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First record of *Trimerodytes praemaxillaris* (Angel, 1929) from Xaisomboun Province, Laos, with additional comments on morphology, natural history, and the type locality

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Abstract. We describe the discovery of the 11th specimen of *Trimerodytes premaxillaris* and use this opportunity to make some clarifying remarks about the history of the species, its type locality, morphology, and natural history. The snake was found at the southernmost locality for the species and represents a new provincial record for Laos. It was in the process of swallowing a juvenile spiny bream (*Scaphiodonichthys acanthopterus*), the first identifiable prey for this snake. The snake was a female carrying two oviductal eggs indicating that the reproductive season of the species likely coincides with the monsoon season. This correlates with the collection of the hatchling type specimens in late 1925 or early 1926. Finally, we provide some additional detail regarding this species' scale and colour pattern, as well as a more detailed account of the type locality and the time when the syntypes were collected.

Keywords. Type locality, Indochina, taxonomy, pholidosis, colouration, prey.

Introduction

Angel's Mountain Keelback, T*rimerodytes praemaxillaris*, was originally described by Angel (1929) from two small specimens in the collection of the Muséum National d'Histoire Naturelle, Paris, France (MNHNP-RA 1928.63–64; Fig. 1) that he placed into the new, monotypic genus *Paratapinophis* based on the presence of "une expansion lamelleuse située dans l'encoche de la plaque rostrale" [a lamellar expansion located in the notch of the rostral plate] (Angel, 1929: 76). Soon afterwards, Pope (1935) synonymised this genus with *Opisthotropis* Günther, 1872 and noted that the lamellar protrusion was merely the egg-tooth of the syntypes demonstrating that the specimens were neonates, also evident from the presence of umbilical scars. It took 55 years from the time of the species description before another snake was collected and it was the first from Thailand, ca. 450 km east of the type locality (Rasmussen, 1982). Murphy et al. (2008) resurrected *Paratapinophis* based on a unique suite of morphological characteristics (head distinct from neck, scale ornamentation only in males with a medial row of tubercles instead of a continuous or serrated keel, sexually dimorphic body colour and pattern, robust body, 18–20 maxillary teeth, two pairs of medial gulars), a decision accepted by David et al. (2015). Most recently, Ren et al. (2019) provided evidence that the characteristics singled out by Murphy et al. (2008) were identical to those of the genus *Trimerodytes* Cope, 1895 and recommended that *praemaxillaris* should be placed into that genus. This conclusion was formalised subsequently by Deepak et al. (2022), who based their taxonomic decision on an analysis of molecular data. The latest account of the species, with some additional data on the type locality and a detailed description was provided by David et al. (2023).

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Figure 1. Syntypes of *Trimerodytes praemaxillaris* (Angel, 1929). Both specimens are hatchlings with umbilical scars still visible that were preserved in a twisted position. (A, A') MNHNP-RA 1928.63 and (B, B') MNHNP-RA 1928.64 in two complementary views to show as much of the dorsal and ventral surfaces as possible. Photos by Antoine Fraysse, downloaded from the website of the Muséum National d'Histoire Naturelle, Paris, France, and used under the CC BY-NC-ND license.

One of the reasons it took almost 100 years to resolve the taxonomy of *T. praemaxillaris* is that very few specimens of this snake exist in museum collections (n = 10; Appendix) and few researchers have evaluated all of them. The first adult individual appeared to be a female collected in Yunnan Province, China in 1982 (Mo et al., 1984), but this specimen was subsequently identified as a member of *T. yapingi* (Guo et al., 2019) by Wang et al. (2022), who removed the species from the list of reptiles found in China. Thus, the first adult specimens were only collected in 2007 during the expedition described by Murphy et al. (2008). We are aware of one additional specimen from Xaisomboun Province in Laos, catalogued in the collections of the National University of Laos as NUOL 00108 (Bryan Stuart, pers. comm.), but we have been unable to obtain a more precise locality and morphological data from this specimen. *Trimerodytes praemaxillaris* has been important in current phylogenetic work on natricine snakes (Ren et al., 2019; Deepak et al., 2022; Bryan Stuart, pers. comm., 2024), especially given its range in the northern parts of Laos and Thailand (Angel, 1929; Rasmussen, 1982; Murphy et al., 2008) where there is a lot of faunal endemism. Below we document a new record for this species, the southernmost in Laos.

Specimen collection. During a recent a field survey for small mammals and other vertebrates in Xaisomboun Province, Laos (Fig. 2) on 11 May 2024 at 19:25 h, we opportunistically encountered and collected a medium-sized snake (total length 762 mm) near the village of Ban Pha Sa-ngop (18.8662°N, 103.1154°E, elevation 1272 m) along a small stream. The snake had settled on a submerged stone near the streambank and was in the process of consuming a fish (Fig. 3A). Upon capture, the snake regurgitated the fish.

The snake was euthanised using a 5% solution of isoflurane. Both snake and fish were then fixed in 10% formalin with a tissue sample for each preserved in 99% ethanol. Snout–vent length (SVL) and tail length (TL) of the snake were measured on the ventral side using a flexible tape measure and total length (TTL) was calculated. Nomenclature and definitions of scales and scale counts follow Dowling (1951) and Kaiser et al. (2019), as modified by Kaiser et al. (2021). In addition to the common terms supralabial and infralabial (Fig. 4A), we also use the term lateral gular, coined by Thakur et al. (2024), to help explain the scale pattern complexity in the throat area of snakes (Fig. 4B). These scales lie parallel to the narrow posterior infralabials on the edge of the gular region and only scales that are fully in contact with infralabial scales are considered lateral gulars. The preserved snake and fish specimens were deposited in the collection of the Faculty of Environmental Sciences, National University of Laos, Vientiane, Lao PDR (FES).

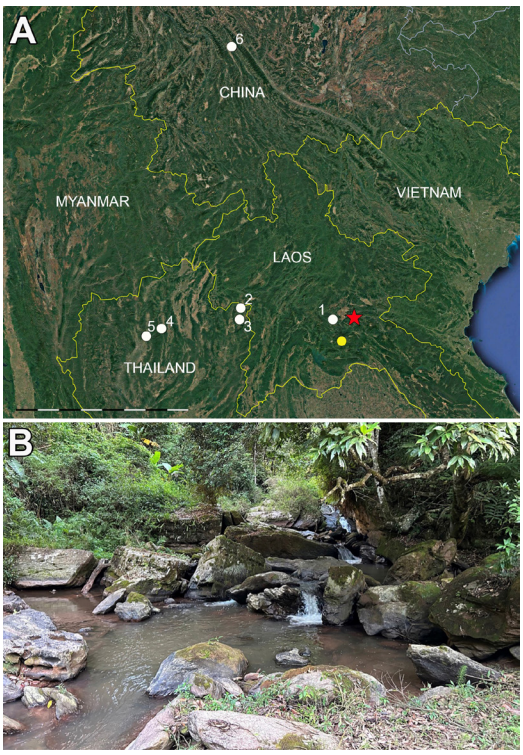

Figure 2. (A) Localities for *Trimerodytes praemaxillaris*, including the type locality Xieng Khouang Province, Laos (red star), the new locality in Xaisomboun Province, Laos (yellow circle), and other confirmed localities (white circles). Locality 6 in China is the locality of a misidentified *T. yapingi*, shown here to avoid future confusion. The scale shows a distance of 400 km in 50-km intervals. Map created by Mark O'Shea using Google Earth. (B) Habitat at the new locality in Xaisomboun Province. Photo by Yanpeng Shen.

Comparative characters. Scale characters and measurements for snakes currently listed under the nomen *praemaxillaris* (a unique species name for reptiles) were summarized from the literature, museum databases, and provided by museum curatorial assistants. Characters of the new specimen (FES. RA.24.001) were directly determined by the authors, and some scale counts were determined by examining photographs (Table 1).

Collection of the *Trimerodytes praemaxillaris* syntypes. The two hatchlings (MNHN-RA 1928.63–64; Appendix) were collected during the third Indochina expedition (Delacour and Jabouille, 1927, 1931) led by Jean Théodore Delacour (1890–1985) and his collaborator Pierre Charles Edmond Jabouille (1875–1947). Their text allows for a more specific assignment of both the date of collection as well as the type locality, neither of which has heretofore been reported with desirable precision. In the original species description, Angel (1929) listed no date for the collection and gave the locality as Xieng-Khouang as documented in the museum ledger. Murphy et al. (2008) also listed no collection date but specified that Xieng-Khouang was located at "about 19°52'N, 103°20'E" and at an elevation of "1094 m". David et al. (2015) provided a date range of "December 1925 or January 1926" (without explanation as to the origin of those dates) and a locality description of "Xieng-Khouang, the former city of Xiengkhuang, now near Phonsavan, Xiangkhoang Province, Laos." Finally, David et al. (2023) listed the locality as "the former city of Xiengkhouang, now Khoune, Khoune District, Xiangkhoang Province, Laos". We used the original texts detailing the journey (Delacour and Jabouille, 1927, 1931; Delacour, 1927, 1933) and were able to pinpoint the exact locality where the specimens were found**.**

Delacour collected these specimens at a locality he listed as "Xiengkhouang" (Delacour and Jabouille, 1931: XXXVIII) and explained that this was the "chef-lieu et province du Laos, appellée également Tranninh (1.200 m)" [capital and province of Laos, also known as Tranninh (1200 m)]. This description is significant because it shows that this locality should be both a capital and a province. Today, Xiengkhouang is the name of a province in Laos (called Tranh Ninh in Vietnamese). We consulted the data associated with some of Delacour's bird collection localities from the third Indochina expedition in the hope that, as an ornithologist, he may have provided more specific data for where he collected. This revealed a locality of "Muang Khoun, Ancienne Xieng Khouang (détruite)" [Muang Khoun, Ancient Xiengkhouang (ruin)] as the locality for the collection of several specimens (e.g., the syntype of *Psittiparus gularis laolianus* Delacour, 1926, MNHNP-ZO-MO 1927-835). Muang Khoun was the French provincial capital of Xiengkhouang Province, a small settlement until it was completely destroyed by U.S. bombing in the early 1970s. It was also the site of what was once the royal seat of the minor kingdom of Xieng Khuang in the sixteenth century. Given that Delacour (1927: VII) stated that the expedition made only a single foray to a pond 40 km northwest of Muang Khoun, we conclude that best notation for the type locality for *T. praemaxillaris* is "near Muang Khoun, Xiengkhouang Province, Laos (19.3280°N, 103.3702°E; elevation 1200 m)".

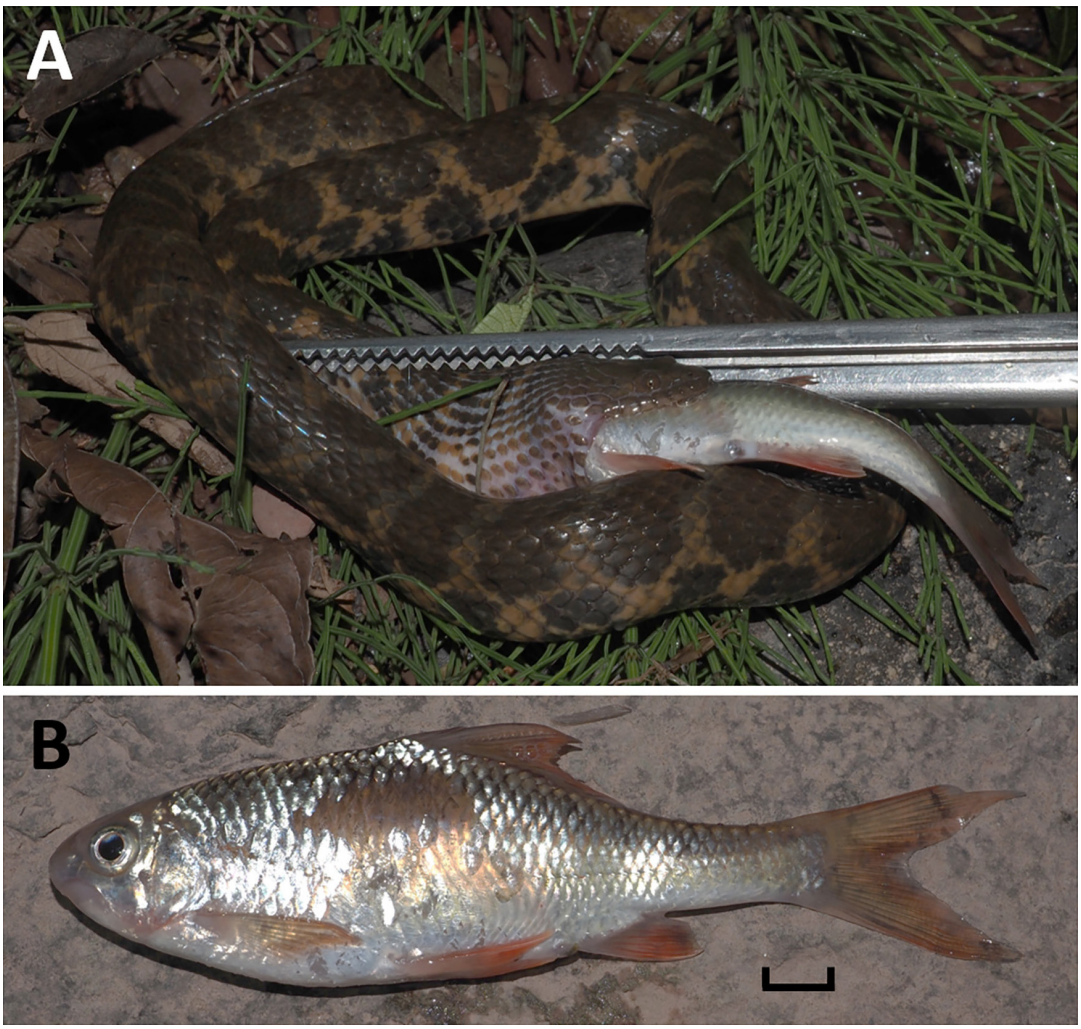

Figure 3. (A) *Trimerodytes praemaxillaris* from Xaisomboun Province, Laos. We prevented the snake's escape using large forceps, which prompted a regurgitation response. (B) A juvenile *Scaphiodonichthys acanthopterus*, the first definitive prey item of *T. premaxillaris*. The scale bar in (B) represents 10 mm. Photos by Kanto Nishikawa.

We note that the coordinates for this locality on the website of the MNHNP are incorrect, placing the marker into the city centre of Phonsavan, the current capital of Xiengkhouang Province. While the expedition arrived in Muang Khoun on 15 December 1925 and departed on 13 January 1926 (Delacour, 1927: VI–VII, 1933: 548), the snake specimens were accessioned at the MNHN only on 15 November 1928.

Measurements and pholidosis of the new specimen. The specimen (FES.RA.24.001) is an adult female with two oviductal eggs (Smith et al., 1989). It is a relatively small individual (584 mm SVL + 142 mm TL = 726 mm TTL) with the following characteristics: (1) rostral does not extend onto the dorsal part of the head, slightly wider than tall (3.4 mm and 2.6 mm, respectively; Fig. 5C); (2) internasals long and flared posterolaterally, about twice as long as wide and similar in length to the nasals (Fig. 5C); (3) prefrontals fused into a single scale with a medial apex directed anteriorly, lateral sides create a wing-like appearance with a lateral edge that curves ventrally, posterior edge almost completely straight, width 3.4 mm at widest point (Fig. 5C); (4) frontal pentagonal with well-formed corners, length 5.9 mm, about ¾ the length of the parietals;

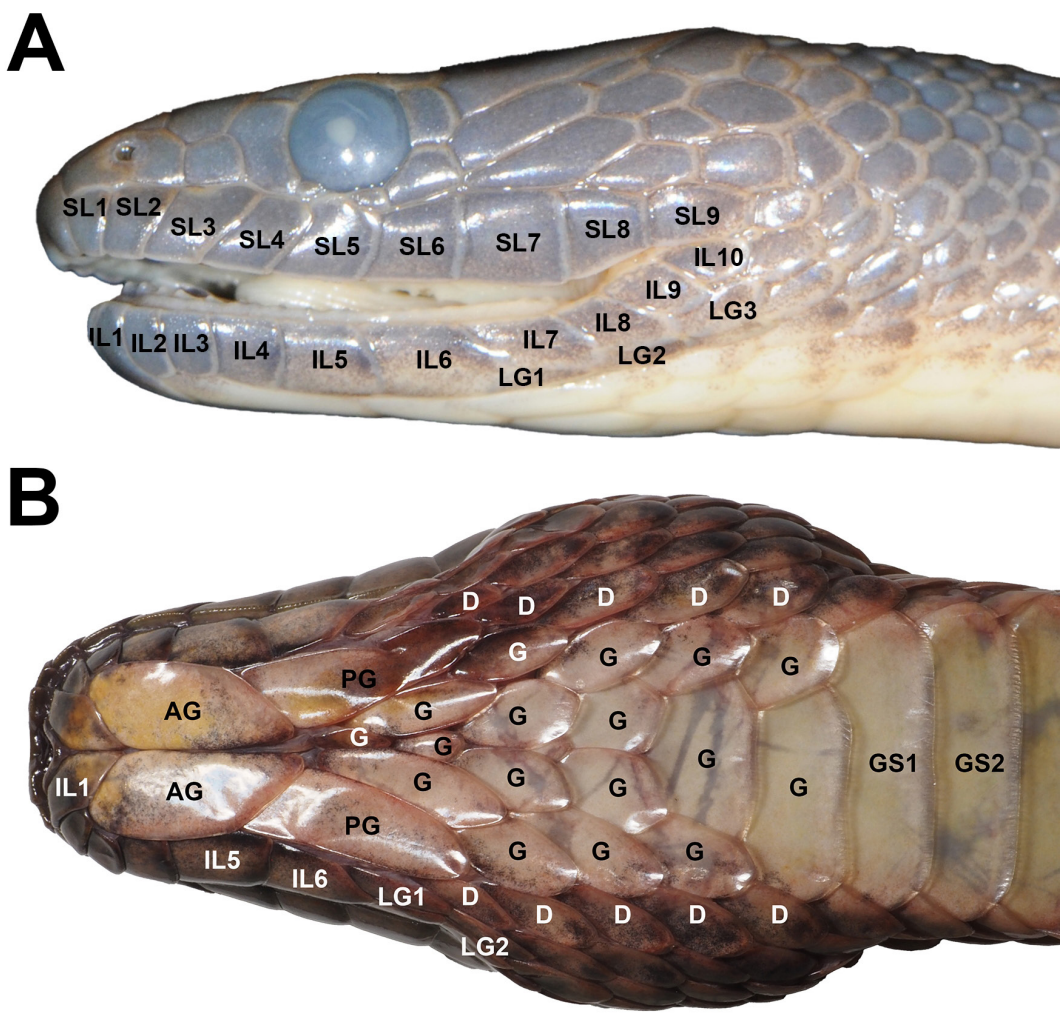

Figure 4. Head scales of two specimens of *Trimerodytes praemaxillaris*, showing (A) a left lateral view of NCSM 79204 with labelled supra- and infralabial scales, and (B) a ventral view of FES.RA.24.001 with labelled chin and throat scales. Labels include supralabials (SL), infralabials (IL), anterior genials (AG), posterior genials (PG), lateral gulars (LG), gulars (G), dorsals (D), and gastrosteges (GS). The positioning of the dorsal scales follows Dowling (1951).

(5) length of parietals 8.1 mm at their longest point, parietal suture about the same length as the frontal; (6) three temporal scales touching the parietals on each side of the head, temporal formula 2+3+3 (Fig. 5D); (7) loreal about as long as wide; (8) on both sides of the head a single, narrow preocular, twice as tall as the loreal, curving around the anterior border of the eye (Fig. 5D); (9) two postoculars of similar size on the left side of the head, the lower curving around the posterior border of the eye to form the separation between SL6 and the eye (Fig. 5D); on the right side, both postoculars are divided into two smaller scales (Fig. 5D'), with the anterior fragment of the lower postocular forming a subocular scale that almost separates SL5 from the eye; (10) supraoculars large, ⅘ the length of the frontal; (11) nine supralabials (SL), two (SL4–5) touching the eye (Fig. 5D); (12) nine infralabials (IL), five (IL1–5) touching the anterior genial, ⅔ of IL5 in contact with the anterior genial; (13) three lateral gulars (LG), LG1 touching the posterior part of IL6 and mostly paralleling IL7, LG3 reaching to the centre of IL10 (Figs. 4B, 5E);

Table 1. Comparative data for museum specimens of *Trimerodytes praemaxillaris*. Measurements for snout–vent length (SVL), tail length (TL), and total length (TTL) are given in mm. Sex is abbreviated as hatchling (H), juvenile (J), male (M), and female (F), and scales are listed as ventrals (V), paired subcaudals (SC), supralabials (SL), and infralabials (IL). Calculations of the dorsal scale ratio (SCR) follow Kaiser et al. (2018). We also provide the numbers of SLs touching the eye (SL_E) and of ILs touching the anterior genial (IL_G), as well as the number of dorsal scale rows in three areas of the body (see text). The plus sign (+) indicates a broken tail, and in those specimens the SCR is an estimate. The missing symbol (⃠) indicates data we were unable to obtain or calculate.

Specimen	Sex	SVL	TL	TTL	V	SC	SCR	Dorsals	SL	SL_E	IL	IL_G
MNHNP-RA 1928.63 (syntype)	H	166	50	216	149	67	0.32	⃠-19-⃠	9	4+5	9	5
MNHNP-RA 1928.64 (syntype)	H	161	47	208	149	63	0.30	⃠-19-⃠	9	4+5	9	5
ZMUC R601134	J	214	63	277	145	64	0.31	⃠-19-⃠	9	4+5	10	5
NCSM 79204	J	211	48	259	157	56	0.26	19-19-17	9	4+5	9	5
FMNH 271443	M	568	144+	712+	155	58+	⃠	19-19-17	9	4+5	9	⃠
FMNH 271445	M	504	125+	629+	154	57+	⃠	19-19-17	9	4+4	11	⃠
THNHM 15363	M	545	134+	679+	154	58+	⃠	19-19-17	9	5	10	⃠
THNHM 15364	F	665	153+	818+	149	55+	⃠	19-19-17	9	5	10	⃠
THNHM 15365	F	770	210+	980+	152	53+	⃠	19-19-17	9	4+5	10	⃠
NUOL 00108	⃠	⃠	⃠	⃠	⃠	⃠	⃠	⃠	⃠	⃠	⃠	⃠
FES.RA.24.001	F	584	142	726	152	58	0.28	19-19-17	9	4+5	9	5

(13) four rows of gular scales separating the posterior genial and the anteriormost gastrostege (the first scale normally considered as the "first ventral" in ventral scale counts of snakes), Row 1 composed of a pair of elongate scales separated by a narrow medial scale ⅓ their size, Rows 2–3 paired rounded scales, and Row 4 a scale with similar dimensions to the first gastrostege but bordered by an additional gular on the left side (Figs. 4B, 5E); (14) 19-19-17 dorsal scale rows, counted one head length behind the head, at midbody, and one head length anterior to the cloacal opening; (15) 152 ventrals, 58 paired subcaudals; (16) two scales covering the cloacal opening, and; (17) tail length about ¼ of total length (subcaudal ratio 0.28).

Morphological variation. The maximum total length of *T. praemaxillaris* is just under 1 m (THNHM 15365), with a hatchling size of about 20 cm, or ⅕ adult maximum size (Table 1). There is little variation in the scale counts, and given the small sample size it is not possible to determine whether there is any sexual dimorphism in ventral and subcaudal scale counts in *T. praemaxillaris*. The two male specimens have 154 and 155 ventrals, a number that is higher but continuous with that in the four female specimens (149–153). Because of broken tails we were only able to determine a complete subcaudal count (58 SC) in a single adult specimen, the female we recently caught (FES.RA.24.001), but if we include immature specimens, the range is 56–67 SC. The only other variation is in the number of infralabials, which includes counts of nine (n = 5), ten (n = 4), and 11 (n = 1). These characters are to a high degree congruent with those in the syntypes (Figs. 1, 6). Additional information can be found in David et al. (2023).

Colouration. The colour in life of our specimen consists of a brown dorsal background with irregular, alternating bands of dark brown and lighter orange brown that shift asymmetrically along the midline (Fig. 5A). The darker bands just barely reach the ventral scales. The venter is cream all along the body, with some dark pigmentation on the infralabials and some dark brown and reddish-brown blotches only on the tail (Fig. 5B). This pattern is also observed in the single observation available on iNaturalist (Bunkhwamdi, 2021), except that the depicted individual is overall darker and there is no asymmetrical pattern shift. The syntypes no longer show any discernible colour pattern (Fig. 1), which if present at the time of collection probably leached out during nearly a century in preservative. Angel (1929) already saw no patterning and described the colouration as "uniform brown above; yellowish white below; the upper and lower labials bordered with brown on their posterior margins." A juvenile specimen (NCSM 79204), slightly longer than the syntypes, has a grey background colour based on a decade in preservative, but the patterning seen in the living adult specimens remains faintly visible (Fig. 7).

Prey species. The fish regurgitated by the snake (FES.FH.24.001; Fig. 3B) is a juvenile spiny bream, *Scaphiodonichthys acanthopterus* (Chanda Vongsombath and Yuichi Kano, pers. comm.) of total length ca. 160 mm.

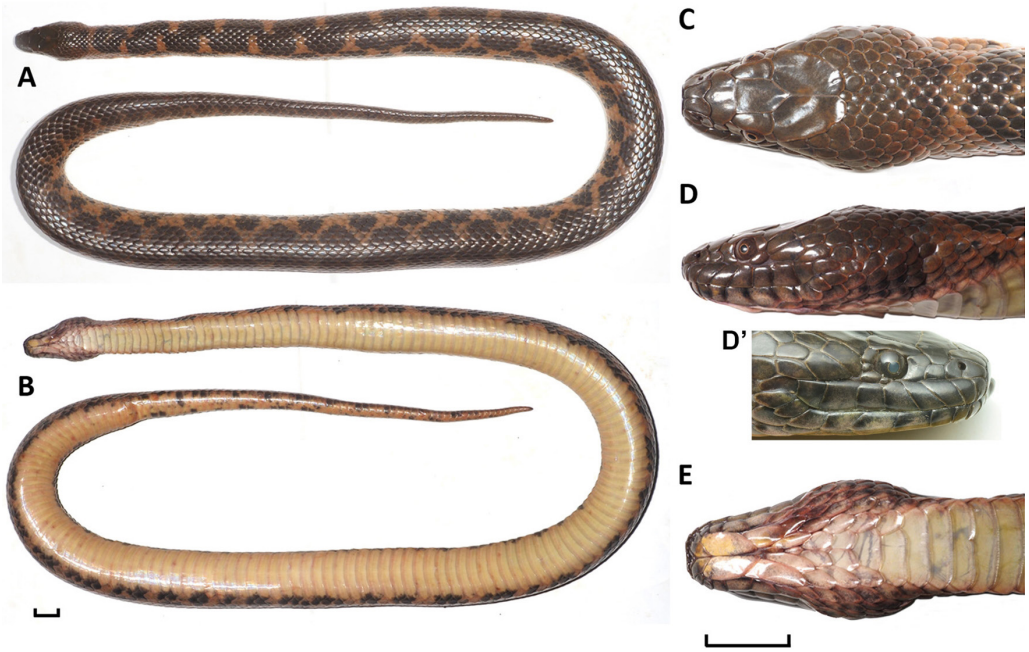

Figure 5. Adult female *Trimerodytes praemaxillaris* (FES.RA.24.001) before preservation. The entire body is shown in (A) dorsal and (B) ventral view. Images of the head include a dorsal view (C), a left lateral view (D), a right lateral view (D'), and a ventral view (E). The scale bars represent 10 mm. The right lateral view (D') is slightly enlarged to show the fragmented postocular scales, so it is not to scale. Photos by Kanto Nishikawa.

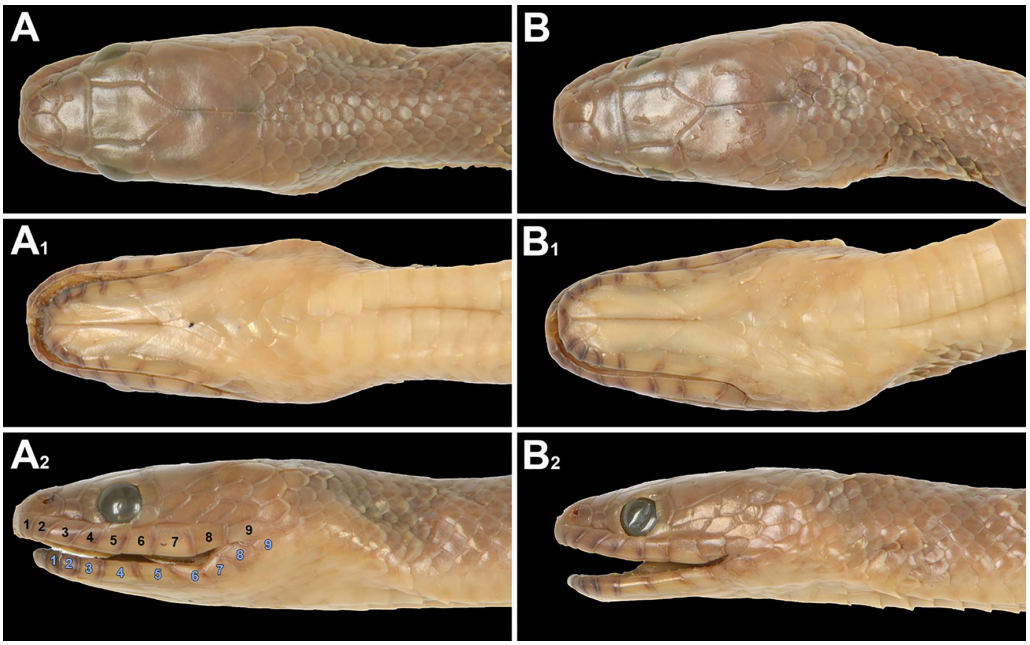

Figure 6. Head views of the *Trimerodytes praemaxillaris* syntypes in (from top to bottom) dorsal, ventral, and left lateral views. Images show MNHNP-RA 1928.63 (A, A1, A2) and MNHNP-RA 1928.64 (B, B1, B2). We added numbers to the supralabials (black) and infralabial (blue) scales to facilitate a correct count. Photos by Antoine Fraysse, downloaded from the website of the Muséum National d'Histoire Naturelle, Paris, France (MNHNP), and used under the CC BY-NC-ND license.

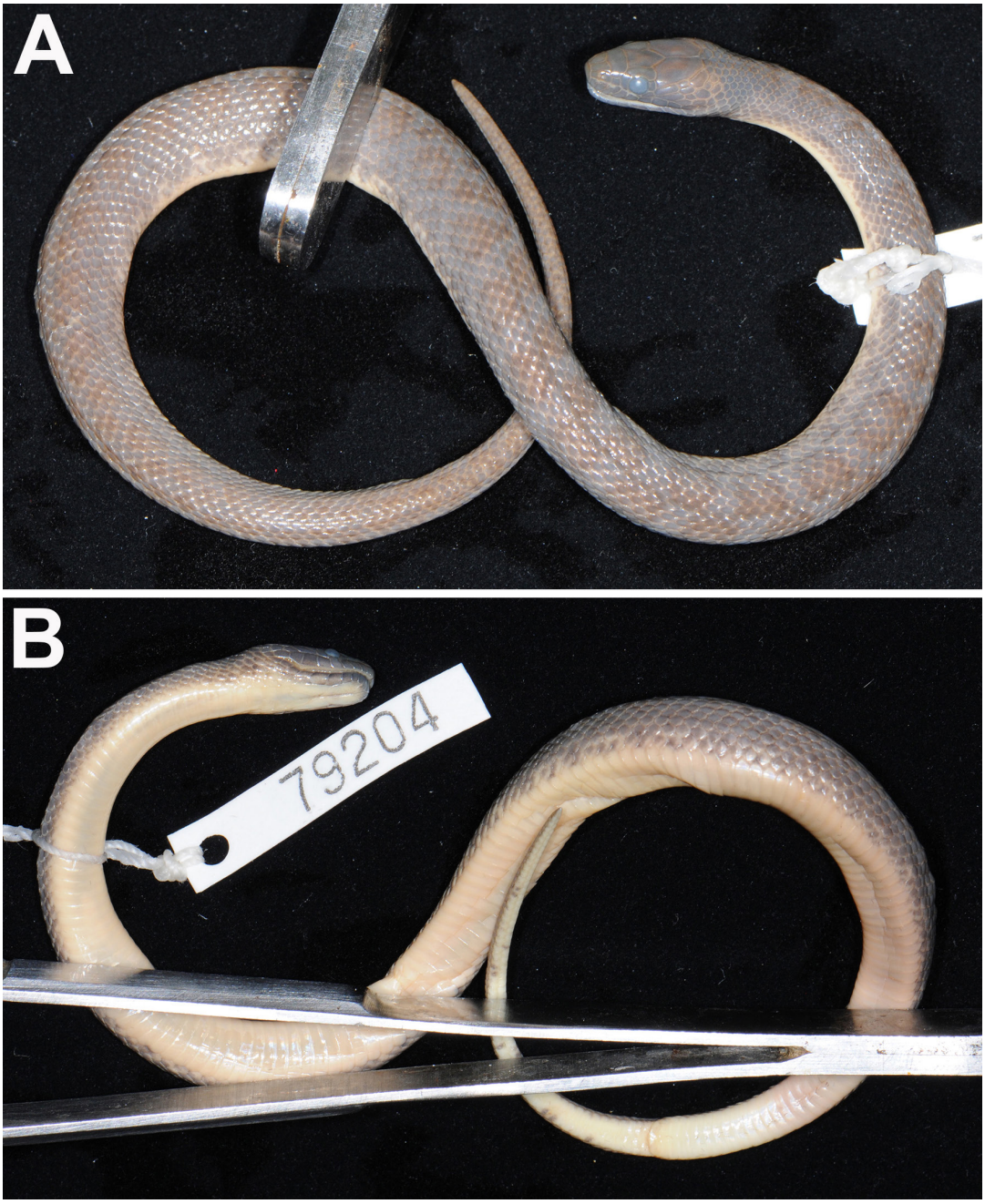

Figure 7. Whole body view of a juvenile *Trimerodytes praemaxillaris* (NCSM 79204) in dorsal (A) and ventral (B) view. The body is only faintly patterned but it appears as described for adults. Photos by Bryan Stuart.

Natural history. Angel (1929) did not include any natural history or habitat information from the work by Delacour and Jabouille (1927) and, given the devastation this region experienced during the Vietnam War, we believe it is relevant to recount some of this information here. Delacour (1927: VI) reported that:

> "The valley and the hills close to Xieng-Khouang are somewhat cultivated or covered with tall grasses and bushes, with isolated trees, but the higher, more distant areas are largely covered with forest. These woods present a surprising appearance: some appear

> tropical, with palm trees, orchids, aroids [Family Araceae], ferns, and vines, while the others, contiguous, are covered in pines, oaks, and deciduous trees, reminiscent of our temperate regions; it does not seem, moreover, that elevation or exposure plays a role in this." [our translation from the original French]

This account documents a mixed-vegetation area with agricultural activity on the level ground, some level of habitat modification in places near the town, but with some high-quality forest of two different types, where collecting also took place. Plates II and III in Delacour and Jabouille (1927) illustrate these habitats. The area was strongly impacted by bombing during the Vietnam War, which unfortunately created environmental changes.

In addition to habitat considerations, it is of interest to note that the hatchling snakes were collected in December or January, months considered to be part of the dry season in Laos. In fact, Delacour (1927: VI–VII) made the following statement about the weather during their stay in Muang Khoun:

> "At the time of our visit, the temperature in Tranninh was very pleasant, dry and sunny, quite hot during the day, but very cold at night; several times it even froze hard, and all the gardens were as burned and browned by frost as those of France can be at this time of the year; the temperature sometimes goes down, it is said, to –7°C. However, we see banana trees, papaya trees, palm trees, and other tropical plants that grow back in spring and bear fruit in summer, despite this harsh winter, which completely stops their vegetation. While it freezes in the valleys, the higher elevations are unaffected, and the plants there, more delicate, that would not resist the cold in the lower lands, grow abundantly. During our stay, a violent storm broke out followed by rain, but it was a completely exceptional phenomenon in January." [our translation from the original French]

This description shows that *T. praemaxillaris* has a reproductive season that likely begins with the monsoon rains in May (WB/ADB, 2011), leading to hatching at the beginning of the dry season in October. Shifts in rainfall patterns and other environmental factors influence this, as the presence of egg-tooth-bearing hatchlings (the syntypes) and a juvenile (NCSM 79204) in February (late in the season), and a hatchling in October (early in the season; Rasmussen, 1982) indicates. The observation that the specimen we collected in Xaisomboun Province in May carries oviductal eggs fits this timeline. That time of the year would allow hatchling snakes, whose diet at least partly consists of fish and would require safe passage in and along streams, to experience low water conditions instead of the fast flow brought by extended periods of rain during May–October.

Comments on the more recent collection of specimens are sparse but appear to support the concept of this species as a habitat generalist. For example, Rasmussen (1982) reported that the Copenhagen specimen, a juvenile (TTL = 277 mm; Table 1), was collected on 3 October 1981in what appears to be pristine habitat, a 2-m wide, fast-flowing forest stream bordered by bamboo scrub (Doi Saket District, Chiang Mai Province, Thailand). The largest number of snakes (n = 5) was collected at night at Wang Pian Waterfalls, Nan Province, Thailand in excellent forest habitat, where the Nan River is surrounded by mixed deciduous forest and bamboo scrub along its banks (Murphy et al., 2008). From the description of these encounters, we concur with Murphy et al. (2008) that the species is likely nocturnal and at least semi-aquatic, especially given its ability to prey on a fish species as agile as *Scaphiodonichthys acanthopterus*. Whereas Murphy et al. (2008) documented the presence of fish scales in two of their specimens (as well as nematode infestations), we here provide the first information regarding the identity of a prey species.

Range. Specimens of *T. praemaxillaris* have now been collected in two countries (Laos, Thailand) at elevations from ca. 475–1200 m. In terms of elevational range (725 m), it appears that this species is able to tolerate varying climatic conditions and, if the range is continuous, must be able to survive at least intermittently in less-than-ideal habitat. The north–south exent of the range is rather narrow compared to the elevation, which perhaps indicates a preferred suite of environmental conditions around 19–20°N. This range is at the crossroads of three significant biodiversity hotspots, the Indo-Burma Region, the Mountains of Southwest China, and the Eastern Himalayas Region. The influence of mountains in the region is interesting because of the narrow, deep river valleys with a north–south orientation. This means that the mountain slopes either face east or west, resulting in a more moderate and warmer climate than non-mountainous areas at the same latitude, and they support subalpine coniferous forests in addition to more tropical forest habitats. These mountains are ancient, resulting in an accumulation of rich species diversity and their geography creates barriers to the migration of terrestrial organisms. This makes *T. praemaxillaris*, with its wide elevational and narrow latitudinal range, a species of great interest.

Conclusions. Our new record for *T. praemaxillaris* is the first for the mountainous Xaisomboun Province in Laos and the southernmost location for the species so far (8 km further south than specimens collected near Doi Saket District, Thailand; see Appendix), extending the range by about 58 km southwest of the type locality. It is also the first specimen with oviductal eggs, confirming this reproductive mode for the species, and it was caught in the act of consuming a fish, confirming this dietary component. Given the confusion with the nomenclature and position of chin and throat scales (i.e., genials, gulars, lateral gulars), we consider these variable characters to the extent that they may not be taxonomically informative. Perhaps with larger sample sizes (at least ten males and ten females by our estimation) a reassessment of the chin and throat pholidosis can build a reliable character set.

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Appendix. Specimens of *Trimerodytes praemaxillaris* in museum collections. Acronyms follow Sabaj (2020), with the addition of the collection in the Faculty of Environmental Sciences, National University of Laos (FES) and the use of the older acronym for the Natural History Museum of Denmark, University of Copenhagen (ZMUC). We do not include the specimen at the National University of Laos (NUOL 00108) for which we were unable to obtain any information.

LAOS (*n* = 4): XAISOMBOUN PROVINCE, ca. 6 km by road southeast of Ban Mouang Cha (18.8662°N, 103.1154°E; elevation 1272 m), FES.RA.24.001. XIANGKHOANG PROVINCE, in a tributary entering the Nam Ngum River north of Ban Xamthong Village (19.2869°N, 102.9242°E; elevation 1100 m), NCSM 79204. XIENG-KHOUANG PROVINCE, surroundings of Muang Khoun Village (19.3280°N, 103.3702°E; elevation 1072 m), MNHNP-RA 1928.63–64 (syntypes).

THAILAND (*n* = 6): CHIANG MAI PROVINCE, Doi Saket (ca. 19°N, 99.15°E; elevation 700 m), ZMUC-R601134. NAN PROVINCE, Chaloem Pra Kiat District, Huai Kon Subdistrict, Wang Pian Waterfall (ca. 19.54°N, 101.07°E; elevation 475 m), FMNH 21443, 271445, THNHM 15363–65.

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