A New Striped Ichthyophis (Amphibia: Gymnophiona) from Mt. Kinabalu, Sabah, Malaysia

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Abstract: A new striped *Ichthyophis* is described based on one adult male collected from the southeastern slope of Mt. Kinabalu, Sabah, East Malaysia. The new species is characterized by the absence of yellow marking on the jaw angle and the presence of a lateral stripe on most of the collar region, and is distinguished from all other striped congeners by a combination of characters that includes body size and proportion, position of tentacles, shape of annular grooves, and number of annuli, scale rows, and splenial teeth. The anterior phallodeum morphology is also described for the new species.

Key words: Caecilian; Ichthyophis; New species; Mt. Kinabalu; Borneo

INTRODUCTION

Southeast Asia is the center of species diversity of the Ichthyophiidae, which encompasses a total of 53 species (Frost, 2013). This family is the largest among the order Gymnophiona after recent taxonomic revision at the family level (Wilkinson et al., 2011; Frost, 2013), and consists of two genera, *Ichthyophis* Fitzinger, 1826 and *Uraeotyphlus* Peters, 1880. Presently, the genus *Ichthyophis* includes 46 species from South and Southeast Asia, and the southernmost part of East Asia. The taxonomy of the species belonging to *Ichthyo*.

phis is very problematic because most of them have very similar morphology.

The component species of Ichthyophis can be divided into two color types, one with a pair of yellow or cream-colored lateral stripes (striped type) and the other lacking such stripes (unstriped type). They are also divided into two tooth series types, one with a splenial tooth series on the lower jaw (formerly, Ichthyophis sensu stricto), and the other lacking the series (formerly, Caudacaecilia: synonymized with Ichthyophis by Nishikawa et al., 2012a). Division of *Ichthyophis* by these colors and/or tooth series types is not supported by molecular phylogenetic analyses (Gower et al., 2002; Nishikawa et al., 2012a), but the combination of these characters is extremely useful for identification of conge-

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neric species (Taylor, 1968; Wilkinson et al., 2007).

In 2006, we collected a specimen of Ichthyophis species with a striped body and a splenial tooth series from Poring Station of Kinabalu National Park, Sabah, Malaysian part of Borneo Island. From Borneo, two species of striped Ichthyophis with a splenial tooth series have been known: I. atricollaris Taylor, 1965 from East Kalimantan, Indonesia and I. biangularis Taylor, 1965 from western Sarawak, Malavsia. The present Ichthyophis from Sabah has a distinctive combination of morphological characteristics that distinguishes it from these two Bornean species, as well as from all the other congeners. We therefore describe this caecilian as a new species.

MATERIALS AND METHODS

A field survey of caecilians was made at Poring Station of Kinabalu National Park, Ranau, Sabah, Malaysia in 2005 and 2006 and at Kubah National Park, Sarawak, Malaysia in 2009 and 2012. Adults were sexed by direct observation of the gonads. After tissues were taken for genetic analysis, specimens were fixed in 10% formalin, transferred to 70% ethanol, and identified by examining morphological characters. Voucher specimens are stored at the Graduate School of Human and Environmental Studies, Kyoto University (KUHE).

We measured the following morphometric characters to the nearest 0.1 mm with a dial caliper following Nishikawa et al. (2012b): total length (TL); head length (HL) from tip of snout to first collar groove, measured dorsally; trunk length (TRL) from first collar groove to posterior end of vent; tail length (TAL) from posterior end of vent to tail tip; vent length (VL); snout length (SL) from tip of snout to jaw angle; lower jaw length (LJL) from tip of lower jaw to jaw angle; snout-2nd collar groove length (S2CL), measured ventrally; snout-3rd collar groove length (S3CL), measured dorsally; 1st collar length (1CL), measured laterally; 2nd collar length (2CL), measured laterally; head width (HW) at jaw angle; maximum head width (MXHW); body width at middle (BWM); tail width at posterior vent (TAW); lateral stripe width at middle (LSWM); interorbital distance (IOD); intertentacle distance (ITD); internarial distance (IND); eyenostril distance (END); eye-tentacle distance (ETD); tentacle-nostril distance (TND); and eye-jaw angle distance (EJD).

The following meristic characters were counted: total annuli (TA); annuli interrupted by vent (VA); post-vent annuli (PVA); dorsal transverse grooves on 2nd collar (DTG); premaxillary-maxillary teeth (PMM); vomeropalatine teeth (VP); dentary teeth (DE); splenial teeth (SP); and vertebrae (VER). The number of vertebrae was counted from a soft X-ray photograph using Fuji Medical X-Ray Film (RX-U).

Since the single adult proved to be a male, its phallodeum was everted after anesthetization and fixed by 10% formalin injection. For describing the everted morphology of the anterior phallodeum, we followed the terminology of Gower and Wilkinson (2002) and Kupfer and Müller (2004) with addition of two characters: central tuberosity of the left dorsolateral longitudinal ridge (c.ldl) and central tuberosity of the right dorsolateral longitudinal ridge (c.rdl).

SYSTEMATICS

Ichthyophis pauli sp. nov. Figs. 1–4

Ichthyophis sp. 4: Nishikawa et al., 2012a, p. 716.

Diagnosis

An *Ichthyophis* with broad and uninterrupted lateral stripes extending from the posterior end of the collar to the end of the vent; body uniformly slate dorsally, slightly paler ventrally; total length of the single male 331.5 mm; TL/BWM ratio=29.1; 335 annuli, of which six are on the tail; 22 splenial teeth; TND/ETD ratio=2.5; scales from 30th annuli



FIG. 1. Holotype of Ichthyophis pauli sp. nov. (KUHE 39361) in life.

to the end of the body, number of rows increasing in posterior annuli up to seven.

Holotype

KUHE 39361 (Figs. 1–4), an adult male (wrongly presented as adult female in Nishikawa et al., 2012a) from a small tributary of Sg. (Sungei=River) Kipungit I in the Poring Station of Kinabalu National Park (6°2'57"N, 116°42'00"E, a. 600 m asl), about 15 km north of the central Ranau District, State of Sabah, Malaysia, collected by Kanto Nishikawa and Paul Yambun, at 1220 h on 26 November 2006. The GenBank accession numbers of mtDNA sequences are AB686129 (12S rRNA and 16S rRNA) and AB686064 (cytochrome b).

Description of holotype (measurements in mm)

Moderately sized (TL 331.5); body subcylindrical, slightly depressed dorsoventrally, tapering posteriorly, more abruptly at about onesixth of body, ending in blunt tail tip (tip damaged), head widened slightly just behind jaw angle; snout rounded anterior to tentacles, slightly longer (10.0) than lower jaw (9.2); intertentacle distance (7.5) larger than interorbital distance (6.4), which in turn is much larger than internarial distance (3.3); eyes slightly protruding, almost midway between top of head and edge of mouth in lateral view, slightly inset from edge of head in dorsal view; tentacles two and a half times as far from nostrils than from the eyes (TND/ETD=2.5); eye-jaw angle distance (2.9) larger than eyetentacle distance (1.5) but smaller than tentacle-nostril distance (3.8); tentacles very close to edge of mouth, long and thin in life, tip slightly protruding from tentacular sheath in preservative; second collar (4.6) much longer than first collar (2.9); nostrils round, positioned closely at anterior margin of mouth in dorsal and lateral views, invisible in ventral view.

Collar region slightly wider than head and anterior body in dorsal and ventral views, not



FIG. 2. Holotype of *Ichthyophis pauli* sp. nov. (KUHE 39361) in dorsal (top), ventral (middle), and lateral (bottom) views. Scale=20 mm.

higher than head and anterior body in lateral view; first collar groove evident as constriction separating head and trunk, curving slightly anteriorly towards dorsal midline, where the groove becomes incomplete; second collar groove evident ventrally but not apparent dorsally, parallel to first groove laterally, fading out near lateral midline; third collar groove not clearly differentiated from anteriormost annular grooves of trunk, but recognized as first groove crossing lateral to ventral body; third collar groove dorsally complete, curving slightly anteriorly towards dorsal midline; dorsal transverse groove (DTG) absent.

Annular count 335; annular grooves complete dorsally; dorsally, annular grooves curving slightly anteriorly towards midline on anterior three-fifths of body and nearly orthoplicate on posterior two-fifths of body; ventrally, grooves strongly angulate posteriorly towards midline, degree of curvature decreasing posteriorly to becoming orthoplicate at ca. one-twentieth of body; number of scale rows one from anteriormost 30th to around 80th annuli, two to 175th, three or four to 280th, five to 300th, six to 310th, and seven to the end.

Longitudinal vent surrounded by small and whitish subcircular disc; five denticulations on each side of vent and each one small denticulation on anterior and posterior ends; no papillae on disc; four annuli in vent slit including denticulations and six in tail.

Teeth on premaxillary-maxillopalatine 44, vomeropalatine 44, dentary 44, splenial 22; choanae elongated, about three times as long as broad, obliquely extending posterolaterally,



FIG. 3. Holotype of *Ichthyophis pauli* sp. nov. (KUHE 39361). From top to bottom: head and anterior body in dorsal, ventral, and lateral views; posterior body in ventral view. Scale=10 mm.

without a flap on edge.

Anterior phallodeum with a pair of blind sacs laterally and longitudinal ridges dorsolaterally, laterally, and ventrolaterally (Fig. 4); ventrolateral longitudinal ridges slightly smaller than dorsolateral longitudinal ridges, but almost same as lateral longitudinal ridges; each longitudinal ridge with a posterior tuberosity but lacking distinct anterior tuberosity; central tuberosities only on dorsolateral longitudinal ridges; no mid-dorsal longitudinal ridge; a mid-dorsal knob.

Color

In life, ground color of dorsum uniform slate; pale lilac ventrally (Figs. 1–2); lateral stripe bright yellow, broad, and uninterrupted throughout the body, extending from posterior end of

second collar to posterior end of vent disc; head with several pale yellowish markings dorsally; eye surrounded by narrow whitish ring; tentacles and surrounding tentacle apertures whitish; vent disc whitish. In preservative, color and pattern faded but not obviously changed.

Comparisons

Ichthyophis pauli differs from other striped Ichthyophis with splenial teeth from Borneo in the following way (topotypic specimens of I. biangularis examined by us are shown in Table 1, and data of I. atricollaris and the holotype of I. biangularis are taken from Taylor, 1965). It differs from I. atricollaris and I. biangularis by having larger (TL= 331.5 mm vs. 204.0-285.0 mm in I. atricollaris and 237.5–285.0 mm in I. biangularis) and thinner body (TL/BWM=29.1 vs. 25.5-26.8 in I. atricollaris and 23.9-28.4 in I. biangularis), larger number of splenial teeth (SP=22 vs. 13–16 in *I. atricollaris* and 3–6 in I. biangularis), and tentacles closer to eyes (TND/ETD=2.5 vs. 1.7-2.0 in I. atricollaris and 1.8–2.0 in *I. biangularis*). The new species also differs from I. atricollaris in lacking a distinct yellow spot on the jaw angle (vs the presence of a yellow spot on the jaw angle in I. atricollaris) and in having ventral annular grooves strongly angulated posteriorly (weakly angulated in I. atricollaris), and from I. biangularis in lacking scales on the anterior 29 annuli and having scales up to seven (having scales from the first annuli and which number up to five in *I. biangularis*).

The new species differs from other striped *Ichthyophis* with splenial teeth in the following way (the specimens examined by us are shown in Appendix 1 and data of the remaining species are from Taylor, 1960, 1965, 1968, 1973; Salvador, 1975; Pillai and Ravichandran, 1999; Kupfer and Müller, 2004; Wilkinson et al., 2007; Kamei et al., 2009; Mathew and Sen, 2009). It differs from all the other species (i.e., *I. alfredi*, *I. bannanicus*, *I. beddomei*, *I. bernisi*, *I. daribokensis*, *I. davidi*, *I. elongatus*, *I. garoensis*, *I. glutinosus*, *I. humphreyi*, *I. hypocyaneus*, *I. khumhzi*, *I. kodaguen*



FIG. 4. Anterior phallodeum of holotype of *Ichthyophis pauli* sp. nov. (KUHE 39361) in dorsal (top left), ventral (top right), left lateral (bottom left), right lateral (bottom right), and distal views (center). c.ldl: central tuberosity of l.dl; c.rdl: central tuberosity of r.dl; ebs: entrance of blind sac; eu: entrance of urodeum; l.dl: left dorsolateral longitudinal ridge; mdk: mid-dorsal knob; l.vl: left ventrolateral longitudinal ridge; p.ldl: posterior tuberosity of l.dl; p.lvl: posterior tuberosity of right lateral longitudinal ridge; p.rdl: posterior tuberosity of right dorsolateral longitudinal ridge; p.rvl: posterior tuberosity of right ventrolateral longitudinal ridge; r.dl: right dorsolateral longitudinal ridge; r.l: right lateral longitudinal ridge; r.vl: right ventrolateral longitudinal ridge. Scale=10 mm.

	<i>Ichthyophis pauli</i> sp. nov.	I. atricollaris			I. biangularis			
Locality	Poring, Sabah, Malaysia	Long Bloee, Boven Mahakkam, Indonesia	Balik Papan, Indonesia	Boven Mahakkam, Indonesia		Matang, Sara	wak, Malaysia	
Types	Holotype	Holotype	Paratype	Paratype	Holotype	Topotype	Topotype	Topotype
		RMNH	RMNH	RMNH	BMNH			
Specimen No.	KUHE 39361	10684*	10685*	6912D*	72.2.19.59.A*	KUHE 53016	KUHE 53017	KUHE 54550
Sex	Male	Unknown	Unknown	Unknown	Unknown	Female	Female	Female
Morphometri	с							
TL	331.5	285.0	255.0	204.0	258.0	239.0	237.0	249.5
HL	13.7	10.0	11.0	9.0	10.0	10.2	10.4	9.8
TRL	310.0	—	—	—	—	230.0	228.5	237.5
TAL	4.7	4.8	5.1	4.0	5.8	3.7	3.6	4.5
VL	2.1	_	_	—	—	1.7	1.3	1.4
SL	10.0	_	_	—	—	6.8	7.0	7.3
LJL	9.2	_	_	_		6.3	6.1	6.7
S2CL	15.4	13.7	13.2	11.0	12.5	11.7	12.5	11.3
S3CL	19.7	17.2	17.0	13.4	16.5	14.6	15.3	15.0
ICL	2.9	_	_	_	—	2.3	2.5	2.8
2CL	4.6	_	_	_	_	3.2	3.0	3.0
HW	10.0	_	_		_	6.7	7.0	6.3
MXHW	11.0	9.9	9.0	7.7	8.2	7.4	7.6	7.2
BWM	11.4	11.0	9.5	8.0	9.8	9.3	9.9	8.8
TAW	4.0	—	—	—	—	3.2	3.9	3.5
LSWM	2.5	_	_	_	—	1.4	1.9	1.1
IOD	6.4	_	_	_	_	4.6	4.9	5.2
IID	7.5	—	—	—	—	5.2	5.4	5.4
IND	3.3	_	_	_	_	2.8	2.5	2.9
END	5.0			_	3.5	3.0	3.3	3.5
ETD	1.5	1.5	1.5	1.3	1.2	1.1	1.3	1.3
TND	3.8	3.0	2.5	2.4	2.4	2.1	2.3	2.4
EJD	2.9	_	_	_	_	1.8	1.9	1.6
Morphomeris	225	262 275	200 210	202 202	220 222	205	216	210
IA	333	203-275	300-310	293-303	330-333	325	310	310
VA	4	_	_	_	—	4	4	4
PVA	6	_	_	_	_	0	0	6
DIG	20/24			24/24	25/26	24/22	22/22	1
PMM	20/24	22/22	25/27	24/24	25/26	24/22	22/23	20/20
VP	21/23	22/23	20/20	20/19	24/24	1//18	19/20	18/21
DE	22/22	19/20	19/19	18/19	19/19	15/1/	1//18	1//1/
SF VED	11/11	8/8	8/3+	8/8	2/2	2/2	2/1	3/3
VEK Datio	108	—	_	_	_	109	108	108
TI /DWM	20.1	25.0	26.0	25 5	26.2	25.7	22.0	20 4
1L/DWM	29.1	23.9	20.8	20.0	20.3	23.7	23.9	28.4
IND/EID	2.5	2.0	1.7	1.8	2.0	1.9	1.8	1.8

TABLE 1. Measurements of striped *Ichthyophis* with splenial teeth from Borneo. RMNH: Nationaal Natuurhistorisch Museum; BMNH: The Natural History Museum. *Data were taken from the original description (Taylor, 1965).

sis, I. kohtaoensis, I. longicephalus, I. moustakius, I. nguyenorum, I. nokrekensis, I. paucisulcus, I. pseudoangularis, I. sendenyu, I. supachaii, and I. tricolor) in lacking yellow spots on jaw angles and stripes on most of the collar region except for the posterior end (having the spots on jaw angles and/or a lateral stripe crossing most of the collar region in all of the remaining species). The new species also differs from I. bannanicus, I. beddomei, I. davidi, I. elongatus, I. garoensis, I. glutinosus, I. khumhzi, I. kodaguensis, I. kohtaoensis, I. longicephalus, I. moustakius, I. paucisulcus, I. sendenyu, and I. tricolor in having a smaller number of splenial teeth (SP=22 vs. 24-31 in I. bannanicus, 52 in I.beddomei, 29-40 in I. davidi, 28-32 in I. elongates, 29 in I. garoensis, 30 in I. glutinosus, 40-46 in I. khumhzi, 25-31 in I. kodaguensis, 30-38 in I. longicephalus, 34-36 in I. moustakius, 28 in I. paucisulcus, 43-45 in I. sendenyu, and 47–57 in I. tricolor), from I. supachaii in having a larger number of splenial teeth (SP=22 vs. 11-18 in I. supachaii), and from I. glutinous, I. peninsularis, and I. pseudoangularis in having central tuberosities on the dorsolateral longitudinal ridges of the phallodeum (the tuberosities are lacking in I. glutinous, I. peninsularis, and I. pseudoangularis).

Finally, the mean of uncorrected pairwise sequence divergences (p-distance) in 2700 bp of 12S rRNA and 16S rRNA mitochondrial genes and 1140 bp of complete cytochrome b between the new species and *I. biangularis* are very large: 8.1% (range 8.1–8.2%) in 12S rRNA and 16S rRNA and 13.4% (range 13.1–14.3%) in cytochrome b genes (data re-calculated from Nishikawa et al. [2012a]). The new species is also differentiated from all of the remaining congeners examined at a distinct species level (Nishikawa et al., 2012a).

Range

Known only from the type locality on the southeastern slope of Mt. Kinabalu (location is shown as Sample 3 in Fig. 1 of Nishikawa et al. [2012a]).

Natural history

The type locality is in primary forest dominated by dipterocarps. The holotype was collected from inside a rotten log (32 cm in diameter and 125 cm in length) buried about 10 cm deep in wet soil close to a small stream (100 cm in width and <20 mm in depth). The streambed was a mixture of mud and sand, and the water was clear. Air, water, and soil temperatures at the time of collection of the holotype were 26.7, 22.6, and 23.6 C, respectively. Information on breeding, larvae, and metamorphosis is lacking.

The following Amphibian species have been found sympatric with the new species: *Ichthyophis* cf. asplenius, Ansonia longidigita, Bufo juxtasper, Fejervarya limnocharis, Hylarana picturata, Ingerana baluensis, Leptolalax pictus, Limnonectes finchi, L. kuhlii, Megophrys nasuta, Meristogenys dyscritus, M. orphnocnemis, M. whiteheadi, Metaphrynella sundana, Occidozyga baluensis, Odorrana hosii, Polypedates otilophus, Rhacophorus gauni, Staurois guttatus, and S. tuberilinguis.

Etymology

The species name is dedicated to Mr. Paul Yambun (Sabah Parks), who is one of the collectors of this species and has supported our field survey in Sabah.

DISCUSSION

Three Bornean striped species, I. atricollaris, I. biangularis, and the present new species I. pauli have superficially similar morphology, although at least the latter two species are clearly genetically distinct from each other (Nishikawa et al., 2012a). Because only a single specimen of the new species has been obtained, we cannot preclude variation in the diagnostic characteristics proposed. Especially, the lack of a yellow spot on the jaw angle can be variable. Such a variation has been found in *I. biangularis* compared above. This species was long known only from a holotype collected in 1872 (the year estimated by Taylor [1965]) by A. H. Everett from

Matang, Kuching, Sarawak (presently, Kubah National Park). However, we collected the second and third adult specimens (KUHE 53016 and 53017) from the type locality in 2009, possibly 137 years after the collection of the holotype. The holotype has been reported to have a spot (Taylor, 1965), and this was confirmed in the two topotypic specimens (measurement data in Table 1). Thus we first considered this trait (presence of a spot on the jaw angle) to be a stable characteristic, usable for taxonomic purpose. However, the third topotypic specimen collected more recently in 2012 (KUHE 54550, data also in Table 1) completely lacked the spot on both jaw angles, in spite of the fact that its conspecific status with the other two specimens was confirmed by molecular analysis. Thus the presence of a spot on the jaw angle is not a stable character in *I. biangularis*. This suggests the possible occurrance of intraspecific variation in the spot on the jaw angle also in the present new species. Even so, correct identification of the new species can be efficiently made by the other characteristics described above.

External characteristics like spots, markings, and stripes have been regarded as taxonomically important in the striped species of *Ichthyophis* (e.g., Taylor, 1968), which are otherwise very similar in morphology. Furthermore, species description has usually been made based on a small number of specimens. Thus we need to reevaluate the taxonomic utility of the characteristics by examining sufficient numbers of additional specimens.

Mt. Kinabalu, the highest mountain in Southeast Asia, is well known for its rich amphibian fauna with the known species numbering at least 80 (Malkmus et al., 2002; Nishikawa et al., 2012c). Description of the present new species *I. pauli* (*Ichthyophis* sp. 4 in Nishikawa et al., 2012a) resulted in the known presence of a total of three caecilian species from Mt. Kinabalu. Of these, *Ichthyophis lakimi* (*Ichthyophis* sp. 3 in Nishikawa et al., 2012a) is distributed at 960 m asl on the northwestern slope (Sg. Wariu) and at 580 m (Sg. Mamut) on the southeastern slope of the mountain, while the present new species and Ichthyophis cf. asplenius (as Caudacaecilia sp. 1 in Nishikawa et al., 2012a) occur sympatrically at ca. 550–600 m on the southeastern slope (Sg. Kipungit I). However, Malkmus et al. (2002) recorded an unstriped species I. monochrous from Sg. Kipungit (I or II, not mentioned), but the species is most probably I. lakimi, and therefore, it is probable that the three species occur sympatrically at low altitude on the southeastern slope of Mt. Kinabalu. If this is the case, the number of sympatric Ichthyophis species on Mt. Kinabalu equals that of Kubah National Park, Kuching, Sarawak (Nishikawa et al., 2012a), and is the highest among known localities of the genus.

Nishikawa et al. (2012c) reported the large size of larval *I. lakimi*, which they attributed to long larval life. They further surmised that such a life history is probably related to the cool montane habitats of the species on Mt. Kinabalu. In contrast, we have never collected any larvae of the present new species or of *Ichthyophis* cf. *asplenius*, in spite of our intensive field survey of habitats similar to those where we found larval *I. lakimi*. There might be subtle ecological differences in larval habitat and/or life history among these sympatric species on Mt. Kinabalu.

For striped caecilians, Nishikawa et al. (2012a) reported four species of striped Ichthyophis, two lineages of Ichthyophis cf. asplenius, Ichthyophis cf. nigroflavus, and the one corresponding to the present new species, from Sabah. Additionally, Inger (1966) reported a striped species, I. glutinosus, from Ranau and Kinabatangan districts in Sabah. However, I. glutinosus is now known to be restricted to Sri Lanka, and the specimens from Sabah should represent a species different from I. glutinosus. Unfortunately, we cannot at present determine to which species of Nishikawa et al. (2012a) Inger's (1966) species corresponds, but it is certain that striped Ichthyophis species are far more diverse than was formerly considered. Compared with the rich anuran fauna, which is still expected to increase (Matsui, 2006), caecilian

diversity in Sabah is doubtlessly much smaller. Even so, its diversity remains much less completely surveyed than in anurans because of the greater difficulty in studying this group of animals that are fossorial in habits and are extremely similar in morphology.

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APPENDIX 1

Specimens examined (DWNP: Department of Wildlife and National Parks, Malaysia; FMNH: Field Museum of Natural History; USNM: National Museum of Natural History, Smithsonian Institution; VNMN: Vietnam National Museum of Nature; ZISP: Zoological Institute, Russian Academy of Sciences, St. Petersburg)

Ichthyophis bannanicus: KUHE 42464-67 (topotypes) from Mengla, Yunnan, China.

I. dulitensis: FMNH 67349 from Lawas, Sarawak, Malaysia.

I. hypocyaneus: KUHE 53313 from Gn. Ledang National Park, Johor, Malaysia.

I. kohtaoensis: USNM 72293 (holotype) and KUHE 54567 (topotype) from Ko Tao, Surat Thani, Thailand

I. lakimi: KUHE 38275 (holotype) from Sayap Station, Kota Belud, Sabah, Malaysia.

I. larutensis: KUHE 15460, 54054, 97, 54145 and DWNP 4461 (topotypes) from Larut Hills, Perak, Malaysia.

I. mindanaoensis: FMNH 50957 (paratype) from Davao, Mindanao, The Philippines.

I. nguyenorum: ZISP 10711 (holotype), KUHE 55007, and VNMN 3481 (paratypes) from Kon Plong, Kon Tum, Vietnam.

I. nigroflavus: USNM 129462 (holotype) from Kuala Lumpur, Selangor, Malaysia.

I. paucidentulus: USNM 70671 (holotype) from Kapahiang, Sumatra, Indonesia.

I. paucisulcus: USNM 103565 (holotype) from Siantar, Sumatra, Indonesia.

I. sumatranus: USNM 70667 (paratype) from Kaba Wetan, Sumatra, Indonesia.

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