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Expanded morphological definition and molecular phylogenetic position of the Tam Dao mountain stream keelback *Opisthotropis tamdaoensis* (Squamata: Natricidae) from Vietnam

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Abstract: The description of *Opisthotropis tamdaoensis* Ziegler, David & Vu, 2008, which was based on the male holotype only, is expanded herein on the basis of four newly collected specimens from the type locality of the species, including three adult females. Based on the enlarged sample size and thus extended range of morphological characters in *O. tamdaoensis*, not all characters mentioned in the original description as being distinctive between the latter species and *O. lateralis* Boulenger, 1903, a morphologically similar species, could withstand, such as number and arrangement of preocular, temporal and subocular scales, as well as total size. Presently, the number and arrangement of supralabials in concert with the dorsal colour pattern and the course of the dark lateral stripe still serve as good diagnostic characters to morphologically distinguish *O. tamdaoensis* from *O. lateralis*. Thus, on the basis of the new morphological and for the first time also molecular data, the validity of *O. tamdaoensis* as a distinct species is confirmed. The molecular analyses based on the mitochondrial cytochrome *b* gene revealed *O. tamdaoensis* to be distinct by about 6% genetic divergence from *O. lateralis*, with which it forms a sister relationship.

Keywords: Redescription - morphology - molecular phylogeny - *Opisthotropis lateralis*

INTRODUCTION

Water snakes of the genus *Opisthotropis*, often referred to as Mountain stream keelbacks, are highly aquatic snakes which inhabit flowing streams of hills and mountains of tropical and subtropical Asia. Mountain stream keelbacks are distributed across the mainland of Southeast Asia to

Sumatra (Indonesia), the Philippines and the Ryukyu Archipelago of Japan. This genus, which currently comprises 21 species, is still imperfectly known (Teynié *et al.*, 2013). No less than five *Opisthotropis* species have been discovered in the past decade only: *O. laui* from China, *O. maculosa* from Thailand and China, *O. durandi* from Laos, and *O. cucuae* as well as *O. tamdaoensis* from

Vietnam (Stuart & Chuaynkern, 2007; Ziegler *et al.*, 2008; David *et al.*, 2011; Teynié *et al.*, 2013; Yang *et al.*, 2013).

From Vietnam, eight species of mountain stream keelbacks have been recorded so far (David *et al.*, 2011; Nguyen *et al.*, 2017), most of which are rare or at least rarely collected and thus poorly known. One of these uncommon mountain stream keelbacks from Vietnam is *Opisthotropis tamdaoensis*, a species recently described from the Tam Dao mountain ridge in northern Vietnam. The original description was based on a single male individual only, which, however, showed peculiar morphological characters compared with its congeners which were the crucial factor for scientific description (Ziegler *et al.*, 2008). Recently, Ziegler *et al.* (2015) reported about another sighting of *O. tamdaoensis* in a forest stream in the surroundings of the Melinh Station for Biodiversity in Vinh Phuc Province, which borders Tam Dao National Park in the West.

During recent herpetological field work in Tam Dao, further *Opisthotropis* individuals were collected in the Bac (Silver) stream, the type locality of *O. tamdaoensis*. Based on this new collection from the type locality, which morphologically was clearly assignable to *O. tamdaoensis*, we herein expand the morphological definition of the species, for the first time including adult female individuals. Based on this new collection we also conducted molecular analyses based on the mitochondrial cytochrome *b* gene to test the distinct taxonomic status and to define for the first time the phylogenetic position within the genus *Opisthotropis*.

The Tonkin mountain stream keelback, *O. lateralis* Boulenger, 1903, is morphologically similar to *O. tamdaoensis*. This species was originally described from northern Vietnam (Manson Mt., nowadays Mao Son Mt., Lang Son Province), and currently is known from central and northern Vietnam as well as from southern China (Guangxi, Guizhou, Hong Kong) (Ziegler *et al.*, 2008; Nguyen *et al.*, 2009; Hecht *et al.*, 2013; Gawor *et al.*, 2016). Based on new collections of the Tonkin mountain stream keelback from northern Vietnam's Bac Giang, Cao Bang and Quang Ninh provinces we additionally provide new information on its morphometry and scalation and morphologically and for the first time also genetically compare *O. lateralis* with *O. tamdaoensis*.

MATERIAL AND METHODS

This study is based on four newly collected *Opisthotropis tamdaoensis* and nine newly collected *O. lateralis*.

Tissue samples were preserved separately in 95% ethanol and voucher specimens were anaesthetized with ethyl acetate, fixed in approximately 85% ethanol, and then transferred to 70% ethanol for permanent storage.

Individuals were subsequently deposited in the following collections:

- IEBR Institute of Ecology and Biological Resources, Vietnamese Academy of Science and Technology, Hanoi, Vietnam
- MHNG Muséum d'histoire naturelle, Geneva, Switzerland
- VNMN Vietnam National Museum of Nature, Hanoi, Vietnam
- ZFMK Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

The holotype of *O. tamdaoensis* is deposited in the Zoological Museum, Vietnam National University, Hanoi, Vietnam (VNUH).

Opisthotropis tamdaoensis: IEBR A.2016.32, Suoi Bac (Silver stream), Tam Dao, northern Vietnam, coll. Thanh Ngoc Vu, 29 June 2008. – IEBR A.2016.33, Suoi Bac (Silver stream), Tam Dao, northern Vietnam, coll. Cuong The Pham, 31 May 2014. – MHNG 2767.60, Suoi Bac (Silver stream), Tam Dao, northern Vietnam, coll. Thanh Ngoc Vu, July 2007. – ZFMK 100000, Suoi Bac (Silver stream), Tam Dao, northern Vietnam, coll. Thanh Ngoc Vu.

Opisthotropis lateralis: IEBR 3629, Son Dong, Tay Yen Tu, Bac Giang Province, coll. Truong Quang Nguyen, Tung Thanh Tran & Cuong The Pham, 07 April 2008. – IEBR 3644, Son Dong, Tay Yen Tu, Bac Giang Province, coll. Truong Quang Nguyen, Tung Thanh Tran & Cuong The Pham, 09 April 2008. – IEBR 3645, Son Dong, Tay Yen Tu, Bac Giang Province, coll. Truong Quang Nguyen, Tung Thanh Tran & Cuong The Pham, 09 April 2008. – IEBR A.2016.35, Dong Son Ky Thuong, Bac Giang / Quang Ninh provinces, coll. Ha Thuy Duong, June 2013. – IEBR A.2016.36, Tay Yen Tu, Bac Giang Province, coll. Cuong The Pham & Mona van Schingen, 15 May 2015. – VNMN A.2016.14, Bai Tu Long, Quang Ninh Province, coll. Tao Thien Nguyen & Cuong The Pham, 19 September 2009. – VNMN A.2016.15, Cao Bang Province, coll. Tao Thien Nguyen, 08 June 2009. – ZFMK 100805, Tay Yen Tu, Bac Giang Province, coll. Truong Quang Nguyen & Thomas Ziegler, May 2009. – ZFMK 100806, Tay Yen Tu, Bac Giang Province, coll. Truong Quang Nguyen & Thomas Ziegler, 16 May 2014.

In addition, *O. lateralis* specimens recorded in Ziegler *et al.* (2008), Hecht *et al.* (2013) and Gawor *et al.* (2016) were reexamined.

Morphological examination: Identification of sex was performed by dissection (inspection of gonads and inspection of presence of hemipenes). Measurements were taken after preservation with a measuring tape. The number of ventral scales was counted according to Dowling (1951). The numbers of dorsal scale rows are given at one head length behind head, at midbody, and at one head length before vent, respectively. Maxillary teeth were counted by dissecting the right maxilla for

teeth / alveoles. Scallation and maxillary teeth number were studied by using a binocular. We herein use the term precloacal instead of anal.

Abbreviations of morphological characters used in the text are as follows.

Measures and ratios: SVL: snout-vent length. – TaL: tail length. – TL: total length (SVL + TaL). – TaL/TL: ratio tail length/total length.

Meristic characters: ATem: anterior temporal scales (in contact with postocular scale / scales). – DSR: formula of dorsal scale rows. – IL: infralabial scales. – Lor: loreal scales. – PreOc: preocular scales. – PreVen: preventral scales. – PostOc: postocular scales. – PTEM: posterior temporal scales (in contact with anterior temporal scale / scales). – SL: supralabial scales. – SL/orbit: supralabial scale / scales touching the orbit. – Subc: subcaudal scales (without tail tip). – SubOc: subocular scales. – Ven: ventral scales.

Molecular analyses: The mitochondrial cytochrome *b* gene was employed in this study, because it has been successfully used in previous molecular analyses of *Lycodon* (e.g. Guo *et al.*, 2012). We included three new sequences from samples collected in Vietnam, IEBR A.2016.33 (*Opisthotropis tamdaoensis*) from Tam Dao National Park, VNMN A.2016.14 (*O. lateralis*) from Bai Tu Long, and ZFMK 100806 (*O. lateralis*) from Tay Yen Tu (GenBank MF477899 through MF477901). Another sequence of *O. lateralis* (GenBank accession number CG281782) originated from Guangxi Province, China. Other sequences of related species were obtained from GenBank. Three species, *Sinonatrix aequifasciata*, *S. annularis*, and *S. percarinata* were used as outgroups based on their phylogenetic relationships to the genus *Lycodon* (Guo *et al.*, 2012) (Fig. 5).

We used the protocols of Le *et al.* (2006) for DNA extraction, amplification, and sequencing. A fragment of the mitochondrial cytochrome *b* was amplified using the primer pair L14910/H16064 (Burbrink *et al.*, 2000). After sequences were aligned by Clustal X v2 (Thompson *et al.*, 1997), data were analyzed using maximum parsimony (MP) and combined (single model of molecular evolution) maximum likelihood (ML) as implemented in PAUP*4.0b10 (Swofford, 2001), partitioned ML (mixed models of molecular evolution based on codon positions) in IQTree v1.5.5 (Nguyen *et al.*, 2015), and Bayesian combined and partitioned analysis (BA) as implemented in MrBayes v3.2 (Ronquist *et al.*, 2012). Settings for MP, combined ML, and Bayesian analyses followed Le *et al.* (2006), except that the number of generations in the Bayesian analysis was increased to 1×10^7 and the number of bootstrap replicates in ML to 1000. Bootstrap support in IQTree was calculated using the ultrafast option (Bui *et al.*, 2013). For MP analysis, heuristic analysis was conducted with 100 random taxon addition replicates using tree-bisection and reconnection (TBR) branch

swapping algorithm, with no upper limit set for the maximum number of trees saved. Bootstrap support was calculated using 1000 pseudo-replicates and 100 random taxon addition replicates. All characters were equally weighted and unordered. The optimal model for nucleotide evolution was set to GTR+I+G for combined ML and Bayesian analyses as selected by ModelTest v3.7 (Posada & Crandall, 1998). In the partitioned Bayesian analysis, models of molecular evolution identified by ModelTest for codon position one, two, and three were GTR+I, TrN+I+G, and TVM+G, respectively. In the partitioned ML analysis, they were determined by IQTree as TN+I, TN+G, and TPM+G, respectively. The cutoff point for the burn-in function was set to 13 and 16 in combined and partitioned Bayesian analyses, respectively, as $-\ln L$ scores reached stationarity after 13 000 and 16 000 generations in both runs. Nodal support was evaluated using Bootstrap replication (BP) as estimated in PAUP and posterior probability (PP) in MrBayes v3.2. $BP \geq 70\%$ and $PP \geq 95\%$ are regarded as strong support for a clade. Uncorrected pairwise divergences (p-distance) were calculated in PAUP*4.0b10.

RESULTS

The new *Opisthotropis* series from Silver Stream in Tam Dao was collected in secondary monsoon tropical evergreen forest on granitic soil. Individuals were discovered in between 09:00 to 12:00 am at elevations in between 1200 to 1500 m above sea level. The snakes were in the shallow water in stream sections with open forest.

Subsequent dissections revealed the specimens to represent one adult male and three adult females. The females, which all were collected during the summer, contained large eggs besides small oocytes: IEBR A.2016.33 with eggs up to 24 mm in size (in May), IEBR A.2016.32 with eggs up to 19 mm in size (in June), and MHNG 2767.60 with eggs up to 23 mm in size (in July). Morphometrical data, scalation and dentition of the new *Opisthotropis* series from the type locality of *O. tamdaoensis* are summarized in Table 1. Morphologically, the new individuals (Figs 1-3) could be clearly identified as *O. tamdaoensis*. However, based on the meanwhile extended sample size, compared with the original description, which was based on a single male individual only, the morphological description of the species must be expanded as follows (based on two adult males, including the holotype, and three adult females): Maximum known total length 555 mm (maximum known snout vent length 475 mm, maximum known tail length 82 mm); tail / total length ratio 0.143-0.157; body stout, cylindrical; head not distinct from neck, dorsally covered with large shields; eye small, with round pupil. Maxillary teeth 25-29. Rostral broader than high; internasals in contact with rostral, nasals, and single prefrontal;

Table 1. Sex, morphometry and scalation of the holotype of *Opisthotropis tamdaoensis* (after Ziegler *et al.*, 2008) and the new series from Tam Dao; values given in brackets indicate infrequent condition.

	VNUH 010606 (holotype)	ZFMK 100000	Range (males)	MHNG 2767.60	IEBR A.2016.32	IEBR A.2016.33	Range (females)	Range (total)
Sex	male	male		female	female	female		
TL	555	537	max. 555	459+	522	456	max. 522	max. 555
SVL	475	460	max. 475	420	440	384	max. 440	max. 475
TaL	80	77	max. 80	39+	82	72	max. 82	max. 82
TaL/TL	0.144	0.143	0.143-0.144	-	0.157	0.157	0.157	0.143-0.157
Teeth max	25-26	28	25-28	-	29	-	29	25-29
SL	8/9	9/9	9(8)	9/9	9/9	9/9	9	9(8)
SL/orbit	0/5	5-6/5	5(0, 5-6)	5-6/5	5-6/5-6	5/5	5-6(5)	5, 5-6(0)
IL	10/9	9/10	9-10	10/11	9/10	10/9	10(9,11)	10(9, 11)
PreOc	1/1	1/2	1(2)	1/1	1/2	2/2	1-2	1-2
SubOc	1/1	0/1	1(0)	0/1	0/0	1/1	0-1	1(0)
PostOc	2/2	2/2	2	2/2	2/2	2/2	2	2
Lor	1/2	1/1	1(2)	1/1	1/1	1/1	1	1(2)
Atem	2/2	1/1	1-2	1/1	1/1	1/1	1	1(2)
PTem	4/3	4/3	3-4	2/2	2/3	2/3	2(3)	2-3(4)
DSR	19-17-17	19-17-17	19-17-17	19-17-17	19-17-17	19-17-17	19-17-17	19-17-17
PreVen	4	0	0-4	3	2	3	2-3	0-4
Ven	171	176	171-176	165	163	162	162-165	162-176
Prec	divided	divided	divided	divided	divided	divided	divided	divided
Subc	49+	51	49+-51	-	48	50	48-50	48-51

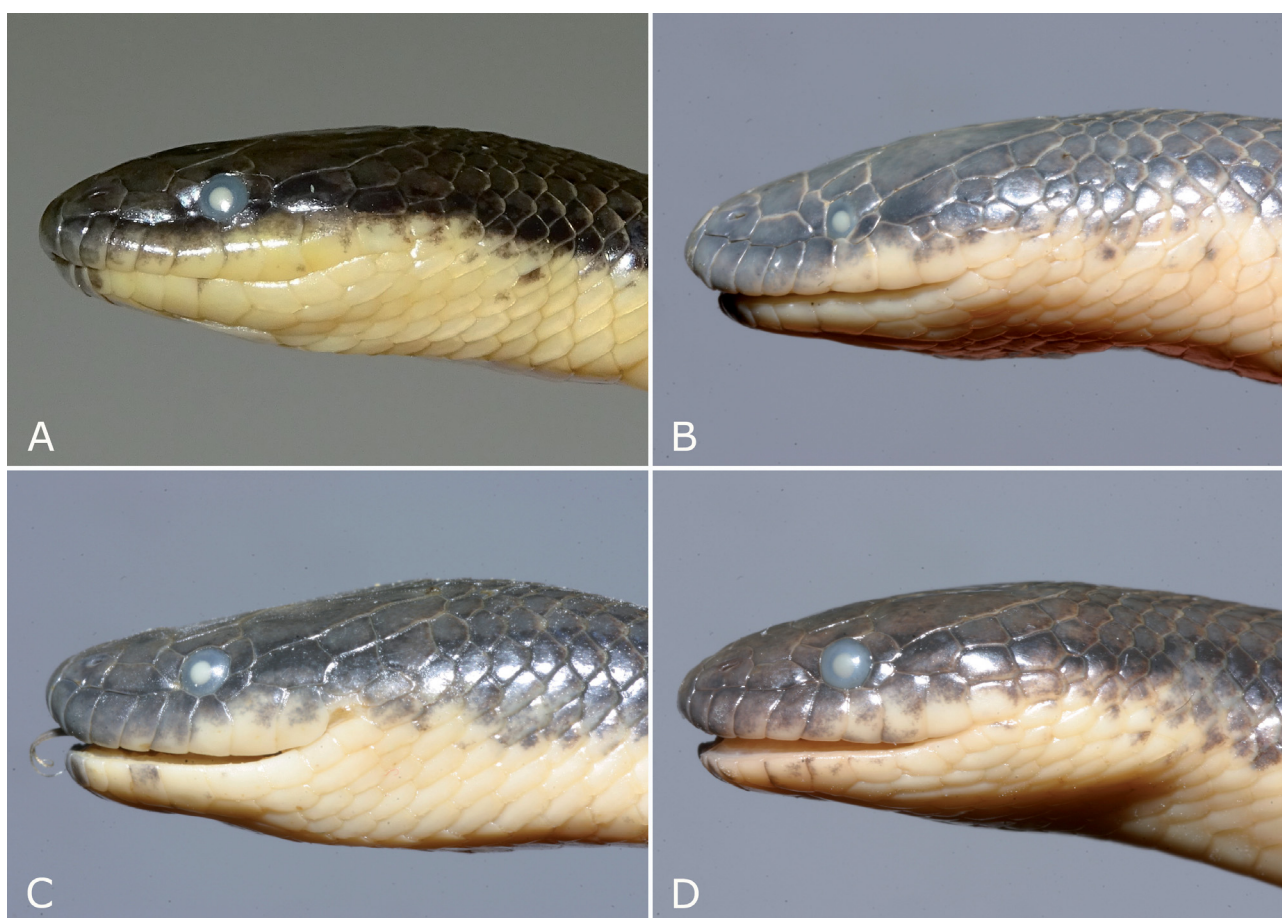


Fig. 1. Head portraits of the new series of *Opisthotropis tambdaensis* in preserved state, showing the head scalation and the insertion of the black lateral stripe in the midst of the dark dorsal colouration. (A) Female IEBR A.2016.33. (B) Male ZFMK 100000. (C) Female IEBR A.2016.32. (D) Female MHNG 2767.60. Photos: T. Ziegler

frontal pentagonal, widest anteriorly; nasal not divided below nostril; one (rarely two) elongated loreals; loreals not in contact with internasals; one or two preoculars (one preocular in the holotype), two postoculars, one supraocular; one (rarely none) subocular; postoculars followed by one (rarely two) anterior temporals, in the rare latter case the upper one being larger and elongate; anterior temporal(s) followed by (i.e., in contact with) two or three (rarely four) posterior temporals (holotype with 2 anterior and 3-4 posterior temporals); only the holotype shows an additional “postsubocular” scale that is surrounded by the lower anterior temporal, the lower postocular, subocular, and two supralabials; nine (rarely eight) supralabials, the fifth or fifth and sixth (rarely none) in contact with eye; first supralabial not vertical, but directed backward, anterior supralabials distinctly higher than long; mental triangular-shaped, wider than high; ten (rarely nine or eleven) infralabials; first pair of chin shields in contact with first four to five infralabials, and being larger and longer than the second pair of chin shields; posterior chin shields separated by two to three smaller scales.

Dorsal scales in 19 rows at anterior body, in 17 rows at midbody and at posterior body, dorsals finely tuberculate, smooth anteriorly, keeled posteriorly; tail surface distinctly keeled; 0-4 pre- and 162-176 ventrals; preloacal divided; 48-51 divided subcaudals.

Dorsum in preservative nearly uniform olive grey or grey above and paler below, without sharp transition (ca. at the second to third dorsal scale row); dorsum sometimes with rudiments of thin black longitudinal stripes; a more or less distinct dark longitudinal lateral stripe of about 1-2 mm width extends from the eye along the lowermost 3-5 dorsal body scale rows towards the tail tip; supralabials except the completely dark anteriormost ones dark above and pale below; centre of mental and anteriormost infralabials dark; tip of subcaudal region usually with dark mottling. There exists sexual dimorphism related to the number of ventrals, which is higher in males than in females (171-176 versus 162-165) and the relative length of the tail (ratio Tal / TL 0.143-0.144 in males versus 0.157 in females); in addition, males appear to be more slender than the females.

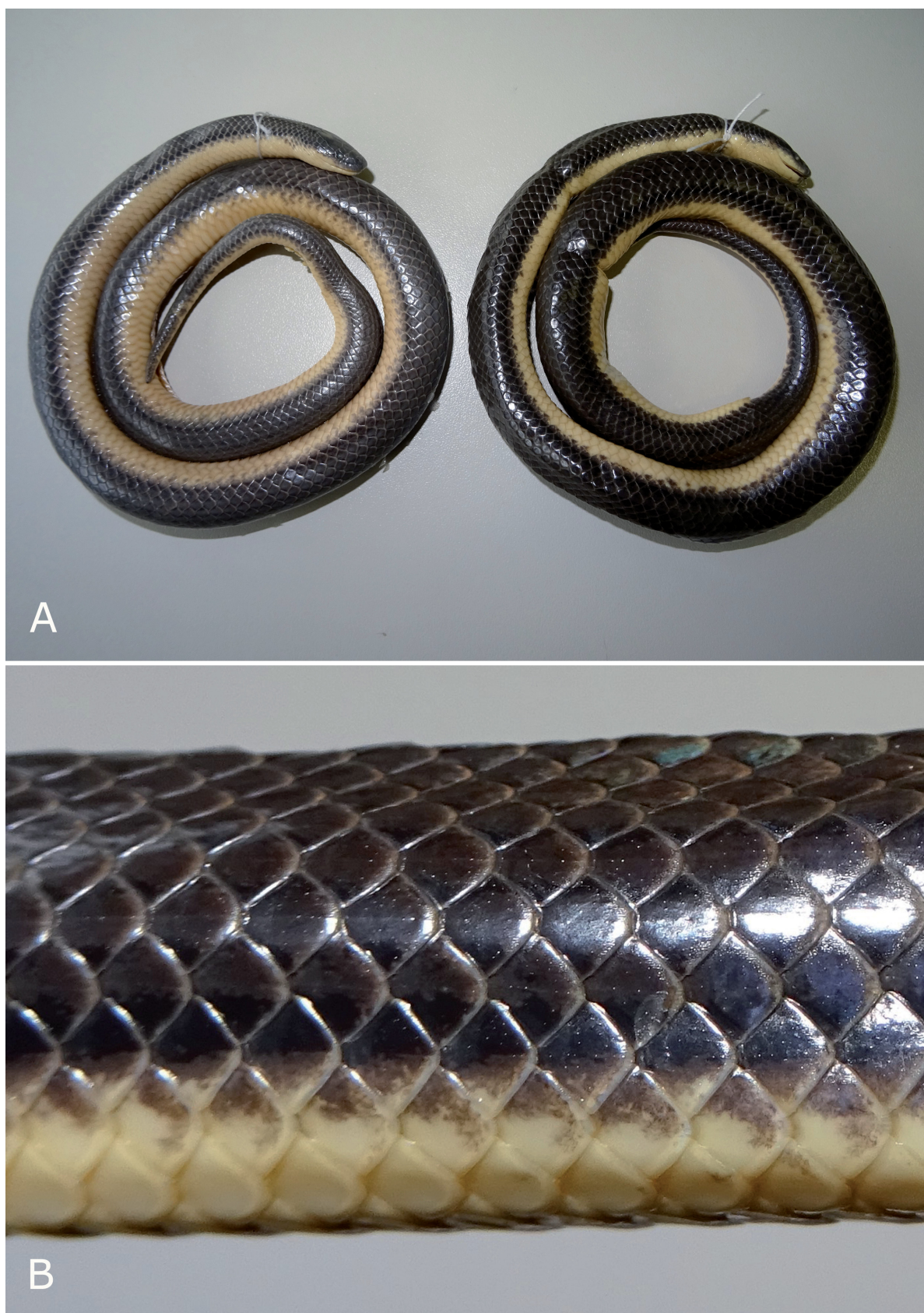


Fig. 2. Characteristic feature of *Opisthotropis tamdaoensis*: the black lateral stripe in the midst of the dark dorsal colouration. (A) Male ZFMK 100000 (left), and female IEBR A.1016.32 (right) in preserved state. (B) Detail of the body side of the female IEBR A.1016.33 in preserved state. Photos: T. Ziegler

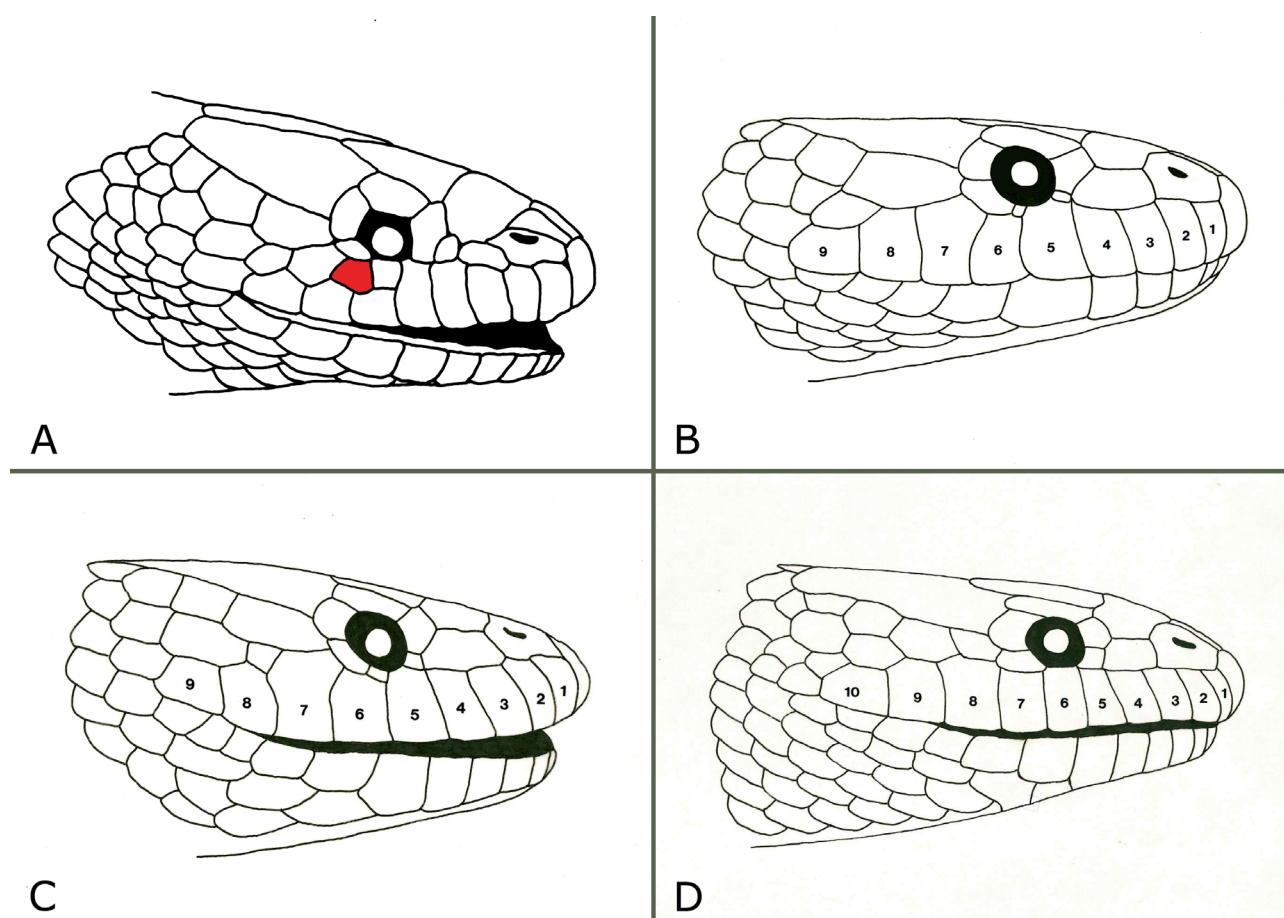


Fig. 3. Drawings showing the head scalation in *Opisthotropis tamdaoensis*. (A) Male holotype after Ziegler *et al.* (2008), with the additional scale below the eye earmarked. (B) Female IEBR A.1016.33. (C) Male ZFMK 100000) compared to *O. lateralis* (D: Male IEBR 3645). Supralabials are numbered to show the differences between the new series of *O. tamdaoensis* (B, C) and *O. lateralis* (D). Drawings: T. Ziegler

Based on the enlarged sample size for *O. tamdaoensis*, the combination of diagnostic characters must be expanded as follows:

- (1) nasal not divided below nostril;
- (2) 1-2 loreals, not in contact with internasals;
- (3) 1-2 preoculars; 2 postoculars; usually 1 subocular;
- (4) 1-2 anterior and 2-4 posterior temporals;
- (5) 9 (rarely 8) supralabials, only the fifth or fifth to sixth supralabial (rarely none) in contact with the eye;
- (6) 9-10 (rarely 11) infralabials;
- (7) first pair of chin shields longer than the second pair;
- (8) dorsal scales smooth anteriorly, keeled posteriorly; in 19-17-17 rows;
- (9) 0-4 pre- and 162-176 ventrals; preloocal divided; 48-51 divided subcaudals;
- (10) uniform olive grey dorsum, with a dark longitudinal lateral stripe within the dark flank coloration; ventral side pale, without sharp transition towards the dark dorsal coloration, tip of the subcaudal region may bear dark mottling.

In the molecular analyses, the final matrix consisted of 1100 aligned characters, of which 268 were parsimony informative. The alignment did not contain gaps. Maximum parsimony analysis of the dataset recovered a single most parsimonious tree with 654 steps (CI = 0.73; RI = 0.71). In the ML analysis, the score of the single best tree found was 4252.62 after 287 arrangements were tried. All ingroup nodes received strong support values from all analyses, except for the placement of *Opisthotropis cheni* + *O. latouchii*, which was only strongly corroborated by the MP analysis. *O. tamdaoensis* was recovered as a sister taxon of *O. lateralis* with high statistical values from all analyses (Fig. 5). Two taxa showed about 6% genetic divergence. The *O. lateralis* from Guangxi in southern China was estimated to be about 2% divergence towards Vietnamese *O. lateralis*.

Based on the meanwhile enlarged sample size and thus extended range of morphological characters in *O. tamdaoensis*, not all characters mentioned in Ziegler *et al.* (2008) as being distinctive between the latter species and *O. lateralis* could withstand, such as number



Fig. 4. Lateral views of two of the newly collected *Opisthotropis lateralis* in life. (A) Male ZFMK 100805. (B) Juvenile ZFMK 100806; the characteristic black lateral stripe that sharply separates the dark dorsal colouration from the light venter is well discernible. Photos: T. Ziegler

and arrangement of preoculars (only one preocular present in the holotype), temporals (2 anterior and 3–4 posterior temporals in the holotype) and subocular scales (existence of an additional “postsubocular” scale that is surrounded by the lower anterior temporal, the lower postocular, subocular, and two supralabials in the holotype), as well as total size.

However, there remain still clear morphological differences between the sister taxa [after Pope (1935), Bourret (1936), Smith (1943), and our own data presented herein, see Tables 2-3, Figs 3-4]:

- 1) *O. tamdaoensis* has 9 (rarely 8) supralabials versus 10 [very rarely 9 or 11] in *O. lateralis*;
- 2) *O. tamdaoensis* has only the fifth or fifth and sixth supralabials (very rarely none) in contact with the eye, whereas in *O. lateralis* very rarely the fifth or even none supralabial, but usually supralabials 5-6, 6, 6-7, or 5-7 are entering the orbit, and
- 3) *O. tamdaoensis* has a black lateral stripe that does not sharply separate the dark dorsum from the pale ventral pattern (sharply separated in the case of *O. lateralis*) and rather takes course within the dark flank coloration; dark dorsum in *O. tamdaoensis* without sharp transition towards the light venter.

DISCUSSION

Based on a new *Opisthotropis* collection from the type locality of *O. tamdaoensis* the morphological definition of the species could be expanded, for the first time also including complete subcaudal counts and female individuals. The existence of an additional “postsubocular” scale that is surrounded by the lower anterior temporal, the lower postocular, subocular, and two supralabials, considered as a diagnostic character by Ziegler *et al.* (2008), revealed to be an abnormality of the holotype. The molecular analyses revealed *O. tamdaoensis* to be the sister species of *O. lateralis*, which is morphologically similar. Based on the herein expanded morphological definition of *O. tamdaoensis*, not all characters given as distinctive between the latter species and *O. lateralis* in Ziegler *et al.* (2008) could withstand. However, the number and arrangement of supralabials in concert with the dorsal colour pattern and the course of the dark lateral stripe still serve as good diagnostic characters to morphologically distinguish *O. tamdaoensis* from *O. lateralis*. The distinct specific status of the latter taxa is also corroborated by the molecular differentiation of about 6% between both species.

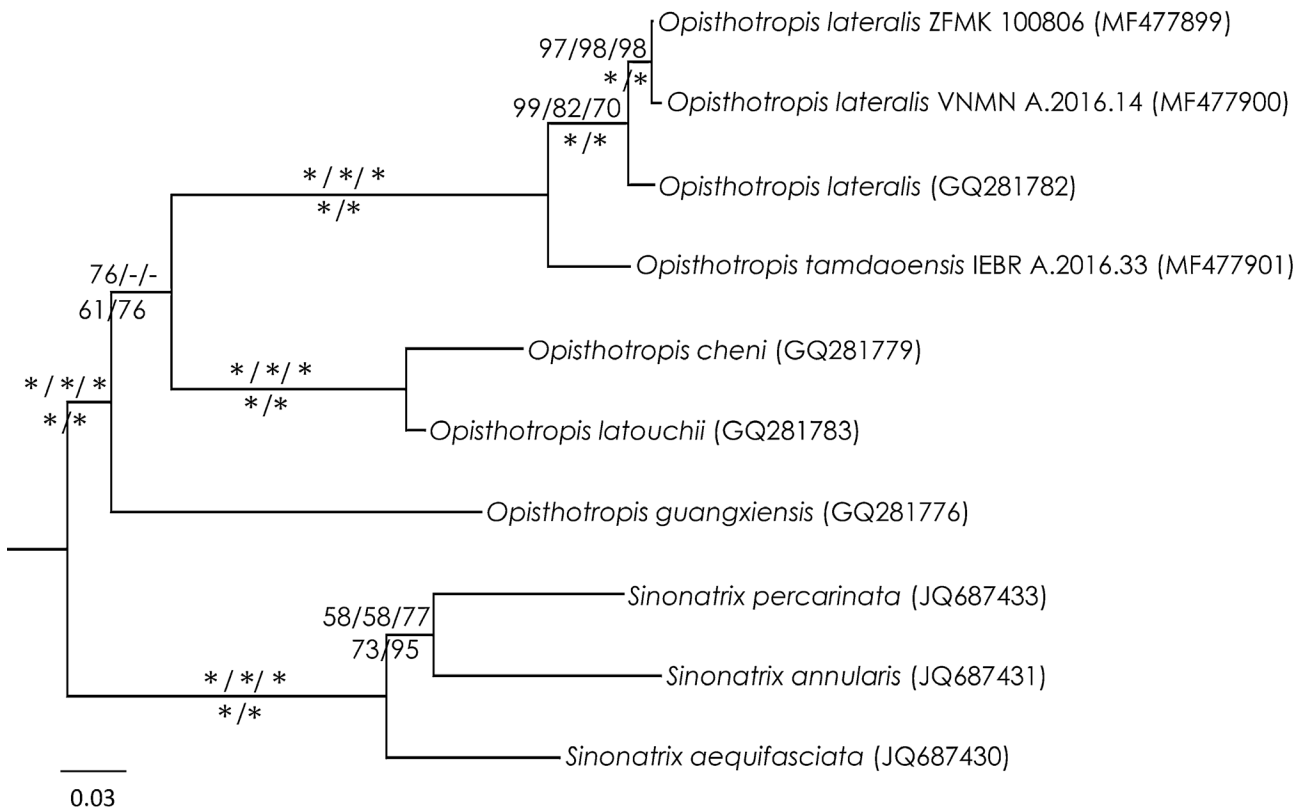


Fig. 5. Combined Bayesian phylogram based on a partial cytochrome *b* fragment. Numbers above and under branches are MP/combined ML/partitioned ML bootstrap values and combined/partitioned Bayesian posterior probabilities (>50%), respectively. Hyphen and asterisk denote <50% and 100% values, respectively.

Table 2. Sex, morphometry and scalation of the new series of *Opisthotropis lateralis* from northern Vietnam's Bac Giang, Cao Bang and Quang Ninh provinces; values given in brackets indicate infrequent condition.

	IEBR 3629	IEBR 3644	IEBR 3645	IEBR A.2016.35	ZFMK 100805	Range (males)	IEBR A.2016.36	VNMN A.2016.15	VNMN A.2016.14	Range (females)	ZFMK 100806	Range (total)
Sex	male	male	male	male	male	male	female	female	female	female	juv.	
TL	465	456	463	485	460	Max. 485	490	522	361	Max. 522	223	Max. 522
SVL	397	398	396	420	395	Max. 420	417	438	316	Max. 438	193	Max. 438
TaL	68	68	67	65	65	Max. 68	73	84	45	Max. 84	30	Max. 84
TaL/TL	0.148	0.149	0.144	0.134	0.141	0.134-0.149	0.148	0.160	0.124	0.124-0.160	0.134	0.124-0.160
Teeth max		27-28	-	-	-	27-28	-	27-28	27	27-28	-	27-28
SL	10/10	10/10	10/10	10/10	10/10	10	10/10	10/10	10/10	10	11/11	10(11)
SL/orbit	6-7/6-7	6/6	6/6	5/6	6/6	6(5, 7)	6/6	6-7/5-6	5-6/6	5-6(7)	0	5-7(0)
IL	10/10	8/10	10/10	10/10	10/10	10(8)	10/10	10/10	9/10	10(9)	10/10	10(8, 9)
PreOc	1/1	1/1	2/2	2/1	2/2	1-2	2/2	1/1	1/2	1-2	2/2	1-2
SubOc	1/1	1/1	1/1	1/1	0	1(0)	1/1	1/1	1/1	1	1/2	1(0, 2)
PostOc	2/2	2/2	2/2	2/3	2/3	2(3)	2/2	2/2	2/2	2	2/2	2(3)
Lor	1/1	1/1	1/1	1/1	1/1	1	1/1	1/1	1/1	1	2/1	1(2)
Atem	1/1	2/2	1/1	1/1	1/1	1(2)	1/1	2/1	1/1	1(2)	2/2	1(2)
PTem	2/2	2/3	1/1	3/2	2/2	2(1,3)	3/2	4/2	2/2	2(3,4)	2/2	2(1,3,4)
DSR	19-17-17	19-17-17	19-17-17	19-17-17-	19-17-17	19-17-17	19-17-17	19-17-17	19-17-17	19-17-17	19-17-17	19-17-17
PreVen	2	2	2	2	3	2-3	3	0	2	0-3	2	0-3
Ven	186	183	182	186	186	182-186	176	186	167	167-186	186	167-186
Prec	divided	divided	divided	divided	divided	divided	divided	divided	divided	divided	divided	divided
Subc	-	51	50	48	50	48-51	52	45	-	45-52	51	45-52

Table 3. Sex, morphometry and scalation data of *Opisthotropis lateralis* from the literature (data from Hecht *et al.*, 2013, and Gawor *et al.*, 2016 modified) M: in males, F: in females.

Sex	Pope (1935)	Bourret (1936)	Smith (1943)	Ziegler <i>et al.</i> (2008) male (IEBR 83)	Hecht <i>et al.</i> (2014) male (ZFMK 93904)	Gawor <i>et al.</i> (2016) female (IEBR A.2013.54)
TL	437	360	360	417	472	462
SVL	-	-	-	355	407	387
TaL	-	-	-	62	65	75
TaL/TL	-	-	-	0.149	0.138	0.162
Teeth max	-	-	-	26	-	-
SL	10(9, 11)	10	10-11	11/10	10/10	10/10
SL/orbit	5-7	5-6	5-6	6-7/6	6/6	5-6/5-6
IL	-	-	-	10/10	9/9	9/9
PreOc	1	2	2	2/2	2/2	2/2
SubOc	-	-	-	0/1	0	0
PostOc	2	2	2	2/2	2/2	2/2
Loreal	-	-	-	1/1	1/1	1/1
ATem	1	1	1	1/1	1/1	1/1
PTem	2	2	2	3/3	3/2	2/2
DSR	17 at midbody	17 at midbody	17 at midbody	19-17-17	19-17-17	17-17-17
PreVen	-	-	-	4	2	2
Ven	M: 161-173 F: 159-162	172	159-173	183	184	166
Prec	-	-	-	divided	divided	divided
Subc	M: 51-54 F: 49-56	45	49-56	51	49	45

Concerning the morphological examination of a new series of *O. lateralis* from Vietnam, the dorsal scale row count at the neck in the *O. lateralis* specimen IEBR A.2013.54 from Bai Tu Long was divergent (17 instead 19). However, this seems to represent an abnormality, as another individual from Bai Tu Long (VNMNA.2016.14) showed the species specific dorsal scale row count at the neck (19) and furthermore showed no divergent position in the phylogenetic tree compared to other *O. lateralis* from Vietnam.

The examination of the new series of *O. lateralis* from Vietnam further revealed different ventral scale counts compared with data sorted by sex provided by Pope (1935) for *O. lateralis* from China: 182-186 ventrals in males studied by us from Vietnam versus 161-173 ventrals in males from China, and 166-186 ventrals in females studied by us from Vietnam versus 159-162 in females from China. The herein exemplarily counted maxillary teeth for Vietnamese *O. lateralis* (26-28, n = 4: 2 males, 2 females) agreed well with the known maxillary teeth count of the holotype from northern Vietnam (27); according to Pope (1935), who referred to Chinese *O. lateralis*, Mell (1930) and Fan (1931) only mentioned 18 and 18-20 maxillary teeth respectively, and Pope (1935) furthermore stated how difficult and uncertain this character is. The *O. lateralis* from Guangxi in southern China (Guo *et al.*, 2012) included in the molecular tree (Fig. 5) also showed some genetic divergence towards Vietnamese *O. lateralis*. As recent taxonomic research in a semiaquatic squamate reptiles living in the Vietnam – China border region revealed distinct taxa to be involved (van Schingen *et al.*, 2016), further taxonomic research of *O. lateralis* thus could be interesting and reveal the presence of an undescribed species.

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