

## ORIGINAL ARTICLE

# Systematic revision of mountain dragons (Reptilia: Agamidae: *Diploderma*) in China, with descriptions of six new species and discussion on their conservation

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## Funding information

STEP Program of China, Grant/Award Number: 2019QZKK0501; National Key Research and development Program of China, Grant/Award Number: 2017YFC0505202; Strategic Priority Research Program of CAS, China, Grant/Award Number: XDA19050303; The Ministry of Ecology and Environment of China, Grant/Award Number: 2019HJ2096001006; National Science Foundation of USA, Grant/Award Number: DEB 1657648, IOS 1353683, GRFP 2017216966 and EAPSI 171400

## Abstract

Cryptic diversity not only introduces confusion to taxonomic studies, but it also poses major challenges to conservation and environmental legislation. One such troubling group are the Mountain Dragons in the genus *Diploderma* in Southwest China. Previous studies have suggested that the genus contains considerable cryptic diversity, particularly in the *D. flaviceps* complex. Owing to taxonomic confusion, micro-endemic lineages are still neglected by the Chinese wildlife protection laws, despite their urgent conservation needs. Combining multivariate morphological and multi-locus phylogenetic data, we provide the first integrative systematic revision of the genus *Diploderma*. Specifically, we confirm that the six examined populations of *D. cf. flaviceps* from the upper Jinsha and Yalong River Valleys in Sichuan and Yunnan Provinces represent six cryptic, undescribed lineages, and we describe each of them as a new species. With the updated taxonomy and distribution information, we discuss the taxonomy of the *D. flaviceps* complex in Southwest China, provide an updated diagnostic key along with distributional ranges for all species of the genus, and discuss some of the suspicious records of other congeners in China. Lastly, we evaluate the IUCN status of each of the six new species and highlight the major challenges for *Diploderma* conservation in China due to delayed environmental legislation and misleading conservation assessments.

## KEYWORDS

Draconinae, IUCN, *Japalura* sensu lato, taxonomy, Wildlife Protection Act of China

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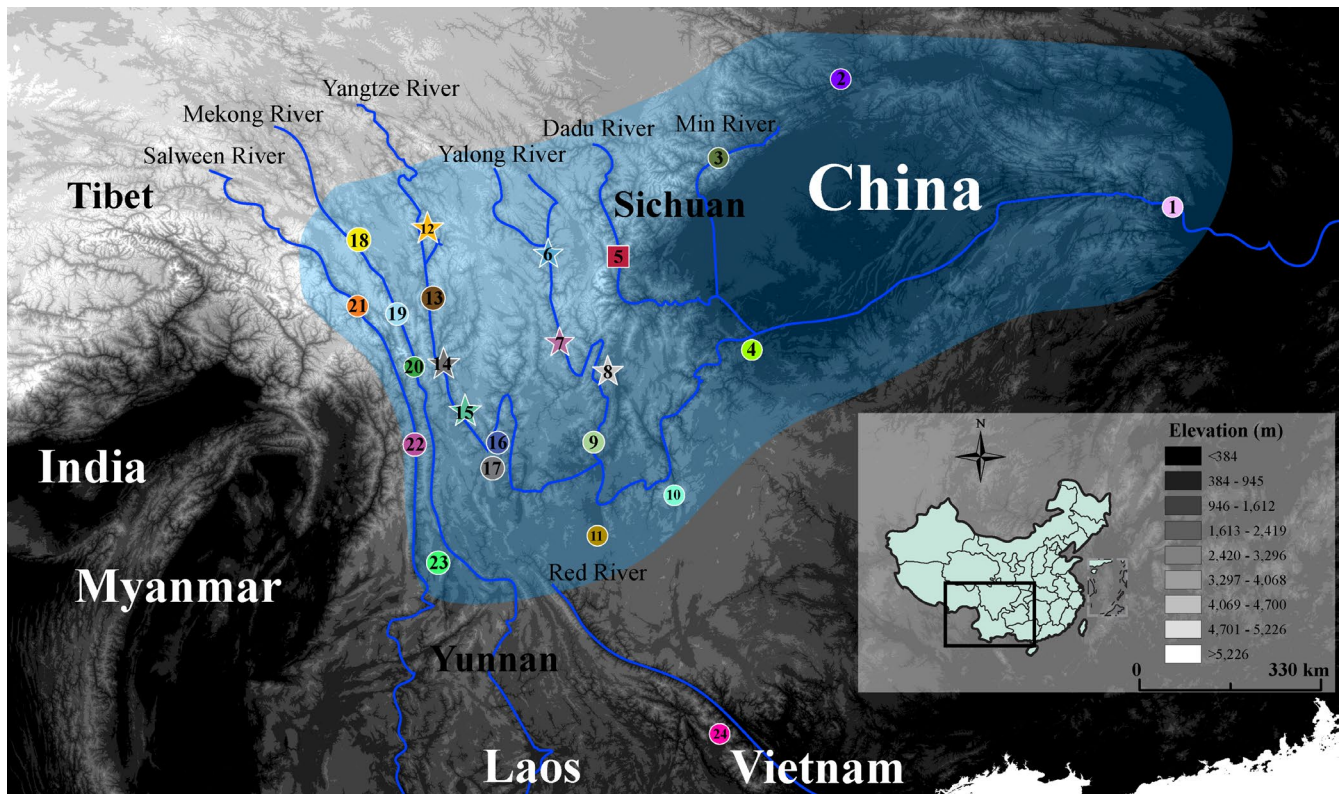
## 1 | INTRODUCTION

The genus *Diploderma* Hallowell, 1861, commonly known as Mountain Dragons, was resurrected recently from the paraphyletic genus *Japalura* sensu lato Gray, 1853 (Wang, Che, Lin, et al., 2019). Despite the recent split, *Diploderma* still comprises a major portion of the diversity in the subfamily Draconinae, with a total of 25 species recognized to date (Wang, Che, et al., 2019; Wang, Jiang, Ren, et al., 2019; Wang, Wu, Jiang, et al., 2019). Most congeners are found in the Hengduan Mountain Region (HMR) in Mainland Southwest China and Taiwan (Manthey, 2010; Wang, Che, et al., 2019), and the major portion of the diversity (12 species) belongs to a single species complex, the *D. flaviceps* (Barbour & Dunn, 1919) complex (Figure 1; Manthey, Wolfgang, Hou, & Wang, 2012; Wang, Jiang, Ren, et al., 2019).

First described based on specimens from the upper Dadu River Valley in central Sichuan Province, China, the type specimen (holotype MCZ R-12469) of *D. flaviceps* was deposited in the United States. With no access to the type specimen and logistical obstacles to accessing the type locality, early Chinese herpetologists misinterpreted the diagnosis of *D. flaviceps*, particularly regarding the coloration and ornamentation patterns of the head and body. In fact, incorrect diagnostic characters were widely recognized for years in early Chinese literature, including the supposed presence

of greenish body coloration, colorful gular spots, and distinct radial stripes around the eyes (Hu et al., 1987; Zhao, Zhao, & Zhou, 1999). As a result, nearly all *Diploderma* populations in Southwest and central China were long considered as *D. flaviceps*, a species believed to have the widest distribution among all Chinese congeners (Yang & Rao, 2008; Yao & Gong, 2012; Zhao et al., 1999).

Recent re-examination of *D. cf. flaviceps* populations across China have restricted the range of true *D. flaviceps* to the upper Dadu River Valley only, and studies have shown that the majority of congeners from the HMR are micro-endemic lineages restricted to only specific sections of isolated river valleys (Manthey et al., 2012; Wang et al., 2015, 2016; Wang, Jiang, Ren, et al., 2019). Therefore, populations of previously identified *D. cf. flaviceps* outside of the upper Dadu River Valley represent a large species complex of misidentified congeners. Since the early 2000s, multiple distinct evolutionary lineages have been discovered from the *D. flaviceps* complex across the HMR, including *D. batangense* (Li, Deng, Wu, Wang, 2001), *D. brevicaudum* (Manthey, Wolfgang, Gou, Wang, 2012), *D. drukdaypo* (Wang, Ren, Jiang, Zou, Wu, Che, Siler, 2019), *D. iadinum* (Wang, Jiang, Zou, Yan, Siler, Che, 2016), *D. laeiventre* (Wang, Jiang, Zou, Yan, Siler, Che, 2016), *D. micangshanense* (Song, 1987), *D. vela* (Wang, Jiang, Pan, Hou, Siler, Che, 2015), *D. yulongense* (Manthey, Wolfgang, Hou, Wang, 2012), and *D. zhaermii* (Gao, Hou, 2002; Figure 1). However,



**FIGURE 1** Distributions of *Diploderma* species in East Asia. Shaded region represents the range of the *D. flaviceps* complex in China. Numbered shapes represent type localities of *Diploderma* species: The rectangle represents true *D. flaviceps* (5), stars represent the new species described here (6: *D. panchi* sp. nov.; 7: *D. angustelinea* sp. nov.; 8: *D. panlong* sp. nov.; 12: *D. flavilabre* sp. nov.; 14: *D. aorun* sp. nov.; and 15: *D. qilin* sp. nov.), and circles represent type localities of the remaining recognized congeners (1: *D. splendidum*; 2: *D. micangshanense*; 3: *D. zhaermii*; 4: *D. grahami*; 9: *D. swild*; 10: *D. dymondi*; 11: *D. varcoae*; 13: *D. batangense*; 16: *D. brevicaudum*; 17: *D. yulongense*; 18: *D. drukdaypo*; 19: *D. vela*; 20: *D. iadinum*; 21: *D. laeiventre*; 22: *D. slowinskii*; 23: *D. yunnanense*; and 24: *D. chapaense*)

despite the well-recognized suspicion of taxonomic identities of *D. cf. flaviceps* and the recent efforts in taxonomic studies of the *D. flaviceps* complex, the status of many questionable populations of *D. cf. flaviceps* in the HMR still remains unexamined. This is particularly true for populations from the valleys of the Jinsha River and its main tributary, the Yalong River, in Yunnan and Sichuan Provinces (Wang, Ren, Jiang, et al., 2019).

In Yunnan Province, Yang and Rao (2008) reported on questionable records of *D. cf. flaviceps* from the Jinsha Valley in Deqin County and Shangri-La County (=Xianggelila). Based on their descriptions, these Yunnan populations of *D. cf. flaviceps* possess distinct dark radial stripes around the eyes and colorful gular spots, which contradict the revised diagnoses of true *D. flaviceps* (radial stripes around the eyes absent or faint; gular spots absent; Manthey et al., 2012; Wang et al., 2015; Wang et al., 2016; Wang, Ren, Jiang, et al., 2019). As coloration and ornamentation patterns have proved reliable as diagnostic characters for members of the genus *Diploderma* (Wang et al., 2015, 2016, 2017; Wang, Jiang, Ren, et al., 2019; Wang, Ren, Jiang, et al., 2019; Wang, Wu, Jiang, et al., 2019), these Yunnan populations with such contradicting ornamentation patterns warrant further investigation.

In Sichuan Province, Zhao (2003) recorded *D. cf. flaviceps* from Mianning and Muli Counties, without providing any vouchered information of referred specimens; however, both of the mentioned counties are along the Yalong River Valley, which is isolated from the restricted range of the true *D. flaviceps* (i.e., Dadu River Valley) by the continuous Hengduan Mountains. Because these populations of *D. cf. flaviceps* in Sichuan Province are from localities that are allopatric from the known range of true *D. flaviceps*, separated by known biogeographic barriers (i.e., Hengduan Mountains; Lei, Qu, Song, Alström, & Fjeldså, 2015; Yang, Yi, Pan, & Guo, 2012), they may also represent overlooked cryptic diversity within the genus.

Furthermore, in addition to the abovementioned suspect populations of *D. cf. flaviceps*, many suitable valleys in Sichuan Province have not yet been surveyed for *Diploderma* diversity, including the upper reaches of the Jinsha and Yalong Rivers in Baiyu and Yajiang Counties, respectively. Given the consistent distributional patterns of *Diploderma* restricted to the major rivers in the HMR (Wang, Jiang, Ren, et al., 2019), these un-surveyed valleys also may harbor additional undescribed diversity.

To decipher cryptic diversity within the *D. flaviceps* species complex, an integrative approach must be taken. However, due to the lack of specimens and genetic samples, not only were the majority of the previous taxonomic studies on the genus *Diploderma* based on morphological data only (Manthey et al., 2012; Rao, Vindum, Ma, Fu, & Wilkinson, 2017; Wang, Jiang, Ren, et al., 2019; Wang et al., 2017), but the few recent integrative taxonomic studies of the genus also have limited taxa or gene coverage (Wang, Che, et al., 2019; Wang, Ren, Jiang, et al., 2019; Wang, Wu, Jiang, et al., 2019). Some recognized species still lack molecular data, and their phylogenetic relationships with congeners remain unknown. Such paucity of comprehensive genetic data and phylogenetic relationships among recognized species hinders the discovery processes of cryptic diversity in this group.

Lastly, the current unresolved taxonomy poses major challenges to the conservation of the genus *Diploderma* in China. Cryptic, undescribed species and species recently discovered are left out of endangered species listings, and taxonomic confusion has resulted in misleading conservation assessments (Wang, Jiang, Ren, et al., 2019; Wang, Ren, Jiang, et al., 2019). With the rapidly expanding human settlements in the HMR, this lag between species discovery and environmental legislation and conservation action is an urgent concern that needs to be addressed.

During herpetological surveys between 2015 and 2019, we collected specimens of the genus *Diploderma* across the HMR in Southwest China (denoted in stars numbered 6, 7, 8, 12, 14, and 15 in Figure 1). Based on these collections, we take the first comprehensive, integrative approach to investigating diversity within the *D. flaviceps* complex in Southwest China, using multi-locus phylogenetic and morphological analyses. Our results indicate that members of the *D. flaviceps* complex are paraphyletic, and the six examined populations identified previously as *D. cf. flaviceps* from Yunnan and Sichuan Provinces represent undescribed, micro-endemic diversity within the genus that are facing urgent conservation needs. Herein, we describe six new species of *Diploderma* from the *D. flaviceps* complex, provide an updated diagnostic key of the genus, and discuss the possible solutions to the major conservation challenges that these Chinese endemic species face due to delayed conservation assessments and legislation.

## 2 | MATERIALS AND METHODS

### 2.1 | Taxonomic sampling

Specimens of the genus *Diploderma* were collected in southwestern China from 2015 to 2019, including 54 specimens from six populations of *D. cf. flaviceps*: three from the upper Jinsha River Valley and three from the Yalong River Valley (Figure 1; for detailed population sampling see Appendix 1 and Table S1). In the field, specimens were euthanized, tissue samples were taken from livers and preserved in 95% ethanol, and voucher specimens were fixed in 10% buffered formalin and later transferred to 70% ethanol for long-term preservation. All newly collected specimens were deposited at the Museum of Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ).

In addition to specimens collected, specimens in major museum collections were also examined, which included 223 specimens of 22 recognized species of the genus *Diploderma* (Table S1). To avoid possible taxonomic confusion over cryptic diversity, morphological data were taken from type specimens, topotypic specimens, or specimens with confirmed taxonomic status whenever possible. Museum abbreviations follow Sabaj (2016), which included the following: Museum of California Academy of Sciences (CAS), San Francisco, CA, USA; Chengdu Institute of Biology, Chinese Academy of Sciences (CIB); Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ), Kunming, Yunnan, China; University of Kansas Biodiversity Institute (KU), Lawrence, KS, USA; Field Museum of Natural History (FMNH), Chicago, IL, USA; Museum

of Comparative Zoology (MCZ), Cambridge, MA, USA; Natural History Museum (NHM), London, UK; and Smithsonian National Museum of Natural History (USNM).

## 2.2 | Morphological data and statistical analyses

Morphometric measurements and pholidosis data were taken from a subset of the examined specimens (Tables S2 and S3). Morphometric data were taken with a digital slide caliper by KW to the nearest 0.1 mm. Focal characters and character definitions follow Wang, Wu, Jiang, et al. (2019), including snout–vent length (SVL); tail length (TAL); head width (HW); head length (HL); head depth (HD); snout–eye length (SEL); length of tallest nuchal crest (TNC); fore-limb length (FLL); hind limb length (HLL); Toe IV length (T4L); trunk length (TRL); supralabial count (SL); infralabial count (IL); number of scales between nasal and first supralabials (NSL); number of scale rows between supralabials and orbit circle (SOR); enlarged, modified, post-occipital scale count (POS); enlarged, modified, post-tympanic scale count (PTY); enlarged, modified, post-rectal scale count (PRS); Finger IV subdigital lamellae count (F4S); Toe IV subdigital lamellae count (T4S); middorsal scale count (MD); and keel status of ventral body scales (KVS). Values for paired pholidosis characters (SL, IL, NSL, SOR, F4S, T4S, POS, PTY, and PRS) were recorded from both sides of the body, with counts provided in left/right order, while for paired morphometric data (FLL and HLL), a single value was taken at the left side.

Because coloration and ornamentation are both diagnostic (Wang, Jiang, Ren, et al., 2019; Wang et al., 2016, 2017; Wang, Ren, Jiang, et al., 2019; Wang, Wu, Jiang, et al., 2019) and play important roles in the sexual selection processes for agamid lizards (Stuart-Fox & Ord, 2004), data of coloration and ornamentation were also collected from both live and preserved specimens, including (a) presence or absence of gular spot; (b) coloration of gular spot, if present; (c) presence or absence of dorsolateral stripes on the body; (d) shape of dorsolateral stripe of body (strongly jagged, feebly jagged, or smooth-edged), if present; (e) coloration of dorsolateral stripes of body, if present; (f) shape of vermiculated stripes on ventral head (reticulated versus scattered); (g) coloration of inner lips; (h) coloration of oral cavity and tongue; and (i) coloration of ventrolateral body. Color descriptions were standardized using terminology and codes in Köhler (2012).

To account for the allometry between adults and juveniles, which is known in the genus *Diploderma* (Wang et al., 2015, 2016, 2017), data of juvenile and subadult specimens were excluded from comparisons and morphometric analyses. Principal component analysis (PCA) and discriminant analysis of principal components (DAPC) were performed to examine whether the questionable populations of *D. cf. flaviceps* from Yunnan and Sichuan Provinces occupy distinct morphological spaces with respect to true *D. flaviceps* and other morphologically similar congeners. These combined analyses allowed us to determine whether the morphological clustering coincided with the clades recovered from our molecular data set.

Because species of the genus *Diploderma* are known to be sexually dimorphic in morphometric measurements (Manthey et al., 2012;

Wang et al., 2015, 2018; Wang, Jiang, Ren, et al., 2019), morphometric data of each sex are treated separately for analyses and comparisons. Due to a limited sample size for *D. druckdaypo*, only females were included for the morphometric analyses (males  $n < 3$ ). Raw morphometric measurements were used for statistical analyses, while relative ratios of raw measurements (i.e., TAL/SVL, FLL/SVL, HLL/SVL, TRL/SVL, HW/SVL, HD/SVL, HL/SVL, HW/HL, HD/HL, HD/HW, and SEL/HL) were used for comparisons among species, in order to remove covariance among raw morphological measurements.

On the other hand, as scale counts are less prone to sexual dimorphism and allometry (Manthey et al., 2012; Wang, Jiang, Ren, et al., 2019; Wang et al., 2016; Wang, Wu, Jiang, et al., 2019), pholidosis data of both sexes and juveniles/subadults were combined in analyses and comparisons. A total of nine pholidosis counts (SL, IL, SOR, F4S, T4S, MD, POS, PTY, and PRS) were used for the analyses. For each of the paired counts (SL, IL, SOR, F4S, T4S, POS, PTY, and PRS), the mean values of counts from both sides of the body of each individual were calculated and rounded to the nearest whole numbers for the statistical analyses.

All morphological data were square root transformed prior to the statistical analyses and scaled to their standard deviation in order to normalize their distribution. PCA was performed using the `prcomp` command in R v. 3.2.1. Major PCs that explain at least 95% of the total variance and the major discriminant functions were retained and used for DAPC analyses, also using R v. 3.2.1. The first two major principal components from PCA and the results of DAPC analyses were plotted using `ggplot2` in R with 95% confidence ellipses.

Furthermore, one-way analysis of variance (ANOVA) was used to search for the significant variation in morphometric data among the putative new species and their morphologically similar congeners; and if ANOVA yields significant variation, then Tukey's HSD test was used to determine whether the putative new species are statistically different from each of the given congeners. Both statistical tests were done using R.

## 2.3 | Molecular data and phylogenetic analyses

Sequence data of 69 individuals were generated in this present study and deposited in GenBank (Accession numbers MT577892–578014 and MT659027–659119; Appendix 1). In addition, a total of 48 individuals of 18 species of *Diploderma* and seven species of three outgroup agamid genera (*Acanthosaura*, *Calotes*, and *Pseudocalotes*) were obtained from GenBank (Appendix 1). The outgroup selection followed the most recent phylogenetic studies of Draconinae (Wang, Che, et al., 2019).

Genomic DNA was extracted from liver samples stored in 95% ethanol using Fujita's guanidine thiocyanate protocol (Esselstyn, Garcia, Saulog, & Heaney, 2008). Fragments of a single mitochondrial (mt) DNA locus, NADH dehydrogenase subunit 2 gene (*ND2*), and the nearby tRNAs (*Trp*, *Ala*, *Asn*), and three nuclear DNA loci, namely brain-derived neurotrophic factor (*BDNF*), oocyte maturation factor (*CMOS*), and RNA fingerprint protein 35 (*R35*) were amplified using published primers and PCR protocols (Crottini et al., 2009;

Wang, Che, et al., 2019; Whiting, Bauer, & Sites, 2003; Table 1), and the PCR products are about 1,200 bp, 200 bp, 600 bp, 500 bp, and 800 bp, respectively. After sequencing and trimming, the alignments of new sequences are 1,032 bp, 184 bp, 567 bp, 391 bp, and 641 bp for *ND2*, tRNAs, *BDNF*, *CMOS*, and *R35*, respectively. When included and aligned with the GenBank data, the final alignments are 1,032 bp, 392 bp, 567 bp, 539 bp, and 641 bp for the five genes, respectively. Amplified products were visualized on 1.5% agarose gels, and clean single banded products were purified with 1  $\mu$ L of a 20% dilution of ExoSAP-IT (US78201, Amersham Biosciences). Cycle sequencing reactions were carried out using ABI Prism BigDye Terminator chemistry (Ver. 3.1; Applied Biosystems), and purified with Sephadex (NC9406038, Amersham Biosciences) in Centri-Sep 96 spin plates (CS-961, Princeton Separations). Purified products were sent to Eurofins Genomics for analysis.

Raw sequences were assembled and aligned using Geneious v.10.0 with minor subsequent manual adjustments. The final alignments and resulting topologies are deposited in Data Dryad (<https://doi.org/10.5061/dryad.7sqv9s4qc>). Pairwise genetic distances of the *ND2* coding region among species of the genus *Diploderma* were calculated using PAUP v. 4.0 b10 (Swofford, 2002).

The phylogenetic trees were generated using both maximum-likelihood and Bayesian analyses. To assess phylogenetic congruence between the mitochondrial and nuclear data, we inferred the phylogeny for each gene independently using likelihood and Bayesian analyses. As no strongly supported incongruences between mitochondrial and nuclear data were observed visually, we concatenated the two data sets for the final analyses.

Partitioned Bayesian analyses were conducted using the program MRBAYES v. 3.2.7a on CIPRES (Ronquist et al., 2012). All protein-coding genes were partitioned by codon positions, except for the mitochondrial tRNAs, which were combined and treated as a single partition (Table 1). The best model of nucleotide substitution was selected for each partition by the Akaike information criterion (AIC), implemented in JMODELTEST2 v. 2.1.10 (Darriba, Taboada,

Doallo, & Posada, 2012; Guindon & Gascuel, 2003). A rate multiplier model was used to allow substitution rates to vary among subsets. Two independent Markov chain Monte Carlo analyses were run, each with four Metropolis-coupled chains. Because the analyses did not converge under default settings, we adjusted the melting temperature (from 0.2 to 0.1). All Bayesian analyses were run for 2,000,000,000 generations, with parameters and topologies sampled every 2,000 generations. Stationarity and convergence were assessed with TRACER v. 1.6.0 (Rambaut, Suchard, & Drummond, 2013). We conservatively discarded the first 20% of samples as burn-in.

Partitioned maximum-likelihood analyses were performed using RAxML-VI-HPC v. 8.2.10 (Stamatakis, 2014) on the final data set using the same partition strategy as for Bayesian analyses. The most complex model (GTR +  $\Gamma$ ) was applied for all subsets, with 1,000 replicate ML inferences run. Each inference was initiated with a random starting tree, and nodal support was assessed with 1,000 bootstrap pseudoreplicates. Nodes having ML bootstrap values of 70 and above and BI posterior probabilities of 0.95 and above were considered well-supported.

### 3 | RESULTS

#### 3.1 | Molecular results

The topologies of the consensus trees obtained from the ML and BI analyses were very similar, except for three nodes (within the outgroup genus *Pseudocalotes*, the node inside of node E, and node Q), which either have low support in the ML analyses and are not resolved in the BI analyses (for the first and last cases) or different topologies (regarding the relationships between *D. swinhonis* and *D. polygonatum*; Figure 2). Tip nodes that unify recognized species are all well-supported (bootstrap support > 90, Bayesian posterior probability > 0.95, herein all given in such order).

**TABLE 1** Partition strategies, primers, and corresponding annealing temperatures for PCR of all genetic markers used in this study

Gene	Codon	Substitution model	Primer name	Primer info	References
<i>BDNF</i>	1	GTR	BDNF.F	CCCAATGAAAGAAGTGASCCTC	Crottini et al. (2009)
	2	HKY + $\Gamma$	BDNF.R	TGGGTAGTTCGGCACTGAGAATTC	
	3	JC69			
<i>CMOS</i>	1	JC69	G73.1	GGCTRTAAARCARGTGAAGAAA	Whiting et al. (2003)
	2	HKY + $\Gamma$	G74.1	GARCWTCCAAAGTCTCCAATC	
	3	HKY + $\Gamma$			
<i>R35</i>	1	GTR + $\Gamma$	R35.F	GACTGTGGAYGAYCTGATCAGTGTTGG	Whiting et al. (2003)
	2	HKY	R35.R	GCCAAAATGAGSGAGAARCCTTCTG	
	3	GTR + $\Gamma$			
<i>ND2</i>	1	GTR + $\Gamma$	Jap_70F	CCACCAAACAACCTACACCTA	Wang, Che, et al. (2019)
	2	GTR + $\Gamma$			
	3	GTR + $\Gamma$	Jap_1559R	GGATTAATGCCCTCTGGATT	
tRNAs	1	GTR + $\Gamma$			

The genus *Diploderma* is recovered as monophyletic (100/1.00). Both *D. drukdaypo* and *D. iadinum* are recovered as members of the genus *Diploderma*, as morphological data suggested. Members of the *D. flaviceps* complex are paraphyletic, as members of the complex are scattered across the genus (Figure 2). Within the genus *Diploderma*, two major clades, Clade A (100/1.00) and Clade B (78/0.96), are recovered with strong support. For Clade A, two major subclades, Clade C and Clade F, are recovered. In Clade C, true *D. flaviceps* is most closely related to *D. splendidum* (100/1.00), and the entire group is sister to Clade E, which contains all species from East Asian islands (100/1.00). Within Clade F, *D. zhaoermii* and *D. micangshanense*, *D. varcoae* and *D. dymondi*, and *D. swild* and the previously identified *D. cf. flaviceps* from Miansha County, southern Sichuan Province (population 8 in Figure 1), each form a monophyletic group with strong support (Clades G [100/1.00], I [99/1.00], and J [96/1.00], respectively).

All of the remaining populations of *D. cf. flaviceps* are recovered within the second major clade, Clade B, and most populations are paraphyletic with respect to each other, except the two populations from Yajiang County and Shangri-La/Deqin County, which form Clade J (Figure 2). *Diploderma iadinum* is recovered as the most basal lineage in Clade B, which is followed by Clade K (100/1.00) that unifies *D. yunnanense* and *D. chapaense* and Clade L (100/1.00) that unifies *D. laeviventre* and *D. slowinskii*. The remaining recognized species and all remaining populations of *D. cf. flaviceps* (populations 6, 7, 12, 14, and 15) are recovered within the next clade, Clade N (100/1.00). Within Clade N, previously identified *D. cf. flaviceps* from Baiyu County of Sichuan Province (population 12) is the most basal, which is followed by *D. batangense* (Node O, 99/1.00). Although relationships of *D. yulongense* and the population of *D. cf. flaviceps* from Muli County, southern Sichuan Province (population 7) are not resolved (Node Q, 48/-), the remaining three populations of *D. cf. flaviceps* are all nested within the next more crown clade, Clade R (95/1.00), where the population from Shangri-La County, northwest Yunnan Province (population 15) is the most basal one, and populations from Yalong County, Sichuan Province (population 6), and Deqin County, Northwest Yunnan Province (population 14), form a monophyletic group with strong support (Clade T, 92/1.00), sister to the Clade U that unifies *D. vela* and *D. drukdaypo* (98/1.00; Figure 2).

The uncorrected pairwise distances are more than 12% between true *D. flaviceps* and members of the *D. flaviceps* complex, and more than 5.7% among the six examined populations of *D. cf. flaviceps* from Sichuan and Yunnan Provinces (Table S4). The lowest interspecific genetic distance is between *D. drukdaypo* and *D. vela*, which is 2.4%–2.7%, while the highest is between *D. dymondi* and *D. laeviventre*, which is 20.5%–22.1%. In addition, two species show high intraspecific genetic variation, namely *D. splendidum* (6.1%) and *D. chapaense* (5.7%) (Table S4).

### 3.2 | Morphological results

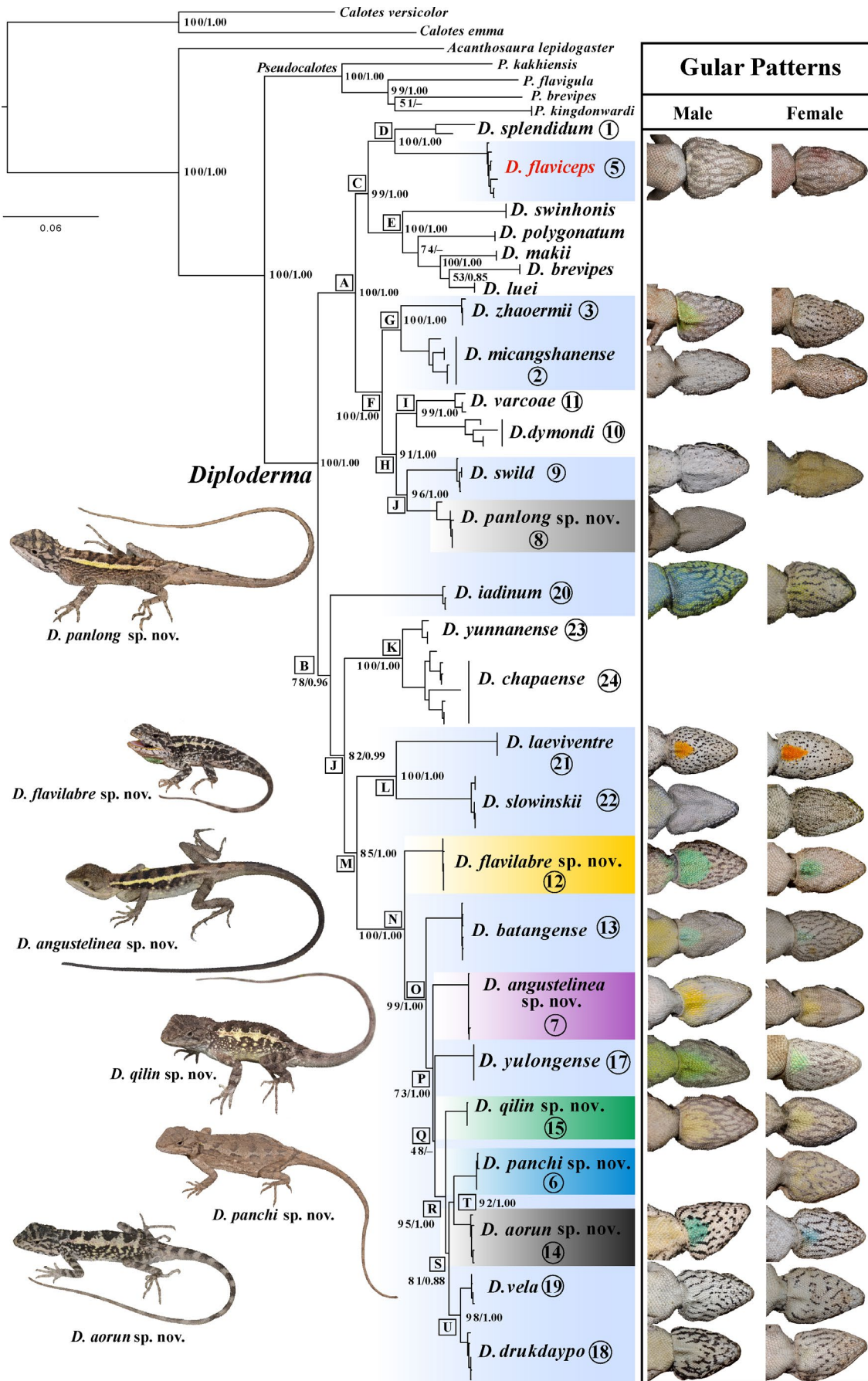
For pholidosis data, the first eight principal components (PC) explain 96.5% of the total variance, in which the first four PCs have eigenvalues greater than one. The four major PCs that have eigenvalues greater than one load most heavily on PRS, MD, PTY, and SOR, respectively (Table S5). When plotting the first two PCs, most populations of the *D. cf. flaviceps* are clustered together, except population 8 from the middle Yalong River; and true *D. flaviceps* only overlaps partially with the main cluster of *D. cf. flaviceps* (Figure 3). Using the first eight PCs and three discriminant functions, although DAPC analyses still cannot separate most of the examined *D. cf. flaviceps* populations from recognized congeners, they further separate the population 8 of *D. cf. flaviceps* from the middle Yalong River and true *D. flaviceps* from the main cluster of *D. cf. flaviceps* (Figure 3).

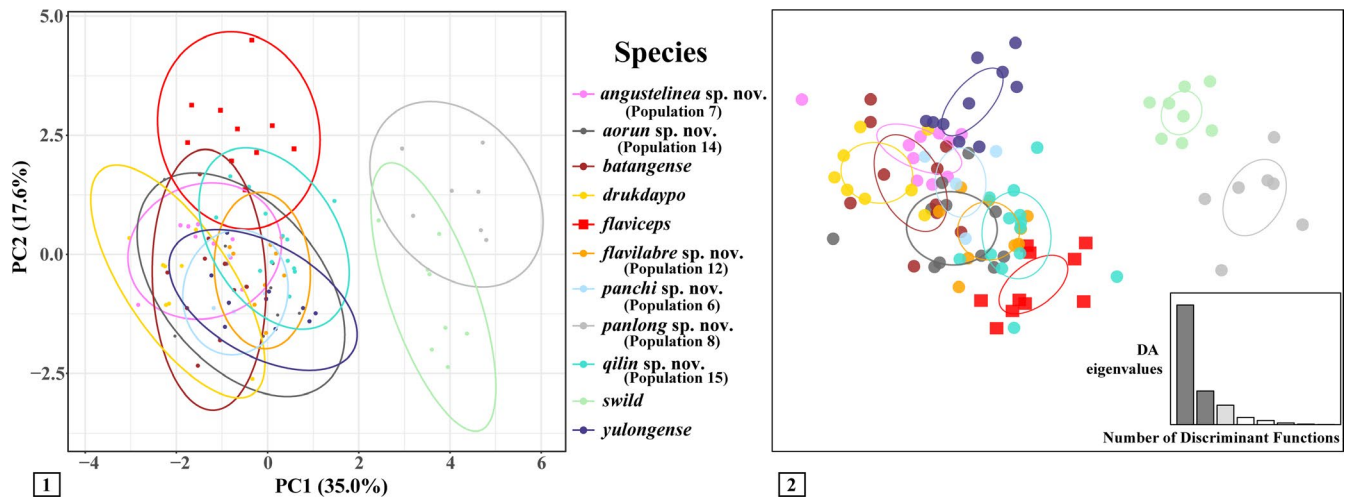
For morphometric data of males, the first three PCs explain 95.4% of the total variance, in which only the first PC has an eigenvalue greater than one (Table S6). For the first PC, it loads most heavily on SVL and HL, and the remaining two major PCs load most heavily on TAL and FLL. When plotting the first two PCs, similar to the PCA results of pholidosis data, most of the examined populations of *D. cf. flaviceps* are still clustered together, except population 12 from the far upper Jinsha River and population 8 from the middle Yalong River; and true *D. flaviceps* only overlap partially with the main cluster of *D. cf. flaviceps* (Figure 4). Using the first three PCs and two discriminant functions, DAPC analyses further separates the cluster, particularly between the true *D. flaviceps* and the six examined *D. cf. flaviceps* populations, and between the main cluster and population 8 along the middle Yalong River and population 12 from the far upper Jinsha River (Figure 4).

For morphometric data of females, the first four PCs explain 96.5% of the total variance, in which the first two PCs have eigenvalues greater than one (Table S7). For the first two PCs, they load most heavily on HD, HL, TAL, and TRL. Unlike the pattern for the males, PCA plots of the first two PCs show two major clusters for females: One contains four of the six examined populations of *D. cf. flaviceps*, true *D. flaviceps*, and three of the included recognized species of the complex (i.e., *D. batangense*, *D. swild*, and *D. yulongense*), while the other one cluster consists of two population of *D. cf. flaviceps* (populations 6 and 12), as well as *D. drukdaypo* (Figure 4). Using the first four PCs and two of the discriminant functions, DAPC analyses further separate the clusters, including the true *D. flaviceps* from the main cluster (Figure 4).

Despite the overlapping clustering among many of the examined *D. cf. flaviceps* populations in morphospace, when comparing coloration/ornamentation (i.e., shape and color of dorsolateral stripes, gular coloration, ventrolateral coloration, and oral coloration) and

**FIGURE 2** Phylogenetic relationships of the genus *Diploderma* inferred from a concatenated multi-locus data set (ND2, RNAs, BDNF, CMOS, and R35), with gular patterns of males and females in life of the *D. flaviceps* complex shown on the side. All tip nodes that unify each individual species are well-supported (BS > 90, BP > 0.98). “-” indicates non-resolved or differential relationship in Bayesian analyses. Shaded species are members of the *D. flaviceps* complex, while new species described here are shaded with the same color as they appear in the map in Figure 1. The circled number of each species corresponds to the number shown in Figure 1. Photographs by Kai WANG and Christian WEINERT





**FIGURE 3** PCA (1) and DAPC plots (2) with 95% confidence ellipses based on nine pholidosis characters (SL, IL, SOR, F4S, T4S, MD, POS, PTY, and PRS) for the six examined populations of *D. cf. flaviceps* and their morphologically similar congeners. The embedded figure in the DAPC plot indicates the DA eigenvalue for each of the major discriminant functions, where the shaded ones were obtained for the DAPC analyses. See methods for abbreviations and their morphological definitions

development statuses of pholidosis characters (i.e., degree of modification of conical scales on the head and crest shape), *D. cf. flaviceps* populations that overlap in morphospace of morphometric and pholidosis characters can be readily distinguished from each other and from all recognized congeners (see comparison sections below for details; Tables 2–4; Figures 2, 11, 12).

In conclusion, the six examined populations of *D. cf. flaviceps* from Yunnan and Sichuan Provinces are similar to members of the *D. flaviceps* complex in terms of morphometric and pholidosis characters, but each of them can still be diagnosed readily from all recognized species particularly using coloration and ornamentation characters. In addition, the genealogy from the multi-locus data set shows that each of the six populations also forms a monophyletic group, which is paraphyletic to true *D. flaviceps*. Furthermore, each of the six populations also exhibits considerable genetic distance from all other recognized congeners and from each other (>5.7%). Therefore, adopting the evolutionary species concept, we here consider each of the six examined *D. cf. flaviceps* populations as distinct new species.

### 3.3 | Taxonomic accounts

#### 3.3.1 | *Diploderma angustelina* sp. nov. Wang, Ren, Wu, Che, Siler

(Population 7 in Figure 1; Figures 2, 5, 11, 12; Tables 2–4; Table S8 (1); ZooBank ID urn:lsid:zoobank.org:act:E709207E-3FC6-45EF-9D54-8CADA8949A8).

##### Synonym

*Japalura flaviceps* Zhao et al. (1999: 111–115), in part; Zhao (2003: 84), in part.

##### Holotype

KIZ 029703, adult male from Maidilong Village, Muli Tibetan Autonomous County, Liangshan Prefecture, Sichuan Province, China (28.594° N, 101.226° E, elevation 2017 m, WGS 84). Collected by locals on June 10, 2016.

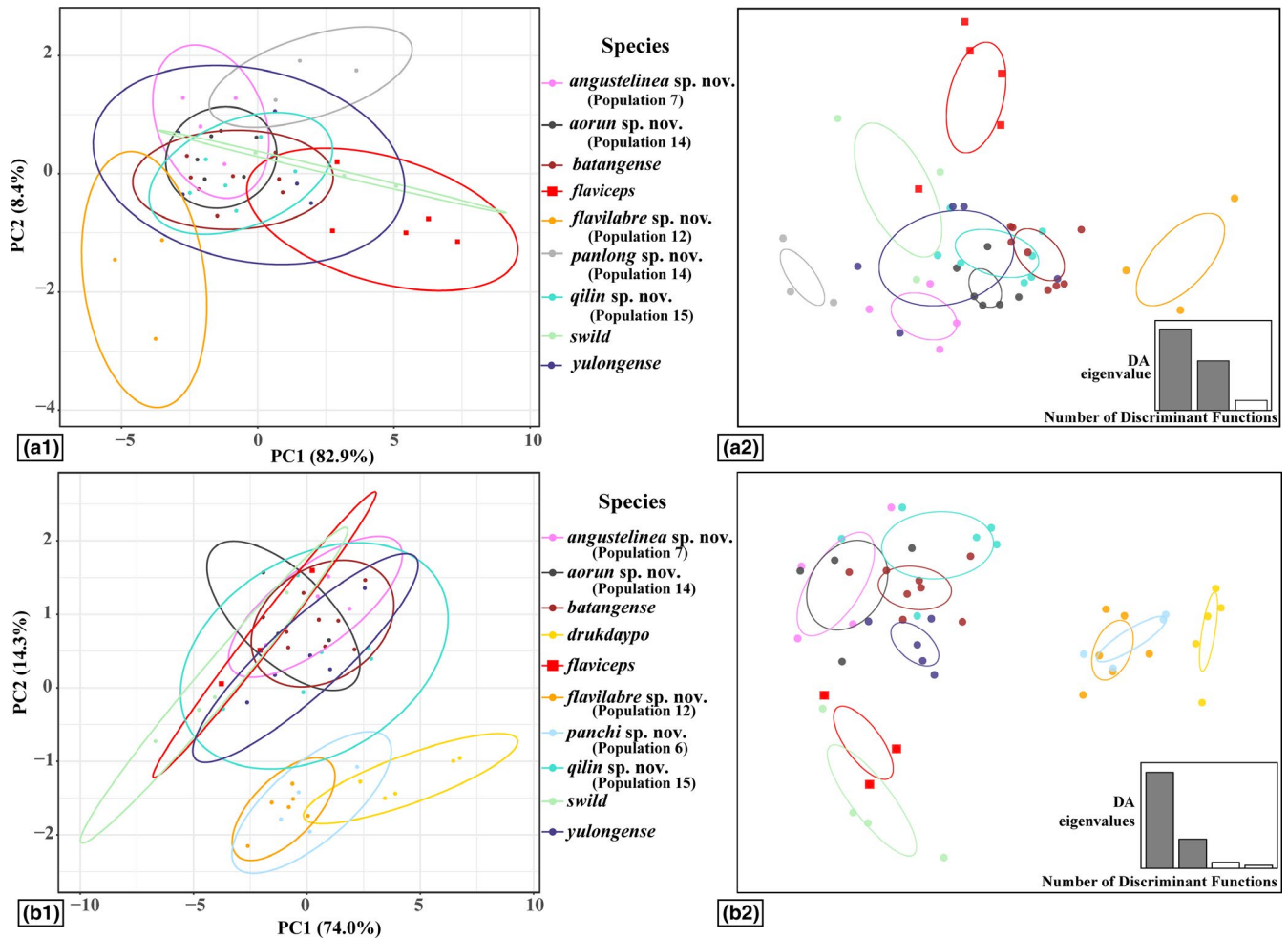
##### Paratopotypes

KIZ 044484, 044796, 044797, adult males; collected by Kai Wang, Zhuoyu Lu, and Xiankun Huang on June 25, 2019. KIZ 029704–029708, 029710, adult females, same collecting information as for the holotype.

##### Diagnosis

The new species can be diagnosed from congeners by a combination of the following morphological characteristics: (1) body size moderate, SVL 56.8–60.2 mm in males, 59.0–67.8 mm in females; (2) tail long, TAL 230.2%–249.1% SVL in males, 194.30%–222.3% in females; (3) hind limbs moderate, HLL 71.1%–80.2% SVL in males, 74.4%–79.2% in females; (4) head width moderate, HW 66.6%–73.9% HL, HD 72.7%–79.3% HW; (5) MD 41–49; (6) F4S 14–19; (7) T4S 21–26; (8) post-rectal sub-pyramidal scales weakly developed and few, 0–3; (9) tympanum concealed; (10) nuchal crest scales weakly developed without skin folds in both sexes, slightly raised and serrated in males; (11) distinct transverse gular fold present, deep; (12) ventral scales of head and body distinctively keeled; (13) gular spots always present in males, mostly in females, Spectrum Yellow (Color 79) to Dark Spectrum Yellow (Color 78) in life, absent after preservation; (14) no dark vermiculate stripes on ventral head; (15) dorsolateral stripes narrow, feebly jagged, Spectrum Yellow (Color 79), present in both sexes; (16) dark radial stripes around eyes indistinct or absent; (17) distinct, clear separation between the Jet Black (Color 300) or Burnt Umber (Color 48) coloration of dorsolateral body and white coloration of ventrolateral body; and (18) oral cavity and tongue Light Flesh Color (Color 250).





**FIGURE 4** PCA (1) and DAPC plots (2) with 95% confidence ellipses based on nine morphometric characters (SVL, TAL, HL, HW, HD, SEL, FLL, HLL, and TRL) for both males (a) and females (b) of the examined populations of *D. cf. flaviceps* and their morphologically similar congeners. The embedded figure in the DAPC plot indicates the DA eigenvalue for each of the major discriminant functions, where the shaded ones were obtained for the DAPC analyses. See methods for abbreviations and their morphological definitions. For population 6 and population 14, as only female and male specimens were collected from each population, respectively, the analyses for each sex only have representation from five *D. cf. flaviceps* populations in total

### Comparisons

*Diploderma angustelina* sp. nov. was confused historically with *D. flaviceps*, with both species having faint, indistinct, or no dark radial stripes around eyes. However, the new species can be distinguished from the latter by having feebly developed nuchal crests without skin folds in both sexes (versus well-developed on skin folds in both sexes), a relatively longer tail in males (TAL 230.2%–249.1% SVL versus 181.8%–210.8% SVL), fewer and weakly developed post-rital modified scales (0–3, average 1, sub-pyramidal-shaped and weakly developed versus 3–9, average 6, conical-shaped and well-developed), feebly jagged, narrow dorsolateral stripes in both sexes (versus strongly jagged and wide), a sharp transition in body coloration from dorsolateral Jet Black (Color 300) or Burnt Umber (Color 48) coloration to ventral white (versus gradual transition from Pale Pinkish Buff [Color 3] to white), and by the presence of distinct gular spots in both sexes (versus absence), and absence of reticulated, vermiculate black patterns on the gular region (versus presence).

The new species is morphologically most similar to *D. laeviventre*, in which both species possess yellowish gular spots, distinct transverse gular folds, and none or few weakly developed post-rital modified scales. However, *D. angustelina* sp. nov. can be differentiated from the latter species by having distinctively keeled ventral scales (versus feebly keeled or smooth), fewer middorsal scales (41–49 versus 57–59), slightly jagged, narrower dorsolateral stripes (versus completely smooth-edged and wide), and by the absence of heavy black speckles on dorsal, lateral, and ventral surfaces of head (versus presence).

*Diploderma angustelina* sp. nov. differs from all remaining recognized congeners by having narrow, dorsolateral stripes in both sexes (versus thick and wide). Specifically, *D. angustelina* differs from *D. brevicaudum* and *D. drukdaypo* by having a longer tail (230.2%–249.1% SVL in males, 194.3%–222.3% SVL in females versus 140.0% in male, 125.0%–145.0% in females for *D. brevicaudum*; 153.0%–154.4% in males, 132.8%–144.0% in females for *D. drukdaypo*) and

**TABLE 2** Comparisons of morphometric data among the six new species described here (*Diploderma angustelinea* sp. nov., *D. aorun* sp. nov., *D. flavilabre* sp. nov., *D. panlong* sp. nov., *D. qilun* sp. nov., and *D. panchi* sp. nov.) and their morphologically similar congeners (*D. batangense*, *D. drukdaypo*, *D. flaviceps*, *D. swild*, *D. vela*, and *D. yulongense*). See methods for abbreviations and their morphological definitions. Average values are given in parentheses

Species	Sex	Sample size	SVL	TAL/SVL (%)	FLL/SVL (%)	HLL/SVL (%)	HL/SVL (%)	HD/HW (%)	HW/HL (%)
<i>D. angustelinea</i> sp. nov.	M	4	56.8–60.2 (58.5)	230.2–249.1 (235.3)	45.7–46.5 (46.4)	71.1–80.2 (77.0)	27.8–30.1 (29.4)	73.3–78.7 (76.4)	66.6–70.8 (68.7)
	F	6	59.0–67.8 (63.1)	194.3–222.3 (207.3)	40.8–46.2 (43.7)	74.4–79.2 (75.9)	27.3–29.3 (28.2)	72.7–79.3 (75.9)	67.0–73.9 (68.9)
<i>D. aorun</i> sp. nov.	M	7	56.3–61.2 (58.7)	212.0–221.1 (216.4)	43.7–50.4 (47.7)	73.7–81.7 (78.6)	29.2–31.4 (29.9)	71.4–80.2 (75.4)	67.8–72.7 (70.8)
	F	4	60.8–66.5 (63.8)	191.4–207.7 (199.2)	45.0–52.8 (47.9)	71.5–80.5 (75.3)	27.3–30.2 (28.9)	66.7–78.0 (74.0)	66.8–70.4 (68.7)
<i>D. flavilabre</i> sp. nov.	M	3	50.8–55.2 (53.5)	149.7–179.3 (176.0)	43.1–48.3 (45.8)	66.9–74.8 (71.5)	31.2–32.2 (31.6)	70.1–75.5 (72.4)	70.7–73.1 (71.6)
	F	6	64.2–72.9 (67.5)	140.2–152.2 (146.4)	40.1–43.5 (41.2)	62.0–65.6 (63.0)	27.1–29.3 (28.6)	68.6–75.1 (71.3)	70.1–74.9 (71.8)
<i>D. panchi</i> sp. nov.	F	4	59.6–67.7 (65.2)	141.8–151.5 (148.1)	39.3–41.7 (40.0)	60.2–65.8 (62.6)	27.0–28.8 (28.0)	63.3–74.3 (69.0)	69.5–73.6 (71.6)
<i>D. panlong</i> sp. nov.	M	4	64.2–71.7 (64.8)	248.2–268.0 (257.1)	44.9–46.9 (46.3)	77.7–83.2 (80.5)	29.1–31.6 (30.7)	77.8–79.5 (78.5)	63.4–67.3 (65.0)
<i>D. qilun</i> sp. nov.	M	7	55.9–66.5 (55.9)	201.0–218.2 (208.6)	44.3–48.5 (46.4)	73.3–78.4 (75.8)	28.8–31.2 (31.2)	73.9–82.7 (80.4)	65.0–72.7 (68.1)
	F	6	55.3–72.0 (61.0)	174.3–199.7 (187.5)	44.7–51.8 (46.8)	72.5–80.4 (74.5)	26.6–28.9 (28.0)	72.3–80.4 (76.2)	69.6–73.2 (71.1)
<i>D. batangense</i>	M	6	55.5–62.8 (59.3)	187.3–206.5 (194.6)	46.0–49.8 (47.9)	74.7–79.8 (76.4)	28.8–32.2 (30.9)	71.7–75.3 (73.6)	66.3–67.3 (67.0)
	F	5	54.7–63.1 (60.0)	171.8–203.1 (186.9)	46.2–51.2 (48.4)	73.4–79.2 (76.9)	28.5–31.7 (30.2)	68.4–75.9 (72.5)	65.3–71.5 (68.1)
<i>D. drukdaypo</i>	M	2	49.9–51.5 (50.7)	153.1–154.4 (153.7)	37.9–45.4 (41.6)	58.2–63.8 (61.0)	27.2–33.2 (30.2)	71.1–73.2 (72.1)	65.9–66.7 (66.3)
	F	6	50.2–58.9 (54.3)	132.8–143.9 (138.0)	37.5–42.6 (39.4)	59.7–62.8 (60.8)	27.8–30.2 (28.9)	66.3–73.8 (68.7)	66.4–72.1 (70.5)
<i>D. flaviceps</i>	M	5	68.5–82.1 (74.9)	181.8–210.8 (191.6)	42.3–45.6 (44.2)	69.7–73.5 (71.9)	30.7–32.7 (31.9)	76.7–85.1 (81.2)	63.1–65.4 (64.4)
	F	3	59.6–69.3 (64.2)	191.5–205.7 (197.0)	44.7–46.0 (45.4)	69.3–77.8 (73.7)	31.6–31.8 (31.7)	75.1–81.0 (78.3)	64.5–67.9 (66.5)
	M	3	59.8–71.7 (66.6)	224.4–239.0 (233.3)	46.3–48.7 (47.2)	72.0–78.1 (75.1)	31.2–32.5 (32.0)	73.4–83.4 (78.6)	65.8–71.5 (67.9)
<i>D. swild</i>	F	4	59.7–76.8 (68.8)	200.4–221.0 (208.8)	41.9–49.2 (44.9)	69.4–75.9 (70.7)	30.8–34.6 (32.1)	77.0–80.6 (78.5)	64.9–70.0 (67.2)
	M	10	51.6–64.5 (58.2)	174.6–238.1 (199.3)	43.5–53.1 (47.9)	67.5–85.6 (75.6)	30.5–32.8 (31.4)	66.7–76.7 (73.3)	64.5–69.3 (67.8)
<i>D. vela</i>	F	10	54.1–64.2 (59.3)	159.8–202.2 (180.0)	43.3–51.8 (47.0)	65.7–81.6 (72.9)	28.2–30.4 (29.7)	67.6–73.8 (70.7)	65.2–69.8 (67.8)
	M	9	56.2–70.7 (62.9)	193.7–244.3 (223.0)	42.9–47.9 (45.1)	69.1–78.0 (74.4)	29.3–32.3 (30.7)	77.9–88.3 (82.4)	62.1–72.4 (67.2)
<i>D. yulongense</i>	F	6	56.2–69.2 (62.5)	182.2–211.3 (194.4)	42.0–45.3 (44.0)	68.8–74.9 (71.2)	27.8–30.2 (29.1)	73.4–83.8 (78.9)	63.7–68.5 (66.4)

**TABLE 3** Comparisons of pholidosis data among the six new species described here (*Diploderma angustelinea* sp. nov., *D. aorun* sp. nov., *D. flavilabre* sp. nov., *D. panlong* sp. nov., *D. qilin* sp. nov., and *D. panchi* sp. nov.) and their morphologically similar congeners (*D. batangense*, *D. drukdaypo*, *D. flaviceps*, *D. swild*, *D. vela*, and *D. yulongense*). See methods for abbreviations and their morphological definitions. Average values are given in parentheses. For keel status of ventral scale, S: strongly keeled; N: not keeled; W: weakly keeled

Species	Sample Size	F4S	T4S	MD	PTS	PTY	PRS	KVS
<i>D. angustelinea</i> sp. nov.	10	14–19 (17)	21–26 (23)	41–49 (45)	1–5 (4)	1–4 (2)	0–3 (1)	S
<i>D. aorun</i> sp. nov.	11	12–18 (15)	16–24 (21)	35–46 (40)	1–4 (3)	2–6 (4)	1–7 (4)	S
<i>D. flavilabre</i> sp. nov.	9	13–16 (15)	19–22 (21)	39–43 (41)	3–6 (4)	3–7 (5)	4–9 (6)	S
<i>D. panchi</i> sp. nov.	4	14–17 (15)	20–24 (22)	42–46 (45)	2–5 (3)	2–6 (4)	3–7 (4)	S
<i>D. panlong</i> sp. nov.	7	18–24 (20)	22–27 (25)	39–46 (42)	2–6 (4)	6–12 (9)	9–13 (11)	S
<i>D. qilin</i> sp. nov.	13	15–19 (17)	21–25 (22)	38–45 (41)	2–5 (4)	3–8 (6)	3–8 (5)	S
<i>D. batangense</i>	11	13–17 (15)	18–24 (21)	41–53 (44)	2–5 (3)	1–5 (3)	0–3 (2)	S
<i>D. drukdaypo</i>	8	13–17 (15)	18–23 (20)	43–56 (48)	1–5 (3)	1–4 (2)	0–3 (2)	N or W
<i>D. dymondi</i>	12	16–21 (19)	22–27 (24)	41–51 (45)	2–5 (3)	4–9 (6)	6–10 (9)	S
<i>D. flaviceps</i>	11	15–22 (18)	22–27 (24)	45–56 (51)	2–6 (4)	4–8 (6)	3–9 (6)	S
<i>D. swild</i>	9	18–22 (20)	23–27 (25)	35–44 (42)	1–3 (2)	3–7 (5)	5–10 (8)	S
<i>D. vela</i>	28	14–18 (16)	20–25 (22)	40–50 (44)	2–5 (4)	1–5 (3)	0–6 (3)	S
<i>D. yulongense</i>	14	15–19 (17)	21–26 (24)	38–44 (40)	1–5 (3)	1–3 (2)	0–4 (2)	S

much longer hind limbs (HLL 71.1%–80.2% versus 60.0%–64.0% in *D. breccicaudum*, 58.2%–63.8% in *D. drukdaypo*); from *D. batangense*, *D. iadinum*, *D. vela*, *D. yulongense*, and *D. zhaormii* by having weakly developed nuchal crests without skin folds (versus well-developed on raised on skin folds in males) and distinct coloration of gular spots (Dark Spectrum Yellow [Color 78] versus Pale Cyan [Color 157] in *D. batangense*; Caribbean Blue [Color 168] and Medium Greenish Yellow [Color 88] males and females in *D. iadinum*, respectively; Chartreuse [Color 89] in *D. yulongense* and *D. zhaormii*; and no gular spots in *D. vela*); from *D. chapaenses*, *D. micangshanense*, *D. varcoae*, *D. yunnanenses*, and all island species (*D. brevipes*, *D. luei*, *D. makii*, *D. polygonatum*, and *D. swinhonis*) by the presence of a distinct, deep, transverse gular fold (versus absence); from *D. fasciatum* by the feebly developed nuchal crests (versus well-developed and differentiated from dorsal crests), and by the presence of dorsolateral stripes (versus absence) and the absence of hourglass-shaped pattern on the mid-dorsum (versus presence); from *D. dymondi*, *D. slowinskii*, *D. swild*, and *D. varcoae* by having a concealed tympanum (versus exposed); from *D. splendidum* by having a smaller maximum body size (SVL  $\leq$  67.8 mm versus  $\leq$  92.0 mm), homogeneous ventral head scales (versus heterogeneous), and distinct, deep, transverse gular fold (versus shallow); from *D. hamptoni* by having parallel dorsolateral stripes (versus diagonally away from vertebral line posteriorly), a distinct transverse gular fold (versus shallow), and by the absence of distinct dark stripes on gular region (versus presence).

#### Description of holotype

Medium-sized agamid, SVL 57.6 mm, body slender, not dorsally compressed; tail slender, long, TAL 230.2% SVL; limbs moderate in length, FLL 45.8% SVL, HLL 79.1% SVL; head robust, HW 70.6% HL, HD 75.84% HW, 53.5% HL; snout pointy, SEL 36.9% HL. Rostral

rectangular, four times wider than high, one or two small scales in direct contact between rostral and nasal; nasal oval, naris positioned mediodorsally; supralabials 9/9, anteriormost supralabial single scale away from nasal on both sides, posteriormost longest, approximately three times longer than others, each bearing single, weak, lateral keel; infralabials 9/9, posteriormost shortest, each bearing single, lateral keel toward inferior side; conical or subpyramidal post-rectal scales, 2/2, relatively weak; suborbital scale rows 4/4, subequal in sizes; enlarged, elongated, keeled scales between posterior orbit and anterosuperior tympanum, 7/7; tympana concealed under fine scales; post-tympanic conical scales well-developed, protruding, 2/5.

Dorsal head scales keeled, heterogeneous in size and shape; single Y-shaped ridge formed by series of hexagon-shaped, enlarged scales on dorsal snout, with end of Y-shaped ridge two small scales posterior to rostral, tips of Y-shaped ridge consisting of single pair of distinctively enlarged, protruding scales, lining up at line between anterior orbits; supraciliaries 7/7, overlapping more than one third of total length with neighboring scales; enlarged, somewhat elongated, oval-shaped, protruding scale dorsoposterior to orbit, 1/1; interparietal enlarged, irregular-shaped, with distinct parietal eye; two lateral series of four enlarged, slightly protruding scales symmetrical along vertebral axis posterior to interparietal on each side of occipital head; enlarged, conical scales on post-occipital head, 4/6, dorsally fattened, pointing posteriorly.

Dorsal body scales heterogeneous in size and shape, all distinctively keeled; axillary scales smaller than background dorsal scales, non-granular in shape; enlarged scales two to four times larger than surrounding background scales, some arranged in three parallel, dorsolateral rows on each side of body: first row two scales inferior to vertebral crest, second row through dorsolateral stripe, last row four

**TABLE 4** Comparisons of coloration and ornamentation data among the six new species described here (*Diploderma angustelinea* sp. nov., *D. aaron* sp. nov., *D. flavilabre* sp. nov., *D. panlong* sp. nov., *D. qilin* sp. nov., and *D. panchi* sp. nov.) and their morphologically similar congeners (*D. batangense*, *D. drukdaypo*, *D. flaviceps*, *D. swild*, *D. vela*, and *D. yulongense*). Abbreviations see methods. "+": present; "-": absent; SFNC: Skin Fold under Nuchal Crest; SFDC: Skin Fold under Dorsal Crest; CSSE: Crest Scale Strongly Erected; For color codes see Köhler (2012)

Species	Sex	SFNC	SFDC	CSSE	Inner-Lip Coloration	Tongue Coloration	Pharyngea and Palatum Coloration	Gular Spot	Gular Spot Coloration	Dorsolateral Stripe Shape	Ventral Body Coloration	Ventrolateral Body Coloration
<i>D. angustelinea</i> sp. nov.	M	-	-	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+	Dark Spectrum Yellow (78)	Feebly jagged	White	White or Light Buff (Color 1)
	F	-	-	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+	Dark Spectrum Yellow (78)	Feebly jagged	White	White or Light Buff (Color 1)
<i>D. aaron</i> sp. nov.	M	+	+	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+	Light Cyan (159)	Strongly jagged	White or Pale Sulphur Yellow (Color 79)	White or Light Buff (Color 1)
	F	-	-	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+	Light Cyan (159)	Strongly jagged	White	White or Light Buff (Color 1)
<i>D. flavilabre</i> sp. nov.	M	+	+	+	Spectrum Yellow	Light Flesh Color (250)	Light Flesh Color (250) speckled with Pale Neutral Gray (296)	+	Pale Emerald Green (141) to Light Turquoise Green (146)	Strongly jagged	Pale Greenish Yellow (Color 86)	Pale Buff (1)
	F	-	-	+	Spectrum Yellow	Light Flesh Color (250)	Light Flesh Color (250) speckled with Pale Neutral Gray (296)	+	Pale Emerald Green (141) to Light Turquoise Green (146)	Strongly jagged	White	White or Light Buff (Color 1)
<i>D. panchi</i> sp. nov.	F	-	-	+	Spectrum Yellow	Light Flesh Color (250)	Light Flesh Color (250) speckled with Pale Neutral Gray (296)	+	Pale Emerald Green (141) to Light Turquoise Green (146)	Strongly jagged	White	White or Light Buff (Color 1)
<i>D. panlong</i> sp. nov.	M	-	-	+	Dark Spectrum Yellow (78)	Dark Spectrum Yellow (78)	Dark Spectrum Yellow (78)	-	-	Smooth	White	White
<i>D. qilin</i> sp. nov.	M	+	+	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+	Light Sulphur Yellow (Color 93)	Strongly jagged	White	Light Sulphur Yellow (93)
	F	-	-	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+	Light Sulphur Yellow (Color 93)	Strongly jagged	White	White
<i>D. batangense</i>	M	+	+	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+	Pale Cyan (157)	Strongly jagged	Sulphur Yellow (Color 79)	Sulphur Yellow (Color 79)
	F	-	-	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+	Pale Cyan (157)	Strongly jagged	White	White or Light Buff (Color 1)

(Continues)

TABLE 4 (Continued)

Species	Sex	SFNC	SFDC	CSSE	Inner-Lip Coloration	Tongue Coloration	Pharyngea and Palatum Coloration	Gular Spot	Gular Spot Coloration	Dorsolateral Stripe Shape	Ventral Body Coloration	Ventrolateral Body Coloration
<i>D. drukdaypo</i>	M	-	-	-	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	-	-	Strongly jagged	White	White or Light Buff (Color 1)
	F	-	-	-	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	-	-	Strongly jagged	White	White or Light Buff (Color 1)
<i>D. dymondi</i>	M	-	-	+	Smoky White (261)	Light Flesh Color (250)	Spectrum Violet (186) to Jet Black (300)	-	-	Smooth	White	White or Light Buff (Color 1)
	F	-	-	+	Smoky White (261)	Light Flesh Color (250)	Spectrum Violet (186) to Jet Black (300)	-	-	Smooth	White	White or Light Buff (Color 1)
<i>D. flaviceps</i>	M	+	+	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	-	-	Strongly jagged	White	White or Light Buff (Color 1)
	F	+	-	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	-	-	Strongly jagged	White	White or Light Buff (Color 1)
<i>D. swild</i>	M	-	-	+	Light Chrome Orange (76)	Light Chrome Orange (76)	Light Chrome Orange (76)	-	-	Smooth	White	White or Light Buff (Color 1)
	F	-	-	+	Light Chrome Orange (76)	Light Chrome Orange (76)	Light Chrome Orange (76)	-	-	Smooth	White	White or Light Buff (Color 1)
<i>D. vela</i>	M	+	+	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	-	-	Strongly jagged	White	White or Light Buff (Color 1)
	F	-	-	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	-	-	Strongly jagged	White	White or Light Buff (Color 1)
<i>D. yulongense</i>	M	+	-	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+	Chartreuse (89) to Opaline Green (106)	Strongly jagged	White	Pale Green (99) to Chartreuse (89)
	F	-	-	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+	Chartreuse (89) to Opaline Green (106)	Strongly jagged	White	White or Light Buff (Color 1)



**FIGURE 5** Male holotype (a1 and a2; KIZ 029703) and female paratopotype (b1 and b2 KIZ 029706) of *Diploderma angustelinea* sp. nov. in life. Photographs by JR

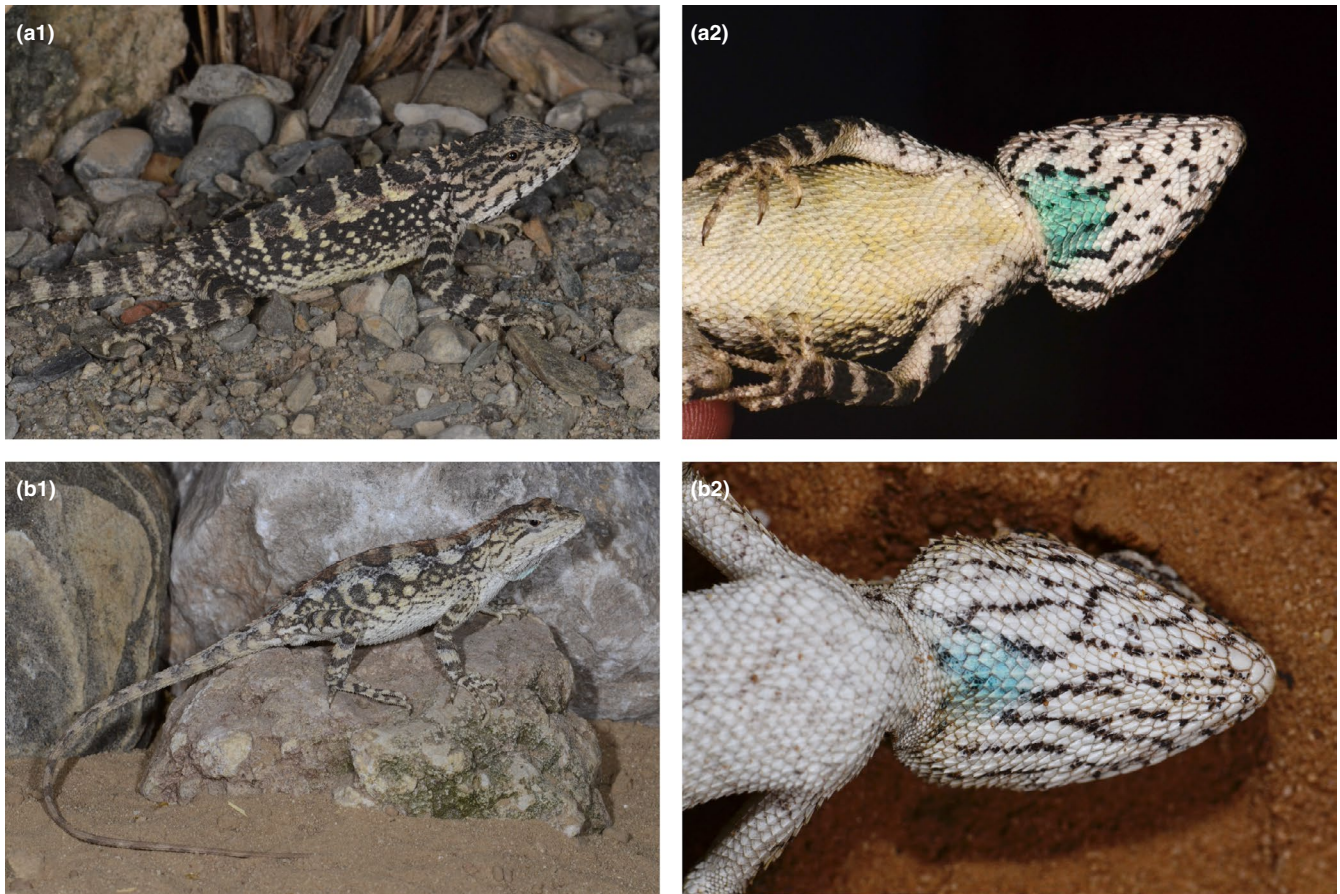
to five scales inferior to dorsolateral stripe; remaining enlarged dorsal scales scattered randomly. Middorsal scale count 45; nuchal crest scales serrated, slightly erect on weak skin fold in life (indistinct after preservation), short, CL 3.3% HL; dorsal crest scales relatively low, enlarged, roughly equal in size to enlarged dorsal scales, serrated. Dorsal limb scales distinctively keeled, homogeneous in size on forelimbs, heterogeneous on hind limbs, with enlarged scales possessing protruding keels on posterior lateral thigh. Finger I shortest, Finger IV longest, F4S 16/16; Toe IV longest, T4S 24/26.

Ventral head scales distinctively keeled, mostly homogeneous in size and shape, except three scales at center of gular pouch, which are slightly enlarged; mental pentagonal in shape, sandwiched between first pair of chin shields; all chin shields except first pair separated from infralabials by one to three rows of small, elongated scales; first two pairs of chin shields largest; gular pouch well-developed in life, indistinct after preservation; transverse gular fold present, deep, distinct. Scales on ventral body, limb, tail mostly homogeneous in size, shape, distinctively keeled, regularly arranged; keels of ventral tail scales carinate in lateral rows.

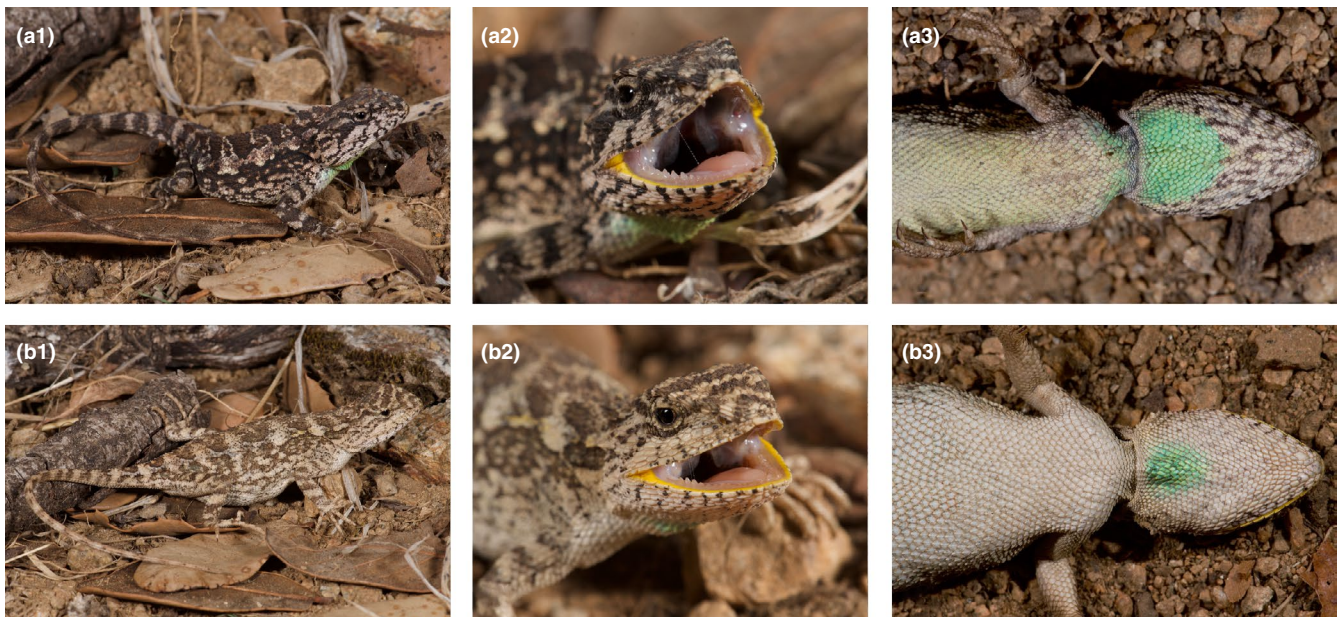
#### *Coloration of holotype in life*

The background color of the dorsal and lateral surfaces of the head is uniform Medium Neutral Gray (Color 298), and the coloration is

much darker toward the occipital region of the head. Two transverse bands occur between the eyes, which are more distinct toward the terminal ends on both sides; and both bands are Robin Rufous (Color 29) on the terminal ends and gradually fade into Buff (Color 5) toward the middle. Jet Black (Color 300) to Dark Neutral Gray (Color 299) radial stripes are present around the eyes, where most stripes extend outside of the orbit circle except ones that are inferior to the orbit. Radial stripes around the eyes are somewhat faint and indistinct, except the posterior one that is toward the rictus on each side, which is the broadest and most distinct stripe. A single Cream Color (Color 12), distinct suborbital stripe is present below the eye on each side of the head, extending from the posterior nasal scale to the rictus and beyond on each side. A somewhat faint, dark stripe, which is formed by two rows of heavily speckled scales (Medium Neutral Gray, Color 298), is present below the suborbital stripe from the anteriormost supralabial to the second most posterior supralabial scale. Supralabial scales are Light Yellow Ocher (Color 13), distinct from the infralabial scales. Background color on the post-tympanic regions of the head is Smoky White (Color 261). Two short, longitudinal, Dark Neutral Gray (Color 299) streaks (less than 10 scales in length) are present on each side, which are parallel to each other and positioned at the superior and inferior edges of the tympanum, respectively. For the remaining scales of the post-tympanic and



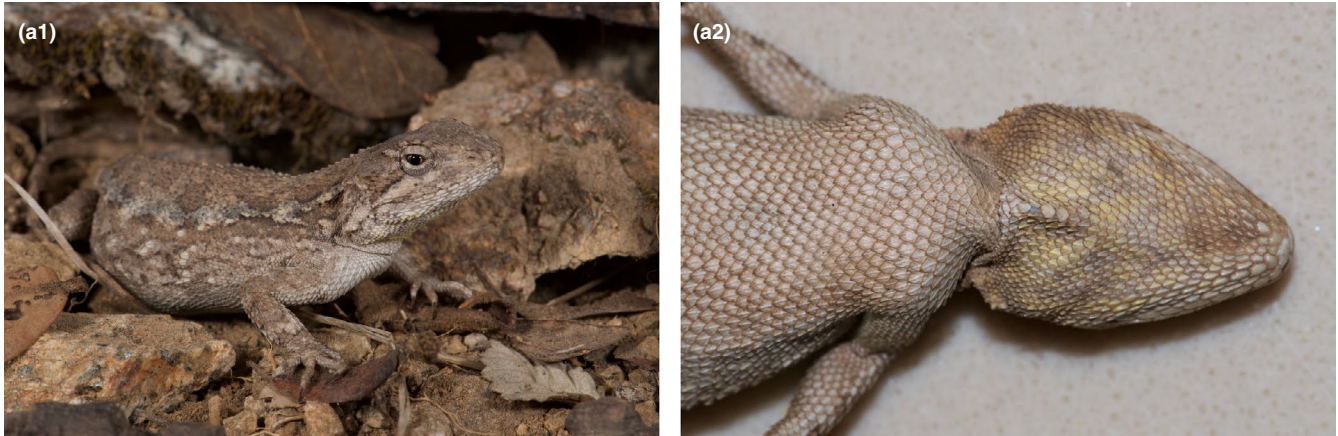
**FIGURE 6** Male paratype (a1 and a2; KIZ 044764) and female paratype (b1 and b2 KIZ 032735) of *Diploderma aorun* sp. nov. in life. Photographs by KW



**FIGURE 7** Male holotype (a1–a3; KIZ 032693) and female paratopotype (b1–b3; KIZ 032695) of *Diploderma flavilabre* sp. nov. in life. Photographs by KW

post-riotal regions of the head, the keels and conical tips of all scales are Sulphur Yellow (Color 80). The oral cavity and tongue are uniform Light Flesh (Color 250) colored in life.

Two narrow, Sulphur Yellow (Color 80) dorsolateral stripes are present from the posterior occipital region to the pelvis, one on each side of the vertebral crest, parallel to each other. The dorsal region



**FIGURE 8** Female holotype (KIZ 032715) of *Diploderma panchi* sp. nov. in life. Photographs by KW

between the two dorsolateral stripes is Orange-Rufous (Color 56), with five rectangular, Burnt Umber (Color 48) patches scattered evenly from the neck to the pelvis. Body surfaces inferior to the dorsolateral stripes are Jet Black (Color 300) on the anterior part of the body, fading into Burnt Umber (Color 48) and eventually to Drab-Gray (Color 256) posterior to the pelvis. Ventrolateral surfaces of the body are Smoky White (Color 261) to white, which is distinct from the blackish coloration below the dorsolateral stripes. Some of the enlarged scales on the lateral body surfaces inferior to the dorsolateral stripes are much lighter, which bear an either Flesh Ocher (Color 57) or Sulphur Yellow (Color 80) medial keel. The dorsal surfaces of the limbs are uniform Pratt's Payne's Gray (Color 293), with keels of individual scales in Olive Sulphur Yellow (Color 90). The dorsal and lateral tail surfaces are Pale Neutral Gray (Color 296), with Flesh Ocher (Color 57) scales scattered randomly near the tale base. Numerous faint Light Flesh Color (Color 250) bands are scattered evenly on the tail from one third of its length posteriorly, and the color eventually fades into uniform Drab-Gray (Color 256) toward the end.

The background coloration of the ventral surface of the head is white. A distinct, Spectrum Yellow (Color 79) gular spot is present on the center of the gular pouch. Scales surrounding the gular spot bear Spectrum Yellow (Color 79) keels. No distinct dark vermiculate stripes are present on the ventral surfaces of the head. The ventral surface of the body is uniform white with no distinct color pigmentation, and the ventral surfaces of the tail are uniform Smoky White (Color 261).

#### *Coloration of holotype in preservation*

Ornamentation patterns remain largely consistent after preservation; however, some observed coloration patterns fade, including the Spectrum Yellow (Color 79) color of the gular spot and the Sulphur Yellow (Color 80) color of the dorsolateral stripes turn to white, and the Burnt Umber (Color 48) coloration of the dorsolateral regions of the body become Dark Neutral Gray (Color 299) after long-term preservation.

#### *Variation*

Morphometric and pholidosis variation of the type series is summarized in Table S8. Although the sample size is limited,

sexual dimorphism is evident in *D. angustelinea* sp. nov., with males differing from females by having a longer tail (TAL 230.2%–249.1% SVL versus 194.3%–222.3%), more developed and serrated nuchal crests (versus less developed), and brighter dorsolateral stripes (versus duller with less distinct edges), and by the absence of distinct chevron patterns along dorsal mid-line between dorsolateral stripes (versus presence). For some females (KIZ 029704, 029708), the dorsolateral stripes are not continuous, with three to four short breaks (one to four scales in length) along the stripes, and a single female (KIZ 029704) lacks the gular spot.

#### *Etymology*

The Latin specific name, "*angustelinea*", comprises two parts: *anguste* meaning "narrow" and *linea* meaning "stripe" or "line." Together, the specific name describes the diagnostic narrow, thin, dorsolateral stripes present in the species. We recommend Narrow-striped Mountain Dragon as its English common name and 细纹龙蜥 (Pinyin: Xi Wen Long Xi) as its Chinese common name.

#### *Natural History and conservation status*

The new species was found in arid grassy valleys along the middle Yalong River (Figure 13a). Individuals were observed to be terrestrial, basking and seeking shelters in rock crevices (sandstone) during the day, but sleeping on bushes at night (i.e., *Rumex hastatus*, the most common bush species in their habitats). Only a single female was gravid (KIZ 029705), with all the remaining females showing characters of recent oviposition (i.e., empty stomach and extra skin folds on ventrolateral and lateral trunk), which suggests that mid-June is toward the end of its breeding season. Currently, the new species is known only from its type locality only in the upper Yalong River Valley. Although no further information is available about its distribution range, rapid township expansion and major hydropower developments were observed near the type locality, which pose major threats to the habitats of the species in the hot-dry valleys. We recommend Data Deficient (DD) for its IUCN classification, but call for future ecological and population studies of this species.





FIGURE 9 Male holotype (KIZ 040138) of *Diploderma panlong* sp. nov. in life. Photographs by KW

### 3.3.2 | *Diploderma aorun* sp. nov. Wang, Jiang, Zheng, Xie, Che, Siler

(Population 14 in Figure 1; Figures 2, 6, 11, 12; Tables 2–4; Table S8 (2); ZooBank ID urn:lsid:zoobank.org:act:E81CAE00-16CA-4D9A-8BD5-0B49158DFFF0).

#### Synonym

*Japalura flaviceps* Zhao and Yang (1997: 165–167), in part; Zhao et al. (1999: 111–115), in part; Yang and Rao (2008: 200), in part.

#### Holotype

KIZ 044735, adult male, from Dari Village, Deqin County, Yunnan Province, China (99.1733° E, 28.5804° N, elevation 2,198 m, WGS 84). Collected by Kai WANG, Xiankun HUANG, and Zhuoyu LU on June 17, 2019.

#### Paratypes

KIZ 032734, 032736, 032737, adult males; KIZ 032735, adult female, all from areas near Benzilan township, Deqin County, Yunnan Province, China (99.3827° E, 28.1774° N, elevation 2010 m, WGS 84); collected by Kai WANG, Shuqi LI, and Gadeng Nima on June 4, 2017. KIZ 044431, adult male, KIZ 044432, 044433, adult females, from Rongzong Village, Deqin County, Yunnan Province, China (99.1733° E, 28.5804° N, elevation 2,198 m, WGS 84); KIZ 044740, adult male, KIZ 044742, adult female, near Zhidu, Deqin County, Yunnan Province, China (99.2241° E, 28.3545° N, elevation 2037 m, WGS 84); CIB 116315–16, subadult females, CIB 116318, adult male, all from Songmai Township, Derong County, Sichuan Province (99.292382° E, 28.701581° N, elevation 2520m, WGS 84), collected by Gang Wang and Puyang Zheng on August 29, 2019; KIZ 044764, adult male near Derong township, Sichuan Province, China (99.2773° E, 28.6714° N, elevation 2,412 m, WGS 84); all collected by Kai WANG, Zhuoyu LU, and Xiankun HUANG on June 19, 2019.

#### Diagnosis

The new species can be diagnosed from congeners by a combination of the following morphological characteristics: (1) body size moderate, SVL 56.3–61.2 mm in males, 57.0–66.5 mm in females; (2) tail long, TAL 212.0%–221.1% SVL in males, 191.4%–207.7% in females; (3) hind limbs moderate, HLL 73.7%–82.7% SVL in males, 71.8%–80.5% in females; (4) head moderate, HW 66.8%–75.1% HL; (5) MD 36–45;

(6) T4S 19–24; (7) post-riatal conical or sub-pyramidal scales weak and few, 1–3; (8) tympanum concealed; (9) nuchal crest well-developed on strong skin folds, serrated; (10) distinct transverse gular fold present; (11) ventral scales of head and body distinctively keeled; (12) ventral head scales and ventrolateral body scales homogeneous in size; (13) gular spots present in both sexes, Pale Cyan (Color 157) to Light Caribbean Blue (Color 163) in life, Plumbeous (Color 295) after long-term preservation; (14) dorsolateral stripes strongly jagged, Cream (Color 12) in males, white in females in life; (15) dark ornamentations (i.e., transverse bands, radial stripes around eyes) with strong contrast; (16) no distinct ornamentation pattern on ventrolateral body; (17) ventral body white in most individuals, sometimes pale yellowish in males; and (18) oral cavity, inner lips, and tongue light flesh color (Color 250).

#### Comparisons

The new species was confused with *D. flaviceps*, but it can be differentiated from the latter by having a smaller body size in males (SVL 56.3–61.2 mm versus 68.5–82.1 mm), fewer middorsal crest scales (MD 35–46, average 40 versus 45–56, average 51), solid patches along dorsal midline in both sexes (versus hollow, rhomboid-shaped patterns), as well as by the presence of distinct radial stripes around eyes (versus absence or faint), the presence of gular spots in both sexes (versus absence), the absence of crest skin folds in females (versus absence), and the absence of reticulated, vermiculate patterns on the gular region (versus presence).

*Diploderma aorun* sp. nov. is morphologically most similar to *D. batangense*, which is found further upstream along the Jinsha River. However, *D. aorun* sp. nov. can still be differentiated from *D. batangense* by having a longer tail in males (TAL 212.0%–221.1% SVL, average 216.4% versus 187.3%–206.5%, average 194.6%; Tukey's HSD test,  $p < .05$ ), strongly developed skin fold of nuchal and dorsal crests in males (versus weak and often indistinct), and much stronger contrast between the dorsal dark and light ornamentations (versus much weaker contrast and faint).

For the remaining species in the same clade (Figure 2), *Diploderma aorun* sp. nov. differs from *D. drukdaypo*, *D. vela*, and *D. slowinskii* by the presence of distinct gular spots in both sexes (versus absence in both sexes); from *D. iadinum* by having fewer dorsolateral rows of enlarged keeled scales on each side of the body (1 versus 2–3), strongly jagged dorsolateral stripes (versus smooth), distinct body coloration in both sexes (Pale Buff [Color 1] in males, Chamois [Color 84] in females versus Yellowish Spectrum Green [Color 128] to Emerald



**FIGURE 10** Male holotype (a1–a3; KIZ 028332) and female paratype (b1–b3; KIZ 044820) of *Diploderma qilin* sp. nov. in life. Photographs by KW

Green [Color 143] in males, Buff [Color 5] to Pale Greenish Yellow [Color 86]), and a distinct gular coloration (Pale Cyan [Color 157] to Light Caribbean Blue [Color 163] in both sexes versus Caribbean Blue [Color 168] in males, Medium Greenish Yellow [Color 88] in females); from *D. yulongense* by having a distinct coloration for gular spots in life (Pale Cyan [Color 157] to Light Caribbean Blue [Color 163] versus Chartreuse [Color 89] to Opaline Green [Color 106]) and dorso-lateral stripes (white to Cream Color [Color 12] versus Pale Greenish Yellow [Color 86]), as well as by the absence of green patches on the dorsolateral surface of body (versus presence); from *D. laeiventre* by having distinctively keeled ventral scales (versus smooth or feebly keeled) and distinct gular coloration (Pale Cyan [Color 157] to Light Caribbean Blue [Color 163] versus Light Chrome Orange [Color 76]); from *D. chapaense* and *D. yunnanense* by the presence of a distinct transverse gular fold (versus absence) and differential coloration of gular spot (Pale Cyan [Color 157] to Light Caribbean Blue [Color 163] versus Light Chrome Orange [Color 76]).

For the remaining species in the different phylogenetic clade, *D. aorun* sp. nov. differs from *D. micangshanense*, *D. varcoae*, and all species from East Asian islands (*D. brevipes*, *D. luei*, *D. makii*, *D. polygonatum*, and *D. swinhonis*) by the presence of a distinct transverse gular fold (versus absence); from *D. dymondi*, *D. swild*, *D. slowinskii*, and *D. varcoae* by having a concealed tympanum (versus exposed) and distinct coloration of oral cavity (Light Flesh Color [Color 250] versus Light Chrome Orange [Color 76] in *D. swild* and *D. varcoae*; Jet Black [Color 300] or Spectrum Violet [Color 186] in *D. dymondi*); from *D. splendidum* by having distinct transverse gular fold (versus feeble), homogeneous ventral head scales (versus heterogeneous), and jagged dorsolateral stripes in males (versus smooth-edged); and from *D. zhaoermii* by having a smaller body size (maximum SVL 61.2 mm in males versus up to 81.7 mm), distinct vermiculate stripes on the ventral head (versus faint or absence), and a distinct

gular coloration (Pale Cyan [Color 157] to Light Caribbean Blue [Color 163] versus Chartreuse [Color 89]).

For the species that lack genetic data, *D. aorun* sp. nov. differs from *D. brevicaudum* by having a longer tail (TAL  $\geq 191.4\%$  versus  $\leq 160.0\%$ ) and longer hind limbs ( $>71.5\%$  versus  $\leq 64.0\%$ ) and the presence of gular spots after preservation (versus absence); from *D. grahami* by having distinct appearance of dorsal body scales (spiky versus granular), a distinct transverse gular fold (versus feebly), and a larger body size (56.3–66.5 mm versus 49.3 mm); from *D. fasciatum* by having smaller and non-differentiated nuchal crest scales (versus much larger and distinctively differentiated from dorsal crests), the presence of dorsolateral stripes (versus absence), and by the absence of single hourglass-shaped pattern on the mid-dorsum (versus presence); and from *D. hamptoni* by having parallel dorsolateral stripes on dorsal body (versus diagonally away from dorsal midline).

For new species described above, *D. aorun* sp. nov. differs from *D. angustelinea* sp. nov. by having wider and strongly jagged dorsolateral stripes in males (versus much narrower, smooth or feebly jagged), a distinct gular spot coloration (Pale Cyan [Color 157] to Light Caribbean Blue [Color 163] versus Dark Spectrum Yellow [Color 78]), a much gradual transition from dorsal to ventral coloration (versus sharp and distinct), and by the presence of strongly developed skin folds under nuchal and dorsal crests in males (versus absence), and the presence of distinct black vermiculate stripes on ventral head (versus absent).

#### *Description of holotype*

Body size moderate, not dorsally compressed, SVL 56.3 mm; tail slender, long, TAL 213.63% SVL; limbs moderate, FLL 48.3% SVL, HLL 80.8% SVL; head relatively wide and robust, HW 72.7% HL, HD 75.8% HW; snout pointy, SEL 40.8% HL. Rostral rectangular, three times wider than height, two scales away from nasal; nasal

oval, single scale away from first supralabial; supralabials 9/8, feebly keeled, more distinct on last five; infralabials 11/11, feebly keeled; suborbital scale rows 3/3, middle row slightly enlarged, each scale bearing distinct, lateral keel; supraciliaries 6/6, overlap one half of total length with succeeding ones; enlarged, protruding scales between posterior orbit and tympanum, 6/7, each bearing single distinct, lateral keel; tympanum concealed under fine scales; enlarged, conical scales post-tympanic, 6/5, one of which much taller than others on each side; enlarged post-rectal scales 4/5, sub-pyramidal in shape. Dorsal head scales heterogeneous in size and shape, all distinctively keeled; single, laterally oriented, Y-shaped ridge present on dorsal snout, starting three scales posterior of rostral to posterior end of orbit; interparietal slightly enlarged, parietal eye distinct; postciliary scale much enlarged, subpyramidal shape, with multiple keels; post-occipital scales well-differentiated, conical or subpyramidal in shape, 4/3.

Dorsal body scales distinctively keeled, heterogeneous in size and shape; axillary scales fine, much smaller than remaining dorsals; enlarged scales mostly randomly scattered, except ones close to dorsal midline and ones along medial line of dorsolateral stripes, which arranged in dorsolateral rows from neck to pelvis on each side; nuchal, dorsal crests well-developed on skin folds, crest scales erected, serrated, differentiated from nearby dorsal scales; middorsal scales 38. Scales of dorsal limbs distinctively keeled, homogeneous on forelimbs, heterogeneous on hind limbs, with few enlarged, subpyramidal ones on posterior lateral thigh and dorsal crus; Finger IV and Toe IV longest, Finger IV subdigital lamellae 14/15, Toe IV subdigital lamellae 21/21.

Ventral head scales homogeneous in size and shape, distinctively keeled except chin shields, regularly arranged; mental pentagonal, not completely enclosed by first pair of chin shields; chin shields 5/5, smooth, two scale rows from infralabials. Gular pouch present, well-developed in life, indistinct after preservation; distinct transverse gular fold present, deep. Ventral body and limb scales distinctively keeled, keels more pronounced than those of ventral head, homogeneous in size and shape, mostly regularly arranged.

#### *Coloration of holotype in life*

The background coloration of the dorsal surface of the head is Smoky White (Color 261). Four Dark Neutral Gray (Color 299) transverse bands are evenly distributed on the dorsal surface of head, with the last one between posterior margins of the orbits. A thin, incomplete, transverse band is between the 2nd and the 3rd and between 3rd and 4th thick bands. All of these transverse bands except the most anterior three enter orbits on both sides, which form the radial stripes superior of the eyes. Temporal and occipital regions of the head are dirty Light Neutral Gray (Color 297) to Jet Black (Color 300), with irregular Dark Neutral Gray (Color 299) to Jet Black (Color 300) spots and streaks. The ground coloration of the lateral surface of the head is white. Jet Black (Color 300) radial stripes are present around eyes, where the posterior two stripes are the broadest: One of which extends from the superior posterior corner of orbit to region above the concealed tympanum, while the

other extends from inferior posterior corner of orbit to region just superior to the rictus. Some Irregular Dark Neutral Gray (Color 299) speckles are present on the lateral surfaces of head, particularly posterior to orbits.

The ground coloration of the dorsal and lateral surface of body is Pale Buff (Color 1). A single strongly jagged, Cream Colored (Color 12) dorsolateral stripe is present from neck to pelvis on each side of the body. Six Jet Black (Color 300) rectangular patches are present on the dorsal body along dorsal midline from neck to pelvis between dorsolateral stripes. Each of the rectangular patches is separated from each other by a Cream Colored (Color 12) transverse streak, which connects the dorsolateral stripes on both sides of the body. Lateral surfaces of the body that are inferior to dorsolateral stripes are Jet Black (Color 300), with Cream Colored (Color 12) scales densely scattered. Dorsal surfaces of limbs are white, with Dark Neutral Gray (Color 299) to Jet Black (Color 300) transverse bands across. The bands are much distinct on forelimbs than hind limbs. The dorsal surface of tail is Smoky White (Color 261). Faint Dark Neutral Gray (Color 299) or Jet Black (Color 300) transverse bands are evenly scattered on the tail from the vent to two third of its length, and the remaining distal portion of the tail is more or less uniform Drab-Gray (Color 256).

The ground coloration of the ventral surface of the head is white. Short, Jet Black (Color 300) streaks and speckles are present, some of which connect and form vermiculated patterns. A distinct Medium Blue (Color 169) gular spot is present on the posterior center of ventral head, relatively large in size. Such gular spot ends before the transverse gular fold and does not extend into anterior chest. The ventral surface of the body is uniform white without any distinct ornamentation. The hands and feet are uniform pale Tawny Olive (Color 17), while the remaining ventral surfaces of limbs are uniform white. The ventral surface of the anterior two third of tail is white, while the remaining parts gradually become Smoky White (Color 261) toward the tip.

#### *Coloration of holotype in preservation*

Ornamentation remains largely the same after preservation, but coloration fades. Specifically, the Cream Color (Color 12) of dorsolateral stripes and scattered scales on the lateral surface of the body fade into white, and the Medium Blue (Color 169) gular spot becomes Light Sky Blue (Color 191).

#### *Variation*

Morphometric and pholidosis variation of the type series is summarized in Table S8. The dorsal coloration of a single male (KIZ 044740) is Vandyke Brown (Color 282) to Jet Black (Color 300), with no distinct dorsolateral stripes. For the coloration of the gular spot, some individuals (i.e., KIZ 032734, 032736, 032737) are much lighter than others, showing a Pale Cyan Color (Color 157). Although sample size is limited, sexual dimorphism is evident in the species, where similar to congeners, males of *D. aorun* sp. nov. show tendency toward a longer tail (TAL 212.0%–221.1% SVL in males versus 178.85%–207.7% in females). Furthermore, female

specimens possess distinct coloration and ornamentation patterns compare to males, including having a distinct coloration of dorsolateral stripes (Smoky White [Color 261], Sulphur Yellow [Color 80], or entirely absent in females versus Cream Color [Color 12] in males), background coloration of lateral head, lateral body inferior to dorsolateral stripes, and dorsal limbs (Chamois [Color 84] in live females versus white in males), and by the presence of Peach Red (Color 70) vertebral stripe pattern from dorsal head to the vent in female (versus absence in males). Males tend to have brighter and larger gular spots than females.

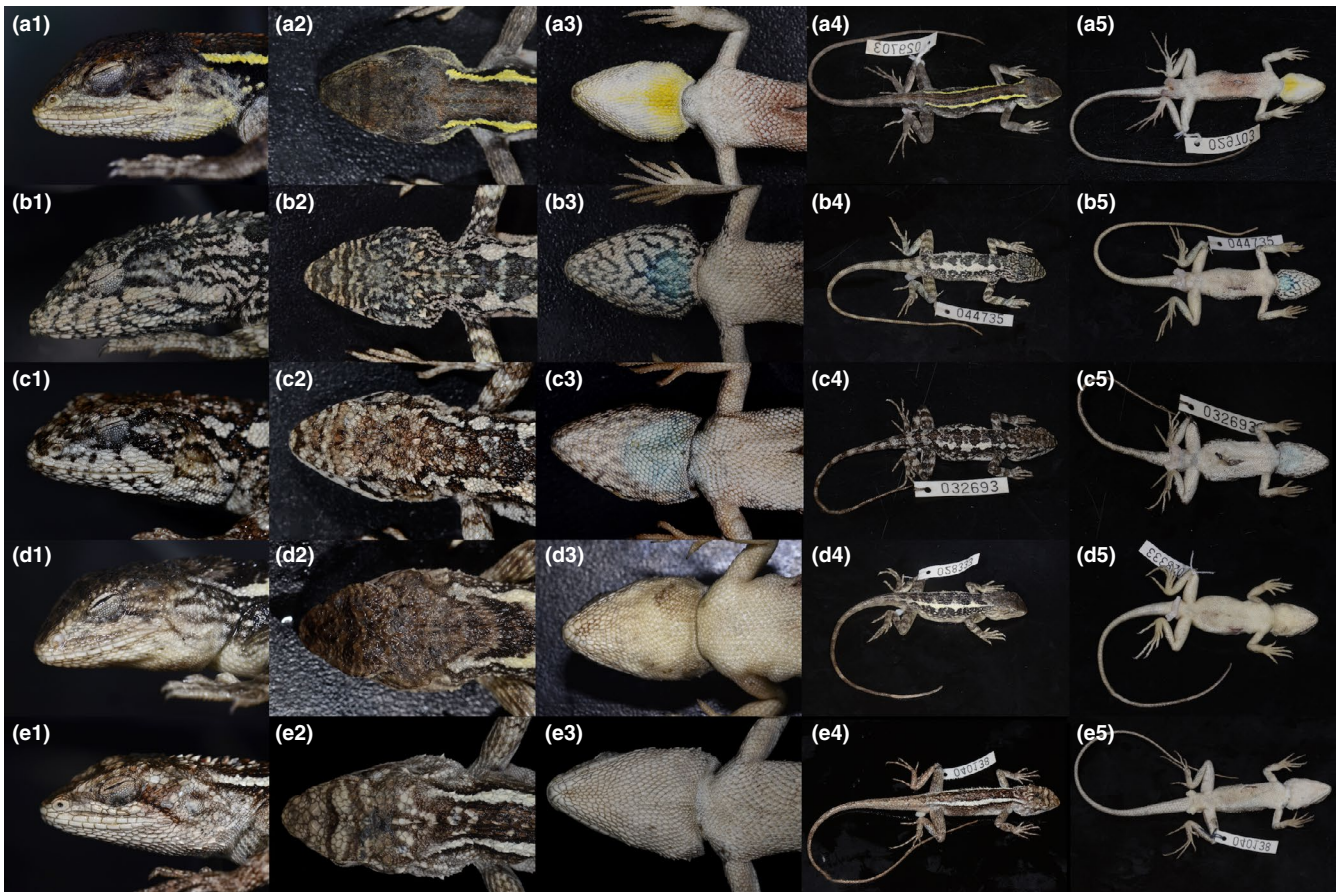
#### Etymology

The species name “*aorun*” is derived from the name of the legendary Dragon Lord in Chinese mythology (Chinese 敖闰, Pinyin: Ao Run), who is the guardian of the West Ocean and is responsible for creating precipitation. We name the new species after the guardian of the ocean in the hope that the recognition of its endangered status will bring protection to the fragile valley habitats that the species is endemic to, just like the dragon lord protecting its realm in the mythology. We recommend Aorun Mountain Dragon as its English common name and 敖闰龙蜥 (Pinyin: Ao Run Long Xi) as its Chinese common name.

#### Natural History and conservation

*Diploderma aorun* sp. nov. inhabits hot-dry valley below 3,000 m of elevation along the upper Jinsha River, from Zongrong Village of Derong County, Sichuan Province, to areas 14 km south of Benzilan, Deqin County, Northwest Yunnan Province, China. Its habitat is the most arid among all new species described here, which comprises of most rocky outcrops (mostly sandstone) and very little vegetation (Figure 13b). The species is terrestrial, basking on large rocks or open grounds within patches of cactus (an introduced alien species) during the day, but most individuals were observed sleeping on bushes or grass stems at night. Road-kill individuals were commonly seen along the highway through the valley. *Elaphe taeniura* and *Gekko scabridus* were found co-distributed at the type locality.

Based on our surveys, the known extent of occurrence of *D. aorun* sp. nov. is only approximately 550 km<sup>2</sup>, which includes low-elevation (i.e., <3,500 m), hot-dry valleys along the isolated upper Jinsha River (from Benzilan to Zongrong Village) and its immediate tributaries (i.e., Dingqu and East Wangxuqu). Although the Baima Snow Mountain Nature Reserve protects the west side of the Jinsha Valley within the range of *D. aorun* sp. nov., being the most peripheral parts of the reserve, much of the habitats still



**FIGURE 11** Comparisons of lateral head view (1), dorsal head view (2), ventral head view (3), dorsolateral overview (4), and ventral overview (5) of preserved specimens among males of *Diploderma angustelinea* sp. nov. (a), *D. aorun* sp. nov. (b), *D. flavilabre* sp. nov. (c), *D. qilin* sp. nov. (d), and *D. panlong* sp. nov. (e). Photographs by KW

overlap greatly with rapid human developments, national highways, and tourist infrastructures. In fact, multiple illegal cement mills were observed at the type locality of the species, which devastate the limestone habitats around them. Additionally, the recent major landslides in 2018 and the discharge of its resulting barrier lake on the Jinsha River have led to severe habitat destructions along the Jinsha Valley, and the follow-up road repairs after the natural disaster further destroyed the low-elevation habitats. Despite the abundant individuals in some regions, the population density varies drastically across its range, and numerous human settlements fragment the continuous distribution of the species, leading to isolated populations along the valleys. Therefore, following IUCN criteria D2, we recommend listing *D. aorun* sp. nov. as Vulnerable (VU).

### 3.3.3 | *Diploderma flavilabre* sp. nov. Wang, Che, Siler

(Population 12 in Figure 1; Figures 2, 7, 11, 12; Tables 2–4; Table S8 (3); ZooBank ID urn:lsid:zoobank.org:act:90059942-6615-4C6A-834A-C427B1AA9BE6).

#### Synonym

*Japalura flaviceps* Zhao et al. (1999: 111–115), in part; Zhao (2003: 84), in part.

#### Holotype

KIZ 032693, adult male from Jinsha River Valley at Yebatan, Gaiyu County, northwest Sichuan Province, China, on May 28, 2017 (98.9642° E, 30.7385° N, elevation 2,845 m, WGS 84).

#### Paratopotypes

KIZ 032692, 032694, adult males; KIZ 032695–032699, KIZ 032730, adult females; all collected from the same locality as the holotype by Kai WANG and Gadeng NIMA.

#### Diagnosis

The new species can be diagnosed from congeners by a combination of the following morphological characteristics: (1) body size small, SVL 50.8–55.2 mm in males, 64.2–72.9 mm in females; (2) tail short, TAL 149.7%–179.3% SVL in males, 140.2%–152.2% in females; (3) head wide, HW 70.01%–73.0% HL, HD 68.6%–75.5% HW; (4) hind limb short, HLL 66.9%–74.8% SVL in males, 61.7%–63.9% in females; (5) tympanum concealed; (6) transverse gular fold present, deep; (7) MD 39–43; (8) F4S 13–16; (9) T4S 19–22; (10) post-riatal conical scales well-developed, 4–9; (11) nuchal and dorsal crest well-developed with strong skin folds in males only; (12) ventral head scales smooth or feebly keeled; (13) ventral body scales distinctively keeled; (14) inner lips Dark Spectrum Yellow (Color 78) in both sexes in life, distinct from background coloration of oral cavity; (15) background coloration of oral cavity Light Flesh Color (Color 250) in life; (16) palate and tonsils speckled heavily with Light Neutral Gray (Color 297) in

both sexes in life; (17) gular spots present in both sexes, Pale Emerald Green (Color 141) to Light Turquoise Green (Color 146) in life; and (18) ventral body Pale Greenish Yellow (Color 86) in live males.

#### Comparisons

The new species was confused with *Diploderma flaviceps*, but it can be distinguished from *D. flaviceps* readily by having a much smaller adult body size in males (SVL 50.8–55.2 mm versus 68.5–82.1 mm), a relatively shorter tail (TAL 149.7%–179.3% SVL in males, 140.2%–152.2% in females versus 181.8%–210.8% in males, 191.5%–205.7% in females), distinct coloration of inner lips (dark spectrum yellow coloration versus same as rest of oral cavity, flesh color), as well as by the presence of gular spots in both sexes (versus absence), presence of distinct radial stripes around eyes (versus faint or absence), presence of distinct dark spectrum yellow along inner lips in both sexes (versus absence), absence of reticulated dark patterns on gular region (versus presence), and by the absence of hallow, brown rhomb-shaped patterns with distinct yellow centers along dorsal midline (versus presence).

*Diploderma flavilabre* sp. nov. is morphologically most similar to *D. batangense* and *D. vela*, with all three species possessing distinct black radial stripes around eyes, blackish dorsal background coloration, and raised nuchal and dorsal crests on skin folds in males. However, the new species can be differentiated from both *D. batangense* and *D. vela* by having a distinct coloration color of inner lips in life for both sexes (Dark Spectrum Yellow [Color 78] versus flesh color, same as the rest of oral cavity) and the tendency toward a relatively shorter tail (ANOVA  $p = .031$ ; TAL 149.7%–179.3% SVL in males, 140.2%–152.2% in females versus 187.3%–206.5% in males, 171.8%–203.1% in females for *D. batangense* [Tukey's HSD  $p = .041$ ]; 174.6%–238.1% in males, 159.8%–202.7% in females for *D. vela* [Tukey's HSD  $p = .034$ ]). In addition, it differs from *D. batangense* by having more post-riatal modified conical or sub-pyramidal scales (4–9 versus 0–3); and from *D. vela* by having a relatively wider head (HW 70.1%–73.0% HL versus 65.2%–69.8%), discontinuous skin folds between nuchal and dorsal sections in males (versus continuous), distinct coloration of dorsolateral stripes in females (Sulphur Yellow [Color 80] versus Medium Chrome Orange [Color 75]), and by the presence of gular spots in both sexes (versus absence).

For remaining closely distributed congeners in the northern HMR, the new species can be differentiated from all species by the distinct dark spectrum yellow coloration of inner lips in life for both sexes (versus same flesh color as the rest of oral cavity). Furthermore, it can be differentiated from *D. brevicaudum* by the presence of distinct gular spots in both sexes after preservation (versus absence); from *D. laeiventris* and *D. drunkdaypo* by having distinctively keeled ventral head and body scales (versus smooth or feebly keeled); from *D. slowinskii* by a smaller body size (SVL 50.8–55.2 mm in males, 64.2–72.9 mm in females versus 81.0–95.5 mm in males, 74.8–91.7 mm in females) and a concealed tympanum (versus exposed); from *D. yulongense* by having a much shorter tail (TAL 149.7%–179.3% SVL in males, 140.2%–152.2% in females

versus 211.3%–247.6% in males, 182.1%–227.3% in females), as well as by the absence of greenish ventrolateral patches of body (versus presence); and from *D. iadinum* by the distinct body coloration in males (Jet Black [Color 300] background coloration of dorsal body, with Pale Horn Color [Color 11] dorsolateral stripes versus Yellowish Spectrum Green [Color 128] to Emerald Green [Color 143] background coloration, with same colored dorsolateral stripes), shape of dorsolateral stripes in males (strongly jagged versus smooth-edged), and fewer dorsolateral ridges on body in females (1 versus 2 or 3).

For the remaining recognized congeners, in addition to the differential Dark Spectrum Yellow (Color 78) coloration of inner lips (versus same coloration as in the oral cavity), the new species differs from *D. varcoae*, *D. dymondi*, and *D. swild*, by having a concealed tympanum (versus exposed); from *D. chapaense*, *D. grahami*, *D. mi-cangshanense*, *D. yunnanense*, and all island species (*D. brevipes*, *D. luei*, *D. makii*, *D. polygonatum*, and *D. swinhonis*) by having a distinct transverse gular fold (versus absence or feeble); from *D. fasciatum* by the absence of single hourglass-shaped pattern on the mid-dorsum (versus presence); from *D. splendidum* by much smaller adult body size (SVL 50.8–55.2 mm in males, 64.2–72.9 mm in females versus >80.0 mm in both sexes) and much shorter tail (TAL < 180.0% SVL in males, <153.0% in females versus >200% in both sexes); and from *D. zhaermii* by a smaller adult body size in males (SVL < 55.2 mm versus > 64 mm) and more T4S (T4S 19–22 versus 23–27).

Lastly, for the other new species described here, *D. flavilabre* sp. nov. differs from all by the differential coloration of inner lips (versus same coloration as rest of the oral cavity). Specifically, it differs from *D. angustelinea* sp. nov. by having a relatively shorter tail (TAL 149.7%–179.3% SVL in males, 140.2%–152.2% in females versus 230.2%–249.1% in males, 194.3%–222.3% in females), more and better developed conical or sub-pyramidal post-riktal scales (4–9 versus 0–3), distinct coloration of gular spots (Pale Emerald Green [Color 141] versus Spectrum Yellow [Color 79]), wider and strongly jagged dorsolateral stripes (versus narrow, weakly jagged or smooth), as well as by the presence of raised, well-developed nuchal and dorsal crests on skin folds in males (versus absence); and from *D. aorun* sp. nov. by having a smaller body size in males (SVL 50.8–55.2 mm versus 58.4–61.2), a shorter tail (TAL 149.7%–179.3% SVL in males, 140.2%–152.2% in females versus 212.0%–221.1% in males, 191.4%–207.7% in females), shorter hind limbs (HLL 66.9%–74.8% in males, 62.0%–65.6% in females versus 73.7%–82.7% in males, 71.8%–80.5% in females), and a distinct gular coloration (Pale Emerald Green [Color 141] versus Pale Cyan [Color 157] to Light Caribbean Blue [Color 163]).

#### Description of holotype

Small-sized agamid, SVL 50.8 mm; tail short, TAL 172.8% SVL; limbs relatively short, FLL 48.3% SVL, HLL 74.8% SVL; head wide, robust, HW 71.2% HL, HD 75.5% HW; snout pointy, SEL 37.1% HL. Rostral rectangular; nasal oval-shaped, nostril close to posterior end, two scales away from the rostral, one scale away from first supralabial; supralabials 9/8 (left/right), feebly keeled;

infralabials 10/8, smooth; loreal approximately equal size, irregularly arranged, keeled; suborbital scale rows 3/4, keeled, central row slightly enlarged; supraciliaries 7/7, each greatly overlapped two third total length with posterior scale. Tympanum concealed under fine scales; two enlarged, sub-pyramidal scales anterior tympanum; enlarged, conical, post-tympanic scales 6/6, one of which distinctively taller on each side; enlarged, conical or sub-pyramidal, post-riktal scales 8/8, one/two much taller than others on each side. Dorsal head scales keeled, heterogeneous in size and shapes; enlarged, hexagon-shaped scales forming Y-shaped ridge on dorsal snout anterior to eyes; interparietal not much differentiated, parietal eye indistinct; single enlarged, sub-pyramidal scale dorsoposterior to orbit on each side of head; enlarged conical scales 7/5 post-occipital.

Dorsal body scales heterogeneous, strongly keeled; axillary scales granular, much smaller than other dorsal scales; enlarged, sub-pyramidal scales, each with single distinct medial keel, scattered across dorsum; enlarged scales mostly irregularly arranged, except some arranged in paravertebral row superior to dorsolateral stripes on each side of body. Middorsal scales 41; nuchal crest scales serrated, erected, much larger than neighboring dorsal scales; dorsal crest scales less erected than nuchal, serrated; both crests on well-developed skin folds in life, with distinct break in between; both skin folds of crests shrunken after preservation. Dorsal limb scales distinctively keeled, homogeneous in size on forelimbs, heterogeneous on hind limbs, with some enlarged sub-pyramidal ones on posterior lateral thigh and dorsal crus. Finger IV and Toe IV longest, Finger IV subdigital lamellae 16/16, Toe IV subdigital lamellae 20/20.

Ventral head scales homogeneous in size and shape mostly, with few slightly enlarged toward center of gular, regularly arranged, smooth or feebly keeled; mental pentagonal in shape, enclosed by first pair of chin shields, which compressed and elongated; chin shield 5/4, smooth, 2–3 scale rows from infralabials. Gular pouch present in life, well-developed; distinct transverse gular fold present across neck, deep. Ventral body scales mostly homogeneous in size and shape, distinctively keeled. Ventral limb and tail scales distinctively keeled; ventral thigh scales regularly arranged in rows in proximal–distal direction, smaller toward posterior lateral sides.

#### Coloration of holotype in life

The background of the anterior part of dorsal head is white to Smoky White (Color 261). A single V-shaped, Jet Black (Color 300) patterns on the dorsal anterior snout, with its branches terminate on the nasal scales, and the root terminates at the posterior edge of the first enlarged, keeled scale of the Y-shaped ridge on the snout. Three Orange-Rufous (Color 56) transverse bands with distinct Dark Neutral Gray (Color 299) edges are present on the dorsal surface of head, where the first one is short and centered on the dorsal snout between the anterior borders of orbit circle. The background coloration of the temporal region of the head is Smoky Gray (Color 266), with irregular ornamentation patterns of Ducky Brown (Color 285) to Jet Black (Color 300).

Lateral surface of head is white to Light Buff (Color 2). Distinct Jet Black (Color 300) radial stripes are around the eyes, eight and nine on each side. Of these radial stripes, three stripes are below eyes in subocular and loreal regions, and all of them continue to extend to lower jaw. The two posteriorly directed stripes from the posterior corner of each eye (one extending slightly dorsally, the other extending slightly ventrally) are the broadest among all, where the ventrally extending one terminated at the anterior end of tympanic region. The inner surfaces of both upper and lower lips, as well as corners of the mouth, are Dark Spectrum Yellow (Color 78). The tongue and gum are uniform Light Flesh Color (Color 250), whereas the palate and tonsils are speckled heavily with Light Neutral Gray (Color 297).

Background coloration of the dorsal surface of the body is Jet Black (Color 300). A distinct Pale Horn Color (Color 11), zig-zag-shaped, dorsolateral stripe is present on each side of the vertebral crest, running from neck to pelvis, sympatric to each other along the vertebral line. The pointy edges of the jagged dorsolateral stripe extend dorsally and almost connect with the symmetric edges from the other side at the dorsal midline. As the individual become stressed or when it was basking, the coloration of dorsolateral stripes may become dirty with pale Salmon Color (Color 58). A total of six solid, dark patches are present along the dorsal midline between two dorsolateral stripes from neck to vent, which are Mahogany Red (Color 34) in the center and gradually transition to Jet Black (Color 300). Except the first and the fourth patches, which are in rectangular and irregular shape, respectively, the remaining four dark patches are in rhomb shape. Irregular light spots of white to Pale Pinkish Buff (Color 3) coloration are scattered inferior to the dorsolateral stripe on each side. Those light spots become larger and longer as moving toward ventral direction, which separates the background Jet Black (Color 300) coloration into thin reticulated patterns on ventrolateral sides of body. Dorsal surfaces of limbs are Jet Black (Color 300). Distinct Pale Buff (Color 1) to Pale Pinkish Buff (Color 3) transverse bands are present on dorsal limbs, evenly scattered from proximal to distal end. Similar transverse bands are also present on dorsal surfaces of limb digits. A white, narrow stripe is present from the base of thigh to the knee joint on the posterior ventrolateral side of hind limb on each side.

The background coloration of the ventral surface of the head is white. A relatively large, two-centered arch-shaped, gular spot is present on the posterior central region of the ventral head, Pale Emerald Green (Color 141) in coloration. Jet Black (Color 300) vermiculated stripes are present on the remaining areas of ventral head outside of the gular spot. Ventral surface of neck and the very anterior portion of the ventral surface of the chest are also Pale Emerald Green (Color 141) as in the gular spot. This Pale Emerald Green coloration gradually fades into Pale Greenish Yellow (Color 86) as moving posteriorly to the chest and abdomen; and coloration continues to fade, where it eventually becomes Pale Buff (Color 1) at the very posterior portion of the ventral body. No other distinct ornamentation patterns are present on ventral surface of body.

Ventral surfaces of limbs are uniform Pale Buff (Color 1), which becomes darker and transitions to Pale Pinkish Buff (Color 3) on ventral hands and feet.

Background coloration of the tail is Pale Pinkish Buff (Color 3). Distinct, dark transverse bands are present on dorsal and lateral surfaces of tail, which do not fully enclose the tail on the ventral side. Coloration of transverse bands changes from Medium Neutral Gray (Color 298) at the proximal end to Salmon Color (Color 58) at the distal end.

#### *Coloration of holotype in preservation*

While the ornamentation patterns remain the same after preservation, coloration of the holotype fades significantly. Specifically, the Pale Horn (Color 11) coloration of the dorsolateral stripes, the Pale Pinkish Buff (Color 3) coloration of irregular spots on the dorsal surface of the body, and the Dark Spectrum Yellow (Color 78) coloration of the inner lips fade into white; the Mahogany Red (Color 34) coloration of the dorsal body becomes Burnt Umber (Color 48); the Pale Emerald Green (Color 141) gular spot fades into Pale Cyan (Color 157); and the Pale Greenish Yellow (Color 86) coloration of the anteroventral region of the body fades into Cyan White (Color 156) or white.

#### *Variation*

Morphometric and pholidosis variation of the type series is summarized in Table S8. Although the sample size is small, it is evident that the new species is sexually dimorphic. Males possess relatively a relatively longer tail (TAL 172.8%–179.3% SVL in males versus 140.2%–152.2% in females), relatively longer hind limbs (HLL 66.9%–74.8% SVL in males versus 61.7%–65.6% in females) and raised crests on skin folds (versus absence). Furthermore, males of the new species differ from females in coloration and ornamentation patterns, including having distinct background coloration of dorsum (Jet Black [Color 300] to Mahogany Red [Color 34] in males versus Tawny Olive [Color 17] to Clay Color [Color 18] in females) and presence of distinct Pale Horn Color (Color 11) dorsolateral stripes in males (versus absence or in faint Sulphur Yellow [Color 80]).

Among females, the transverse bands on the dorsal head and dark rhomb-shaped patches along dorsal body midline of KIZ 032697 are Light Pratt's Rufous (Color 71); the same specimen also has irregular Drab-Gray (Color 256) patterns on the anterior and central abdomen, and its gular spot is Greenish Turquoise (Color 166). KIZ 032699 has the faintest vermiculated stripes on the ventral head. KIZ 032700 has Grayish Horn (Color 268) coloration, irregular stripes and patches on the chest region of ventral body.

#### *Etymology*

The Latin species name, *flavilabre*, means “yellow-lipped,” which describes the diagnostic dark spectrum yellow coloration of inner lips of the species. We recommend Yellow-lipped Mountain Dragon as its English common name and 黄唇龙蜥 (Pinyin: Huang Chun Long Xi) as its Chinese common name.

### Natural History and Conservation

The overall habitat of the new species is warm, semi-arid valley with considerable amount of vegetation coverage, which is very distinct from habitats of congeners in lower reaches of the river (e.g., *D. batangense* and *D. aorun* sp. nov.). Individuals were observed inhabiting rock piles (sandstone) among shrubs and forest edges (Figure 13c). Females and juveniles seem to be less selective for weather conditions and were active even in during cloudy weather, whereas males were only observed during the hottest time of the sunny days. All observed females, including ones that were collected, were gravid, suggesting June is during the breeding season of the species. Considerable amount of ant remains were found in the feces of the collected individuals. Possible predations are likely from birds and snakes (*Elaphe taeniura*).

The type locality of *D. flavilabre* sp. nov. is less than five km away from the biggest hydropower station in the upper Jinsha River, the Yebatan Hydropower Station, which was under active construction at the time of collection in 2017. Several habitat destructions were observed at the time, with explosions and drainage alterations. No lizards were found close to the construction site, and population density was much lower than any other new species described here. Furthermore, the recent major landslide and subsequent flooding in 2018 might have led to further massive habitat destructions and population decline of the new species.

Because we did not find any *D. flavilabre* sp. nov. near Baiyu Township, which is approximately 60km linear distance north of the type locality of *D. flavilabre* sp. nov., the potential distribution range of the new species is only less than 140km linear distance of low-elevation habitats along a single, isolated river valley, and the estimated extent of occurrence is less than 400 km<sup>2</sup>. Given the endemic nature and limited range, fragile ecosystem where the species inhabits, and several, continuous habitat destructions from both natural and anthropogenic causes, we propose to list the species as Vulnerable (VU) based on IUCN criteria D2.

### 3.3.4 | *Diploderma panchi* sp. nov. Wang, Zheng, Xie, Che, Siler

(Population 6 in Figure 1; Figures 2, 8, 12; Tables 2–4; Table S8 (4); ZooBank ID urn:lsid:zoobank.org:act:833577B9-CF79-4E8E-AC83-D8E913DF8DBA).

#### Synonym

*Japalura flaviceps* Zhao et al. (1999: 111–115); Zhao (2003: 84).

#### Holotype

KIZ032715, adult female from upper Yalong River Valley near Yajiang Township, Yajiang County, Ganzi Tibetan Autonomous Prefecture, northwest Sichuan Province, China (30.0414° N, 101.0108° E, elevation 2,663 m). Collected by Kai WANG and Nima DADENG in May 22, 2017.

#### Paratopotypes

KIZ 032716, 032717, 032729, adult females, same collecting information as for the holotype.

#### Diagnosis

The new species can be diagnosed from congeners by a combination of the following morphological characteristics: (1) body length moderate SVL 59.6–67.3 mm; (2) tail short TAL/SVL 141.8%–151.5%; (3) hind limbs short HLL/SVL 60.2%–65.8%; (4) head width moderate HW/HL 69.5%–73.6%; (5) MD 42–46; (6) F4S 14–17; (7) T4S 20–24; (8) conical or sub-pyramidal post-rectal scale moderately developed, 3–7; (9) tympanum concealed; (10) nuchal crest feebly developed with no skin folds; (11) transverse gular fold present, distinct; (12) ventral scales of head and body distinctively keeled; (13) ventral head scales and ventrolateral body scales homogeneous in size; (14) distinct gular spots absent in females, but mosaic Light Sulphur Yellow (Color 93) patterns present; (15) dorsolateral stripes strongly jagged, White, Light Buff (Color 2), or Light Sulphur Yellow (91); (16) ventral body uniform Pale Buff (Color 1); and (17) inner lips, oral cavity, and tongue uniform flesh color.

#### Comparisons

Because all species of *Diploderma* are sexually dimorphic, and since we only have females of *D. panchi* sp. nov., comparisons are carried out for females only. *Diploderma panchi* sp. nov. was confused as *D. flaviceps*, but it can be differentiated from the latter species by having feebly developed nuchal crests with no skin folds in females (versus erected on well-developed skin folds), a relatively shorter tail  $TAL \leq 151.0\%$  SVL in females (versus  $\geq 191.5\%$ ), as well as by the distinct coloration of gular patterns (Light Sulphur Yellow [Color 93] blotches versus Jet black [Color 300] reticulated stripes), and the absence of dark rhomb-shaped patterns along dorsal midline in females (versus presence).

The new species was morphologically most similar to *D. brevicaudum* and *D. drukdaypo*, with all three species having a dwarf appearance (i.e., disproportionally short tail and short limbs). However, the new species can be differentiated from *D. brevicaudum* by having more middorsal scales (MD 42–46 versus 34–40) and the presence of mosaic gular patterns in females (versus absence); and from *D. drukdaypo* by having distinctively keeled ventral scales (versus smooth or feebly keeled), distinct coloration of dorsolateral stripes (Light Yellow Ocher [Color 13] to Pale Buff [Color 1] versus Medium Chrome Orange [Color 75]), and presence of mosaic gular patterns in females (versus absence).

For remaining congeners, *D. panchi* sp. nov. differs from all by having a much shorter tail in females ( $TAL < 151.7\%$  SVL in females versus  $>160.0\%$ ), shorter hind limbs ( $HLL \leq 65.8\%$  SVL versus  $>69.0\%$ ), and differential gular patterns (mosaic pattern versus no gular spots or single distinct gular spot). Specifically, *D. panchi* sp. nov. differs from *D. fasciatum* by the absence of transverse hourglass-shaped pattern on mid-dorsum (versus presence) and presence of dorsolateral stripes (versus absence); from *D. batangense*, *D. iadidum*, and *D. yulongense* by differential gular coloration and patterns in females (Light Sulphur Yellow [93], mosaic patterns versus single



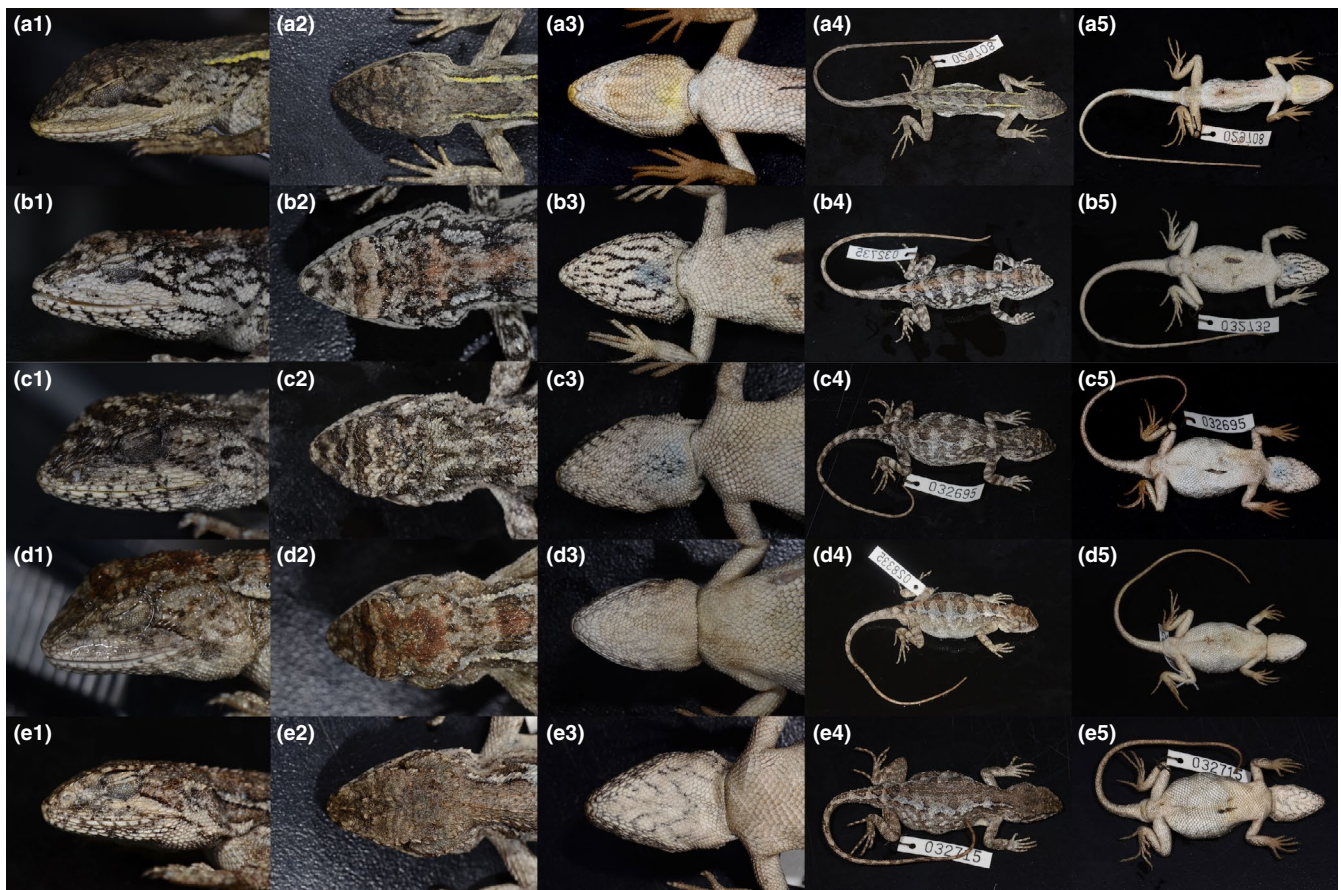
spot, Pale Cyan [Color 157] in *D. batangense*, Medium Greenish Yellow [Color 88] in *D. iadinum*, and Chartreuse [Color 89] in *D. yulongense*; from *D. chapaense*, *D. micangshanense*, *D. varcoae*, *D. yunnanense*, and all species from oceanic islands (*D. brevipes*, *D. luei*, *D. makii*, *D. polygonatum*, and *D. swinhonis*) by the presence of distinct transverse gular fold (versus absence); from *D. swild* and *D. splendidum* by having homogeneous ventral head scales (versus heterogeneous); from *D. laeiventre* by distinctively keeled ventral scales (versus smooth or feebly keeled); from *D. dymondi*, *D. slowinskii*, and *D. varcoae* by having a concealed tympanum (versus exposed); and from *D. vela* by differential coloration of dorsolateral stripes in females (Light Sulphur Yellow [Color 93] versus Medium Chrome Orange [Color 75]).

For the new species described here, *D. panchi* sp. nov. differs from all but *D. flavilabre* sp. nov. by having a much short tail in females (TAL  $\leq$  151.0% SVL versus  $\geq$  174.3%). In addition, *D. panchi* sp. nov. differs from *D. angustelinea* sp. nov. by having more conical or sub-pyramidal post-rectal scales (3–7 versus 0–3) and strongly jagged and wide dorsolateral stripes in females (versus feebly jagged and thin); from *D. aorun* sp. nov. by distinct gular coloration (Light Sulphur Yellow [Color 93], mosaic patterns versus single spot, Pale Cyan [Color 157] to Light Caribbean Blue [Color 163]). For *D. flavilabre* sp. nov., *D. panchi* sp. nov. differs by having a distinct gular pattern and coloration (Light Sulphur Yellow [Color 93], mosaic patterns versus

Pale Emerald Green [Color 141] to Light Turquoise Green [Color 146] gular spots) and a distinct lip coloration (Light Flesh Color [Color 250] versus Dark Spectrum Yellow [Color 78]).

#### Description of holotype

Adult female, body slightly compressed dorsally, SVL 67.3 mm. Tail slender, short, TAL 151.5% SVL. Limbs short, FLL 40.0% SVL, HLL 61.2% SVL. Head slightly compressed dorsally, HW 71.5% HL, HD 68.8% HW; snout pointy, SEL 37% HL. Rostral rectangular, two scales away from nasal; nasal oval shape, single scale away from first supralabial; supralabial 9/8, keeled; suborbital scale rows 4/4, distinctively keeled, third row from bottom enlarged; numerous enlarged scales between posterior orbit and tympanum. Tympanum concealed under fine scales; enlarged, conical, or sub-pyramidal scales post-tympanic, 4/5. Sub-pyramidal, post-rectal scales moderately developed, 5/6. Dorsal head scales heterogeneous, distinctively keeled; Y-shaped ridge present on dorsal snout, formed by enlarged, modified scales, from two small scales posterior to rostral extending across forehead to approximately three scales anterior of interparietal. Interparietal enlarged, tear shape, distinct parietal eye present. Single, elongated, subpyramidal scale present on each side post-orbit dorsally. Enlarged, conical or subpyramidal scales post-temporal, 4/2, with outer most one twice as large as adjacent one.



**FIGURE 12** Comparisons of lateral head view (1), dorsal head view (2), ventral head view (3), dorsolateral overview (4), and ventral overview (5) of preserved specimens among females of *Diploderma angustelinea* sp. nov. (a), *D. aorun* sp. nov. (b), *D. flavilabre* sp. nov. (c), *D. qilin* sp. nov. (d), and *D. panchi* sp. nov. (e). Photographs by KW

Dorsal body scales heterogeneous in size, with enlarged, modified scales scattered across. Nuchal crest feebly developed with no skin folds, indistinguishable from dorsal crest; crest scales serrated, slightly erected, larger than nearby dorsal scales. Two lateral rows of enlarged scales forming dorsolateral ridges, parallel to vertebral ridge on each side of body from neck to pelvis. Dorsal limb scales distinctively keeled, homogeneous on forelimbs, heterogeneous on hind limbs, with enlarged scales in single oblique row on thigh and crus, respectively; enlarged conical scales present on posterior thigh. Tail scales homogeneous, distinctively keeled, craniate in lateral rows.

Ventral head scales homogeneous, distinctively keeled; mental pentagonal in shape, enclosed by first pair of chin shields; chin shields keeled, 6/6, separated from infralabials by two rows of small scales. Gular pouch present in life, moderately developed, indistinct after preservation; transverse gular fold present, distinct. Ventral body, limb scales homogeneous, distinctively keeled. Finger I shortest, Finger IV longest, F4S 16/14, T4S 20/20.

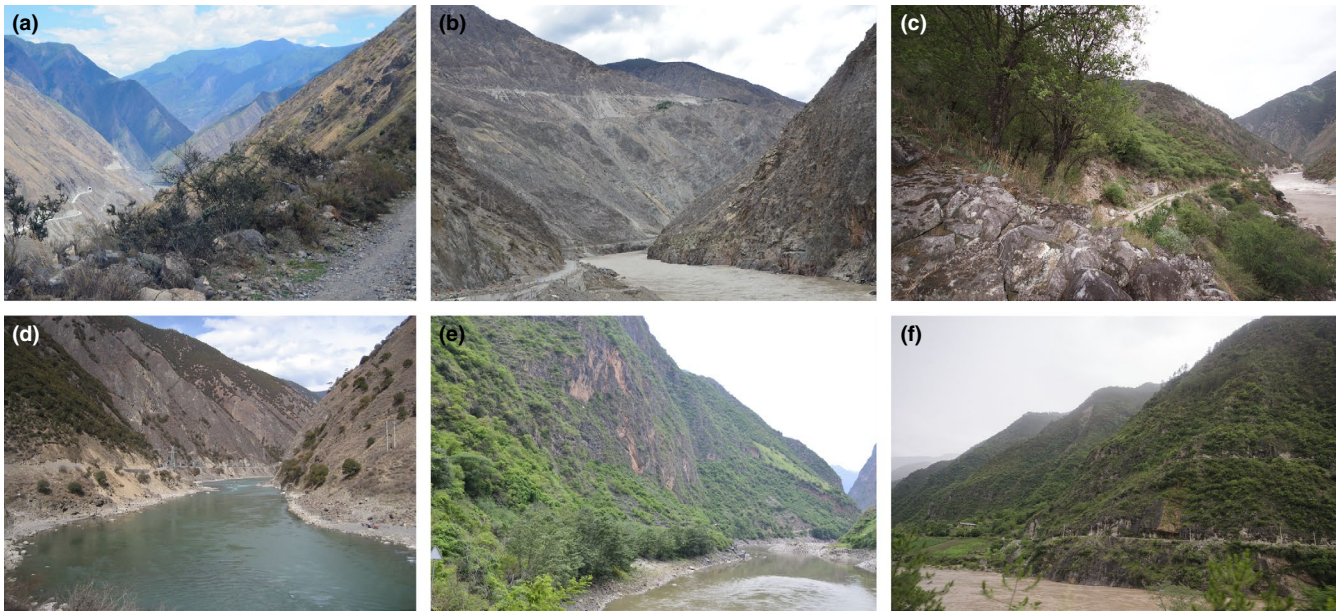
#### Coloration of holotype in life

The dorsal surface of the head is mostly uniform Cinnamon-Drab (Color 50), with some unclear Light Buff (Color 2) transverse streaks between orbits. The background coloration of the lateral surfaces of the head is Light Buff (Color 2). Burnt Umber (Color 48) to Dark Neutral Gray (Color 299) radial stripes are present around eyes, whereas the stripe from posterior–inferior corner of the eye to the rictus and the one from posterior–superior corner of the eye to the enlarged conical scale post-supraciliaries are the darkest and

longest. Remaining radial stripes that are inferior to the orbit are unclear and faint. The background coloration of the lateral head is Light Buff (Color 2). Light Neutral Gray (Color 297) marble patterns are present on the loreal region of head, giving a dirty appearance. The area of lateral head that are in between and posterior to the two darkest radial stripes and anterior to tympanum are Light Russet Vinaceous (Color 246). Scales covering tympanum are Fawn Color (Color 258).

Background coloration of dorsal and lateral surfaces of limbs, body, and tail are Cinnamon-Drab (Color 50). A strongly Jagged, zigzag-shaped, dorsolateral stripe is present on each side of the body from neck to base of tail, with the most anterior one third of dorsolateral stripe faint Light Yellow Ocher (Color 13), and the remaining parts of the stripe Pale Buff (Color 1). The boarding regions along the superior and inferior edge of dorsolateral stripes are Raw Umber (Color 280), particularly in the valleys region of the zigzag dorsolateral stripe along the superior side of the dorsolateral stripe. The dark coloration of each valley along each dorsolateral stripe forms a dark patch, symmetrical to the corresponding one on the other side of the body. Area along the vertebrate between dorsolateral stripes is dirty Salmon Color (Color 58). Randomly scattered enlarged scales on lateral and ventrolateral body are Pale Buff (Color 1). Coloration of lateral body gradually fades and transition into white inferiorly toward ventral body.

Faint Pale Buff (Color 1) and Salmon Color (Color 58) transverse streaks are present on the dorsal forelimbs and hind limbs, respectively. A Pale Buff (Color 1), narrow stripe with Raw Umber (Color 280) edges is present from the base of thigh to the knee joint on the posterior ventrolateral side of hind limb on each side.



**FIGURE 13** Habitats of the six new species at their type localities in the Hengduan Mountain Region. (a) *Diploderma angustilinea* sp. nov.: near Maidilong Village, Muli County, Liangshan Prefecture, Sichuan Province, China; (b) *D. aorun* sp. nov.: near Benzilan Township, Deqin County, Yunnan Province, China; (c) *D. flavilabre* sp. nov.: near Yebatan Hydropower Station, Baiyu County, Ganzi Prefecture, Sichuan Province, China; (d) *D. panchi* sp. nov.: near Yajiang Township, Yajiang County, Ganzi Prefecture, Sichuan Province, China; (e) *D. panlong* sp. nov.: near Miansha Village, Mianning County, Liangshan Prefecture, Sichuan Province, China; and (f) *D. qilin* sp. nov.: near Wujin Village, Shangri-La County, Yunnan Province, China

Four Salmon Colored (Color 58) triangular patterns with Raw Umber (Color 280) outlines are present on the dorsal surface from the pelvis to one fifth of the tail from the vent. The remaining parts of the tail are patterned with Drab (Color 19) spots or transverse streaks.

The background coloration of the ventral surface of the head is Pale Buff (Color 1). Faint Jet Black (Color 300) vermiculated stripes are present on the ventral head, some of which are interconnected and form a web pattern. Light Sulphur Yellow (Color 93) patches are present in between the faint Jet Black vermiculate stripes, forming a mosaic pattern on the gular. Ventral surfaces of the body and limbs are uniform Pale Buff (Color 1) with no distinct ornamentations, and the ventral hands and feet, as well as the ventral surface of the distal portion of the tail are pale Tawny Olive (Color 17).

#### Coloration of holotype in preservation

Most ornamentation patterns remain the same after preservation, except for the Light Sulphur Yellow (Color 93) reticulated patterns of gular disappear. Additionally, most coloration remains the same except the Light Yellow Ocher (Color 13) and Pale Buff (Color 1) coloration of the dorsolateral stripes, which fade to Smoky White (Color 261).

#### Variation

Morphometric and pholidosis variation of the type series is summarized in Table S8. For coloration and ornamentations, all paratopotypes (KIZ 032717, 032716, and 032729) have reduced black vermiculated patterns on the ventral surface of the head, and paratype KIZ 032717 has the most reduced patterns.

#### Etymology

The species name "*panchi*" is derived from the name of female dragons (Chinese 蟠螭, Pinyin: Pan Chi) in the ancient Chinese literature, 《汉书·司马相如传》. We recommend Panchi Mountain Dragon as its English common name and 蟠螭龙蜥 (Pinyin: Pan Chi Long Xi) as its Chinese common name.

#### Natural History and conservation

*Diploderma panchi* sp. nov. inhabits the warm-dry valley along the upper Yalong River, which is predominantly coniferous forest along with tall bush species (i.e., *Lonicera tangutica*; Figure 13d). The new species is terrestrial, basking in the open areas in sunny days and seeking rock crevices or fallen woodpiles for shelters when disturbed. Individuals were observed to sleep on bushes at night. Lizard-feeding snakes such as *Elaphe carinata* may represent predators of the new species.

Based on our surveys, habitats of the new species overlap greatly with human inhabitants, township developments, and hydropower developments (i.e., Lianghekou Station) in Yajiang County, Sichuan Province. Although the exact distribution range of the new species is still unknown, its distribution is unlikely to expand much farther away from the type locality in Yajiang County. We recommend Data Deficient (DD) as its IUCN assessments, and we call for future ecological studies on the population size and distribution range of the new species.

### 3.3.5 | *Diploderma panlong* sp. nov. Wang, Che, Siler

(Population 8 in Figure 1; Figures 2, 9, 11; Tables 2–4; Table S8 (5); ZooBank ID urn:lsid:zoobank.org:act:79DA84FF-CA00-4C19-9D7D-3F3071C2AC8F).

#### Synonyms

*Japalura dymondi* Deng, Yu, and Cao (1991: 27), in part. Zhao et al. (1999: 110–111), in part. Zhao (2003: 82–83), in part.

*Japalura flaviceps* Deng et al. (1991: 27); Zhao et al. (1999: 111–115); Zhao (2003: 84), in part.

#### Holotype

KIZ 040138, adult male collected near Siyinuo Village, Mianning County, Liangshan District, Sichuan Province, China (101.8806° E, 28.3569° N, elevation 1,430 m, WGS 84). Collected by Kai Wang and Gadeng Nima on April 25, 2018.

#### Paratopotypes

KIZ 040137, 040139, 040140, 040143, adult males; 040141, 040142, young adult males. All share same collecting information as the holotype.

#### Diagnosis

The new species can be diagnosed from congeners by a combination of following morphological characters (1) body size moderate, SVL 60.2–71.7 in males; (2) tail long, TAL 248.2%–268.0% SVL in males; (3) hind limbs moderate, HLL 77.7%–83.2% SVL; (4) head moderate, HW 63.4%–67.3% HL; (5) MD 39–46; (6) F4S 18–24; (7) T4S 22–27; (8) conical, post-riatal scales strongly developed, 9–13; (9) tympana mostly exposed; (10) nuchal crest moderately developed, TNC 5.4%–7.7% HL; (11) transverse gular fold present in life, shallow, sometimes indistinct after preservation; (12) ventral head and body scales homogeneous, distinctively keeled; (13) gular spots absent in either sexes; (14) dorsolateral stripes smooth-edged, narrow, Sulphur Yellow (Color 80); (15) distinct radial stripes present around eyes except suborbital regions; (16) distinct white lip stripe present on each side below eye; (17) gradual transition from Tawny (Color 60) or Amber (Color 51) dorsolateral body coloration to Light Flesh (Color 250) coloration of ventrolateral body surface and eventually to Light Buff (Color 2) coloration of ventral body surface; and (18) oral cavity Dark Spectrum Yellow (Color 78), tongue Light Chrome Orange (Color 76).

#### Comparisons

The new species is most similar to *D. swild*, with both species having exposed tympana (in most individuals of *D. panlong* sp. nov.), smooth dorsolateral stripes, and Dark Spectrum Yellow (Color 78) to Light Chrome Orange (Color 76) oral coloration, and both species are found along the Yalong River Valley. However, *D. panlong* sp. nov. differs from *D. swild* by having a relatively longer tail in males (TAL 248.2%–268.0% SVL versus 225.5%–239.0%), lower and less differentiated nuchal crest scales (TNC 5.4%–7.7% HL versus

12.0%–12.4%), homogeneous scales on the ventral surface of head (versus heterogeneous), distinct coloration of dorsolateral stripes in males (Sulphur Yellow [Color 80] versus Chartreuse [Color 89]), and a terrestrial life style (versus arboreal).

For other species that also have exposed tympana, the new species differs from *D. dymondi* by having a distinct coloration of the oral cavity (Light Chrome Orange [Color 76] versus Spectrum Violet [Color 186] to Jet Black [Color 300]) and tongue (Light Chrome Orange [Color 76] versus Pale Pinkish Buff [Color 3]), and a terrestrial lifestyle (versus arboreal); from *D. varcoae* by having a distinct coloration of the posterior surface of the palate and deep throat in life (marbled Dark Neutral Gray [Color 299] versus uniform Light Orange Yellow [Color 77]), smooth dorsolateral stripes in males (versus strongly jagged), and by the presence of a transverse gular fold (versus absence).

For the remaining species in the same clade (Figure 2), *D. panlong* sp. nov. differs from all congeners by having a distinct oral cavity and tongue coloration in life (Light Chrome Orange [Color 76] versus Light Flesh Color [Color 250]). Furthermore, *D. panlong* sp. nov. differs from *D. flaviceps* by having exposed tympana in most individuals (versus always concealed), a shallow transverse gular fold (versus deep and well-developed), uniform white ventral head coloration with no gular patterns (versus dark reticulated gular stripes), smooth-edged dorsolateral stripes (versus strongly jagged), and by the presence of distinct radial stripes around the eyes (versus absence or faint); from *D. micangshanense* by the presence of a transverse gular fold (versus absence), absence of strong skin folds of the nuchal and dorsal crests in males (versus presence), absence of regular triangular or rhomboid-shaped patterns along the vertebral line between dorsolateral stripes (versus presence), and by having smooth dorsolateral stripes in males (versus strongly jagged); from *D. zhaoermii* by having smooth-edged, dorsolateral stripes (versus strongly jagged), the presence of distinct white lip stripes (versus absence), and absence of gular spots and skin folds under the nuchal and dorsal crests in males (versus presence). Additionally, from the island congeners *D. brevipes*, *D. luei*, *D. makii*, *D. polygonatum*, and *D. swinhonis*, *D. panlong* sp. nov. can be diagnosed by having exposed tympana in most individuals (versus always concealed) and a terrestrial lifestyle (versus arboreal), and by the presence of a transverse gular fold (versus absence).

For species in Clade B (Figure 2), *D. panlong* sp. nov. differs from all congeners by having exposed tympana in most individuals (versus always concealed), and from all except *D. chapaense* and *D. yunnanense* by having a distinct oral coloration in life (Light Chrome Orange [Color 76] versus Light Flesh Color [Color 250]). Additionally, the new species differs from *D. batangense*, *D. laeviventre*, and *D. yulongense* by having a greater number of, and better developed, post-riatal conical scales (versus fewer and weaker), and by the absence of gular spots (versus presence in both sexes); from *D. drukdaypo* by having a longer tail (TAL  $\geq$  248.0% SVL versus  $<$ 154.0%) and hind limbs (HLL  $>$  77.0% SVL versus  $<$ 64.0%); from *D. slowinskii* by having a smaller maximum body size (SVL  $\leq$  71.7 mm

versus  $\leq$ 98.3 mm), fewer middorsal scales (39–46 versus 47–53), a distinct coloration of dorsolateral stripes (Sulphur Yellow [Color 80] versus Light Emerald Green [Color 143]), and a distinct dorsal limb coloration (Light Buff [Color 2] to Pale Pinkish Buff [Color 3] versus Parrot Green [Color 121] to Greenish Olive [Color 125]); from *D. vela* by having a distinct dorsal background coloration (Brussels Brown [Color 33] to Maroon [Color 39] versus Jet Black [Color 300]) and by the absence of sail-like skin folds of the crests in males (versus presence); from *D. iadinum* by having a longer tail (TAL  $\geq$  248.0% SVL versus  $<$ 206.0%), a distinct background body coloration (Brussels Brown [Color 33] to Maroon [Color 39] versus Yellowish Spectrum Green [Color 128] to Emerald Green [Color 143]), and by the absence of gular spots (versus presence); and from *D. chapaense* and *D. yunnanense* by having shorter and less well-defined nuchal crest scales (versus taller and strongly defined), and by the absence of gular spots (versus presence), absence of a W-shaped ridge on the occipital region of the head (versus presence), and by the presence of a transverse gular fold (versus absence).

For species that lack genetic data, the new species differs from all by having mostly exposed tympana (versus always concealed). Additionally, it differs from *D. brevicadum* by having a longer tail (TAL  $>$  248.0% SVL versus  $\leq$ 154.0%) and longer hind limbs (HLL  $>$  77.0% SVL versus  $\leq$ 64.0%); from *D. grahami* by having more middorsal scales (39–46 versus 8) and by the absence of granular scales on the dorsal body surface (versus presence); from *D. hamptoni* by having a transverse gular fold (versus absence) and distinct, parallel dorsolateral stripes (versus faint, diagonally away dorsal midline posteriorly); and from *D. fasciatum* by having weakly developed nuchal crests (TNC  $\leq$  7.1% HL in males versus  $\geq$ 8.9% in males) and by the absence of transverse, hourglass-shaped ornamentation patterns on the dorsal midbody (versus presence).

For the new species described here, *D. panlong* sp. nov. differs from all by having exposed tympana in most individuals (versus always concealed), taller nuchal crests, and better developed, higher numbers of conical scales on the post-riatal and post-tympanic regions. In particular, *D. panlong* sp. nov. differs from *D. angustelinea* sp. nov. by having more and better developed conical scales on the post-riatal region (PRS 9–13 versus 0–3), a narrower head (HW 63.4%–67.3% HL versus 67.0%–73.9%), a distinct oral coloration in life (Light Chrome Orange [Color 76] versus Light Flesh Color [Color 250]), and by the absence of gular spots (versus presence); from *D. aorun* sp. nov. by having a narrower head (HW 63.5%–67.3% HL versus 67.8%–72.7%), a tendency toward more lamellae scales under Finger IV (18–24 versus 12–19), more and better developed conical scales on the post-riatal region (PRS 9–13 versus 1–7), distinct shapes of dorsolateral stripes (smooth-edged versus strongly jagged), weakly developed nuchal and dorsal crests without distinct skin folds (versus strongly developed with skin folds), and by the absence of gular spots (versus presence); from *D. flavilabre* sp. nov. by having a larger adult body size (SVL 60.2–71.7 mm versus 50.8–55.2 mm), a longer tail (TAL 248.2%–268.0% SVL versus 149.7%–179.3%), longer hind limbs (HLL 77.7%–83.2% SVL versus 66.9%–74.8%), having more and better developed conical scales on the post-riatal region (PRS 9–13

versus 4–9), distinct dorsal body coloration (Pale Pinkish Buff [Color 3] to Light Flesh Color [Color 250] versus Jet Black [Color 300]), distinct oral and inner coloration (uniform Light Chrome Orange [Color 76] versus Light Flesh Color [Color 250] for oral cavity and tongue, only inner lips uniform Dark Spectrum Yellow [Color 78]), and by the absence of gular spots (versus presence).

For *D. panchi* sp. nov., although we only have data of the opposite sex for each species (males for *D. panlong* sp. nov. and females for *D. panchi* sp. nov.), which surrenders comparisons of morphometric and coloration data due to sexual dimorphism, however, *Diploderma panlong* sp. nov. can still be differentiated from *D. panchi* sp. nov. in pholidosis characters that are not known to be sexually dimorphic, including having more lamellae scales under Finger IV (18–24 versus 14–17), and more and better developed conical scales on the post-tympanic (6–12 versus 2–6) and post-rectal regions of head (9–13 versus 3–7).

#### Description of holotype

Adult male, moderate-sized agamid, SVL 71.7 mm, body not compressed dorsally; tail long, slender, TAL 248.2% SVL; limbs moderate, FLL 44.9% SVL, HLL 78.1% SVL. Head moderate, HW 65.9% HL, HD 79.5% HW; snout pointed, SEL 39.05% HL. Rostral rectangular, approximately three times longer than height, separated from nasal by two scales; nasal polygonal-shaped, in brief contact with first supralabial; supralabials 7/8, all feebly keeled, posteriormost longest; two scale rows between supralabials and fine scales around orbit, superior row much larger, all distinctively keeled; supraciliaries 7/7, overlapping between one half to two third of its length; elongated, sub-pyramidal, convex scale dorsoposterior to orbit on each side, posterior to last supraciliaries, 1/2; enlarged, convex, keeled scales between posterior orbit and anterosuperior tympanum, 6/6, forming lateral ridge between orbit and tympanum on each side; tympana exposed, somewhat oval shape, TD 46.0% OD; scales enclosing tympana fine, much smaller than other scales nearby; strongly developed, enlarged, conical scales posterior to tympana, 9/9, two of which much taller and larger on each side.

Dorsal head scales heterogeneous in size and shape, all distinctively keeled; six enlarged, keeled scales forming Y-shaped arrangement on dorsal snout anterior to anterior margins of orbit, with base of such Y-shaped arrangement two small scales posterior to rostral; interparietal scale in elongated hexagonal shape, parietal eye distinct; four enlarged, convex scales forming cluster on each side of interparietal, symmetrical to other side along dorsal midline; enlarged, tall, conical scales post-occipital on each side, 4/6, one of which much taller, located on far lateral position on each side.

Dorsal body scales all distinctively keeled, heterogeneous in size and shape; nuchal crest scales in low triangular shape, highly serrated, slightly taller and differentiated from following dorsal crests; dorsal crest highly serrated, differentiated from remaining dorsal scales; middorsal scale 43; enlarged dorsal body scales randomly scattered for the most parts, except some arranged in two paravertebral rows on each side of body first row approximately two scale rows away from dorsal crest, second row along superior

border of dorsolateral stripe; tips of all distinctively enlarged dorsal body scales raised, protruding slightly backwards and upwards. Dorsal forelimb scales homogeneous on upper arm, heterogeneous on lower arm, with few enlarged, subpyramidal scales on posterior lateral side; dorsal hind limb scales heterogeneous, with enlarged scales on posterior lateral thigh.

Mental pentagonal in shape, in contact with first pair of supralabial and first pair of chin shield; chin shields 4/5, one to two scale rows away from infralabials; infralabials 10/9, all distinctively keeled, each bearing single lateral keel; remaining ventral scales all distinctively keeled, homogeneous in size and shape; post-rectal modified scales conical in shape, well-developed, 13/14, distinctively raised, giving spiky appearance. Gular pouch present, distinct in life, indistinct after preservation; lateral gular fold present in life, absent after preservation; transverse gular fold present across throat, shallow. Ventral body scales all distinctively keeled, homogeneous in size and shape. Ventral limb scales homogeneous in size and shape, all distinctively keeled; Finger VI and Toe VI longest; subdigital lamellae well-modified, F4S 19/19, T4S 25/26. Tail scales all distinctively keeled, carinate in lateral rows.

#### Coloration of holotype in life

The background coloration of the dorsal surface of the head is Pale Buff (Color 1). Two Sepia (Color 279) transverse patterns are present on the dorsal surface of the head between the orbit. The first pattern is a transverse streak between the middle points of the orbit, and the second pattern is a compressed X-shape between the posterior ends of the orbit. Both ornamentation patterns extend laterally and inferiorly into the orbit on both sides of the head, forming parts of the radial patterns above the eyes. The background coloration of the lateral surface of the head is also Pale Buff (Color 1). Distinct Sepia (Color 279) or Jet Black (Color 300) radial stripes are present around the eyes, except the suborbital region. Of the radial stripes, the one from the posterior–inferior corner of the eye to the anterior edge of the tympanum and the rictus is the broadest. A distinct white lip stripe is present from the nasal scale to the rictus on each side of the head. The oral cavity is Dark Spectrum Yellow (Color 78), and the tongue is Light Chrome Orange (Color 76).

The background coloration of the lateral surface of the body is Brussels Brown (Color 33) to Maroon (Color 39), which gradually transitions to Jet Black (Color 300) as it gets closer to the inferior edges of the dorsolateral stripes. Short, Light Buff (Color 2) to Pale Pinkish Buff (Color 3) streaks or spots are densely distributed on the lateral surfaces of the body inferior to the dorsolateral stripes, cutting the background coloration of the lateral body surfaces into a reticulated pattern. The dorsolateral stripes are smooth-edged and relatively narrow, Sulphur Yellow (Color 80) in color, extending from the neck to the pelvis. The dorsal region of the body between the dorsolateral stripes is Clay Color (Color 18) to Brussels Brown (Color 33). Sepia (Color 286) to Jet Black (Color 300) rectangular or chevron-shaped patterns are present along the dorsal midline of the body between the neck and the base of the tail.

The dorsal surfaces of the limbs and tail are Pale Pinkish Buff (Color 3) to Light Flesh Color (Color 250). Light Buff (Color 2) transverse bands with incomplete Jet Black (Color 300) edges are present on the forelimbs, where such bands are indistinct and close to the background color of the limbs. A single Pale Buff (Color 1) circular patch with Jet Black (Color 300) is present on the elbow on each side. The dorsal surface of the tail is mostly uniform Pale Pinkish Buff (Color 3) to Light Flesh Color (Color 250), with a few faint bands with slightly darker color.

The ventral surface of the head is uniform white. The ventral surface of the body, limbs, and tail are faint Light Flesh Color (Color 250) with no distinct ornamentations.

#### Coloration of holotype in preservative

Ornamentations remain the same after preservation, but the coloration fades and changes as follows: The Pale Buff (Color 1) color on the dorsal and lateral surfaces of the head and the Light Buff (Color 2) transverse bands on the forelimbs all fade into white; the Brussels Brown (Color 33) to Maroon (Color 39) lateral body coloration becomes Brunt Umber (Color 48); and the Sulphur Yellow (Color 80) dorsolateral stripes fade to white.

#### Variation

Morphometric and pholidosis variation of the type series is summarized in Table S8. Coloration and ornamentation patterns among the type series are consistent with the holotype. Two of the paratopotype specimens (KIZ 040139, 040143) each has a concealed tympanum.

#### Etymology

The specific name "*panlong*" is derived from the Chinese word 蟠龙 (Pinyin: Pan Long), from the ancient Chinese literature, 《广雅》 (Pinyin: Guang Ya). The name refers to dragons that are terrestrial and are not able to fly, which matches the terrestrial lifestyle of the new species. We recommend Pan Long Mountain Dragon as its English common name and 蟠龙龙蜥 (Pinyin Pan Long Long Xi) as its Chinese common name.

#### Natural history and conservation status

The new species inhabits valleys along the middle reaches of the Yalong River. The environment is more humid than the type localities of other *Diploderma* at the same latitude (i.e., *D. batangense* and *D. vela*), where trees and leafy shrubs (i.e., *Pueraria peduncularis*, *Dalbergia* sp., and *Pterocarya* sp.) form the main plant community (Figure 13e). Individuals were found basking on low bushes and rock piles (sandstone) along the forest edge in the afternoon, and lizards took shelter in rock crevices or dense vegetation when disturbed. At night, individuals sleep on thin stems of bushes above ground. Other herpetofauna such as *Ptyas dhumnades*, *Brachytarsophrys* sp., *Bufo gargarzians*, *Odorrana* sp. also were observed at the type locality.

Habitats of *D. panlong* sp. nov. overlap greatly with human habitations, road construction, and major hydropower station (i.e., Jinping Hydropower Station), which have resulted in deforestation

and pose serious threats to the remaining habitat of the new species. Although the extent distribution range of the species is still unknown, given our preliminary surveys, the estimated extent of occurrence of the new species is less than 600 km<sup>2</sup> along the Yalong River Valley between Jiulong County and Xichang in Sichuan Province. Given the restricted range along a single, highly developed river valley, the observed declines of habitat quality, and the existing development plans of the Yalong River by the government, we recommend listing the species as Vulnerable (VU) according to IUCN criteria D2.

### 3.3.6 | *Diploderma qilin* sp. nov. Wang, Ren, Che, Siler

(Population 15 in Figure 1; Figures 2, 10, 11, 12; Tables 2–4; Table S8 (6); ZooBank ID urn:lsid:zoobank.org:act:AE454658-7AC6-4436-9636-15EC789329FA).

#### Synonym

*Japalura flaviceps*: Zhao and Yang (1997: 165–167), in part; Zhao et al. (1999: 111–115), in part; Yang and Rao (2008: 200), in part.

#### Holotype

KIZ 028332, adult male, from Jinsha River Valley in Balong, Deqin County, northwest Yunnan Province, China (27.7017° N, 99.4563° E, elevation 1982 m, WGS 84). Collected by Kai WANG and Jinlong REN on July 9, 2016.

#### Paratopotypes

KIZ 028333, adult male, same collecting information as for the holotype; KIZ 028334–336, adult females, same collecting information as for the holotype.

#### Paratypes

KIZ 044412, 044413, adult males, near Baka Village, Shangri-La County, NW Yunnan Province, China (27.8066° N, 99.4527° E, elevation 2028 m); KIZ 044405, 044407, adult males, KIZ 044408, adult female, near Meiding Village, Shangri-La County, NW Yunnan Province, China (27.8811 N, 99.4440 E, elevation 1950 m); KIZ 044745, adult male, KIZ 044744, adult female, near Cangjue Village, Shangri-La County, NW Yunnan Province, China (27.6087 N, 99.5226 E, 1,939 m); KIZ 044820, adult female, near Pengnanshou Bridge, Shangri-La County, NW Yunnan Province, China (28.0301 N, 99.4215 E, elevation 2,619 m); all collected by Kai WANG, Zhuoyu LU, and Xiankun HUANG on June 15, 2019.

#### Diagnosis

The new species can be diagnosed from congeners by a combination of the following morphological characteristics: (1) body length moderate, SVL 55.9–66.5 mm in males, 55.3–61.7 mm in females; (2) tail long, TAL 201.0%–218.2% SVL in males, 174.3%–199.7% in females; (3) hind limbs moderate HLL 73.3%–78.4% SVL in males, 72.5%–80.4% in females; (4) head relatively robust, HW 65.0%–73.2% HL,

HD 72.3%–82.8% HW; (5) MD 38–45; (6) F4S 15–19; (7) T4S 21–25; (8) conical or subpyramidal, post-rectal scales moderately developed, 3–8; (9) tympanum concealed; (10) transverse gular fold present, distinct; (11) ventral scales of head and body distinctively keeled; (12) gular spots present in both males and females, Light Sulphur Yellow (Color 93); (13) oral cavity uniformly Light Flesh Color (Color 250); (14) dorsolateral stripes present, jagged, always in males, sometimes in females, Cream Yellow (Color 82) in males, Beige (Color 254) in females; (15) ventrolateral body Light Sulphur Yellow (Color 93) in males; and (16) ventral body uniform white or Pale Buff (Color 1) in both sexes.

### Comparisons

*Diploderma qilin* sp. nov. was confused as *D. flaviceps*, but it can be differentiated from the latter by having a smaller maximum adult body size in males (SVL up to 66.5 mm versus up to 82.1 mm), weaker skin folds under crests in males, absent in females (versus strongly developed, raised in both sexes), less developed conical scales on the post-occipital and post-rectal regions (sub-pyramidal shape versus tall conical shape), as well as by the presence of gular spots in both sexes (versus absence), presence of distinct radial stripes around eyes (versus absence), and the absence of dark rhomboid-shaped patterns with distinct light centers on dorsal body along dorsal midline (versus presence).

For closely distributed congeners along the upper Yangtze River in the HMR, *D. qilin* sp. nov. differs from *D. batangense* by having a tendency toward more MD (38–45 versus 41–53), a different gular coloration (Light Sulphur Yellow [Color 93] versus Pale Cyan [Color 157]) and a different coloration of ventral body in males (white or Pale Buff [Color 1] versus Spectrum Yellow [Color 79]); from *D. brevicaudum* by having a longer tail (TAL  $\geq$  174.3% SVL versus  $<$ 145.0%) and longer hind limbs (HLL  $\geq$  72.5% of SVL versus  $<$ 64.0%); and from *D. yulongense* by having different coloration of gular spots in males (Light Sulphur Yellow [Color 93] versus Opaline Green [Color 106]), as well as by the presence of distinct reticulated patterns on the ventral head in males (versus absence), the absence of gular spots in females (versus presence), and by the absence of Greenish Yellow (Color 88) ventrolateral patches of body (versus presence).

For congeners distributed in different river valleys in the HMR, *D. qilin* sp. nov. differs from *D. drunkdaypo* by having a longer tail (TAL  $\geq$  174.3% versus  $\leq$ 154.4%), longer hind limbs (HLL  $\geq$  72.5% SVL versus  $\leq$ 63.8%), better developed crest scales in males (erected and serrated on skin folds versus not erected or serrated, skin fold absence), distinctively keeled ventral scales (versus feebly keeled or smooth), and by the presence of gular spots in males (versus absence); from *D. iadinum* by having a distinct body coloration (Emerald Green [Color 143] versus True Cinnamon [Color 260] to Burnt Umber [Color 48]) and different coloration of gular spot (Light Sulphur Yellow [Color 93] in both sexes versus Caribbean Blue [Color 168] in males, Medium Greenish Yellow [Color 88] in females); from *D. laeiventre* by distinctively keeled ventral scales (versus smooth or feebly keeled), fewer MD (38–45 versus 57–59),

and different coloration of gular spots (Light Sulphur Yellow [Color 93] in both sexes versus Medium Chrome Orange [Color 75] in both sexes); from *D. vela* by weaker and discontinuous skin fold of crests in males (versus sail-like, continuous skin fold under crests) and by the presence of gular spots (versus absence); from *D. slowinskii* by a concealed tympanum (versus exposed), a smaller body size (SVL  $<$  64 mm versus SVL  $>$  74 mm), fewer T4S (19–25 versus 25–30), jagged dorsolateral stripes (versus smooth-edged), different body coloration of dorsolateral stripes (Cream Color [Color 82] versus Opaline Green [Color 106]), and by the presence of gular spots in males (versus absence).

For remaining congeners, the new species differs from *D. dymondi*, *D. swild*, and *D. varcoae* by having a concealed tympanum (versus exposed) and differential oral coloration (Flesh Color [Color 250] versus Light Chrome Orange [Color 76] in *D. swild* and *D. varcoae*; Spectrum Violet [Color 186] to Jet Black [Color 300] in *D. dymondi*); from *D. grahami* by distinct appearance of dorsal body scales (protruding and spiky versus granular), more middorsal scales (38–45 versus 8), and a larger body size (55.94–63.44 mm versus 49.29 mm); from *D. fasciatum* by the absence of single hourglass-shaped pattern on the mid-dorsum (versus presence); from *D. hamptoni* by having small scales between nasal and first supralabial (versus in direct contact) and parallel dorsolateral stripes on dorsal body (versus diagonally away from dorsal midline); from *D. chapaense*, *D. micangshanense*, *D. yunnanense*, and all species from islands (*D. brevipes*, *D. makii*, *D. luei*, *D. polygonatum*, and *D. swinhonis*) by having a distinct transverse gular fold (versus absence); from *D. splendidum* by having homogeneous ventral head scales (versus heterogeneous) and strongly jagged dorsolateral stripes (versus smooth-edged); and from *D. zhaoermii* by a longer tail (TAL  $>$  200.0% SVL in males,  $>$ 174.0% in females versus  $<$ 190.0% in males,  $<$ 160.0% in females) and different coloration of gular spots (Light Sulphur Yellow [Color 93] versus Chartreuse [Color 89]).

For the new species described here, *D. qilin* sp. nov. differs from *D. angustelina* sp. nov. by having more developed nuchal and dorsal crests on skin folds (versus feebly developed), wider and strongly jagged dorsolateral stripes in both sexes (versus narrow, feebly jagged), and by the different coloration of gular spots (Light Sulphur Yellow [Color 93] versus Sulphur Yellow [Color 80] to Dark Spectrum Yellow [Color 78]); from *D. aorun* sp. nov. by having distinct gular coloration (Light Sulphur Yellow [Color 93] versus Pale Cyan [Color 15] to Light Caribbean Blue [Color 163]); from *D. flavilabre* sp. nov. by having a longer tail (TAL  $\geq$  201.0% SVL in males,  $\geq$ 174.3% in females versus  $\leq$ 179.3% in males,  $<$ 152.2% in females), different gular coloration in males (Sulphur Yellow [Color 80] versus Pale Emerald Green [Color 141]), different inner-lip coloration (Light Flesh Color [Color 250] versus Spectrum Yellow [Color 79]), as well as by the absence of gular spots in females (versus presence); from *D. panchi* sp. nov. by having a longer tail (TAL 174.3%–199.7% SVL in females versus 141.8%–167.8%), a tendency toward a more robust head (HD 72.3%–80.41% HW in females versus 63.3%–74.3%), and by the absence of mosaic gular patterns (versus presence); and from *D. panlong* sp. nov. by having a shorter tail (TAL

202.0%–218.2% in males versus 248.2%–268.0%), a wider (HW 68.12%–74.76% HL versus 63.4%–67.3%) and more robust head (HD 51.5%–60.2% HL versus 49.3%–52.4%), concealed tympana (versus mostly exposed), deeper transverse gular folds (versus shallow), distinct shape of dorsolateral stripes (strongly jagged versus smooth-edged), and by the presence of distinct gular spots in males (versus absence).

#### *Description of holotype*

Adult male, body size moderate, SVL 55.9 mm; tail slender, TAL 208.6% SVL; limbs moderate, FLL 46.4% SVL, HLL 75.8% SVL; head robust, HW 68.1% HL, HD 80.4% HW; snout pointy, SEL 37.4%. Rostral rectangular, two scales away from nasal; nasal oval shape, single scale away from first supralabial; nostril centered in nasal; supralabials keeled, 10/10; subocular scale rows 5/5, all keeled, third row from bottom enlarged than others. Tympanum concealed under fine scales; 7/8 modified scales post-tympanic, some in conical shape and better developed; single distinctively enlarged, subpyramidal scale anterior to tympanum. Infralabials keeled, 12/13; post-rectal modified scales 5/7, moderately developed. Dorsal head scales keeled, heterogeneous in size and shape; distinct Y-shaped ridge present on dorsal snout from midpoint of posterior nasal to midpoint of anterior orbit, constituted by enlarged, modified scales; interparietal enlarged, somewhat rectangular, with parietal eye; post-occipital scales strongly modified in conical shape, 5/4.

Dorsal body scale heterogeneous, strongly keeled; axillary scales much smaller than other dorsals; enlarged, subpyramidal-shaped, keeled scales scattered across dorsum, mostly irregularly arranged, some arranged in paravertebral row superior to dorsolateral stripe from neck to pelvis on each side. Antehumeral fold present, distinct; axillary fold present, indistinct. Crest scales serrated, larger than neighboring dorsal scales; middorsal scale count 41; nuchal and dorsal crests erected on weak skin folds in life, more distinct on nuchal section, with distinct break in between, both shrunk after preservation. Dorsal limb scales distinctively keeled, homogeneous in size on forelimbs, heterogeneous on hind limbs; enlarged, subpyramidal scales on posterior lateral thigh; F4S 16/16; T4S 21/21.

Ventral head scales mostly homogeneous, slightly enlarged toward center, all distinctively keeled; first pair of chin shield in contact with each other, mental, first pair of infralabials; remaining chin shields 2–3 scale rows away from infralabials; transverse gular fold present, distinct; gular pouch well-developed with distinct lateral gular fold in life, indistinct after preservation. Ventral body scales homogeneous, distinctively keeled. Tail scales distinctively keeled; keels aligned in regular rows from base to tip.

#### *Coloration of holotype in life*

The dorsal surface of the head is Sinnamon-Drab (Color 50). A single Warm Sepia (Color 40) transverse band stretches across the forehead between the eyes. Loreal and suborbital regions of the head are Pale Buff (Color 1). Warm Sepia (Color 40) radial stripes are present around the eyes, of which the inferior ones are faint and indistinct. The stripe from the posterior corner of the eye to the rictus is the broadest. The

lateral postorbital region of the head is Beige (Color 254). The oral cavity and inner lips are uniform Light Flash Color (Color 250).

The background coloration of the dorsum is True Cinnamon (Color 260). The background coloration is darker and becomes Brunt Umber (Color 48) when it is close to the edge of the dorsolateral stripes. A strongly jagged, Light Sulphur Yellow (Color 93) dorsolateral stripe is present on each side of the body from the neck to the pelvis. In between the two dorsolateral stripes, five Brunt Umber (Color 48), somewhat rectangular patches are equally spaced along the dorsal midline of the body from the neck to the pelvis. Irregular Cream Color (Color 12) to Light Sulphur Yellow (Color 93) spots are present inferior to the dorsolateral stripes. Dorsal surfaces of the limbs are Pale Buff (Color 1) to pale Cinnamon-Drab (Color 50), with broad Beige (Color 254) to Burnt Umber (Color 48) transverse bands scattered from the proximal to distal ends. A white, narrow stripe with Raw Umber (Color 280) edges is present from the area lateral and superior to the cloaca to approximately 0.5 cm from the base of thigh on the posterior ventrolateral side of the hind limb on each side. The ventrolateral surfaces of the body are light Sulphur Yellow (Color 93). Dorsal and lateral surfaces of the tail are mostly uniform Beige (Color 254).

The background coloration of the ventral surface of the head is Pale Buff (Color 1). Reticulated, Drab-Gray (Color 256) vermiculate stripes are present on the ventral surface of head. A Light Sulphur Yellow (Color 93) gular spot is present on the center of the gular pouch. Ventral surfaces of the body, limbs, and the tail are mostly uniform Pale Buff (Color 1). Coloration of the ventral body is slightly yellowish toward the most anterior and lateral portions.

#### *Coloration of holotype in preservation*

Coloration and ornamentation patterns remain the same after preservation with the exception of the following: (1) Light Sulphur Yellow (Color 93) coloration of the gular spot, dorsolateral stripes, and irregular spots on the dorsal surface of the body fade into white, and (2) the remaining dark coloration of the dorsal body surface becomes slightly darker.

#### *Variation*

Morphometric and pholidosis variation of the type series is summarized in Table S8. Sexual dimorphism is evident in our current samples, in which males differ from females in both morphometric measurements and coloration. Specifically, males have relatively longer tails (TAL 202.0%–218.2% SVL in males versus 174.3%–199.7% in females) and relatively shorter trunks than females (TRL 44.0%–48.1% SVL in males versus 47.8%–56.9% in females). For ornamentations and coloration, males possess distinct coloration of dorsolateral stripes (Light Sulphur Yellow [Color 93] versus either indistinct [as in KIZ 028336] or in the same coloration as the True Cinnamon [Color 260] background of dorsum) and a larger and more distinct Light Sulphur Yellow (Color 93) gular spots (versus smaller and fainter).

Among females, one individual (KIZ 028336) possesses no transverse bands on dorsal head, no dorsolateral stripes, and indistinct Brunt Umber (Color 48) patches along the dorsal midline of body;



instead, the dorsal surface of its head is uniform Peach Red (Color 70), and this coloration continues posteriorly as a uniform, vertebral stripe until the base of the tail.

#### Etymology

The specific name, *qilin*, is derived from the Chinese name of the legendary beast (麒麟). According to Chinese mythology, Qilin is the son of the dragon, with a golden yellow body coloration, which matches the diagnostic gular color of the new species. We suggest its English common name as Qilin Mountain Dragon and Chinese common name as 麒麟龙蜥 (Pinyin: Qi Lin Long Xi).

#### Natural History and conservation

The new species inhabits mix forests along the upper Jinsha River Valley (Figure 13f). Although individuals were found in the forests, *D. qilin* sp. nov. was observed to be mostly terrestrial, foraging on the ground and basking on rock piles and bases of tree trunks. Individuals were observed sleeping on bushes (i.e., *Rumex hastatus*) at night. Lizard-eating snakes are common at the site (including *Elaphe carinata*, *Ptyas nigromarginata*, and *Sibynophis collaris*), which may be the main source of predation of the new species. Locals believe the meat of the new species has certain medical properties, and lizards were collected and dried as traditional medicine.

The distribution range of the species is the low-elevation valley below 3,300 m along the upper Jinsha River Valley, from the Cangjue Village of Shangri-La County to the areas approximately 13 km southeast of Benzilan Township. The estimated extent of occurrence is approximately 700 km<sup>2</sup> along the Jinsha River Valley. Most of the habitats overlapped with human inhabitations and major highways and are not covered by any existing natural reserves. Continuous expansions of agriculture and tourist infrastructure were observed between 2016 and 2019, which had led to serious habitat destructions of the species. According to IUCN criteria D2, we recommend listing the species as Vulnerable (VU).

## 4 | DISCUSSION

### 4.1 | Taxonomy of the *D. flaviceps* complex

Similar to previous studies, our results show that most members of the *D. flaviceps* complex are paraphyletic with respect to true *D. flaviceps* (Wang, Che, et al., 2019; Wang, Ren, Jiang, et al., 2019; Wang, Wu, Jiang, et al., 2019; Figures 1, 2). Furthermore, although species of the complex were confused with *D. flaviceps* historically, they are morphologically distinct from true *D. flaviceps* in pholidosis, morphometric, as well as coloration and ornamentation patterns (Figures 2–4). However, excluding the true *D. flaviceps*, members of the complex are indeed similar in terms of morphometric and pholidosis characters (Figures 3 and 4), and the most distinct diagnostic characters are usually coloration and ornamentation patterns (Figure 2). As coloration fades away after long-term preservation, the similar external morphology explains the previous taxonomic

confusion over these taxa. Our results further highlight the importance of coloration data in the taxonomy of agamid lizards.

Regarding the generic affiliation of recognized species, *D. iadinum* was described initially in the paraphyletic genus *Japalura* (i.e., *Japalura iadina*) based on morphological data, and it was thought to be most similar to *D. splendidum* (Wang et al., 2016; Xu & Zhang, 2011). Although it was transferred to the genus *Diploderma* later, such taxonomic change was based on morphological diagnosis only (Wang, Che, et al., 2019). Our phylogenetic results confirm the generic affiliation of the species in the genus *Diploderma*, supporting the previous morphological hypothesis. However, we show that *D. iadinum* is not closely related to either *D. flaviceps* or *D. splendidum* as morphological data suggested (Figure 2). Instead, *D. iadinum* is the sister taxon to all species of the second major clade of *Diploderma* that inhabit the HMR.

Similarly, *D. drukdaypo* was also described as a member of the paraphyletic genus *Japalura* based on morphological data only (i.e., *Japalura drukdaypo*, Wang, Jiang, Ren, et al., 2019). At the time, authors suggested that *J. drukdaypo* should belong to the Indochinese group of the paraphyletic genus *Japalura* sensu lato (which includes the genera *Diploderma* and *Pseudocolotes*; Wang, Che, et al., 2019), as it resembles *D. vela* (considered as *J. vela* at the time) in external morphology (Wang, Jiang, Ren, et al., 2019). Recent studies followed such conclusions and reassigned the species to the genus *Diploderma* based on morphological diagnosis (Denzer, Manthey, & Campbell, 2019; Wang, Ren, Jiang, et al., 2019). Our phylogenetic data show that *D. drukdaypo* indeed belongs to the genus *Diploderma*, and it is the sister of *D. vela* as morphological data suggested (Figure 2). Interestingly, although the uncorrected pairwise genetic distance of *ND2* is relatively small between *D. drukdaypo* and *D. vela* (2.4%–2.7%, Table 2), each species occupies a distinct section of the Mekong River at different elevations. Additionally, each species can be distinguished readily by non-overlapping morphological characters (i.e., relative limb length, tail length, and keel status of ventral body scales; Wang, Che, et al., 2019). It is likely that *D. drukdaypo* represents a recently diverged species that is adapted to higher-elevation habitats in the upper Mekong River Valley. Future population genetic and ecological studies are needed to gain a better understanding of gene flow and speciation mechanisms between *D. drukdaypo* and its sister species *D. vela*.

### 4.2 | Suspicious records of other Chinese congeners

Similar to *D. flaviceps*, other species of the genus *Diploderma* also possess multiple suspicious records in China that warrant future confirmation (Wang, Ren, Jiang, et al., 2019; Wang, Wu, Jiang, et al., 2019). For the records of *D. cf. splendidum* from southern Gansu and Shaanxi Province (no vouchered information mentioned; Yao & Gong, 2012; Zhao et al., 1999), not only do habitats of these regions differ from the rest of the confirmed range of *D. splendidum*, but also, if these records are valid, they support sympatric distributions for *D. splendidum* and *D. micangshanense* at the exact same sites. However, such sympatric distributions of congeners on mainland Asia have yet to be reported for any other

species, and the similar, confirmed cases of supposed sympatric distributions have now been shown to be the result of misidentification (Wang, Ren, Jiang, et al., 2019). Therefore, these records of *D. splendidum* remain highly questionable, and likely represent misidentifications of *D. micangshanense*. For the records of *D. cf. splendidum* in the Nu River (=Salween River) Valley in western Yunnan Province (vouchered numbers: KIZ 78II003, 78II0034, 78II0048, 78II0060, 78II0061, 78I066, 78I071, 78I078, 78I079, 730047-49, 730100, 730084, 730085, 730088; Zhao et al., 1999; unable to examine here due to political reasons), as they are isolated from the rest of the recognized range of *D. splendidum* by a known biogeographic barrier (i.e., Hengduan Mountains), they should also represent misidentification of congeners, which are most likely to be the recently described species, *D. slowinskii* (Rao et al., 2017). Future taxonomic studies are needed to confirm these suspect records and continue to clarify the distributions of *Diploderma* species in China.

### 4.3 | Diagnostic key to and revised distribution of the genus *Diploderma*

Despite being one of the most diverse agamid genera in Asia, the genus *Diploderma* still lacks an updated, comprehensive key (Pope, 1935; Smith, 1935; Wang, Che, et al., 2019; Wang, Jiang, Ren, et al., 2019; Wang, Jiang, Wang, et al., 2019; Wang, Ren, Jiang, et al., 2019; Wang, Wu, Jiang, et al., 2019; Zhao et al., 1999). With the addition of the six new species described here, a total of 31 species of *Diploderma* are now recognized (Wang, Che, et al., 2019; Wang, Jiang, Ren, et al., 2019; Wang, Ren, Jiang, et al., 2019; Wang, Wu, Jiang, et al., 2019), including *D. angustelinea*, *D. aorun*, *D. batangense*, *D. chapaense*, *D. brevicaudum*, *D. brevipes*, *D. drukdaypo*, *D. dymondi*, *D. fasciatum*, *D. flaviceps*, *D. flavilabre*, *D. grahami*, *D. hamptoni*, *D. iadinum*, *D. laeiventre*, *D. luei*, *D. makii*, *D. micangshanense*, *D. panchi*, *D. panlong*, *D. polygonatum*, *D. qilin*, *D. slowinskii*, *D. splendidum*, *D. swinhonis*, *D. swild*, *D. varcoea*, *D. vela*, *D. yulongense*, *D. yunnanense*, and *D. zhaoermii*.

To facilitate future taxonomic and systematic studies of this unique lizard radiation and make information more accessible for conservation and law enforcement agencies, we provide the first updated, comprehensive diagnostic key and revised distribution to all recognized members of the genus *Diploderma* (diagnostic key modified from Ota, [1989] and Zhao et al. [1999]; distribution data modified from Wang, Ren, Jiang, et al. [2019] and Manthey & Denzer [2012]).

**1a.** Single Light Pistachio (Color 101) hourglass-shaped, transverse ornamentation pattern present on mid dorsum in both sexes, no dorsolateral stripes or dorsolateral series of ornamentations in either sex-----  
-----*D. fasciatum* (China: Yunnan, Sichuan, Guizhou, Guangdong, Guangxi, Jiangxi, and Hunan; Vietnam: Lao Cai)

**1b.** No transverse hourglass-shaped pattern on mid dorsum, males always have dorsolateral stripes, dorsolateral series of spots, or multiple transverse bands on dorsal body-----**2**

**2a.** Tympanum exposed-----**3**  
**2b.** Tympanum concealed-----**7**  
**3a.** Transverse gular fold absent; dorsolateral stripes strongly jagged; oral cavity and tongue Light Orange Yellow (Color 77) to Light Chrome Orange (Color 76) in life; TAL <200% SVL-----  
-----*D. varcoea* (China: Yunnan and Guizhou)  
**3b.** Transverse gular fold present; dorsolateral stripes with smooth edges; TAL >200% SVL-----**4**  
**4a.** Nuchal crest scale tall, CL/HL >8%; enlarged scales scattered on ventral head and ventrolateral body; oral cavity and tongue Light Chrome Orange (Color 76) in life-----*D. swild* (China: Sichuan)  
**4b.** Nuchal crest scales low, CL/HL <8%; ventral head and ventrolateral scales of body homogeneous in size-----**5**  
**5a.** Conical scales on post-occipital head strongly developed, distinctively keeled, oriented backwards; suborbital scales with distinct black edges; lip stripes absent; oral cavity Light Flesh (Color 250) in life-----*D. slowinskii* (China: Yunnan)  
**5b.** Conical scales on post-occipital head less developed, oriented more straight upwards; suborbital scales without black edges; light-colored lip stripes present; oral cavity and tongue not light flesh color in life-----**6**  
**6a.** Tympana relatively small, TD 33.24–51.87%; oral cavity and tongue Light Chrome Orange (Color 76) in life; dorsolateral stripes Sulphur Yellow (Color 80) in males-----*D. panlong* (China: Sichuan)  
**6b.** Tympana relatively large, TD 49.39–61.15%; Oral cavity Spectrum Violet (Color 186) or Jet Black (Color 300) in life; dorsolateral stripes Chartreuse (Color 89) in males-----  
-----*D. dymondi* (China: Yunnan and Sichuan)  
**7a.** Transverse gular fold present-----**8**  
**7b.** Transverse gular fold absent-----**23**  
**8a.** Ventral scales smooth or feebly keeled-----**9**  
**8b.** Ventral scales distinctively keeled-----**10**  
**9a.** Middorsal scale count 57–59; nuchal crest scales well developed in males, raised on skin folds; tail long, TAL/SVL > 190% in males, > 168% in females; hind limbs long, HLL/SVL > 70% in males, > 64% in females; dorsolateral stripes smooth edged; gular spots present in both sexes, Light Chrome Orange (Color 76) in life-----  
-----*D. laeiventre* (China: Tibet)  
**9b.** Middorsal crest scale count <56; nuchal crest feebly developed without skin folds in males; tail short, TAL/SVL <155% in males, <144% in females; hind limbs short, HLL/SVL <64% in males, <62% in females; dorsolateral stripes strongly jagged; gular spots absent in both sexes-----*D. drukdaypo* (China: Tibet)  
**10a.** TAL/SVL ≤ 150%; Toe IV lamellae 16–20; middorsal crest scale counts 34–40-----*D. brevicaudum* (China: Yunnan)  
**10b.** TAL/SVL > 160%-----**11**  
**11a.** Transverse gular fold shallow, feeble-----**12**  
**11b.** Transverse gular fold deep, forming a distinct pouch across the throat-----**13**  
**12a.** Dorsolateral stripes parallel to vertebral line in males; suborbital scales without dark edges, forming single white lip-stripe on each side-----*D. splendidum* (China: Sichuan, Yunnan, Guizhou [?], Chongqing, and Hubei)

- 12b.** Dorsolateral stripes diagonally away from vertebral line toward posterior end in male; suborbital scales with dark edges, distinct white lip-stripe absent-----  
-----*D. hamptoni* (Myanmar: Mandalay)
- 13a.** Both males and females with well-developed skin folds under nuchal crest; modified, conical, post-rectal scales well developed, 3–8; dark radial stripes around eyes absent or faint; brownish, rhomb-shaped, hollow patterns with yellow centers along dorsal midline from neck to pelvis; dark, reticulated patterns on gular region; gular spots absent in both sexes-----  
-----*D. flaviceps* (China: Sichuan)
- 13b.** Skin folds under nuchal crest absent entirely or present in males only; either with no radial stripes around eyes but with distinct gular spots, or with distinct radial stripes around eyes with no gular spots; dark ornamentations on gular region not in dense reticulated pattern-----  
-----**14**
- 14a.** Dorsal background coloration Yellowish Spectrum Green (Color 128) to Emerald Green (Color 143) in males, Pale Greenish Yellow (Color 86) in females; dorsolateral stripes always present in males, sometimes in females, smooth-edged, same color as body background; females with Cinnamon (Color 255) cross-bands; gular spots present in both sexes, Caribbean Blue (Color 168) in live males, Medium Greenish Yellow (Color 88) in live females-----  
-----*D. iadinum* (China: Yunnan)
- 14b.** Dorsal background coloration not green in live males; dorsolateral stripes smooth or jagged-----  
-----**15**
- 15a.** TAL/SVL  $\leq 151\%$  in females; ventral head with faint mosaic Light Sulphur Yellow (Color 93) patterns in live females-----  
-----*D. panchi* (China: Sichuan)
- 15b.** TAL/SVL  $> 159\%$  in females; yellow mosaic patterns absent on ventral head in live females-----  
-----**16**
- 16a.** Dorsolateral stripes narrow in both sexes, feebly jagged; gular spot Spectrum Yellow (Color 79) or Dark Spectrum Yellow (Color 80) in life, always present in males, sometimes in females; nuchal and dorsal crests weakly developed, with feeble skin fold under nuchal crest only-----  
-----*D. angustelinea* (China: Sichuan)
- 16b.** Dorsolateral stripes wide and strongly jagged in males; nuchal and dorsal crests well developed, nuchal crest with much better developed skin fold-----  
-----**17**
- 17a.** Both nuchal and dorsal crests on continuous, sail-like skin folds in males; gular spot absent in both sexes; dorsolateral stripes Sulphur White (Color 96) or Pale Greenish White (Color 97) in males, Medium Chrome Orange (Color 75) in females -----  
-----*D. vela* (China: Yunnan and Tibet)
- 17b.** Vertebral crest discontinuous between nuchal and dorsal sections with a distinct gap; gular spots always present in males, absent or present in females; dorsolateral stripes not orange in females-----  
-----**18**
- 18a.** Head more robust, head depth mostly  $> 80\%$  head width; gular spots present in males only, light Sulphur Yellow (Color 93) in life, absent after preservation; ventrolateral light Sulphur Yellow (Color 93) in live males, white after preservation-----  
-----*D. qilin* (China: Yunnan)
- 18b.** Head more slender, head depth mostly  $< 80\%$  of head width; gular spots present in both sexes, greenish in color; ventrolateral body not Sulphur Yellow (Color 93) in life-----  
-----**19**
- 19a.** Tail short, TAL/SVL  $< 180\%$  in males,  $< 152\%$  in females; inner lips bright spectrum yellow in both sexes in life-----  
-----*D. flavilabre* (China: Sichuan and Tibet)
- 19b.** Tail long, TAL/SVL  $> 200\%$  in males,  $> 175\%$  in females; inner lips Smoky White (Color 261) to Light Flesh Color (Color 250)-----  
-----**20**
- 20a.** Medium or pale greenish yellow patch present on each side of ventrolateral body; gular spots present in both sexes, Chartreuse (89) or Opaline Green (Color 106) in life, dark blue or black after preservation; radial stripes below eyes absent; distinct white subocular lip stripe present-----  
-----*D. yulongense* (China: Yunnan)
- 20b.** No distinct ornamentation or coloration on ventrolateral body; dark radial stripes present below eyes; distinct white lip stripe absent below eyes-----  
-----**21**
- 21a.** Body size large, SVL up to 81 mm; gular spots present in males only, large, extending to anterior chest, Light Yellow-Green (Color 100) in life, absent after preservation; transverse streaks on dorsal head and radial stripes around eyes Smoky Gray (Color 267) or Olive Gray (Color 265)-----  
-----*D. zhaermii* (China: Sichuan)
- 21b.** Body size relative small, SVL up to 65 mm; gular spots present in both sexes (rarely absent in females), Pale Emerald Green (Color 141), Light Turquoise Green (Color 146), or Pale Cyan (Color 157) in life, dark bluish or black after preservation; dorsal head transverse streaks and radial stripes around eyes Jet Black (Color 300) or Raw (Color 280)-----  
-----**22**
- 22a.** Tail relatively long, TAL/SVL 212–221% in males; vertebral crest skin folds strongly developed in males; stronger contrast of dorsal dark ornamentation-----  
-----*D. aorun* (China: Yunnan and Sichuan)
- 22b.** Tail relatively short, TAL/SVL 188–206% in males; vertebral crest less developed in males; less contrast of dorsal dark ornamentation-----  
-----*D. batangense* (China: Sichuan and Tibet)
- 23a.** HW/HL  $> 64\%$ -----  
-----**24**
- 23b.** HW/HL  $< 64\%$ -----  
-----**27**
- 24a.** Tail short, TAL 164.3% SVL; granular scales present on head and body-----  
-----*D. grahami* (China: Sichuan)
- 24b.** Tail long, TAL  $> 190\%$  SVL; granular scales absent on head and body-----  
-----**25**
- 25a.** Nuchal crest scales in approximately same shape as dorsal crest; ventrolateral body scales homogeneous in sizes; gular spots absent in both sexes; oral cavity and tongue Light Flesh Color (Color 250) in life-----  
-----*D. micangshanense* (China: Sichuan, Gansu, Shanxi, Shaanxi, Hubei, and Henan)
- 25b.** Nuchal crest scales distinctively differentiated from dorsal in both sexes, much taller and wider; ventrolateral body scales heterogeneous in sizes; yellow gular spots present in both sexes; oral cavity and tongue Light Orange Yellow (Color 77) in life-----  
-----**26**
- 26a.** Middorsal scale counts 39–46; tail relatively long, TAL/SVL  $> 250\%$  in males,  $> 237\%$  in females-----  
-----*D. yunnanense* (China: Yunnan; Myanmar: Kachin; Thailand: Chiang Mai)

- 26b. Middorsal scale counts 34–42; tail relatively short, TAL/SVL < 250% in males, < 228% for females-----  
-----*D. chapaense* (China: Yunnan; Vietnam: Lao Cai)
- 27a. Enlarged scales of dorsum in transverse or V-shaped rows; body coloration Tawny Olive (Color 17) to Olive Horn (Color 16) (sometimes Pistachio (Color 102) for individuals from Eastern Taiwan); white circular patterns present on ventral head; no distinct gular spot-----*D. swinhonis* (China: Taiwan)
- 27b. Enlarged scales of dorsum not in transverse or V-shaped rows-----28
- 28a. Multiple Opaline Green (Color 106) to Light Emerald Green (Color 141) transverse bands present on dorsal body in males; males with distinct Spectrum Yellow (Color 79) gular spots; oral cavity and tongue Light Flesh (Color 250) or slightly yellowish-----  
-----*D. makii* (China: Taiwan)
- 28b. No transverse bands absent on dorsal body in males-----29
- 29a. Scales of dorsal snout smooth; dorsolateral series of chevron- or diamond-shaped patterns present on lateral dorsum; oral cavity and tongue Light Chrome Orange (Color 76)-----  
-----*D. luei* (China: Taiwan)
- 29b. Scales of dorsal snout strongly keeled; chevron- or diamond-shaped patterns absent on lateral dorsum-----30
- 30a. Oral cavity Light Neutral Gray (Color 297); gular spots absent in males-----*D. brevipes* (China: Taiwan)
- 30b. Oral cavity lighter colored, Light Flesh (Color 250), Light Orange Yellow (Color 77), or Beige (Color 254); prominent gular spots present in males-----  
-----*D. polygonatum* (China: Taiwan; Japan: Okinawa)

#### 4.4 | Challenges to *Diploderma* conservation in China

Although recent discoveries of endemic species of *Diploderma* in Southwest China highlight the incredible biodiversity of this region, such discoveries also create major challenges for wildlife conservation and legislation in the country. Because the Endangered Species List of China (ESLC) has changed little since 1988, the protection status of most listed species has not been re-evaluated or modified in decades. New species described since 1988 have not been added to the protection list, despite their endangered status and urgent conservation threats (Hou et al., 2014; Yang & Chan, 2015; Jiang et al., 2016). Such problems are particularly true for *Diploderma* diversity in China. None of the previously recognized species are listed as nationally protected in the current ESLC (Wang, Jiang, Ren, et al., 2019). Although the government is currently updating the ESLC, and despite the fact that the new list might give protection status to many of the recognized species (i.e., *D. iadinum*, *D. splendidum*, *D. slowinskii*, *D. varcoae*, *D. vela*, *D. yulongense*, *D. yunnanense*, and *D. zhaermii*; personal communication), new species that are more recently described will still be left unprotected by the new law (i.e.,

*D. drukdaypo*, *D. swild*, and the six new species described here), until the next updating cycle in five years. Because habitat destruction and illegal harvesting for pet trade are the two top threats for the genus, and since the ranges of most threatened species are not covered by existing nature reserves or national parks, such lack of species protection status may lead to irreversible habitat destruction and severe population declines during this 5-year period.

With the high level of cryptic diversity and the rapidly changing taxonomy of the Chinese herpetofauna (Wang et al., 2020), as well as the fixed update schedule for the ESLC, we recommend taking a more general approach to endangered species listing in China. Instead of listing individual species that may be subject to taxonomic changes and ignore any cryptic diversity, we recommend listing major groups (i.e., at the unit of genus) under protection, and extend the protection status to new species that are recently split from previously protected species, at least until the next re-assessment effort. We call for systematic, objective updates to the conservation assessments of the Chinese herpetofauna. As for *Diploderma* diversity in China, to avoid the complications and confusion arising from taxonomic changes and descriptions of new taxa, we recommend the following: (a) listing *D. iadinum* as Class I protected under the ESLC based on current data, due to its threaten status and the urgent conservation needs; (b) listing all members of the genus *Diploderma*, with the exception of *D. fasciatum*, *D. chapaense*, *D. micangshanense*, *D. yunnanense*, and *D. zhaermii* as Class II protected under the ESLC, due to the continuous and increasing threats from habitat destruction across their ranges, lack of protection from existing natural reserves, and existing and apparent illegal pet trade.

Lastly, for the habitats covered by protected areas in the HMR, we recommend these existing reserves (i.e., Baima Snow Mountain Nature Reserve and The Three Parallel Rivers of Yunnan Protected Areas) increase conservation efforts for *Diploderma* species in the peripheral, low-elevation regions and increase law enforcements for habitat destructions such as illegal mining. For habitats that are not already covered by existing protected areas, given the large extents of existing human settlements and infrastructures in the valleys, we recommend establishing micro-reserves to restore microhabitats in the remaining non-disturbed regions, and we call for stricter environmental evaluations for any future developments in these regions.

#### ACKNOWLEDGEMENTS

Collection of all animals used for this present study abides by the Wildlife Protection Act of PR China. Research approvals were issued by the Kunming Institute of Zoology, Chinese Academy of Sciences (BBCJ-2014-001). We followed IACUC protocols (IACUC R13-11) and protocols of the Animal Care and Ethics Committee of the KIZ, CAS for the proper treatments of animals in the field. We thank Mrs. H. Xu, K. Xu, K. Lei, H. Yu, M. Fu, J. Yang, G. Nima, C. Zhongyang, L. He, B. Miao, D. Zou, and Dr. F. Yan for their assistances in the field; Dr. V. Deepak for his help in examining specimens and taking photographs at NHM; Mr. C. Weinert for providing photographs of the live female individual of *D. yulongense*; Dr. J. Li (CIB), Drs. R. Brown and L. Welton (KU), Mr. W.

Addison (NMNH), Mr. J. Vindum and Ms. L. Scheinberg (CAS), and Drs. J. Hanken and J. Losos (MCZ) for their support in allowing us to examine specimens or facilitate specimen loans; and Drs. H. Lanier, L. Weider, R. Lupia, and K. Marske (OU) for their helpful feedback on the manuscript. This research was supported by the Second Tibetan Plateau Scientific Expedition and Research (STEP) program (2019QZKK0501), the National Key Research and Development Program of China (2017YFC0505202), the Strategic Priority Research Program of Chinese Academy of Sciences (XDA19050303), and the Animal Branch of the Germplasm Bank of Wild Species of CAS (the Large Research Infrastructure Funding) to JC, NSF IOS 1353683 and DEB 1657648 to CDS, NSF GRFP 2017216966 and EAPSI 1714006 to KW, and the Biodiversity Survey and Assessment Project of the Ministry of Ecology and Environment (2019HJ2096001006) to JJQ and FX.

#### AUTHOR CONTRIBUTIONS

The study was conceived and designed by KW, JC, and CDS; field-work was conducted by KW, JR, JW, KJ, FX, and PZ; data collected by JJ, SH, and KW; data analyzed and figures made by KW and CDS; manuscript written by KW, CDS, and JC, with input from all remaining authors; and manuscript revised by KW, JR, CDS, and JC.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Specimens of recognized species of the genus *Diploderma* examined in this study.

**Table S2.** Subsets of specimens that were measured for morphometric analyses.

**Table S3.** Subsets of specimens used for pholidosis analyses.

**Table S4.** Uncorrected pairwise genetic distances among members of the *Diploderma flaviceps* complex and other closely-related congeners based on ND2 coding region (1,032 bp). All numbers are in %.

**Table S5.** Summary Statistics of the PCA analyses of the pholidosis characters among selected members of the *Diploderma flaviceps* complex.

**Table S6.** Summary Statistics of the PCA analyses of the morphometric characters of males among selected members of the *Diploderma flaviceps* complex.

**Table S7.** Summary Statistics of the PCA analyses of the morphometric characters of females among selected members of the *Diploderma flaviceps* complex.

**Table S8.** Detailed morphological measurements and pholidosis characters of majority of the type specimens of the six new species described.

**How to cite this article:** Wang K, Ren J, Wu J, et al. Systematic revision of mountain dragons (Reptilia: Agamidae: *Diploderma*) in China, with descriptions of six new species and discussion on their conservation. *J Zool Syst Evol Res*. 2020;00:1–39. <https://doi.org/10.1111/jzs.12414>

## APPENDIX 1.

Genetic sequence data used for the present study. The accession numbers that are in bold indicate sequences generated in this present study, where the remaining ones are downloaded from GenBank. “–” indicates missing data. Museum abbreviations include CAS = California Academy of Sciences, USA; MCZ = Museum of Comparative Zoology, USA; KIZ = Kunming Institute of Zoology, Chinese Academy of Sciences, China; TNHC = Texas Memorial Museum, USA; WK-JK = Mr. Kai Wang's personal collection; and ZMMU = Zoological Museum of Lomonosov Moscow State University, Russia.

Vouchered Number	Species	Locality	GenBank Accession Number			
			ND2	BDNF	CMOS	R35
KIZ 029704	<i>Diploderma angustelina</i>	Muli, Sichuan, China	MT577930	MT578009	MT659049	MT659093
KIZ 029705	<i>D. angustelina</i>	Muli, Sichuan, China	MT577924	MT577998	MT659044	MT659087
KIZ 029708	<i>D. angustelina</i>	Muli, Sichuan, China	MT577931	MT577993	MT659050	MT659094
KIZ 029710	<i>D. angustelina</i>	Muli, Sichuan, China	MT577927	MT578005	–	MT659090
KIZ 032488	<i>D. angustelina</i>	Muli, Sichuan, China	MT577925	MT578006	MT659045	MT659088
KIZ 032489	<i>D. angustelina</i>	Muli, Sichuan, China	MT577926	MT577994	MT659046	MT659089
KIZ 032490	<i>D. angustelina</i>	Muli, Sichuan, China	MT577928	MT578000	MT659047	MT659091
KIZ 032491	<i>D. angustelina</i>	Muli, Sichuan, China	MT577929	MT577992	MT659048	MT659092
KIZ 032733	<i>D. aorun</i>	Benzilan, Yunnan, China	MT577938	MT577964	MT659052	MT659096
KIZ 032734	<i>D. aorun</i>	Benzilan, Yunnan, China	MT577939	MT577990	MT659053	MT659097
KIZ 032735	<i>D. aorun</i>	Benzilan, Yunnan, China	MT577937	MT577989	–	MT659095
KIZ 032736	<i>D. aorun</i>	Benzilan, Yunnan, China	MT577936	–	MT659051	–
KIZ 032737	<i>D. aorun</i>	Benzilan, Yunnan, China	MT577940	MT577977	MT659054	MT659098
KIZ 019278	<i>D. batangense</i>	Zhubalong, Markam, Tibet, China	MT577932	–	–	–
KIZ 019279	<i>D. batangense</i>	Zhubalong, Markam, Tibet, China	MT577933	–	–	–
KIZ 019281	<i>D. batangensis</i>	Batang, Sichuan, China	MT577934	–	–	–
KIZ 19314	<i>D. batangensis</i>	Zhubalong, Markam, Tibet, China	MT577935	MT577991	–	–
KIZ 040147	<i>D. dymondi</i>	Panzhuhua, Sichuan, China	MT577899	–	–	–
KIZ 040148	<i>D. dymondi</i>	Panzhuhua, Sichuan, China	MT577900	–	–	–
KIZ 040149	<i>D. dymondi</i>	Panzhuhua, Sichuan, China	MT577901	–	–	–
KIZ 019575	<i>D. flaviceps</i>	Kangding, Sichuan, China	MT577896	MT577971	MT659061	MT659107
KIZ 019576	<i>D. flaviceps</i>	Kangding, Sichuan, China	MT577897	MT577968	MT659062	MT659108
KIZ 019577	<i>D. flaviceps</i>	Kangding, Sichuan, China	MT577895	MT577970	–	MT659106
KIZ 019578	<i>D. flaviceps</i>	Kangding, Sichuan, China	MT577894	MT577969	MT659060	MT659105
KIZ 019579	<i>D. flaviceps</i>	Kangding, Sichuan, China	MT577898	MT577967	MT659063	MT659109
KIZ 032692	<i>D. flavilabre</i>	Baiyu, Sichuan, China	MT577916	MT578002	MT659037	MT659079
KIZ 032694	<i>D. flavilabre</i>	Baiyu, Sichuan, China	MT577917	MT578001	MT659038	MT659080
KIZ 032695	<i>D. flavilabre</i>	Baiyu, Sichuan, China	MT577918	MT578003	MT659039	MT659081
KIZ 032696	<i>D. flavilabre</i>	Baiyu, Sichuan, China	MT577919	MT578004	MT659040	MT659082
KIZ 032697	<i>D. flavilabre</i>	Baiyu, Sichuan, China	MT577915	MT578007	MT659036	MT659078
KIZ 032698	<i>D. flavilabre</i>	Baiyu, Sichuan, China	MT577920	MT577999	MT659041	MT659083
KIZ 027697	<i>D. iadinum</i>	Degong Village, Yunling, Deqin, Yunnan, China	MT577956	MT577987	MT659034	MT659076

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## APPENDIX I (Continued)

Vouchered Number	Species	Locality	GenBank Accession Number			
			ND2	BDNF	CMOS	R35
KIZ 027702	<i>D. iadinum</i>	Degong Village, Yunling, Deqin, Yunnan, China	MT577957	MT577988	MT659035	MT659077
KIZ 027706	<i>D. iadinum</i>	Degong Village, Yunling, Deqin, Yunnan, China	MT577955	MT577986	MT659033	MT659075
KIZ 027691	<i>D. laeviventre</i>	Basu, Markam, Tibet, China	MT577892	MT577965	MT659031	MT659073
KIZ 027692	<i>D. laeviventre</i>	Basu, Markam, Tibet, China	MT577893	MT577966	MT659032	MT659074
KIZ 032715	<i>D. panchi</i>	Yajiang, Sichuan, China	MT577946	MT577980	MT659056	MT659100
KIZ 032716	<i>D. panchi</i>	Yajiang, Sichuan, China	MT577944	MT577982	MT659055	MT659099
KIZ 032717	<i>D. panchi</i>	Yajiang, Sichuan, China	MT577947	MT577981	MT659057	MT659101
KIZ 032729	<i>D. panchi</i>	Yajiang, Sichuan, China	MT577945	MT577983	-	-
KIZ 040136	<i>D. panlong</i>	Miansha, Liangshan, Sichuan, China	MT577906	-	-	-
KIZ 040138	<i>D. panlong</i>	Miansha, Liangshan, Sichuan, China	MT577907	-	-	-
KIZ 040139	<i>D. panlong</i>	Miansha, Liangshan, Sichuan, China	MT577908	-	-	-
KIZ 040140	<i>D. panlong</i>	Miansha, Liangshan, Sichuan, China	MT577905	-	-	-
KIZ 040141	<i>D. panlong</i>	Miansha, Liangshan, Sichuan, China	MT577909	-	-	-
KIZ 040143	<i>D. panlong</i>	Miansha, Liangshan, Sichuan, China	MT577904	-	-	-
KIZ 027543	<i>D. slowinskii</i>	Fugong, Gongshan, Yunnan, China	MT577910	MT577958	MT659027	MT659069
KIZ 027544	<i>D. slowinskii</i>	Fugong, Gongshan, Yunnan, China	MT577911	MT577960	MT659028	MT659070
KIZ 027572	<i>D. slowinskii</i>	Qiunatong, Gongshan, Yunnan, China	MT577912	MT577959	MT659029	MT659071
KIZ 027573	<i>D. slowinskii</i>	Qiunatong, Gongshan, Yunnan, China	MT577913	MT577961	MT659030	MT659072
KIZ 034893	<i>D. swild</i>	Panzhuhua, Sichuan, China	MN266297	MT577972	MT659064	MT659111
KIZ 034894	<i>D. swild</i>	Panzhuhua, Sichuan, China	MN266300	MT577976	-	MT659114
KIZ 034895	<i>D. swild</i>	Panzhuhua, Sichuan, China	MN266298	MT577973	MT659065	MT659112
KIZ 034914	<i>D. swild</i>	Panzhuhua, Sichuan, China	MN266299	MT577975	MT659066	MT659113
KIZ 034915	<i>D. swild</i>	Panzhuhua, Sichuan, China	MN266301	MT577974	MT659067	MT659115
KIZ 029711	<i>D. varcoae</i>	Dali, Yunnan, China	MT577902	MT577962	MT659068	MT659116
KIZ 027672	<i>D. vela</i>	Tongsha, Markam, Tibet, China	MT577949	MT578011	MT659059	MT659104
KIZ 027673	<i>D. vela</i>	Tongsha, Markam, Tibet, China	MT577948	MT578010	MT659058	MT659103
KIZ 028291	<i>D. yulongense</i>	Middle Hutiaoxia, Shangri-La, Yunnan, China	MT577921	MT577979	-	MT659086

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## APPENDIX I (Continued)

Vouchered Number	Species	Locality	GenBank Accession Number			
			ND2	BDNF	CMOS	R35
KIZ 028292	<i>D. yulongense</i>	Middle Hutiaoxia, Shangri-La, Yunnan, China	MT577922	MT577978	MT659043	MT659085
KIZ 028300	<i>D. yulongense</i>	Baishuitai, Shangri-La, Yunnan, China	MT577923	MT578008	MT659042	MT659084
KIZ 040193	<i>D. yunnanense</i>	Yingjiang, Yunnan, China	MT577914	-	-	-
KIZ 027627	<i>D. drukdaypo</i>	Jinduo, Chamdo, Tibet, China	MT577950	MT578013	-	-
KIZ 027628	<i>D. drukdaypo</i>	Zhuka, Chamdo, Tibet, China	MT577592	MT578012	-	-
KIZ 027629	<i>D. drukdaypo</i>	Zhuka, Chamdo, Tibet, China	MT577593	-	-	-
KIZ 016486	<i>D. drukdaypo</i>	Chamdo City, Tibet, China	MT577951	-	-	MT659102
KIZ 027630	<i>D. drukdaypo</i>	Zhuka, Chamdo, Tibet, China	MT577954	MT578014	-	-
KIZ 028332	<i>D. qilin</i>	Balong, Deqin, Yunnan, China	MT577941	MT577995	-	-
KIZ 028335	<i>D. qilin</i>	Balong, Deqin, Yunnan, China	MT577943	MT577997	-	-
KIZ 028333	<i>D. qilin</i>	Balong, Deqin, Yunnan, China	MT577942	MT577996	-	-
WK-JK 011	<i>D. varcoae</i>	Yuxi, Yunnan, China	MT577903	MT577963	-	-
KIZ 034923	<i>D. chapaense</i>	Lvchun, Honghe, Yunnan, China	MG214263	MK001526	MK001494	MK001474
KIZ 019276	<i>D. batangense</i>	Batang, Sichuan, China	MK001413	-	-	-
KIZ 09404	<i>D. batangense</i>	Zhubalong, Tibet, China	MK001412	-	-	-
NMNS 19607	<i>D. brevipes</i>	Taiwan, China	MK001429	MK001540	MK001506	MK001464
NMNS 19608	<i>D. brevipes</i>	Taiwan, China	MK001430	MK001541	MK001507	MK001465
KIZ 040145	<i>D. chapaense</i>	Dali, Yunnan, China	MK578667	-	-	-
KIZ 046954	<i>D. chapaense</i>	Jingdong, Yunnan, China	MK578660	-	-	MT659117
KIZ 046970	<i>D. chapaense</i>	Jingdong, Yunnan, China	MK578659	-	-	MT659118
KIZ 047085	<i>D. chapaense</i>	Jingdong, Yunnan, China	MK578661	-	-	MT659119
KIZ 034921	<i>D. chapaense</i>	Lvchun, Yunnan, China	MG214264	MK001525	MK001502	MK001475
ZMMUNAP-01911	<i>D. chapaense</i>	Chapa, Vietnam	MG214262	-	-	-
KIZ 040639	<i>D. dymondi</i>	Dongchuan, Yunnan, China	MK001422	MK001545	MK001513	MK001477
KIZ 040640	<i>D. dymondi</i>	Dongchuan, Yunnan, China	MK001423	MK001546	MK001514	MK001478
KIZ 01851	<i>D. flaviceps</i>	Luding, Sichuan, China	MK001416	MK001528	MK001512	MK001473
KIZ 01852	<i>D. flaviceps</i>	Luding, Sichuan, China	MK001417	MK001544	MK001505	MK001472
KIZ 014037	<i>D. laeiventre</i>	Basu, Markam, Tibet, China	MK001407	MK001529	-	MK001466
NMNS 19604	<i>D. luei</i>	Taiwan, China	MK001433	MK001532	MK001510	MK001462
NMNS 19605	<i>D. luei</i>	Taiwan, China	MK001434	MK001533	MK001511	MK001463
NMNS19609	<i>D. makii</i>	Taiwan, China	MK001431	MK001536	MK001508	MK001460
NMNS19610	<i>D. makii</i>	Taiwan, China	MK001432	MK001537	MK001509	MK001461
KIZ 023231	<i>D. micangshanense</i>	Xixia, Henan, China	MK578664	-	-	-

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## APPENDIX I (Continued)

Vouchered Number	Species	Locality	GenBank Accession Number			
			ND2	BDNF	CMOS	R35
KIZ 032801	<i>D. micangshanense</i>	Shiyan, Hubei, China	MK578665	MT577984	-	MT659110
KIZ 032802	<i>D. micangshanense</i>	Shiyan, Hubei, China	MK578666	MT577985	-	-
KIZ 06850	<i>D. micangshanense</i>	Longnan, Gansu, China	MK001424	MK001559	-	MK001452
WK-JK 037	<i>D. micangshanense</i>	Wenxian, Gansu, China	MK578662	-	-	-
WK-JK 038	<i>D. micangshanense</i>	Wenxian, Gansu, China	MK578663	-	-	-
NMNS 19598	<i>D. polygonatum</i>	Taiwan, China	MK001427	MK001538	MK001515	MK001458
NMNS 19599	<i>D. polygonatum</i>	Taiwan, China	MK001428	MK001539	MK001516	MK001459
CAS 214906	<i>D. slowinskii</i>	Gongshan, Yunnan, China	MK001405	-	-	-
CAS 214954	<i>D. slowinskii</i>	Gongshan, Yunnan, China	MK001406	-	-	-
KIZ 015973	<i>D. splendidum</i>	Yichang, Hubei, China	MK001418	MK001522	MK001492	MK001476
NMNS 19592	<i>D. swinhonis</i>	Taiwan, China	MK001419	MK001534	MK001495	MK001456
NMNS 19593	<i>D. swinhonis</i>	Taiwan, China	MK001420	MK001535	MK001496	MK001457
KIZ 026132	<i>D. varcoae</i>	Mengzi, Honghe, Yunnan, China	MK001421	MK001523	MK001493	MK001471
KIZ 034925	<i>D. vela</i>	Quzika, Markam, Tibet, China	MK001415	MK001531	MK001497	MK001449
KIZ 019299	<i>D. vela</i>	Quzika, Markam, Tibet, China	MK001414	MK001530	MK001499	MK001448
KIZ 09399	<i>D. yulongense</i>	Xianggelila, Yunnan, China	MK001410	MK001542	MK001498	MK001450
KIZ43196	<i>D. yulongense</i>	Xianggelila, Yunnan, China	MK001411	MK001543	-	MK001451
KIZ 040193	<i>D. yunnanense</i>	Yingjiang, Yunnan, China	MK578658	-	-	-
CAS 242271	<i>D. yunnanense</i>	Baoshan, Yunnan, China	MK001408	MK001527	MK001517	MK001469
CAS 242183	<i>D. yunnanense</i>	Baoshan, Yunnan, China	MK001409	MK001524	MK001518	MK001470
KIZ 019564	<i>D. zhaoermii</i>	Wenchuan, Sichuan, China	MK001425	MK001547	MK001500	MK001467
KIZ 019565	<i>D. zhaoermii</i>	Wenchuan, Sichuan, China	MK001426	MK001548	MK001501	MK001468
KIZ 015975	<i>Pseudocalotes kakhienensis</i>	Gongshan, Yunnan, China	MK001435	MK001549	MK001489	MK001447
CAS 241966	<i>P. kingdonwardi</i>	Dulongjiang, Yunnan, China	MK001436	MK001550	MK001503	MK001453
CAS 242628	<i>P. kingdonwardi</i>	Dulongjiang, Yunnan, China	MK001437	MK001551	MK001504	MK001454
MVZ 216622	<i>D. zhaoermii</i>	Wenchuan, Sichuan, China	AF128500	-	-	-
MVZ 224106	<i>P. brevipes</i>	Vinh Phuc, Vietnam	AF128499.1	-	-	-
TNHC 58040	<i>P. flavigula</i>	Perak, Malaysia	AF128503.1	-	-	-
CAS 194476	<i>D. splendidum</i>	Yaan, Sichuan, China	AF128501	-	-	-
-	<i>Acanthosaura lepidogaster</i>	-	AF128499	MK001552	MK001490	MK001455
CAS 223063	<i>Calotes emma</i>	-	DQ289460	-	-	MK792530