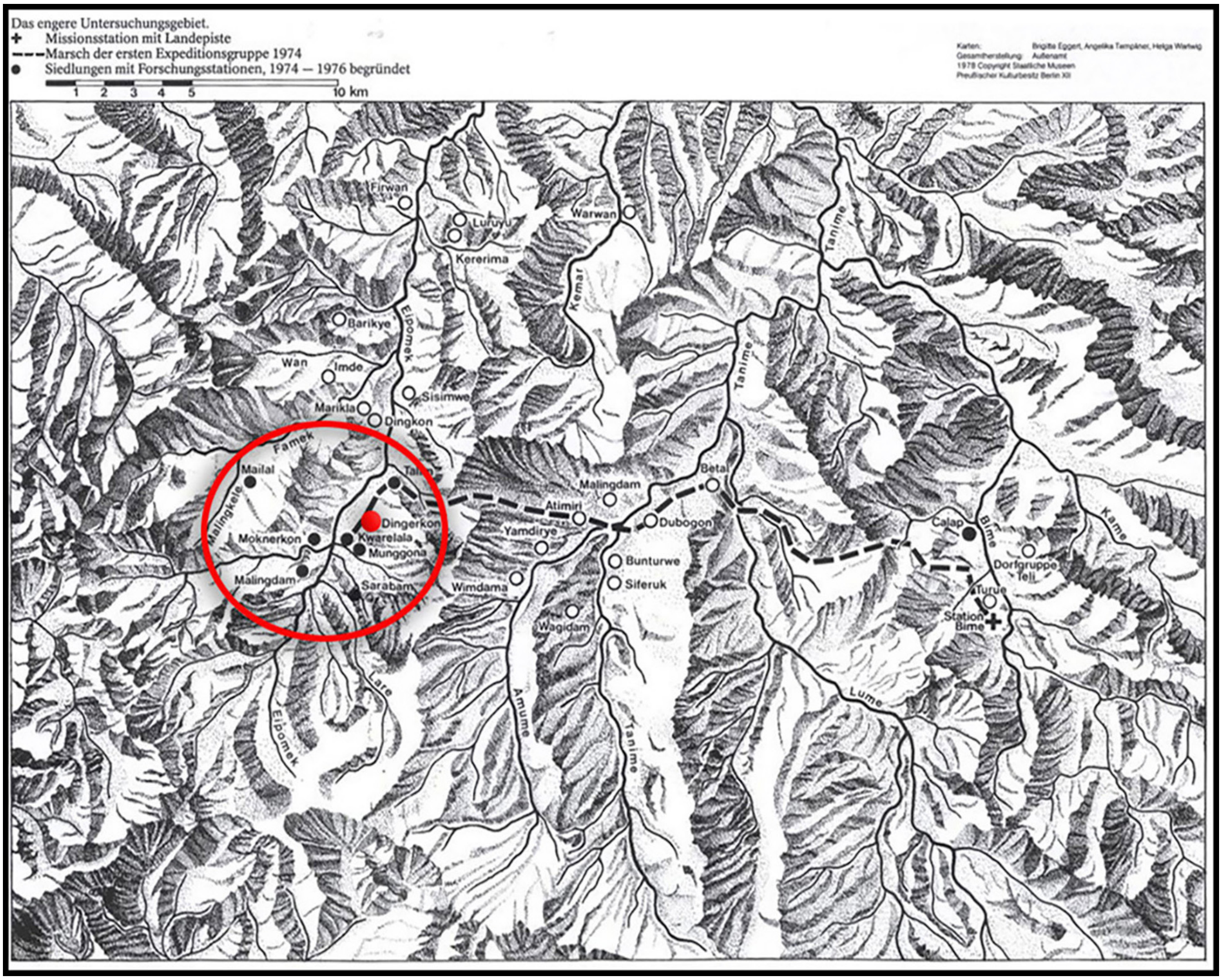

Fig. 7. Map of the 1976 expedition to the Eipomek Valley, West New Guinea, Indonesia, modified from Ploeg (2004: 38). The red dot marks Dingerkon, where the specimen of *Toxicocalamus ernstmayri* (ZSM 55/2015) was collected. The red circle indicated the broader area in which expedition members studied the language and culture of the Eipo community, as well as the area's natural history. Scale is present above the map.

Richmond "Sandy" Wollaston (1875–1930; Fig. 10A) and the British zoologist Cecil Boden Kloss[8] (1877–1949; Fig. 10B) during the Wollaston Expedition[9] to Dutch New Guinea in 1912–13. The expedition journeyed up the Setekwa River branch of the Utekwa River, following the same initial route and using the same campsites as the Van der Bie Expedition[10] of two years earlier, which were referred to as "Base Camp" and "Canoe Camp" (Wollaston 1933). While Wollaston gave no clue to the location of his own site, called Launch Camp, the English naturalist Albert Stewart Meek (1871–1943; Fig. 10C), who had accompanied the earlier Van der Bie Expedition, did refer to a likely location for this camp when he wrote:

8 Cecil Boden Kloss learnt his trade as a museum conservator in the natural history museum in Kuala Lumpur, Malaya, from 1908, and he would go on to become Director of the Raffles Museum, in Singapore (1923–1932). It is likely his presence on the Wollaston Expedition ensured that the zoological specimens were correctly and expertly fixed and curated.

9 This was Wollaston's second expedition to New Guinea. His first was the British Ornithologists' Union expedition of 1910–11. He was attempting to reach Mt. Carstensz (now Puncak Jaya), at 4994 m the highest peak in New Guinea in the Nassau Mountains (now Sudirman Range) in Dutch New Guinea. The 1910–11 expedition ascended the Mimika River but failed to reach Mt. Carstensz, whereas the 1912–13 expedition used the Setekwa and Utekwa Rivers and came very close to succeeding.

10 Dutch military officers J.J. van der Bie and P.F. Postema, along with the naturalist Joannes Maximiliaan Dumas (1856–1931), explored the Setekwa and Utekwa River on a multipurpose military mission in 1910–11 (LeCroy & Jansen 2011). This expedition also included the English naturalist collector A.S. Meek (see below).

Fig. 8. An overgrown garden plot in Dingerkon, West New Guinea, where the recently identified specimen of *Toxicocalamus ernstmayri* (ZSM 55/2015) was collected. The snake was observed in the grass during the day and killed by a villager. Photo by Paul Blum.

> "*At the mouth of the Oetakwa River we disembarked our baggage into launches. The stores for the Dutch expedition filled nine big boats and my stores another big boat. This string of boats was taken in tow by a steam launch, and like a great snake it wound its way up the river, a full day's journey. This was the end of navigable water for the steam launch. At this stage, which was called the Launch Stage, I encountered Captain Van der Bie and discussed my arrangements with him. Then two days' journey further up the river by canoe brought us to what was called the Canoe Stage."* (Meek 1913: 211f)

With Meek's term "stage" clearly synonymous to a site where expeditions are staged (i.e., a camp or landing stage), it is most likely that Base Camp and Launch Camp are one and the same location, with deep enough water for a motor launch and two days downstream from Canoe Camp (see Wollaston's map; Fig. 12). This would suggest that the camp from which the expedition originated lay in the very low reaches of the Setekwa River, with an elevation of only 20–30 m. The distribution of *Toxicocalamus* can be loosely summarised as "highland or island" but from the above account it might be assumed that, unlike other mainland New Guinea *Toxicocalamus*, especially unlike *T. ernstmayri*, *T. grandis* defies that rule and is a southern lowland species.

However, there is a problem with this supposition. In her compilation of her husband's posthumously published letters and diaries[11] Mary Wollaston added the following note:

> "December 8. Up river to 'Canoe Camp'
> *At this point in the diary A.F.R.* [Sandy Wollaston] *makes the following note: 'On March 9, 1913, coming down the river from Canoe Camp to Base Camp, my canoe upset in a dangerous rapid, so that I was nearly drowned, and I lost the greater part of my baggage, cameras, medicine chest, maps and diaries. Now I have to begin to write over again my diary from December 8, to March 9 – so far as I can remember it. A.F.R.W. March 19, 1913.*"
> (Wollaston 1933: 135)

11 After a life time of living dangerously, which included two expeditions to New Guinea, one to East Africa, participation in the first ever attempt to ascend Mt. Everest with George Mallory (1886–1924), and Royal Naval service in both the Great War and the Russian Civil War, Sandy Wollaston was shot dead by a deranged student at Cambridge University on 3 June 1930 (Wollaston 2003).

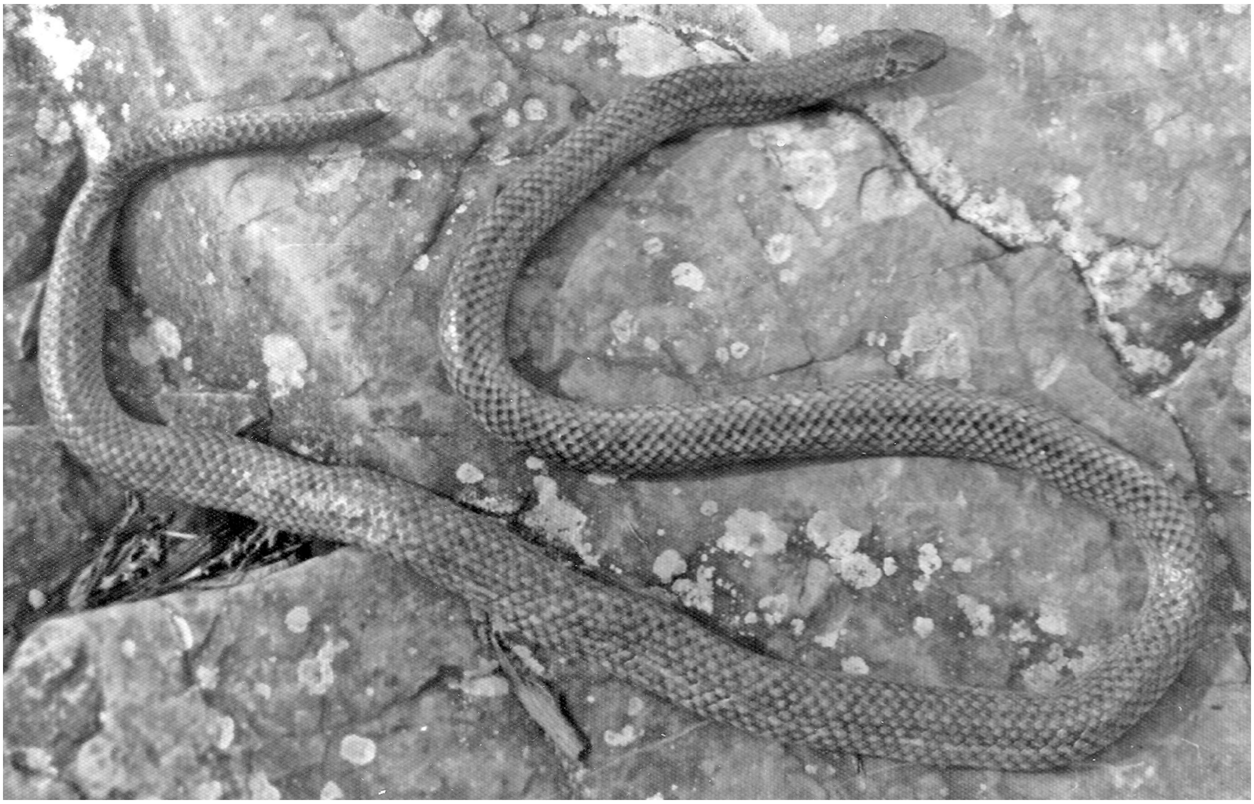

Fig. 9. The freshly killed *Toxicocalamus ernstmayri* (ZSM 55/2015), photographed by Paul Blum on 18 June 1976.

Since Wollaston and other naturalist collectors of his era were more interested in birds, beetles, or butterflies than reptiles and amphibians it is likely that they were not as diligent with their recording of specific collection localities for herpetological specimens. Given that Wollaston had lost his diary and been forced to rewrite his journey, from the Setekwa and Utekwa Rivers uphill to an elevation of 4700 m on the slopes of Mt. Carstensz (today Puncak Jaya) and then downhill, weeks after the events had taken place, it is not surprising that no mention was made of an obscure snake.

Furthermore, listing this snake along with a great many other herpetological specimens from the Wollaston Expedition (Boulenger 1914; O'Shea 2013) as originating from the expedition's launching point, Launch Camp, is no different than when the Italian naturalist collector Luigi Maria d'Albertis (1841–1901) listed the collection locality for many of the herpetological specimens collected quite far upriver on the Fly River during his three expeditions (1875–77) as Kataw (or Katau), which was actually his base camp on the south coast, a mooring in the mouth of the Binaturi River, southern Western Province, PNG, and demonstrably not their true collection localities (d'Albertis 1879, 1880; O'Shea & Kaiser 2018). Therefore, without proof that *T. grandis* really does occupy the lower reaches of the Setekwa River and should be aligned ecologically with this lowland locality, there is a higher probability that it was obtained in an area that is ecologically a better match for a species so similar to the montane *T. ernstmayri*. We consider the likeliest collection area to be much further upstream, on the southern versant of the Sudirman Range, and Wollaston would have collected it on the trip during which he lost his diary, between 8 December 1912 and 9 March 1913.

The two main mountain ranges of Papua Province, WNG, that combined form the Maoke Mountains, formerly Snow Mountains, are the Jayawijaya Range in the east, and the Sudirman Range to the west (Fig. 1). The Jayawijaya Range, formerly known as the Orange Range, extends for 380 km westward from the Star Mountains, which straddle the border between Western and Sandaun Provinces, PNG, and Papua Province, WNG. The highest point in the Jayawijaya Range is Puncak Mandala, formerly Juliana Summit (4760 m). The Sudirman Range, formerly the Nassau Range, is located to the west of the Jayawijaya Range, and it extends the central cordillera a further 692 km westwards, with its highest point at Puncak Jaya, formerly the Carstensz Pyramid (4884 m), a peak so high it was snow-capped until the early 1960s and which still retains some small, but rapidly shrinking, glaciers (Löffler 1982). Both ranges provide a wide range of habitats and exhibit considerable vertebrate diversity and endemicity (Allison 2007; Beehler 2007;

Fig. 10. Portraits of (**A**) Alexander Frederick Richmond "Sandy" Wollaston (1875–1930) photographed in Dutch New Guinea in 1912, and (**B**) Cecil Boden Kloss (1877–1949) photographed in the field (date and location unknown). Both gentlemen display the attire and character typical of early 20th Century explorers. Note their similarities: both bearded, both behatted, both with belted field kit, both with walking canes (Wollaston always carried his ice-axe), both in cut-off shorts and puttees, both photographed surrounded by field camp debris in an "active pose," with one leg forward. Images courtesy of (**A**) Royal Geographical Society and (**B**) Kevin Tan, National University of Singapore.

Brongersma & Venema 1962). The Jayawijaya and Sudirman Ranges are separated, at an elevation of 1600–1700 m, by the 80 km long and 20 km wide Baliem River Valley, another biodiversity hotspot which was explored by the 3rd Archbold Expedition of 1938–39 (Archbold et al. 1942), and other expeditions have followed subsequently. The Baliem Valley has been called "an important zoogeographic divide and a potential important area of interchange" with regards to mammals (Helgen 2007: 736) and it may also act as a barrier between the two montane herpetofaunas. If *T. ernstmayri* and *T. grandis* are ecologically similar species, large diurnal members of a genus that feeds exclusively on annelids, especially large earthworms, it is possible that they evolved through allopatric speciation, *T. ernstmayri* in the Jayawijaya and Star Mountains, and *T. grandis* in the Sudirman Range. A third relatively large, stocky and poorly known species, *T. pachysomus* Kraus, 2009, is known from its holotype, collected in the Cloudy Mountains at the southeastern end of the Owen Stanley Range. It may also occupy a similarly montane vermivorous niche, albeit at a lower elevation of 715 m.

The discovery of *T. ernstmayri* in the WNG mountains and our sleuthing of historical records to better align *T. grandis* with the ecology expected of a large *Toxicocalamus* lend further support to the 'highlands or islands' biogeographic hypothesis for *Toxicocalamus* diversity. Our findings also provide important insights into how these species may have evolved on the New Guinea mainland, via allopatric speciation, one mountain chain at a time, with the mountain ranges acting like archipelagos in the sky, separating populations with lowland or submontane valleys. The apparent allopatric mountain-derived speciation in *T. ernstmayri* and *T. grandis* means that some of the widely distributed montane species on mainland New Guinea may in reality represent species-complexes, and with this in mind we are currently examining *T. loriae* (Boulenger, 1898), *T. stanleyanus* Boulenger, 1903, and *T. preussi* more closely. *Toxicocalamus* appears to provide a small yet interesting example for the evolution of biodiversity on the world's largest tropical island.

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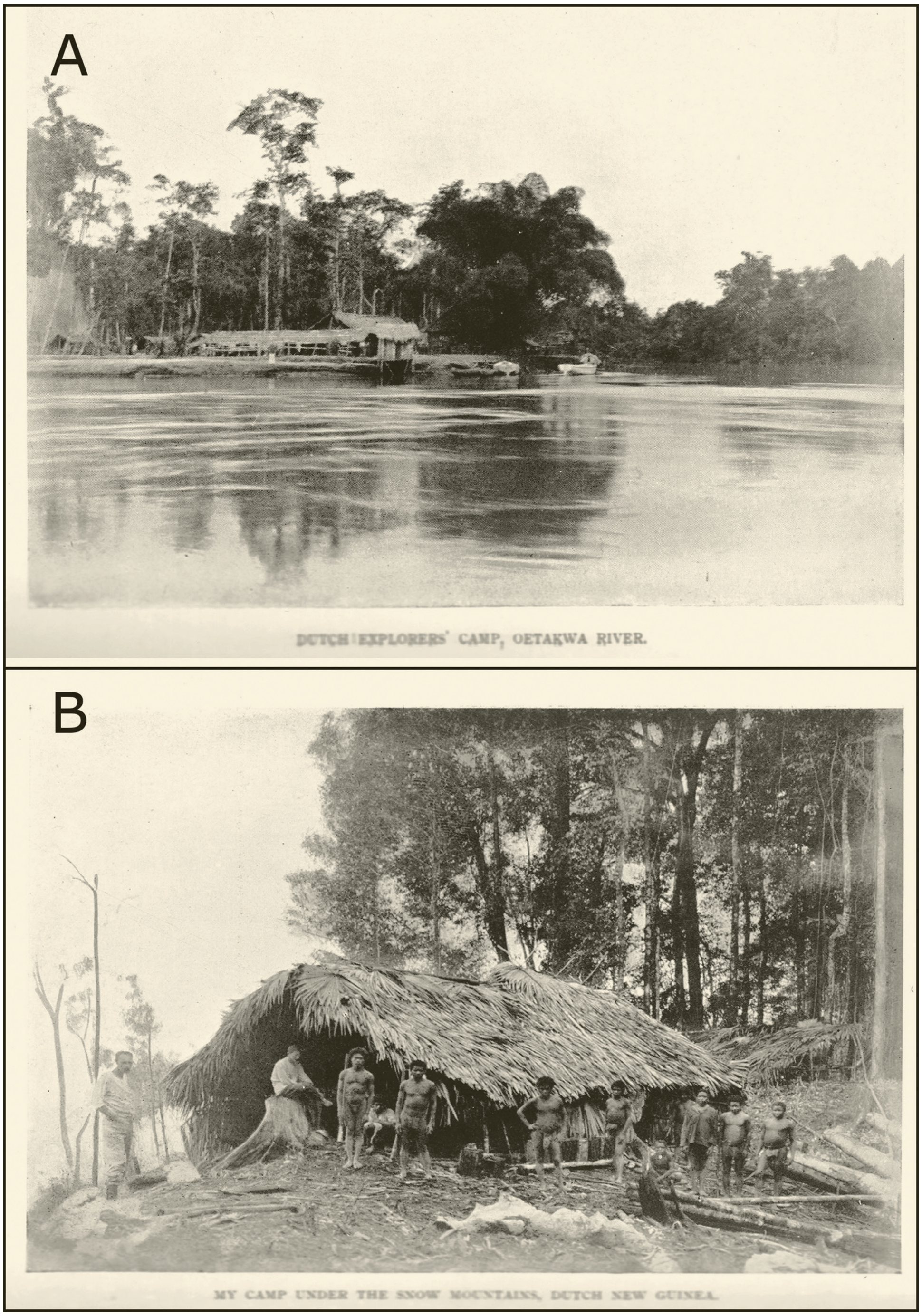

Fig. 11. Two photographs from the book *A Naturalist in Cannibal Land* by Albert Stewart Meek (1871–1943). (**A**) "Dutch Explorers' Camp, Oetakwa River" shows the lower reaches of the Oetakwa (Utekwa) River. This is either the unnamed camp (Fig. 12: Location 3) at the confluence of the Utekwa and Setekwa Rivers, or Base Camp (Fig. 12: Location 4) at the confluence of the Setekwa and Mamoa Rivers, since the Setekwa is a branch of the Utekwa[12]. The river is wide and probably deep enough for a motor launch, and canoes and European skiff-like boats for the journey up-stream are visible in the image. This location could also be the same as Launch Camp, the location Wollaston listed as his purported collection locality for the holotype of *T. grandis*. (**B**) Meek's campsite in the Maoke Mountains (historically known as the Snow Mountains) in 1910–11, captioned "My camp under the Snow Mountains, Dutch New Guinea". Meek is seen sitting on the tree stump. This photograph was taken on Meek's second venture into Dutch New Guinea, up the Eilanden (Island) River further to the east, so the camp is located in the Jayawijaya (then Orange) Range, the eastern portion of the Maoke Mountains, while the Utekwa and Setekwa Rivers lead to the Sudirman (then Nassau) Range, the western portion of the Maoke Mountains (see Fig. 1).

12 Meek (1913: 213) referred to Canoe Camp as being on "the right-hand branch of the Oetakwa," which is the Setekwa River.

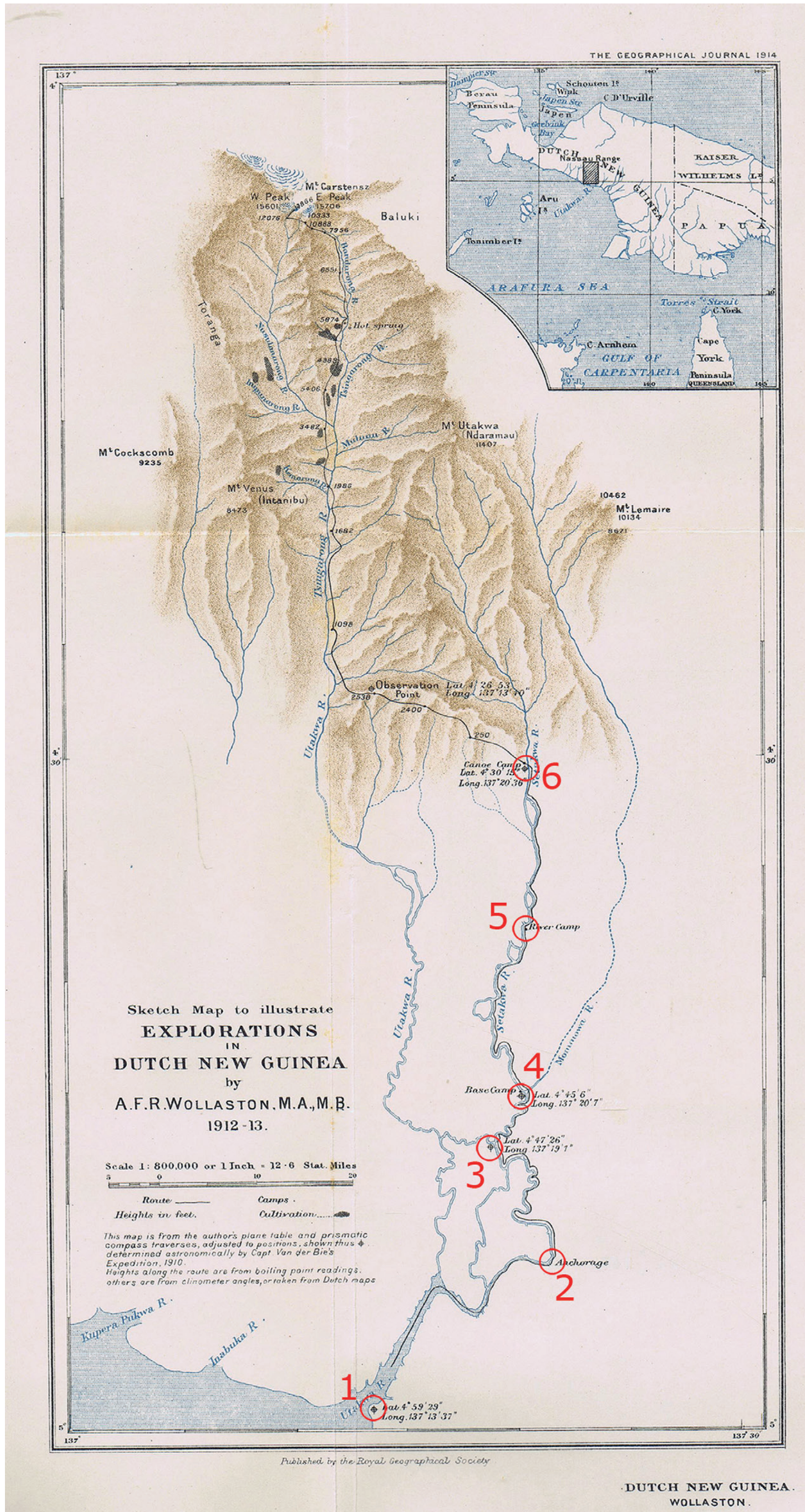

Fig. 12. Map of the Explorations in Dutch New Guinea by A.F.R. Wollaston in 1912–13. This is the approximate area identified by the white frame in Fig. 1. In the lowlands below the mountains there are six camps or locations indicated (numbered red circles): (1) an unnamed camp at the mouth of the Utekwa River; (2) an anchorage on a wide bend in the Setekwa branch of the river; (3) an unnamed camp at the confluence of the Utekwa and Setekwa Rivers; (4) Base Camp at the confluence of the Setekwa with the Mamoa River; (5) River Camp on the Setekwa River; and (6) Canoe Camp at the base of the mountains. From Canoe Camp the expedition struck out across land. It is proposed that "Launch Camp" is either synonymous with Base Camp (from where the expedition was launched), or it could be the unnamed camp at the Utekwa-Setekwa confluence.

hospitality and the generous use of their facilities during his 2015 visit.

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