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 prevelar, 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 inframarginal shield lacking, three pairs of inframarginals, the first pair distinctly elongated, posterior inframarginals 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. wasakii* (Maki); *P. komaii* (Maki); *P. macularius* (Theobald); *P. mengziensis* 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. vindalum* 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 *Eberharditia tonkinensis* Angell, 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, Teynić & 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.
Infrafalabials 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 μl using NanoDrop 2000 (Thermo Scientific), and adjusted it to ca. 100 ng DNA/μL. 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; Loredo 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 μl reactions using ca. 50 ng genomic DNA, 10 nmol of each primer, 15nmol 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.
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 *Astenodipsas* as well as *Aplopeltura boa*. The sequence of *Xylophis captaini* (Pariedae: *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-selecction 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 *Astenodipsas*. The monophyly of the genus *Astenodipsas* 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  | *Pareas andersonii*      | Myanmar, Chin, Mt. Natmataung      | MT968772| MW287040| MW287022 | this work       |
| NMNS 05594  | *Pareas atayal*          | China, Taiwan, Yilan, Beiheng      | KJ642124| MW287041| KJ642198 | *You et al.* 2015 |
| KIZ 09965   | *Pareas boulengeri*      | China, Hubei, Enshi                | JF827678| MW287056| MK135141 | *Guo et al.* 2011 |
| GP1079      | *Pareas carinatus*       | Peninsular Malaysia                | MK135110| MK805378| MK135162 | *Wang et al.* 2020 |
| CIB 098269  | *Pareas chinensis*       | China, Sichuan, Tianquan          | JF827691| MW287069| MK135137 | *Guo et al.* 2011 |
| NMNH 05637  | *Pareas formosensis*     | China, Taiwan, Nantou              | MK135068| MK805333| MK135117 | *Wang et al.* 2020 |
| YBU 12015   | *Pareas formosensis*     | China, Hainan                      | MK135068| MW287043| MW287024 | this work       |
| H26-HAM01   | *Pareas formosensis*     | China, Guangdong                   | MW287061| MW287043| MW287024 | this work       |
| ZMMUR-16684 | *Pareas formosensis*     | Vietnam, Cao Bang, Phia Oac NP     | MW287062| MW287044| MW287025 | this work       |
| FMNH 255567 | *Pareas formosensis*     | Vietnam, Nghe An, Pu Mat NP       | AV425806| —       | —        | unpublished     |
| ZMMUR-NAP-08868 | *Pareas formosensis* | Vietnam, Quang Nam, Song Thanh NP | MW287063| MW287045| MW287026 | this work       |
| ZMMUR-13709 | *Pareas formosensis*     | Vietnam, Lam Dong, Bidoup - Nui Ba NP | MW287064| MW287046| MW287027 | this work       |
| ZMMUR-14072 | *Pareas formosensis*     | Vietnam, Dak Lak, Chu Yang Sin NP  | MW287065| MW287047| MW287028 | this work       |
| ZMMUR-16333 | *Pareas formosensis*     | Vietnam, Gia Lai, Kon Chu Rang NR  | MW287066| MW287048| MW287029 | this work       |
| DL2019072910 | *Pareas geminatus* sp. nov. | China, Yunnan, Jiangcheng       | MW287067| —       | —        | this work       |
| CIB 118021  | *Pareas geminatus* sp. nov. | China, Yunnan, Jiangcheng      | MW287068| —       | —        | this work       |
| CIB 118022  | *Pareas geminatus* sp. nov. | China, Yunnan, Jiangcheng      | MW287069| —       | —        | this work       |
| CIB 118023  | *Pareas geminatus* sp. nov. | China, Yunnan, Jiangcheng      | MW287070| —       | —        | this work       |
| DL2019093001 | *Pareas geminatus* sp. nov. | China, Yunnan, Jiangcheng     | MW287071| —       | —        | this work       |
| DL2019093002 | *Pareas geminatus* sp. nov. | China, Yunnan, Jiangcheng     | MW287072| —       | —        | this work       |
| ZMMUR-16695 | *Pareas geminatus* sp. nov. | Laos, Xaisomboun, Long Tien    | MW287073| MW287049| MW287030 | this work       |
| ZMMUR-16478 | *Pareas geminatus* sp. nov. | Thailand, Chiang Mai, Doi Inthanon NP | MW287074| MW287050| MW287031 | this work       |
| ZMMUR-16477 | *Pareas geminatus* sp. nov. | Thailand, Chiang Mai, Mae Kampong | MW287075| MW287051| MW287032 | this work       |
| AUP-00176   | *Pareas geminatus* sp. nov. | Thailand, Chiang Mai, Doi Inthanon NP | MW287076| MW287052| MW287033 | this work       |
| YPX 18219 (GP5127) | *Pareas hamptoni* s. str. | Myanmar, Kachin                 | MK135077| MK805342| MK135126 | *Wang et al.* 2020 |
| YPX 18604   | *Pareas hamptoni* s. str. | Myanmar, Kachin                 | MK135078| MK805343| MK135127 | *Wang et al.* 2020 |
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  | *Pareas hamptoni* s. str. | Myanmar, Kachin, Putao, Naung Mon | MW287077 | — | MW287034 | this work |
| ROM 38104   | *Pareas hamptoni* s. str. | Vietnam, Lao Cai, Sa Pa | KX694896 | — | — | Alencar et al. 2016 |
| ZMMU NAP-09087 | *Pareas hamptoni* s. str. | Vietnam, Lao Cai, Bat Xat NR | MW287078 | MW287054 | MW287035 | this work |
| ZMMU NAP-09088 | *Pareas hamptoni* s. str. | Vietnam, Lao Cai, Bat Xat NR | MW287079 | MW287053 | MW287036 | this work |
| NMNS 05655  | *Pareas iwasakii* | Japan, Okinawa, Ishigaki | KJ642160 | — | KJ642198 | You et al. 2015 |
| NMNS 05654  | *Pareas iwasakii* | Japan, Okinawa, Iriomote | KJ642156 | — | KJ642207 | You et al. 2015 |
| NMNS 05625  | *Pareas komaii* | China, Taiwan, Hualien | KJ642189 | MW287055 | MW287024 | You et al. 2015 |
| NMNS 05618  | *Pareas komaii* | China, Taiwan, Taitung, Lijia | KJ642185 | MW287056 | MW287024 | You et al. 2015 |
| ZMMU R-16629 | *Pareas macularius* | Myanmar, Sagaing, Ban Mauk | MT968771 | MW287057 | MW287037 | this work |
| M01         | *Pareas margaritophorus* | Vietnam, Binh Phuoc, Bu Gia Map NP | KJ642195 | MW287058 | MW287038 | this work |
| GP1292      | *Pareas menglaensis* | China, Yunnan, Mengla | MK135113 | MK805378 | MK135162 | Wang et al. 2020 |
| YBU14288    | *Pareas mengiensis* | China, Yunnan, Mengzi | MK135083 | MK805348 | MK135132 | Wang et al. 2020 |
| MZMU 1293   | *Pareas modestus* | India, Mizoram, Aizawal, Tanhril | MT968773 | — | — | Vogel et al. 2020 |
| GP2027      | *Pareas monticola* | China, Xizang (Tibet), Motuo | MK135107 | MK805372 | MK135156 | Wang et al. 2020 |
| CHS 656     | *Pareas nigriceps* | China, Yunnan, Gaoligongshan | MK201455 | — | — | Li et al. 2020 |
| FK 2626     | *Pareas nuchalis* | Brunei, Brunei Darussalam | U49311 | — | — | Kraus & Brown 1998 |
| HM 2007-S001 | *Pareas stanleyi* | China, Guangxi, Guilin | JN230704 | JN230705 | MK135135 | Guo et al. 2011 |
| CAS 248147  | *Pareas vindumi* | Myanmar, Kachin, Chipwi, Lukpwi | MW287080 | MW287059 | MW287039 | this work |
| BNHS 3575   | *Pareas sp.* | India, Arunachal Pradesh | MT188734 | — | — | Bhosale et al. in press |
| KIZ 011963  | *Aplopeletura boia* | Peninsular Malaysia | JF827673 | JF827650 | JF827696 | Guo et al. 2011 |
| —           | *Asthenodipsas troidonotus* | Indonesia | AY425808 | — | — | unpublished |
| LSUHC 9098  | *Asthenodipsas lasgalenensis* | Malaysia, Pahang, Fraser’s Hill | KC916755 | — | — | Loredo et al. 2013 |
| —           | *Asthenodipsas vertebralis* | Peninsular Malaysia | AY425807 | — | — | unpublished |
| FMNH 241296 | *Asthenodipsas laevis* | Malaysia, Sabah, Lahad Datu | KX660468 | KX660596 | KX660335 | Figueroa et al. 2016 |
| FMNH 273617 | *Asthenodipsas borneensis* | Malaysia, Sarawak, Bintulu | KX660469 | KX660597 | KX660336 | Figueroa et al. 2016 |
| BNHS 3376   | *Xylophis captaini* | India | MK340914 | MK340912 | MK344195 | Deepak et al. 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, Luikwi (Vogel 2015); Pareas nigriceps: (3) China, Yunnan, Gaoligongsan (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 Uthang 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 Eberharditia 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 iwasaki: (33) Japan, Okinawa, Ishigaki (Maki 1937, You et al. 2015), (34) Japan, Okinawa, Iriomote (You et al. 2015).
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**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 Jiangchen 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. iwasekii 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 |
|------|-------------|------------------|-----------------|-----------|
| cyt b | L14910      | forward          | 5'-GACCTGTGATMTGAAAACAYCGTTG-3' | de Queiroz et al. 2002 |
| cyt b | H16064      | reverse          | 5'-CTTTGTTTCTACAGAACAATGTGTTA-3' | de Queiroz et al. 2002 |
| ND4  | ND4F        | forward          | 5'-ACCTATGACTACCAAAAGCTCATGTAAGGC-3' | Salvi et al. 2013 |
| ND4  | ND4LEUR     | reverse          | 5'-CATTACTTTTACTTTGGATTGACCA-3' | Salvi et al. 2013 |
| e-mos | cmos S77    | forward          | 5'-CATGGACTGAGGATGTATG-3' | Slowinski & Lawson 2002 |
| e-mos | cmos S78    | reverse          | 5'-CCTTGTTGTGATTTCCTACCT-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 |
|---------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| *Pareas andersonii* | —  | 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|
| *Pareas atayal*      | 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| 1.3| 1.5| 1.2| 1.1| 1.2|
| *Pareas boulenieri*   | 20.2| 17.1| —  | 1.3| 0.8| 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|
| *Pareas carinatus*    | 22.3| 22.5| 21.5| —  | 1.2| 1.2| 1.2| 1.3| 1.3| 1.2| 1.3| 1.2| 1.3| 1.0| 1.3| 1.2| 1.7| 1.2| 1.3| 1.2|
| *Pareas chinensis*    | 18.8| 18.2| 9.0 | 21.9| —  | 1.1| 1.1| 1.2| 1.2| 1.1| 1.2| 1.1| 1.2| 1.1| 1.3| 1.6| 1.2| 1.2| 1.3|
| *Pareas formosensis*  | 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|
| *Pareas gaminatus* 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|
| *Pareas hamptoni*     | 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|
| *Pareas iwassakii*    | 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|
| *Pareas komai*        | 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| 1.2| 1.4| 1.2| 1.2| 1.1| 1.2|
| *Pareas macularius*   | 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|
| *Pareas margaritophorus* | 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|
| *Pareas menglaenos*   | 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|
| *Pareas mengiensis*   | 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|
| *Pareas modestus*     | 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|
| *Pareas monticola*    | 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|
| *Pareas nigriceps*    | 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|
| *Pareas stanleyi*     | 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|
| *Pareas vindumi*      | 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|
| *Pareas 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 (21.20756 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.
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; 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, Country                                      | SVL  | TaL  | KMD  | VSE  | VEN  | SC   | SL   | IL   | Tem  | Lor  | Lor-E | PrO  | SoO  | PoO  |
|-----------|-------------|-------------------------------------------------------|------|------|------|------|------|------|------|------|------|-------|-------|------|------|------|
| Males     |             |                                                       |      |      |      |      |      |      |      |      |      |       |       |      |      |      |
| CIB 118021 | MNHN 0171S  | Jiangcheng, Yunnan, China                            | 428  | 138  | 5    | 1    | 180  | 79   | 6/7  | 8/8  | 1+2  | 1/1   | N     | 1/1   | Full |
| DL2019093002 | DL2019072910 | Jiangcheng, Yunnan, China                            | 348  | 103  | 5    | 1    | 170  | 75   | 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    |      |      |      |       |       |       |      |      |      |
| Females   |             |                                                       |      |      |      |      |      |      |      |      |      |       |       |      |      |      |
| 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   |      |      |      |       |       |       |      |      |      |
| Parasitic |             |                                                       |      |      |      |      |      |      |      |      |      |       |       |      |      |      |
| NHMUK 1904.4.26.16 |                | 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    |      |      |      |       |       |       |      |      |      |
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 |
|--------------------|----|----|----|----|----|----|----|----|----|----|----|
| *P. geminatus* sp. nov | 0  | 0  | 0  | 1  | 1  | Fused | Fused | 8  | 1+2 or 2+3 | 3–5 | 1  |
| *P. andersonii*     | 0  | 0  | 0  | 1  | 1  | 1   | 1   | 7–8 | 2+3           | 5–9 | 0  |
| *P. atayal*         | 0  | 0  | 0  | 1  | 1  | 1   | 1   | 7–9 | 2+4           | 5–9 | 3  |
| *P. boulengeri*     | 0  | 0  | 1  | 1  | 0  | Fused | Fused | 8 (7, 9) | 2+3 (1+2) | 0   | 0  |
| *P. carinatus*      | 1  | 1  | 0  | 0  | 1  | 1   | 1   | 7–9 | 3+4 or 3+3 | 0–11 | 3  |
| *P. chinensis*      | 0  | 0  | 0(1) | 1  | 1  | 1   | 1   | 8 (7, 9) | 2+3           | 0 (7) | 3  |
| *P. formosensis*    | 0  | 0  | 0  | 1  | 1  | 1   | 1   | 6–8 | 2+3           | 0   | 3  |
| *P. hamptoni*       | 0  | 0  | 0  | 1  | 1  | 1   | 1   | 6–9 | 1+2 or 2+3 | 5–9 | 1  |
| *P. iwassii*        | 0  | 0  | 0  | 1  | 1  | 1   | 1   | 9–11 | 3+4 or 2+3 | 5–7 | 1  |
| *P. komaii*         | 0  | 0  | 0  | 1  | 1  | 1   | 1   | 6–9 | 3+4 or 2+3 | 9–13 | 3  |
| *P. macularius*     | 0  | 0  | 0  | 1  | 1  | 1   | 1   | 7   | 2+3           | 7–13 | 0  |
| *P. marginiphorus*  | 0  | 0  | 0  | 1  | 1  | 1   | 1   | 7   | 2+3           | 0   | 0  |
| *P. menglaensis*    | 1  | 1  | 0  | 0  | 2  | 1–3 | 1–2 | 7–8 | 3+4 or 3+3 | 5–11 | 3  |
| *P. mengiensis*     | 0  | 0  | 0  | 1  | 1  | Fused | Fused | 89  | 2+3           | 3–9 | 3  |
| *P. modestus*       | 0  | 0  | 0  | 1  | 1  | 1   | 1   | 7   | 2+3           | 3–5 | 0  |
| *P. monticola*      | 0  | 0  | 1  | 1  | 1   | 1   | 1   | 7   | 2+3           | 0   | 1–3 |
| *P. nigricep*       | 0  | 0  | 0  | 0 or 1 | 1   | Fused | Fused | 7   | 1+2 or 1+3 | 5–9 | 1  |
| *P. nuchalis*       | 1  | 1  | 0  | 1  | 1   | 1–3 | 1–2 | 7 (6, 8) | 3+3 or 3+4 | 0   | 1–3 |
| *P. stanleyi*       | 0  | 0  | 1  | 1  | 0  | 1   | 1   | 7 (8) | 2+2 or 2+3 | 13  | 0  |
| *P. vindumi*        | 0  | 0  | 1  | 1  | 1   | 0   | 1   | 6   | 2+3 keel     | 0   | 0  |
### 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 |
|---------|----|----|-----------------------|--------|
| *P. andersonii* | 141–162 | 35–47 | No markings on the head, no collar | 9, 10 |
| *P. atayal* | 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 |
| *P. boulengeri* | 164–187 | 63–78 | A black line from behind eye to angle of mouth | 6, 10 |
| *P. carinatus* | 158–190 | 54–84 | A black line from eye to nape, and another from behind eye to angle of mouth | 5, 10 |
| *P. chinensis* | 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 |
| *P. formosensis* | 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 |
| *P. hamptoni* | 185–195 | 91–99 | Two black longitudinal streaks on the back of the head and nape | 10 |
| *P. iwasakii* | 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 |
| *P. komaii* | 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 |
| *P. macularius* | 151–173 | 39–53 | A pink, cream or yellow entire or tripartite collar or spot without fine brown speckling | 9, 10 |
| *P. margaritophorus* | 133–160 | 35–54 | A butterfly or W shaped collar with moderate or dense speckling | 9, 10 |
| *P. menglaensis* | 176–177 | 65–79 | A thin postorbital stripe extending from postocular to neck | 8 |
| *P. mengziensis* | 167–173 | 54–61 | A large black area on the back of head, two black spots on each side of head | 8 |
| *P. modestus* | 151–159 | 35–46 | No markings on the head, no collar | 9, 10 |
| *P. monticola* | 178–199 | 69–90 | A black line from eye to nape, and another from behind eye to angle of mouth | 3, 10 |
| *P. nigriceps* | 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 |
| *P. nuchalis* | 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 |
| *P. stanleyi* | 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 |
| *P. vindumi* | 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.
**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 scation 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 vertebrales 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. iwasaki* by 8 infralabials (vs 9–11) and a lower number of ventrals 170–188 (vs 189–194); from *P. komai* 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,
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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 “伯仲钝头蛇” (bó zhòng dùn tóu shé) 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. iwasakii*, and *P. komai*) 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 sympathy in the southwestern part of China. The sympathy 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 sympathy. *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**: Khou Tcheoumon, 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. Jiguang, Sichuan Province: DL 051; Hongya Xian, Sichuan Province: FMNH 232812–14; Sichuan Province: FMNH 170632; Mt. Jiguang, 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 *Eberharditia 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, Patau 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'ungan Hsien 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 Hills, Assam: NHMUK 1946.1.20.5 (holotype of *Dipsas monticola*); Khali 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, Arunchal 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 gernatianus* sp. nov. (12 ex.): **China**: Jiangcheng, Yunnan Province: CIB 118021–23, DL20190930001–2, DL2019072910. **Laos**: Houaphanh Province: MNHN 1718; 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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