A new species in the *Pareas hamptoni* group (Squamata, Pareidae) from southeastern Laos

Bryan L. Stuart[1,*], Sengvilay Seateun[2], Niane Sivongxay[3], Siliphone Souvannavong[2], Somphouthone Phimmachak[2]

1 *North Carolina Museum of Natural Sciences, 11 West Jones Street, Raleigh, North Carolina 27601, USA*

2 *Department of Biology, Faculty of Natural Sciences, National University of Laos, Dongdok Campus, P.O. Box 7322, Vientiane, Laos*

3 *SEAMEO Regional Centre for Community Education Development, Ministry of Education and Sports, Dongdok, Xaithany District, P.O. Box 67, Vientiane, Laos*

Corresponding author, E-mail: bryan.stuart@naturalsciences.org

ABSTRACT

The slug-eating snakes of the *Pareas hamptoni* species group consist of approximately 15 species distributed across mainland Southeast Asia into northeastern India and southern China. A single specimen collected from the Dakchung Plateau in Xekong Province of southeastern Laos is shown to be molecularly and morphologically distinct from all related species in the *P. hamptoni* species group and is described as a new species. *Pareas capitulatus* **sp. nov.** is a smooth-scaled species having a distinctively narrow head and pattern on the nuchal region that was recovered as the sister taxon to approximately half of the members of the *P. hamptoni*

species group. The inclusion of additional samples of *P. geminatus* from northern Laos demonstrated the non-monophyly of that taxon with respect to the morphologically similar *P. xuelinensis* and *P. yunnanensis*, all of which have type localities in Yunnan Province of southern China. To reconcile this taxonomic problem, *P. geminatus* and *P. xuelinensis* are treated as junior synonyms of *P. yunnanensis*. With these revisions, three species in the *P. hamptoni* species group are recognized from Laos: *P. capitulatus* **sp. nov**., *P. formosensis*, and *P. yunnanensis*. Further field surveys on the Dakchung Plateau and vicinity are needed to determine the geographic distribution and morphological variation in *P. capitulatus* **sp. nov**.

Keywords: Dakchung Plateau, integrative taxonomy, *Pareas geminatus, Pareas xuelinensis, Pareas yunnanensis*

Running title: New *Pareas* from Laos

INTRODUCTION

The slug-eating snakes of the genus *Pareas* Wagler, 1830 consist of approximately 31 species distributed from the Sundaic islands of Southeast Asia northward onto the mainland throughout Indochina into northeastern India and southern China (Uetz et al., 2024). Numerous, recent, molecular phylogenetic and morphological analyses have resulted in the recognitions of species groups as well as partitioning of geographically widespread species into more narrowly endemic species (e.g., Ding et al., 2020; Vogel et al., 2020; Wang et al., 2020; Poyarkov et al., 2022; Liu et al., 2023a,b, 2024). Poyarkov et al. (2022) recognized six species groups within two subgenera

of *Pareas*, specifically the *P. carinatus* and *P. nuchalis* groups within the subgenus *Pareas*, and the *P. chinensis*, *P. hamptoni*, *P. margaritophorus*, and *P. monticola* species groups within the subgenus *Eberhardtia*.

The *P. hamptoni* group contains nearly half of the currently recognized species diversity of the genus. *Pareas hamptoni* (Boulenger, 1905) with Mogok, Myanmar as type locality was long considered to be a single geographically widespread species across mainland Southeast Asia and southern China. Recent taxonomic revisions, aided by molecular data, have resulted in the current recognition of 15 species in the *P. hamptoni* group (You et al., 2015; Ding et al., 2020; Wang et al., 2020; Liu & Rao, 2021; Poyarkov et al., 2022; Liu et al., 2023a,b, 2024).

In May 2011, we collected a single specimen of the *P. hamptoni* species group from the Dakchung Plateau in Xekong Province of southeastern Laos (Figure 1) that differed morphologically from other members of the group, notably in head shape and color pattern on the nuchal region. In this study, the Dakchung Plateau taxon is compared to its relatives using molecular phylogenetic and morphological data, and based on the findings, is described as a new species. Other samples of *Pareas* from our collaborative fieldwork are also included in the molecular phylogenetic analyses, and the findings showed that *P. geminatus* Ding, Chen, Suwannapoom, Nguyen, Poyarkov & Vogel, 2020 from northern Laos and Thailand is more closely related to *P. xuelinensis* Liu & Rao, 2021 and *P. yunnanensis* (Vogt, 1922) from Yunnan, China, than to the holotype and topotypes of *P. geminatus* from Yunnan, China, necessitating taxonomic revision.

MATERIALS AND METHODS

Specimens were collected by hand, photographed in life, humanely euthanized by cardiac injection of a high concentration of tricaine methanesulfonate (MS-222), and fixed in 10% formalin after preserving liver tissue in 20% DMSO-salt saturated storage buffer, RNAlater (Invitrogen), or 95–100% ethanol. Specimens were later soaked in water for several hours to remove formalin and transferred to 70% ethanol for permanent storage at the North Carolina Museum of Natural Sciences, Raleigh, USA (NCSM) and Department of Biology, Faculty of Natural Sciences, National University of Laos (NUOL).

Morphology

Measurements were taken to the nearest 0.1 mm with dial calipers under a dissecting microscope except snout-vent length (SVL) and tail length (TaL) were taken to the nearest mm with a soft measuring tape. Measurements and meristic counts were taken following Wang et al. (2020) and Gong et al. (2023). Measurements taken were snout-vent length (SVL); tail length (TaL); total length (TL), obtained by adding SVL and TaL; relative tail length (TaL/TL); head length from tip of snout to commissure of jaws (HLJ); head length from tip of snout to rear of maxilla (HLM); maximum head width (HW); and eye diameter (ED). Meristic characters taken were number of dorsal scales counted at one head length behind the head (ASR), mid-body (MSR), and one head length before vent (PSR); number of enlarged vertebral scale rows (VSE); number of keeled dorsal scale rows at mid-body (KMD); number of ventral scales (VEN), counted following Dowling (1951); number of subcaudal scales (SC), not including terminal scute; number of cloacal plates (CP); number of supralabials (SL); number of infralabials (IL); number of loreals (LOR); number of supraoculars (SupraOc); number of preoculars (PreOc); number of

presuboculars (PreSubOc); number of suboculars (SubOc); number of postoculars (PostOc); number of anterior temporal scales (At); and number of posterior scales (Pt). Paired meristic characters are given as right/left. Color terminology and codes follow Köhler (2012).

Comparative data for *P. formosensis* (Van Denburgh, 1909) were taken from the original description, examined material (Appendix I), and expanded descriptions (Ota et al., 1997; You et al., 2015; David et al., 2023). Comparative data for other species were taken from their original descriptions (Boulenger, 1905; Pope, 1928; Ding et al., 2020; Liu & Rao, 2021; Liu et al., 2024) as well as expanded descriptions of *P. hamptoni*, *P. niger* (Pope, 1928), and *P. yunnanensis* (Ding et al., 2020; Wang et al., 2020; Liu et al., 2023b). The description format generally follows Liu et al. (2024). Ocular scales (notably presubocular, subocular, and postocular scales) appear to be inconsistently interpreted by authors and are not used in comparisons based on literature.

Molecular sequencing

Total genomic DNA was extracted from liver tissue from 42 *Pareas* specimens (Table 1) using the DNeasy Blood and Tissue Kit (Qiagen). A 1,150–1,1153 nucleotide basepair (bp) fragment of mitochondrial (mt) DNA that encodes part of the tRNA-Glu, the complete cytochrome *b*, and part of the tRNA-Thr genes (cyt *b*), was amplified at annealing temperature (T_m) 49ºC using the primers L14910 and H16064 (Burbrink et al., 2000). An 862-868 bp fragment of mt DNA that encodes part of the NADH dehydrogenase subunit 4 gene, the complete tRNA-His and tRNA-Ser genes, and part of the tRNA-Leu gene (ND4) was amplified at T_m 52ºC using the primers ND4 and Leu (Arèvalo et al., 1994). A 570 bp fragment of nuclear (nu) DNA that encodes part

of the oocyte maturation factor Mos (c-*mos*) gene was amplified at T_m 52ºC using the primers S77 and S78 (Lawson et al., 2005).

PCR products were cleaned using ExoSAP-IT and sequenced in both directions by direct double strand cycle sequencing using the BigDye Terminator version 3.1 Cycle Sequencing Kit and the amplifying primers on a 3500xl DNA Analyzer (all by Applied Biosystems). The internal primers L15584 (Burbrink et al., 2000) and H15149 (Kocher et al., 1989) were also used in the cyt *b* sequencing reactions. Sequences were edited using Geneious Prime 2024.0.7 (Biomatters Ltd.) and deposited in GenBank under accession numbers PQ677119–PQ677197, PQ677274–PQ677315.

Phylogenetic analysis

Homologous sequences of all currently recognized species of *Pareas* (primarily based on the datasets of Guo et al., 2011; Ding et al., 2020; Wang et al., 2020; Poyarkov et al., 2022), representatives of the pareid genera *Aplopeltura*, *Asthenodipsas*, and *Xylophis*, and the viperid outgroup *Ovophis tonkinensis* (following Pyron et al., 2013; Figueroa et al., 2016) were downloaded from GenBank (Table 1). Newly generated and downloaded sequences were aligned using the default parameters in the MAFFT 7.45 alignment algorithm (Katoh & Standley, 2013) implemented in Geneious Prime 2024.0.7 (Biomatters Ltd.). Alignments were visually checked to ensure that insertion-deletions did not disrupt translation of coding regions. The dataset was partitioned by tRNA and codon positions of cyt *b*, ND4, and c-*mos* for a total of 10 partitions. The best-fit partitioning scheme and models of sequence evolution were selected using the

Akaike Information Criterion (AICc) in Partition Finder 2 (Lanfear et al., 2017). Six partitions were selected with the models GTR+I+G for tRNA, cyt *b*, and ND4 first codon positions; GTR+I+G for cyt *b* second codon positions; GTR+I+G for cyt *b* and ND4 third codon positions; GTR+I+G for ND4 second codon positions; GTR+G for c-*mos* first and third codon positions; and GTR+G for c-*mos* second codon positions.

Bayesian inference (BI) was performed on the partitioned dataset using MrBayes 3.2.7a (Ronquist et al., 2012) on the Cyber infrastructure for Phylogenetic Research (CIPRES) Science Gateway version 3.3 (Miller et al., 2010). In each of four independent analyses, four chains were run for 20 million generations using the default priors, trees were sampled every 4,000 generations, and the first 25% of trees were discarded as 'burn-in'. The resulting trace plots were viewed using Tracer v.1.7 (Rambaut et al., 2018). A 50% majority-rule consensus of the post burn-in trees was constructed to calculate the posterior probabilities (PP) of nodes. Maximum likelihood (ML) analysis was performed on the partitioned dataset using raxml GUI 2.0 (Edler et al., 2021). The GTR+I+G model was applied to the six partitions selected by PartitionFinder 2 (Lanfear et al., 2017) in a single analysis. Nodal support values were estimated by the thorough bootstrap (BS) with 1,000 pseudoreplicates. Nodes with posterior probabilities ≥ 0.95 and bootstrap values ≥ 70 were considered supported. Uncorrected pairwise (*p*) distances were calculated using Geneious Prime 2024.0.7 (Biomatters Ltd.).

RESULTS

Phylogenetic analysis

The dataset contained 2,645 aligned characters and 219 taxa. In the BI analysis, the standard deviation of split frequencies was 0.004321 among the four runs, and the Estimated Sample Sizes (ESS) of parameters were ≥ 1,574. The ML analysis recovered a single tree with log likelihood of -38861.615473. The BI and ML trees had very similar topologies.

The Dakchung Plateau taxon was deeply nested within the *P. hamptoni* species group (sensu Poyarkov et al. 2022) and recovered with strong support (PP 1.00/BS 100) as the sister taxon to a clade containing *P. formosensis*, *P. "geminatus"*, *P. guanyinshanensis*, *P. hamptoni*, *P. niger*, *P. "xuelinensis"*, and *P. yunnanensis* (Figure 2). The Dakchung Plateau taxon had uncorrected pairwise divergences in the coding region of cyt *b* of 8.4–15.2% from these taxa.

Pareas "*geminatus*" was recovered as a broadly non-monophyletic taxon with respect to *P. "xuelinensis"* and *P. yunnanensis* (Figure 2B). The holotype and topotypes of *P. "geminatus"* were recovered as more closely related to topotypes of *P. yunnanensis* than to paratypes and referred localities of *P. "geminatus"* from Thailand and Laos (Ding et al., 2020; David et al., 2023). *Pareas* "*xuelinensis*" was also nested within referred localities of *P. "geminatus"* from Thailand and Laos (Ding et al., 2020; David et al., 2023).

Taxonomy

The clade containing *P. yunnanensis*, *P. "xuelinensis"*, and *P. "yunnanensis"* exhibited similar genetic structure to that observed in the geographically widespread species *P. formosensis* (Figure 2B). Moreover, samples from localities spanning this clade, including Phou Phan in Xamneua District, Houaphanh Province, Laos through northern Thailand to the type locality in Yunnan Province, China, were all referred to a single morphological species in the account of *P.*

"geminatus" by David et al. (2023). To resolve the non-monophyly of *P. geminatus* Ding, Chen, Suwannapoom, Nguyen, Poyarkov & Vogel, 2020 with respect to *P. xuelinensis* Liu & Rao, 2021 and *P. yunnanensis* (Vogt, 1922), *P. geminatus* and *P. xuelinensis* are treated as subjective junior synonyms of *P. yunnanensis*, the oldest available name for this clade.

***Pareas yunnanensis* (Vogt, 1922)**

Chresonymy:

Amblycephalus yunnanensis Vogt, 1922:142; Mell, 1922:125; Pope, 1935:381.

Amblycephalus monticola yunnanensis Mell, 1931:216.

Pareas yunnanensis Rao & Yang, 1992:140; Guo, Wang & Rao, 2020:565; Liu, Zhang, Poyarkov, Hou, Wu, Rao, Nguyen & Vogel, 2023:9; Liu, Mo, Li, Li, Luo, Rao & Li, 2024:4.

Pareas chinensis (part) Zhao & Adler, 1993:249.

Pareas hamptoni Vogel, 2010:219.

Pareas cf. *yunnanensis* Poyarkov, Nguyen, Pawangkhanant, Yushchenko, Brakels, Nguyen, Nguyen, Suwannapoom, Orlov & Vogel, 2022:33.

Synonymy:

Pareas geminatus Ding, Chen, Suwannapoom, Nguyen, Poyarkov & Vogel, 2020:184; Liu & Rao, 2021:121; Yang, Yeung, Huang & Yang, 2021:41; Wang, Lyu, Wang, Qi & Che, 2022:9; Maury, David & Sudavanh, 2022:88; Poyarkov, Nguyen, Pawangkhanant, Yushchenko, Brakels, Nguyen, Nguyen, Suwannapoom, Orlov & Vogel, 2022:14; David, Teynié & Vogel, 2023:723; Gong, Wu, Huang, Xu, Yang, Liu, Liang & Lee, 2023:3; Liu, Yang, Rao, Guo & Rao, 2023:170; Liu, Zhang, Poyarkov, Hou, Wu, Rao, Nguyen &

Vogel, 2023:4; Poyarkov, Nguyen, Popov, Geissler, Pawangkhanant, Neang, Suwannapoom, Ananjeva & Orlov, 2023:385; Liu, Mo, Li, Li, Luo, Rao & Li, 2024:3.

Pareas xuelinensis Liu & Rao, 2021:128; Yang, Yeung, Huang & Yang, 2021:41; Poyarkov, Nguyen, Pawangkhanant, Yushchenko, Brakels, Nguyen, Nguyen, Suwannapoom, Orlov & Vogel, 2022:14; Wang, Lyu, Wang, Qi & Che, 2022:9; Gong, Wu, Huang, Xu, Yang, Liu, Liang & Lee, 2023:3; Liu, Yang, Rao, Guo & Rao, 2023:170; Liu, Zhang, Poyarkov, Hou, Wu, Rao, Nguyen & Vogel, 2023:5; Liu, Mo, Li, Li, Luo, Rao & Li, 2024:2.

Revised diagnosis. A species in the *P. hamptoni* group (sensu Poyarkov et al., 2022) having 3–7 rows of keeled (sometimes weakly) dorsal scale rows on posterior portion of body; supralabials 6–8; infralabials 6–8; loreal rarely in narrow contact with eye; ventrals 169–188; subcaudals 59–93; top of head usually dark brown or black, with two broad dark bands extending from parietal to transverse dark bar on neck; and side of head without stripes, but one or more dark spots often present (Vogt, 1922; Pope, 1935; Ding et al., 2020; Liu & Rao, 2021; Liu et al., 2023b).

Revised geographic distribution. *Pareas yunnanensis* occurs in southern China (Yunnan Province), northern Thailand, and northern Laos (Vogt, 1922; Pope, 1935; Vogel, 2010; Ding et al., 2020; Liu & Rao, 2021; David et al. 2023; Liu et al., 2023b; this study). It is expected to also occur in northeastern Myanmar and northwestern Vietnam.

The Dakchung Plateau taxon was recovered as a basal taxon that was phylogenetically and morphologically very dissimilar to other members of the *P. hamptoni* species group. As a result of these corroborating lines of evidence, it is described as a new species as follows.

***Pareas capitulatus* sp. nov.**

Holotype: NCSM 78628 (field tag BLS 14402), adult female, Laos, Xekong Province, Dakchung District, Dakchung Plateau, Phou Ajol, 15.68239ºN, 107.19424ºE, 1,475 m.a.s.l., coll. 19 May 2011 by Bryan L. Stuart, Somphouthone Phimmachak, and Sengvilay Seateun (Figures 3, 4).

Diagnosis: *Pareas capitulatus* **sp. nov.** is distinguished from all other species of *Pareas* by having the combination of yellow-brown colouration with transverse dark bars on body; frontal shield-shaped, with lateral sides converging posteriorly; all body scales smooth; single vertebral scale row slightly enlarged; head distinctly narrow, with eyes projecting beyond parallel lateral margins of head in dorsal view; supralabials seven; infralabials six; ventral scales 175; subcaudals 75; a complete light band on occiput followed posteriorly by a complete dark nuchal marking; and two dark stripes on side of head consisting of an oblique dark stripe from posterior margin of eye to mouth and a transverse dark stripe from top of head to near corner of mouth.

Description of holotype: Adult female, SVL 461 mm, TaL 125 mm, TL 586 mm, TaL/SVL 0.27, TaL/TL 0.21; body elongated, laterally compressed; head elongate, in dorsal view oval, slightly distinct from neck, eyes projecting beyond lateral margins of head, lateral margins of head parallel (Figure 5); snout truncate in dorsal view, rounded in lateral view, projecting beyond lower jaw, HLJ 13.3 mm, HLM 17.0 mm, HW 7.8 mm; rostral wider (3.6 mm) than high (2.8 mm), slightly visible from above, with inverted U-shaped notch in lower margin at mouth; nasal undivided; internasal elongated, in contact with rostral, nasal, loreal, and prefrontal; prefrontal

trapezoidal, in contact with internasal, loreal, preocular, eye, supraocular, and frontal; frontal shield-shaped, longer (5.5 mm) than wide (4.2 mm), lateral sides converging posteriorly and not parallel to body axis; parietals large, longer (7.2/7.1) than wide (3.7/3.7), narrowing posteriorly, median suture (4.8 mm) slightly shorter than length of frontal (5.5 mm); loreal single, not in contact with eye; eye round, slightly enlarged, pupil vertical, elliptical, ED 3.4 mm; supraocular one, approximately triangular; preocular one; presubocular one, elongate, extending from preocular to point below first one-third of eye; subocular one, in contact with most of central portion of lower margin of eye; postoculars two, upper larger; anterior temporals two, posterior temporals three; supralabials 7/7, first and second in contact with nasal, not in contact with eye; infralabials 6/6, anterior-most in contact with its opposite between mental and anterior chin shield; mental ovoid; chin shields in three pairs, interlaced, anterior shield in contact with first through third infralabials, second shield in contact with third through fifth infralabials, no mental groove under chin and throat; ventral scales 175; cloacal plate undivided; subcaudals 75, paired; dorsal scales in 15–15–15 rows, all smooth and without apical pits, single vertebral scale row slightly enlarged.

Coloration of holotype*:* In life (Figure 3), head and dorsal surfaces of body yellow-tan (Light Yellow Ocher Color 13) with dark brown (Dark Drab Color 45) speckling; top of head mostly dark brown (Drab Color 19) with dark brown (Drab Color 19) oblique stripe from posterior margin of prefrontal through eye to mouth and a second dark brown (Drab Color 19) transverse stripe from dark marking on top of head through posterior temporals to mouth; large dark brown (Dark Drab Color 45) blotch on nape, complete across vertebrals, approximately nine body scale rows in length, completely separated (4–5 scale rows) from dark marking on top of head;

approximately 40 transverse, dark brown (Drab Color 19), irregular stripes on each side of body, darker and wider (2–3 scale rows) and sometimes X-shaped or contacting adjacent stripe on anterior portion of body, becoming lighter and narrower (1–2 scale rows) and sometimes incomplete on posterior portion of body, stripes becoming irregular spots on tail; venter light yellow (Pale Horn Color 11) with dark brown (Dark Drab Color 45) speckling; eye greenish-yellow (Olive Horn Color 16). In preservative (Figure 4), yellow-tan (Light Yellow Ocher Color 13) on head and dorsal surfaces of body slightly faded (Buff Color 5).

Distribution and natural history: *Pareas capitulatus* **sp. nov.** is currently only known by the holotype from Dakchung District, Xekong Province, Laos (Figure 1) at 1,475 m.a.s.l. The holotype was found at night (1922 hours) in wet evergreen forest on a shrub approximately 1 m above the ground, not in the immediate proximity of a water body. The species occurs in near sympatry with *P. formosensis* from adjacent Phou Koungking in Dakchung District (NUOL 01812–13).

Etymology: The specific epithet *capitulatus* is a Latin adjective for "having a small head," in reference to the distinctly narrow head of the new species. Suggested common names are Narrow-headed Snail-eating Snake (English) and ງູນ້ອຍດັກຈິ (phonetically *Ngou Nasan Dakchung*; Lao).

Comparisons: *Pareas capitulatus* **sp. nov.** is most closely related (Figure 2) and morphologically similar to other members of the *P. hamptoni* species group, consisting of *P. formosensis*, *P. guanyinshanensis* Liu, Mo, Li, Li, Luo, Rao & Li, 2024, *P. hamptoni*, *P. niger*,

and *P. yunnanensis* (this concept of *P. yunnanensis* includes *P. "geminatus"* and *P. "xuelinensis"*).

Pareas capitulatus **sp. nov.** differs from all of these species by having a distinctly narrow head with eyes projecting beyond parallel lateral margins of head in dorsal view (posterior head region wider than anterior head region and eyes not projecting beyond lateral margins of head in dorsal view in these species); and by having a complete light band on occiput followed posteriorly by a complete dark nuchal marking (solid black head marking extending onto dorsum in *P. niger*, light vertebral stripe on nuchal region in *P. formosensis*, *P. guanyinshanensis*, *P. hamptoni*, and *P. yunnanensis*). *Pareas capitulatus* **sp. nov.** further differs from all of these species except *P. formosensis* by having smooth body scales (3–9 keeled dorsal scale rows in *P. guanyinshanensis*, *P. hamptoni*, *P. niger*, and *P. yunnanensis*). *Pareas capitulatus* **sp. nov.** further differs from *P. niger* by having yellow-brown body colouration with narrow, dark, transverse bands (dorsum mostly black in *P. niger*). *Pareas capitulatus* **sp. nov.** further differs from *P. yunnanensis* by having an oblique dark stripe from posterior margin of eye to mouth and a transverse dark stripe from top of head to near corner of mouth (side of head without stripes, sometimes one or more dark spots present, in *P. yunnanensis*).

DISCUSSION

Samples of the *P. hamptoni* species group from Laos were found to phylogenetically belong to three separate clades: a smooth-scaled clade from throughout the country referred to *P. formosensis*, a moderately-keeled clade from northern Laos referred here to *P. yunnanensis* (with *P. geminatus* and *P. xuelinensis* as its junior synonyms), and a smooth-scaled clade from the

Dakchung Plateau of southeastern Laos with distinctive head shape and colouration that is the sister taxon to all of these species, as well as to *P. niger*, *P. guanyinshanensis*, and *P. hamptoni*, that is newly described here as *P. capitulatus* **sp. nov.**

Pareas yunnanensis was considered a distinct taxon at the times of the descriptions of *P. geminatus* and *P. xuelinensis*, but molecular data for *P. yunnanensis* did not yet exist (Guo et al., 2020; Ding et al., 2020; Liu & Rao, 2021). Liu et al. (2023b) generated invaluable topotypic sequences of *P. yunnanensis* from Dali, Yunnan, China, but all phylogenetic studies that utilized those sequences also included only topotypic sequences of *P. "geminatus"* from Jiangcheng, Yunnan, China (Liu et al., 2023a,b, 2024). By incorporating all available sequences of *P. "geminatus*," including paratypes and localities of other specimens referred morphologically to that species from Laos and Thailand (Ding et al., 2020; David et al., 2023), this study found *P. "geminatus"* to be broadly non-monophyletic with respect to *P. "xuelinensis"* and *P. yunnanensis*. Likewise, the inclusion of a topotype of *P. berdmorei unicolor* from Kampong Speu Province, Cambodia, in this study found the subspecies *P. b. unicolor* as defined by Poyarkov et al. (2022) to be broadly non-monophyletic with respect to *P. b. berdmorei* and *P. b. truongsonicus* (Figure 2A), necessitating further taxonomic work.

Only a single specimen of *P. capitulatus* **sp. nov.** is currently known, despite multiple field trips by the authors to the Dakchung Plateau (approximately 13 days of fieldwork in 2011, 25 days in 2022–2023). Phou Ajol has been designated as a National Protection Forest to serve as biodiversity offset from wind farm projects being developed on the Dakchung Plateau.

NOMENCLATURAL ACTS REGISTRATION

http://zoobank.org/45953DF0-0C4C-4B24-97FC-92F936433644

COMPETING INTERESTS

The authors declare that they have no competing interests.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Fieldwork in Laos was made possible by the Biodiversity Conservation Project, a cooperative agreement between the Wildlife Conservation Society Laos Program and the National University of Laos, with fieldwork permission and specimen export permits to the North Carolina Museum of Natural Sciences provided by the Ministry of Natural Resources and Environment (MoNRE), Vientiane. Fieldwork in Cambodia was made possible by the Fauna & Flora International Cambodia Program, Wild Earth Allies Cambodia Program, and the Ministry of Environment, Kingdom of Cambodia, with specimen export permits to the North Carolina Museum of Natural Sciences provided by the Ministry of Environment, Kingdom of Cambodia. Fieldwork in Vietnam was made possible by the Vietnam Ministry of Agriculture and Rural Development and the staff of Bidoup Nui-Ba National Park (permit number 3023/GT-BNN-KL).

AUTHOR CONTRIBUTIONS

B.L.S. and S.P. designed the study; all authors collected materials for study; B.L.S., S.S., S.S., and S.P. obtained morphological data; B.L.S. performed molecular and phylogenetic analyses;

B.L.S. and S.P. prepared the manuscript; all authors edited, revised, and approved the final version of the manuscript.

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APPENDIX I. COMPARATIVE MATERIAL EXAMINED.

Pareas formosensis.— LAOS: NCSM 77920–23, NUOL 00552, Champasak Province, Pakxong District, Dong Hua Sao National Park; NCSM 76555, Savannakhet Province, Vilabouli District; NCSM 85477, Khammouan Province, Boualapha District, Nakai-Nam Theun National Park; NUOL 00553, Xaisomboun Province, Hom District. VIETNAM: NCSM 77337, NCSM 80353–54, Lam Dong Province, Lac Duong District, Bi Doup-Nui Ba National Park; NCSM 79202, Quang Nam Province, Phuoc Son District, Song Thanh National Park; NCSM 79758, Kon Tum Province, Dak Glei District, Ngoc Linh National Park; FMNH 255567, Nghe An Province, Tuong Duong District, Pu Mat National Park; NCSM 79759, Nghe An Province, Que Phong District, Pu Hoat Proposed Nature Reserve.

Pareas yunnanensis.—LAOS: NCSM 86599, NUOL 00551, Houaphanh Province, Xamneua District, Phou Phan (= Phou Luang); NCSM 80841, Xieng Khouang Province, Kham District.

Table 1 Samples of *Pareas* and outgroup taxa used in the molecular phylogenetic analyses. Institutional and collector abbreviations of vouchers are defined in the source publications.

Species	Voucher	Locality	cyt *b*	ND4	c-*mos*	Sources
Aplopeltura boa	KIZ 011963	Malaysia	JF827673	JF827650	JF827696	Guo et al. (2011)
Asthenodipsas laevis	FMNH 241296	Malaysia, Sabah, Lahad Datu	KX660468	KX660596	KX660335	Figueroa et al. (2016)
Asthenodipsas lasgalenensis	LSUHC 9098	Malaysia, Pahang, Fraser's Hill	KC916755	MZ712267	MZ712299	Loredo et al. (2013), Poyarkov et al. (2022)
Ovophis tonkinensis	KIZ 011602	Vietnam, Phu Tho, Xuan Son	OP441880	OP441822	OP441931	Zeng et al. (2023)
Pareas abros	ZMMU R-14788	Vietnam, Thua Thien-Hue, A Roang	MZ712237	MZ712264	MZ712295	Poyarkov et al. (2022)
P. abros	ZMMU R-16392	Vietnam, Thua Thien-Hue, A Roang	MZ712236	MZ712263	MZ712294	Poyarkov et al. (2022)
P. abros	ZMMU R-16393	Vietnam, Quang Nam, Song Thanh N.P.	MZ712235	MZ712262	MZ712293	Poyarkov et al. (2022)
P. andersonii	CAS 235359	Myanmar, Chin, Nat Ma Taung N.P.	MT968772	MW287040	MW287022	Ding et al. (2020), Vogel et al. (2020)
P. atayal	HC 000618	China, Taiwan, Yilan	JF827685	JF827662	JF827711	Guo et al. (2011)
P. atayal	HC 000628	China, Taiwan, Taoyuan	JF827686	JF827663	JF827712	Guo et al. (2011)
P. atayal	HC 000711	China, Taiwan, Taipei	JF827688	JF827665	JF827714	Guo et al. (2011)
P. atayal	NMNS 05594	Taiwan, Taoyuan, Beiheng	KJ642124	MW287041	KJ642198	You et al. (2015), Ding et al. (2020)
P. baiseensis	ANU 000220008 = HSR 22185	China, Guangxi, Baise	OQ054328	OQ054329	—	Gong et al. (2023)
P. berdmorei "unicolor"	NCSM 84985	Laos, Savannakhet, Vilabouli	PQ677125	PQ677277	PQ677167	This study
P. berdmorei "unicolor"	NCSM 84988	Laos, Savannakhet, Vilabouli	PQ677126	PQ677278	PQ677168	This study
P. berdmorei "unicolor"	NCSM 99032	Cambodia, Kampot, Teuk Chou, Bokor N.P.	PQ677129	PQ677281	—	This study

P. berdmorei "unicolor"	SIEZC 20216	Vietnam, Lam Dong, Di Linh	MZ712228	MZ712254	MZ712284	Poyarkov et al. (2022)
P. berdmorei "unicolor"	ZMMU R-13679-1	Vietnam, Dong Nai, Cat Tien N.P.	MZ712229	MZ712255	MZ712285	Poyarkov et al. (2022)
P. berdmorei "unicolor"	ZMMU R-13679-2	Vietnam, Dong Nai, Cat Tien N.P.	MZ712230	MZ712256	MZ712286	Poyarkov et al. (2022)
P. berdmorei "unicolor"	ZMMU R-13753-1	Vietnam, Dong Nai, Ma Da N.R.	MZ712223	MZ712249	MZ712279	Poyarkov et al. (2022)
P. berdmorei "unicolor"	ZMMU R-13753-2	Vietnam, Dong Nai, Ma Da N.R.	MZ712224	MZ712250	MZ712280	Poyarkov et al. (2022)
P. berdmorei "unicolor"	ZMMU R-14013	Vietnam, Dong Nai, Ma Da N.R.	MZ712225	MZ712251	MZ712281	Poyarkov et al. (2022)
P. berdmorei "unicolor"	ZMMU R-14165	Vietnam, Binh Puoc, Bu Gia Map N.P.	MZ712231	MZ712257	MZ712287	Poyarkov et al. (2022)
P. berdmorei "unicolor"	ZMMU R-14263	Vietnam, Tay Ninh, Lo Go - Xa Mat N.P.	MZ712226	MZ712252	MZ712282	Poyarkov et al. (2022)
P. berdmorei "unicolor"	ZMMU R-14421	Vietnam, Lam Dong, Loc Bao	MZ712227	MZ712253	MZ712283	Poyarkov et al. (2022)
P. berdmorei berdmorei	AUP 01573	Thailand, Chiang Mai	MZ712218	MZ712244	MZ712276	Poyarkov et al. (2022)
P. berdmorei berdmorei	CAS 240362	Myanmar, Mon, Kin Pon Chaung	MZ712219	MZ712245	MZ712277	Poyarkov et al. (2022)
P. berdmorei berdmorei	CIB 098270	China, Yunnan, Mengla	JF827676	JF827652	JF827701	Guo et al. (2011)
P. berdmorei berdmorei	GP 1292	China, Yunnan, Mengla	MK135113	MK805378	MK135162	Wang et al. (2020)
P. berdmorei berdmorei	NCSM 79506	Laos, Luang Phabang, Luang Phabang	PQ677120	PQ677313	PQ677162	This study
P. berdmorei berdmorei	NCSM 79507	Laos, Xaignabouli, Xaignabouli	PQ677121	PQ677314	PQ677163	This study
P. berdmorei berdmorei	NCSM 80692	Laos, Phongsaly, Boun Tai	PQ677122	PQ677315	PQ677164	This study
P. berdmorei berdmorei	YBU 14124 = GP 3356	China, Yunnan, Mengla	MK135114	MK805379	MK135163	Wang et al. (2020)
P. berdmorei berdmorei	YBU 14141 = GP 3376	China, Yunnan, Mengla	MK135115	MK805380	MK135164	Wang et al. (2020)
P. berdmorei berdmorei	YBU 14142 = GP 3377	China, Yunnan, Mengla	MK135116	MK805381	MK135165	Wang et al. (2020)
P. berdmorei berdmorei	ZMMU R-16803	Thailand, Ratchaburi, Suan Phueng	MZ712220	MZ712246	MZ712278	Poyarkov et al. (2022)
P. berdmorei truongsonicus	NCSM 80935	Laos, Bolikhamxay, Viengthong, Nam Kading N.P.A.	PQ677123	PQ677275	PQ677165	This study
P. berdmorei truongsonicus	ZMMU R-14796	Vietnam, Quang Binh, Thanh Thach	MZ712222	MZ712248	MZ712289	Poyarkov et al. (2022)
P. berdmorei truongsonicus	ZMMU R-16801	Laos, Khammouan, Nahin	MZ712221	MZ712247	MZ712288	Poyarkov et al. (2022)

P. berdmorei unicolor	NCSM 79596	Cambodia, Kampong Speu, Aural, Phnom Aural W.S.	PQ677124	PQ677276	PQ677166	This study
P. berdmorei unicolor	NCSM 98703	Cambodia, Sihanoukville, Sihanoukville	PQ677127	PQ677279	PQ677169	This study
P. berdmorei unicolor	NCSM 98722	Cambodia, Sihanoukville, Sihanoukville	PQ677128	PQ677280	PQ677170	This study
P. boulengeri	GP 207	China, Sichuan, Anxian	MK135091	MK805356	MK135140	Wang et al. (2020)
P. boulengeri	GP 2923	China, Guizhou, Jiangkou	MK135090	MK805355	MK135139	Wang et al. (2020)
P. boulengeri	GP 3428	China, Anhui, Yixian	MK135094	MK805359	MK135143	Wang et al. (2020)
P. boulengeri	GP 4716	China, Hubei, Yidu	MK135093	MK805358	MK135142	Wang et al. (2020)
P. boulengeri	HSR 18074	China, Anhui, Qimen, Haungjialing	MN866896	MN866896	—	Huang et al. (2020)
P. boulengeri	KIZ 09965	China, Hubei, Enshi	JF827678	JF827655	JF827704	Guo et al. (2011)
P. boulengeri	KIZ 09966	China, Hubei, Jiannan	JF827679	JF827656	JF827705	Guo et al. (2011)
P. boulengeri	KIZ 09967	China, Hubei, Jianzhuxi	JF827680	JF827657	JF827706	Guo et al. (2011)
P. boulengeri	KIZ 09968	China, Hunan, Luxi	JF827681	JF827658	JF827707	Guo et al. (2011)
P. boulengeri	KIZ 09969	China, Hubei, Shennongjia	JF827682	JF827659	JF827708	Guo et al. (2011)
P. boulengeri	KIZ 09970	China, Hunan, Luxi	JF827683	JF827660	JF827709	Guo et al. (2011)
P. boulengeri	KIZ 09971	China, Hubei, Shennongjia	JF827684	JF827661	JF827710	Guo et al. (2011)
P. boulengeri	YBU 13323A = GP 3095	China, Hubei, Wufeng	MK135092	MK805357	MK135141	Wang et al. (2020)
P. boulengeri	YBU 17155 = GP 4827	China, Zhejiang, Chunan	MK135095	MK805360	MK135144	Wang et al. (2020)
P. boulengeri	YBU 17245 = GP 4886	China, Zhejiang, Chunan	MK135096	MK805361	MK135145	Wang et al. (2020)
P. capitulatus **sp. nov.**	NCSM 78628	Laos, Xekong, Dakchung, Phou Ajol	PQ677119	PQ677274	PQ677161	This study
P. carinatus carinatus	DL 2008-S039	Malaysia	JF827677	JF827653	JF827702	Guo et al. (2011)
P. carinatus carinatus	GP 1079	Malaysia	MK135110	MK805375	MK135159	Wang et al. (2020)
P. carinatus carinatus	KIZ 011970 = GP 5129	Malaysia	MK135112	MK805377	MK135161	Wang et al. (2020)

P. carinatus carinatus	KIZ 011972 = GP 5131	Malaysia	MK135111	MK805376	MK135160	Wang et al. (2020)
P. carinatus carinatus	LSUHC 10604	Malaysia, Kedah, Sungai Sedim	KC916748	MZ712261	MZ712292	Loredo et al. (2013), Poyarkov et al. (2022)
P. carinatus tenasserimicus	CAS 247982	Myanmar, Tanintharyi, Yaephyu	MZ712233	MZ712259	MZ712291	Poyarkov et al. (2022)
P. carinatus tenasserimicus	ZMMU R-16800	Thailand, Ratchaburi, Suan Phueng	MZ712234	MZ712260	MZ712290	Poyarkov et al. (2022)
P. chinensis	CIB 010140	China, Sichuan, Baoxing	JF827690	JF827667	JF827716	Guo et al. (2011)
P. chinensis	CIB 010141	China, Sichuan, Baoxing	JF827692	JF827669	JF827718	Guo et al. (2011)
P. chinensis	CIB 010144	China, Sichuan, Baoxing	JF827693	JF827670	JF827719	Guo et al. (2011)
P. chinensis	CIB 098269	China, Sichuan, Tianquan	JF827691	JF827668	JF827717	Guo et al. (2011)
P. chinensis	CIB 098272	China, Sichuan, Tianquan	JF827694	JF827671	JF827720	Guo et al. (2011)
P. chinensis	GP 2196	China, Sichuan, Junlian	MK135088	MK805353	MK135137	Wang et al. (2020)
P. chinensis	GP 2383	China, Sichuan, Hongya	MK135089	MK805354	MK135138	Wang et al. (2020)
P. dulongjiangensis	KIZ R201607	China, Yunnan, Gongshan	OQ718498	—	—	Liu et al. (2023a)
P. formosensis	FMNH 255567	Vietnam, Nghe An, Tuong Duong, Pu Mat N.P.	AY425806	—	MZ712274	Poyarkov et al. (2022), GenBank unpublished
P. formosensis	FMNH 258687	Laos, Champasak, Pakxong	AY425809	—	—	GenBank unpublished
P. formosensis	GP 2164	China, Hainan	MK135069	MK805334	MK135118	Wang et al. (2020)
P. formosensis	GP 2165	China, Hainan	MK135070	MK805335	MK135119	Wang et al. (2020)
P. formosensis	GP 4581	China, Zhejiang, Jingning	MK135072	MK805337	MK135121	Wang et al. (2020)
P. formosensis	H26-HAM01	China, Guangdong	MW287061	MW287043	MW287024	Ding et al. (2020)
P. formosensis	LSU 2020MLTWDT01	China, Zhejiang, Lishui, Baiyunshan	MW531674	MW531674	—	Liu et al. (2021)
P. formosensis	NCSM 77337	Vietnam, Lam Dong, Lac Duong, Bi Doup-Nui Ba N.P.	PQ677130	PQ677282	PQ677171	This study
P. formosensis	NCSM 77920	Laos, Champasak, Pakxong, Dong Hua Sao N.P.	PQ677131	PQ677283	PQ677172	This study

P. formosensis	NCSM 77921	Laos, Champasak, Pakxong, Dong Hua Sao N.P.	PQ677132	PQ677284	PQ677173	This study
P. formosensis	NCSM 77922	Laos, Champasak, Pakxong, Dong Hua Sao N.P.	PQ677133	PQ677285	PQ677174	This study
P. formosensis	NCSM 77923	Laos, Champasak, Pakxong, Dong Hua Sao N.P.	PQ677134	PQ677286	PQ677175	This study
P. formosensis	NCSM 79202	Vietnam, Quang Nam, Phuoc Son, Song Thanh N.P.	PQ677135	PQ677287	PQ677176	This study
P. formosensis	NCSM 79758	Vietnam, Kon Tum, Dak Glei, Ngoc Linh N.R.	PQ677136	PQ677288	PQ677177	This study
P. formosensis	NCSM 79759	Vietnam, Nghe An, Que Phong, Pu Hoat	PQ677137	PQ677289	PQ677178	This study
P. formosensis	NCSM 80353	Vietnam, Lam Dong, Lac Duong, Bi Doup-Nui Ba N.P.	PQ677138	PQ677290	PQ677179	This study
P. formosensis	NCSM 80354	Vietnam, Lam Dong, Lac Duong, Bi Doup-Nui Ba N.P.	PQ677139	PQ677291	PQ677180	This study
P. formosensis	NCSM 85477	Laos, Khammouan, Boualapha, Nakai-Nam Theun N.P.	PQ677140	PQ677292	PQ677181	This study
P. formosensis	NMNS 05637	China, Taiwan, Nantou	MW287060	MW287042	MW287023	Ding et al. (2020)
P. formosensis	NUOL 00552	Laos, Champasak, Pakxong, Dong Hua Sao N.P.	PQ677141	PQ677293	PQ677182	This study
P. formosensis	NUOL 00553	Laos, Xaisomboun, Hom	PQ677142	PQ677294	PQ677183	This study
P. formosensis	NUOL 01809	Laos, Bolikhamxay, Xaychamphone	PQ677143	PQ677295	—	This study
P. formosensis	NUOL 01810	Laos, Xaisomboun, Hom	PQ677144	PQ677296	—	This study
P. formosensis	NUOL 01812	Laos, Xekong, Dakchung, Phou Koungking	PQ677145	PQ677297	—	This study
P. formosensis	NUOL 01813	Laos, Xekong, Dakchung, Phou Koungking	PQ677146	PQ677298	—	This study
P. formosensis	SYS r001444 = CHS 738	China, Guangdong, Dawuling	MK201495	—	—	Li et al. (2020)
P. formosensis	YBU 12015 = GP 2146	China, Hainan	MK135068	MK805333	MK135117	Wang et al. (2020)
P. formosensis	YBU 12032 = GP 2170	China, Hainan	MK135071	MK805336	MK135120	Wang et al. (2020)

P. formosensis	YBU 12090 = GP 2332	China, Guizhou, Leishan	MK135074	MK805339	MK135123	Wang et al. (2020)
P. formosensis	YBU 12115 = GP 2384	China, Guizhou, Rongjiang	MK135075	MK805340	MK135124	Wang et al. (2020)
P. formosensis	YBU 14508 = GP 3911	China, Guangxi	MK135076	MK805341	MK135125	Wang et al. (2020)
P. formosensis	YBU 17029 = GP 4659	China, Hainan	MK135073	MK805338	MK135122	Wang et al. (2020)
P. formosensis	ZMMU NAP-08868	Vietnam, Quang Nam, Song Thanh N.P.	MW287063	MW287045	MW287026	Ding et al. (2020)
P. formosensis	ZMMU R-13709	Vietnam, Lam Dong, Bidoup-Nui Ba N.P.	MW287064	MW287046	MW287027	Ding et al. (2020)
P. formosensis	ZMMU R-14072	Vietnam, Dak Lak, Chu Yang Sin N.P.	MW287065	MW287047	MW287028	Ding et al. (2020)
P. formosensis	ZMMU R-16333	Vietnam, Gia Lai, Kon Chu Rang N.R.	MW287066	MW287048	MW287029	Ding et al. (2020)
P. formosensis	ZMMU R-16684	Vietnam, Cao Bang, Phia Oac N.P.	MW287062	MW287044	MW287025	Ding et al. (2020)
P. guanyinshanensis	KIZ 2023038	China, Yunnan, Yuanyang	PP215390	PP215399	—	Liu et al. (2024)
P. guanyinshanensis	KIZ 2023039	China, Yunnan, Yuanyang	PP215389	PP215398	—	Liu et al. (2024)
P. guanyinshanensis	KIZ 2023040	China, Yunnan, Yuanyang	PP215388	PP215397	—	Liu et al. (2024)
P. hamptoni	CAS 221489	Myanmar, Kachin, Putao, Naung Mon	MW287077	—	MW287034	Ding et al. (2020)
P. hamptoni	KIZ 201903001	China, Yunnan, Hekou	PP215383	PP215392	—	Liu et al. (2024)
P. hamptoni	KIZ 20210517	China, Yunnan, Malipo	PP215386	PP215395	—	Liu et al. (2024)
P. hamptoni	KIZ 20210518	China, Yunnan, Hekou	PP215385	PP215394	—	Liu et al. (2024)
P. hamptoni	KIZ 20210519	China, Yunnan, Hekou	PP215384	PP215393	—	Liu et al. (2024)
P. hamptoni	KIZ 2023046	China, Yunnan, Jianshui	PP215387	PP215396	—	Liu et al. (2024)
P. hamptoni	KIZ L2020018	China, Yunnan, Malipo	PP215382	PP215391	—	Liu et al. (2024)
P. hamptoni	ROM 38104	Vietnam, Lao Cai	KX694896	—	KX694789	Alencar et al. (2016)
P. hamptoni	YPX 18219 = GP 5127	Myanmar, Kachin	MK135077	MK805342	MK135126	Wang et al. (2020)
P. hamptoni	YPX 18604 = GP 5128	Myanmar	MK135078	MK805343	MK135127	Wang et al. (2020)
P. hamptoni	ZMMU NAP-09087	Vietnam, Lao Cai, Bat Xat N.R.	MW287078	MW287054	MW287035	Ding et al. (2020)
P. hamptoni	ZMMU NAP-09088	Vietnam, Lao Cai, Bat Xat N.R.	MW287079	MW287053	MW287036	Ding et al. (2020)

P. iwasakii	I03-ISG1	Japan, Okinawa, Ishigaki	KJ642158	—	KJ642207	You et al. (2015)
P. iwasakii	NMNS 05654	Japan, Okinawa, Iriomote	MZ712216	—	MZ712270	Poyarkov et al. (2022)
P. kaduri	BNHS 3574	India, Arunachal Pradesh, Lohit, Kamlang W.S.	MW026190	—	—	Bhosale et al. (2020)
P. kaduri	BNHS 3575	India, Arunachal Pradesh, Lohit, Kamlang W.S.	MT188734	—	—	Bhosale et al. (2020)
P. komaii	HC 000669	China, Taiwan, Taidong	JF827687	JF827664	JF827713	Guo et al. (2011)
P. komaii	NMNS 05618	China, Taiwan, Taitung, Lijia	KJ642185	MW287056	KJ642210	You et al. (2015), Ding et al. (2020)
P. komaii	NMNS 05625	China, Taiwan, Hualien	MZ712215	MZ712240	MZ712269	Poyarkov et al. (2022)
P. kuznetsovorum	ZMMU R-16802	Vietnam, Phu Yen, Song Hinh	MZ712232	MZ712258	MZ712296	Poyarkov et al. (2022)
P. macularius	GP 2110	China, Hainan	MK135102	MK805367	MK135151	Wang et al. (2020)
P. macularius	GP 815	China, Hainan	MK135101	MK805366	MK135150	Wang et al. (2020)
P. macularius	NCSM 77325	Vietnam, Lam Dong, Lac Duong, Bi Doup-Nui Ba N.P.	PQ677147	PQ677299	PQ677184	This study
P. macularius	NCSM 77926	Laos, Champasak, Pakxong, Dong Hua Sao N.P.	PQ677148	PQ677300	PQ677185	This study
P. macularius	NCSM 80842	Laos, Xieng Khouang, Kham	PQ677149	PQ677301	PQ677186	This study
P. macularius	NCSM 80843	Laos, Xieng Khouang, Kham	PQ677150	PQ677302	PQ677187	This study
P. macularius	NCSM 85521	Laos, Xieng Khouang, Kham	PQ677151	PQ677303	PQ677188	This study
P. macularius	YBU 12016 = GP 2147	China, Hainan	MK135103	MK805368	MK135152	Wang et al. (2020)
P. macularius	YBU 17030 = GP 4660	China, Hainan	MK135104	MK805369	MK135153	Wang et al. (2020)
P. macularius	YBU 17062 = GP 4699	China, Yunnan, Jingdong	MK135106	MK805371	MK135155	Wang et al. (2020)
P. macularius	YBU 17078 = GP 4715	China, Yunnan, Jingdong	MK135105	MK805370	MK135154	Wang et al. (2020)
P. macularius	ZMMU R-16628	Laos, Xaisomboun, Long Tien	MT968770	MZ712241	MZ712271	Vogel et al. (2020), Poyarkov et al. (2022)
P. macularius	ZMMU R-16629	Myanmar, Sagaing, Ban Mauk	MT968771	MW287057	MW287037	Ding et al. (2020), Vogel et al. (2020)

P. margaritophorus	CIB 098267	China, Hainan	JF827675	—	JF827700	Guo et al. (2011)
P. margaritophorus	FMNH 258638	Laos, Xekong, Kaleum	AY425805	—	—	GenBank unpublished
P. margaritophorus	GP 4437	China, Guangxi, Cangwu	MK135099	MK805364	MK135148	Wang et al. (2020)
P. margaritophorus	NCSM 79504	Laos, Luang Phabang, Luang Phabang	PQ677152	PQ677304	PQ677189	This study
P. margaritophorus	NCSM 79505	Laos, Xaignabouli, Xaignabouli	PQ677153	PQ677305	PQ677190	This study
P. margaritophorus	NCSM 79753	Vietnam, Nghe An, Que Phong, Pu Hoat	PQ677154	PQ677306	PQ677191	This study
P. margaritophorus	NCSM 80936	Laos, Bolikhamxay, Viengthong, Nam Kading N.P.A.	PQ677155	PQ677307	PQ677192	This study
P. margaritophorus	NCSM 99031	Cambodia, Kampot, Teuk Chou, Bokor N.P.	PQ677156	PQ677308	PQ677193	This study
P. margaritophorus	YBU 16061 = GP 4410	China, Guangxi, Cangwu	MK135097	MK805362	MK135146	Wang et al. (2020)
P. margaritophorus	YBU 16095 = GP 4465	China, Guangxi, Cangwu	MK135100	MK805365	MK135149	Wang et al. (2020)
P. margaritophorus	YBU 17164 = GP 4837	China, Guangxi, Cangwu	MK135098	MK805363	MK135147	Wang et al. (2020)
P. margaritophorus	ZMMU NAP-09759	Thailand, Ratchaburi, Suan Phueng	MZ712217	MZ712243	MZ712273	Poyarkov et al. (2022)
P. margaritophorus	ZMMU R-13451 = M01	Vietnam, Binh Puoc, Bu Gia Map N.P.	KJ642195	MW287058	MW287038	You et al. (2015), Ding et al. (2020)
P. modestus	MZMU 1293	India, Mizoram, Aizawl, Tanhril	MT968773	—	—	Vogel et al. (2020)
P. monticola	GP 2027	China, Tibet, Motuo	MK135107	MK805372	MK135156	Wang et al. (2020)
P. monticola	KIZ 014167 = GP 5133	China, Tibet, Motuo	MK135109	MK805374	MK135158	Wang et al. (2020)
P. monticola	KIZ 047036 = GP 5132	China, Yunnan, Pingbian	MK135108	MK805373	MK135157	Wang et al. (2020)
P. monticola	SYN U04(II)149	China, Tibet, Motuo	JF827689	JF827666	JF827715	Guo et al. (2011)
P. monticola	ZMMU R-16630	Myanmar, Kachin, Indwgyi	MW438295	—	MW438303	Vogel et al. (2021)
P. monticola	ZMMU R-16631	Myanmar, Sagaing, Ban Mauk	MW438296	MW438301	MW438304	Vogel et al. (2021)
P. monticola	ZMMU R-16632	Myanmar, Sagaing, Ban Mauk	MW438297	—	MW438305	Vogel et al. (2021)
P. monticola	ZMMU R-16633	Myanmar, Sagaing, Ban Mauk	MW438298	—	MW438306	Vogel et al. (2021)
P. monticola	ZMMU R-16634	Myanmar, Sagaing, Ban Mauk	MW438299	—	MW438307	Vogel et al. (2021)

P. niger	GP 1294	China, Yunnan, Mengzi	MK135079	MK805344	MK135128	Wang et al. (2020)
P. niger	HS 11012 = CHS 018	China, Yunnan, Mengzi	MK201239	—	—	Li et al. (2020)
P. niger	KIZ 059339	China, Yunnan, Kunming	MW436706	—	—	Liu and Rao (2021)
P. niger	MTPA 20200811031	China, Guizhou	ON961770	—	—	GenBank unpublished
P. niger	MTPA 20200811032	China, Guizhou	ON961771	—	—	GenBank unpublished
P. niger	MTPA 20200811033	China, Guizhou	ON961772	—	—	GenBank unpublished
P. niger	YBU 14251 = GP 3551	China, Yunnan, Mengzi	MK135080	MK805345	MK135129	Wang et al. (2020)
P. niger	YBU 14252 = GP 3552	China, Yunnan, Mengzi	MK135081	MK805346	MK135130	Wang et al. (2020)
P. niger	YBU 14253 = GP 3553	China, Yunnan, Mengzi	MK135082	MK805347	MK135131	Wang et al. (2020)
P. niger	YBU 14288 = GP 3588	China, Yunnan, Mengzi	MK135083	MK805348	MK135132	Wang et al. (2020)
P. niger	YBU 15100 = GP 4122	China, Yunnan, Mengzi	MK135084	MK805349	MK135133	Wang et al. (2020)
P. niger	YBU 15114 = GP 4123	China, Yunnan, Mengzi	MK135085	MK805350	MK135134	Wang et al. (2020)
P. nigriceps	SYS r001222 = CHS 656	China, Yunnan, Gaoligongshan N.R.	MK201455	—	—	Li et al. (2020)
P. nuchalis	FK 2626	Brunei Darussalam, Belait	MZ603794	U49311	—	Kraus and Brown (1998), Le et al. (2021)
P. nuchalis	FMNH 269040	Malaysia, Sarawak, Bintulu	PQ677157	PQ677309	PQ677194	This study
P. stanleyi	GP 229	China, Guangxi	MK135086	MK805351	MK135135	Wang et al. (2020)
P. stanleyi	HM 2007-S001	China, Guangxi, Guilin	JN230704	JN230705	JN230703	Guo et al. (2011)
P. stanleyi	LSU 2020MLFJDT01	China, Fujian, Nanping, Mt. Wuyi N.P.	MW531673	MW531673	—	X. Yang et al. (2021)
P. stanleyi	YBU 12094 = GP 2343	China, Guizhou, Leishan	MK135087	MK805352	MK135136	Wang et al. (2020)
P. temporalis	SIEZC 20215	Vietnam, Lam Dong, Di Linh	MZ712239	MZ712266	MZ712298	Poyarkov et al. (2022)
P. temporalis	UNS 09992	Vietnam, Lam Dong, Da Huoai	MZ603793	MZ603792	—	Le et al. (2021)
P. temporalis	ZMMU R-13656	Vietnam, Lam Dong, Cat Loc	MZ712238	MZ712265	MZ712297	Poyarkov et al. (2022)

P. tigerinus	KIZ 20210703	China, Yunnan, Menghai	OP752143	—	—	Liu et al. (2023b)
P. tigerinus	KIZ 20210704	China, Yunnan, Menghai	OP752144	—	—	Liu et al. (2023b)
P. tigerinus	KIZ 20210705	China, Yunnan, Menghai	OP752145	—	—	Liu et al. (2023b)
P. victorianus	CAS 235254	Myanmar, Chin, Nat Ma Taung N.P.	MW438300	MW438302	MW438308	Vogel et al. (2021)
P. vindumi	CAS 248147	Myanmar, Kachin, Lukpwi	MW287080	MW287059	MW287039	Ding et al. (2020)
P. vindumi	KFBG 14360	China, Yunnan, Gaoligongshan N.R.	MZ169542	—	—	J. H. Yang et al. (2021)
P. yunnanensis	KIZ 2022033	China, Yunnan, Dali	OP752146	—	—	Liu et al. (2023b)
P. yunnanensis	KIZ 2022034	China, Yunnan, Dali	OP752147	—	—	Liu et al. (2023b)
P. yunnanensis	KIZ 2022035	China, Yunnan, Dali	OP752148	—	—	Liu et al. (2023b)
P. yunnanensis	KIZ 2022036	China, Yunnan, Dali	OP752149	—	—	Liu et al. (2023b)
P. yunnanensis (*P. "geminatus"*)	AUP 00176	Thailand, Chiang Mai, Doi Inthanon N.P.	MW287076	MW287052	MW287033	Ding et al. (2020)
P. yunnanensis (*P. "geminatus"*)	CIB 118021	China, Yunnan, Jiangcheng	MW287068	—	—	Ding et al. (2020)
P. yunnanensis (*P. "geminatus"*)	CIB 118022	China, Yunnan, Jiangcheng	MW287069	—	—	Ding et al. (2020)
P. yunnanensis (*P. "geminatus"*)	CIB 118023	China, Yunnan, Jiangcheng	MW287070	—	—	Ding et al. (2020)
P. yunnanensis (*P. "geminatus"*)	DL 2019072910	China, Yunnan, Jiangcheng	MW287067	—	—	Ding et al. (2020)
P. yunnanensis (*P. "geminatus"*)	DL 2019093001	China, Yunnan, Jiangcheng	MW287071	—	—	Ding et al. (2020)
P. yunnanensis (*P. "geminatus"*)	DL 2019093002	China, Yunnan, Jiangcheng	MW287072	—	—	Ding et al. (2020)
P. yunnanensis (*P. "geminatus"*)	KIZ L2020020	China, Yunnan, Jiangcheng, Pu'er	MW436707	—	—	Liu and Rao (2021)
P. yunnanensis (*P. "geminatus"*)	KIZ L2020024	China, Yunnan, Jiangcheng	MW436708	—	—	Liu and Rao (2021)
P. yunnanensis (*P. "geminatus"*)	NCSM 80841	Laos, Xieng Khouang, Kham	PQ677158	PQ677310	PQ677195	This study
P. yunnanensis (*P. "geminatus"*)	NCSM 86599	Laos, Houaphanh, Xamneu	PQ677159	PQ677311	PQ677196	This study
P. yunnanensis (*P. "geminatus"*)	NUOL 00551	Laos, Houaphanh, Xamneu	PQ677160	PQ677312	PQ677197	This study
P. yunnanensis (*P. "geminatus"*)	ZMMU R-16477	Thailand, Chiang Mai, Mae Kampong	MW287075	MW287051	MW287032	Ding et al. (2020)
P. yunnanensis (*P. "geminatus"*)	ZMMU R-16478	Thailand, Chiang Mai, Doi Inthanon N.P.	MW287074	MW287050	MW287031	Ding et al. (2020)

P. yunnanensis (*P. "geminatus"*)	ZMMU R-16695 = NAP 09280	Laos, Xaisomboun, Long Tien	MW287073	MW287049	MW287030	Ding et al. (2020)
P. yunnanensis (*P. "xuelinensis"*)	KIZ-XL1	China, Yunnan, Lancang, Xuelin, Pu'er	MW436709	—	—	Liu and Rao (2021)
P. yunnanensis (*P. "xuelinensis"*)	KIZ-XL2	China, Yunnan, Lancang, Xuelin, Pu'er	MW436710	—	—	Liu and Rao (2021)
Xylophis perroteti	BNHS 3582	India, Tamil Nadu, Nilgiri, Sholur	MN970042	MN970046	MN970049	Deepak et al. (2020)

Figure 1 Map illustrating the type locality of *Pareas capitulatus* sp. nov. (star) and molecular-verified localities of *Pareas yunnanensis* (circles; Table 1). This concept of *Pareas yunnanensis* includes treating *Pareas "geminatus"* and *Pareas "xuelinensis"* as its junior synonyms. The geographic coordinates for the holotype locality of *Pareas geminatus* in Yunnan Province, China, provided in Ding et al. (2020) erroneously correspond to Chin State, western Myanmar, and are not included here.

Figure 2 Fifty percent majority-rule consensus phylogram resulting from partitioned Bayesian analysis of 2,645 aligned characters of the mitochondrial cytochrome *b* (cyt *b*) gene and flanking tRNAs, the mitochondrial NADH dehydrogenase subunit 4 (ND4) and flanking tRNAs, and the nuclear oocyte maturation factor Mos (c-*mos*) gene from pareid snakes. Numbers at nodes are Bayesian posterior probabilities on left and bootstrap values from a separate maximum likelihood analysis on right. Sample information is provided in Table 1. The entire tree is shown in inset. A: All taxa other than the *Pareas hamptoni* species group. B: The *Pareas hamptoni* species group.

Figure 3 Holotype female (NCSM 78628) of *Pareas capitulatus* sp. nov. in life. A: Anterior body in dorsolateral view. B: Head and neck in dorsolateral view.

Figure 4 Holotype female (NCSM 78628) of *Pareas capitulatus* sp. nov. in preservative. A: Whole body in lateral view. B: Whole body in ventrolateral view. C: Lateral view of head. D: Dorsal view of head.

Figure 5 Dorsal view of heads (left to right) of holotype female of *Pareas capitulatus* sp. nov. (NCSM 78628), *Pareas yunnanensis* (NCSM 86599), and *Pareas formosensis* (NCSM 77920) in preservative. Note the complete dark nuchal band and narrow head of *Pareas capitulatus* **sp. nov.**