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A NEW SPECIES OF THE *Pareas hamptoni* COMPLEX (SQUAMATA: SERPENTES: PAREIDAE) FROM THE GOLDEN TRIANGLE

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Abstract

An investigation of the taxonomic status of *Pareas hamptoni* (Hampton's Slug snake) based on morphological and molecular data revealed a new distinct species from the Golden Triangle region (comprising parts of southern China, and adjacent Laos and Thailand). The new species is shown to be a sister species to *P. hamptoni* but can be separated from the latter by having 3–5 dorsal scale rows at midbody slightly keeled (*vs* 5–9 scales strongly keeled); a lower number of ventrals, 170–188 (*vs* 185–195); and a lower number of subcaudals, 67–91 (*vs* 91–99). The new species is currently known from northwestern Thailand, northern Laos, and the southern part of Yunnan Province in China at elevations of 1,160–2,280 m a.s.l. We suggest that the new species to be considered of Least Concern (LC) in the IUCN's Red List categories. Problems of taxonomy and actual distribution of the *P. hamptoni* complex are briefly discussed; our results show *P. hamptoni* is now reliably known only from Myanmar and Vietnam, but its occurrence in Yunnan Province of China is likely.

Key words: China, Indo-Burma, Laos, *Pareas formosensis*, *Pareas mengziensis*, Thailand

Introduction

The Asian snail-eating genus *Pareas* Wagler, 1830 (Pareidae) occurs throughout southern and south-eastern Asia. These snakes are mainly arboreal, nocturnal, and generally feed on slugs and snails (You *et al.* 2015, Uetz *et al.* 2020).

The genus *Pareas* is morphologically characterized by having medially smooth or keeled dorsal scales in 15 rows throughout the body; the ventrals preceded by a strongly enlarged preventral, larger than the ventrals; the subcaudals divided; the absence of mental

groove; suboculars are usually present; supralabials usually not touching the eye (except in *P. monticola* and *P. stanleyi*); the anterior single inframaxillary shield lacking, three pairs of inframaxillaries, the first pair distinctly elongated, posterior inframaxillaries usually as long as wide or wider than long (Grossmann & Tillack 2003). The reported high degree of morphological similarity makes species delineation in this genus quite challenging (Guo & Deng 2009, Vogel 2015). Application of the integrative taxonomic approach combining evidence from morphological and molecular data resulted in the discovery of several previously unnoticed taxa (You *et al.* 2015, Wang *et al.* 2020, Vogel *et al.* 2020). Currently 19 species in the genus *Pareas* are regarded as valid, namely *Pareas andersonii* Boulenger; *P. atayal* You, Poyarkov & Lin; *P. boulengeri* (Angel); *P. carinatus* (Wagler); *P. chinensis* (Barbour); *P. formosensis* (Van Denburgh); *P. hamptoni* (Boulenger); *P. iwasakii* (Maki); *P. komaii* (Maki); *P. macularius* (Theobald); *P. menglaensis* Wang, Che, Liu *et al.*; *P. mengziensis* Wang, Che, Liu *et al.*; *P. margaritophorus* (Jan); *P. monticola* (Cantor); *P. modestus* Theobald; *P. nigriceps* Guo & Deng; *P. nuchalis* (Boulenger); *P. stanleyi* (Boulenger); and *P. vindumi* Vogel (see Guo *et al.* 2011, You *et al.* 2015, Uetz *et al.* 2020, Vogel *et al.* 2020). Hampton's Slug snake, *Pareas hamptoni*, was originally described by G.A. Boulenger in 1905 based on one single adult male from Mandalay Division, Myanmar (Boulenger 1905). This species has been reported to be widely distributed, ranging across mainland Southeast Asia from Myanmar in the west to Thailand, Indochina and southern China (Yunnan, Hainan, Guangdong and Guangxi provinces) in the east (Nguyen *et al.* 2009). However, since geographic variation of this species has never been examined across the different regions, its taxonomic status remained controversial and a number of misidentifications were made in the past (see You *et al.* 2015). Recently You *et al.* (2015) demonstrated that specimens identified as *P. hamptoni* from mainland China and Vietnam were closely related to *P. formosensis* that previously, was considered to be endemic to Taiwan. More recently, Wang *et al.* (2020) revised the taxonomy of this group, restricted the distribution of *P. hamptoni sensu stricto* to Myanmar, assigned populations from the south-eastern part of mainland China to *P.*

formosensis, and described a new species, *P. mengziensis*, from western Yunnan, China. However, the actual extent of the distribution of these species, as well as the taxonomic status of two *P. hamptoni* synonyms remains unclear. Presently *Eberhardtia tonkinensis* Angel, 1920 and *Amblycephalus carinatus hainanus* Smith, 1923 are considered to be junior synonyms of *Pareas hamptoni* (Wallach *et al.* 2014, Uetz *et al.* 2020). During our recent herpetological surveys throughout the Golden Triangle region (encompassing the southern part of Yunnan Province of China, Laos and Thailand), we collected a series of *Pareas* specimens which were originally identified as *P. hamptoni* (Vogel 2009, Teynié & David 2010, Nguyen *et al.* 2020). However, further comprehensive analyses of molecular and morphological characters have demonstrated that these specimens form a lineage within the genus *Pareas*, which is different from all known congeners including *P. hamptoni sensu stricto*. Therefore, we herein describe it as a new species.

Material and methods

Material examined: For this study, a total 25 preserved specimens of the *P. hamptoni* complex were examined for their external morphological characters; eight specimens of the new species from China, Laos, and Thailand, 12 specimens of *P. formosensis* from eastern Indochina and southern China, and five specimens of *P. hamptoni* including the holotype. Measurements were taken with a slide-caliper to the nearest 0.1 mm, except body and tail lengths, which were measured to the nearest one millimetre with a measuring tape. The number of ventral scales was counted according to Dowling (1951). The first enlarged scute preceding the ventrals (larger than the ventrals itself) was regarded as preventral; it was present in all examined specimens. Half ventrals were counted as one. The first scale under the tail meeting its opposite was regarded as the first subcaudal, and the terminal scute was not included in the number of subcaudals. The dorsal scale rows were counted at one head length behind head, at midbody, and at one head length before vent. The keeling was checked at midbody around half of the body length. The same was done for examination of the enlarged middorsal scale rows. In the number of supralabials touching the subocular, those only touching the presubocular were not included.

Infralabials were considered to be those shields that were completely below a supralabial and bordering the mouth gap. Usually the last supralabial shield was a very large shield, much larger than other supralabials. Smaller shields behind this enlarged shield do not border the mouth gap (only the connecting muscle) and were excluded from the sublabial scale count, despite the fact that they were covered by the supralabials. Values for paired head characters were recorded on both sides of the head and were reported in a left/right order. The sex was determined by dissection of the ventral tail base. The examined materials for *Pareas* are listed in the Appendix. For comparison with other taxa, we relied on previously published data (e.g., Jiang 2004, Guo & Zhao 2004, Guo & Deng 2009, Stuebing *et al.* 2014, You *et al.* 2015, Vogel 2015, Vogel *et al.* 2020).

Museum abbreviations: AUP, School of Agriculture and Natural Resources, University of Phayao, Phayao, Thailand; CAS, California Academy of Sciences Museum, California, USA; CIB, Chengdu Institute of Biology, Chengdu, People's Republic of China; DL, Ding Lee's private collection, Chengdu, People's Republic of China; FMNH, Field Museum of Natural History, Chicago, USA; GP, Guo Peng's private collection, College of Life Science and Food Engineering, Yibin University, Yibin, People's Republic of China; LSUHC, La Sierra University Herpetological Collection, Riverside, California, USA; KIZ, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, People's Republic of China; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHMUK, The Natural History Museum, London, UK; NMNS, National Museum of Natural Science, Taichung, Taiwan, China; NMW, Naturhistorisches Museum Wien, Vienna, Austria; QSMI, Queen Saovabha Memorial Institute, Thai Red Cross Society, Bangkok, Thailand; YPX, Field number of KIZ; ZMB, Zoologisches Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany; ZMH, Zoologisches Institut und Museum, Universität Hamburg, Hamburg, Germany; ZMMU, Zoological Museum of Moscow University, Moscow, Russia. **Other abbreviations:** SVL, snout-vent length; TaL, tail length; TL, total length; Mt., mountain; NP, national park; NR, natural reserve; a.s.l., above sea level.

Molecular methods: For those specimens for which tissue samples were available, we

performed molecular phylogenetic analyses to test the differences observed from the morphological data (Table 1). For molecular analyses, we extracted the total genomic DNA from ethanol-preserved liver or muscle tissue using standard phenol-chloroform-proteinase K extraction protocol following Hillis *et al.* (1996), with consequent isopropanol precipitation. The isolated genomic DNA was visualized in agarose electrophoresis in the presence of ethidium bromide. We measured DNA concentration in 1 μ l using NanoDrop 2000 (Thermo Scientific), and adjusted it to ca. 100 ng DNA/ μ L. To assess the phylogenetic relationships within the Pareidae, we amplified 1126 bp long fragment of mtDNA cytochrome b gene (*cyt b*), 680 bp long fragment of mtDNA NADH dehydrogenase subunit 4 gene (*ND4*), and a 734 bp long fragment of nuclear oocyte maturation factor *mos* gene (*c-mos*). These genes are widely applied as phylogenetic markers in biodiversity surveys in various snake groups, including the family Pareidae (e.g. Guo *et al.* 2011; Loredó *et al.* 2013; You *et al.* 2015; Deepak *et al.* 2020; Li *et al.* 2020; Wang *et al.* 2020; Vogel *et al.* 2020). We performed DNA amplification in 20 μ l reactions using ca. 50 ng genomic DNA, 10 nmol of each primer, 15 nmol of each dNTP, 50 nmol additional MgCl₂, Taq PCR buffer (10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.1 mM MgCl₂ and 0.01% gelatine) and 1 U of Taq DNA polymerase. Primers used in PCR and amplification are summarized in Table 2. The PCR conditions for *cyt b* and *c-mos* genes followed You *et al.* (2015) and included denaturation at 94 °C for 3 min, followed by 35 cycles at 94 °C for 30 s, 52 °C for 40 s and 72 °C for 90 s, with a final extension at 72 °C for 10 min. The PCR conditions for *ND4* gene were as follows: initial denaturation at 94 °C for 3 min, followed by 15 cycles at 94 °C for 60 s, annealing for 60 s and 72 °C for 60 s, with annealing temperature reducing 0.5 °C every cycle from 60 °C, followed by 19 cycles at 92 °C for 60 s, 52 °C for 60 s and 72 °C for 60s, with a final extension step at 72 °C for 15 min. All amplifications were run using an iCycler Thermal Cycler (Bio-Rad). PCR products were loaded onto 1.5% agarose gels in the presence of ethidium bromide and visualized in electrophoresis. The successful targeted PCR products were outsourced to Evrogen® (Moscow, Russia) for PCR purification and sequencing; sequence data collection and visualization was performed on an ABI 3730xl

Automated Sequencer (Applied Biosystems). We deposited the newly obtained sequences in GenBank under the accession numbers MW287022–MW287080 (Table 1).

Phylogenetic analyses: To reconstruct the phylogenetic relationships within the genus *Pareas*, we aligned the newly obtained *cyt b*, *ND4* and *c-mos* sequences together with representative sequences of all 19 currently recognized species of *Pareas* and one undescribed species *Pareas* sp. from northeastern India, as well as five outgroup species of *Asthenodipsas* as well as *Aplopeltura boa*. The sequence of *Xylophis captaini* (Pareidae: Xylophinae) was used to root the tree following the phylogenetic data of Deepak *et al.* (2018, 2020) (Table 1). In total, sequences for 52 specimens of Pareidae were included in the final analysis, comprising all currently recognized species of the genus *Pareas*, and including 34 sequences of *Pareas hamptoni* species group members from India, Myanmar, China, southernmost Japan, Vietnam, Laos, and Thailand (Fig. 1). The nucleotide sequences were initially aligned in MAFFT v.6 (Katoh *et al.* 2002) with default parameters, and were subsequently checked by eye in BioEdit 7.0.5.2 (Hall 1999) and slightly adjusted. The mean uncorrected genetic *p*-distances between sequences were calculated with MEGA 6.0 (Tamura *et al.* 2013). Phylogenetic trees were estimated for the combined mitochondrial DNA fragments (*cyt b* and *ND4*) and nuclear gene (*c-mos*) dataset. The total evidence analysis was performed as the approximately unbiased tree-selection test (AU-test; Shimodaira 2002) conducted using Treefinder v. March 2011 (Jobb 2011) did not reveal statistically significant topological differences between mtDNA and nuDNA topologies. Phylogenetic relationships of Pareinae were inferred using Bayesian Inference (BI) and Maximum Likelihood (ML) approaches. A Maximum Likelihood (ML) analysis was implemented using the IQ-TREE webserver (Nguyen *et al.* 2015; Trifinopoulos *et al.* 2016) preceded by the selection of substitution models using the Bayesian Information Criterion (BIC) in ModelFinder (Kalyaanamoorthy *et al.* 2017) which selected GTR+I+G for the first and the third codon positions of *cyt b*, GTR+G for the second codon position of *cyt b*, and the third codon position of *ND4* and *c-mos*, HKY+G for the first and the second codon positions of *ND4*, K2P for the first

codon position of *c-mos*, and K2P+I for the second codon position of *c-mos*, as suggested by the Akaike Information Criterion (AIC). When the same model was proposed to different codon positions of a given gene, they were treated as a single partition; which resulted in seven partitions in total. One-thousand bootstrap pseudoreplicates via the ultrafast bootstrap (UB; Hoang *et al.* 2018) approximation algorithm were employed, and nodes having UB values of 95 and above were considered strongly supported (Minh *et al.* 2013). We considered nodes with values of 90–94 to be well-supported. A Bayesian phylogenetic tree (BI) was estimated using MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003). Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analyses were run with one cold chain and three heated chains for one million generations and sampled every 100 generations. Two independent MCMCMC runs were performed and checked for the effective sample sizes (ESS) were all above 200 by exploring the likelihood plots using TRACER v1.6 (Rambaut & Drummond 2007). We discarded the initial 1000 trees as burn-in. We assessed the confidence in tree topology by the posterior probability (PP) (Huelsenbeck & Ronquist 2001). Nodes with Bayesian posterior probabilities (BPP) of 0.95 and above were considered strongly supported (Wilcox *et al.* 2002). We considered nodes with values of 0.90–0.94 as well-supported.

Results

Phylogenetic data: The ML and BI analyses recovered trees with very similar topologies, and the ML topology used here (Fig. 2) agreed well with the earlier phylogenies of the genus *Pareas* (Guo *et al.* 2011, You *et al.* 2015, Wang *et al.* 2020, Vogel *et al.* 2020). Phylogenetic relationships among the three genera of Pareidae were resolved sufficiently, suggesting sister relationships between the genera *Aplopeltura* and *Pareas* (96/1.0; hereafter nodal support values given for UB/BPP, respectively), and a more distant phylogenetic position of *Asthenodipsas*. The monophyly of the genus *Asthenodipsas* was poorly supported (93/0.86), while the monophyly of the genus *Pareas* with respect to other genera was strongly supported (97/1.0) (Fig. 2). All species of *Pareas* were clustered in five major clades, corresponding to groups of closely related species, in accordance with the results of Vogel *et al.* (2020):

Table 1. Sequences and voucher specimens of *Pareas* and outgroup taxa used in the molecular analyses for this study. Numbers in sampling localities of *P. hamptoni* species group members refer to Figure 1.

Specimen ID	Species	Locality	cyt b	ND4	cmos	Reference
CAS 235359	<i>Pareas andersonii</i>	Myanmar, Chin, Mt. Natmataung	MT968772	MW287040	MW287022	this work
NMNS 05594	<i>Pareas atayal</i>	³² China, Taiwan, Yilan, Beiheng	KJ642124	MW287041	KJ642198	You et al. 2015
KIZ 09965	<i>Pareas boulengeri</i>	China, Hubei, Enshi	JF827678	JF827656	MK135141	Guo et al. 2011
GP1079	<i>Pareas carinatus</i>	Peninsular Malaysia	MK135110	MK805378	MK135162	Wang et al. 2020
CIB 098269	<i>Pareas chinensis</i>	China, Sichuan, Tianquan	JF827691	JF827669	MK135137	Guo et al. 2011
NMNH 05637	<i>Pareas formosensis</i>	²⁷ China, Taiwan, Nantou	MW287060	MW287042	MW287023	You et al. 2015
YBU 12015	<i>Pareas formosensis</i>	²⁴ China, Hainan	MK135068	MK805333	MK135117	Wang et al. 2020
H26-HAM01	<i>Pareas formosensis</i>	²⁵ China, Guangdong	MW287061	MW287043	MW287024	this work
ZMMU R-16684	<i>Pareas formosensis</i>	²³ Vietnam, Cao Bang, Phia Oac NP	MW287062	MW287044	MW287025	this work
FMINH 255567	<i>Pareas formosensis</i>	²¹ Vietnam, Nghe An, Pu Mat NP	AY425806	—	—	unpublished
ZMMU NAP-08868	<i>Pareas formosensis</i>	²⁰ Vietnam, Quang Nam, Song Thanh NP	MW287063	MW287045	MW287026	this work
ZMMU R-13709	<i>Pareas formosensis</i>	¹⁷ Vietnam, Lam Dong, Bidoup - Nui Ba NP	MW287064	MW287046	MW287027	this work
ZMMU R-14072	<i>Pareas formosensis</i>	¹⁸ Vietnam, Dak Lak, Chu Yang Sin NP	MW287065	MW287047	MW287028	this work
ZMMU R-16333	<i>Pareas formosensis</i>	¹⁹ Vietnam, Gia Lai, Kon Chu Rang NR	MW287066	MW287048	MW287029	this work
DL2019072910	<i>Pareas geminatus</i> sp. nov.	¹¹ China, Yunnan, Jiangcheng	MW287067	—	—	this work
CIB 118021	<i>Pareas geminatus</i> sp. nov.	¹¹ China, Yunnan, Jiangcheng	MW287068	—	—	this work
CIB 118022	<i>Pareas geminatus</i> sp. nov.	¹¹ China, Yunnan, Jiangcheng	MW287069	—	—	this work
CIB 118023	<i>Pareas geminatus</i> sp. nov.	¹¹ China, Yunnan, Jiangcheng	MW287070	—	—	this work
DL2019093001	<i>Pareas geminatus</i> sp. nov.	¹¹ China, Yunnan, Jiangcheng	MW287071	—	—	this work
DL2019093002	<i>Pareas geminatus</i> sp. nov.	¹¹ China, Yunnan, Jiangcheng	MW287072	—	—	this work
ZMMU R-16695	<i>Pareas geminatus</i> sp. nov.	¹³ Laos, Xaisomboun, Long Tien	MW287073	MW287049	MW287030	this work
ZMMU R-16478	<i>Pareas geminatus</i> sp. nov.	¹⁵ Thailand, Chiang Mai, Doi Inthanon NP	MW287074	MW287050	MW287031	this work
ZMMU R-16477	<i>Pareas geminatus</i> sp. nov.	¹⁴ Thailand, Chiang Mai, Mae Kampong	MW287075	MW287051	MW287032	this work
AUP-00176	<i>Pareas geminatus</i> sp. nov.	¹⁵ Thailand, Chiang Mai, Doi Inthanon NP	MW287076	MW287052	MW287033	this work
YPX 18219 (GP5127)	<i>Pareas hamptoni</i> s. str.	Myanmar, Kachin	MK135077	MK805342	MK135126	Wang et al. 2020
YPX 18604	<i>Pareas hamptoni</i> s. str.	Myanmar, Kachin	MK135078	MK805343	MK135127	Wang et al. 2020

A NEW SPECIES OF THE GENUS *Pareas* FROM THE GOLDEN TRIANGLE

Table 1 continued. Sequences and voucher specimens of *Pareas* and outgroup taxa used in the molecular analyses for this study. Numbers in sampling localities of *P. hamptoni* species group members refer to Figure 1.

Specimen ID	Species	Locality	cyt b	ND4	cmos	Reference
CAS 221489	<i>Pareas hamptoni</i> s. str.	⁵ Myanmar, Kachin, Putao, Naung Mon	MW287077	—	MW287034	this work
ROM 38104	<i>Pareas hamptoni</i> s. str.	⁷ Vietnam, Lao Cai, Sa Pa	KX694896	—	—	Alencar <i>et al.</i> 2016
ZMMU NAP-09087	<i>Pareas hamptoni</i> s. str.	⁶ Vietnam, Lao Cai, Bat Xat NR	MW287078	MW287054	MW287035	this work
ZMMU NAP-09088	<i>Pareas hamptoni</i> s. str.	⁶ Vietnam, Lao Cai, Bat Xat NR	MW287079	MW287053	MW287036	this work
NMNS 05655	<i>Pareas iwasakii</i>	³³ Japan, Okinawa, Ishigaki	KJ642160	—	KJ642198	You <i>et al.</i> 2015
NMNS 05654	<i>Pareas iwasakii</i>	³⁴ Japan, Okinawa, Iriomote	KJ642156	—	KJ642207	You <i>et al.</i> 2015
NMNS 05625	<i>Pareas komaii</i>	³¹ China, Taiwan, Hualien	KJ642189	MW287055	KJ642210	You <i>et al.</i> 2015
NMNS 05618	<i>Pareas komaii</i>	³⁰ China, Taiwan, Taitung, Lijia	KJ642185	MW287056	KJ642210	You <i>et al.</i> 2015
ZMMU R-16629	<i>Pareas macularius</i>	Myanmar, Sagaing, Ban Mauk	MT968771	MW287057	MW287037	this work
M01	<i>Pareas margaritophorus</i>	Vietnam, Binh Phuoc, Bu Gia Map NP	KJ642195	MW287058	MW287038	this work
GP1292	<i>Pareas menglaensis</i>	China, Yunnan, Mengla	MK135113	MK805378	MK135162	Wang <i>et al.</i> 2020
YBU14288	<i>Pareas mengziensis</i>	¹⁰ China, Yunnan, Mengzi	MK135083	MK805348	MK135132	Wang <i>et al.</i> 2020
MZMU 1293	<i>Pareas modestus</i>	India, Mizoram, Aizawl, Tanhril	MT968773	—	—	Vogel <i>et al.</i> 2020
GP2027	<i>Pareas monticola</i>	China, Xizang (Tibet), Motuo	MK135107	MK805372	MK135156	Wang <i>et al.</i> 2020
CHS 656	<i>Pareas nigriceps</i>	³ China, Yunnan, Gaoligongshan	MK201455	—	—	Li <i>et al.</i> 2020
FK 2626	<i>Pareas nuchalis</i>	Brunei, Brunei Darussalam	—	U49311	—	Kraus & Brown 1998
HM 2007-S001	<i>Pareas stanleyi</i>	China, Guangxi, Guilin	JN230704	JN230705	MK135135	Guo <i>et al.</i> 2011
CAS 248147	<i>Pareas vindumi</i>	² Myanmar, Kachin, Chipwi, Lukpwi	MW287080	MW287059	MW287039	this work
BNHS 3575	<i>Pareas</i> sp.	¹ India, Arunachal Pradesh	MT188734	—	—	Bhosale <i>et al.</i> in press
KIZ 011963	<i>Aplopeltura boa</i>	Peninsular Malaysia	JF827673	JF827650	JF827696	Guo <i>et al.</i> 2011
—	<i>Asthenodipsas tropidonotus</i>	Indonesia	AY425808	—	—	unpublished
LSUHC 9098	<i>Asthenodipsas lasgatenensis</i>	Malaysia, Pahang, Fraser's Hill	KC916755	—	—	Loredo <i>et al.</i> 2013
—	<i>Asthenodipsas vertebralis</i>	Peninsular Malaysia	AY425807	—	—	unpublished
FMNH 241296	<i>Asthenodipsas laevis</i>	Malaysia, Sabah, Lahad Datu	KX660468	KX660596	KX660335	Figueroa <i>et al.</i> 2016
FMNH 273617	<i>Asthenodipsas borneensis</i>	Malaysia, Sarawak, Bintulu	KX660469	KX660597	KX660336	Figueroa <i>et al.</i> 2016
BNHS 3376	<i>Xylophis captaini</i>	India	MK340914	MK340912	MK344195	Deepak <i>et al.</i> 2020



Figure 1. Distribution of *Pareas hamptoni* species complex: type localities (star); populations for which molecular/morphological data available (filled icons, colours correspond to those in Fig. 2); populations of unclear taxonomic status (white icons).

Pareas* sp.:** (1) India, Arunachal Pradesh (Bhosale *et al.* in press); ***Pareas vindumi*:** (2) Myanmar, Kachin, Chipwi, Lukpwi (Vogel 2015); ***Pareas nigriceps*:** (3) China, Yunnan, Gaoligongshan (Guo & Deng 2009); ***Pareas hamptoni sensu stricto*:** (4) Myanmar, Mandalay, Mogok (Boulenger 1905), (5) Myanmar, Kachin, Putao, Naung Mon (this paper), (6) Vietnam, Lao Cai, Bat Xat NR (this paper), (7) Vietnam, Lao Cai, Sa Pa (Alencar *et al.* 2016); ***Amblycephalus yunnanensis: (8) China, Yunnan, Talifu [Dali County] (Vogt 1922); ***Amblycephalus niger***: (9) China, Yunnan, Kunming (Pope 1928); ***Pareas mengziensis*:** (10) China, Yunnan, Mengzi (Wang *et al.* 2020); ***Pareas geminatus sp. nov.*:** (11) China, Yunnan, Jiangcheng (this paper), (12) Laos, Houaphanh (this paper), (13) Laos, Xaisomboun, Long Tien (this paper), (14) Thailand, Chiang Mai, Mae Kampong (this paper), (15) Thailand, Chiang Mai, Doi Inthanon NP (this paper), (16) Thailand, Tak, between Uphang and Mae Sot (Vogel 2010, this paper); ***Pareas formosensis*:** (17) Vietnam, Lam Dong, Bidoup-Nui Ba NP (this paper), (18) Vietnam, Dak Lak, Chu Yang Sin NP (this paper), (19) Vietnam, Gia Lai, Kon Chu Rang NR (this paper), (20) Vietnam, Quang Nam, Song Thanh NP (this paper), (21) Vietnam, Nghe An, Pu Mat NP (this paper), (22) Vietnam, Vinh Phuc, Tam Dao NP (Angel 1920; type locality of *Eberhardtia tonkinensis*), (23) Vietnam, Cao Bang, Phia Oac NP (this paper), (24) China, Hainan (Smith 1923; type locality of *Amblycephalus carinatus hainanus*), (25) China, Guangdong (this paper), (26) China, Taiwan, Kanshirei [Kuantzu Ling] (Van Denburgh 1909; type locality of *Amblycephalus formosensis*), (27) China, Taiwan, Nantou (You *et al.* 2015); ***Amblycephalus kuangtungensis***: (28) China, Guangdong, Mt. Longtoushan (Vogt 1922); ***Pareas komaii*:** (29) China, Taiwan, Arisan [Alishan NP] (Maki 1931), (30) China, Taiwan, Taitung, Lijia (You *et al.* 2015), (31) China, Taiwan, Hualien (You *et al.* 2015); ***Pareas atayal*:** (32) China, Taiwan, Yilan, Beiheng Rd. (You *et al.* 2015); ***Pareas iwasakii*:** (33) Japan, Okinawa, Ishigaki (Maki 1937, You *et al.* 2015), (34) Japan, Okinawa, Iriomote (You *et al.* 2015).

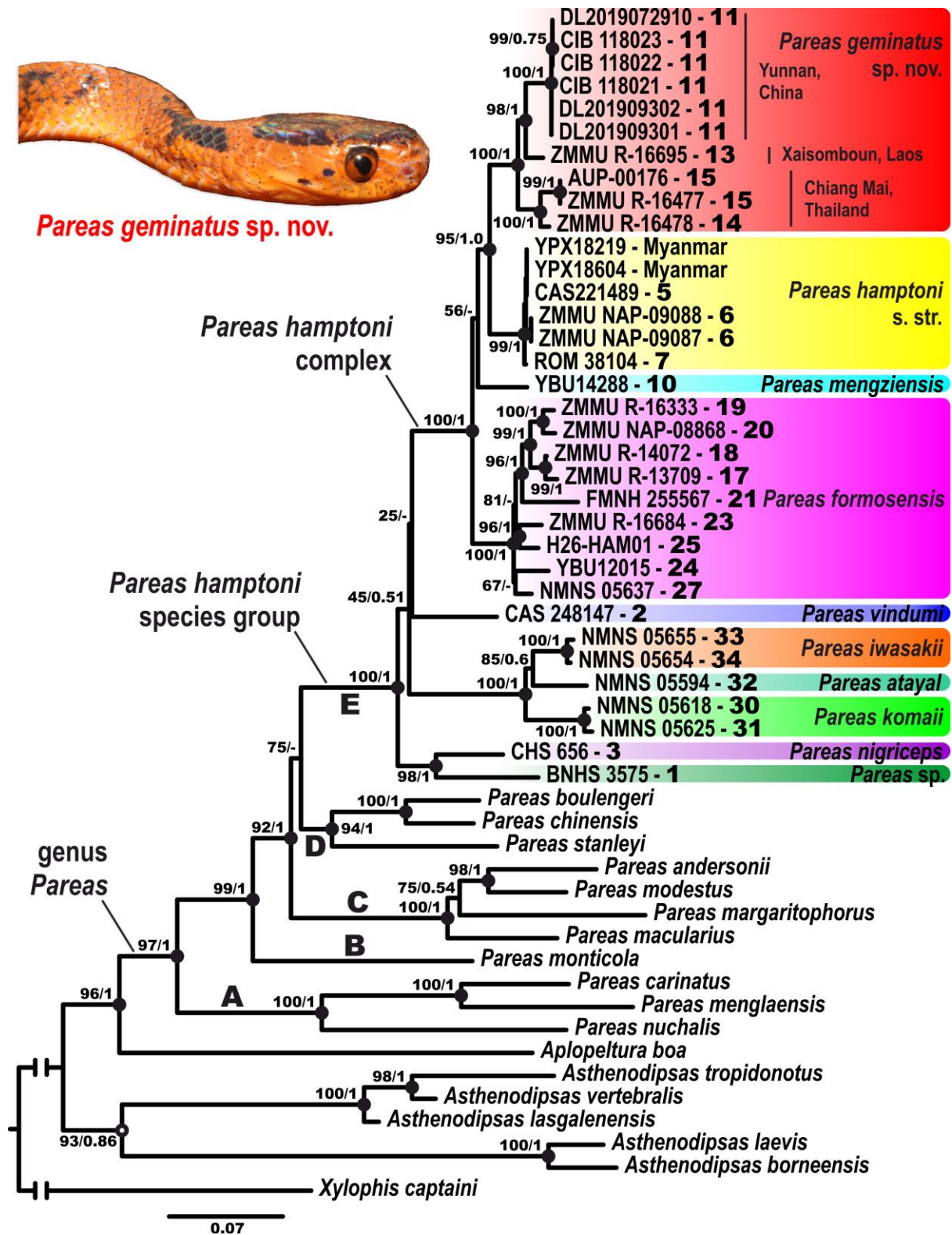


Figure 2. Majority-rule consensus tree from 1000 ML bootstrap pseudoreplicates of the *Pareas hamptoni* species group derived from the analysis of 1 126 bp of *cyt b*, 678 bp of *ND4*, and 734 bp of *c-mos* gene fragments. Black circles represent nodes the UB and BPP support > 90 and 0.90, respectively; the white circle represents a node with UB support > 90 only; nodes lacking circles are unsupported. For voucher specimen information and GenBank accession numbers see Table 1; values in bold after specimen ID correspond to locality numbers (Fig. 1 and Table 1). Photograph showing *Pareas geminatus* sp. nov. from Jiangcheng County, Yunnan Province, China, by Shengchao Shi.

- (1) *Pareas carinatus* species group (Fig. 2, clade A; 100/1.0) is composed of *P. carinatus*, *P. menglaensis*, and *P. nuchalis*; the former two species form a clade (100/1.0). This species group forms a highly divergent lineage, sister to all other congeners (99/1.0).
- (2) *Pareas monticola* (Fig. 2, lineage B; 100/1.0) is an orphaned species from Himalaya that forms a well-supported sister lineage with respect to all remaining *Pareas* species of clades C–E (92/1.0); phylogenetic relationships among the latter clades are essentially not resolved.
- (3) *Pareas margaritophorus* species group (Fig. 2, clade C; 100/1.0) is composed of *P. margaritophorus*, *P. macularius*, *P. modestus* and *P. andersonii*; phylogenetic relationships among the members of this group are not resolved, though the two latter species form a clade (98/1.0).
- (4) *Pareas chinensis* species group (Fig. 2, clade D; 94/1.0) is composed of *P. chinensis*, *P. boulengeri* and *P. stanleyi*; with the former two species forming a clade (100/1.0).
- (5) *Pareas hamptoni* species group (Fig. 2, clade E; 100/1.0) includes at least ten lineages with species level of differentiation from Himalaya, northern Indochina, Annamite (Truong Son) Range., southern China, including the islands of Hainan and Taiwan, and the southernmost islands of the Ryukyu Archipelago (Yaeyama Group) of Japan (Fig. 1).

Phylogenetic relationships among the species composing the *P. hamptoni* species group remain essentially unresolved. An undescribed species, *Pareas* sp. from East Himalaya in India, formed a well-supported clade with *P. nigriceps* from the Mt. Gaoligongshan in western Yunnan, China (98/1.0; see Figs. 1 and 2). A group of closely-related species from the Pacific islands of Taiwan and the Yaeyama Group of the Ryukyus formed a strongly supported monophylum composed of *P. atayal*, *P. iwasakii* and *P. komaii* (100/1.0; Figs. 1 and 2). The phylogenetic position of *P. vindumi* from northern Myanmar within the group remained unresolved (Figs. 1 and 2). Finally, the lineages until recently regarded as *P. hamptoni sensu lato*

formed a strongly supported clade (100/1.0), which we now refer to as *P. hamptoni* complex (Fig. 2). Overall, our analysis revealed the four major lineages of species-level differentiation within the *P. hamptoni* complex (Fig. 2). The sample of *P. formosensis* from Taiwan (locality 27, Fig. 1) clustered in one group with specimens from southern China (localities 24 previously referred to as *Amblycephalus carinatus hainanus*, Fig. 1), northern Vietnam (localities 21–23 previously referred to as *Eberhardtia tonkinensis*, Fig. 1), and the mountains of the Tay Nguyen Region in central and southern Vietnam (localities 17–20, Fig. 1). The sample of *P. mengziensis* from eastern Yunnan in China formed a lineage with unresolved phylogenetic affinities (locality 10, Figs. 1 and 2). The samples of *P. hamptoni* (95/1.0) were divided into two reciprocally monophyletic lineages, one of which included samples from northern Myanmar (locality 5) and the Mt. Hoang Lien Son in the north-eastern part of Vietnam (localities 6–7, Fig. 1), and corresponded to *P. hamptoni sensu stricto* (99/1.0). The second lineage (100/1.0) included samples from the mountains of southern Yunnan (locality 11), Laos (locality 13) and northern Thailand (localities 14–15, Fig. 1).

Genetic distances: The interspecific uncorrected genetic *p*-distances in *cyt b* gene within *Pareas* varied from $p=5.5\%$ (between *P. hamptoni sensu stricto* and *P. mengziensis*) to $p=25.3\%$ (between *P. menglaensis* and *Pareas* sp. from India). The divergence between the two sister lineages of ‘*P. hamptoni*’ was found to be $p=7.6\%$; while the intraspecific distances varied from 0.5% within *P. hamptoni sensu stricto* to $p=4.0\%$ within the new lineage from southern Yunnan, Laos and Thailand (Table 3).

Taxonomy

Based on our updated phylogeny of Pareinae, and the high degree of uncorrected pairwise sequence divergence between the two lineages presently assigned to ‘*P. hamptoni*’ as well as the stable morphological and chromatical differences reported below, we hypothesize that the populations of the *P. hamptoni* complex from the Golden Triangle region (northwestern Thailand, northern Laos and southernmost part Yunnan Province in China) represent a discretely diagnosable lineage which shows no evidence of reciprocity with any other lineage and as such, should be accorded species status, and is formally described below.

Table 2. Primers used for DNA amplification and sequencing

Gene	Primer Name	Primer direction	Primer sequence	Reference
<i>cyt b</i>	L14910	forward	5'-GACCTGTGATMTGAAAAACCAACCAATGTTGT-3'	de Queiroz <i>et al.</i> 2002
<i>cyt b</i>	H16064	reverse	5'-CTTTGGTTTACAAGAACAATGCITTA-3'	de Queiroz <i>et al.</i> 2002
<i>ND4</i>	ND4F	forward	5'-CACCTATGACTACCAAAAAGCTCATGTAGAAGC-3'	Salvi <i>et al.</i> 2013
<i>ND4</i>	ND4LEUR	reverse	5'-CATTACTTTTACTTGGATTGGACCA-3'	Salvi <i>et al.</i> 2013
<i>c-mos</i>	cmos S77	forward	5'-CATGGACTGGGATCAGTTATG-3'	Slowinski & Lawson 2002
<i>c-mos</i>	cmos S78	reverse	5'-CCTTGGGIGTGATTTTCTCACCT-3'	Slowinski & Lawson 2002

Table 3. Genetic divergence (uncorrected *p*-distance, %) between the mtDNA sequences of *cyt b* gene fragment (below the diagonal) and error estimate (above the diagonal) for the genus *Pareas* members; the within-lineage genetic *p*-distances are shown on the diagonal.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Pareas andersonii</i>	—	1.2	1.3	1.1	1.1	1.3	1.4	1.4	1.3	1.2	1.0	1.2	1.2	1.3	1.0	1.1	1.6	1.4	1.3	1.3
<i>Pareas atayal</i>	20.2	—	1.3	1.2	1.2	1.0	1.0	1.1	0.7	0.8	1.3	1.3	1.3	1.0	1.2	1.3	1.5	1.2	1.1	1.2
<i>Pareas boulengeri</i>	20.2	17.7	—	1.3	0.8	1.1	1.1	1.1	1.2	1.2	1.0	1.3	1.2	1.2	1.3	1.4	1.6	1.2	1.3	1.3
<i>Pareas carinatus</i>	22.3	22.5	21.5	—	1.2	1.2	1.2	1.3	1.3	1.2	1.2	1.3	1.0	1.3	1.2	1.2	1.7	1.2	1.3	1.2
<i>Pareas chinensis</i>	18.8	18.2	9.0	21.9	—	1.1	1.1	1.2	1.2	1.2	1.1	1.2	1.1	1.2	1.1	1.3	1.6	1.2	1.2	1.3
<i>Pareas formosensis</i>	22.0	14.9	16.7	23.1	17.7	4.9	0.7	0.7	1.0	1.0	1.3	1.3	1.1	0.8	1.3	1.3	1.1	1.3	1.0	1.0
<i>Pareas geminatus</i> sp. nov.	22.2	14.3	16.7	22.9	18.7	9.5	4.0	0.7	1.0	1.0	1.3	1.4	1.2	0.7	1.3	1.3	1.1	1.2	1.0	1.0
<i>Pareas hamptoni</i>	22.1	14.1	16.6	22.6	17.8	8.0	7.6	0.5	1.1	1.1	1.4	1.4	1.2	0.7	1.4	1.4	1.2	1.3	1.0	1.1
<i>Pareas iwasakii</i>	20.2	6.9	16.8	23.4	17.5	14.2	14.1	13.6	0.8	0.8	1.3	1.3	1.3	0.9	1.2	1.3	1.5	1.1	1.1	1.1
<i>Pareas komaii</i>	19.4	9.2	17.7	23.6	17.8	14.7	15.4	14.8	8.4	1.8	1.1	1.2	1.1	1.1	1.1	1.2	1.4	1.2	1.1	1.2
<i>Pareas macularius</i>	14.4	18.3	18.7	20.7	17.4	19.6	20.0	18.7	18.9	18.7	—	1.0	1.2	1.4	0.9	1.1	1.6	1.2	1.4	1.3
<i>Pareas margartiophorus</i>	15.2	19.1	19.1	23.1	18.2	20.5	21.4	20.7	19.2	19.5	14.6	—	1.3	1.4	1.0	1.1	1.7	1.2	1.3	1.4
<i>Pareas menglaensis</i>	23.2	22.2	22.9	14.5	24.4	23.2	22.7	22.5	23.2	23.2	21.4	24.0	—	1.2	1.2	1.2	1.6	1.3	1.3	1.2
<i>Pareas mengziensis</i>	20.9	14.1	17.0	22.1	17.6	8.1	7.0	5.5	13.4	14.7	18.9	19.5	22.2	—	1.3	1.3	1.2	1.3	1.0	1.1
<i>Pareas modestus</i>	11.2	17.7	19.1	23.2	18.3	19.7	20.1	19.0	19.1	17.3	11.9	13.7	22.7	18.7	—	1.2	1.5	1.2	1.3	1.2
<i>Pareas monicola</i>	19.7	17.4	18.6	22.0	18.0	19.6	19.7	19.1	17.8	18.2	17.3	19.8	21.6	18.8	18.5	—	1.6	1.3	1.4	1.3
<i>Pareas nigriceps</i>	18.8	15.6	16.9	22.9	16.2	13.4	13.4	12.6	16.0	16.2	19.3	18.8	23.3	12.7	16.4	19.3	—	1.6	1.2	1.1
<i>Pareas stanleyi</i>	20.6	19.0	15.4	23.9	15.2	19.4	19.7	18.4	18.3	17.2	18.1	19.9	24.6	19.5	19.1	19.4	19.0	—	1.2	1.3
<i>Pareas vindumi</i>	20.9	14.8	18.2	23.3	17.6	12.7	12.5	11.7	14.4	14.9	19.0	20.3	23.5	11.2	19.3	18.3	12.3	19.2	—	1.1
<i>Pareas</i> sp.	21.6	16.0	19.9	23.0	19.9	14.5	14.4	13.7	15.7	16.7	20.9	21.6	25.3	13.3	19.7	19.3	10.4	20.9	13.4	—

Pareidae Romer, 1956
Pareas Wagler, 1830

***Pareas geminatus* sp. nov.**

[urn:lsid:zoobank.org:act:8F0D1286-933F-45A7-B557-FEBC23751B53]

(Figs. 3–4; Table 4)

Pareas hamptoni — Vogel 2010; Teynié & David 2010 [*partim*].

Holotype. Adult male, CIB 118021, collected from Jiangcheng County (21.207556 N, 94.020056 E; alt. 2,280 m a.s.l.), Yunnan Province, China, by Ding Li on 21 May 2006.

Paratypes (n=5). Adult females, CIB 118022 and CIB 118023, collected from Jiangcheng County (22.603453 N, 101.882167 E; alt. 1,272 m a.s.l.), Yunnan Province, China; adult male, MNHN 0171S, collected from Houaphanh Province, Laos (no exact locality data); subadult male, ZMMU R-16695, collected from Long Tien, Xaisomboun Province, Laos; adult female, QSMI 1013, collected from Tak Province (approx. 16.425833 N, 99.000000 E; alt. 1,160 m a.s.l.), Thailand.

Other material examined (n=6). Adult male, DL20190930002 (22.619374 N, 101.473156 E, alt. 1,253 m a.s.l.); adult male, DL2019072910 (22.603453 N, 101.882167 E; alt. 1,272 m a.s.l.); adult female, DL2019093001 (22.603424 N, 101.882041 E, alt. 1,227 m a.s.l.); all from Jiangcheng County, Yunnan Province, China; adult males, AUP-00176, ZMMU R-16477, ZMMU R-16478, collected from Doi Inthanon NP, Chiang Mai Province, Thailand.

Diagnosis. *Pareas geminatus* sp. nov. differs from all congeners by the combination of the following morphological characters: a slender, yellow-brown, medium-sized snake (total length 566 mm); one or two anterior temporals; loreal not contacting the eye; prefrontal contacting the eye; one preocular; slightly enlarged median vertebral row; usually 7 (6–8) supralabials; 8 infralabial scales; 3–5 scale rows slightly keeled at midbody; 170–188 ventrals lacking lateral keels; 75–91 subcaudals, all divided; slightly billowing vertical dark bars on the trunk; two slight thin black postorbital stripes starting from lower and upper edges of postorbital scales; lower postorbital stripe reaching the anterior part of seventh supralabial, not continuing to the lower jaw and chin; the left and right upper postorbital stripes merge forming a black nuchal collar.

Description of the holotype: Body slender and laterally flattened; head comparatively large, elongate, clearly distinct from the thin neck (head more than twice the width of the neck near the head base); snout blunt; eye rather large, pupil vertical and slightly elliptical. SVL 428 mm; TaL 138 mm; TL 566 mm; TaL/TL: 0.244. Dorsal scales in 15-15-15 rows, slightly keeled in 5 scale rows at midbody, lacking apical pits; vertebral scales slightly enlarged (one mesial row); outermost dorsal scale rows not enlarged; ventrals 180 (+1 preventral), lacking lateral keels; subcaudals 79, all divided; cloacal plate single.

Rostral not visible from above; single nasal; two internasals, much wider than long, narrowing and slightly curving back laterally (in dorsal view), anteriorly in contact with rostral, laterally in contact with nasal and loreal, posteriorly in contact with prefrontal, not contacting preocular; two large irregular pentagonal prefrontals, much larger than internasals and with a slightly diagonal suture between them, contacting the eye; frontal hexagonal in shape with the lateral sides converging posteriorly, longer than wide, smaller than parietals; presubocular absent; on the both sides subocular and postocular fused into a crescent-shaped scale; one large loreal, not contacting the eye, contacting prefrontal, internasal, nasal, 2nd supralabial and subocular; 6/7 supralabials, 3rd–5th SL touching the subocular, none reaching the eye, 6th by far the largest, elongate; 1/1 supraocular; 1/1 anterior temporals; 2/2 posterior temporals; 8/8 infralabials, anterior most in contact with opposite one along midline, bordering mental, anterior 5 pairs of infralabials bordering anterior chin shields; 4 pairs of chin shields interlaced, 2nd pair very small, no mental groove under chin and throat; anterior chin shields relatively large, much longer than broad, followed by two pairs of chin shields that are much broader than long.

Colouration. In preservative, dorsal surface head black, two black spots behind each eye and above the angle of the mouth respectively on each side of head; ventral surface of head uniformly yellowish. Dorsal surface body yellowish-brown, with about 56 dark faint bands and a few tiny black spots on each scale of the back; the black bands tapering downward on the sides of body and tail, sometimes crossing the vertebral; ventral surface body and tail pale with very sparse small black spots concentrating laterally, tail tip black.

A NEW SPECIES OF THE GENUS *Pareas* FROM THE GOLDEN TRIANGLE

Table 4. Measurements and scale counts of *Pareas geminatus* sp. nov. and *P. hamptoni*. H, Holotype; TaL, tail length; KMD, number of keeled dorsal scale rows at midbody; VSE, number of vertebral scales enlarged; VEN, ventrals; SC, subcaudals; SL, supralabials; SL, infralabials; IL, infralabials; Tem, anterior + posterior temporals; Lor, loreals; Lor-E, loreal scale contact eyes or not; PrO, preoculars; SoO, suboculars; PoO, postoculars; Y, yes; N, no.; SoO-PoO: full: fused into one crescent-shaped scale

Sp.	Cat. No.	Locality	SVL	TaL	KMD	VSE	VEN	SC	SL	IL	Tem	Lor	Lor-E	PrO	SoO	PoO
<i>Pareas geminatus</i> sp. nov.	CIB 118021 ^H	Jiangcheng, Yunnan, China	428	138	5	1	180	79	6/7	8/8	1+2	1/1	N	1/1		Full
	DL2019093002	Jiangcheng, Yunnan, China	348	103	5	1	170	75	7/7	8/8	2+2	1/1	N	1/1		Full
	DL2019072910	Jiangcheng, Yunnan, China	411	110	5	1	182	77	7/7	8/8	2+2	1/1	N	1/1		Full
	MNHN 0171S	Huaphanh, Laos	290	102	3	1	175	91	8/8	8/8	2+3	1/1	N	1/1		Full
		Min	290	102	3	1	170	75								
	Max	428	138	5	1	182	91									
	Mean	369	113	4	1	177	81									
	±SD	63	17	1	0	5	7									
<i>Pareas hamptoni</i>	QSMI 1013	Tak, Thailand	225	72	0	1	188	87	7/7	8/8	2+2	1/1	N	1/1		Full
	CIB 118022	Jiangcheng, Yunnan, China	305	81	5	1	186	67	7/7	8/8	1+2	1/1	N	1/1		Full
	CIB 118023	Jiangcheng, Yunnan, China	317	82	5	1	181	70	7/7	8/8	2+2	1/1	N	1/1		Full
	DL2019093001	Jiangcheng, Yunnan, China	362	94	5	1	174	67	7/7	8/8	2+2	1/1	N	1/1		Full
		Min	225	72	0	1	174	67								
	Max	362	94	5	1	188	87									
	Mean	302	82	4	1	182	73									
	±SD	57	9	2	0	6	10									
<i>Pareas hamptoni</i>	NHMUK 1904.4.26.16 ^H	Mandalay, Myanmar	403	142	5	3	195	96	7/8	6/7	1+2	1/1	N	1/1		Full
	CAS 221489	Putao, Kachin, Myanmar	469	134	9	1	194	91	7/7	8/7	2+3	1/1	Y	1/0	1/1	1/1
	MNHN-RA 1935.0087	Sa Pa, Lao Cai, Vietnam	483	?	5	3	185	92	7/7	7/7	2+3	1/1	N	1/1	1/1	1/1
	MNHN-RA 1935.0088	Sa Pa, Lao Cai, Vietnam	446	155	7	3	193	99	7/7	8/8	2+3	1/1	N	1/1	1/1	1/1
	RMNH 6512	Sa Pa, Lao Cai, Vietnam	471	164	7	1	194	96	8/7	9/8	2+3	1/1	N	1/1		Full
	Min	403	134	5	1	185	91									
	Max	483	164	9	3	195	99									
	Mean	454	149	7	2	192	95									
	±SD	32	13	2	1	4	3									

Plate 51

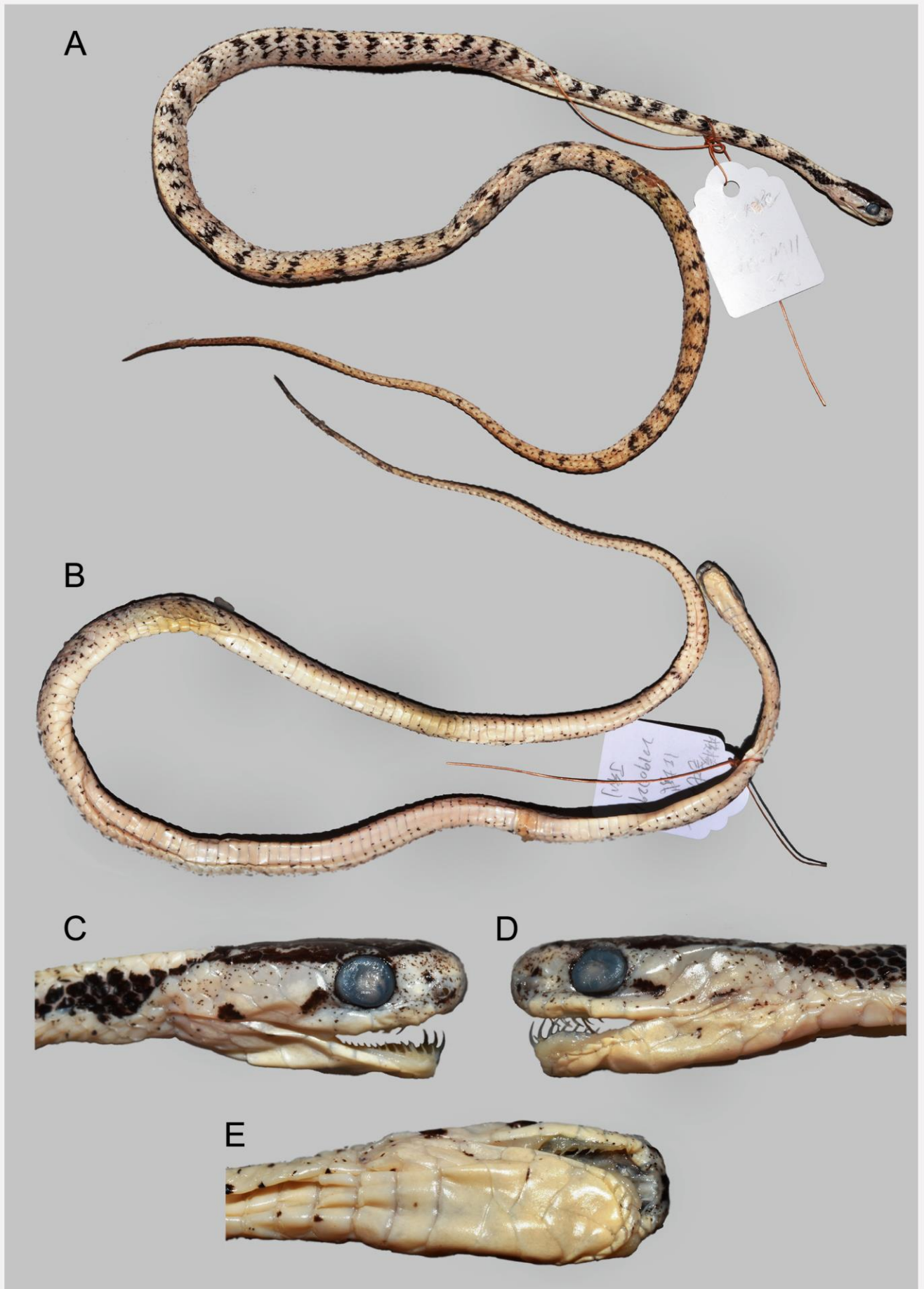


Figure 3. Holotype of *Pareas geminatus* sp. nov. (CIB 118021, adult male): (A) dorsal and (B) ventral views of the body; and the head in (C) lateral (right side), (D) lateral (left side), and (E) ventral views. © Photos G. Vogel

Table 5. Diagnostic features of scalation and color pattern of *Pareas geminatus* sp. nov. in comparison with currently recognized species of the genus *Pareas*. Exceptional values are shown in parentheses. **Symbol characters:** ① Frontal scale shape: 0= subhexagonal with the lateral sides converging posteriorly, 1= hexagonal with the lateral sides parallel; ② Anterior pair of chin shields: 0= longer than broad, 1= broader than long; ③ Loreal-eye contact: 0 = yes, 1 = no; ④ Prefrontal-eye contact: 0= yes, 1= no; ⑤ Number of preoculars; ⑥ Number of suboculars; ⑦ Number of postoculars; ⑧ Number of infralabials; ⑨ Number of temporals; ⑩ Number of keeled dorsal scale rows at midbody; ⑪ Number of enlarged vertebral scales.

Species	①	②	③	④	⑤	⑥	⑦	⑧	⑨	⑩	⑪
<i>P. geminatus</i> sp. nov.	0	0	0	1	1	Fused	Fused	8	1+2 or 2+3	3-5	1
<i>P. andersonii</i>	0	0	0	1	1	1	1	7-8	2+3	5-9	0
<i>P. atayal</i>	0	0	0	1	1	1	1	7-9	2+4	5-9	3
<i>P. boulengeri</i>	0	0	1	1	0	Fused	Fused	8 (7, 9)	2+3 (1+2)	0	0
<i>P. carinatus</i>	1	1	0	0	1	1-3	1 (0)	7-9	3+4 or 3+3	0-11	3
<i>P. chinensis</i>	0	0	0(1)	1	1	1	1	8 (7, 9)	2+3	0 (7)	3
<i>P. formosensis</i>	0	0	0	1	1	1	1	6-8	2+3	0	3
<i>P. hamptoni</i>	0	0	0	1	1	1 or Fused	1 or Fused	6-9	1+2 or 2+3	5-9	1
<i>P. iwasakii</i>	0	0	0	1	1	1	1	9-11	3+4 or 2+3	5-7	1
<i>P. komati</i>	0	0	0	1	1	1	1	6-9	3+4 or 2+3	9-13	3
<i>P. macularius</i>	0	0	0	1	1	1	1	7	2+3	7-13	0
<i>P. margaritophorus</i>	0	0	0	1	1	1	1	7	2+3	0	0
<i>P. menglaensis</i>	1	1	0	0	2	1-3	1-2	7-8	3+4 or 3+3	5-11	3
<i>P. mengziensis</i>	0	0	0	1	1	Fused	Fused	89	2+3	3-9	3
<i>P. modestus</i>	0	0	0	1	1	1	1	7	2+3	3-5	0
<i>P. monticola</i>	0	0	1	1	1	1	1	7-8	2+3	0	1-3
<i>P. nigriceps</i>	0	0	0	0 or 1	1	Fused	Fused	7	1+2 or 1+3	5-9	1
<i>P. nuchalis</i>	1	1	0	1	1	1-3	1-2	7 (6, 8)	3+3 or 3+4	0	1-3
<i>P. stanleyi</i>	0	0	1	1	0	1	1	7 (8)	2+2 or 2+3	13	0
<i>P. vindami</i>	0	0	1	1	1	0	1	6	2+3	keel	0

A NEW SPECIES OF THE GENUS *Pareas* FROM THE GOLDEN TRIANGLE

Table 5 continued. Diagnostic features of scalation and color pattern of *Pareas geminatus* sp. nov. in comparison with currently recognized species of the genus *Pareas*. Exceptional values are shown in parentheses. **Symbol characters:** ⑫ Number of Ventrals; ⑬ Number of Subcaudals.

Species	⑫	⑬	Head and neck pattern	Source
<i>P. geminatus</i> sp. nov.	170–188	75–91	Two black longitudinal streaks on the back of the head and nape	10
<i>P. andersonii</i>	141–162	35–47	No markings on the head, no collar	9, 10
<i>P. atayal</i>	174–188	71–79	Two black lines from postorbital, lower reaching mouth angle, upper going behind head basis and contacting with short black line on neck	5, 10
<i>P. boulengeri</i>	164–187	63–78	A black line from behind eye to angle of mouth	6, 10
<i>P. carinatus</i>	158–190	54–84	A black line from eye to nape, and another from behind eye to angle of mouth	5, 10
<i>P. chinensis</i>	169–180	69–76	A black line from eye extending along nape, and another from the eye to the angle of the mouth	1, 6, 10
<i>P. formosensis</i>	170–180	69–82	A black line from rear of the supraocular to neck, and another from lower anterior-temporal to angle of mouth	5, 10
<i>P. hamptoni</i>	185–195	91–99	Two black longitudinal streaks on the back of the head and nape	10
<i>P. iwasaki</i>	189–194	76–84	A vertical black line from behind eye to neck, another line from behind eye to angle of mouth and to chin	5, 10
<i>P. komaii</i>	162–182	60–76	Two black lines from postorbital, lower reaching mouth angle, upper going behind head basis and contacting with short black line on neck	5, 10
<i>P. macularius</i>	151–173	39–53	A pink, cream or yellow entire or tripartite collar or spot without fine brown speckling	9, 10
<i>P. margaritophorus</i>	133–160	35–54	A butterfly or W shaped collar with moderate or dense speckling	9, 10
<i>P. menglaensis</i>	176–177	65–79	A thin postorbital stripe extending from postocular to neck	8
<i>P. mengziensis</i>	167–173	54–61	A large black area on the back of head, two black spots on each side of head	8
<i>P. modestus</i>	151–159	35–46	No markings on the head, no collar	9, 10
<i>P. monticola</i>	178–199	69–90	A black line from eye to nape, and another from behind eye to angle of mouth	3, 10
<i>P. nigriceps</i>	175–184	73–77	A big black oval patch on back of head, two round black spots on each side of head, a black nuchal band	3, 10
<i>P. nuchalis</i>	201–220	102–120	Oblique black line from lower corner of eye to front edge of last upper labial, and usually a thin, vertical black line at rear of head	4, 10
<i>P. stanleyi</i>	151–160	48–60	A big black spot on the back of the head which separates into two vertical black lines behind the neck; a black line from behind the eye to the nape	2, 10
<i>P. vindumi</i>	178	61	No markings on the head, no collar	6, 10

Source: 1= Jiang (2004); 2= Guo *et al.* (2004); 3= Guo & Deng (2009); 4= Stuebing *et al.* (2014); 5= You *et al.* (2015); 6= Vogel (2015); 7= Yang *et al.* (2019); 8= Wang *et al.* (2020); 9= Vogel *et al.* (2020); 10= our data.

Plate 52



Figure 4. *Pareas geminatus* sp. nov. in life: (A & B) adult males from Jiangchen County, Yunnan, China (not collected, © photos Shengchao Shi); (C) subadult male from Long Tien, Xaisomboun, Laos (ZMMU NAP09280, © photo Parinya Pawangkhanant); (D) adult male from Doi Inthanon NP, Chiang Mai, Thailand (AUP-00176, © photo N.A. Poyarkov)

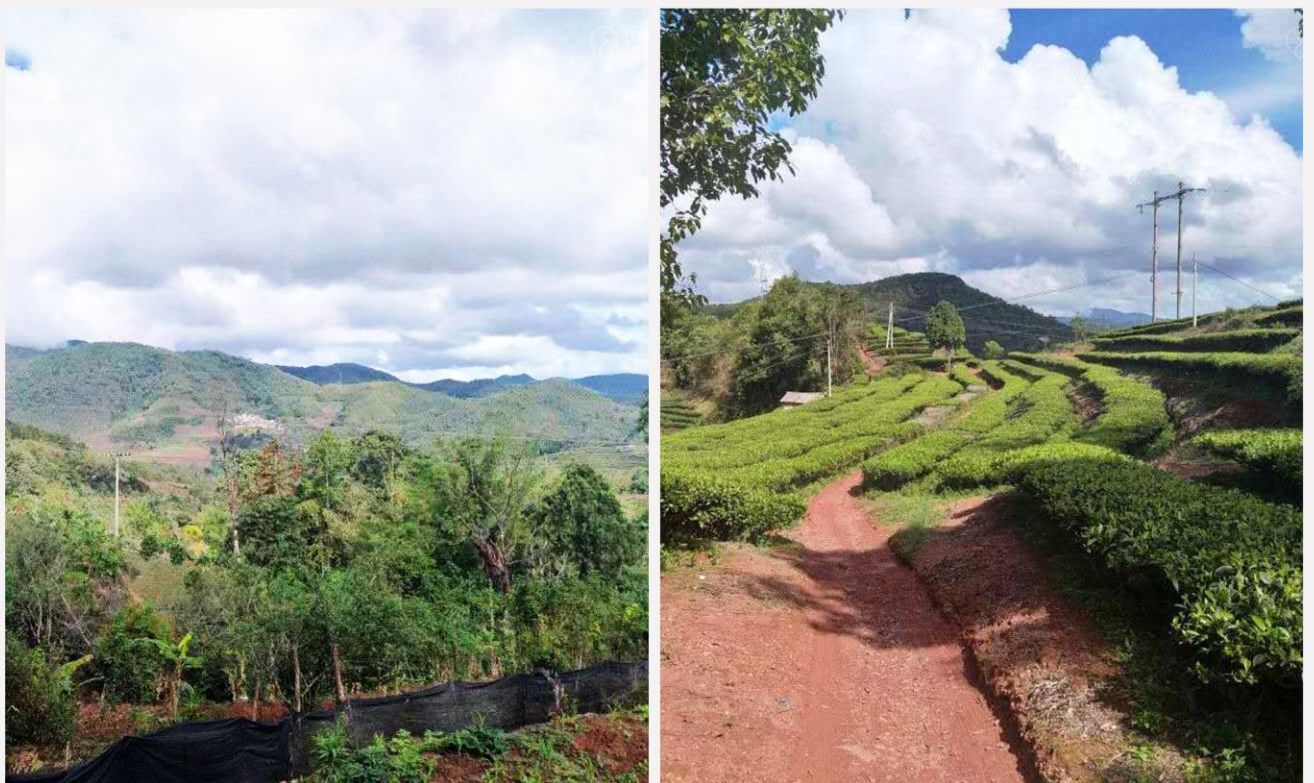


Figure 5. Habitats of *Pareas geminatus* sp. nov. (type locality) © photo Shengchao Shi

Variation. Morphometric and meristic data for the type series are provided in Table 4 and Fig. 4. Paratypes generally agree with the holotype in scalation features. Some variation in body coloration is observed among specimens from China, Laos and Thailand. The topotype specimens from Jiangcheng County, Yunnan Province, China, vary in the degree of development of dark markings on dorsum, neck and dorsal surfaces: in some darker-colored specimens dark cross-bands on dorsum comprise two scales in width, and dark markings in nuchal area connect to dark brown spot covering almost all dorsal surfaces of the head (Fig. 4A), while in other specimens the dark patch on head abruptly terminates at the posterior edge of parietals, separated from much weaker nuchal dark markings by a light-orange collar (Fig. 4B). The adult male AUP-00176 is uniform reddish-brown dorsally, orange-yellow ventrally, with weak dark markings in nuchal area and on the dorsal surface of the head, and very weak almost indiscernible dorsal cross-bands (Fig. 4C). The characteristic dark postocular streaks are prominent in all specimens examined (Figs. 3, 4A–C) but the AUP-00176 (Fig. 4D). Iris reddish in life in all specimens.

Comparisons. Comparative morphological information of species considered to be diagnostic in the genus *Pareas* is summarized in Table 5. The new species is easily distinguishable from the *P. margaritophorus* group [including *P. andersonii*, *P. margaritophorus*, *P. macularius*, and *P. modestus*] by pale brown body coloration with bands (vs uniform dark grey or with bicoloured dots); from the *P. carinatus* group [including *P. carinatus*, *P. nuchalis*, and *P. menglaensis*] by the frontal scale shape subhexagonal with the lateral sides converging posteriorly (vs hexagonal with the lateral sides parallel), the anterior pair of chin shields longer than broad (vs broader than long), the prefrontal contacting eye (vs not in contact), and one or two anterior temporals (vs usually three); from *P. monticola* by the loreal not contacting the eye (vs usually contacting), the absence of a presubocular (vs present), 3–5 slightly keeled dorsal scale rows at midbody (vs all smooth), and the eye separated from the labials by a subocular scale (vs 4th or 4th–5th supralabials touching the eye); from *P. boulengeri* by the loreal not contacting the eye (vs usually contacting), 3–5 slightly keeled dorsal scale rows at midbody (vs usually all smooth), a single row of enlarged vertebral

scales (vs vertebrals not enlarged), and a higher number of subcaudals 75–91 (vs 63–78); from *P. chinensis* by a single row of enlarged vertebral scales (vs 3 rows) and a higher number of subcaudals 75–91 (vs 69–76); from *P. stanleyi* by the loreal not contacting the eye (vs usually contacting), the supralabials not touching the eye (vs in contact with the eye), a lower number of keeled dorsal scales at midbody 3–5 (vs 13), a single row of enlarged vertebral scales (vs not enlarged), a higher number of ventrals 170–188 (vs 151–160), and a higher number of subcaudals 75–91 (vs 48–60).

Comparisons of *Pareas geminatus* sp. nov. with other members of the *P. hamptoni* group appear to be the most pertinent. The new species differs from *P. atayal* by 3–5 medial dorsal scale rows slightly keeled at midbody (vs 5–9 strongly keeled scales), a single row of enlarged vertebral scales (vs 3 rows), and the iris colour reddish (vs yellow); from *P. iwasakii* by 8 infralabials (vs 9–11) and a lower number of ventrals 170–188 (vs 189–194); from *P. komaii* by a lower number of keeled dorsal scales at midbody 3–5 (vs 9–13), a single row of enlarged vertebral scales (vs 3 rows), and a higher number of subcaudals 75–91 (vs 60–76); from *P. mengziensis* by the pale brown coloration of dorsum with indistinct darker crossbars (vs solid black marking on back of head extending to dorsum), a single row of enlarged vertebral scales (vs 3 rows), and a higher number of ventrals 170–188 (vs 167–173); from *P. nigriceps* by a slightly higher number of subcaudals 75–91 (vs 73–77) and indistinct transverse bands on the body (vs distinct); from *P. vindumi* by the absence of a presubocular (vs presence), 7 supralabials (vs 6), a single row of enlarged vertebral scales (vs not enlarged), a higher number of subcaudals 75–91 (vs 61), and dark collar and cross bands on body present (vs absent); from *P. formosensis* by 3–5 dorsal scale rows at midbody keeled (vs all smooth) and a single row of enlarged vertebral scales (vs 3 rows); and finally from its sister species, *P. hamptoni*, by 3–5 dorsal scale rows at midbody slightly keeled (vs 5–9 scales strongly keeled), a lower number of ventrals 170–188 (vs 185–195) and a lower number of subcaudals 67–91 (vs 91–99).

Moreover, the new species differs from the two species described from northern Vietnam (*Eberhardtia tonkinensis* Angel, 1920, type locality: Tam Dao NP., Vinh Phuc Province, Vietnam) and from Hainan Is. of China (*Amblycephalus carinatus hainanus* Smith,

1923, type locality: Hainan) that are currently considered junior synonyms of *P. hamptoni*. Both of these species have completely smooth dorsal scale rows, which agrees with the diagnosis of *P. formosensis* and distinguishes them from the new species (3–5 slightly keeled dorsal scale rows at midbody in *Pareas geminatus* sp. nov.). As we demonstrate below, based on the analysis of topotypic material from northern Vietnam and Hainan, *Eberhardtia tonkinensis* Angel, 1920 and *Amblycephalus carinatus hainanus* Smith, 1923 have to be considered junior synonyms of *P. formosensis*.

Etymology. The specific epithet “*geminatus*” is a Latin adjective in nominative singular (masculine gender) derived from the Latin “*geminus*”, for “twin”, “double”, and is given in reference to the similarity in morphology of the new species to its sister taxon, *P. hamptoni*, with which it was confused for a long time. We suggest the following common names: “Twin Slug snake” (English) and “Bó Zhòng Dùn Tóu Shé” (伯仲钝头蛇) in Chinese.

Distribution and natural history. The known distribution of *Pareas geminatus* sp. nov. is shown in Fig. 1. The new species is currently known from the Golden Triangle area, including the southernmost part of Yunnan Province, the northwestern part of Thailand, and the northern part of Laos. The occurrence of the new species in the extreme eastern corner of the Shan Plateau in Myanmar is anticipated. At the type locality in Jiangcheng County, Yunnan, China, *Pareas geminatus* inhabits tropical monsoon forests with clearly defined dry and wet seasons at elevations from 1,160 to 2,280 m asl. The new species was also recorded in highly modified secondary habitats with tea plantations (Fig. 5). The specimens of *Pareas geminatus* were observed at night after 2100 h while perching on vines or bushes ca. 1.0–1.5 m above the ground, waiting for prey. In China, the new species is threatened by intensifying human activity due to increasing deforestation for tea cultivation.

Conservation status. Further research is required to clarify the extent of the distribution, population trends and conservation status of the new species. *Pareas geminatus* sp. nov. is distributed over a large area including several protected areas. Across its range the new species seems not to be especially rare. Thus, we tentatively suggest *P. geminatus* be considered a Least Concern (LC) species following the IUCN’s Red List categories (IUCN Standards and Petitions Committee 2019).

Discussion

Our study provides an updated phylogeny for the genus *Pareas* including 20 nominal species and one undescribed population, *Pareas* sp. from Indian East Himalayas (Fig. 1, locality 1). Our phylogenetic results are concordant with the earlier works (You *et al.* 2015, Wang *et al.* 2020, Vogel *et al.* 2020) in recognizing the monophyly of the genus *Pareas* encompassing five major species groups (Fig. 2A–E). Though the phylogenetic relationships within the *P. hamptoni* species group remain essentially unresolved, our study provides insights on diversity and distribution of the group members.

The undescribed *Pareas* sp. from India forms a well-supported clade (98/1.0) with *P. nigriceps* from Mt. Gaoligongshan in western Yunnan. Monophyly of the clade encompassing the three species from the East Asian islands (Taiwan and Yaeyama Group: *P. atayal*, *P. iwakii*, and *P. komaii*) is strongly supported (100/1.0) (Fig. 2).

Pareas vindumi from the northeastern part of Kachin State of Myanmar, which originally described without assignment to any species group of *Pareas* (Vogel 2015), is confirmed as the member of *P. hamptoni* species group (Fig. 2). We have for the first time confirmed the actual distribution limits of *P. formosensis*, which remained unclear after the review by Wang *et al.* (2020). According to our data, this species inhabits not only the island of Taiwan, but also the southern parts of mainland China including Guangdong Province, Hainan Island, and is also found in Vietnam from the north (Cao Bang and Vinh Phuc provinces) southwards along the Truong Son (Annamite) Mountain Range to the Kontum and Langbian plateaus in the south (Fig. 1: localities 17–27), and most certainly also can be found in the Cambodian and Laotian parts of the Annamite Range.

Eberhardtia tonkinensis Angel, 1920 (from Tam Dao NP., Vinh Phuc Province, northern Vietnam, Fig. 1: locality 22) and *Amblycephalus carinatus hainanus* Smith, 1923 (from Hainan, Fig. 1: locality 24) were examined and fall into the range of *P. formosensis sensu lato* and also agree with the morphological diagnosis of the latter species (smooth dorsal scales). With this new data we now consider *Eberhardtia tonkinensis* Angel, 1920 and *Amblycephalus carinatus hainanus* Smith, 1923 to be subjective junior synonyms of *Amblycephalus formosensis* van Denburgh, 1909.

Several *Pareas* species described from southern China in the early 20th century and presently considered junior synonyms of *P. chinensis* (Wallach *et al.* 2014) or *P. hamptoni* (Uetz *et al.* 2020) still remain poorly understood. The type localities of *Amblycephalus yunnanensis* Vogt, 1922 and *Amblycephalus niger* Pope, 1928 are also located in the northern part of Yunnan Province, China (Fig. 1: localities 8–9); both species may represent valid taxa according to our ongoing studies. The type locality of *Amblycephalus kuangtungensis* Vogt, 1922 described from Guangdong Province in southern China (Fig. 1: locality 28) is placed within the range of *P. formosensis sensu lato*, and it is likely that they are conspecific. The identity of these three taxa has yet to be clarified based on an integrative approach combining morphological examination of type specimens and molecular data from the topotypic materials.

Despite the fact that *P. hamptoni* has been known since 1905 and is regularly mentioned in scientific publications, this species seems to be very rare in collections. Most specimens that we located actually belong to *P. geminatus* sp. nov. or to *P. formosensis*. It is not clear whether the distributions of *P. hamptoni* and *P. geminatus* sp. nov. overlap but it seems to be likely that both species live in sympatry in the southwestern part of China. The sympatry of three other members of the *P. hamptoni* group (*P. formosensis*, *P. komaii*, and *P. atayal*) was recently reported from Taiwan Island (You *et al.* 2015); however such cases are not yet known from the Asian mainland. Although we do not report different species of the *P. hamptoni* group occurring sympatric in the present paper, the demonstrated high diversity of the group members in the mountains of southern Yunnan and northwestern Vietnam implies that some of them might be found in sympatry. *Pareas vindumi* and *P. nigriceps* are expected to be sympatric with *P. hamptoni sensu stricto* in the montane areas of western Yunnan and the eastern part of Kachin State of Myanmar. The ranges of *P. hamptoni sensu stricto*, *P. geminatus* sp. nov. and *P. mengziensis* most surely overlap in southern Yunnan, while *P. formosensis* is distributed to the east of the range of *P. geminatus* sp. nov., and the cases of sympatric or parapatric occurrence of these two species cannot be excluded in northern Vietnam and Laos. Finally, the significant degree of molecular divergence along with the differences

in morphology and coloration observed between the populations of *P. geminatus* sp. nov. from China, Laos and Thailand suggest that further studies on the phylogeography and distribution patterns of this new species are required to assess its intraspecific variation.

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Appendix. Specimens Examined

- Pareas atayal* (4 ex.): Taiwan:** Yang-Ming-Shan: FMNH 169392; Yang-Ming-Shan: Yung-foh-lee: FMNH 127998, 169315; Yang-Ming-Shan: Mt. Agr. Area: FMNH 169395.
- Pareas boulengeri* (9 ex.): China:** Kouy Tcheounow, Guizhou Province: MNHN 1912.0349–0351 (syntypes of *Amblycephalus boulengeri*); Fangxiang Village, Leishan County, Guizhou Province: CIB 10084; Ebian County, Sichuan Province: DL 026; Xingou village, Ya'an City, Sichuan Province: DL 2019.09.23.04; Xianju County, Zhejiang Province: DL 2018.06.29.01–02.
- Pareas chinensis* (7 ex.): China:** Mt. Jiguan, Sichuan Province: DL 051; Hongya Xian, Sichuan Province: FMNH 232812–14; Sichuan Province: FMNH 170632; Mt. Jiguan, Sichuan Province: NMW 39540.1–2.
- Pareas formosanus* (12 ex.): Taiwan:** Tsu-Shari: NMW 28130:3, 7–9; Formosa: NMW 28130:12, 14, 16, 18; Kosango: NMW 28130:20; Suisharya: ZMB 30585. **Vietnam:** Lao-Kay (now Sapa District, Lao Cai Province): MNHN 1908.206 (holotype of *Eberhardtia tonkinensis*). **China:** Kachei near Five Finger Mount, Hainan Province: NHMUK 1924.5.22.11 (holotype of *Amblycephalus carinatus hainanus*).
- Pareas hamptoni* (5 ex.): Myanmar:** Mogok, Upper Burma now Mandalay Division: NHMUK 1904.4.26.16 (holotype of *Amblycephalus hamptoni*); Naung Mon, Putao District, Kachin State: CAS 221489. **Vietnam:** Sa Pa District, Lao Cai Province: MNHN-RA 1935.0087-88, RMNH 6512.
- Pareas stanleyi* (4 ex.): China:** Fujian Province: CIB 10165; Fukien, Ch'unganHsien now Wuyishan City, Fujian Province: FMNH 24990–92.
- Pareas vidumi* (1 ex.): Myanmar:** Chipwi Township, Lukpwi Village, Kachin State: CAS 248147 (holotype of *Pareas vidumi*).
- Pareas monticola* (24 ex.): India:** Naga Hillas, Assam: NHMUK 1946.1.20.5 (holotype of *Dipsas monticola*); Khasi Hills, Meghalaya: NHMUK 1907.12.16.26, 60.3.19.1312; Darjiling, west Bengal: NHMUK 1909.3.9.18–21, 80.11.10.147, NMW 28127, ZMH R05510; Jaipur, Rajasthan" (erroneous): NHMUK 1910.12.36.7; Mishmi Hills, Arunachal Pradesh: NHMUK 1940.3.7.2; Abor Hills, Arunachal Pradesh: NHMUK 1940.3.9.15–16; Mizoram: MZMU 851, 1335, 1485–1486. **China:** Motuo, Xizang: CIB 10163. **Myanmar:** Indawgyi, Kachin: ZMMU R-16630; Ban Mauk, Sagaing: ZMMU R-16631–16634.
- Pareas geminatus* sp. nov. (12 ex.): China:** Jiangcheng, Yunnan Province: CIB 118021–23, DL20190930001–2, DL2019072910. **Laos:** Houaphanh Province: MNHN 171S; Long Tien, Xaisomboun Province: ZMMU R-16695. **Thailand:** Tak Province: QSMI 1013; Doi Inthanon NP, Chiang Mai Province: AUP-00176, ZMMU R-16477–8.

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