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On the taxonomic status of the Thai endemic freshwater snake *Parahelicops boonsongi*, with the erection of a new genus (Squamata: Natricidae)

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Abstract

Parahelicops boonsongi Taylor & Elbel, 1958 is known from only three specimens from Thailand. It has been placed either in the genus *Parahelicops* Bourret, 1934, along with *Parahelicops annamensis* Bourret, 1934, or in the genus *Opisthotropis* Günther, 1872. We compared its morphological characters with those of *P. annamensis* and with three other relevant genera, *Opisthotropis*, *Pararhabdophis* Bourret, 1934, and *Paratapinophis* Angel, 1929. *Parahelicops boonsongi* is phenotypically distinct from *Parahelicops annamensis*, *Opisthotropis*, and all other natricine genera. We consequently erect a new genus, *Isanophis* gen. nov., to accommodate *Parahelicops boonsongi*.

Key words: Serpentes, Natricidae, *Parahelicops*, *Parahelicops annamensis*, *Isanophis* gen. nov., *Opisthotropis*, *Pararhabdophis*, *Paratapinophis*

Introduction

Several species of the snake fauna of the Indochinese region, including Thailand, are still known only from their holotype or type series, or at best a handful of specimens. For instance, *Paratapinophis praemaxillaris* Angel, 1929, has been known from two syntypes from northern Laos, and six other specimens from China and Thailand (Mo *et al.* 1984, Murphy *et al.* 2008). Two other natricine species, *Pararhabdophis chapaensis* Bourret, 1934 and *Parahelicops annamensis* Bourret, 1934, were previously also known from their respective holotypes. However, Stuart (2006) described a second specimen of *Parahelicops annamensis*, from Laos. Currently, following intensive fieldwork in northern Vietnam and Laos, both *Parahelicops annamensis* and *Pararhabdophis chapaensis* are known from about 10 specimens each (unpublished data; see Appendix).

Another rare species, *Parahelicops boonsongi* Taylor & Elbel, 1958 was described on the basis of a single specimen from Loei Province in northeastern Thailand. Subsequently, Cox (1995) recorded two additional specimens, also from Loei Province. Taylor & Elbel (1958) referred their new species to the genus *Parahelicops* Bourret, 1934 because of some morphological similarities with *P. annamensis*, such as the single prefrontal. However, the generic status of *Parahelicops* has been controversial nearly since its description. It was established by Bourret (1934b: 170 [separate: p. 6]) for a new species, *Parahelicops annamensis* Bourret, 1934, on the basis of a single specimen with the following characters: 25 subequal maxillary teeth, the last two enlarged (in fact we counted 26+2 teeth on the same specimen); head quite distinct from the neck; eye small with a round pupil; nostrils directed upwards; two internasals, a single prefrontal; elongated body, slightly laterally compressed; dorsal scales keeled, without apical pits, in 15 rows; tail long; subcaudals paired; hypapophyses developed throughout the vertebral column. Bourret (1934b) further commented that this genus was similar to *Opisthotropis* Günther, 1872 but differed by its dentition, its head distinct from the neck and its elongated body.

Since its description in 1934, the systematic position of the genus *Parahelicops* has been debated by several authors. Smith (1943: 334), although recognizing the validity of the characters on which Bourret (1934b) based his description, synonymized *Parahelicops* with the genus *Opisthotropis* Günther, 1872 in extending the definition of this latter one. In contrast, Taylor & Elbel (1958: 1156) did not accept this synonymy and recognized the distinct generic status of *Parahelicops*; these authors placed in this latter genus their new species from northern Thailand, *Parahelicops boonsongi*. This arrangement was followed by Taylor (1965) and Cox (1991). However, most authors have referred this species to as *Opisthotropis boonsongi*, such as Brown & Leviton (1961), Cox (1995), Chan-ard *et al.* (1999), David *et al.* (2011), and Wallach *et al.* (2014). Lastly, Stuart (2006), although recognizing the validity of the genus *Parahelicops*, at least for *P. annamensis*, also suggested a close relationship of *Parahelicops* with *Opisthotropis*.

The availability of a series totalling 13 specimens of *Parahelicops annamensis* made it possible to both define variation in this latter species and establish a detailed comparison between *P. annamensis* and the three available specimens of *P. boonsongi*. Results and systematic implications are presented below. As a consequence the status of *Parahelicops boonsongi* Taylor & Elbel, 1958 is re-evaluated and a new genus is erected to accommodate this species. We also compared this latter species with the genera *Pararhabdophis* Bourret, 1934 and *Paratapinophis* Angel, 1929.

Material and methods

This work is based on external morphological characters and dentition regarded as taxonomically significant in natricid genera such as *Amphiesma* Duméril, Bibron & Duméril, 1854 (see Malnate 1960; Malnate & Underwood 1988; David & Vogel 2010; David *et al.* 2007, 2013) and *Opisthotropis* (see Brown & Leviton 1961; Stuart & Chuaynkern 2007; Ziegler *et al.* 2008; David *et al.* 2011; Yang *et al.* 2011; Teynié *et al.* 2014a). A total of 554 specimens were examined, comprising 15 specimens of *Parahelicops annamensis*, 47 specimens of *Opisthotropis*, 3 specimens of “*Parahelicops*” *boonsongi*, 8 specimens of *Pararhabdophis chapaensis* (plus an unpreserved specimen cited by Teynié *et al.* 2014b), 7 specimens of *Paratapinophis praemaxillaris*, and 474 specimens of 29 species of the genus *Amphiesma* as currently defined. Examined specimens of *Parahelicops annamensis* and of “*Parahelicops*” *boonsongi* are listed under the respective species accounts; specimens of the genera *Amphiesma* are those listed in David & Vogel (2010) and David *et al.* (2007; 2013; 2014) and will not be repeated here. Lastly, examined specimens of *Opisthotropis*, *Pararhabdophis* and of *Paratapinophis* are listed in the Appendix.

Maxillary teeth were counted by dissecting the right maxilla of one specimen and, for other specimens, in removing the exterior gum surfaces of the jaw *in situ*. Dentition data of other species were obtained in the same way (tooth sockets were included in the counts in cases of tooth loss). Measurements, except body and tail lengths, were taken with a slide-calliper to the nearest 0.1 mm; body and tail lengths were measured to the nearest millimetre. The number of ventral scales is counted according to Dowling (1951). The numbers of dorsal scale rows are given at one head length behind head, at midbody (i.e. at the level of the ventral plate corresponding to half of the total ventral number), and at one head length before vent respectively. The terminal scute is not included in the number of subcaudals. Values for symmetric head characters are given in left / right order.

Abbreviations. *Measures and ratios:* HL:head length. SVL:snout-vent length. TaL:tail length. TL:total length. TaL / TL: ratio: tail length / total length.

Meristic characters: DSR: dorsal scale rows. IL:infralabials. SC: subcaudals. SL: supralabials. VEN: ventrals.

Museum abbreviations: AMNH: The American Museum, New York, USA. BMNH: Natural History Museum, London, UK. CAS: California Academy of Sciences, San Francisco, USA. CIB: Chengdu Institute of Biology, Chengdu, People’s Republic of China. FMNH: Field Museum of Natural History, Chicago, USA. IEBR: Institute for Ecology and Biological Resource, Hanoi, Vietnam. MNHN: Muséum National d’Histoire Naturelle, Paris, France. NCSM: North Carolina Science Museum, Raleigh, USA. NMW: Naturhistorisches Museum Wien, Wien, Austria. RMNH: Nationaal Natuurhistorisch Museum (formerly the Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands. ROM: Royal Ontario Museum, Toronto, Canada. SMF: Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt-am-Main, Germany. THNHM: Thailand Natural History Museum, Pathum Thani, Thailand. TNRC: Thai National Reference Collection, National Research Council of Thailand, Bangkok, Thailand. VNMN: Vietnam National Museum of Nature, Hanoi, Vietnam. ZFMK: Zoologisches Forschungsmuseum

Alexander Koenig, Bonn, Germany. ZISP: Zoological Institute, Russian Academy of Science, St. Petersburg, Russia. ZMB: Zoologisches Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany. ZSM: Zoologische Staatssammlung, München, Germany.

Results

Taylor & Elbel (1958) referred their new species to the genus *Parahelicops*, seemingly mainly on the basis of the presence of a single prefrontal scale, but noticed several major morphological differences between *P. boonsongi* and *P. annamensis*. Furthermore, Taylor & Elbel (1958: 1158) were incorrect in stating that *Parahelicops annamensis* has an entire anal plate. However, the availability of additional specimens of *Parahelicops annamensis* shows that “*Parahelicops*” *boonsongi* differs by the following series of characters: (1) body stout in “*Parahelicops*” *boonsongi* vs. elongate in *P. annamensis*, (2) head well distinct from the neck vs. head moderately distinct from the neck, (3) three strongly enlarged posterior maxillary teeth vs. maxillary teeth progressively increasing in size with last two moderately enlarged, (4) nostrils dorsolateral and directed distinctly upwards vs. nostrils piercing obliquely dorsolaterally, (5) eye large, diameter distinctly greater than the distance between its lower margin and the margin of the lip vs. eye moderate in size, (6) dorsal scales strongly keeled throughout the body with a thick median keel vs. moderately keeled at midbody, strongly keeled posteriorly, with a thin median keel, (7) 19 DSR at midbody vs. 15 or 17 rows, (8) 136–140 vs. 158–172 VEN, (9) 60 in a single specimen vs. 116–146 SC, (10) anterior supralabials distinctly higher than long vs. all SL distinctly longer than high, and (11) 2 anterior temporals vs. 1 in all known specimens of *P. annamensis*.

On another side, the holotype and other specimens of “*Parahelicops*” *boonsongi* do not agree with important characters of the definition of the genus *Opisthotropis* as given by, for example, Boulenger (1893), Pope (1935), Bourret (1936), Smith (1943), Brown & Leviton (1961), Stuart & Chuaynkern (2007), Murphy *et al.* (2008), Ziegler *et al.* (2008), David *et al.* (2011), Yang *et al.* (2011), and Teynié *et al.* (2014a). “*Parahelicops*” *boonsongi* differs from all species of *Opisthotropis* by (1) posterior maxillary teeth strongly enlarged vs. maxillary teeth subequal in *Opisthotropis*, (2) head clearly distinct from the neck vs. head barely distinct from the neck, (3) eye large, i.e. distinctly greater than the distance between its lower margin and the margin of the lip, vs. small, i.e. diameter distinctly less than the distance between its lower margin and the margin of the lip, (4) dorsal scales strongly keeled with a thick median longitudinal keel vs. smooth or feebly keeled, and (5) tail rather long, 24% of TL vs. tail short or average, usually below 20% of TL. In contrast, “*Parahelicops*” *boonsongi* and *Opisthotropis* share the following characters: (1) nostrils directed distinctly upwards, (2) prefrontal single, (3) anterior supralabials distinctly higher than long, and (4) dorsal color pattern more or less uniform, or with crossbars.

The differences between *Parahelicops annamensis* and “*Parahelicops*” *boonsongi* are at least as significant as those distinguishing “*Parahelicops*” *boonsongi* from *Opisthotropis*. *Parahelicops boonsongi* differs by a series of at least five characters from all species of the homogeneous genus *Opisthotropis*. Although there is no phylogenetic analysis including all of the relevant taxa, existing data suggest that *Parahelicops* is not a natural group. Given the current poor understanding of evolutionary relationships among natricids in general, we think there is more to gain by emphasizing the phenetic diversity among these snakes than there is in recognizing heterogenous, possibly non-monophyletic, groups. Hence, we propose a new genus for *Parahelicops boonsongi*.

Isanophis gen. nov.

(Fig. 1A–D)

Type species. *Parahelicops boonsongi* Taylor & Elbel, 1958 by present designation.

Diagnosis. A genus of snake of the family Natricidae characterized by (1) posterior maxillary teeth strongly enlarged, (2) nostrils dorsolateral and directed obliquely upwards; (3) eye diameter slightly greater than the eye-nostril distance and distinctly greater than the distance between its lower margin and the margin of the lip, (4) pupil round, (5) dorsal scales strongly keeled with a thick median keel throughout the body, (6) body stout, (7) head strongly distinct from neck, and (8) prefrontal scale single.

Etymology. The generic nomen *Isanophis* is derived from the word “Isan”, the Thai name of the north-eastern

region of Thailand, and from the Greek word *ophis*, meaning “snake”. It describes the limited known range of this genus. This generic nomen is masculine in gender.

We suggest the following common generic names in English / French / German respectively: Isan Keeled Stream Snakes / Isanophides / Isan Gebirgswassernattern.

Contents. This genus contains a single species, *Isanophis boonsongi* (Taylor & Elbel, 1958), currently known only from north-eastern Thailand.

***Isanophis boonsongi* (Taylor & Elbel, 1958) comb. nov.**

(Fig. 1A–D)

Parahelicops boonsongi Taylor & Elbel, 1958: 1156, Fig. 31. **Type locality.** Mt. Phu Nam Lang, 1,780 m, Ban Khok, Na Phung, Dan Sai District, Loei Province, Thailand. **Holotype.** FMNH 135328 (originally EHT-HMS 31707), adult female; collected by Robert E. Elbel, 2 June 1955.

Material examined. Thailand. Loei Province. FMNH 135328 (holotype), see locality above.

Additional material. Specimens cited by Cox (1995) were deposited as TNRC 52-3884, and TNRC 52-3885, both adult, unsexed specimens from Nam San Noi Stream, Phu Ruea District, Loei Province, Thailand, 700 m a.s.l. In spite of extensive searches made by one of us (O.S.G.P.) in August 2014, these specimens could not be traced. Nevertheless, M. J. Cox (pers. comm to PD, July 2012) kindly communicated some morphological characters of these two specimens which were used in the present paper.

Taxonomic comments. This species has been known from only the holotype until Cox (1995) recorded two additional specimens about 40 km east of the type locality. One of the specimens was depicted in Cox *et al.* (1998, 2012). This species is monotypic.

Diagnosis. See above the generic characters plus: (1) large size, up to at least 990 mm; (2) 19–19–17 DSR, all strongly keeled; (3) 29 maxillary teeth in the holotype, the last three distinctly enlarged; (4) a long tail, with a ratio TaL / TL reaching at least 0.24; (5) 136–140 VEN, 60 SC in the holotype; (6) 8–9 SL; (7) 2 anterior temporals; (8) body uniformly dark ochre-brown (dark chestnut brown in life), somewhat paler and more beige on the lower part of the sides (dark reddish-brown); and (9) venter uniformly pale ochre-brown (pale yellowish-brown in life).

Description. Body cylindrical, thick and stout; head elongate, well distinct from the neck, flattened; snout elongate, flat, broadly rounded, approximately 24 % of HL, or 1.1–1.4 times as long as the horizontal diameter of eye; nostrils placed dorsolaterally on the snout and directed obliquely upwards; eye diameter 1.5 times as large as the distance between its lower margin and the margin of the lip, with a round pupil; tail long and tapering.

The maximal total length known is 990 mm (SVL 750 mm; TaL 240 mm; specimen depicted in Cox *et al.* 1998, 2012).

Ratio TaL / TL: 0.242 in the only specimen with a complete tail (same specimen as above; sex unrecorded).

Dentition. 29–30 maxillary teeth, the last three distinctly enlarged, without diastema.

Body scalation. DSR: 19–19–17; scales notched posteriorly, strongly keeled throughout, with a thick keel; 1st DSR weakly keeled anteriorly, distinctly keeled posteriorly.

Scale row reductions (holotype): 19→17 DSR at VEN 78 (left) & 84 (right).

VEN: 136–140 (plus 1 preventral); SC: 60 in the only specimen with a complete tail, all paired; anal plate divided.

Ratio VEN / SC 2.33 (in the only specimen with complete tail). Position of the reduction to 6 scale rows around the tail: 11th SC.

Head scalation. Rostral wider than high, slightly visible from above; nasals subrectangular, elongate, vertically divided, with the posterior part shorter than anterior one; nostril small, oval, piercing in the middle of the nasal; internasals small, triangular, in broad contact, barely longer than the prefrontal, longer than wide, distinctly narrowed forward with an anterior margin about 0.4 times the width of the posterior margin, rounded posteriorly; prefrontal single, rather narrow, about twice as wide as long; frontal hexagonal, shield-like, rather small, 1.5 times longer than wide, about 2.2 times as long as the prefrontal; supraocular 1 / 1, large, subtriangular, longer than wide, nearly twice as wide as internasals; parietals large, much longer than the frontal; loreal scale 1 / 1, trapezoidal, as high as long, in broad contact with the nasal; SL 8 or 9, the first five higher than long; 1st, 2nd and 3rd SL small and short, in contact with the nasal, 3rd and 4th SL in contact with the loreal, SL 3–4, 4–5 or 4–6 entering orbit, 6th and 7th or 7th and 8th SL largest; 1 or 2 small suboculars usually present above SL 6; preoculars 1 / 1 (2 specimens) or 2 / 2



FIGURE 1. *Isanophis boonsongi* new comb., preserved holotype (FMNH 135328). From top to bottom: Dorsal view - Ventral view - Lateral view of the head and neck, left side. Photographs by Patrick David.

(1 specimen); postoculars 2–4, small; temporals 2+3, anterior ones larger; IL 10 / 10 in all known specimens, IL 1–5 in contact with anterior chin shields, 6th IL largest; 1 pair of posterior chin shields much longer than anterior ones, narrowly divided anteriorly.

Coloration and pattern. The upper surface of the body is uniformly dark ochre-brown (dark chestnut brown in life), possibly with some very faint, irregular, darker areas, progressively paler and more reddish-beige on the lower part of the sides (dark reddish-brown in life), especially on the 1st and 2nd DSR. Tail as the body, paler on its lower sides.

Head dark ochre-brown (dark olive-brown in life), paler on the side of the snout and anterior SL (yellowish-brown); posterior supralabials pale greyish-yellow (yellow in life), contrasting abruptly with the upper head surface; IL, chin and throat uniformly pale ochre-brown (pale yellowish-brown), brighter yellow on IL and sides of the throat. Iris black.

Venter uniformly pale ochre-brown (pale yellowish-brown in life). Under surface of tail as the venter, irregularly mottled with dark greyish-brown.

Hemipenes. Unknown.

Sexual dimorphism. Unknown.

Distribution. Thailand. *Isanophis boonsongi* is known only from Dan Sai District and Phu Ruea [or Phu Rua] District, Loei Province. Based on the distributions of other species (e.g., *Paratapinophis praemaxillaris* Angel, 1929), we think it is likely to occur in north-western Laos.

Biology. This species has been recorded from 700 m up to 1,780 m a.s.l. Specimens mentioned by Cox (1995) were taken from a mountain stream.

Recognition of *Isanophis* requires a redefinition of *Parahelicops*, which is currently monotypic:

***Parahelicops* Bourret, 1934**

Parahelicops Bourret, 1934b: 170 [separate: p. 6].—**Type species.** *Parahelicops annamensis* Bourret, 1934 by monotypy.

Diagnosis. A genus of medium-sized snakes of the family Natricidae characterized by (1) body elongate, (2) head moderately distinct from the neck, (3) eye moderate in size with a round pupil, (4) maxillary teeth progressively increasing in size in a continuous series, last 2 moderately enlarged, not separated from anterior teeth by a diastema, (5) nostrils piercing distinctly dorsolaterally, (6) upper head scales complete as for typical colubroids but prefrontal single in most specimens, (7) internasals distinctly narrowed anteriorly, (8) all SL distinctly longer than high, (9) dorsal scales in 15 or 17 rows at midbody, moderately keeled at midbody, strongly keeled posteriorly, especially before vent, (10) caudal scales around the base of the tail very strongly keeled, (11) more than 110 SC, paired, (12) hemipenes short, thin, single, and spinose.

Although *Parahelicops annamensis* usually has a single prefrontal, as in most species of *Opisthotropis*, it differs from this latter genus, as defined above, by (1) maxillary teeth enlarged vs. subequal teeth in *Opisthotropis*, (2) tail long vs. rather short or average in *Opisthotropis* (see the descriptions), (3) head moderately distinct from the neck vs. barely distinct in *Opisthotropis*, (4) eye large vs. small in *Opisthotropis*, (5) nostrils directed dorsolaterally vs. directed upwards in *Opisthotropis*, (6) SL much longer than high vs. distinctly higher than long in *Opisthotropis*, and (7) dorsal pattern with two rows of large rusty blotches, vs. more or less uniform, or with crossbars in species of *Opisthotropis*.

Contents As currently defined, the genus *Parahelicops* includes only a single species, *Parahelicops annamensis* Bourret, 1934.

***Parahelicops annamensis* Bourret, 1934**

(Fig. 3A–D, 4A–C)

Parahelicops annamensis Bourret, 1934b: 170, Fig. 2. **Type locality.** “Bana, station d’altitude située à 1500 m d’altitude au bord de la Baie de Tourane”, now Ba Na Nature Reserve, Da Nang City, Vietnam. **Holotype.** MNHN 1938.0117, adult male; collected by René Bourret, 1934.

Material examined (15 specimens). **Vietnam.** Ha Tinh Province. AMNH 147129, Po Mu forest (18°20'26"N, 105°14'13"E), Rao An, Huong Son District, elev. 870 m; ZISP NLO-2478, Rao An, elev. 300 m. Quang Binh Province. ZFMK 86457, ZISP NLO-2714, IEBR A.2013.16–17, Phong Nha - Ke Bang National Park, Hoa Son Commune, Minh Hoa District, 17°42.654'N, 105°52.708'E, elev. 527 m. Quang Tri Province. ZISP NLO-3257, Ban Cup, Huong Hoa District, 16°57.434'N, 106°35.329'E elev. 490 m. Thua Thien-Hue Province. ZFMK 83513, Bach Ma National Park; ZISP NLO-2790, Bach Ma National Park, elev. 1,350 m. Da Nang City. MNHN 1938.0117 (holotype of *Parahelicops annamensis*), "Bana", now Ba Na Nature Reserve, elev. 1,500 m; ZISP NLO-2831, Ba Na Nature Reserve, elev. 1,400 m. Kon Tum Province. IEBR 371, ZISP NLO-3435, Mang Canh village (14°41'950N, 108°14'642E), Kon Plong District, elev. 1,200–1,250 m. **Laos.** Xékong Province. FMNH 258637, Xe Sap National Biodiversity Conservation Area, 16°04'10"N-106°58'45"E, Kaleum District, elev. 1,280–1,500 m; NCSM 78632, Phou Ajol, 15.68516°N-107°1981°E, Dakchung District, elev. 1,450 m.

Taxonomic comments. For a long time, this species has been known from only the holotype collected in central Vietnam. The second known specimen, and first recorded from Laos, was described by Stuart (2006). Subsequently, more specimens became available, especially from central Vietnam. This species is monotypic.

Diagnosis. A species of the genus *Parahelicops* characterized by the combination of (1) body elongate in males and females; (2) tail long with a ratio TaL / TL at least equal to 0.30, (3) maxillary teeth 28–34, the last two moderately enlarged; (4) DSR 15 or 17 at midbody, moderately keeled at midbody, strongly keeled posteriorly, usually smooth on the 1st dorsal scale row; (5) scales around the base of the tail very strongly keeled; (6) background colour chestnut brown, dark brown or dark greyish-brown; (7) dorsal pattern with isolate, bright orange or rusty-red blotches (cream or yellowish-ochre in preservative), usually horizontally elongate or vertically elongate as crossbars anteriorly, then becoming irregular, broken spots posteriorly; (8) postocular streak short, narrow, oblique, reaching the neck behind the corner of the mouth; (9) a broad, oblique and elongate orange or rusty blotch (cream or yellowish-ochre in preservative) present on the nape; (10) SL dark as the upper head surface, without defined spots or blotches, (11) venter pale in its central half with outer tips of ventral scales very dark; (12) eye moderate, 1.2–1.4 times the distance between the lower margins of eye and of lip; (13) VEN 158–172, SC 116–146, paired; (14) internasals narrowed anteriorly; (15) SL 8 or 9; (16) prefrontal scale often single; and (17) anterior temporal single.

With its typical dorsal and ventral patterns and its long tail, *Parahelicops annamensis* cannot be confused with any species of the genera *Opisthotropis*, *Paratapinophis*, *Amphiesma* and *Rhabdophis* recorded from Vietnam and Laos. It is however much similar with *Pararhabdophis chapaensis* Bourret, 1934 (see below). It can be distinguished from this latter species by its pale venter, at least in its central area, vs. the venter entirely black in *Pararhabdophis*.

In collections, specimens of *Parahelicops annamensis* have been misidentified as *Amphiesma modestum* (Günther, 1875), an Indo-Himalayan species unknown east of Myanmar (our data, in prep.). Nevertheless, *A. modestum* has 19 DSR at midbody, 143–163 VEN, scales in the region of the base of the tail feebly keeled, and an ochre or pale brown venter.

Description. The body is moderately robust but elongate (more gracile in males) and cylindrical; head oval, rather short, moderately distinct from the rather thick neck, flattened anteriorly; snout long, 2.0–2.2 times as long as horizontal diameter of eye, flat, blunt or slightly rounded seen from above, blunt and subrectangular seen in profile, no canthus rostralis; nostril directed distinctly dorsolaterally, small, rounded, piercing in the middle of the divided nasal; eye moderately sized or small, diameter about 1.2–1.4 times the distance between the lower margins of eye and of lip, with a round pupil; tail long, thin and tapering.

The maximum known length is 796 mm for a male (SVL 528 mm, TaL 268 mm; specimen ZISP NLO-3257). The longest known female is 685 mm long (SVL 465 mm, TaL 220 mm; ZISP NLO-2831).

Ratio TaL / TL 0.297–0.337, without clear sexual dimorphism (6 males: 0.301–0.337; 3 females: 0.297–0.321).

Maxillary teeth. Total of 28–34 maxillary teeth, gradually enlarged in a continuous series, the last 2 moderately enlarged, without diastema.

Body scalation. DSR 17–19 – 15–17 – 15–17; dorsal scales rhomboedric, normal in shape, distinctly keeled on 2nd–10th rows, moderately on the anterior part of the body, strongly posteriorly, very strongly in the region of the vent and on the base of the tail; scales smooth on 1st row or feebly keeled posteriorly; VEN 158–172 (plus 1 or 2 preventrals), with a sexual dimorphism (see below); SC 116–146, all paired, with a sexual dimorphism (see below); anal plate divided; ratio VEN / SC 1.18–1.43.

The number of DSR is quite variable in this species. In the 13 available specimens, the formulae are: 18–15–15 (1 specimen), 19–15–15 (3), 17–17–17 (1), 18–17–15 (2), 18–17–17 (2), and 19–17–17 (4).

Scale row reductions: first reduction (18 or 19→17) at VEN 56–89; second reduction (17→15) at VEN 98–128.

Head scalation. Complement of upper head scales complete but with prefrontals variable, including 2 internasals, 1 or 2 prefrontals (see below), 2 supraoculars, 1 frontal, and 2 parietals. Rostral hexagonal, wider than high, barely visible from above; nasal subrectangular, elongate, vertically divided by a furrow, with the fore and hind parts of similar size, altogether about 1.3–1.5 times longer than high; internasals distinctly subtriangular, elongate, in broad contact with each other, 1.2–1.4 times longer than wide, distinctly narrowed anteriorly with anterior margin about 0.4–0.5 times the width of the posterior margin; prefrontal 1 (in 10 / 13 specimens), wide and shield-like, or 2 (3 / 13), large, subrectangular, broader than long, in both cases 0.9–1.2 times as long as internasals, in broad contact with loreal; supraocular 1 / 1, entire, subtriangular, rather broad, 1.8–2.2 times longer than wide, slightly narrower than internasals, about 0.5 times as wide as frontal; frontal hexagonal, shield-like, rather wide but short, its apex directed posteriorly, 1.0–1.2 times longer than wide, 1.7–2.0 times longer than prefrontals; parietals large, long and wide, 1.7–2.1 times longer than frontal and in contact for a length 1.2 times as great as the frontal length; loreal scale 1 / 1, large, rectangular, elongate, 1.5–1.8 times longer than high, in broad contact with the nasal; SL 8 or 9, 1st as long as high, 2nd–5th longer than high, other SL as long as high, 1st–2nd SL, small and short or, exceptionally 1st–3rd SL, in contact with nasal, 2nd–3rd or 3rd–4th SL in large contact with the loreal, 4th–5th SL, or exceptionally solely 4th, only 5th, 4th–6th or 5th–6th SL, entering orbit; 6th–7th or 7th–8th SL largest; preoculars 2 / 2 in all known specimens, subequal; postoculars 2 or rarely 3, small, the upper one largest; anterior temporal 1, narrow and elongate, in all known specimens with complete temporal formulae as 1+1+2 or rarely 1+2+2 or 1+3 (this latter met only in the type); IL 10 (rarely 8 or 9), 1st pair in contact behind the mental, 1st–5th IL in contact with anterior chin shields, 5th IL largest; mental triangular; anterior pair of chin shields equal to or slightly longer than posterior shields.

Coloration and pattern. In preservative, the dorsal and lateral surfaces of body are dark chestnut brown, dark brown or dark greyish-brown, darker above than on the sides, either nearly uniform or, more usually, profusely variegated with darker brown, diffuse blotches, larger on the upper parts of the sides than on the back; in 3 of 15 specimens, a faint dorsolateral stripe is present on 5th–7th dorsal rows, barely paler than the background color and poorly distinct; on each side, a series of about 50 to 70 distinct dorsolateral blotches, cream, ochre, yellowish-brown, pinkish-brown or orange-brown on 5th–7th dorsal rows, separated from each other by 2–3 dorsal scales, forming a discontinuous dorsolateral stripe; these blotches are large, thick and horizontally elongate on the fore part of the body from behind the neck to the first anterior quarter to third of the body, or, often, vertically elongate on a short part of the body up to forming a few vertical, more or less narrow crossbars reaching downwards to the level of the 3rd scale row; progressively these blotches are reduced to irregular or broken spots, or are absent posteriorly; a short, cream ventrolateral stripe on the anterior part of the body, up to 20th to 30th VEN. Upper surface of tail as the body, either uniform or with only a few pale dots.

Head dark chestnut-brown, more or less variegated above with ochre yellow or pale yellowish-brown, often with numerous minute scattered dark dots; an ochre yellow or pale yellowish-brown sagittal line present, but faint, or absent; last three posterior supralabials irregularly and faintly edged with ochre-yellow anteriorly; a short, narrow or relatively broad, oblique, more or less distinct postocular streak on anterior and lower posterior temporals, and on top of 8th and 9th SL, reaching the neck behind the corner of the mouth and continuing as a large, cream or yellowish-ochre oblique, elongate blotch on the nape, connecting the posterior end of the postocular streak with the first dorsolateral blotch. The throat, chin and IL are cream or pale yellowish-ochre, more or less heavily spotted with dark brown spots; IL heavily marbled or spotted with dark brown. Iris deep black in life.

Venter cream, pale yellowish-ochre or light brown, with outer tips of ventral scales dark brown or dark greyish-brown, progressively widening posteriorly; often some irregular dark spots scattered on the pale part. Under surface of tail as the venter but the pale central part narrower than the dark outer parts anteriorly, the tail becoming progressively entirely dark below.

It should be noted that the holotype has a venter much darker than other specimens (perhaps due to an inadequate preservation), but the bicolour ventral pattern typical of this species is nevertheless present.

In life, the background coloration is bright chestnut-brown or dark purplish-brown; the dorsolateral blotches

are bright orange or rusty-brown, a colour often still seen in recently preserved specimens. The postocular streak is yellow turning to orange on the neck. Lastly, the pale area of the venter is orange or reddish-pink.

Hemipenis. In situ, it is short, reaching the level of the 8th SC, rather thin, and single although forked at its tips, the tips stemming from the face bearing the sulcus. The organ is calyculate on its lower proximal part, along about 1/6 of the organ length, then covered with medium-sized spines; some spines are larger and hooked near the limit between the calyculate and the spinose areas and on the most proximal part, shorter but more densely spaced towards the distal area. The sulcus is not conspicuous and mostly straight.

Sexual dimorphism. It is expressed in (1) the difference in the number of VEN: 7 males: 168–172 ($x = 169.7$, $s = 1.7$); 6 females: 158–167 ($x = 164.2$, $s = 3.4$); (2) difference in the number of SC: 6 males: 126–146 ($x = 138.7$, $s = 6.9$); 3 females: 116–126 ($x = 119.7$, $s = 5.5$); and (3) difference in the position (counted in SC) to the reduction from 6 to 4 scale rows around the tail of SC: males: 12th–16th SC; females: 4th–7th SC.

Distribution (Fig. 2). **Vietnam.** This species is known from the centre of the country, in the following provinces (from north to south): Ha Tinh (Huong Son District); Quang Binh (Phong Nha - Ke Bang National Park, Minh Hoa District); Quang Tri (Huong Hoa District); Thua Thien-Hue (Bach Ma National Park); Da Nang City (Ba Na Nature Reserve), and Kon Tum (Kon Plong District, Ngoc Linh Nature Reserve). – **Laos.** Known only from the southwest of the country: Xékong Province (Xe Sap National Biodiversity Conservation Area, Kaleum District; Phou Ajol, Dakchung District).

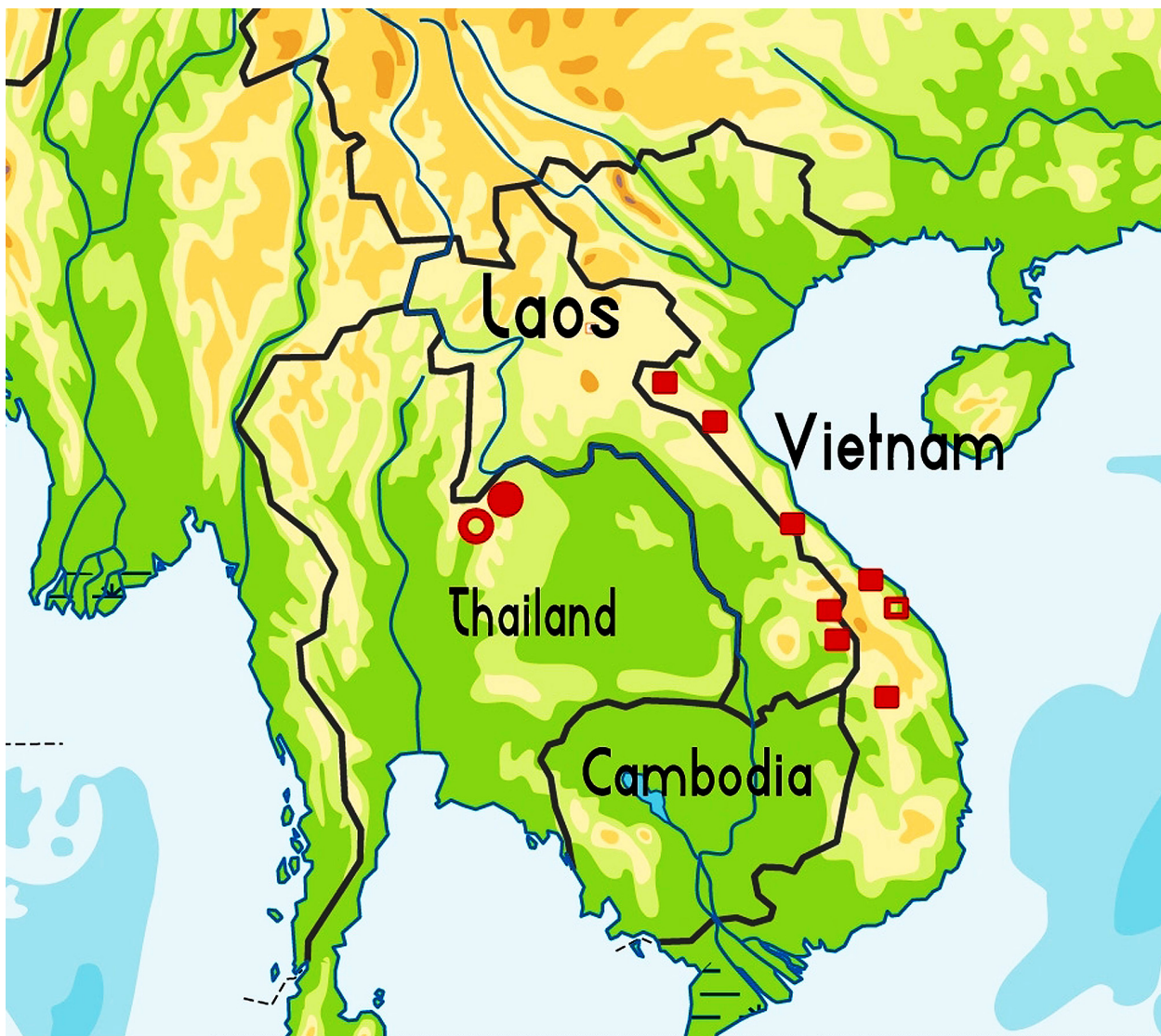


FIGURE 2. Map showing the localities of *Isanophis boonsongi* (solid circle, type locality as a hollow circle) and *Parahelicops annamensis* (solid squares, type locality as a hollow square).



FIGURE 3. *Parahelicops annamensis*, preserved holotype (MNHN 1938.0117). From top to bottom: Dorsal view - Ventral view - Lateral view of the head and neck, left side - Dorsal view of head. Photographs by Patrick David.



FIGURE 4. *Parahelicops annamensis*, (IEBR A.2013.16; male) alive, Phong Nha - Ke Bang National Park, Hoa Son Commune, Minh Hoa District, Quang Binh Province, Vietnam. Photograph by Truong Quang Nguyen.

Biology. Stuart (2006) provided the first data on the ecology of this species. *Parahelicops annamensis* inhabits regions covered with tropical wet evergreen forest and subtropical montane evergreen forests between about 300 and 1,500 m a.s.l., although most specimens for which we have data were collected between 1,200 and 1,400 m a.s.l. All were collected in primary tropical or montane evergreen forests and in close association with fast-moving, rocky forest streams. This species seems to be mainly nocturnal and aquatic, although one specimen was found on the ground, under a log on the bank of a 4 m wide rocky stream. Specimen ZFMK 86457 was captured in the evening in the leaf litter of a forest stream at 510 m a.s.l., with only the snout tip protruding from the surface of the water. The diet and reproductive habits of *Parahelicops annamensis* are still unknown.

Discussion

Morphological comparison with some other Asian natricid genera. Morphological characters separating *Isanophis* nov. gen. from *Parahelicops* and *Opisthotropis* have been given above in the introduction to results. The main characters allowing an immediate recognition of *Isanophis* are (1) head clearly distinct from neck, (2) posterior maxillary teeth strongly enlarged, and (3) dorsal scales strongly keeled throughout the body with a thick median keel. Characters separating these three genera as well as *Paratapinophis* and *Pararhabdophis*, discussed below, are summarized in Table 1.

TABLE 1.

Characters	<i>Isanophis</i> gen. nov.	<i>Parahelicops</i>	<i>Opisthotropis</i>
Head / neck	Clearly distinct	Moderately distinct	Barely distinct
Position of nostrils	Dorsolateral	Dorsolateral	Dorsal
Direction of nostrils	Obliquely upwards	Dorsolaterally	Upwards
Eye relative size (1)	Large	Moderate or small	Small
Prefrontal	Single	Single or paired	Single
Internasals shape	Narrowed forward	Narrowed forward	Narrowed forward
Anterior temporals	2	1	1 or 2
DSR at midbody	19	15–17	15–19 (23 in <i>O. laui</i>)
DSR keeling	Strongly keeled throughout; thick median keel	Moderately anteriorly, strongly posteriorly; thin median keel	Smooth or moderately keeled, more strongly keeled posteriorly; thin median keel
Posterior maxillary teeth	Last three distinctly enlarged	Last 2 moderately enlarged	Teeth subequal

continued.

Characters	<i>Paratapinophis</i>	<i>Pararhabdophis</i>
Head / neck	Distinct	Distinct
Position of nostrils	Lateral / dorsolateral	Lateral
Direction of nostrils	Slightly dorsolaterally	Slightly dorsolaterally
Eye relative size (1)	Small	Moderate
Prefrontal	Single	Paired
Internasals shape	Narrowed forward	Truncated anteriorly
Anterior temporals	2	2
DSR at midbody	19	17
DSR keeling	Smooth; tuberculate posteriorly	Moderately anteriorly, strongly posteriorly; thin median keel
Posterior maxillary teeth	Last 3 or 4 slightly enlarged	Last 2 or 3 strongly enlarged

(1) Small: horizontal diameter of the eye smaller than the distance between the eye and the lower margin of lip. Moderate: horizontal diameter of the eye 1.0–1.2 times the distance between the eye and the lower margin of lip. Large: horizontal diameter of the eye at least 1.4 times the distance between the eye and the lower margin of lip.

Another poorly known genus found in Thailand is *Paratapinophis* Angel, 1929 (Type species: *Paratapinophis praemaxillaris* Angel, 1929, by monotypy), the position of which has long been controversial. Angel (1929: 76) erected this genus for its sole included species, *P. praemaxillaris* Angel, 1929 (p. 78, Fig. A–D. Type locality: “Xieng-Khouang”, the former city of Xiengkhuang, now near Phonsavan, Xiangkhoang Province, Laos. Syntypes. MNHN 1928.0063, neonate, probably male, and MNHN 1928.0064, neonate, probably female; collected by M. Jean Delacour, December 1925 or January 1926). One of the most salient characters pointed out by Angel to define the new genus was the presence of a short, external process that extends anteriorly the premaxillary bone. Pope (1935) discovered that this process was in fact the neonate’s egg tooth, a temporary “tooth” allowing the snake to cut the shell of its egg; Pope (1935: 164) referred *Paratapinophis* to the synonymy of *Opisthotropis* Günther, 1872, in pointing out, however, that *P. praemaxillaris* differed by some characters from other species of the genus *Opisthotropis*. This position was accepted by Smith (1943) and subsequent authors, at the exception of Deuve (1970) who retained the validity of the genus *Paratapinophis*. Subsequently, other specimens were recorded from northern Thailand (Rasmussen 1982) and China (Yunnan Province; Mo *et al.* 1984) respectively. Eventually, Murphy *et al.* (2008), on the basis of five fresh specimens collected in northern Thailand, redefined the species and presented evidence for recognizing *Paratapinophis* as a genus valid and distinct from *Opisthotropis*.

The genus *Paratapinophis* is diagnosed by (1) body robust, subrectangular in section, with a laterally compressed tail, (2) head distinct from the neck, (3) eye rather small with a round pupil, (4) maxillary teeth progressively increasing in size in a continuous series, last 3 or 4 slightly enlarged, not separated from anterior teeth by a diastema, (5) nostrils piercing slightly dorsolaterally, more laterally than dorsally, (6) upper head scales complement complete as for typical colubroids but prefrontal single, (7) internasals narrowed anteriorly, (8) anterior supralabials distinctly higher than long, (9) 2 parallel pairs of posterior chin shields, (10) 19 DSR at midbody, mostly smooth but with scales of the 3rd–10th rows on the posterior part of body with rows of small tubercles in the middle of the scale in males, smooth throughout in females, (11) caudal scales around the base of the tail not keeled, and (12) anal plate divided.

Paratapinophis is morphologically close to *Opisthotropis* but, according to Pope (1935) and Murphy *et al.* (2008), it differs by (1) the sexually dimorphic ornamentation of dorsal scales, made of a longitudinal row of tubercles on scales of the posterior part of the body in males, vs. smooth in both sexes in all known species of *Opisthotropis*, (2) the presence of two parallel pairs of posterior chin shields vs. 1 pair, (3) head well distinct from the neck vs. barely distinct, (4) fewer maxillary teeth, and (5) a sexually dimorphic pattern, such a dimorphism being unknown in *Opisthotropis*. Furthermore, *Isanophis* differs from *Paratapinophis* by (1) posterior maxillary teeth strongly enlarged vs. slightly enlarged, (2) dorsal scales strongly keeled vs. smooth or with rows of small tubercles posteriorly in males, (3) eye large vs. small, (4) posterior chin shields in 1 pair vs. 2 pairs, and (5) dorsal pattern uniform vs. banded.

Lastly, another genus of Asian Natricidae, *Pararhabdophis* Bourret, 1934, remains poorly known. It was erected by Bourret (1934a: 131 [Separate: p. 3]; type species: *Pararhabdophis chapaensis* Bourret, 1934, by monotypy) for its sole included species, *Pararhabdophis chapaensis* Bourret, 1934, also described on the basis of a single specimen (Bourret 1934a: 131 [Separate: p. 3], Fig. 2. Type locality: “Chapa, province de Laokay (Tonkin), à l’altitude moyenne de 1600 m”, now Sa Pa, Lao Cai Province, Vietnam, ca. 1,600 m elevation; holotype MNHN 1938.0125, adult male; collected by René Bourret). This genus has been consistently considered to be valid (Bourret 1936; Smith 1943; Nguyen & Ho 1996; Nguyen *et al.* 2005, 2009; Wallach *et al.* 2014) but never re-evaluated, possibly because of the lack of additional material.

Pararhabdophis was established on the basis of the following characters: maxillary teeth 32, subequal, of which the last three ones are strongly enlarged, and a small eye with a vertical pupil; other characters included a head well distinct from the neck, 2 internasals and 2 prefrontals, an elongate, slightly laterally compressed body, dorsal scales feebly keeled, without apical pits, in 17 rows, tail long, SC paired and hypapophyses developed throughout along the vertebral column. Smith (1943) accepted the validity of this genus solely on the basis of the vertical pupils of the holotype. Otherwise, Smith stated that he would have placed it in the large genus *Natrix* Laurenti, 1768 as understood at that time. In fact, the diagnosis of the genus has been somewhat biased by Bourret (1934a). The holotype is in bad condition and strongly desiccated. After a careful examination under a powerful incident light, the pupil of the holotype became quite visible. It is indeed elliptic at left but nearly circular at right, where it is much more difficult to see. Most probably, Bourret was misled by the poor condition of his specimen, perhaps found dead on road. We suggest that the desiccation of this specimen may have altered the shape of the eye. All other specimens of our material agree in all points with the holotype but have a round pupil. As a consequence, and on the basis of 9 specimens available to us, we here redefine *Pararhabdophis chapaensis* as follows: (1) body elongate, (2) head clearly distinct from the neck, (3) eye moderate, 1.0–1.2 times the distance between the lower margins of eye and of lip, with a round pupil, (4) maxillary teeth 29–32, progressively increasing in size in a continuous series, last 2 or 3 abruptly and strongly enlarged, not separated from anterior teeth by a diastema, (5) nostrils piercing laterally or slightly dorsolaterally, (6) upper head scales complete as for typical colubroids, with 2 prefrontals, (7) internasals abruptly truncated anteriorly, (8) SL distinctly longer than high, (9) dorsal scales in 17 rows at midbody, distinctly keeled at midbody, strongly keeled posteriorly, especially before vent, (10) supracaudal scales around the base of the tail very strongly keeled, (11) VEN 159–174, (12) SC 90–114, (13) background colour dark brown or blackish-brown, with the dorsal pattern made of more or less elongate cream, pale yellow or pale orange-brown blotches on a faint dorsolateral stripe, (14) an elongate, cream or pale ochre-yellow blotch, or isolated blotches present on the nape, and (15) venter dark, blackish-brown or black, with some paler, more or less faint longitudinal streaks.

Pararhabdophis chapaensis can be confused only with *Parahelicops annamensis*. *P. chapaensis* can be distinguished from the latter by (1) its venter entirely blackish-brown or black vs. pale, at least in its medial

portion, (2) internasals abruptly truncated vs. narrowed anteriorly, and (3) fewer SC, 90–114 vs. 116–146. *Isanophis* differs from *Pararhabdophis* by the following series of characters: (1) body stout in *I. boonsongi* vs. elongate in *P. chapaensis*, (2) nostrils dorsolateral and directed distinctly upwards vs. nostrils piercing laterally or slightly obliquely dorsolaterally, (3) eye large, distinctly larger than the distance between its lower margin and the margin of the lip vs. eye moderate in size, (4) dorsal scales strongly keeled throughout the body with a thick median keel vs. distinctly to strongly keeled posteriorly but with a thin median keel, (5) dorsal scale in 19 rows at midbody vs. 17 rows, (6) VEN 136–140 vs. 159–174, (7) SC 60 in a single specimen vs. 90–114, (8) anterior SL distinctly higher than long vs. all SL distinctly longer than high, (9) anterior temporals 2 vs. 1 in all known specimens of *P. chapaensis*, and (10) a different color pattern (see in respective diagnoses).

Lastly, *Isanophis* differs from other genera of Natricidae present in the Indochinese Peninsula and Thailand, such as *Xenochrophis* Günther, 1864, *Sinonatrix* Rossman & Eberle, 1977, *Rhabdophis* Fitzinger, 1843, and *Amphiesma* Duméril, Bibron & Duméril, 1854 by the very peculiar morphology of the keels of dorsal scales and its single prefrontal scale. Besides these distinctive characters, it differs from *Xenochrophis* and *Sinonatrix* and most species of *Amphiesma* by strongly enlarged posterior maxillary teeth; it differs from *Amphiesma* and *Rhabdophis* by the dorsolateral position of its nostrils, directed obliquely upwards vs. laterally directed.

Conclusion

On the basis of its morphological characters, *Isanophis boonsongi* new comb. does not match any genus of Natricidae, although most similarities seem to be with *Opisthotropis*. However, referring *I. boonsongi* to this latter genus, otherwise very homogeneous, would require to a significant expansion of its definition. In the absence of a phylogenetic hypothesis including all the relevant taxa, we think there is more to gain by erecting a new genus rather than expanding the definitions of existing genera.

The relationships of Asian Natricidae remain unclear. For example, several characters found in *Parahelicops*, i.e. the enlarged posterior maxillary teeth, the average eye with a round pupil, the dorsolateral nostrils, the distinctly keeled dorsal scales, the long, keeled tail, supralabials longer than high and the general blotched pattern on a dark brown or black background, are typical of the group of *Amphiesma venningi* (Wall, 1910), as defined by Malnate (1960), a group of largely Indo-Himalayan species to which we refer *Amphiesma taronense* (Smith, 1940), *A. venningi* (Wall, 1910), *A. deschauenseei* (Taylor, 1934), *A. groundwateri* (Smith, 1922), and other taxa that need to be described or resurrected at full species status (David *et al.*, in prep). Nevertheless, preliminary molecular data (unpublished) suggest that *Parahelicops* forms a clade distinct from the one containing the genus *Amphiesma* as currently conceived. On this basis, we retain the validity of the genus *Parahelicops* Bourret, 1934 but its morphological affinities are definitely more with the genus *Amphiesma* than with *Opisthotropis*.

The case is rather similar for *Pararhabdophis*. Its posterior maxillary teeth are strongly enlarged, a character found in the genera *Rhabdophis* and some species of the genus *Amphiesma*, such as *Amphiesma stolatum* (Duméril, Bibron & Duméril, 1854), and in the Himalayan species *Amphiesma platyceps* (Blyth, 1854). The overall morphology and scalation of the head, and the scalation of the body do not agree with characters that define *Rhabdophis*. Rather, they fall within the variation met in the genus *Amphiesma* as currently conceived.

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APPENDIX. List of additional examined specimens.

- Opisthotropis atra* (n = 1). “West Africa”. BMNH 1946.1.15.31 (holotype), no locality.
- Opisthotropis andersoni* (n = 1). China. FMNH 71136, “Hong Kong, Hong Kong Island, 950 ft.”
- Opisthotropis balteata* (n = 5). Vietnam. Bac Giang Province. IEBR A.0861, ZFMK 94229, Tay Yen Tu Nature Reserve, Son Dong District. North Vietnam. NMW 22979, “Tonkin”.—Cambodia. NMW 22978:1–2, no locality.
- Opisthotropis cucae* (n = 1). Vietnam. Kon Tum Province. IEBR A.0924 (holotype), Chu Mom Ray National Park, Sa Thay District, (14°26.227'N, 107°43.268'E), 740 m.
- Opisthotropis daovantieni* (n = 3). Vietnam. Gai Lai Province. FMNH 252009 (holotype), Buon Luoi village, 14°20'N 108°36'E, Kannack town, 20 km to the northwest from Kannack, Annam mountains, Ankhe District, 700–750m; FMNH 252008 (paratype), Buon Luoi village, Kannack town, 14°20'N–108°36'E, 20 km to the northwest from Kannack, Annam

mountains, Anke District, 700–750 m. Kon Tum Province. ZISP 26073, Kon Plong Forest, Xa Hieu, Kon Plong District (14°41.447'N–108°22.376'E, 1,170 m).

Opisthotropis durandi (n = 2). **Laos**. Louangphabang Province. MNHN 2013.1001 (holotype), vicinity of Muang Ngoi (20°42'10"N, 102°41'21"E), Ngoi District; IEBR A.2013.26 (paratype), Mork or Mok Waterfall (20°39'N, 102°42'E), at about 4 km east of Ban Sopkhong or Ban Sop Keng, a village on Nam Ou River located between Nuang Kiea and Muang Ngoi, Ngoi District.

Opisthotropis guangxiensis (n = 3). **China**. Guangxi Province. CIB 9972–4, Dayao Shan (Mt. Dayao).

Opisthotropis jacobi (n = 7). **Vietnam**. Lao Cai Province. IEBR 2910, Sa Pa; MNHN 1933.0010, MNHN 1935.0083, MNHN 1938.0126–0127, “Chapa, Tonkin”, now Sa Pa. Vinh Phuc Province. MNHN 1935.0457, CAS-SU 9147, Tam Dao.

Opisthotropis kuantunensis (n = 1). **China**. Guangdong Province. ZSM 85/1941, “Kuantung”, 2,000 m.

Opisthotropis lateralis (n = 5). **Vietnam**. Bac Giang Province. IEBR 3644–3645, Tay Yen Tu Nature Reserve, Son Dong District. Quang Nam Province. IEBR 83, Tra My, Tra Don Commune, Mt. Ngoc Linh.—**China**. Guangxi Province. RMNH.REBA 5886, “Lo Shiang, Yao Shan”, now Luoxiang, Dayao Shan; ZMB 70758 (holotype of *Tapinophis shini* Mell, 1930), Loshiang or Chinsi Le.

Opisthotropis latouchii (n = 11). **China**. Fujian Province. FMNH 24858, FMNH 24860, FMNH 24862, FMNH 24863–65, FMNH 24867, “Ch’ungan Hsien”, now Chongan County. Guangdong Province. ZSM 901/37, “Kuantung”, 2000 m. Jiangxi Province. NMW 26028: 1–2, “Pingshiang, Kiangsi Province”, now Pingxiang; SMF 19378, “Ping-Shiang”, now Pingxiang.

Opisthotropis multicincta (n = 1). **China**. Guangxi Province. RMNH 5885, “Lo-Shiang, Jao Shan”, now Luoxiang, Dayao Shan.

Opisthotropis rugosa (n = 1). **Indonesia**. Sumatra. Province of Sumatera Barat. RMNH 4330 (Holotype), Kayutanam.

Opisthotropis spenceri (n = 2). **Thailand**. Lampang Province. BMNH 1946.1.15.31, BMNH 1965.640, “Muang Ngow, N. Siam”, at present Ngao.

Opisthotropis tamdaoensis (n = 1). **Vietnam**. Vinh Phuc Province. VNUH 010606, Tam Dao, ca. 195 m a.s.l.

Opisthotropis typica (n = 2). **Federation of Malaysia**. Borneo. State of Sabah. MNHN 1889.0216, “Mt. Kina-Balu, Alt. 4175 m (Nord Borneo)”, Mt. Kinabalu.—**The Philippines**. Palawan Island. CAS 28676, about 7 km NW of Iwahig.

Pararhabdophis chapaensis (n = 9). **Vietnam**. Lao Cai Province. IEBR 2907–2909, Cat Cat, I Ninh Ho, Sa Pa; MNHN 1938.0125 (holotype of *Pararhabdophis chapaensis*), Sa Pa, ca. 1600 m a.s.l.; ROM 38195, Lao Cai.—Cao Bang Province. ROM 28636, Cao Bang.—**Laos**. Houaphan Province. NCSM 77924, Phou Louey National Protected Area, near Tad Loi Waterfall, 20.23253°N–103.2108°E, Viengthong District, elev. 1,186 m; 1 non preserved specimen, near Viengthong, Viengthong District, elev. 1,050m. – Louangphabang Province. NCSM 77925, Hoay Tala 1, branch of the Nam Madao, 19.30189°N–102.5736°E, Phoukhoume District, elev. 1,269 m.

Paratapinophis praemaxillaris (n = 7). **Laos**. Xiangkhoang Province. MNHN 1928.0063–0064, “Xiengkhouang”.—**Thailand**. Nan Province. FMNH 271443, FMNH 271445, THNHM 15363–365 (formerly FMNH 271444, FMNH 271446 & FMNH 271447, respectively), Wang Pian Waterfalls, Nan River (about 19°31'N–101°05'11.8"E), Huia Gon Subdistrict, Chaloeprakiat District, 475 m.