A new species of the Southeast Asian genus *Opisthotropis* (Serpentes: Colubridae: Natricinae) from western Hunan, China

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**ABSTRACT**

A new species of natricine snake of the Southeast Asian genus *Opisthotropis* Günther, 1872 is described from western Hunan Province of China based on both mitochondrial DNA and morphological data. The new species is morphologically most similar and genetically most closely related to *O*. *cheni* Zhao, 1999 and *O*. *latouchii* (Boulenger, 1899), but possesses considerable genetic divergence (p-distance 5.1%–16.7%) and can be differentiated from all other congeners by a combination of the following morphological characters: (1) body size large (total length 514–586 mm) and strongly built; (2) dorsal scale rows 17 throughout, feebly keeled anteriorly and moderately keeled posteriorly; (3) ventral scales 147–152, subcaudal scales 54–62; (4) preocular absent, loreal elongated and touching orbit; (5) supralabials 8–9, fifth and sixth entering orbit; (6) anterior temporals short, length 1.74–2.04 times longer than width; (7) maxillary teeth subequal, 28–30; (8) dorsal surface of head with distinct irregular yellow stripes and markings edged with ochre; (9) body with clear black and yellow longitudinal streaks, partly fused to several lighter patches or thicker stripes anteriorly; and (10) venter pale yellow, with asymmetric blackish speckles along outer margin. We present an updated diagnostic key to all members of the genus *Opisthotropis*, and recommendations on the ecological study for the group are provided.

**Keywords:** Distribution; Natricinae; Natural history; Taxonomy; *Opisthotropis*; *Opisthotropis zhaoermii* sp. nov.

**INTRODUCTION**

The snakes of the family Colubridae represent the most specious group of extant Serpentes (Figuerola et al., 2016; Pyron et al., 2013). Within this diverse group, keelback snakes of the subfamily Natricinae exhibit adaptations to aquatic habitats to different degrees, and include aquatic specialists of the genus *Opisthotropis* Günther, 1872 (Guo et al., 2014; Zhao et al., 1998). The generic nomenclature of *Opisthotropis* means “keeled backwards”, based on its distinct morphological adaptations for an aquatic lifestyle (Günther, 1872; Ziegler et al., 2008). The natricine genus *Opisthotropis* is distributed across southern China and Southeast Asia, and inhabits flowing streams or waterfalls in low to moderate altitude forested areas (Pope, 1935; Zhao, 2006). Currently, the genus *Opisthotropis* includes 22 species, with 12 currently recorded in China: *O*. *andersonii* (Boulenger, 1888), *O*. *balteata* (Cope, 1895), *O*. *latouchii* (Boulenger, 1899), *O*. *lateralis* Boulenger, 1903, *O*. *maxwellii* Boulenger, 1914, *O*. *kuatunensis* Boulenger, 1938, *O*. *maxwellii* Boulenger, 1914, *O*. *kuatunensis* Boulenger, 1938, *O*. *guangxiensis* Zhao, Jiang and Huang, 2006.

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Despite the remarkable ecological adaptations and rich diversity of *Opisthotropis*, little attention has been given to its taxonomy until recently (Chuaynkern et al., 2014; David et al., 2011; Iskandar & Kamsi, 2009; Murphy et al., 2008; Wang et al., 2017). This is particularly true for congeners in southern China. Prior to 2010, no modern taxonomic work on Chinese *Opisthotropis* had been conducted, and our understandings of the genus were based on study that dated back to the nineteenth century (Pope, 1935; Smith, 1943; Taylor, 1965; Zhao & Adler, 1993; Zhao et al., 1998; Zheng, 1992). Although a few recent taxonomic works using genetic methods have revealed surprising endemism and cryptic diversity within the genus, these studies have focused on areas around the Fujian-Guangdong Coast Subregion of southern China, with many areas in southern China remaining under-surveyed in regard to *Opisthotropis* diversity (Wang et al., 2017; Yang et al., 2011, 2013). As *Opisthotropis* congeners are ecological specialists with narrow niches and limited dispersal abilities, it is possible that previous records of widespread congeners may represent overlooked distinct and cryptic species (Wang et al., 2017; Zhao et al., 1998; Zhao, 2006).

During field surveys of Hunan Province in 2017, three adult specimens of *Opisthotropis* were collected in western Hunan, China. Detailed morphological comparisons and phylogenetic analyses showed that the western Hunan population of *Opisthotropis* represents a distinct evolutionary lineage that can be diagnosed readily from closely related congeners. Therefore, we describe the Hunan population of *Opisthotropis* as a new species herein.

**MATERIALS AND METHODS**

**Sampling**

Three adult *Opisthotropis* specimens (two females and one male) were collected from Guzhang, western Hunan, China on 22, 23, and 24 August 2017 (Figures 1, 2, 3A, 4A, 6). After each collection, the temperature and pH of the water were measured immediately using a liquid-in-glass thermometer and digital pH meter (calibrated), respectively. After euthanization, liver tissues were taken and preserved in 95% ethanol for DNA extraction, with all specimens preserved in 10% formalin in the field and transferred to 75% ethanol for permanent storage after fieldwork. All vouchedered specimens and tissue samples were deposited in the Museum of Herpetology, Chengdu Institute of Biology (CIB), Chinese Academy of Sciences (CAS).

**MOLECULAR ANALYSES**

**DNA extraction, amplification, and sequencing**

Genomic DNA was extracted from macerated liver tissue samples using a TIANamp Genomic DNA kit (Tiangen Biotech, China), according to the protocols of the manufacturer. Mitochondrial gene cytochrome b (cyt b) was targeted and amplified using primers L14919 (5’–AACCACCGTTGTTATTCAACT–3’) and H16064 (5’–CTTTGGTTTACAAGAACAATGTTTA–3’) (Burbrink et al., 2000; Guo et al., 2012). Polymerase chain reactions (PCR) were performed at 25 μL volume, and amplified DNA was produced after initial denaturing for 7 min at 94 °C, 41 cycles of denaturation for 40 s at 94 °C, annealing for 30 s at 46 °C, extension for 1 min at 72 °C, and final extension for 8 min at 72 °C. The PCR products were purified using...
Figure 2  Dorsal and ventral views of *Opisthotropis zhaoermii* sp. nov. holotype CIB109999 (adult female) and CIB109998 (adult male) (Photos by Jin-Long Ren)

A: Dorsal view of female holotype; B: Ventral view of female holotype; C: Dorsal view of male paratype; D: Ventral view of male paratype.

Figure 3  Lateral head (column 1), dorsal head (column 2), and ventral head (column 3) comparisons of *Opisthotropis zhaoermii* sp. nov., *O. cheni*, and *O. latouchii* (Photos by Jin-Long Ren)

Row A: Lateral head (A1), dorsal head (A2), and ventral head (A3) views of *Opisthotropis zhaoermii* sp. nov. (holotype CIB109999); Row B: Lateral head (B1), dorsal head (B2), and ventral head (B3) views of *O. cheni* (YBU071050); Row C: Lateral head (C1), dorsal head (C2), and ventral head (C3) views of *O. latouchii* (CIB9989).

Phylogenetic analyses

*Natrix natrix* (Linnaeus, 1758), *Rhabdophis leonardi* (Wall, 1923), and *Hebius johannis* (Boulenger, 1908) were selected as the outgroups for phylogenetic analyses (Figueroa et al., 2016). We downloaded all 26 available cyt b sequences of congeners and the above outgroups from GenBank (Table 1). The dataset was aligned using MEGA 6 with default parameters (Tamura et al., 2013), and adjusted manually. Possible saturation of substitution types was checked using DAMBE (Xia & Xie, 2001).

Bayesian inference (BI) and maximum likelihood (ML) analyses were conducted. The DNA substitution model was calculated by PartitionFinder 2 (Lanfear et al., 2017) using Akaike Information Criterion (AIC), which is a GTR+I+G model for the first and second codon positions and a TIM+G model for
the third position. The BI analyses were conducted using MrBayes 3.1.2, as described in Ronquist & Huelsenbeck (2003). Two independent runs of four Markov Chains for 10 000 000 generations were summarized by the BI, and sampled every 100 generations. The first 25% were discarded as “burn-in”. Bayesian posterior probability (BPP) was determined to test the confidence of tree topology, where nodes with BPP≥95% were considered strongly supported. Convergence and effective sample size (ESS) of the parameters were investigated in Tracer 1.6 (Rambaut & Drummond, 2013).

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Figure 4  Anterior dorsal (column 1), dorsolateral (column 2), and ventral coloration (column 3) comparisons of *Opisthotropis zhaoermii* sp. nov., *O. cheni*, and *O. latouchii* (Photos by Jin-Long Ren)

Row A: Anterior dorsal (A1), dorsolateral (A2), and ventral coloration (A3) of *Opisthotropis zhaoermii* sp. nov. (holotype CIB109999); Row B: Anterior dorsal (B1), dorsolateral (B2), and ventral coloration (B3) of *O. cheni* (YBU071050); Row C: Anterior dorsal (C1), dorsolateral (C2), and ventral coloration (C3) of *O. latouchii* (CIB9989).

Figure 5  BI phylogenetic tree estimated from cyt *b* sequences depicting phylogenetic relationships of *Opisthotropis* (numbers above branches are BPP and numbers below branches are BSP (>70 retained))
Figure 6  Type localities of species of the *Opisthotropis latouchii* group (created from MAP WORLD, http://www.tianitdu.com)

Star: Type locality of *Opisthotropis zhaoermii* sp. nov. (western Hunan); Circle: Type locality of *O. cheni* (southern Hunan); Square: Type locality of *O. latouchii* (northern Fujian).

### Table 1  Samples and sequences used in molecular analysis

| Genus     | Species         | Locality                                                | Voucher No. | GenBank accession No. |
|-----------|-----------------|---------------------------------------------------------|-------------|-----------------------|
| *Opisthotropis* | zhaoermii sp. nov | Guzhang County, Hunan Province, China | CIB109998   | MG012799*             |
| *Opisthotropis* | zhaoermii sp. nov | Guzhang County, Hunan Province, China | CIB109999   | MG012800*             |
| *Opisthotropis* | zhaoermii sp. nov | Guzhang County, Hunan Province, China | CIB110000   | MG012801*             |
| *cheni*    |                 | Nanling National Nature Reserve, Ruyuan County, Guangdong Province, China | YBU071040   | GQ281779*             |
| *cheni*    |                 | Shimentai Nature Reserve, Yingde City, Guangdong Province, China | SYS r001422 | KY594741*             |
| *latouchii* |                 | Fujian Province, China                                 | –           | GQ281783*             |
| *latouchii* |                 | Guadun Village, Wuyishan City, Fujian Province, China  | SYS r000670 | KY594742*             |
| *kuatunensis* |              | Qixiling Nature Reserve, Yongxin County, Jiangxi Province, China | SYS r000998 | KY594745*             |
| *kuatunensis* |              | Wulong Village, Shanghang County, Fujian Province, China | SYS r001008 | KY594746              |
| *kuatunensis* |              | Mt. Wutong, Shenzhen City, Guangdong Province, China   | SYS r001081 | KY594747              |
| *lateralis* |                 | Guangxi Province, China                                | –           | GQ281782*             |
| *lateralis* |                 | Heishiding Nature Reserve, Fengkai County, Guangdong Province, China | SYS r000951 | KY594743              |
| *lateralis* |                 | Mt. Wutong, Shenzhen, Guangdong Province, China        | SYS r001080 | KY594744              |
| *laui*     |                 | Shangchuan Island, Taishan County, Guangdong Province, China | SYS r001161 | KY594738*             |
| *laui*     |                 | Shangchuan Island, Taishan County, Guangdong Province, China | SYS r001170 | KY594739              |
| *laui*     |                 | Shangchuan Island, Taishan County, Guangdong Province, China | SYS r001171 | KY594740              |
| *maxwelli* |                 | Nan’ao Island, Nan’ao County, Guangdong Province, China | SYS r000841 | KY594736*             |
| *maxwelli* |                 | Huboliao Nature Reserve, Nanjing County, Fujian Province, China | SYS r001053 | KY594737              |
| *andersonii* |              | Mt. Wutong, Shenzhen City, Guangdong Province, China   | SYS r001020 | KY594732*             |
| *andersonii* |              | Mt. Wutong, Shenzhen City, Guangdong Province, China   | SYS r001082 | KY594733              |
| *andersonii* |              | Mt. Maofeng, Guangzhou City, Guangdong Province, China  | SYS r001382 | KY594734              |
Continued

| Genus        | Species       | Locality                                         | Voucher No. | GenBank accession No. |
|--------------|---------------|--------------------------------------------------|-------------|-----------------------|
| Opisthotropis| andersonii    | Mt. Maocheng, Guangzhou City, Guangdong Province, China | SYS r001383 | KY594735              |
|              | andersonii    | Tai Tam, HK Island, Hong Kong                     | SYS r001423 | KY594730              |
|              | andersonii    | Tai Mo Shan, Hong Kong                            | SYS r001424 | KY594731              |
|              | shenzhenensis | Mt. Wutong, Shenzhen, Guangdong Province, China   | SYS r001018 | KY594727*             |
|              | shenzhenensis | Shenzhen City, Guangdong Province, China          | SYS r001021 | KY594728              |
|              | shenzhenensis | Mt. Tiantou, Shenzhen City, Guangdong Province, China | SYS r001032 | KY594729              |
|              | maculosa      | Heishiding Nature Reserve, Fengkai County, Guangdong Province, China | SYS r000946 | KY594748*             |
|              | guangxiensis  | Guangxi Province, China                           | –           | GQ281776*             |
| Natrix       | natrix        | S Borup, Zealand, Denmark                         | MTD T 9269  | HF680010              |
| Rhabdophis   | leonardi      | Panzhihua City, Sichuan Province, China           | SCUM090009  | KF800933              |
| Hebius       | johannis      | Yunnan Province, China                            | GP897       | KJ685708              |

GenBank accession No. marked with * represents sequence used in the genetic distance analysis to represent respective species; “–” indicates missing voucher information.

The ML analyses were performed in RAxML 8.2.10 (Stamatakis, 2014) under the most complex substitution model (GTRGAMMA) based on the AIC model assessment results. Partitions were unlinked and bootstrap proportions (BSP) were investigated with 1 000 bootstrap replicates using the fast bootstrapping algorithm, otherwise under default parameters. Nodes of the ML tree with BSP ≥ 70 were significantly supported.

Uncorrected pairwise distance (p-distances) of the sequenced cyt b data among congeners was calculated using MEGA 6 (Tamura et al., 2013).

Morphological analyses

In addition to the three newly collected specimens, a total of 33 vouchered specimens were also examined for morphological data (Appendix). As the genus is understudied and contains cryptic diversity, only toptotypic or paratopotypic specimens were examined if available to avoid taxonomic confusion. Additional museum abbreviations include Yibin University, Yibin, China (YBU); Museum of Biology, Sun Yat-Sen University, Guangzhou, China (SYS); Institute of Ecology and Biological Resources, Vietnamese Academy of Science and Technology, Hanoi, Vietnam (IEBR); Zoological Museum, Vietnam National University, Hanoi, Vietnam (VNUH).

Measurements were taken by Jin-Long Ren with a digital slide-caliper to the nearest 0.1 mm, except for total lengths (TL), which were measured using a measuring tape to the nearest 1 mm. Measurement methods and their definitions followed Zhao (2006), and included: total length (TL), snout-vent length (SVL), tail length (TaL), head length (HL), and head width (HW). In addition, the following morphometric characters were examined in this study: rostral length (RL): distance from tip of snout to anterior edges of eyes; rostral width (RW): maximum distance between supralabials at the anterior edges of eyes; interorbital distance (IOD): distance between upper edges of eyes; eye width (EW): maximum horizontal eye width; distance between the lower margins of eye and of lip (SoL); maximum loreal length (LoL); maximum loreal depth (LoD); maximum anterior temporal length (ToL); and maximum anterior temporal depth (ToD).

The following pholidosis characteristics were also recorded (character definition and counting methods followed Zhao (2006)): internasal counts (IN), prefrontal counts (PrF), frontal counts (F), parietal counts (P), loreal counts (L), preocular counts (PrO), postocular counts (PtO), supraocular counts (SpO), subocular counts (SbO), supralabial counts (SL), infralabial counts (IL), temporal counts (TEM), chin shield counts, maxillary tooth counts (MT), dorsal scale row counts (DSR), ventral counts (VEN), and subcaudal counts (SC).

In addition to the vouched specimens examined (Appendix), morphological data of congeners were also obtained from the literature, including original descriptions and redescriptions (Angel & Bourret, 1933; Boulenger, 1888, 1899, 1903, 1914; Cope, 1895; David et al., 2011, 2015; Günther, 1872; Li et al., 2010; Pope, 1928; Stuart & Chuaynkern, 2007; Teynié et al., 2014; Wang et al., 2017; Yang et al., 2013; Zhao et al., 1978, 1998; Zhao, 1999, 2005, 2006; Ziegler et al., 2008).

RESULTS

For the 29 aligned sequences of the congeners, a total of 406 variable and 367 parsimony informative sites were identified. The uncorrected pairwise sequence divergence of 11 sampled Opisthotropis species ranged from 5.0% to 17.8% (Table 2). The three sampled individuals of the Hunan population shared
respectively. Such divergences are higher than the recognized Table 2  Uncorrected pairwise sequence divergence among cyt b mtDNA gene sequences of Opisthotropis species

|        | A    | B    | C    | D    | E    | F    | G    | H    | I    | J    | K    | L    | M    | N    | O    |
|--------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| O. zhaonmi sp. nov. (MG012799) (A) |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| O. zhaonmi sp. nov. (MG012800) (B) | 0.0% |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| O. zhaonmi sp. nov. (MG012801) (C) |      | 0.0% |      |      |      |      |      |      |      |      |      |      |      |      |      |
| O. cheni (GQ281779) (D) | 5.6% | 5.6% | 5.6% |      |      |      |      |      |      |      |      |      |      |      |      |
| O. cheni (KY594741) (E) | 5.6% | 5.6% | 5.6% | 0.5% |      |      |      |      |      |      |      |      |      |      |      |
| O. latouchii (GQ65783) (F) | 5.1% | 5.1% | 5.1% | 5.1% | 5.0% |      |      |      |      |      |      |      |      |      |      |
| O. latouchii (KY594742) (G) | 5.1% | 5.1% | 5.1% | 5.1% | 5.0% | 0.0% |      |      |      |      |      |      |      |      |      |
| O. kuatunensis (KY594745) (H) | 14.8%| 14.8%| 14.8%| 14.2%| 14.3%| 13.8%| 13.8%|      |      |      |      |      |      |      |      |
| O. lateralis (GQ281783) (I) | 16.1%| 16.1%| 16.1%| 15.6%| 15.6%| 15.9%| 15.9%| 16.5%|      |      |      |      |      |      |      |
| O. laui (KY594738) (J) | 16.4%| 16.4%| 16.4%| 16.5%| 16.6%| 16.3%| 16.3%| 18.8%| 15.0%|      |      |      |      |      |      |
| O. maxwelli (KY594736) (K) | 15.2%| 15.2%| 15.2%| 15.9%| 15.8%| 15.5%| 15.5%| 15.9%| 13.3%| 11.4%|      |      |      |      |      |
| O. andersonii (KY594732) (L) | 16.0%| 16.0%| 16.0%| 17.4%| 17.3%| 16.0%| 16.0%| 16.7%| 14.8%| 12.2%| 11.8%|      |      |      |      |
| O. shenzhenensis (KY594727) (M) | 16.2%| 16.2%| 16.2%| 17.2%| 17.3%| 16.5%| 16.5%| 17.8%| 14.8%| 14.3%| 11.2%| 11.7%|      |      |      |
| O. maculosa (KY594748) (N) | 16.7%| 16.7%| 16.7%| 17.5%| 17.4%| 16.5%| 16.5%| 15.9%| 17.7%| 16.5%| 15.0%| 16.7%| 16.5%|      |      |
| O. guangxiensis (GQ281776) (O) | 15.9%| 15.9%| 15.9%| 16.6%| 16.3%| 15.5%| 15.5%| 15.7%| 16.9%| 16.3%| 15.5%| 14.9%| 16.6%| 16.0%|      |

For phylogenetic analyses, a majority rule consensus tree inferred from BI (-lnL=-531.011 3; average standard deviation of split support=0.002 005; ESS>200) was consistent with the ML tree (Figure 5). Opisthotropis was recovered as monophyletic with current samplings. Although interspecific relationships among congeners within Opisthotropis were not fully resolved, the final consensus tree yielded high support (BPP=0.97; BSP=93) for key nodes concerning the relationship between the Hunan population with recognized congeners. The Hunan population was recovered as a monophyletic clade (BPP=0.95; BSP>70) for key nodes concerning the relationship among congeners within Opisthotropis species group (Figure 5).

The new species differs from all congeners by a combination of the following morphological characters: (1) head barely distinct from neck; (2) body and tail moderately slender; (3) prefrontal single, much broader than long; (4) nostrils directed upwards; (5) eyes small; (6) maxillary teeth subequal; (7) anterior neck dorsal scales smooth, middle body with faint keels, tending to moderately keeled rear body and on tail.

Diagnosis A large-sized species of Opisthotropis diagnosed by the following morphological characters: (1) body size large (TL 514–586 mm); (2) tail moderate (Ta/TL 0.20–0.21); (3) dorsal scale rows 17:17:17; (4) ventral scales 147–152; (5) subcaudal scales 54–62; (6) preocular absent; (7) loreal elongated and entering orbit; (8) supralabials mostly 9 (rarely 8), fifth and sixth entering orbit; (9) anterior temporals short, ToL/ToD 1.74–2.02; (10) maxillary teeth 28–30; (11) irregular yellow stripes edged with ochre present on dorsal and lateral head; (12) clear black and yellow longitudinal streaks present on dorsal and lateral body, some streaks fused to light patches or stripes anteriorly; (13) venter pale yellow in life, with asymmetric blackish speckles along outer margins.
Table 3 Morphological characteristics of the examined specimens of *O. zhaoermii* sp. nov., *O. cheni*, and *O. latouchii* examined in this study

|                  | *O. zhaoermii* sp. nov. | *O. latouchii* | *O. cheni* |
|------------------|--------------------------|----------------|------------|
|                  | male *(n=1)* | female *(n=2)* | male *(n=7)* | female *(n=3)* | male *(n=5)* | female *(n=4)* |
| TL (mm)          | 529.7        | 514.8–586.7    | 384.4–463.6  | 401.2–446.3   | 395.9–564.5  | 433.0–534.7    |
| TaL (mm)         | 108.62       | 101.26–120.49  | 78.89–92.86  | 82.59–91.25   | 86.52–113.48 | 86.45–108.21  |
| Tal/TL           | 0.21         | 0.20–0.21      | 0.20–0.21    | 0.20–0.21     | 0.20–0.22    | 0.18–0.21      |
| HL (mm)          | 12.72        | 12.92–13.61    | 9.94–11.69   | 9.43–11.13    | 10.40–14.03  | 12.33–13.64   |
| HW (mm)          | 8.76         | 9.81–10.84     | 7.11–8.34    | 7.26–8.53     | 8.55–10.25   | 8.22–9.80     |
| TL/HL            | 0.21         | 0.20–0.21      | 0.20–0.21    | 0.20–0.22     | 0.18–0.21    | 0.12–0.14     |
| HL/HW            | 1.45         | 1.26–1.32      | 1.31–1.46    | 1.25–1.30     | 1.21–1.53    | 1.32–1.50     |
| TL (mm)          | 4.60         | 4.57–4.78      | 3.18–3.49    | 3.18–3.55     | 3.59–4.56    | 4.21–4.58     |
| TaL (mm)         | 7.14         | 7.00–8.20      | 4.87–6.27    | 5.62–6.66     | 6.46–7.44    | 6.95–7.14     |
| RL (mm)          | 0.64         | 0.56–0.68      | 0.52–0.70    | 0.53–0.58     | 0.56–0.67    | 0.61–0.65     |
| IOD (mm)         | 5.41         | 5.72–6.10      | 4.20–5.47    | 4.65–4.82     | 4.65–5.68    | 4.94–6.05     |
| IOD/HW           | 0.62         | 0.56–0.58      | 0.54–0.66    | 0.57–0.64     | 0.54–0.64    | 0.54–0.62     |
| EW (mm)          | 1.33         | 1.36–1.60      | 0.87–1.09    | 0.96–1.08     | 1.37–1.51    | 1.29–1.48     |
| EW/HW            | 0.10         | 0.11–0.12      | 0.08–0.10    | 0.09–0.11     | 0.10–0.13    | 0.10–0.12     |
| SOL (mm)         | 1.94         | 1.94–1.98      | 1.32–1.64    | 1.26–1.44     | 1.50–1.94    | 1.46–1.85     |
| SOL/HL           | 0.15         | 0.15           | 0.13–0.16    | 0.13–0.14     | 0.13–0.15    | 0.12–0.14     |
| LoL (mm)         | 2.10         | 2.20–2.32      | 1.47–1.85    | 1.44–1.49     | 1.78–2.46    | 2.11–2.42     |
| LoD (mm)         | 1.31         | 1.04–1.28      | 0.84–1.12    | 0.69–0.86     | 1.02–1.39    | 1.13–1.30     |
| LoL/LoD          | 1.64         | 1.82–2.11      | 1.56–1.96    | 1.68–2.18     | 1.75–1.89    | 1.73–2.07     |
| ToL (mm)         | 2.06         | 2.84–3.01      | 2.00–2.66    | 1.99–2.46     | 2.48–3.56    | 2.57–3.42     |
| ToD (mm)         | 1.19         | 1.41–1.47      | 0.85–1.09    | 0.94–1.00     | 0.95–1.09    | 0.75–1.19     |
| ToL/ToD          | 1.74         | 2.02–2.04      | 1.87–2.80    | 2.08–2.66     | 2.36–3.63    | 2.88–3.47     |
| DSR              | 17:17:17     | 17:17:17       | 17:17:17     | 17:17:17      | 17:17:17     | 17:17:17      |
| SL               | 9            | 8–9            | 8–9          | 7–9           | 7–9          | 8–9           |
| IL               | 8            | 8–10           | 7–9          | 8–9           | 8–10         | 9–10          |
| TEM              | 1+2+2/1+1+2  | 1+2/1         | 1+1/2        | 1+2/1         | 1+1          | 1+1           |
| MT               | 29           | 28–30          | 18–24        | 12–23         | 25–28        | 25–28         |
| VEN              | 152          | 147–152        | 155–161      | 155–159       | 152–162      | 146–153       |
| SC               | 62           | 54–61          | 57–63        | 59–63         | 61–64        | 47–60         |

Abbreviations are listed in Material and Methods.

Description of holotype Body relatively large (TL 586 mm), stout and cylindrical; head short and broad, HL/SVL 0.03, HL/HW 1.26, dorsally depressed, not distinct from neck; eyes small, EW 1.60 mm, EW/HL 0.12; pupils round; interorbital distance medium, IOD/HW 0.56. Nostrils oval, directed upwards, located at inner side of nasals; tail long, TaL/TL 0.21, tapering posteriorly. Maxillary teeth 30, subequal, densely set, not grooved.

Rostral semi-circular, width 1.5 times longer than high, visible from above; nasals subhexagonal, in contact with rostral, not divided, furrow from inferior nostril to edge of nasal, reaching superior margin of second supralabial; internasals quadrangular, longer than wide, away from loreal, contacting nasals laterally, prefrontal posteriorly; prefrontal single, subrectangular, twice as broad than long, protruding anteriorly, posterior edge broadly in contact with frontal, lower corner in contact with supraoculars on both sides; frontal single, subpentagonal, somewhat peach-shaped, slightly broader than long, 1.8 times longer than prefrontal; single pair of parietals present, 1.5 times longer than wide; loreals 1/1, elongated, subrectangular in shape, twice as long than high, about 1.4 times longer than eye diameter, entering orbit, in contact with nasal, prefrontal, supraocular, supralabials (third, fourth, fifth). Preocular absent; postoculars 2/2, upper pair slightly shorter than eye, larger than lower pair; lower postocular in contact with sixth supralabial on left, sixth and seventh on right; supraocular 1/1, large, “B”-shaped, about equal length to loreal; supralabials 8/9, fifth and sixth entering orbit. On left, supralabials 1–5 distinctly higher than long,
supralabials 6–8 longer than high; on right, supralabials 1–6 distinctly higher than long, equal size in seventh, last two longer than high. Temporals 1+2/1+2, anterior ones largest, about two times longer than wide, in contact with supralabials 6–7 on left side, supralabials 7–9 on right; two posterior temporals shorter and smaller than anterior pair, subequal, slightly shorter than loreals; two pairs of chin shields present, anterior ones about 1.2 times longer than posterior ones; posterior chin shields separated from each other by two scales; mental groove apparent; infralabials 9/8, first four in contact with anterior chin shields, fourth and fifth in contact with posterior chin shields; sparse minute granular asperities on head scales. Dorsal scale rows 17:17:17 without apical pits, vertebral not enlarged, dorsal scales smooth anteriorly, gradually keeled from seventh ventral position, weakly keeled anteriorly and stronger posteriorly; outer most dorsal scale rows along both sides of body smooth entirely before cloaca. Ventral 152, precloacal divided; anal divided; subcaudal 60, paired, with single terminal rod.

**Coloration of holotype in life:** In life, the dorsal surface of the head is brownish yellow, mottled with small brownish black spots and patches. Lighter irregular markings are present on the internasals, prefrontal, and frontal, which do not sharply separate the darker center from the brownish yellow background color. Brownish ochre stripes are observed on the posterior edges of frontal and parietals, forming several irregular broken boundary lines. In front of the stripes on the parietals, six thicker oblique stripes are observed. Color patterns are similar on the lateral surface, supralabials 3–6 (3–7 on right) and infralabials 2–8 brownish yellow with anterior blackish borders. The blackish edge of upper part of supralabials 6–8 (7–9 on right), postoculars, and lower part of anterior temporal forming a thick “eyebrow” streak pattern, connecting with the outer most irregular black lateral stripe extended to tail tip. From supralabial 5 to neck, darker brownish yellow background color gradually transitions into light yellow. Tongue is purple with pink markings, gradually turning white at apex. Dorsal scales from row 3 to 15, each scale is black with a subtriangular or rectangular yellow center, thus constituting thirteen clear longitudinal stripes along the whole trunk just after the posterior edges of the parietals. Before 24th ventral position, dorsal scale rows 1 and 17 pale yellow entirely or marked with minute black spots, black upper edges gradually appearing on these two rows of scales after 24th ventral position, forming an extra yellow stripe along each side. Along the vertebral scales on the back, these yellow stripes fuse to seven conspicuous irregular patches or stripes anteriorly, only eight yellow stripes observed at the base of the tail. Chin and anterior venter pale yellow, venter becoming lighter posteriorly. The ventral scales are cream with bold yellow posterior margins, asymmetric black spots present along the outer margins, somewhat transparent. Subcaudal resemble ventral but with a black longitudinal joining stripe after the eleventh subcaudal scale.

**Coloration in preservation** Specimens fixed in formalin and preserved in ethanol resemble the coloration of live animals. However, the yellow longitudinal stripes faded to a dull yellow hue, and the cream venter changed to uniform beige and was no longer transparent (Figures 2A, 2B).

**Variation** Paratypes generally resemble holotype in morphological characters (Figures 1C, 1D, 2C, 2D; Table 3). However, the male paratype CIB109998 differs from the female specimens (CIB109999 and CIB 110000) by smaller body size (TL 514 mm vs. 529–586 mm in females), shorter anterior temporals (To/Td 1.74 vs. 2.02–2.04 in females), and rather irregular yellow patterns within each dorsal scale (vs. regular) (Figures 1C, 1D, 2C, 2D). As the sample size is small, it is unknown whether such differences observed between the two sexes represent sexual dimorphism in this species.

**Distribution and natural history** This species is only known from the type locality presently (Figure 6). *Opisthotropis zhaoermii* sp. nov. inhabits small, fast-flowing mountain streams in forested areas, with water temperature and pH between 19.9–21.2 °C and 7.85–7.93, respectively. Being nocturnal, individuals were seen swimming at the edge of the backwater of travertine waterfalls from 2100h to 0100h at night (Figure 7). The holotype was collected during a heavy rainstorm that caused the water to become extreme turbid, with water temperature and pH measurements of 19.5 °C and 8.13, respectively.

When handled, individuals never stroked or displayed threatening postures. Instead, individuals struggled violently and released a musky, pungent, and enduring defensive odor, much like that of *O. balteata* and *O. kuatunensis* (Pope, 1935). The scales of the snakes become dehydrated and crimped quickly after leaving the water for about 10 min, but recovered rapidly when returned to water. Similar to other congeners in China, the new species may prey on earthworms, tadpoles, freshwater isopods, crabs, and small fish (Pope, 1935). Other herpetofauna, including *Quasipaa boulengeri*, *Odonarra schmackeri*, *Lycodon rufizonatum*, *L. fasciatus*, and *Deinagkistrodon acutus*, were observed sympatric with the new species.

**Etymology** The specific epithet, *zhaoermii*, is derived from the name of an internationally renowned Chinese herpetologist, Prof. Er-Mi Zhao, who unfortunately passed away on 24 December 2016. Designation of this specific epithet honors his great contribution to herpetological research in China, specifically to his contribution to the taxonomy of *Opisthotropis*, including the first description of the sister species (i.e., *O. cheni*, see above) of the newly found species. We suggest Zhao’s Mountain Stream Snake as its English common name, and “Zhao Shi Hou Leng She” (趙氏後棱蛇) as its Chinese common name.

**Comparisons** For pholidosis characteristics, *Opisthotropis zhaoermii* sp. nov. is most similar to *O. cheni* and *O. latouchii* in having the same number of dorsal scale rows (17:17:17) and postoculars (2), and all three species possessing elongated loreals that enter orbits. However, *Opisthotropis zhaoermii* sp. nov. can be distinguished from both recognized species by a suite of morphological characteristics. The new species differs
from O. cheni by having a higher number of maxillary teeth (28–30 vs. 25–28), a different temporal format (1+2 [rarely 1 only] vs. 1+1, occasionally 1+2), shorter anterior temporals (ToL/ToD 1.74–2.04 vs. 2.36–3.63), a larger distance between the lower margins of the eye and of lip (SoL/HL 0.15 vs. 0.12–0.14), and distinct dorsal color patterns (alternate, longitudinal black and yellow stripes vs. uniform dark olive with light-yellow transverse bands); from O. latouchii by having a larger body size (TL 514–586 mm vs. 360–419 mm), a higher number of maxillary teeth (28–30 vs. 12–25), lower ventral counts (147–152 vs. 155–159), a different temporal format (1+2 [rarely 1 only] vs. 1+1, occasionally 1+2), and a distinct dorsal color pattern (alternate longitudinal stripes partly fused vs. distinct stripes never fused together) (Figures 3, 4; Table 3).

For other congeners that also have 17:17:17 dorsal scale rows, Opisthotropis zhaermii sp. nov. differs from O. lateralis and O. maxwelli by having a different loreal position (loreals entering orbits vs. separate from orbits). In addition, the new species differs from O. lateralis by having a lower number of supralabials (8–9 vs. 10–11) and a larger size (TL 514–586 mm vs. 294–461 mm); from O. maxwelli by having a higher number of maxillary teeth (28–30 vs. 22–23) and a higher number of supralabials (8–9 vs. 6–7). Furthermore, Opisthotropis zhaermii sp. nov. differs from O. andersonii by having a higher number of maxillary teeth (28–30 vs. 22–23), a larger body size (TL 514–586 mm vs. 240–462 mm), and a longer tail (TaL/TL 0.20–0.21 vs. 0.15–0.20); from O. daovantieni Orlov, Darevsky and Murphy, 1998 and O. spenceri Smith, 1918 by having a different internasals location (separated from loreals vs. in contact) and fewer ventrals (147–152 vs. 189–194 in O. daovantieni and 178–185 in O. spenceri).

For congeners that have 17 rows of dorsal scales at the midbody, including O. rugosa (Lidth de Jeude, 1890), O. tamdaoensis Ziegler, David and Vu, 2008, and O. atra Günther, 1872, the new species differs from O. rugosa and O. tamdaoensis by having a different dorsal scale formula (17:17:17 vs. 19:17:15 in O. rugosa, 19:17:17 in O. tamdaoensis), and from O. atra by lower number of ventrals (147–152 vs. 170), lower subcaudal counts (54–62 vs. 65), and higher number of supralabials (8–9 vs. 7).

For the remaining congeners, Opisthotropis zhaermii sp. nov. differs from O. guangxiensis, O. jacobi, O. kikuzatoi Okada and Takara, 1958, and O. maculosa by having different dorsal scale rows at the midbody (17 vs. 15) and a lower number of ventrals (147–152 vs. 164–174 in O. guangxiensis, 155–179 in O. jacobi, 180–183 in O. kikuzatoi, and 166–188 in O. maculosa); from O. balteata, O. kuatunensis, O. shenzenensis, O. durandi Teynié, Lottier, David, Nguyen and Vogel, 2013, and O. laui, 2013 by a distinct formula of dorsal scale rows (17:17 vs. 19:19:17 in O. balteata, 19:19:19 in O. kuatunensis and O. shenzenensis, 19:21:17 in O. durandi, and 25:23:23 in O. laui); from O. cucae David, Pham, Nguyen and Ziegler, 2011 by having a distinct position of internasals (truncated anteriorly and separate from loreal vs. curved and in contact with loreal); from O. typica (Mocquard, 1890) and O. alcalai Brown and Leviton, 1961 by having a distinct prefrontal condition (complete vs. divided).

Key to species of Opisthotropis
With the description of this new species, an updated diagnostic key to all species of the genus Opisthotropis is provided here to facilitate future taxonomic work.

1 Prefrontal single ............................................................ 2
   – Prefrontal divided ......................................................... 21
2 Dorsal scale rows 15 at midbody ..................................... 3
   – Dorsal scale rows 17–23 at midbody ......................... 6
3 Supralabials 6–7; dorsal scales keeled posteriorly
Supralabials 7–10; dorsal scales smooth entirely

Dorsal scale rows 17:15:15; dorsal surface with pale yellow crossbars
Dorsal scale rows 15:15:15; dorsal surface without pale yellow crossbars

Anterior chin shields nearly two times longer than posterior ones; dorsal surface uniformly blackish brown
Anterior chin shields and posterior ones about equal length; dorsal surface dark with a yellow spot on each dorsal scale

Dorsal scale rows 19–23 at midbody
Dorsal scale rows 17 at midbody

Dorsal scale rows 17:15:15; dorsal surface with pale yellow crossbars
Dorsal scale rows 15:15:15; dorsal surface without pale yellow crossbars

Anterior temporal scales 2; subocular present
Anterior temporal scales 1; subocular absent

Body size small, total length shorter than 419 mm; maxillary teeth count no more than 25
Body size moderate or large, total length longer than 419 mm; maxillary teeth count no less than 25

Maxillary teeth count 25–28; anterior temporal scales elongated, ToL/ToD 2.63–3.63; dorsal surface dark olive with yellow crossbars
Maxillary teeth count 28–30; anterior temporal scales short, ToL/ToD 1.74–2.04; dorsal surface with longitudinal yellow stripes

Nasal scales paired on both sides
Nasal scales not paired on both sides

Dorsal scale rows 19 at midbody
Dorsal scale rows 21 or 23 at midbody

Internasal in contact with loreal
Internasal not in contact with loreal

Dorsal scale rows 19;19:17; ventral scales 190–205
Dorsal scale rows 19;19:19; ventral scales less than 190

Supralabials 9–10, not divided horizontally; dorsal scales feebly keeled anteriorly, strongly keeled posteriorly; dorsal surface olive-green with fine black mesh pattern
Supralabials 13–16, divided horizontally; dorsal scales strongly keeled entire body; dorsal surface dark brown with black longitudinal lines

Dorsal scale rows 23 at midbody

O. kikuzai
O. maculosa
O. daovantieni
O. tamdaoensis
O. zhaoermii
O. shenzhenensis
O. guangxiensis
O. maxwelli
O. andersonii
O. latouchii
O. tsongcucae
O. maculosa
O. andersonii
O. laui
O. alcalai
O. rugosa
O. typica

DISCUSSION

Although recent taxonomic work has shed light on the taxonomy of Chinese Opisthotropis, research has been focused on the Pearl River Valley only (Wang et al., 2017; Yang et al., 2013), and diversity of the genus in most parts of southern China remained overlooked. Our discovery of the new species Opisthotropis zhaoermii in the Yangtze River Basin highlights the underestimated diversity of the genus in southern China and calls for further fieldwork and continuous taxonomic studies of the group in the under-surveyed regions of southern China.

Despite the recent taxonomic discoveries of Opisthotropis in southern China and northern Indochina, many of the newly described species are known from only a handful of specimens, and in some cases, from a single holotype from the type locality (David et al., 2011; Yang et al., 2013; Ziegler et al., 2008). The low numbers of vouchered specimens and geographic samplings have resulted in limited knowledge on the morphological variations, distribution patterns, and conservation of members of the genus. Furthermore, few studies have reported detailed natural history data of congeners, including color in life, behaviors, reproductive biology, and population statuses. As ecological niche differentiation may be a driver of species diversification in Opisthotropis (Yang et al., 2011), it is important to collect ecological data for different congeners. Here we reported on water temperature and pH data of an Opisthotropis species for the first time, and recommend that future studies collect ecological data of Opisthotropis in the field, including the addition of more parameters such as flow speed of water, canopy coverage, humidity, and prey community structures. We recommend future studies to explore the ecology of this unique group of aquatic snakes and investigate the possible ecological speciation mechanisms of the group.

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APPENDIX

The following specimens were examined in this study:

Opisthotropis cheni (n=9): CIB98273, YBU12110, YBU071040, 071042, 071046–071050, Nanling National Nature Reserve, Ruyuan County, Guangdong Province, China.

Opisthotropis cucae (n=1): IEBR A.0924 (holotype), Chu Mom Ray National Park, Sa Thay District, Kon Tum Province.

Opisthotropis latouchii (n=10): CIB9983, 9988, 9990–9994, 9998–10000, Tongmu Village, Fujian Province, China.

Opisthotropis lateralis (n=12): YBU14465, 14477–14478, Fulong Township, Fangchenggang City, Guangxi Province, China; 14516–14523, Mt Pingtian, Guigang City, Guangxi Province, China; 091014, Guangxi Province, China.

Opisthotropis tamdaoensis (n=1): VNUH010606 (holotype), Tam Dao, Vinh Phuc Province, Vietnam.

Opisthotropis zhaoermii sp. nov. (n=3): CIB109998 (paratype), CIB109999 (holotype), CIB110000 (paratype), Zuolong Gorges, Guzhang County, Tujia-Miao Autonomous Prefecture, Hunan Province, China.