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SYSTEMATICS AND EVOLUTION OF MOUNTAIN DRAGONS OF THE GENUS

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Abstract

To better study and conserve the biodiversity around us, one must have an accurate understanding of their taxonomy. Problematic taxonomy or lack of taxonomic knowledge not only mask signals of unique evolutionary stories, but they can also lead to misleading conservation assessments, resulting in detrimental impacts on endangered species. Being one of the most diverse and unique groups of vertebrates, non-avian reptiles constitute a major portion of the world's biodiversity. Compared to megafauna groups such as birds and mammals, non-avian reptiles are the least studied, and their taxonomy is still far from stable. Such lack of taxonomic knowledge is most evident in the global biodiversity hot spots with a complex geological history, including the Hengduan Mountain Region (HMR) of southwest China. Among the reptilian species of Southwest China, Mountain Dragons of the genus *Diploderma* are of particular research interests: a rich cryptic diversity that remains undescribed in the genus, and this major agamid radiation shows a great potential to tackle the outstanding debates on the complex biogeographic patterns in the HMR.

For Chapter 2, I conducted the first comprehensive, integrative taxonomic study of the genus *Diploderma*, using a multi-locus genetic data and morphological data from densely sampled populations across southwest China. My results reveal that the previously identified *D. flaviceps* complex in HMR consists of six unidentified lineages, all of which are paraphyletic to true *D. flaviceps*. Each of the six lineages is also deeply diverged and morphologically distinct from each other and from all recognized species, showing a 5–15% uncorrected genetic divergence on mitochondrial gene *ND2* and a suite of morphological characteristics, particularly gular coloration. Therefore, adapting the evolutionary species concept, I describe the six lineages of the *D. flaviceps* complex as six new species. Based on my conservation assessments using the

International Union of Conservation of Nature (IUCN) criteria, four of the six new species are considered as Vulnerable (VU) due to habitat destruction, and two are considered Data Deficient (DD). I also discuss the challenges that unstable taxonomy poses on the conservation legislation of China and call for conservation attention of species of the genus *Diploderma*.

Building on the results from Chapter 2, I further examine the evolutionary and biogeographic history of the genus in the Hengduan Mountain Region (HMR) in my third chapter. Bayesian analyses show that the genus *Diploderma* consists of two major clades, and their distributions correspond to the paleo-Red River and paleo-Yangtze River Drainages, respectively, which can be delimited by a botanic biogeographic line, Tanaka-Kaiyong Line (TKL), near perfectly. These results support the TKL as a general biogeographic line and support the previously speculated link between TKL and drainage reorganization. Dated phylogeny of Acrodont lizards placed the divergence time between the two major clades of *Diploderma* in the late Oligocene/early Miocene at around 24 million years ago (Ma), which is consistent with the hypothesized timing of paleo-drainage capture and the timing for the active period of major tectonic faults in the region. These aligned timings further confirm the previously speculated links among biogeographic lines, drainage reorganization, and tectonic faults. In addition, species from the Salween River valley forms the only monophyletic drainage-wide species assemblage, which supports another biogeographic line, Mekong-Salween Divide, as an effective zoogeographic barrier. Model tests using BioGeoBEARS support the paleo-connections between paleo-Jinsha, paleo-Mekong, paleo-Yalong, and paleo-Red Rivers, although the connection between Salween and paleo-Red River drainages remain questionable. Ancestral range reconstruction using BioGeoBEARS shows that the genus *Diploderma* originated in the southern region at low elevation, and species underwent northward dispersals along major rivers into the HMR. The

upper reaches of all major rivers except Salween were colonized from multiple cross-valley dispersal events in the late Miocene through Pliocene, which revealed the possibilities of novel river capture events in northern HMR. Finally, the ancestral state reconstruction shows that the most recent common ancestor of *Diploderma* was arboreal, and subsequent northward dispersal along river valleys fueled the multiple independent evolutions of the terrestrial ecotype.

Lastly, for Chapter 4, I assess the history, contemporary extent, taxonomic and regional preferences, and potential impacts of China's herpetofauna pet trade, using data from four major sources: 20 years of international trade records from the Convention on International Trade in Endangered Species (CITES) and the Law Enforcement Information System of the United States Fish and Wildlife Service (LEMIS) from 2000–2019, online surveys of Chinese social media (WeChat) and online forums for up to two years, online questionnaires of 2,264 herpetoculturists across China, and an online search of confiscation records from 2008 to 2020. Results show that herpetofauna trade in China has a long history tracing back to 1975, and the contemporary herpetofauna pet trade of China is at an exceptionally large scale, with China being both a major consumer and a major supplier. China's trade volume is biased taxonomically, concentrating on a small subset of common species, and the trade shows distinct preferences on species origin and taxonomic groups, biasing for exotic Testudines and native Sauria species in its consumption and supply trade, respectively. Additionally, China's trade also displays a distinct regional pattern among major political regions of China, with Mainland China and Hong Kong being both the main importers and exporters. For legality, a high percentage of recorded exotic CITES species in China's trade does not have legal import records, and a large volume of species was trafficked into and out of China through Hong Kong. The extent of contemporary herpetofauna pet trade by China is overlooked and underestimated, and the resulting lack of effective regulation has led to

major conservation concerns, including high risk of exotic invasion and high exploitation pressures on CITES I endangered species, China's native species in general, and all Testudines species. Based on the results, I provide specific recommendations to the regulatory and law enforcement agencies.

Chapter 1: General Introduction

The interactions between the complex landscapes and the evolution of organisms have always been a hot topic in ecology and evolutionary biology (Thompson 1999; Urban 2011). On the one hand, heterogeneous spatial environments create diverse ecological niches, which facilitate niche partitioning and natural selection (Rainey & Travisano 1998; Rundell et al. 2009). On the other hand, environmental heterogeneity through time also generates multiplex distribution scenarios among species, which lead to differential contacts among populations through time, promoting diversifications (Wake 2001; Secondi et al. 2006; Qiao et al. 2018).

The Hengduan Mountain Region (HMR) in Southwest China represents one of the most complex landscapes in the world (Li 1987, 1989). Adjacent to the Tibetan Plateau, it was the result of the continental collision between India and Euroasia (Yang et al. 1982). Not only does the HMR comprise a heterogeneous landscape today, including the characteristic parallel ridge-gorge system across a sharp transition of ecotones, but it also went through dramatic topographic changes historically (Chen 1992, 1996). Coupling such complex topographies and histories, the HMR also represents a global biodiversity hotspot, harboring a high number of endemic taxa (Tang et al. 2006; Mittermeier et al. 2011). This unique combination of heterogeneous environment, complex geological history, and rich biodiversity of the HMR has led to the discoveries of fascinating biogeographic patterns (He & Jiang 2014), some of which are still actively debated today. In particular, the drainage evolution of the paleo-Red River system and the two major biogeographic lines, namely the Tanaka Kaiyong Line and Mekong Salween Divide, are the most debated ones, with great controversies on their formation time, effectiveness as biogeographic barriers, and the formation mechanisms (Clark et al. 2004; Ye et al. 2017; Zhang et al. 2019).

Among the endemic organisms of the HMR, Mountain Dragons of the genus *Diploderma* show a great potential in tackling these two actively debated biogeographic phenomena. Being one of the most diverse agamid genera in Asia, *Diploderma* represent a unique agamid radiation of 25 recognized species, in which 19 of them are endemic to the HMR (Wang et al. 2019c). In addition to the rich diversity, distributions of the congeners in the HMR are closely associated with the river topographies, displaying a unique combination of parapatric distribution along the same river valley, and allopatric distribution between river valleys (Yang & Rao 1992; Wang et al. 2016, 2019b; Fig. 1). In fact, *Diploderma* is the only known vertebrate group in the HMR that has not only endemic species in both modern and proposed paleo-river valleys, but also expand across both biogeographic lines. Furthermore, comparing to plants and fishes that have been used in previous phylogeographic studies, agamid lizards have a well-documented fossil record (Grismer et al. 2016), allowing robust calibrations of a molecular clock and more accurate estimation of divergence timing. All these above characteristics makes the genus a great study system for investigating the competing hypotheses on paleo-drainage evolution and biogeographic lines in the HMR.

However, in order to reveal clear biogeographic structures across the Hengduan Mountain Region and understand the evolutionary dynamics of organisms inhabiting such landscape, we must first have a good understanding on the biodiversity and their evolutionary relationships. Although it sounds straightforward, a good understanding of the systematics and phylogenetic relationships for many taxa of the HMR is still lacking, and *Diploderma* species are no exceptions. Recent taxonomic works still suggested an rich, underestimated diversity in the HMR (Wang et al. 2015, 2016, 2017, 2019b, 2019c, 2019d), and many of the previously identified populations of *D. flaviceps* remain unexamined. Without an accurate taxonomy that

reflects evolutionary history, it will be impossible to detect and reveal the masked evolutionary stories. Furthermore, with the rapid developments of the region and emerging new threats from illegal wildlife trade, a good understanding of the local diversity and their genetic structures are crucial for effective conservation managements and law enforcement (Bickford et al. 2006).

Lastly, regarding the illegal trade of wildlife, despite the importance of Asian countries in understanding global herpetofauna pet trade, substantial knowledge gaps still exist, especially for major economic entities such as China. Although available studies already show a considerable number of exotic species in domestic markets across China (Feng et al. 2002; Gong et al. 2009; Wang et al. 2017, 2018; Zeng et al. 2017; Ji et al. 2020), and despite that China's native species have appeared regularly in the international markets across the globe (Lee et al. 1999; Stuart et al. 2006; Schlaepfer et al. 2005; Herrel & van der Meijden, 2014; Rowley et al. 2016; Canlas et al. 2017), questions still remain on the the exact extent and characteristics of China's trade at the national scale. Additionally, nothing is known quantitatively about China's trade or the specific characteristics of China's trade. Without these crucial trade statistics, it is impossible to assess and improve the effectiveness of current legislation and law enforcements in China.

For my PhD dissertation, I will first resolve the taxonomy of the genus *Diploderma*, describe cryptic diversity and construct the phylogenetic relationships of the genus. Using the resolved taxonomy, I will then investigate the interactions between the complex landscape of the HMR and the organismal evolution, specifically testing competing hypotheses on biogeographic lines and drainage evolution. Lastly, I will combine trade data from various sources to characterize China's herpetofauna pet trade in the past 20 years and provide specific recommendations on China's conservation policies.

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Chapter 2: Systematic Revision of Mountain Dragons (Reptilia: Agamidae: *Diploderma*) in China, with Descriptions of Six New Species and Discussion on Their Conservation

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 we highlight the major challenges for *Diploderma* conservation in China due to delayed environmental legislation and misleading conservation assessments.

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 et al., 2019a). 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 et al., 2019b, 2019c, 2019d). Most congeners are found in the Hengduan Mountain Region (HMR) in Mainland Southwest China and Taiwan (Manthey, 2010; Wang et al., 2019b), 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 et al., 2019c).

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 US. 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 (Zhao et al., 1999; Yang & Rao, 2008; Yao & Gong, 2012).

Recent re-examinations 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, 2019c). 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, Denzer, Hou, & Wang, 2012), *D. drukdaypo* (Wang, Ren, Jiang, Zou, Wu, Che, & Siler, 2019), *D. iadinum* (Wang, Jiang, Siler, & Che, 2016), *D. laeviventre* (Wang, Jiang, Siler, & Che, 2016), *D. micangshanense* (Song, 1987), *D. vela* (Wang, Jiang, & Che, 2015), *D. yulongense* (Manthey, Denzer, Hou, & Wang, 2012), and *D. zhaoermii* (Gao & Hou, 2002) (Figure 1). However, despite the well-recognized suspicion on 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 remain unexamined, particularly populations from the valleys of the Jinsha River and its main tributary, the Yalong River, in Yunnan and Sichuan Provinces (Wang et al., 2019e).

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, 2016, 2019e). As coloration and ornamentation patterns have proved reliable as diagnostic characters for members of the genus *Diploderma* (Wang et al., 2015, 2016, 2017,

2019c, 2019d, 2019e), 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 above-mentioned 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 et al., 2019c), 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 most 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 et al., 2017, 2019c), but the few recent integrative taxonomic studies of the genus also have limited taxa or gene coverage (Wang et al., 2019b, 2019d, 2019e). 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 et al., 2019c, 2019e). With the rapidly expanding human settlements in the HMR, this lag between species discovery and environmental legislation/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 2018, 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; detailed population sampling see Appendix 1 and Table 5). 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 5). 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: 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 (Table 6, 7). Morphometric data were taken with a digital slide caliper to the nearest

0.1 mm. Focal characters and character definitions follow Wang et al. (2019d), 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); forelimb 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-riotal 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 et al., 2016, 2017, 2019c, 2019d, 2019e) 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: (1) presence or absence of gular-spot; (2) coloration of gular spot, if present; (3) presence or absence of dorsolateral stripes on the body; (4) shape of dorsolateral stripe of body (strongly jagged, feebly jagged, or smooth-edged), if present; (5) coloration of dorsolateral stripes of body, if present; (6) shape of vermiculated stripes on ventral head (reticulated vs. scattered); (7) coloration of inner lips; (8) coloration of oral cavity and tongue; and (9) 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, 2016, 2018a, 2019c), morphometric data of each sex are treated separately for analyses and comparisons. Due to limited sample size, for *D. drukdaypo*, 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 et al., 2016, 2019c, 2019d), 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 yield significant variation, then Tukey's HSD test was used to determine whether the putative new species are statistical 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 number 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 et al., 2019b).

Genomic DNA was extracted from liver samples stored in 95% ethanol using Fujita's Guanidine Thyocyanate 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 (Whiting, Bauer, & Sites, 2003; Crottini et al., 2009; Wang et al., 2019b; Table 1), and the PCR products are about 1200bp, 200bp, 600bp, 500bp, 800bp respectively. After sequencing and trimming, the alignments of new sequences are 1032bp, 184bp, 567bp, 391bp, and 641 bp for *ND2*, tRNAs, *BDNF*, *CMOS*, and *R35*, respectively. When included and aligned with the Genbank data, the final alignments are 1032bp, 392bp, 567bp, 539bp, and 641bp for the five genes, respectively. Amplified products were visualized on 1.5% agarose gels, and clean single banded products were purified with 1 µL of a 20% dilution of ExoSAP-IT (US78201, Amersham Biosciences). Cycle sequencing reactions were carried out using ABI Prism Big-Dye 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 DataDryad (DOI: <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 (Guindon & Gascuel, 2003; Darriba, Taboada, Doallo, & Posada, 2012). 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+ Γ) was applied for all subsets, with 1000 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).

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 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 Mianshi County, southern Sichuan Province (population 8 in Figure 1) each form a monophyletic group with strong support (Clade 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 Shangrila/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* (population 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 Shangrila 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 8). 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 8).

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 9). 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 10). 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 separate the clusters, 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 11). 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* (population 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 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, 10, 11).

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 term 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 dataset 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 angustelinea* sp. nov. Wang, Ren, Wu, Che, Siler

(Population 7 in Figure 1; Figures 2, 5, 11, 12; Tables 2–4, 12 (1); Zoobank ID
urn:lsid:zoobank.org:act:E709207E-3FC6-45EF-9D54-8CADA8E8949A8)

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 10 June 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-riatal 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).

Comparisons

Diploderma angustelinea 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 (vs. well-developed on skin folds in both sexes), a relatively longer tail in males (TAL 230.2–249.1% SVL vs. 181.8%–210.8% SVL), fewer and weakly developed post-riatal modified scales (0–3, average 1, sub-pyramidal shaped and weakly developed vs. 3–9, average 6, conical shaped and well developed), feebly jagged, narrow dorsolateral stripes in both sexes (vs. 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 (vs. gradual transition from Pale Pinkish Buff [Color 3] to white), and by the presence of distinct gular spots in both sexes

(vs. absence), and absence of reticulated, vermiculate black patterns on the gular region (vs. 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-riatal modified scales. However, *D. angustelinea* sp. nov. can be differentiated from the latter species by having distinctively keeled ventral scales (vs. feebly keeled or smooth), fewer middorsal scales (41–49 vs. 57–59), slightly jagged, narrower dorsolateral stripes (vs. completely smooth edged and wide), and by the absence of heavy black speckles on dorsal, lateral, and ventral surfaces of head (vs. presence).

Diploderma angustelinea sp. nov. differs from all remaining recognized congeners by having narrow, dorsolateral stripes in both sexes (vs. thick and wide). Specifically, *D. angustelinea* 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 vs. 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 much longer hind limbs (HLL 71.1–80.2% vs. 60.0–64.0% in *D. brevicaudum*, 58.2–63.8% in *D. drukdaypo*); from *D. batangense*, *D. iadinum*, *D. vela*, *D. yulongense*, and *D. zhaoermii* by having weakly developed nuchal crests without skin folds (vs. well-developed on raised on skin folds in males) and distinct coloration of gular spots (Dark Spectrum Yellow [Color 78] vs. 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. zhaoermii*; and no gular spots in *D. vela*); from *D. chapaenses*, *D. micangshanense*, *D. varcoae*, *D. yunnanense*, 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 (vs. absence); from *D. fasciatum* by the feebly developed nuchal crests (vs. well-developed and differentiated from dorsal crests), and by the presence of dorsolateral stripes (vs. absence) and the absence of hourglass shaped pattern on the mid dorsum (vs. presence); from *D. dymondi*, *D. slowinskii*, *D. swild*, and *D. varcoae* by having a concealed tympanum (vs. exposed); from *D. splendidum* by having a smaller maximum body size (SVL ≤ 67.8 mm vs. ≤ 92.0 mm), homogeneous ventral head scales (vs. heterogeneous), and distinct, deep, transverse gular fold (vs. shallow); from *D. hamptoni* by having parallel dorsolateral stripes (vs. diagonally away from vertebral line posteriorly), a distinct transverse gular fold (vs. shallow), and by the absence of distinct dark stripes on gular region (vs. 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-riatal 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 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 towards 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) towards 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 are 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 post-rictal 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 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) towards 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 Supporting Information Table 12. 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 vs. 194.3–222.3%), more developed and serrated nuchal crests (vs. less developed), and brighter dorsolateral stripes (vs. duller with less distinct edges), and by the absence of distinct chevron patterns along dorsal midline between dorsolateral stripes (vs. 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 Narrowed-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 towards 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 post 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.

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, 12 (2); Zoobank ID urn:lsid:zoobank.org:act:E81CAE00-16CA-4D9A-8BD5-0B49158DFFF0)

Synonym

Japalura flaviceps Zhao et al. (1999:111–115), in part; Yang & 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 2198 m, WGS 84). Collected by Kai WANG, Xiankun HUANG, and Zhuoyu LU on 17 June 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 4 June 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 2198 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 29 August, 2019; KIZ 044764, adult male near Derong township, Sichuan Province, China (99.2773° E, 28.6714° N, elevation 2412 m, WGS 84); all collected by Kai WANG, Zhuoyu LU, and Xiankun HUANG on 19 June 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 subpyramidal 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 vs. 68.5–82.1 mm), fewer middorsal crest scales (MD 35–46, average 40 vs. 45–56, average 51), solid patches along dorsal midline in both sexes (vs. hollow, rhomboid-shaped patterns), as well as by the presence of distinct radial stripes around eyes (vs. absence or faint), the presence of gular spots in both sexes (vs. absence),

the absence of crest skin folds in females (vs. absence), and the absence of reticulated, vermiculate patterns on the gular region (vs. 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% vs. 187.3–206.5%, average 194.6%; Tukey HSD test, $p < 0.05$), strongly developed skin fold of nuchal and dorsal crests in males (vs. weak and often indistinct), and much stronger contrast between the dorsal dark and light ornamentations (vs. 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 (vs. absence in both sexes); from *D. iadinum* by having fewer dorsolateral rows of enlarged keeled scales on each side of the body (1 vs. 2–3), strongly jagged dorsolateral stripes (vs. smooth), distinct body coloration in both sexes (Pale Buff [Color 1] in males, Chamois [Color 84] in females vs. Yellowish Spectrum Green [Color 128] to Emerald 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 vs. 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] vs. Chartreuse [Color 89] to Opaline Green [Color 106]) and dorsolateral stripes (white to Cream Color [Color 12] vs. Pale Greenish Yellow [Color 86]), as well as by the absence of green patches on the dorsolateral surface of body (vs. presence); from *D. laeiventre* by having distinctively keeled ventral scales (vs. smooth or feebly keeled) and distinct gular coloration (Pale Cyan [Color 157] to Light Caribbean Blue [Color 163] vs. Light Chrome

Orange [Color 76]); from *D. chapaense* and *D. yunnanense* by the presence of a distinct transverse gular fold (vs. absence) and differential coloration of gular spot (Pale Cyan [Color 157] to Light Caribbean Blue [Color 163] vs. 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 (vs. absence); from *D. dymondi*, *D. swild*, *D. slowinskii*, and *D. varcoae* by having a concealed tympanum (vs. exposed) and distinct coloration of oral cavity (Light Flesh Color [Color 250] vs. 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 (vs. feeble), homogeneous ventral head scales (vs. heterogeneous), and jagged dorsolateral stripes in males (vs. smooth edged); and from *D. zhaoermii* by having a smaller body size (maximum SVL 61.2 mm in males vs. up to 81.7 mm), distinct vermiculate stripes on the ventral head (vs. faint or absence), and a distinct gular coloration (Pale Cyan [Color 157] to Light Caribbean Blue [Color 163] vs. Chartreuse [Color 89]).

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

hamptoni by having parallel dorsolateral stripes on dorsal body (vs. 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 (vs. much narrower, smooth or feebly jagged), a distinct gular spot coloration (Pale Cyan [Color 157] to Light Caribbean Blue [Color 163] vs. Dark Spectrum Yellow [Color 78]), a much gradual transition from dorsal to ventral coloration (vs. sharp and distinct), and by the presence of strongly developed skin folds under nuchal and dorsal crests in males (vs. absence), and the presence of distinct black vermiculate stripes on ventral head (vs. 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 band. All of these transvers

bands except the most anterior three enter orbits on both side, 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 s 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 end 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) towards 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 Supporting Information Table 12. 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 vs. 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 vs. 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 vs. white in males), and by the presence of Peach Red (Color 70) vertebral stripe pattern from dorsal head to the vent in female (vs. 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 3000 m of elevation along the upper Jinsha River, from Zongrong Village of Derong County, Sichuan Province, to areas 14km 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 km², which includes low-elevation (i.e. <3500m), 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 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, and 12; Tables 2–4, 12 (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 28 May 2017 (98.9642° E, 30.7385° N, elevation 2845 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; (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 vs. 68.5–82.1 mm), a relatively shorter tail (TAL 149.7–179.3% SVL in males, 140.2–152.2% in females vs. 181.8–210.8% in males, 191.5–205.7% in females), distinct coloration of inner lips (dark spectrum yellow coloration vs. same as rest of oral cavity, flesh color), as well as by the presence of gular spots in both sexes (vs. absence), presence of distinct radial stripes around eyes (vs. faint or absence), presence of distinct dark spectrum yellow along inner lips in both sexes (vs. absence), absence of reticulated dark patterns on gular region (vs. presence), and by the absence of hallow, brown rhomb-shaped patterns with distinct yellow centers along dorsal midline (vs. 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] vs. flesh

color, same as the rest of oral cavity) and the tendency toward a relatively shorter tail (ANOVA $p=0.031$; TAL 149.7–179.3% SVL in males, 140.2–152.2% in females vs. 187.3–206.5% in males, 171.8–203.1% in females for *D. batangense* [Tukey HSD $p=0.041$]; 174.6–238.1% in males, 159.8–202.7% in females for *D. vela* [Tukey HSD $p=0.034$]). In addition, it differs from *D. batangense* by having more post-rectal modified conical or sub-pyramidal scales (4–9 vs. 0–3); and from *D. vela* by having a relatively wider head (HW 70.1–73.0% HL vs. 65.2–69.8%), discontinuous skin folds between nuchal and dorsal sections in males (vs. continuous), distinct coloration of dorsolateral stripes in females (Surphur Yellow [Color 80] vs. Medium Chrome Orange [Color 75]), and as well as by the presence of gular spots in both sexes (vs. 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 (vs. 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 (vs. absence); from *D. laevis* and *D. drunkdaypo* by having distinctively keeled ventral head and body scales (vs. 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 vs. 81.0–95.5 mm in males, 74.8–91.7 mm in females) and a concealed tympanum (vs. exposed); from *D. yulongense* by having a much shorter tail (TAL 149.7–179.3% SVL in males, 140.2–152.2% in females vs. 211.3–247.6% in males, 182.1–227.3% in females), as well as by the absence of greenish ventrolateral patches of body (vs. 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 vs. 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 vs. smooth edged), and fewer dorsolateral ridges on body in females (1 vs. 2 or 3).

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

Lastly, for the other new species described here, *D. flavilabre* sp. nov. differs from all by the differential coloration of inner lips (vs. 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 vs. 230.2–249.1% in males, 194.3–222.3% in females), more and better developed conical or sub-pyramidal post-riatal scales (4–9 vs. 0–3), distinct coloration of gular spots (Pale Emerald Green [Color 141] vs. Spectrum Yellow [Color 79]), wider and strongly jagged dorsolateral stripes (vs. narrow, weakly jagged or smooth), as well as by the presence of raised, well developed nuchal and dorsal crests on skin folds in males (vs. absence); and from *D. aorun* sp. nov. by having a smaller body size in males (SVL 50.8–55.2 mm vs. 58.4–61.2), a shorter tail (TAL 149.7–179.3% SVL in males, 140.2–152.2% in females

vs. 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 vs. 73.7–82.7% in males, 71.8–80.5% in females), and a distinct gular coloration (Pale Emerald Green [Color 141] vs. 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-riectal 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), zigzag 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 forth 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 Supporting Information Table 12. 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 vs. 140.2–152.2% in females), relatively longer hind limbs (HLL 66.9–74.8% SVL in males vs. 61.7–65.6% in females) and raised crests on skin folds (vs. 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 vs. Tawny Olive [Color 17] to Clay Color [Color 18] in females) and presence of distinct Pale Horn Color (Color 11) dorsolateral stripes in males (vs. 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 1 3C). 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 5 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 km². 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, 12 (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

KIZ 032715, 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 2663 m). Collected by Kai WANG and Nima DADENG in 22 May 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 subpyramidal post-riotal 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 (vs. erected on well-developed skin folds), a relatively shorter tail $TAL \leq 151.0\%$ SVL in females (vs. $\geq 191.5\%$), as well as by the distinct coloration of gular patterns (Light Sulphur Yellow [Color 93] blotches vs. Jet black [Color 300] reticulated stripes), and the absence of dark rhomb shaped patterns along dorsal midline in females (vs. 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 vs. 34–40) and the presence of mosaic gular patterns in females (vs. absence); and from *D. drukdaypo* by having distinctively keeled ventral scales (vs. smooth or feebly keeled), distinct coloration of dorsolateral stripes (Light Yellow Ocher [Color 13] to Pale Buff [Color 1] vs. Medium Chrome Orange [Color 75]), and presence of mosaic gular patterns in females (vs. 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 vs. $> 160.0\%$), shorter hind-limbs ($HLL \leq 65.8\%$ SVL vs. $> 69.0\%$), and differential gular patterns (mosaic pattern vs. 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 (vs. presence) and presence of dorsolateral stripes (vs. absence); from *D. batangense*, *D. iadium*, and *D. yulongense* by differential gular coloration and patterns in females (Light Sulphur Yellow [93], mosaic patterns vs. 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 (vs. absence); from *D. swild* and *D. splendidum* by having homogeneous ventral head scales (vs. heterogeneous); from *D. laeviventre* by distinctively keeled ventral scales (vs. smooth or feebly keeled); from *D. dymondi*, *D. slowinskii* and *D. varcoae* by having a concealed tympanum (vs. exposed); from *D. vela* by differential coloration of dorsolateral stripes in females (Light Sulphur Yellow [Color 93] vs. 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 vs. $\geq 174.3\%$). In addition, *D. panchi* sp. nov. differs from *D. angustelinea* sp. nov. by having more conical or sub-pyramidal post-riatal scales (3–7 vs. 0–3) and strongly jagged and wide dorsolateral stripes in females (vs. feebly jagged and thin); from *D. aorun* sp. nov. by distinct gular coloration (Light Sulphur Yellow [Color 93], mosaic patterns vs. 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 vs. Pale Emerald Green [Color 141] to Light Turquoise Green [Color 146] gular spots) and a distinct lip coloration (Light Flesh Color [Color 250] vs. 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-rietal 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.

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 are 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 coving 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. 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 Supporting Information Table 12. For coloration and ornamentations, all paratopotypes (KIZ032717, 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 12D). 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, 12 (5); Zoobank ID
urn:lsid:zoobank.org:act:79DA84FF-CA00-4C19-9D7D-3F3071C2AC8F)

Synonyms

Japalura dymondi Deng et al. (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 1430 m, WGS 84). Collected by Kai Wang and Gadeng Nima on 25 April 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-rietal 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 vs. 225.5–239.0%), lower and less differentiated nuchal crest scales (TNC 5.4–7.7% HL vs. 12.0–12.4%), homogeneous scales on

the ventral surface of head (vs. heterogeneous), distinct coloration of dorsolateral stripes in males (Sulphur Yellow [Color 80] vs. Chartreuse [Color 89]), and a terrestrial life style (vs. 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] vs. Spectrum Violet [Color 186] to Jet Black [Color 300]) and tongue (Light Chrome Orange [Color 76] vs. Pale Pinkish Buff [Color 3]), and a terrestrial lifestyle (vs. 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] vs. uniform Light Orange Yellow [Color 77]), smooth dorsolateral stripes in males (vs. strongly jagged), and by the presence of a transverse gular fold (vs. 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] vs. Light Flesh Color [Color 250]). Furthermore, *D. panlong* sp. nov. differs from *D. flaviceps* by having exposed tympana in most individuals (vs. always concealed), a shallow transverse gular fold (vs. deep and well developed), uniform white ventral head coloration with no gular patterns (vs. dark reticulated gular stripes), smooth-edged dorsolateral stripes (vs. strongly jagged), and by the presence of distinct radial stripes around the eyes (vs. absence or faint); from *D. micangshanense* by the presence of a transverse gular fold (vs. absence), absence of strong skin folds of the nuchal and dorsal crests in males (vs. presence), absence of regular triangular or rhomboid shaped patterns along the vertebral line between dorsolateral stripes (vs. presence), and by having smooth dorsolateral stripes in males (vs. strongly jagged); from *D. zhaoermii* by having smooth-edged, dorsolateral stripes (vs. strongly jagged), the presence of distinct white lip stripes (vs. absence), and absence of gular spots and skin folds under the nuchal

and dorsal crests in males (vs. 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 (vs. always concealed) and a terrestrial lifestyle (vs. arboreal), and by the presence of a transverse gular fold (vs. absence).

For species in clade B (Figure 2), *D. panlong* sp. nov. differs from all congeners by having exposed tympana in most individuals (vs. always concealed), and from all except *D. chapaense* and *D. yunnanense* by having a distinct oral coloration in life (Light Chrome Orange [Color 76] vs. 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 (vs. fewer and weaker), and by the absence of gular spots (vs. presence in both sexes); from *D. drukdaypo* by having a longer tail ($TAL \geq 248.0\%$ SVL vs. $< 154.0\%$) and hind limbs ($HLL > 77.0\%$ SVL vs. $< 64.0\%$); from *D. slowinskii* by having a smaller maximum body size (SVL ≤ 71.7 mm vs. ≤ 98.3 mm), fewer middorsal scales (39–46 vs. 47–53), a distinct coloration of dorsolateral stripes (Sulphur Yellow [Color 80] vs. Light Emerald Green [Color 143]), and a distinct dorsal limb coloration (Light Buff [Color 2] to Pale Pinkish Buff [Color 3] vs. 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] vs. Jet Black [Color 300]) and by the absence of sail-like skin folds of the crests in males (vs. presence); from *D. iadinum* by having a longer tail ($TAL \geq 248.0\%$ SVL vs. $< 206.0\%$), a distinct background body coloration (Brussels Brown [Color 33] to Maroon [Color 39] vs. Yellowish Spectrum Green [Color 128] to Emerald Green [Color 143]), and by the absence of gular spots (vs. presence); and from *D. chapaense* and *D. yunnanense* by having shorter and less well defined nuchal crest scales (vs. taller and strongly defined), and by the absence of gular spots (vs.

presence), absence of a W-shaped ridge on the occipital region of the head (vs. presence), and by the presence of a transverse gular fold (vs. absence).

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

For the new species described here, *D. panlong* sp. nov. differs from all by having exposed tympana in most individuals (vs. always concealed), taller nuchal crests, and better developed, higher numbers of conical scales on the post-riotal 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-riotal region (PRS 9–13 vs. 0–3), a narrower head (HW 63.4–67.3% HL vs. 67.0–73.9%), a distinct oral coloration in life (Light Chrome Orange [Color 76] vs. Light Flesh Color [Color 250]), and by the absence of gular spots (vs. presence); from *D. aorun* sp. nov. by having a narrower head (HW 63.5–67.3% HL vs. 67.8–72.7%), a tendency toward more lamellae scales under Finger IV (18–24 vs. 12–19), more and better developed conical scales on the post-riotal region (PRS 9–13 vs. 1–7), distinct shapes of dorsolateral stripes (smooth edged vs. strongly jagged), weakly developed nuchal and dorsal crests without distinct skin folds (vs. strongly developed with skin folds), and by the absence of gular spots (vs. presence); from *D.*

flavilabre sp. nov. by having a larger adult body size (SVL 60.2–71.7 mm vs. 50.8–55.2 mm), a longer tail (TAL 248.2–268.0% SVL vs. 149.7–179.3%), longer hind limbs (HLL 77.7–83.2%SVL vs. 66.9–74.8%), having more and better developed conical scales on the post-rietal region (PRS 9–13 vs. 4–9), distinct dorsal body coloration (Pale Pinkish Buff [Color 3] to Light Flesh Color [Color 250] vs. Jet Black [Color 300]), distinct oral and inner coloration (uniform Light Chrome Orange [Color 76] vs. 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 (vs. 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 vs. 14–17), and more and better developed conical scales on the post-tympanic (6–12 vs. 2–6) and post-rietal regions of head (9–13 vs. 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-riatal 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 Burnt 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 Supporting Information Table 12. Coloration and ornamentation patterns among the type series are consistent with the holotype. Two of the paratopotype specimens (KIZ 040139, 040143) each have 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 (e.g., *Pueraria peduncularis*,

Dalbergia sp., and *Pterocarya* sp.) form the main plant community (Figure 12E). 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 inhabitations, 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 km² 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, 12 (6); Zoobank ID [urn:lsid:zoobank.org:act:AE454658-7AC6-4436-9636-15EC789329FA](https://zoobank.org/urn:lsid:zoobank.org:act:AE454658-7AC6-4436-9636-15EC789329FA))

Synonym

Japalura flaviceps: 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 9 July 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 1950m); KIZ 044745, adult male, KIZ 044744, adult female, near Cangjue Village, Shangri-La County, NW Yunnan Province, China (27.6087 N, 99.5226 E, 1939m); KIZ 044820, adult female, near Pengnanshou Bridge, Shangri-La County, NW Yunnan Province, China (28.0301N, 99.4215 E, elevation 2619 m); all collected by Kai WANG, Zhuoyu LU, and Xiankun HUANG on 15 June 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-riotal 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 vs. up to 82.1 mm), weaker skin folds under crests in males, absent in females (vs. strongly developed, raised in both sexes), less developed conical scales on the post-occipital and post-riotal regions (subpyramidal shape vs. tall conical shape), as well as by the presence of gular spots in both sexes (vs. absence), presence of distinct radial stripes around eyes (vs. absence), and the absence of dark rhomboid-shaped patterns with distinct light centers on dorsal body along dorsal midline (vs. 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 vs. 41–53), a different gular coloration (Light Sulphur Yellow [Color 93] vs. Pale Cyan [Color 157]) and a different coloration of ventral body in males (white or Pale Buff [Color 1] vs. Spectrum Yellow

[Color 79]); from *D. brevicaudum* by having a longer tail ($TAL \geq 174.3\%$ SVL vs. $< 145.0\%$) and longer hind limbs ($HLL \geq 72.5\%$ of SVL vs. $< 64.0\%$); and from *D. yulongense* by having different coloration of gular spots in males (Light Sulphur Yellow [Color 93] vs. Opaline Green [Color 106]), as well as by the presence of distinct reticulated patterns on the ventral head in males (vs. absence), the absence of gular spots in females (vs. presence), and by the absence of Greenish Yellow (Color 88) ventrolateral patches of body (vs. presence).

For congeners distributed in different river valleys in the HMR, *D. qilin* sp. nov. differs from *D. drunkdaypo* by having a longer tail ($TAL \geq 174.3\%$ vs. $\leq 154.4\%$), longer hind limbs ($HLL \geq 72.5\%$ SVL vs. $\leq 63.8\%$), better developed crest scales in males (erected and serrated on skin folds vs. not erected or serrated, skin fold absence), distinctively keeled ventral scales (vs. feebly keeled or smooth), and by the presence of gular spots in males (vs. absence); from *D. iadinum* by having a distinct body coloration (Emerald Green [Color 143] vs. True Cinnamon [Color 260] to Burnt Umber [Color 48]) and different coloration of gular spot (Light Sulphur Yellow [Color 93] in both sexes vs. Caribbean Blue [Color 168] in males, Medium Greenish Yellow [Color 88] in females); from *D. laeviventre* by distinctively keeled ventral scales (vs. smooth or feebly keeled), fewer MD (38–45 vs. 57–59), and different coloration of gular spots (Light Sulphur Yellow [Color 93] in both sexes vs. Medium Chrome Orange [Color 75] in both sexes); from *D. vela* by weaker and discontinuous skin fold of crests in males (vs. sail-like, continuous skin fold under crests) and by the presence of gular spots (vs. absence); from *D. slowinskii* by a concealed tympanum (vs. exposed), a smaller body size (SVL < 64 mm vs. SVL > 74 mm), fewer T4S (19–25 vs. 25–30), jagged dorsolateral stripes (vs. smooth edged), different body coloration of dorsolateral stripes (Cream Color [Color 82] vs. Opaline Green [Color 106]), and by the presence of gular spots in males (vs. absence).

For remaining congeners, the new species differs from *D. dymondi*, *D. swild*, and *D. varcoae* by having a concealed tympanum (vs. exposed) and differential oral coloration (Flesh Color [Color 250] vs. 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 vs. granular), more middorsal scales (38–45 vs. 8), and a larger body size (55.94–63.44 mm vs. 49.29 mm); from *D. fasciatum* by the absence of single hourglass shaped pattern on the mid-dorsum (vs. presence); from *D. hamptoni* by having small scales between nasal and first supralabial (vs. in direct contact) and parallel dorsolateral stripes on dorsal body (vs. 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 (vs. absence); from *D. splendidum* by having homogeneous ventral head scales (vs. heterogeneous) and strongly jagged dorsolateral stripes (vs. smooth edged); and from *D. zhaoermii* by a longer tail (TAL >200.0% SVL in males, > 174.0% in females vs. <190.0% in males, <160.0% in females) and different coloration of gular spots (Light Sulphur Yellow [Color 93] vs. Chartreuse [Color 89]).

For the new species described here, *D. qilin* sp. nov. differs from *D. angustelinea* sp. nov. by having more developed nuchal and dorsal crests on skin folds (vs. feebly developed), wider and strongly jagged dorsolateral stripes in both sexes (vs. narrow, feebly jagged), and by the different coloration of gular spots (Light Sulphur Yellow [Color 93] vs. 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] vs. 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 vs. $\leq$ 179.3% in males, <152.2% in females), different gular coloration in males

(Sulphur Yellow [Color 80] vs. Pale Emerald Green [Color 141]), different inner-lip coloration (Light Flesh Color [Color 250] vs. Spectrum Yellow [Color 79]), as well as by the absence of gular spots in females (vs. presence); from *D. panchi* sp. nov. by having a longer tail (TAL 174.3–199.7% SVL in females vs. 141.8–167.8%), a tendency toward a more robust head (HD 72.3–80.41% HW in females vs. 63.3–74.3%), and by the absence of mosaic gular patterns (vs. presence); and from *D. panlong* sp. nov. by having a shorter tail (TAL 202.0–218.2% in males vs. 248.2–268.0%), a wider (HW 68.12–74.76% HL vs. 63.4–67.3%) and more robust head (HD 51.5–60.2% HL vs. 49.3–52.4%), concealed tympana (vs. mostly exposed), deeper transverse gular folds (vs. shallow), distinct shape of dorsolateral stripes (strongly jagged vs. smooth edged), and by the presence of distinct gular spots in males (vs. 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, sub-pyramidal scale anterior to tympanum. Infralabials keeled, 12/13; post-riotal 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, sub-pyramidal 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, sub-pyramidal 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 Burnt 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 Burnt 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 towards 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 Supporting Information Table 12. 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 vs. 174.3–199.7% in females) and relatively shorter trunks than females (TRL 44.0–48.1% SVL in males vs. 47.8–56.9% in females). For ornamentations and coloration, males possess distinct coloration of dorsolateral stripes (Light Sulphur Yellow [Color 93] vs. 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 (vs. smaller and fainter).

Among females, one individual (KIZ 028336) possesses no transverse bands on dorsal head, no dorsolateral stripes, and indistinct Burnt 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 mixed-forests along the upper Jinsha River Valley (Figure 12F). 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 (e.g. *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 on 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 3300 m along the upper Jinsha River Valley, from the Cangjue Village of Shangri-La County to the areas approximately 13km southeast of Benzilan Township. The estimated extent of occurrence is approximately 700km² 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 et al., 2019b, 2019d, 2019e; 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* (Xu & Zhang, 2011; Wang et al., 2016). Although it was transferred to the genus *Diploderma* later, such taxonomic change was based on morphological diagnosis only (Wang et al., 2019b). 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 et al. 2019c). 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 *Pseudocalotes*; Wang et al., 2019b), as it resembles *D. vela* (considered as *J. vela* at the time) in external morphology (Wang et al., 2019c). Recent studies followed such conclusions and reassigned the species to the genus *Diploderma* based on morphological diagnosis (Denzer, Manthey, & Campbell, 2019; Wang et al., 2019e). 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 et al., 2019b). 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 et al., 2019d, 2019e). For the records of *D. cf. splendidum* from southern Gansu and Shaanxi Province (no vouchered

information mentioned; Zhao et al., 1999; Yao & Gong, 2012), 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 et al., 2019e). 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; Zhao et al., 1999; Wang et al., 2019a, 2019b, 2019c, 2019d, 2019e). With the addition of the six new species described here, a total of 31 species of *Diploderma* are now recognized (Wang et al., 2019b, 2019c, 2019d, 2019e), 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. laeviventre*, *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 et al. [2019e] 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. varcoae*** (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. laeviventre* (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. brevicauda* (China: Yunnan)

10b. TAL/SVL>160%-----**11**

11a. Transverse gular fold shallow, feeble-----**12**

11b. Transverse gular fold deep, forming a distinct pouch across 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 [?], Chongqin, 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-riatal 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. zhaoermii* (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 et al., 2019c). 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. zhaoermii*; 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 five-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: 1) listing *D. iadinum* as Class I protected under the ESLC based on current data, due to its threaten status and the urgent conservation needs; 2) listing all members of the genus *Diploderma*, with the exception of *D. fasciatum*, *D. chapaense*, *D. micangshanense*, *D. yunnanense*, and *D. zhaoermii* 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 enforcement 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.

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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	Reference
<i>BDNF</i>	1	GTR	BDNF.F	CCCCAATGAAAGAAGTGASCCTC	Crottini et al, 2009
	2	HKY+ Γ			
	3	JC69	BDNF.R	TGGGTAGTTCGGCACTGAGAATTCC	
<i>CMOS</i>	1	JC69	G73.1	GGCTR TAAARCARGTGAAGAAA	Whiting et al., 2003
	2	HKY+ Γ			
	3	HKY+ Γ	G74.1	GARCWTCCAAAGTCTCCAATC	
<i>R35</i>	1	GTR+ Γ	R35.F	GACTGTGGAYGAYCTGATCAGTGTGG	Whiting et al., 2003
	2	HKY			
	3	GTR+ Γ	R35.R	GCCAAAATGAGSGAGAARCGCTTCTG	
<i>ND2</i>	1	GTR+ Γ			Wang et al, 2019b
	2	GTR+ Γ	Jap_70F	CCACCAAACA ACTACACCTA	
	3	GTR+ Γ	Jap_1559R	GGATTAATGCCCTCTGGATT	
tRNAs	1	GTR+ Γ			

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. qilin* sp. nov., and *D. yajiangense* 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, and “–” indicate not applicable due to sample size of one.

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	230.2–249.1	45.7–46.5	71.1–80.2	27.8–30.1	73.3–78.7	66.6–70.8
			(58.5)	(235.3)	(46.4)	(77.0)	(29.4)	(76.4)	(68.7)
			59.0–67.8	194.3–222.3	40.8–46.2	74.4–79.2	27.3–29.3	72.7–79.3	67.0–73.9
<i>D. aorun</i> sp. nov.	F	6	(63.1)	(207.3)	(43.7)	(75.9)	(28.2)	(75.9)	(68.9)
			56.3–61.2	212.0–221.1	43.7–50.4	73.7–81.7	29.2–31.4	71.4–80.2	67.8–72.7
			(58.7)	(216.4)	(47.7)	(78.6)	(29.9)	(75.4)	(70.8)
<i>D. flavilabre</i> sp. nov.	M	7	60.8–66.5	191.4–207.7	45.0–52.8	71.5–80.5	27.3–30.2	66.7–78.0	66.8–70.4
			(63.8)	(199.2)	(47.9)	(75.3)	(28.9)	(74.0)	(68.7)
			50.8–55.2	149.7–179.3	43.1–48.3	66.9–74.8	31.2–32.2	70.1–75.5	70.7–73.1
<i>D. panlong</i> sp. nov.	F	6	(53.5)	(176.0)	(45.8)	(71.5)	(31.6)	(72.4)	(71.6)
			64.2–72.9	140.2–152.2	40.1–43.5	62.0–65.6	27.1–29.3	68.6–75.1	70.1–74.9
			(67.5)	(146.4)	(41.2)	(63.0)	(28.6)	(71.3)	(71.8)
<i>D. panchi</i> sp. npv.	F	4	59.6–67.7	141.8–151.5	39.3–41.7	60.2–65.8	27.0–28.8	63.3–74.3	69.5–73.6
			(65.2)	(148.1)	(40.0)	(62.6)	(28.0)	(69.0)	(71.6)
			64.2–71.7	248.2–268.0	44.9–46.9	77.7–83.2	29.1–31.6	77.8–79.5	63.4–67.3
<i>D. qilin</i> sp. nov.	M	4	(64.8)	(257.1)	(46.3)	(80.5)	(30.7)	(78.5)	(65.0)
			55.9–66.5	201.0–218.2	44.3–48.5	73.3–78.4	28.8–31.2	73.9–82.7	65.0–72.7
			(55.9)	(208.6)	(46.4)	(75.8)	(31.2)	(80.4)	(68.1)
<i>D. batangense</i>	F	6	55.3–72.0	174.3–199.7	44.7–51.8	72.5–80.4	26.6–28.9	72.3–80.4	69.6–73.2
			(61.0)	(187.5)	(46.8)	(74.5)	(28.0)	(76.2)	(71.1)
			55.5–62.8	187.3–206.5	46.0–49.8	74.7–79.8	28.8–32.2	71.7–75.3	66.3–67.3
	M	6	(59.3)	(194.6)	(47.9)	(76.4)	(30.9)	(73.6)	(67.0)

<i>D. drukdaypo</i>	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)
	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)
	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)
<i>D. yulongense</i>	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)
	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. yajiangense* 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. npv.	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	20–25	40–50	2–5	1–5	0–6	S

		(16)	(22)	(44)	(4)	(3)	(3)	
		15–19	21–26	38–44	1–5	1–3	0–4	
<i>D. yulongense</i>	14	(17)	(24)	(40)	(3)	(2)	(2)	S

Table 4. Comparisons of coloration and ornamentation 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. yajiangense* 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; “—”: not applicable. Color codes see Köhler (2012).

Species	Sex	Skin Fold under Nuchal Crest	Skin Fold under Dorsal Crest	Crest Scale Strongly Erected	Inner Lip Coloration	Tongue Coloration	Pharyngea and Palatum Coloration	Gular Spot
<i>D. angustelinea</i> sp. nov.	M	—	—	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+
	F	—	—	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+
<i>D. aorun</i> sp. nov.	M	+	+	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+
	F	—	—	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+
<i>D. flavilabre</i> sp. nov.	M	+	+	+	Spectrum Yellow	Light Flesh Color (250)	Light Flesh Color (250) speckled with Pale Neutral Gray (296)	+
	F	—	—	+	Spectrum Yellow	Light Flesh Color (250)	Light Flesh Color (250) speckled with Pale Neutral Gray (296)	+
<i>D. panchi</i> sp. npv.	F	—	—	—	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	—
<i>D. panlong</i> sp. nov.	M	—	—	+	Dark Spectrum Yellow (78)	Dark Spectrum Yellow (78)	Dark Spectrum Yellow (78)	—

<i>D. qilin</i> sp. nov.	M	+	+	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+
	F	—	—	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+
<i>D. batangense</i>	M	+	+	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+
	F	—	—	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+
<i>D. drukdaypo</i>	M	—	—	—	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	—
	F	—	—	—	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	—
<i>D. dymondi</i>	M	—	—	+	Smoky White (261)	Light Flesh Color (250)	Spectrum Violet (186) to Jet Black (300)	—
	F	—	—	+	Smoky White (261)	Light Flesh Color (250)	Spectrum Violet (186) to Jet Black (300)	—
<i>D. flaviceps</i>	M	+	+	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	—
	F	+	—	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	—
<i>D. swild</i>	M	—	—	+	Light Chrome Orange (76)	Light Chrome Orange (76)	Light Chrome Orange (76)	—
	F	—	—	+	Light Chrome Orange (76)	Light Chrome Orange (76)	Light Chrome Orange (76)	—
<i>D. vela</i>	M	+	+	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	—
	F	—	—	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	—
<i>D. yulongense</i>	M	+	—	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+

F	—	—	+	Smoky White (261)	Light Flesh Color (250)	Light Flesh Color (250)	+
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Table 4. Continued.

Species	Sex	Gular Spot Coloration	Dorsolateral Stripe Shape	Ventral Body Coloration	Ventrolateral Body Coloration
<i>D. angusteline</i> a sp. nov.	M	Dark Spectrum Yellow (78)	Feebly jagged	White	White or Light Buff (Color 1)
	F	Dark Spectrum Yellow (78)	Feebly jagged	White	White or Light Buff (Color 1)
<i>D. aorun</i> sp. nov.	M	Light Cyan (159)	Strongly jagged	White or Pale Sulphur Yellow (Color 79)	White or Light Buff (Color 1)
	F	Light Cyan (159)	Strongly jagged	White	White or Light Buff (Color 1)
<i>D. flavilabre</i> sp. nov.	M	Pale Emerald Green (141) to Light Turquoise Green (146)	Strongly jagged	Pale Greenish Yellow (Color 86)	Pale Buff (1)
	F	Pale Emerald Green (141) to Light Turquoise Green (146)	Strongly jagged	White	White or Light Buff (Color 1)
<i>D. panchi</i> sp. npv.	F	—	Strongly jagged	White	White or Light Buff (Color 1)
<i>D. panlong</i> sp. nov.	M	—	Smooth	White	White
<i>D. qilin</i> sp. nov.	M	Light Sulphur Yellow (Color 93)	Strongly jagged	White	Light Sulphur Yellow (93)
	F	Light Sulphur Yellow (Color 93)	Strongly jagged	White	White
<i>D. batangense</i>	M	Pale Cyan (157)	Strongly jagged	Sulphur Yellow (Color 79)	Sulphur Yellow (Color 79)

	F	Pale Cyan (157)	Strongly jagged	White	White or Light Buff (Color 1)
<i>D. drukdaypo</i>	M	—	Strongly jagged	White	White or Light Buff (Color 1)
	F	—	Strongly jagged	White	White or Light Buff (Color 1)
<i>D. dymondi</i>	M	—	Smooth	White	White or Light Buff (Color 1)
	F	—	Smooth	White	White or Light Buff (Color 1)
<i>D. flaviceps</i>	M	—	Strongly jagged	White	White or Light Buff (Color 1)
	F	—	Strongly jagged	White	White or Light Buff (Color 1)
<i>D. swild</i>	M	—	Smooth	White	White or Light Buff (Color 1)
	F	—	Smooth	White	White or Light Buff (Color 1)
<i>D. vela</i>	M	—	Strongly jagged	White	White or Light Buff (Color 1)
	F	—	Strongly jagged	White	White or Light Buff (Color 1)
<i>D. yulongense</i>	M	Chartreuse (89) to Opaline Green (106)	Strongly jagged	White	Pale Green (99) to Chartreuse (89)
	F	Chartreuse (89) to Opaline Green (106)	Strongly jagged	White	White or Light Buff (Color 1)

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. “–” indicate missing data. Museum abbreviations include: CAS= California Academy of Sciences, USA; MVZ= 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
KIZ029704	<i>Diploderma angustelinea</i>	Muli, Sichuan, China	MT57793 0	MT5780 09	MT6590 49	MT6590 93
KIZ029705	<i>D. angustelinea</i>	Muli, Sichuan, China	MT57792 4	MT5779 98	MT6590 44	MT6590 87
KIZ029708	<i>D. angustelinea</i>	Muli, Sichuan, China	MT57793 1	MT5779 93	MT6590 50	MT6590 94
KIZ029710	<i>D. angustelinea</i>	Muli, Sichuan, China	MT57792 7	MT5780 05	–	MT6590 90
KIZ032488	<i>D. angustelinea</i>	Muli, Sichuan, China	MT57792 5	MT5780 06	MT6590 45	MT6590 88
KIZ032489	<i>D. angustelinea</i>	Muli, Sichuan, China	MT57792 6	MT5779 94	MT6590 46	MT6590 89
KIZ032490	<i>D. angustelinea</i>	Muli, Sichuan, China	MT57792 8	MT5780 00	MT6590 47	MT6590 91
KIZ032491	<i>D. angustelinea</i>	Muli, Sichuan, China	MT57792 9	MT5779 92	MT6590 48	MT6590 92
KIZ032733	<i>D. aorun</i>	Benzilan, Yunnan, China	MT57793 8	MT5779 64	MT6590 52	MT6590 96
KIZ032734	<i>D. aorun</i>	Benzilan, Yunnan, China	MT57793 9	MT5779 90	MT6590 53	MT6590 97
KIZ032735	<i>D. aorun</i>	Benzilan, Yunnan, China	MT57793 7	MT5779 89	–	MT6590 95
KIZ032736	<i>D. aorun</i>	Benzilan, Yunnan, China	MT57793 6	–	MT6590 51	–

KIZ032737	<i>D. aorun</i>	Benzilan, Yunnan, China	MT57794 0	MT5779 77	MT6590 54	MT6590 98
KIZ019278	<i>D. batangense</i>	Zhubalong, Markam, Tibet, China	MT57793 2	—	—	—
KIZ019279	<i>D. batangense</i>	Zhubalong, Markam, Tibet, China	MT57793 3	—	—	—
KIZ 019281	<i>D. batangensis</i>	Batang, Sichuan, China	MT57793 4	—	—	—
KIZ 19314	<i>D. batangensis</i>	Zhubalong, Markam, Tibet, China	MT57793 5	MT5779 91	—	—
KIZ 040147	<i>D. dymondi</i>	Panzhihua, Sichuan, China	MT57789 9	—	—	—
KIZ 040148	<i>D. dymondi</i>	Panzhihua, Sichuan, China	MT57790 0	—	—	—
KIZ 040149	<i>D. dymondi</i>	Panzhihua, Sichuan, China	MT57790 1	—	—	—
KIZ019575	<i>D. flaviceps</i>	Kangding, Sichuan, China	MT57789 6	MT5779 71	MT6590 61	MT6591 07
KIZ019576	<i>D. flaviceps</i>	Kangding, Sichuan, China	MT57789 7	MT5779 68	MT6590 62	MT6591 08
KIZ019577	<i>D. flaviceps</i>	Kangding, Sichuan, China	MT57789 5	MT5779 70	—	MT6591 06
KIZ019578	<i>D. flaviceps</i>	Kangding, Sichuan, China	MT57789 4	MT5779 69	MT6590 60	MT6591 05
KIZ019579	<i>D. flaviceps</i>	Kangding, Sichuan, China	MT57789 8	MT5779 67	MT6590 63	MT6591 09
KIZ032692	<i>D. flavilabre</i>	Baiyu, Sichuan, China	MT57791 6	MT5780 02	MT6590 37	MT6590 79
KIZ032694	<i>D. flavilabre</i>	Baiyu, Sichuan, China	MT57791 7	MT5780 01	MT6590 38	MT6590 80
KIZ032695	<i>D. flavilabre</i>	Baiyu, Sichuan, China	MT57791 8	MT5780 03	MT6590 39	MT6590 81

KIZ032696	<i>D. flavilabre</i>	Baiyu, Sichuan, China	MT57791 9	MT5780 04	MT6590 40	MT6590 82
KIZ032697	<i>D. flavilabre</i>	Baiyu, Sichuan, China	MT57791 5	MT5780 07	MT6590 36	MT6590 78
KIZ032698	<i>D. flavilabre</i>	Baiyu, Sichuan, China	MT57792 0	MT5779 99	MT6590 41	MT6590 83
KIZ027697	<i>D. iadinum</i>	Degong Village, Yunling, Deqin, Yunnan, China	MT57795 6	MT5779 87	MT6590 34	MT6590 76
KIZ027702	<i>D. iadinum</i>	Degong Village, Yunling, Deqin, Yunnan, China	MT57795 7	MT5779 88	MT6590 35	MT6590 77
KIZ027706	<i>D. iadinum</i>	Degong Village, Yunling, Deqin, Yunnan, China	MT57795 5	MT5779 86	MT6590 33	MT6590 75
KIZ027691	<i>D. laeviventre</i>	Basu, Markam, Tibet, China	MT57789 2	MT5779 65	MT6590 31	MT6590 73
KIZ027692	<i>D. laeviventre</i>	Basu, Markam, Tibet, China	MT57789 3	MT5779 66	MT6590 32	MT6590 74
KIZ032715	<i>D. panchi</i>	Yajiang, Sichuan, China	MT57794 6	MT5779 80	MT6590 56	MT6591 00
KIZ032716	<i>D. panchi</i>	Yajiang, Sichuan, China	MT57794 4	MT5779 82	MT6590 55	MT6590 99
KIZ032717	<i>D. panchi</i>	Yajiang, Sichuan, China	MT57794 7	MT5779 81	MT6590 57	MT6591 01
KIZ032729	<i>D. panchi</i>	Yajiang, Sichuan, China	MT57794 5	MT5779 83	—	—
KIZ 040136	<i>D. panlong</i>	Miansha, Liangshan, Sichuan, China	MT57790 6	—	—	—
KIZ 040138	<i>D. panlong</i>	Miansha, Liangshan, Sichuan, China	MT57790 7	—	—	—
KIZ 040139	<i>D. panlong</i>	Miansha, Liangshan, Sichuan, China	MT57790 8	—	—	—
KIZ 040140	<i>D. panlong</i>	Miansha, Liangshan, Sichuan, China	MT57790 5	—	—	—

KIZ 040141	<i>D. panlong</i>	Miansha, Liangshan, Sichuan, China	MT57790 9	—	—	—
KIZ 040143	<i>D. panlong</i>	Miansha, Liangshan, Sichuan, China	MT57790 4	—	—	—
KIZ027543	<i>D. slowinskii</i>	Fugong, Gongshan, Yunnan, China	MT57791 0	MT5779 58	MT6590 27	MT6590 69
KIZ027544	<i>D. slowinskii</i>	Fugong, Gongshan, Yunnan, China	MT57791 1	MT5779 60	MT6590 28	MT6590 70
KIZ027572	<i>D. slowinskii</i>	Qiunatong, Gongshan, Yunnan, China	MT57791 2	MT5779 59	MT6590 29	MT6590 71
KIZ027573	<i>D. slowinskii</i>	Qiunatong, Gongshan, Yunnan, China	MT57791 3	MT5779 61	MT6590 30	MT6590 72
KIZ034893	<i>D. swild</i>	Panzhihua, Sichuan, China	MN26629 7	MT5779 72	MT6590 64	MT6591 11
KIZ034894	<i>D. swild</i>	Panzhihua, Sichuan, China	MN26630 0	MT5779 76	—	MT6591 14
KIZ034895	<i>D. swild</i>	Panzhihua, Sichuan, China	MN26629 8	MT5779 73	MT6590 65	MT6591 12
KIZ034914	<i>D. swild</i>	Panzhihua, Sichuan, China	MN26629 9	MT5779 75	MT6590 66	MT6591 13
KIZ034915	<i>D. swild</i>	Panzhihua, Sichuan, China	MN26630 1	MT5779 74	MT6590 67	MT6591 15
KIZ029711	<i>D. varcoae</i>	Dali, Yunnan, China	MT57790 2	MT5779 62	MT6590 68	MT6591 16
KIZ027672	<i>D. vela</i>	Tongsha, Markam, Tibet, China	MT57794 9	MT5780 11	MT6590 59	MT6591 04
KIZ027673	<i>D. vela</i>	Tongsha, Markam, Tibet, China	MT57794 8	MT5780 10	MT6590 58	MT6591 03
KIZ028291	<i>D. yulongense</i>	Middle Hutiaoxia, Shangrila, Yunnan, China	MT57792 1	MT5779 79	—	MT6590 86
KIZ028292	<i>D. yulongense</i>	Middle Hutiaoxia, Shangrila, Yunnan, China	MT57792 2	MT5779 78	MT6590 43	MT6590 85

KIZ028300	<i>D. yulongense</i>	Baishuitai, Shangrila, Yunnan, China	MT57792 3	MT5780 08	MT6590 42	MT6590 84
KIZ 040193	<i>D. yunnanense</i>	Yingjiang, Yunnan, China	MT57791 4	—	—	—
KIZ 027627	<i>D. drukdaypo</i>	Jinduo, Chamdo, Tibet, China	MT57795 0	MT5780 13	—	—
KIZ 027628	<i>D. drukdaypo</i>	Zhuka, Chamdo, Tibet, China	MT57759 2	MT5780 12	—	—
KIZ 027629	<i>D. drukdaypo</i>	Zhuka, Chamdo, Tibet, China	MT57759 3	—	—	—
KIZ 016486	<i>D. drukdaypo</i>	Chamdo City, Tibet, China	MT57795 1	—	—	MT6591 02
KIZ 027630	<i>D. drukdaypo</i>	Zhuka, Chamdo, Tibet, China	MT57795 4	MT5780 14	—	—
KIZ 028332	<i>D. qilin</i>	Balong, Deqin, Yunnan, China	MT57794 1	MT5779 95	—	—
KIZ 028335	<i>D. qilin</i>	Balong, Deqin, Yunnan, China	MT57794 3	MT5779 97	—	—
KIZ 028333	<i>D. qilin</i>	Balong, Deqin, Yunnan, China	MT57794 2	MT5779 96	—	—
WK-JK 011	<i>D. varcoae</i>	Yuxi, Yunnan, China	MT57790 3	MT5779 63	—	—
KIZ 034923	<i>D. chapaense</i>	Lvchun, Honghe, Yunnan, China	MG21426 3	MK0015 26	MK0014 94	MK0014 74
KIZ 019276	<i>D. batangense</i>	Batang, Sichuan, China	MK00141 3	—	—	—
KIZ 09404	<i>D. batangense</i>	Zhubalong, Tibet, China	MK00141 2	—	—	—
NMNS 19607	<i>D. brevipes</i>	Taiwan, China	MK00142 9	MK0015 40	MK0015 06	MK0014 64
NMNS 19608	<i>D. brevipes</i>	Taiwan, China	MK00143 0	MK0015 41	MK0015 07	MK0014 65

KIZ 040145	<i>D. chapaense</i>	Dali, Yunnan, China	MK57866 7	—	—	—
KIZ 046954	<i>D. chapaense</i>	Jingdong, Yunnan, China	MK57866 0	—	—	MT6591 17
KIZ 046970	<i>D. chapaense</i>	Jingdong, Yunnan, China	MK57865 9	—	—	MT6591 18
KIZ 047085	<i>D. chapaense</i>	Jingdong, Yunnan, China	MK57866 1	—	—	MT6591 19
KIZ 034921	<i>D. chapaense</i>	Lvchun, Yunnan, China	MG21426 4	MK0015 25	MK0015 02	MK0014 75
ZMMU NAP- 01911	<i>D. chapaense</i>	Chapa, Vietnam	MG21426 2	—	—	—
KIZ 040639	<i>D. dymondi</i>	Dongchuan, Yunnan, China	MK00142 2	MK0015 45	MK0015 13	MK0014 77
KIZ 040640	<i>D. dymondi</i>	Dongchuan, Yunnan, China	MK00142 3	MK0015 46	MK0015 14	MK0014 78
KIZ 01851	<i>D. flaviceps</i>	Luding, Sichuan, China	MK00141 6	MK0015 28	MK0015 12	Mk0014 73
KIZ 01852	<i>D. flaviceps</i>	Luding, Sichuan, China	MK00141 7	MK0015 44	MK0015 05	Mk0014 72
KIZ 014037	<i>D. laeviventre</i>	Basu, Markam, Tibet, China	MK00140 7	MK0015 29	—	MK0014 66
NMNS19604	<i>D. luei</i>	Taiwan, China	MK00143 3	MK0015 32	MK0015 10	MK0014 62
NMNS19605	<i>D. luei</i>	Taiwan, China	MK00143 4	MK0015 33	MK0015 11	MK0014 63
NMNS19609	<i>D. makii</i>	Taiwan, China	MK00143 1	MK0015 36	MK0015 08	MK0014 60
NMNS19610	<i>D. makii</i>	Taiwan, China	MK00143 2	MK0015 37	MK0015 09	MK0014 61
KIZ 023231	<i>D. micangshanense</i>	Xixia, Henan, China	MK57866 4	—	—	—

KIZ032801	<i>D. micangshanense</i>	Shiyan,Hubei, China	MK57866 5	MT5779 84	—	MT6591 10
KIZ032802	<i>D. micangshanense</i>	Shiyan,Hubei, China	MK57866 6	MT5779 85	—	—
KIZ06850	<i>D. micangshanense</i>	Longnan, Gansu, China	MK00142 4	MK0015 59	—	MK0014 52
WK-JK 037	<i>D. micangshanense</i>	Wenxian, Gansu, China	MK57866 2	—	—	—
WK-JK 038	<i>D. micangshanense</i>	Wenxian, Gansu, China	MK57866 3	—	—	—
NMNS 19598	<i>D. polygonatum</i>	Taiwan, China	MK00142 7	MK0015 38	MK0015 15	MK0014 58
NMNS 19599	<i>D. polygonatum</i>	Taiwan, China	MK00142 8	MK0015 39	MK0015 16	MK0014 59
CAS 214906	<i>D. slowinskii</i>	Gongshan, Yunnan, China	MK00140 5	—	—	—
CAS 214954	<i>D. slowinskii</i>	Gongshan, Yunnan, China	MK00140 6	—	—	—
KIZ 015973	<i>D. splendidum</i>	Yichang, Hubei, China	MK00141 8	MK0015 22	MK0014 92	MK0014 76
NMNS 19592	<i>D. swinhonis</i>	Taiwan, China	MK00141 9	MK0015 34	MK0014 95	MK0014 56
NMNS 19593	<i>D. swinhonis</i>	Taiwan, China	MK00142 0	MK0015 35	MK0014 96	MK0014 57
KIZ 026132	<i>D. varcoae</i>	Mengzi, Honghe, Yunnan, China	MK00142 1	MK0015 23	MK0014 93	MK0014 71
KIZ 034925	<i>D. vela</i>	Quzika, Markam, Tibet, China	MK00141 5	MK0015 31	MK0014 97	MK0014 49
KIZ 019299	<i>D. vela</i>	Quzika, Markam, Tibet, China	MK00141 4	MK0015 30	MK0014 99	MK0014 48
KIZ 09399	<i>D. yulongense</i>	Xianggelila, Yunnan, China	MK00141 0	MK0015 42	MK0014 98	MK0014 50

KIZ 43196	<i>D. yulongense</i>	Xianggelila, Yunnan, China	MK00141 1	MK0015 43	—	MK0014 51
KIZ 040193	<i>D. yunnanense</i>	Yingjiang, Yunnan, China	MK57865 8	—	—	—
CAS 242271	<i>D. yunnanense</i>	Baoshan, Yunnan, China	MK00140 8	MK0015 27	MK0015 17	MK0014 69
CAS 242183	<i>D. yunnanense</i>	Baoshan, Yunnan, China	MK00140 9	MK0015 24	MK0015 18	MK0014 70
KIZ 019564	<i>D. zhaoermii</i>	Wenchuan, Sichuan, China	MK00142 5	MK0015 47	MK0015 00	MK0014 67
KIZ 019565	<i>D. zhaoermii</i>	Wenchuan, Sichuan, China	MK00142 6	MK0015 48	MK0015 01	MK0014 68
KIZ 015975	<i>Pseudocalotes kakhiensis</i>	Gongshan, Yunnan, China	MK00143 5	MK0015 49	MK0014 89	MK0014 47
CAS 241966	<i>P. kingdonwardi</i>	Dulongjiang, Yunnan, China	MK00143 6	MK0015 50	MK0015 03	MK0014 53
CAS 242628	<i>P. kingdonwardi</i>	Dulongjiang, Yunnan, China	MK00143 7	MK0015 51	MK0015 04	MK0014 54
MVZ 216622	<i>D. zhaoermii</i>	Wenchuan, Sichuan, China	AF12850 0	—	—	—
MVZ 224106	<i>P. brevipes</i>	Vinh Phuc, Vietnam	AF12849 9.1	—	—	—
TNHC 58040	<i>P. flavigula</i>	Perak, Malaysia	AF12850 3.1	—	—	—
CAS 194476	<i>D. splendidum</i>	Yaan, Sichuan, China	AF12850 1	—	—	—
—	<i>Acanthosaura lepidogaster</i>	—	AF12849 9	MK0015 52	MK0014 90	MK0014 55
CAS 223063	<i>Calotes emma</i>	—	DQ28946 0	—	—	MK7925 30

Supplementary table S1. Specimens of recognized species of the genus *Diploderma* examined in this study. Museum abbreviations include the following: Museum of Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ); 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 (UHM), London, UK; and Smithsonian National Museum of Natural History (USNM), Washington D.C., USA.

D. batangense (n=18): KIZ 019276–019279, 019281, 019282, 019285, 019286, 044729, 044731, 044765, 044766, 044769, 044783, 044787 (topotypes), Batang, Sichuan, China; KIZ 09404, 019312, 019314, Mangkang, Tibet, China.

D. chapaense (n=6): CIB 2679/583623, KIZ 047085, Jingdong, Yunnan Province, China. KIZ 040145, Dali, Yunnan, China; KIZ 034921–23, Lvchun, Yunnan, China.

D. drukdaypo (n=8): KIZ 027616 (holotype), KIZ 027618, 027619, 027628–027630 (paratypes), Chaya, Chamdo, Tibet, China; KIZ 016486 (paratype), Karuo, Chamdo, Tibet, China.

D. dymondi (n=20): KIZ 040639, 040640 (topotypes), Dongchuan, Yunnan, China; KIZ 040147–040153, CIB 1869/755156, City of Panzhihua, Panzhihua District, Sichuan, China; KIZ 95I1001, 95I1002, 95I1016, 95I1018, 95I1022, KIZ 040645–48, Dayao, Yunnan, China; CIB 1870/65I5020, Yuzha, Huili County, Liangshan Prefecture, Sichuan, China.

D. fasciatum (n=3): CIB 2620–2622, Peng County, Sichuan, China.

D. flaviceps (n=15): CIB 2234, 2332, 2333, 2341, 2354, 2355, 2549, 2554, 2556, 2561, 2567; KIZ 05181, 05182, 84001 (topotypes), Luding, Sichuan, China; KU 208076 (topotype), Luding, Sichuan, China.

D. grahami (n=1): USMN 65500 (holotype), Yibin, Sichuan, China.

D. hamptoni (n=1): BMNH 1908.9.18.1/1946.8.14.1 (holotype), Mogok, Myanmar.

D. iadinum (n=16): KIZ 019321 (holotype), 09398 (allotype), 09401–03, 019322, 019325–019328 (paratypes), Ninong, Deqin, Yunnan, China; KIZ 027702–05, Yunling, Deqin, Yunnan, China.

D. laeviventre (n=5): KIZ 014038 (holotype), 014037, 014041–014043 (paratypes), Markam, Tibet, China.

- D. makii* (n=2): MCZ R-172743 (paratype), R-181443, Nantong, Taiwan, China.
- D. micangshanense* (n=9): CIB 86348, 86351, Xianyang, Shaanxi, China; CIB 86356, 86357, 86360, 86361, Luonan, Shaanxi, China; CIB 2572, 2578, 2582, Wenxian, Gansu, China.
- D. polygonatum* (n=11): MCZ 45954, 45956 (paratypes), CAS 21215, 21355, 21243, 21221, 21244, Okinawa, Japan.
- D. splendidum* (n=6): USNM 35522 (holotype), Yichang, Hubei, China; CIB 2588, 2591, 2596, 72468, 72469, Chongqing, China.
- D. slowinskii* (n=11): KIZ 027541, 027543, 027572–74, 027577, 027579, 027595, 027596, 027598, 027600 (topotypes), Nujiang Prefecture, Yunnan, China.
- D. swild* (n=8): KIZ 034912 (holotype), 034894, 034913, 034914, 040125–27 (paratopotypes), Panzhihua, Sichuan, China; CIB 1871/105074 (paratype), Xichang, Liangshan Prefecture, Sichuan, China.
- D. swinhonis* (n=4): CAS 18085, 18089, 18098, 18099, Taiwan, China.
- D. varcoae* (n=15): KIZ 85I0006, 85I0009, 83001, 034294 (topotypes), Kunming, Yunnan, China; KIZ 015691, Yuxi, Yunnan, China; KIZ 015689, Mengzi, Honghe Prefecture, Yunnan, China; CIB 2682/625219, 2659/625233, 2657/625212, 2660/625213, 2668/625214, 2667/625215, 2666/625217, 2662/625218, 2658/625221, 2679/583623, Jizu Mountain, Dali, Yunnan Province.
- D. vela* (n=31): KIZ 013801 (holotype), KIZ 013802, 013813, 013800, 013805–013811 (paratypes), Jerkalo, Tibet, China; KIZ 027641, 027645–49, Rumei, Markam, Tibet, China; KIZ 027668, 027670–73, Tongsha, Markam, Tibet, China; KIZ 027667, 027693–695, Foshan, Deqin, Yunnan, China; KIZ 027680, 027681, Xilu, Deqin, Yunnan, China; KIZ 027682, 027684, Xidang, Deqin, Yunnan, China.
- D. yulongense* (n=15): KIZ 09399, 09400, 028291–028293, 028294, 028296–028298, 028299, 028300, 028303, 028342–028344, Xianggelila County, Yunnan, China.
- D. yunnanense* (n=8): CIB 2684, 2686, 2687, 2689, KIZ 82081 (topotypes), Longling, Yunnan, China; KIZ 74II0240, 0248, 79I469, Tengchong, Yunnan, China; KIZ 040193, Yingjiang, Yunnan, China.
- D. zhaoermii* (n=14): CIB 2690 (holotype), 86432, 86435, 85721, 85722, 86433, 86434, 86436, Wenchuan, Sichuan, China; CIB 2232, 2244, 2240, KIZ 84032, 85030, Lixian, Sichuan, China.

Supplementary table S2. Subsets of specimens used for morphometric analyses. Museum abbreviations include KIZ: Museum of Kunming Institute of Zoology, Chinese Academy of Sciences; and CIB: Chengdu Institute of Biology, Chinese Academy of Sciences.

Males

Diploderma angustelinea (n=4): KIZ 029703, 044484, 044796, 044797.
D. aorun (n=6): KIZ 032734, 032736, 032737, 044431, 044735, 044764.
D. batangense (n=8): KIZ 019276–019279, 019314, 044765, 044766, 044783.
D. flaviceps (n=5): KIZ 019577, 032683, 032684, 84001, 208076.
D. flavilabre (n=3): KIZ 032692–032694.
D. panlong (n=3): KIZ 040137–040139.
D. qilin (n=7): KIZ 028332, 028333, 044405, 044407, 044412, 044413, 044745.
D. swild (n=3): CIB 1871/10507, KIZ 034912, 040935.
D. yulongense (n=5): KIZ 028292, 028294, 028296, 028298, 028343.

Females

D. angustelinea (n=4): KIZ 029706–029708
D. aorun (n=4): KIZ 032735, 044432, 044433, 044742.
D. batangense (n=8): KIZ 019281, 019285, 019286, 019312, 044729, 044731, 044769, 044787.
D. drukdaypo (n=5): KIZ 026729, 027018, 027617, 027619, 027630.
D. flaviceps (n=3): KIZ 019578, 032685, 57785/5182.
D. flavilabre (n=6): KIZ 032695–032699, 032730.
D. panchi (n=3): KIZ 032715–032717.
D. qilin (n=6): KIZ 028334–028336, 044408, 044744, 044820.
D. swild (n=4): KIZ 034913, 040125–040127.
D. yulongense (n=5): KIZ 028293, 028299, 028300, 028342, 028344.

Supplementary table S3. Subsets of specimens used for pholidosis analyses. Museum abbreviations include KIZ: Museum of Kunming Institute of Zoology, Chinese Academy of Sciences; and KU: University of Kansas Biodiversity Institute.

Diploderma angustelinea (n=10): KIZ 029703, 029703–029708, 029710, 044484, 044796, 044797.

D. aorun (n=11): KIZ 032734–032737, 044431–044433, 044735, 044740, 044742, 044764.

D. batangense (n=10): KIZ 019276–019279, 019281, 019285, 019286, 019312, 019314, 09404.

D. drukdaypo (n=8): KIZ 016486, 026729, 027018, 027616, 027617, 027619, 027628, 027630.

D. flaviceps (n=10): KIZ 019575–019579, 032683, 032685, 57785, 84401; KU 208076.

D. flavilabre (n=9): KIZ 032692–032730.

D. panlong (n=7): KIZ 040137–040143.

D. panchi (n=4): KIZ 032715–032717, 032729.

D. qilin (n=13): KIZ 028332–028336, 044405, 044407, 044408, 044412, 044413, 044744, 044745, 044820.

D. swild (n=8): KIZ 034894, 034912–034914, 040124–040127.

D. yulongense (n=10): KIZ 28292–28294, 28296–28298, 28303, 28342–28344.

Supplementary table S5. Summary Statistics of the PCA analyses of the pholidosis characters among selected members of the *Diploderma flaviceps* complex. Morphological abbreviations are the followings: 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-riotal scale count (PRS); Finger IV subdigital lamellae count (F4S); Toe IV subdigital lamellae count (T4S); and middorsal scale count (MD).

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Standard deviation	1.8711	1.3269	1.1981	0.9961	0.8349	0.7739	0.6535	0.5307	0.4268	0.3523
Proportion of										
Variance	0.3501	0.1761	0.1435	0.0992	0.0697	0.0599	0.0427	0.0282	0.0182	0.0124
Cumulative										
Proportion	0.3501	0.5261	0.6697	0.7689	0.8386	0.8985	0.9412	0.9694	0.9876	1.0000
Eigen	3.5009	1.7606	1.4354	0.9923	0.6970	0.5990	0.4271	0.2816	0.1821	0.1241
MD	-0.2336	0.4587	0.1899	0.3674	-0.3217	0.0258	-0.6062	0.2645	0.1138	0.0966
F4S	0.3547	0.2937	0.4586	-0.0800	0.0175	0.0051	0.0959	-0.0145	-0.6642	0.3469
T4S	0.2587	0.2697	0.5846	-0.2227	0.0849	-0.0325	0.2091	0.0535	0.6067	-0.2148
SL	-0.3961	0.3475	0.0716	0.1181	-0.1855	-0.0085	0.2401	-0.7661	-0.0528	-0.1467
IL	-0.3709	0.3539	-0.1227	0.1446	0.1448	0.1268	0.5792	0.5422	-0.1346	-0.1293
NSL	-0.3289	-0.0718	0.1690	-0.4004	0.2053	0.7789	-0.2067	-0.0414	-0.0279	0.0616
POT	-0.1379	0.4206	-0.2491	-0.4477	0.5229	-0.4160	-0.3018	-0.0407	-0.0457	-0.0153
PTY	0.2965	0.3585	-0.4718	-0.1052	-0.1841	0.2616	0.1653	-0.0863	0.3182	0.5582
PRS	0.4115	0.2563	-0.2771	-0.1409	-0.2547	0.2641	-0.1327	0.0191	-0.2222	-0.6829

SOR	-0.2717	-0.0908	0.0423	-0.6184	-0.6476	-0.2534	0.0878	0.1869	-0.0588	0.0635
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Supplementary table S6. Summary Statistics of the PCA analyses of the morphometric characters of males among selected members of the *Diploderma flaviceps* complex. Morphological abbreviations are the followings: snout–vent length (SVL); tail length (TAL); head width (HW); head length (HL); head depth (HD); snout–eye length (SEL); forelimb length (FLL); hind limb length (HLL); and trunk length (TRL).

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Standard deviation	2.7480	0.8691	0.5306	0.4227	0.2979	0.2415	0.1921	0.1769	0.1336
Proportion of Variance	0.8390	0.0839	0.0313	0.0199	0.0099	0.0065	0.0041	0.0035	0.0020
Cumulative Proportion	0.8390	0.9230	0.9542	0.9741	0.9840	0.9904	0.9945	0.9980	1.0000
eigen	7.5513	0.7553	0.2816	0.1787	0.0888	0.0583	0.0369	0.0313	0.0178
SVL	0.3574	-0.0148	0.0463	-0.2622	0.1251	-0.3641	0.0699	-0.3176	-0.7397
TAL	0.2585	0.7448	0.3993	0.4019	-0.0415	-0.1632	-0.1396	0.0972	0.0109
HL	0.3480	-0.2441	0.0640	0.1289	0.3305	-0.5121	0.4534	0.0287	0.4698
HW	0.3395	-0.3616	0.0340	0.0726	-0.1971	-0.2084	-0.7761	-0.1441	0.2055
HD	0.3400	-0.2668	0.1433	0.2893	-0.7005	0.2285	0.3883	0.0114	-0.1230
SEL	0.3446	-0.1980	0.1093	0.3206	0.5806	0.6039	-0.0704	0.0030	-0.1433
FLL	0.3363	0.1131	-0.6594	0.0260	-0.0261	-0.0683	-0.0633	0.6396	-0.1417
HLL	0.3303	0.3556	-0.4571	-0.1565	-0.0679	0.2467	0.0893	-0.5999	0.3125
TRL	0.3354	0.0713	0.3960	-0.7323	-0.0379	0.2294	0.0025	0.3146	0.1908

Supplementary table S7. Summary Statistics of the PCA analyses of the morphometric characters of females among selected members of the *Diploderma flaviceps* complex. Morphological abbreviations are the followings: snout–vent length (SVL); tail length (TAL); head width (HW); head length (HL); head depth (HD); snout–eye length (SEL); forelimb length (FLL); hind limb length (HLL); and trunk length (TRL).

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Standard deviation	2.5798	1.1351	0.7141	0.4796	0.3732	0.2833	0.2081	0.1813	0.1427
Proportion of Variance	0.7395	0.1432	0.0567	0.0256	0.0155	0.0089	0.0048	0.0037	0.0023
Cumulative Proportion eigen	0.7395	0.8827	0.9393	0.9649	0.9804	0.9893	0.9941	0.9977	1
SVL	6.6556	1.2884	0.5099	0.2300	0.1392	0.0803	0.0433	0.0329	0.0204
TAL	-0.3566	-0.2847	0.2007	-0.0537	0.0234	-0.4500	0.0813	-0.1652	0.7153
HL	-0.2778	0.5397	0.1951	-0.5713	-0.2195	-0.1334	-0.4439	-0.0328	-0.0551
HW	-0.363	-0.1057	-0.3960	-0.0614	0.1424	-0.3334	0.1342	-0.5654	-0.4768
HD	-0.3559	-0.2648	-0.2276	0.1305	0.2832	-0.1858	-0.4791	0.6087	-0.1403
SEL	-0.3646	-0.0582	-0.0979	-0.4616	0.4168	0.5939	0.3016	0.0789	0.1318
FLL	-0.3452	0.0213	-0.4930	0.1551	-0.7142	0.2396	0.0779	0.0968	0.1740
HLL	-0.3415	0.2709	0.2118	0.5936	0.2140	0.3547	-0.3254	-0.3557	0.0937
TRL	-0.3195	0.4407	0.2476	0.2419	0.0342	-0.2567	0.5880	0.3731	-0.1785
	-0.2578	-0.5243	0.5951	-0.0449	-0.3464	0.1794	0.0095	-0.0125	-0.3873

Supplementary table S8. Detailed morphological measurements and pholidosis characters of majority of the type specimens of the six new species described. All raw measurements are in the unit of mm. “–” indicates not available due to missing tail or missing digit. KIZ: Kunming Institute of Zoology, Chinese Academy of Sciences. Morphological abbreviations are the followings: snout–vent length (SVL); tail length (TAL); head width (HW); head length (HL); head depth (HD); snout–eye length (SEL); forelimb 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-riotal scale count (PRS); Finger IV subdigital lamellae count (F4S); Toe IV subdigital lamellae count (T4S); middorsal scale count (MD). All morphometric measurements (SVL, TAL, HL, HW, HD, SEL, FLL, HLL, T4L, TRL) are in the unit of mm. HT: holotype; PT: paratype; PTT: paratopotype.

(1)

<i>Diploderma angustelinea</i> sp. nov.										
Museum Catalog Number	KIZ 029703	KIZ 044484	KIZ 044796	KIZ 044797	KIZ 029704	KIZ 029706	KIZ 029708	KIZ 029710	KIZ 029705	KIZ 029707
Type Status	HT	PTT	PTT	PTT	PTT	PTT	PTT	PTT	PTT	PTT
Sex	M	M	M	M	F	F	F	F	F	F
SVL	57.6	59.3	60.2	56.8	67.8	66.8	62.6	62.9	59.0	59.8
TAL	132.5	137.1	149.9	130.9	–	129.8	136.4	–	115.0	133.0
HL	16.0	17.9	17.9	17.1	19.0	19.4	17.1	17.7	16.3	17.5
HW	11.3	12.6	12.0	11.4	14.0	13.2	11.7	11.9	11.2	11.7
HD	8.6	9.3	9.3	8.9	10.2	10.2	9.1	9.4	8.3	8.7
SEL	5.9	7.3	7.0	6.9	6.8	7.1	6.2	6.4	5.9	6.7
FLL	26.4	27.6	27.5	27.1	27.7	29.0	27.2	29.0	26.8	25.8
HLL	45.5	42.1	46.7	45.6	50.5	50.1	46.6	49.8	45.1	45.4
T4L	11.7	10.5	11.3	11.4	11.9	12.0	11.7	13.1	12.5	12.3
TRL	27.4	28.0	29.3	26.6	32.2	32.3	30.6	31.0	29.5	27.9

TAL/SVL (%)	230.2	231.4	249.1	230.5	–	194.3	217.7	–	195.1	222.3
HL/SVL (%)	27.8	30.1	29.7	30.0	28.0	29.0	27.3	28.1	27.6	29.3
HW/HL (%)	70.6	70.8	66.8	66.6	73.9	68.1	68.4	67.2	68.8	67.0
SEL/HL (%)	36.9	40.7	38.9	40.3	35.7	36.7	36.2	36.4	36.6	38.4
HL/SnL (%)	40.2	73.0	76.4	76.0	67.1	74.6	70.6	74.4	68.8	70.6
HD/HW (%)	75.8	73.3	77.7	78.7	72.7	76.9	78.1	79.3	74.5	73.8
FLL/SVL (%)	45.8	46.5	45.7	47.7	40.8	43.4	43.4	46.2	45.5	43.1
HLL/SVL (%)	79.1	71.1	77.6	80.2	74.6	75.0	74.4	79.2	76.5	75.9
TRL/SVL (%)	47.5	47.2	48.7	46.9	47.6	48.3	48.9	49.3	50.0	46.6
SL	9/9	10/9	9/10	10/9	10/9	9/9	9/10	9/9	10/10	9/8
IL	9/10	10/9	10/11	10/10	11/10	10/10	11/10	11/10	11/11	10/10
NSL	1/1	1/1	1/1	1/1	2/2	1/1	2/1	1/2	1/1	1/1
MD	45	44	48	45	47	41	41	47	49	45
F4S	16/16	17/17	16/16	17/17	19/17	15/15	17/17	16/17	17/19	15/14
T4S	24/26	25/24	22/24	22/21	25/25	24/24	22/23	25/22	24/23	21/21
SOR	3/4	5/5	3/3	4/4	4/4	3/3	4/4	4/4	4/4	3/3
POS	4/5	3/4	3/4	2/3	4/4	4/4	4/4	5/5	4/1	4/5
PTY	2/4	3/2	2/3	3/3	2/2	3/3	1/1	2/3	3/1	2/4
PRS	2/2	2/1	0/1	2/3	0/1	1/1	0/0	1/0	1/1	2/3

(2)

Diploderma aorun sp. nov.

Museum Catalog	KIZ	KIZ	KIZ	KIZ	KIZ	KIZ	KIZ	KIZ	KIZ	KIZ	KIZ
Number	044735	044431	044740	044764	032734	032737	032736	032735	044742	044433	044432
Type Status	HT	PT	PT	PT	PT	PT	PT	PT	PT	PT	PT
Sex	M	M	M	M	M	M	M	F	F	F	F
SVL	56.3	56.9	58.6	59.2	60.5	58.4	61.2	64.9	60.8	66.5	63.0
TAL	120.2	124.3	–	128.1	128.3	126.8	135.4	132.2	117.8	127.4	130.8
HL	17.1	17.1	18.4	17.3	18.0	17.0	18.0	18.6	16.6	19.5	19.0

HW	12.4	11.6	13.0	12.3	13.0	12.1	12.6	13.1	11.7	13.0	12.8
HD	9.4	9.0	9.5	8.8	10.1	8.7	10.1	10.2	9.1	8.7	9.4
SEL	7.0	7.0	7.1	6.6	7.1	6.7	7.1	7.1	6.2	7.9	8.0
FLL	27.2	28.7	27.2	29.4	28.1	25.6	30.0	29.2	28.4	31.3	33.3
HLL	45.5	47.0	45.7	47.3	45.9	43.1	48.6	46.6	43.4	51.5	50.7
T4L	10.5	10.4	9.7	11.1	10.1	9.3	12.2	10.9	8.9	11.7	12.2
TRL	25.3	27.0	28.3	27.3	29.2	27.9	29.0	30.9	31.0	32.3	31.0
TAL/SVL (%)	213.6	218.5	—	216.3	216.9	221.1	212.0	203.8	193.9	191.4	207.7
HL/SVL (%)	30.4	30.0	31.4	29.2	29.2	29.4	29.7	28.7	27.3	29.3	30.2
HW/HL (%)	72.7	67.8	70.5	71.0	71.2	69.9	72.2	70.4	70.2	66.8	67.2
SEL/HL (%)	40.8	40.9	38.8	38.1	39.6	39.3	39.3	38.0	37.4	40.2	42.2
HD/HW (%)	75.8	77.9	73.4	71.4	71.6	80.2	77.8	78.0	77.7	66.7	73.6
FLL/SVL (%)	48.3	50.4	46.4	49.6	43.7	48.9	46.3	45.0	46.7	47.1	52.8
HLL/SVL (%)	80.8	82.7	77.9	79.9	73.7	79.4	75.9	71.8	71.5	77.4	80.5
TRL/SVL (%)	44.9	47.4	48.2	46.2	47.8	47.4	48.2	47.6	51.1	48.5	49.3
SL	9/8	9/9	7/8	9/9	8/9	10/9	9/10	9/9	8/9	10/9	11/10
IL	11/11	10/10	9/10	10/10	10/10	11/9	11/9	10/11	11/11	11/11	13/11
NSL	1/1	1/1	2/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	2/2
MD	38	40	35	42	36	44	38	40	39	38	46
F4S	14/15	15/17	15/15	15/15	15/15	17/16	19/17	15/15	12/13	15/16	18/16
T4S	21/21	20/21	20/20	20/17	21/21	21/20	24/24	20/21	16/17	19/20	24/24
SOR	3/3	4/4	3/3	3/3	3/3	3/4	5/5	4/4	3/4	3/5	4/4
POS	4/3	2/2	4/4	3/3	2/3	4/3	3/3	3/3	1/3	3/3	3/3
PTY	6/5	6/4	5/6	5/6	4/3	3/4	3/2	3/4	4/3	4/5	5/5
PRS	4/5	5/5	6/7	4/5	1/2	3/3	3/3	2/3	2/2	4/4	2/3

(3)

***Diploderma flavilabre* sp. nov.**

Museum Catalog Number	KIZ 032693	KIZ 032692	KIZ 032694	KIZ 032696	KIZ 032695	KIZ 032698	KIZ 032697	KIZ 032730	KIZ 032699
Type Status	HT	PTT	PTT	PTT	PTT	PTT	PTT	PTT	PTT
Sex	M	M	M	F	F	F	F	F	F
SVL	50.8	54.5	55.2	64.2	67.1	72.9	67.7	67.4	66.0
TAL	87.9	81.6	99.0	92.9	100.2	102.2	98.5	98.6	100.5
HL	16.0	17.6	17.2	18.8	19.1	19.8	19.4	19.3	19.3
HW	11.4	12.8	12.2	13.5	13.5	14.2	14.1	13.5	13.7
HD	8.6	9.2	8.5	9.4	9.8	10.4	9.7	10.2	9.5
SEL	6.0	6.9	6.4	6.6	7.2	7.5	7.2	6.8	6.7
FLL	24.5	23.5	25.4	26.8	26.9	29.6	29.5	27.0	27.1
HLL	38.0	36.5	40.1	40.1	41.6	45.0	44.4	42.0	42.2
T4L	9.5	9.9	10.1	9.3	9.5	9.7	10.2	10.1	9.5
TRL	21.3	25.3	25.0	34.6	33.0	39.7	36.5	34.8	35.0
TAL/SVL (%)	172.8	149.7	179.3	144.6	149.4	140.2	145.6	146.3	152.2
HL/SVL (%)	31.5	32.2	31.2	29.3	28.5	27.1	28.6	28.6	29.2
HW/HL (%)	71.2	73.0	70.7	71.7	70.5	71.8	72.9	70.1	71.0
SEL/HL (%)	37.1	39.3	37.4	35.2	37.4	37.7	36.9	35.4	35.0
HD/HW (%)	75.5	71.7	70.1	69.2	72.8	72.9	68.6	75.1	69.7
FLL/SVL (%)	48.3	43.1	46.0	41.7	40.1	40.5	43.5	40.1	41.1
HLL/SVL (%)	74.8	66.9	72.7	62.5	62.0	61.7	65.6	62.4	63.9
TRL/SVL (%)	42.0	46.4	45.3	53.9	49.2	54.4	54.0	51.7	53.0
SL	9/8	9/8	8/9	9/9	8/9	8/10	9/9	9/8	9/8
IL	10/8	9/10	9/9	10/10	8/10	9/9	10/10	10/10	8/9
NSL	1/1	1/1	1/1	1/1	2/2	1/1	1/1	2/1	2/1
MD	41	43	43	41	39	39	41	43	40
F4S	16/16	14/16	16/16	13/14	16/15	14/15	16/15	14/15	16/15
T4S	20/20	22/22	21/22	19/19	21/22	20/19	19/21	19/-	22/22
SOR	3/4	4/4	4/5	4/4	4/4	4/4	4/4	4/4	4/4

POS	7/5	4/4	4/4	3/3	4/3	3/3	5/6	5/5	3/5
PTY	6/6	5/7	6/7	5/4	6/5	4/4	3/5	6/7	4/5
PRS	8/8	7/6	6/5	6/9	8/6	5/5	4/4	5/6	4/6

(4)

Diploderma panchi sp. nov.

Museum Catalog Number	KIZ 032716	KIZ 032717	KIZ 032715	KIZ 032729
Type Status	HT	PTT	PTT	PTT
Sex	F	F	F	F
SVL	67.7	66.0	67.3	59.6
TAL	102.2	93.6	102.0	78.0
HL	19.5	17.8	18.7	17.1
HW	13.5	12.8	13.4	12.6
HD	10.1	8.9	9.2	8.0
SEL	7.2	7.3	6.9	6.8
FLL	26.4	26.0	26.9	24.8
HLL	42.9	39.8	41.2	39.2
T4L	10.1	10.1	9.8	8.8
TRL	36.7	36.5	34.3	29.4
TAL/SVL (%)	151.0	141.8	151.5	—
HL/SVL (%)	28.8	27.0	27.8	28.6
HW/HL (%)	69.5	71.9	71.5	73.6
SEL/HL (%)	36.7	40.9	37.0	39.8
HD/HW (%)	74.3	69.7	68.8	63.3
FLL/SVL (%)	38.9	39.3	40.0	41.7
HLL/SVL (%)	63.4	60.2	61.2	65.8
TRL/SVL (%)	54.3	55.3	51.0	49.3
SL	8/8	9/8	9/8	8/9
IL	10/11	9/9	9/10	9/9
NSL	1/1	1/2	1/1	1/2

MD	46	46	46	42
F4S	15/16	17/15	16/14	15/15
T4S	23/24	20/22	20/20	20/23
SOR	4/4	5/5	5/5	4/5
POS	2/2	3/2	5/3	3/3
PTY	3/2	3/3	4/5	4/6
PRS	4/3	3/4	7/6	4/3

(5)

Diploderma panlong sp. nov.

	KIZ	KIZ	KIZ	KIZ	KIZ	KIZ	KIZ
Museum Catalog Number	040139	040137	040143	040138	040142	040140	040141
Type Status	HT	PTT	PTT	PTT	PTT	PTT	PTT
Sex	M	M	M	M	M (subadult)	M (subadult)	M (subadult)
SVL	64.2	63.1	60.2	71.7	53.7	58.0	54.7
TAL	172.0	160.9	—	178.0	138.0	149.0	139.0
HL	19.5	19.9	18.7	20.9	17.0	17.7	16.7
HW	13.2	12.6	11.9	13.8	10.6	12.0	10.6
HD	10.2	9.8	9.4	10.9	8.6	8.8	8.2
SEL	7.2	7.6	7.1	8.2	7.0	7.2	6.7
FLL	30.0	29.6	28.2	32.2	26.9	26.3	27.5
HLL	53.4	49.4	49.9	55.7	46.1	44.7	44.3
T4L	13.5	12.5	13.9	14.5	12.3	12.0	12.8
TRL	31.0	27.5	30.2	33.6	23.8	26.2	24.8
TAL/SVL (%)	268.0	255.1	—	248.2	257.1	256.7	254.3
HL/SVL (%)	30.4	31.6	31.1	29.1	31.6	30.5	30.6
HW/HL (%)	67.3	63.4	63.5	65.9	62.2	67.6	63.3
SEL/HL (%)	36.7	38.2	37.8	39.1	41.0	40.3	39.8
HD/HW (%)	77.8	77.8	79.0	79.5	81.5	73.2	77.3
FLL/SVL (%)	46.7	46.9	46.7	44.9	50.0	45.3	50.3

HLL/SVL (%)	83.2	78.3	82.9	77.7	85.9	77.1	81.0
TRL/SVL (%)	48.2	43.6	50.1	46.9	44.3	45.2	45.3
SL	6/7	8/7	7/7	7/8	7/8	7/8	8/7
IL	8/7	9/8	9/8	10/9	8/8	9/8	8/9
NSL	1/1	1/1	0/0	1/0	0/0	0/0	0/0
MD	41	42	39	43	39	46	41
F4S	24/22	20/20	18/20	19/19	20/18	21/22	21/21
T4S	27/27	26/25	25/25	25/26	27/24	22/23	25/26
SOR	3/3	3/3	3/3	3/3	3/3	3/3	3/3
POS	3/3	2/3	2/4	4/6	5/4	2/3	5/5
PTY	7/7	8/7	9/8	9/9	10/8	8/6	10/12
PRS	11/10	11/10	11/11	13/14	12/12	11/10	11/13

(6)

Diploderma qilin sp. nov.

Museum	KIZ	KIZ	KIZ	KIZ	KIZ	KIZ	KIZ	KIZ	KIZ	KIZ	KIZ	KIZ	KIZ
Catalog	02833	02833	04441	04440	04440	04441	04474	02833	02833	02833	04482	04440	04474
Number	2	3	2	7	5	3	5	5	4	6	0	8	4
Type Status	HT	PTT	PT	PT	PT	PT	PT	PTT	PTT	PTT	PT	PT	PT
Sex	M	M	M	M	M	M	M	F	F	F	F	F	F
SVL	55.9	58.6	66.5	63.1	64.1	58.7	59.2	61.7	59.8	56.8	55.3	60.8	72.0
TAL	116.7	118.3	139.0	134.9	139.9	119.0	119.0	114.8	119.4	99.0	104.0	118.7	130.8
HL	17.5	17.9	19.7	19.1	19.1	16.9	18.2	17.4	17.2	15.9	15.4	17.5	19.2
HW	11.9	13.0	13.7	12.4	13.0	12.1	12.3	12.1	12.4	11.2	10.8	12.5	14.0
HD	9.6	10.8	10.8	9.3	10.8	8.9	9.4	9.7	9.5	8.5	8.2	9.0	10.8
SEL	6.5	7.0	7.6	7.5	7.3	6.6	7.4	6.6	6.4	5.8	6.5	7.3	7.3
FLL	26.0	28.4	29.5	29.9	29.5	27.1	27.0	29.2	27.2	25.9	24.7	31.5	33.1
HLL	42.4	45.0	48.8	48.9	48.2	45.6	46.4	44.8	43.4	42.1	40.7	48.8	53.2
T4L	10.6	11.3	12.2	11.6	11.6	11.4	9.6	10.6	11.4	11.0	9.2	11.9	12.3
TRL	26.6	28.0	31.4	29.1	28.2	28.3	27.7	35.1	30.7	28.7	30.3	29.0	39.5

TAL/SVL													
(%)	208.6	202.0	209.0	213.7	218.2	202.8	201.0	186.2	199.7	174.3	188.2	195.4	181.6
HL/SVL (%)	31.2	30.6	29.6	30.2	29.7	28.8	30.7	28.2	28.7	28.0	27.8	28.9	26.6
HW/HL (%)	68.1	72.7	69.5	65.0	68.5	71.3	67.8	69.6	72.2	70.4	70.4	71.0	73.2
SEL/HL (%)	37.4	38.9	38.4	39.0	38.2	39.3	40.9	38.1	37.3	36.6	42.3	41.7	38.1
HD/HW (%)	80.4	82.7	79.0	75.0	82.8	73.9	76.0	80.4	76.6	75.7	75.4	72.3	76.8
FLL/SVL (%)	46.4	48.5	44.3	47.3	46.1	46.2	45.6	47.4	45.6	45.6	44.7	51.8	45.9
HLL/SVL													
(%)	75.8	76.7	73.3	77.4	75.1	77.7	78.4	72.6	72.5	74.2	73.6	80.4	73.8
TRL/SVL													
(%)	47.5	47.8	47.1	46.0	44.0	48.1	46.8	56.9	51.3	50.5	54.9	47.8	54.9
SL	10/10	10/9	9/8	9/9	10/9	8/9	8/9	9/10	8/8	8/8	9/8	9/9	10/9
IL	12/13	10/10	8/10	11/10	9/10	9/10	9/10	11/12	9/10	11/11	10/10	11/11	11/10
NSL	1/1	1/1	1/1	2/2	0/1	1/1	1/1	2/2	1/1	1/1	1/1	1/1	1/1
MD	41	39	40	40	41	39	43	40	42	45	42	38	43
F4S	16/17	16/16	15/17	18/17	18/18	17/17	16/16	17/19	18/18	15/17	16/16	18/16	15/16
T4S	23/23	21/21	21/23	23/22	25/23	21/21	22/22	21/24	25/25	21/22	22/22	23/22	22/23
SOR	5/5	3/4	3/4	4/4	3/3	3/3	3/3	4/4	5/5	3/3	3/3	3/3	3/3
POS	4/4	3/3	3/3	5/5	3/3	4/3	3/2	4/4	5/5	4/4	4/4	3/3	5/5
PTY	7/8	6/7	8/4	4/6	7/8	3/5	5/6	4/5	3/5	5/6	3/4	5/6	6/7
PRS	5/7	4/4	5/3	6/7	7/8	5/6	4/4	3/3	4/6	4/3	4/3	4/6	3/3

Figure 1. Distributions of *Diploderma* species in East Asia. Shaded region represents the range of *D. flaviceps* complex in China. Numbered shapes represent type localities of *Diploderma* species: the rectangle represents the 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 the circles represent type localities of remaining recognized congeners (1: *D. splendidum*; 2: *D. micangshanense*; 3: *D. zhaoermii*; 4: *D. grahami*; 5: *D. flaviceps*; 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. laeviventre*; 22: *D. slowinskii*; 23: *D. yunnanense*; and 24: *D. chapaense*).

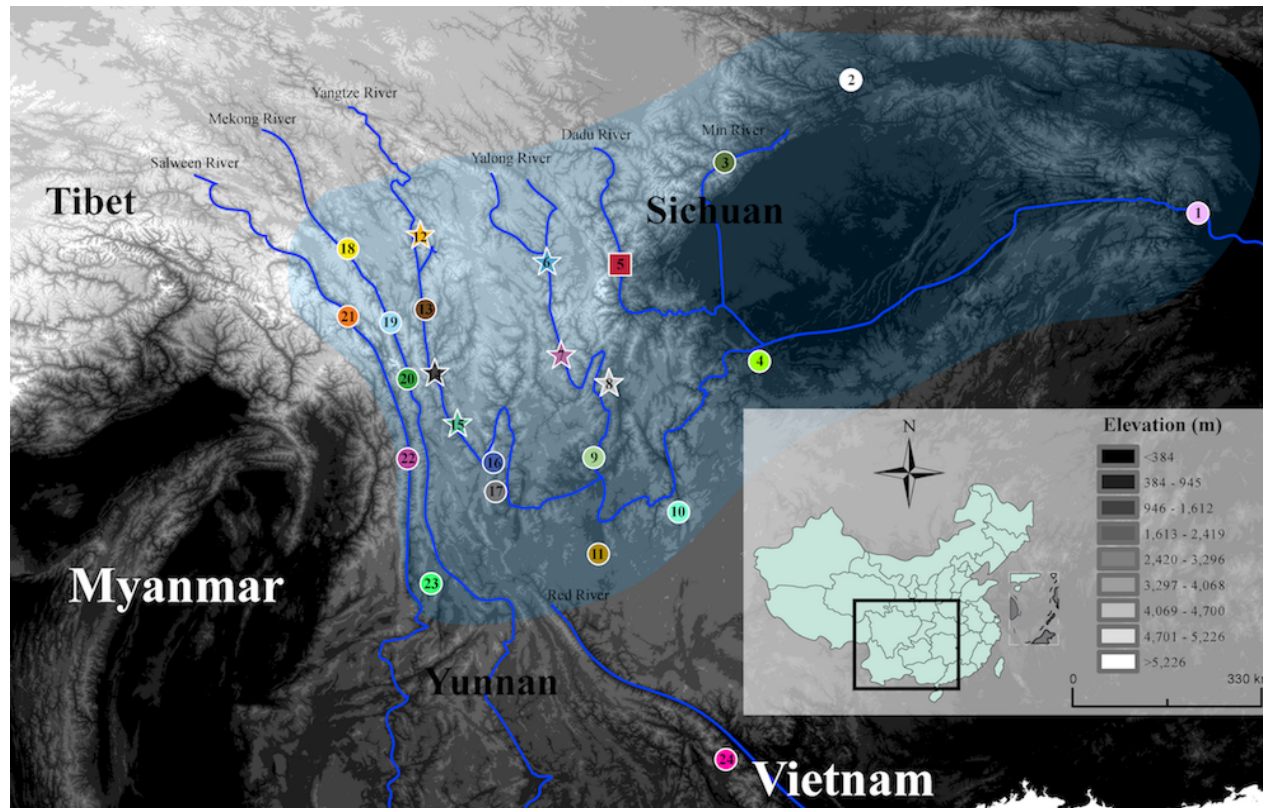


Figure 2. Phylogenetic relationships of the genus *Diploderma* inferred from concatenated multi-locus data set (*ND2*, RNAs, *BDNF*, *CMOS*, and *R35*), with gular patterns of live males and females of the *D. flaviceps* complex illustrated on the side. All tip nodes that unify each individual species 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 correspond to the ones in Figure 1. Photos 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 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.

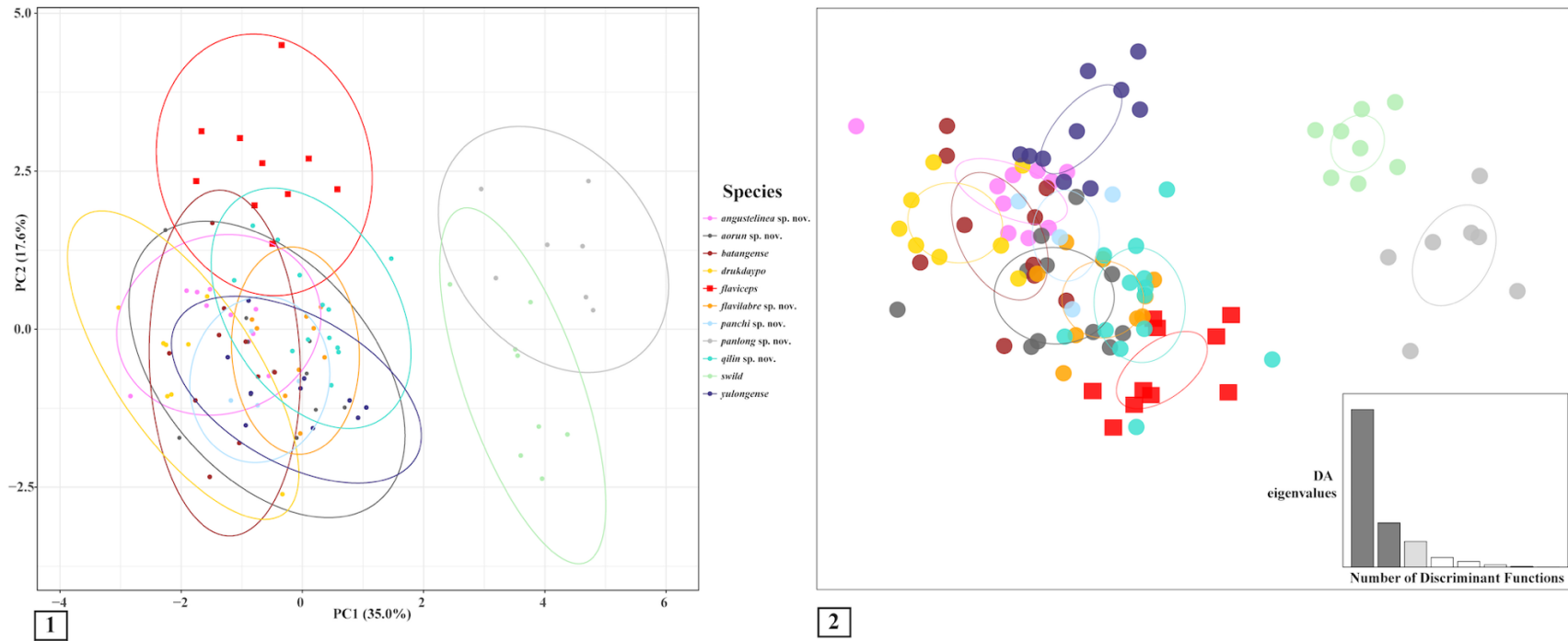


Figure 4. PCA (1) and DAPC plots (2) with 95% confidence ellipses based on nine morphometric characters (SVL, TAL, HL, HW, HD, SEL, FLL, HLL, and TRL) for both males (A) and females (B) of the examined populations of *D. cf. flaviceps* and their morphologically-similar congeners. The embedded figure in 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; therefore, the analyses for each sex only have representations from five *D. cf. flaviceps* populations in total.

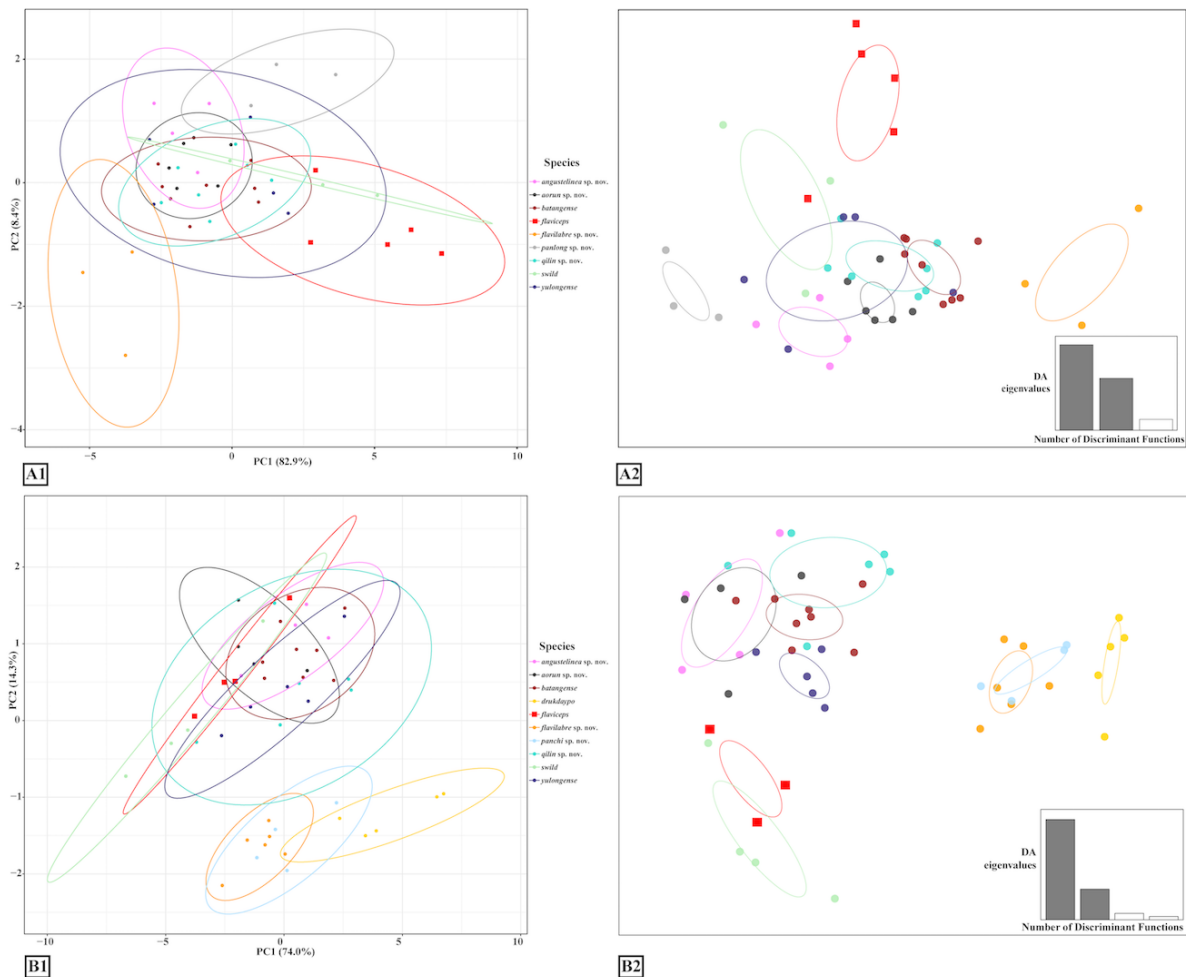


Figure 5. Male holotype (KIZ 029703) and female paratopotype (KIZ 029706) of *Diploderma angustelinea* sp. nov. in life. Photos by JR.



Figure 6. Male paratype (KIZ 044764) and female paratype (KIZ 032735) of *Diploderma aorun* sp. nov. in life. Photos by KW.



Figure 7. Male holotype (KIZ 032693) and female paratopotype (KIZ 032695) of *Diploderma flavilabre* sp. nov. in life. Photos by KW.



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



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



Figure 10. Male holotype (KIZ 028332) and female paratype (KIZ 044820) of *Diploderma qilin* sp. nov. in life. Photos by KW.

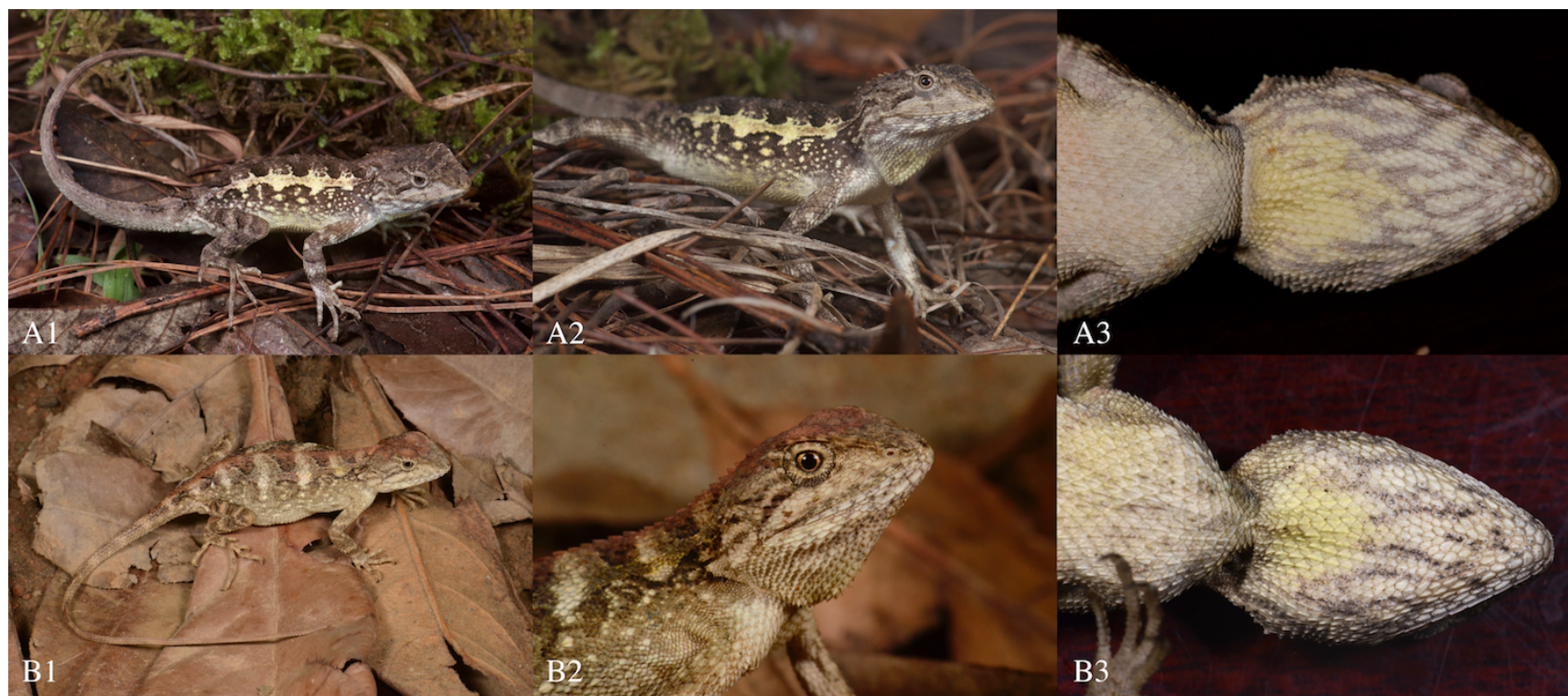


Figure 11. Comparisons of lateral head view (1), dorsal head view (2), ventral head view (3), dorsolateral overview (4), and ventral overview (5) of preserved specimens among males of *Diploderma angustelinea* sp. nov. (A), *D. aorun* sp. nov. (B), *D. flavilabre* sp. nov. (C), *D. qilin* sp. nov. (D), and *D. panlong* sp. nov. (E). Photos by KW.

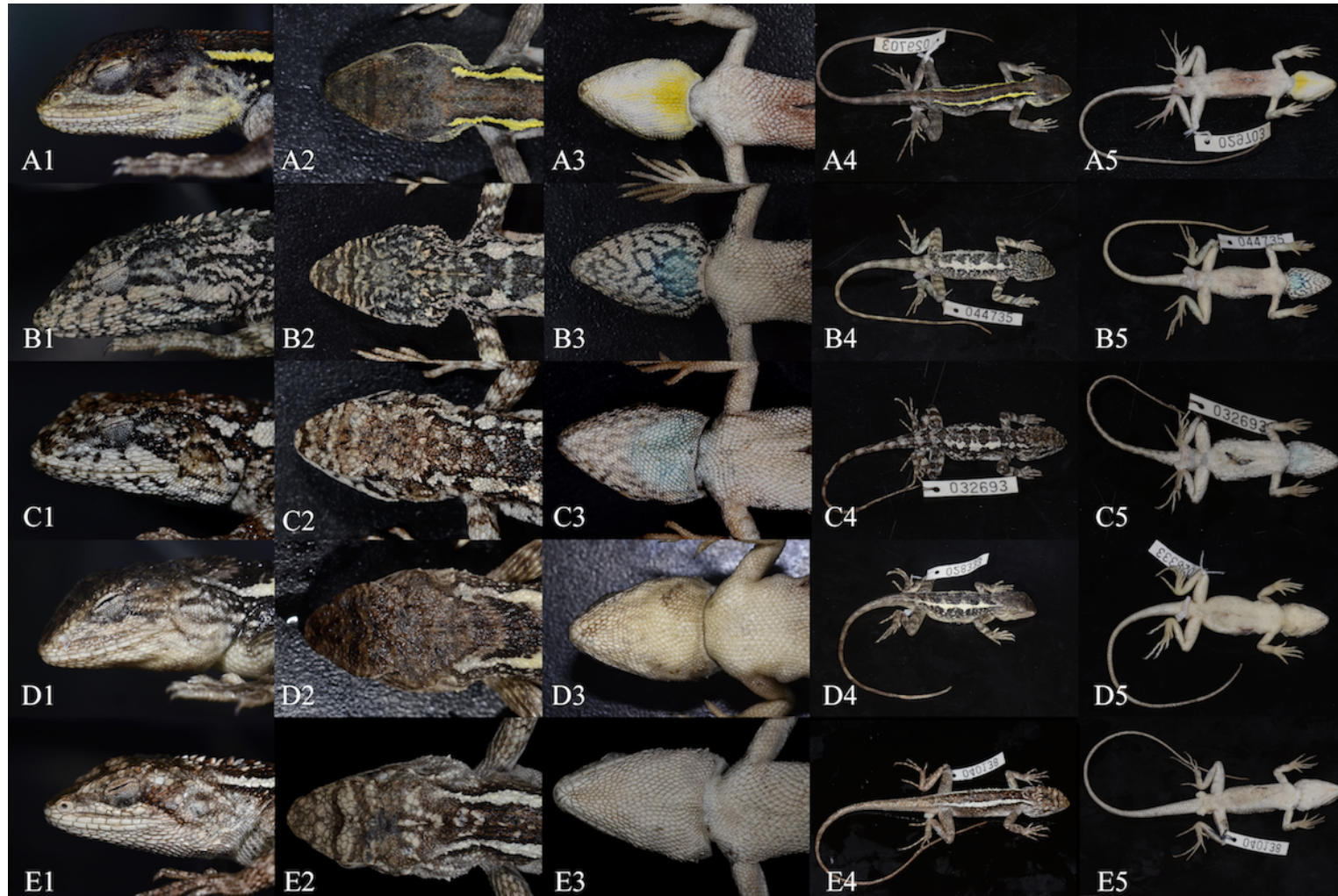


Figure 12. Comparisons of lateral head view (1), dorsal head view (2), ventral head view (3), dorsolateral overview (4), and ventral overview (5) of preserved specimens among females of *Diploderma angustelinea* sp. nov. (A), *D. aorun* sp. nov. (B), *D. flavilabre* sp. nov. (C), *D. qilin* sp. nov. (D), and *D. panchi* sp. nov. (E). Photos by KW.

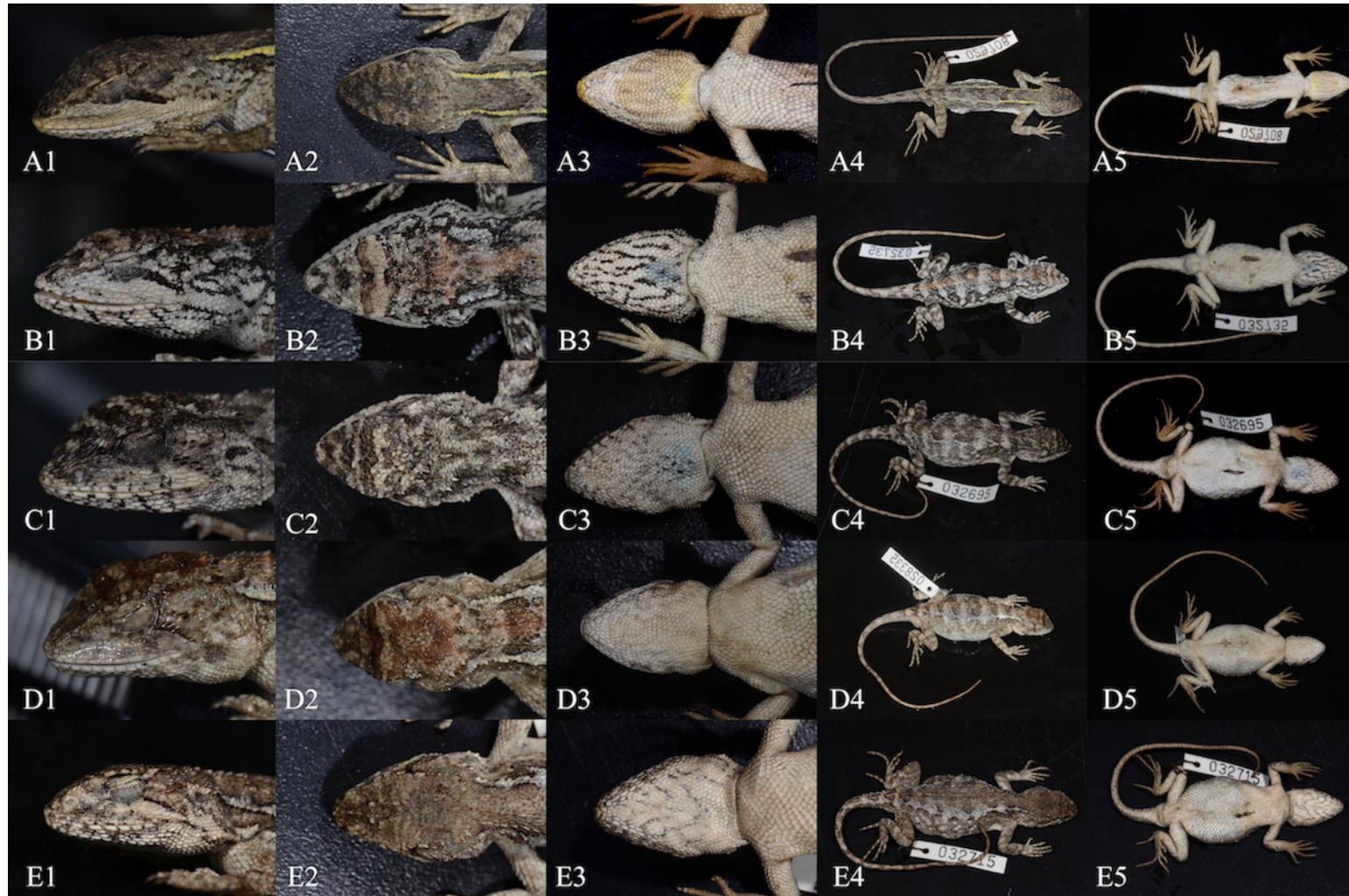
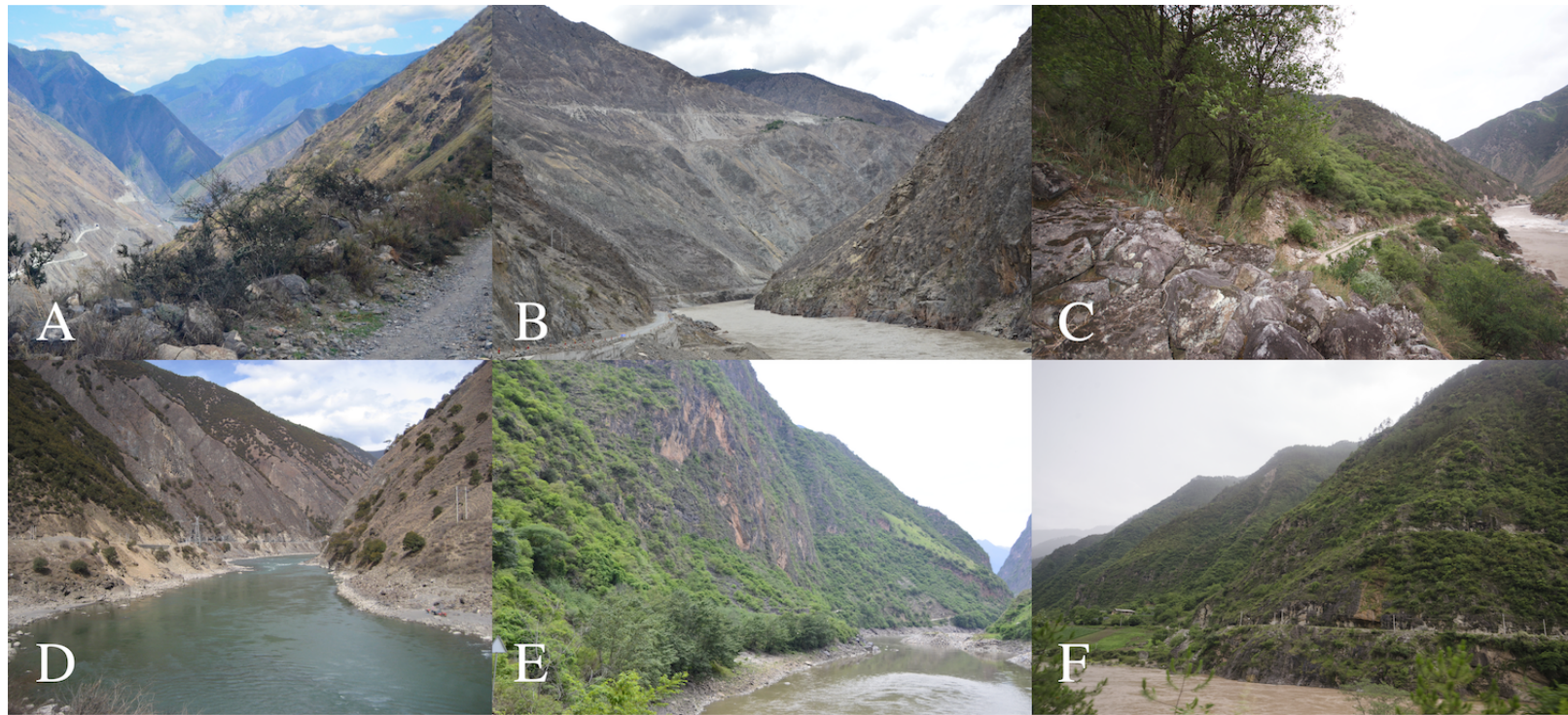


Figure 13. Habitats of the six new species at their type localities in the Hengduan Mountain Region. (A) *Diploderma angustelinea* sp. nov.: near Maidilong Village, Muli County, Liangshan Prefecture, Sichuan Province, China; (B) *Diploderma aorun* sp. nov.: near Benzilan Township, Deqin County, Yunnan Province, China; (C) *Diploderma 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) *Diploderma panlong* sp. nov.: near Miansha Village, Mianning County, Liangshan Prefecture, Sichuan Province, China; and (F) *Diploderma qilin* sp. nov.: near Wujin Village, Shangri-La County, Yunnan Province, China.



Chapter 3: Biogeography of Mountain Dragons (Reptilia: Agamidae: *Diploderma*) Reveals Links between Biogeographic Lines, Paleo-Drainage Reorganizations, and Tectonic Faults in the Mountains of Southwest China

Abstract

Major landscape evolutions can lead to changes in the connectivity among suitable habitats, leaving strong imprints on the species's genetic structure. The Hengduan Mountain Region (HMR) in Southwest China is one of the research hotspots for biogeography. With its rich biota, unique topography, and complex geological history, the HMR harbors some of the most actively debated and most fascinating biogeographic and geological phenomena. Among them, the two major biogeographic lines—Mekong Salween Divide (MSD] and Tanaka Kaiyong Line (TKL)—and the paleo-drainage evolution have the most controversies. Specifically, active debates exist regarding their effectiveness as major dispersal barriers to organisms, timing of formation, and their ultimate driving causes. In addition, the biogeographic lines and drainage evolution have been examined and discussed in nearly independent context without considering others, despite their overlaps in the same geographic area and potential link through the same geological process.

Using agamid lizards of the genus *Diploderma* as the study system, I tackle the existing controversies and test competing hypotheses on the two biogeographic lines and drainage evolution. My results support the existence of a continental paleo-Red River Drainage and subsequent reorganizations of paleo-rivers. Specifically, our drainage evolution model tests using BioGeoBEARS support the connection among paleo-upper Mekong, Jinsha, and Yalong River with the paleo-Red River prior to late Oligocene and early Miocene, and our ancestral range

reconstruction reveals novel and complex dispersal patterns among upper reaches of major rivers in late Miocene and Pliocene, suggesting overlooked river captures and combined roles of mountain building processes and climatic oscillation on organismal diversifications.

Unfortunately, the previously debated connection between paleo-upper Salween and paleo-Red River remains unresolved.

For the biogeographic lines, my results show that both MSD and TKL are effective biogeographic barriers for vertebrate animals as they are for plants: MSD isolates Salween valley from all cross-valley dispersals, and TKL delimits *Diploderma* into two deeply diverged major clades. Moreover, my results show that the seemingly non-structured TKL overlays on top of major tectonic faults in the HMR and delimits the paleo-Red River and paleo-Yangtze River drainages nearly perfectly. The formation time of TKL is also consistent with the most active period of fault movements in late Oligocene and early Miocene, supports the speculated link between biogeographic lines and drainage evolution, and reveals that tectonic faults are the main driver for both phenomena.

Lastly, using the robust fossil calibration method that incorporates all available fossils, we also comment on previous time estimations on the Acrodont evolution, and discuss on the taxonomy and conservation of *Diploderma* in China.

Introduction

Major landscape evolutions can lead to changes on the connectivity among suitable habitats, creating or removing of geographical barriers of gene flows (Hoorn et al. 2018). These changes have substantial impacts on the range evolution and regional assemblage of organisms, leaving strong imprints on species-area relationships (Avice 2000; Julia et al. 2012; He & Jiang 2014; Hoorn et al. 2018). To better understand modern patterns in species-area relationships, biologists use biogeographic lines to delimit these areas of endemism. In most cases, biogeographic lines are intuitive and overlap with contemporary geographies that have existed through the evolutionary time, including most major rivers (Wallace 1854; Nazareno et al. 2019), mountain ranges (Ward 1921; Martín-Piera et al. 1992), or ocean channels (Woodruff 2003; Esselstyn et al. 2010). However, in other cases, biogeographic lines can seem non-structured, with no temporary physical structure as supports (Simpson 1977; Williams 1996), and the natural drivers of these seemingly non-structured lines can be puzzling, including multidimensional factors such as historical geography that are no longer present today (De Bruyn et al. 2005; Parnell 2013).

The Hengduan Mountain Region (HMR) in Southwest China is one of the global biodiversity hotspots with a unique topography: not only does the HMR includes the only north-south trending, parallel ridge-gorge system in the world, but it also expands across a dramatic elevation difference, connecting the high Tibetan Plateau in the northwest and the low tropical northern Indochina in the southeast (Fig. 1). Given its complex topology and rich biota, the HMR has been the focus of biogeographic and evolutionary studies (He & Jiang 2014; Favre et al. 2015; Lei et al. 2015). In the HMR, two major biogeographic lines, namely the Mekong Salween Divide (MSD) (Ward 1921) and the Tanaka -Kaiyong Line (TKL) (Tanaka 1954; Lang 1994), were proposed to delimit floristic and faunal regions (Ye et al. 2017). The MSD overlays on top

of the contemporary Gaoligong Mountain Range, separating the parallel sections of the upper Mekong and the upper Salween River in eastern Tibet and northwestern Yunnan Province (Fig. 1). It has been shown to delimit major fauna groups (Thinh et al. 2010; Geissmann et al. 2011) as well as genetic structures of many plant species (i.e. Li et al. 2011; Luo et al. 2017). On the other hand, the TKL is drawn arbitrarily as two intercepting lines going northeast–southwest and northwest–southeast directions, respectively, cutting through Sichuan and Yunnan Provinces in Southwest China (Fig. 1; Li & Li 1997). Unlike the MSD, TKL was originally proposed to delimit plant endemism only, and it has only been tested explicitly using plants (Zhu & Yuan 2002; Fan et al. 2013; Zhao & Gong 2015; Zhuang et al. 2017).

Both climatic and tectonic mechanisms have been hypothesized as the driver of these two biogeographic lines, and the inferred formation times of biogeographic lines have been used as the main line of evidence in differentiating the two types of mechanisms (Ye et al. 2017). The MSD was initially thought to be driven by the formation of Nu Mountain in Pliocene, resulting in vicariance on two sides of the MSD (Ward 1921; Clark et al. 2004). Such tectonic hypothesis was supported by some biogeographic studies, where the MSD delimits population structure/species distribution of organisms, and the inferred timing of major divergences match the believed formation time of mountain range (Gao et al. 2007; Thinh et al. 2010; Geissmann et al. 2011; Luo et al. 2017). However, other phylogeographic studies show that the inferred timing of genetic divergence on two sides of the MSD postdated the believed formation time of the Nu Mountain during the Pliocene, which rejects the tectonic hypothesis (Li et al. 2011; Meng et al. 2015). Furthermore, the inferred divergence times from these studies match the time for the change in monsoon regime in Pleistocene (Wang et al. 1994), and their ecological modeling showed strong correlation between genetic divergence with the paleoclimate conditions on two

sides of MSD, which favors the climatic hypothesis. To date, no conclusion can be drawn confidently from the contradictory results from past studies. As for the TKL, although early studies have suggested a combined driver of both tectonic and climatic factors (Li & Li, 1997; Li et al. 1999; Zhu & Yuan, 2002), except a single study that supports a combined driver (Zhao & Zhang, 2015), majority of recent phylogeographic studies have favored the climatic hypothesis only, suggesting that the change in either glacial cycles or Pleistocene monsoon regime drove the current genetic structures of plants on two sides of the TKL (Fan et al. 2013; Tian et al. 2015; Zhao & Gong, 2015; Jiang et al. 2018).

Despite the accumulation of literature on the driver of these two biogeographic lines, major limitations and issues exist regarding their evidence (Ye et al. 2017). Firstly, many of the early biogeographic studies were descriptive and lack quantitative evidence (Ward 1921; Li & Li, 1997; Li et al. 1999; Zhu & Yuan, 2002; Thinh et al. 2010; Geissmann et al. 2011). Secondly, while many of the previous studies used timing of genetic divergence as the key evidence to differentiate and test tectonic versus climatic hypotheses, they assumed the incorrect timing for the formation of mountain ranges in the HMR: rather than a late Miocene/Pliocene birth of modern HMR (Li & Fang 1999; Zheng et al. 2000; Mulch & Chamberlain 2006), recent studies indicate that most of eastern Tibet had achieved close to modern heights in either the Eocene (Wang et al. 2012; Hoke et al. 2014) or the early Miocene/Oligocene (Botsyun et al. 2019a), much earlier than previous estimates. Relating to this problematic reference timing, all previous estimations on the divergence times of plants used secondary calibrations (Li et al. 2011; Fan et al. 2013; Meng et al. 2015; Zhao & Gong 2015; Zhao & Zhang 2015; Luo et al. 2017), which can bias dating estimations toward more recent divergences (Gaur & Martin 2004; Sauquet et al. 2012). With contradicting conclusions among studies and major limitations on previous

methodologies, no confident conclusion can be drawn regarding drivers of the two biogeographic lines.

Among the possible tectonic drivers of the two biogeographic lines in the HMR, the reorganization of the paleo-Red River drainage is one of the most heavily debated hypotheses. Based on river topographies, early geologists proposed a continental paleo-Red River drainage that encompassed most of major rivers in East Asia, and they hypothesized that modern rivers experienced numerous captures and reversals before achieving their modern drainage topographies (Fig. 2; Lee 1933; Ding 1933; Barbour 1936; Ren et al. 1959; Brookfield 1998). Clark et al. (2004) synthesized the drainage evolution in the HMR and proposed an east-to-west sequential capture-order of small segments from the Paleo-Red River. However, regardless of decades of research interests, major questions and controversies remain on the connectivity of paleo-drainage and timings of river capture events in the HMR (Ming 2013; Zhang et al. 2019).

Firstly, disagreements exist regarding the connectivity among paleo-rivers (Clark et al. 2004; Clift et al. 2008; Zheng et al. 2013; Wissink et al. 2016; Zhang et al. 2019; Table 1). Early geological studies suggested that the upper reaches of paleo-Jinsha, Mekong and Salween River were all connected to the paleo-Red River (Ren et al. 1959; Brookfield, 1998; Clark et al., 2004). This hypothesis was supported by phylogeographic studies of plants (Zhang et al., 2011; Zhuang & Sun, 2011; Wang et al. 2020), fishes (Guo et al. 2005; He & Chen 2006; Yang et al. 2012; Qi et al. 2015; Li et al. 2016), and frogs (Zhang et al. 2010, 2019), where paleo-drainage better explains the genetic structure of organisms than the contemporary drainage topography. However, later geological studies suggested contradictory results: (1) some cast doubt on the existence of such continental paleo-river system and suggest either no connections between the paleo-Yangtze to the paleo-Red River or an ancient connection prior to Cretaceous (Shen &

Yang 1963; Wissink et al. 2016; Zhang et al. 2017); (2) some argues that the Mekong and Salween Rivers were not part of the paleo-Red River system, and only the paleo-Yangtze and its tributaries drained into the paleo-Red River (Hoang et al. 2009; Zheng et al. 2013); and (3) other studies suggest that only the middle Yangtze drained into the paleo-Red River, with the upper Yangtze (=Jinsha), Mekong, and Salween Rivers draining into a separate paleo-drainage (Clift et al. 2008; Zhang et al. 2017).

Secondly, discrepancies exist regarding the timing of capture events among different studies. Using the proposed capture of Jinsha River from the paleo-Red River as an example, for geological studies, the inferred time of this capture event varies dramatically from Pleistocene (about 2.58 Ma, Ren et al. 1959), late Miocene (about 5 Ma; Wang et al. 2012; Hoang et al. 2009; Su et al. 2019), late Oligocene (24–28 Ma, Clift et al. 2006; 40–45 Ma, Richardson et al., 2010; Zheng et al., 2013), Eocene (about 35 Ma; Zeng 2002), to Cretaceous (before 66 Ma; Wissink et al. 2016; Zhang et al. 2017; Table 1). Given limitations on the sampling sites and issues on result interpretations (Zhang et al. 2019), no confident conclusion can be drawn from geological studies alone. For biogeographic studies, the estimated times are generally younger than geological estimations, ranging from middle Pleistocene (<1.4 Ma) to early Miocene (6.2–6.8 Ma) (He & Chen, 2006; Zhang et al., 2011; Li et al. 2017; Wang et al. 2020).

Finally, relating to the debated on the drivers of biogeographic lines, the specific geological driver of the reorganizations of paleo-drainages is subject to debates. Early geological works propose that the reorganization of paleo-drainages was caused directly by the surface uplift of the Tibetan Plateau in late Miocene (Ren et al. 1959; Brookfield 1989, 1998; Clark et al. 2004). This hypothesis was widely accepted, and the conclusion was used to explain the biogeographic patterns observed in the HMR (Yang et al. 2012; Yue et al. 2012; Li et al. 2016). On the other

hand, other geological studies suggest that much of eastern Tibet (including HMR) have achieved its current height much earlier (as early as Oligocene or late Eocene, no later than Miocene; Tapponnier et al. 2001; Hoke et al. 2014; Li et al. 2015; Su et al. 2018; Botsyun et al. 2019a), which predates the uplift of the main Tibetan plateau. Rather than attributing reorganizations to the rise of the main Tibetan Plateau, a combination of separate uplifts of the HMR and base-level falls due to tectonic faulting were proposed as the possible alternative driver of the drainage reorganizations (Hallet & Molnar, 2001; Kong et al. 2012; Hoke et al. 2014; Gourbet et al. 2016). As geological studies cannot provide robust inferences and the debates on paleo-drainage evolution continue, fine-scale biogeographic studies with robust calibration method may provide a new angle to crack the outstanding geological conundrum in the HMR.

Mountain Dragons of the genus *Diploderma* represent a perfect biological system to study the complex biogeographic patterns and test competing geological hypotheses in the HMR. Of the 35 recognized species of *Diploderma*, 30 species are found across the drainages of the hypothesized paleo-Red River, with their ranges expanding across both sides of the MSD and TKL (Fig. 3). Given their thermal constraints as ectothermic reptiles and the limited dispersal ability due to small body size, species of the genus *Diploderma* are constrained to the warm river valleys at lower elevations in the HMR (Fig. 3; Wang et al. 2019a, 2021a, 2021b; in press). As a result, the evolutionary history of *Diploderma* is likely strongly tied to the geological evolution of major rivers, and the evolutionary relationships and divergence timings among species should reflect connectivity among paleo-rivers and the timing of drainage reorganizations, if such reorganizations ever happened. Moreover, because most species of the genus are micro-endemic to a short, specific section of different rivers (Wang et al. 2019a, 2021a), the biogeographic

inference of *Diploderma* can provide signals of drainage evolution at a fine scale, detecting river capture events that might be overlooked from past broad-scale studies. Lastly, as lizards of the family Agamidae have relatively well-preserved fossil records (Alifanov et al. 2000; Delfino et al. 2008; Wagner et al. 2021), a divergence time inference using independent fossil records will be more robust than all previous estimations using secondary calibrations only. This provides a rare opportunity to examine existing geological hypotheses using robust biological data.

Using a multi-locus genetic data set and a comprehensive taxonomic sampling of the genus *Diploderma* across the hypothesized paleo-Red River drainage, we test the existing geological hypotheses on paleo-drainage evolution, examine the impacts of two well recognized phytogeographic biogeographic lines on the evolution of terrestrial vertebrates. Specifically, we aim to address the following questions: (1) Are the two biogeographic lines effective in delimiting vertebrate animals? (2) When do the two biogeographic lines form, and what are the ultimate drivers for them? (3) Do biogeographic data from valley dwelling lizard support the existence of the paleo-Red River system? (4) Which specific paleo-connectivity pattern do the data of *Diploderma* support? (5) When did the major capture away from the Red River happened? (6) What is the ultimate driver for the paleo-river reorganization? And (7) Is there any overlooked link between biogeographic lines and drainage evolution in the HMR?

Materials and Methods

Taxonomic Samplings

Genetic data of 48 species of outgroup acrodont lizards (agamids and chameleons) and 31 ingroup species of the genus *Diploderma* were downloaded from GenBank, including a single mitochondrial gene *ND2* and three nuclear genes (*BDNF*, *R35*, and *Rag1*; Appendix I and II).

Additionally, we generated additional new sequences for *Diploderma* species (Appendix II). Primers and sequence protocols followed Wang et al. (2021a). The total ingroup consisted of 155 individuals from 73 localities, including 34 recognized species of *Diploderma* in China and nine undescribed species of *Diploderma* (Appendix I, II; Figure 16).

Fossil records of acrodont lizards were recovered by searching the fossil database Fossilworks (Behrensmeyer & Turner 2013). The initial list contained 63 fossil taxa, which were then pruned down by removing unidentified taxa (e.g. Agamidae indet. and Chamaeleonidae indet.), dubious taxa, and taxa with uncertain phylogenetic positions (e.g. †*Tinosaurus* spp., †*Mimeosaurus crassus*, †*Priscagama* spp., †*Agama sinensis*, †*Anhuisaurus* spp., and †*Anqingosaurus* spp.; Gao & Hou, 1995; Smith 2011; Smith et al. 2011; Dong et al. 2016). Additionally, the fossil species †*Rhampholeon* sp., which was thought to be the earliest stem member of the genus *Rhampholeon* (Rieppel et al. 1992) and used in previous biogeographic study (Grismer et al. 2016), was reclassified as a member of the genus *Calumma* (Čerňanský et al. 2020). The final list contained 21 fossil species, including four species in Chamaeleonidae and 17 species in Agamidae (Appendix III).

Phylogenetic Analyses and Divergence Estimations

Sequences were aligned using online MAFFT version 7 under “auto settings” allowing gaps (Kato et al. 2019), and alignments were later manually adjusted using Geneious v10.0.6. As no major, strongly supported conflicts were observed among topologies of different genes through RaxML analyses, sequences were concatenated for final analyses. The final concatenated alignment contained 5,366 bp and was partitioned by genes.

For Bayesian analyses, the dataset was partitioned by genes, and the best partition models for each gene were selected using AIC criteria implemented in jModelTest (Darriba et al. 2012), which were GTR+ Γ for *ND2* and *Rag1*, and HKY+ Γ for *BDNF* and *R35*. Two independent Markov Chain Monte Carlo analyses were run, each with four Metropolis-coupled chains, a melting temperature of 0.02. Each run was conducted with 5×10^8 generations and sampled every 1,000 generations, discarding the first 20% of trees as burnin. Finally, we confirmed convergence of runs with TRACER v. 1.6.0 (visual convergence and ESS>200; Rambaut *et al.* 2013). Analyses were executed on CIPRES (Miller et al. 2010).

The Fossilized Birth-Death Model (FBD) implemented in BEAST 2.6.3 (Bouckaert et al. 2019) was run on the selected subset of samples (one individual per extant species) through CIPRES (Miller et al. 2010). For the few species that have differential nuclear gene coverage among different individuals, their nuclear genes were concatenated to represent the species in the BEAST analyses. The partition scheme and the best evolution models were the same as the Bayesian analyses. All site models were unlinked, but the clock model was linked for all nuclear genes, and the tree model was linked for all genes. Relaxed clock Log Normal was used for the clock model for both mitochondrial and nuclear genes. Diversification prior d was set to be exponential with a value of 2.0 (lineages per million years), which reflects the difficulty in predicting speciation and extinction rates (Smíd & Tolley 2019). Beta distribution was used for SamplingProportionFBD and set to value of 2.0. The ρ parameter was calculated by dividing the sampled number of species by the total number of recognized, extant Acrodont lizards (770 species; Utey et al. 2021), which yielded 0.17. GammaShape priors were all exponential with a mean of 1.0 and offset of 0.0. The Origin was estimated to be 110 Ma using the oldest fossil, which was †*Protodraco* (99 Ma), and the M value was set to 11.0 accordingly. A

lognormal prior distribution for the rate of the mtDNA gene (parameter *ucl.d.mean*: mean= 0.3, SD= 1.0) and an exponential prior distribution for the nDNA genes (*ucl.d.mean*: mean= 0.05) were used (Smíd & Tolley 2019). Rate heterogeneity among lineages (parameter *ucl.d.stdev*) was assumed to have an exponential prior distribution for all partitions (mean= 1.0). Two independent runs each with 5×10^8 generations were conducted using BEAST v. 2.6.3 on CIPRES. Both parameters and trees were sampled every 1,000 generations. Posterior trace plots, stationarity, convergence, and effective sample sizes (ESS) were inspected in Tracer 1.7.1 (Rambaut et al. 2018). The first 20% of sampled trees from each run were discarded as burnin, remaining trees were resampled at frequency of 100,000 using LogCombiner, which resulted in 8,002 combined trees. Fossil samples were removed from the posterior trees, and the maximum clade credibility (MCC) trees with only extant species and mean node height were summarized with mean node heights using TreeAnnotator.

Ancestral Range and Ancestral State Reconstruction

Distributions and ecotypes of species of the genus *Diploderma* were obtained from field surveys, museum specimens, and published literature (Wang et al. 2015, 2016b, 2017, 2019a, 2019b, 2019c, 2021a, 2021b, in press). Ancestral areas were coded as seven regions based on geographic studies of the evolution of East Asian rivers (Clark et al. 2004) and general zoogeography of China (Xie et al. 2004), which include upper Salween River Drainage (USW), middle Salween River Drainage (MSW), upper Mekong River Drainage (UMK), middle Mekong River Drainage (MMK), upper Jinsha River Drainage (UJS), middle Jinsha River Drainage (MJS), Red River and lower tropical Mekong/Salween River Drainage (LTR), upper Yalong

River Drainage (UYL), lower Yalong River Drainage (LYL), and lower Yangtze Drainage (YZ) (Fig. 4; Table 2).

Hypothetical dispersal costs of *Diploderma* across different topography were estimated. Because HMR achieved close to its modern height in prior to the Miocene (Hoke et al. 2014; Li et al. 2015; Botsyun et al. 2019a), all geographic structures that were not specifically tested were assumed to have the same elevation as their modern forms. Previous studies indicated that the upper distribution limit of most *Diploderma* species is 3400 m above sea level (Yang et al. 1987; Wang et al. 2015, 2019a, 2021a, 2021b), therefore any landmass over 3400 m of elevation was assumed as impermeable barrier to the dispersal of *Diploderma* (dispersal ability=0). Landmass below 3400 m was considered as semi-permeable with a dispersal cost (dispersal ability=0.5). For any combinations of dispersal costs, the total cost was the product of all individual costs (e.g. total cost through a dispersible landmass and an additional biogeographic region is $0.5 \times 0.5 = 0.25$; Table 3). If multiple dispersal routes existed between two regions, the one with the lowest dispersal cost was chosen.

Following geological hypotheses, eight possible drainage evolution models (DEMs) defining patterns and changes of connectivity among rivers and a control model (with no dispersal or adjacency constraints) were constructed using time stratified dispersal matrices (Table 4; Figure 18; Appendix IV). For the possible scenarios of the capture of upper Salween River by the paleo-Mekong or paleo-Red River, because no obvious capture-related structures were observed (Clark et al. 2004), we assumed that any structure that led to such possible capture would not be significant enough to cut off dispersal of terrestrial lizards. Therefore, for these scenarios, the dispersal probabilities between upper and lower Salween remain 1, even if the channels of the two river sections were disconnected.

All DEMs were tested with the combination of dispersal-extinction-cladogenesis (DEC; Ree & Smith, 2008), dispersal-vicariance analysis (DIVA; Ronquist, 1997), and Bayesian inference of historical biogeography for discrete areas (BAYAREA, Landis et al. 2013) using BioGeoBEARS (Matzke, 2014) implemented in RASP (Yu et al. 2020). Best model was selected using AIC criteria (lower the value, better fit the model). Models with and without the founder event speciation parameter (j) were compared using Likelihood test scores: significant result (i.e. $p < 0.05$) indicated the model with j parameter conferred different likelihood on the data comparing to the model without j).

The ancestral range was reconstructed using the best fit DEM through BioGeoBEARS implemented in RASP (Yu et al. 2020). A total of 8,002 post burnin trees and the consensus tree from BEAST analyses were used as the input, and 1,000 random trees were drawn from the total input trees. Given that most species of the genus *Diploderma* are micro-endemic (Wang et al. 2021a, 2021b), the maximum area of occupation at a given node was set to two. Adjacency matrices were used to remove the unrealistic states from the state space (Appendix V).

Ecotype was categorized in three groups, including arboreal (spending most time on high vegetations), forestry terrestrial (living in forest, but spending most time on forest floor), and rocky terrestrial (living in hot-dry valley with little vegetation, spending most time on rocks or on ground). Ecotypes of extant species were determined based on published studies (Wang et al. 2015, 2016, 2017, 2019, 2021a, 2021b) and field observations. The ancestral ecotype of the genus *Diploderma* was reconstructed using Bayesian Binary MCMC (BBM) implemented in RASP on the consensus tree from the BEAST analyses. Default setting was used, except the number of states allowed was set to two only, and the null state was unchecked.

Results

Phylogenetic Relationships and Divergence Time

Phylogenetic relationships of the genus *Diploderma* from the Bayesian and BEAST analyses are mostly identical, except a single node with low support in Clade A (Fig. 3). Two major clades are recovered within the genus: Clade A includes species on the west side of the TKL and is associated with the paleo-Red River drainage; and Clade B includes species on the east side of the TKL and is associated with the paleo-Yangtze River drainage (Fig. 3A).

For species in the northern HMR, only species from the Salween River form a monophyletic group, and species from Mekong, Jinsha, and Yalong are all paraphyletic with respect to each other: species from modern allopatric river valleys are more closely related to each other than to their parapatric congeners along the same contemporary river (Fig. 3A). Species from East Asian islands form a monophyletic group within Clade B.

The most recent common ancestor (MRCA) of modern Agamidae originated at about 103.4 Ma (95% HPD 91.8–117.8), and the MRCA of Draconinae originated at about 72.6 Ma (95% HPD 58.0–87.3) (Fig. S1). The MRCA for the genus *Diploderma* originated at about 24.0 Ma (95% HPD 18.3–30.8), and the MRCAs for Clade A and Clade B both originated at about 20 Ma (Clade A: 20.9 Ma, 95% HPD 15.2–27.2; Clade B: 18.9 Ma, 95% HPD 13.7–24.2). In Clade A, most species diversification happened within the last 5 MA; but in Clade B, excluding species of the *D. splendidum* complex, most species diversifications happened earlier before 6 Ma. In Clade B, the MRCA for species from East Asian islands originated about 12.75 Ma (HPD 8.5–17.1) (Fig. 6).

Drainage Evolution, Ancestral Range, and Ancestral State Reconstruction

DEM 2 using DIVALIKE+*j* is the best fit DEM to the modern distribution and species relationship of *Diploderma*, although DEM 1 and 5 using DIVALIKE+*j* are very close (Table 5). All three DEMs support the existence of a large paleo-Red River drainage, where the Mekong, Jinsha, and upper Yalong River all connected to Red River prior to 23 Ma (Fig. 5). Furthermore, all three models support that the connection between upper Yalong and middle Jinsha until 5 Ma. The three models only differ in the connectivity between middle Salween and middle Mekong River prior to 23 Ma, and the timing of disconnection between Salween and Mekong: in DEM 5, middle Salween and middle Mekong were not connected, but in DEM 1 and 2 they were connected; and in DEM 1, such connection lasted until 5 Ma, but in DEM 2 such connection was lost prior to 23 Ma (Fig. 5).

The best fit DEM 5 using DIVALIKE+*j* was used for ancestral range reconstruction because all three close DEMs produced the same overall structure of ancestral range reconstruction. The genus *Diploderma* originated in the lower elevation region in the tropical/subtropical lower Mekong, Salween, and Red River drainage and lower Yangtze Drainage (FJ) about 24 Ma. A major vicariance event happened soon after the emergence of the MRCA of *Diploderma*, which led to the divergence of the two major clades of *Diploderma* (Clade A and B; Fig. 3, 7). Species then migrated northward into the Hengduan Mountain Region through the deeply incised river gorges between 5–23 Ma. In Clade A, species first migrated into the middle Mekong and middle Salween valley at almost the same time around 16–20 Ma, which gave rise to *D. iadinum* in the middle Mekong valley and the MRCA of all remaining modern species in the Hengduan Mountain Region west of the TKL. This MRCA in middle Salween valley then took two different paths: some individuals stayed in the Salween valley and later continued their dispersal northward along the Salween valley at about 11 Ma, giving rise to the modern Salween species

(i.e. *D. laeviventre*, *D. slowinskii*, and *D. yangi*); and other individuals dispersed northeastward into the upper Yalong River, followed by a series of dispersals counterclockwise to the upper Jinsha, middle Jinsha, and finally back to the upper Yalong valley between 5–10 Ma. In Clade B, species dispersed northward into the lower Yalong River, followed by a backward dispersal back to the paleo-Yangtze drainage (Fig. 7).

Between 5 Ma to the present, another series of cross-valley dispersals happened in Clade A. Firstly, species dispersed from upper Yalong to the upper Jinsha again. The population then dispersed in three different directions: back to the upper Yalong valley, west to the upper Mekong valley, and south to the middle Jinsha valley (Fig 20). Each of the above-mentioned dispersals was followed by a vicariance event, except for a single dispersal from the middle Jinsha to the upper Yalong in 0–5 Ma.

Ancestral state reconstruction showed that the MRCA of *Diploderma* was arboreal. Both arboreal and terrestrial ecotypes re-evolved multiple times independently, including four independent evolutions of the terrestrial ecotype and three independent evolutions of the arboreal ecotype (Fig. 8). The evolution of the terrestrial ecotype is associated with the northward dispersal into the higher elevation valleys of the Hengduan Mountain Region.

Discussion

Paleo-Drainage and Species Evolution in the HMR

As in previous biogeographic and phylogeographic studies (Guo et al. 2005; He & Chen 2006; Zhang et al., 2010, 2011, 2019; Zhuang & Sun, 2011; Yang et al. 2012; Qi et al. 2015; Li et al. 2016; Wang et al. 2020), our data support the existence of a paleo-Red River drainage and subsequent drainage reorganization through river captures and reversals (Brookfield, 1998; Clark

et al. 2004). The inferred phylogeny of *Diploderma* reveals non-monophyletic species assemblages along the currently allopatric Jinsha, Mekong, and Yalong Rivers, which indicates multiple dispersals among these modern allopatric valleys. These relationships are indications for paleo-river connections (Tagliacollo et al. 2015). In addition, the three best fit drainage evolution models (DEM 1, 2, and 5) all support the paleo-connections between Mekong, Jinsha, and the upper Yalong Rivers to the Paleo-Red River and the subsequent reorganizations through time (Table 5; Fig. 5). The dated phylogeny of *Diploderma* put the capture time of the lower Jinsha from the Paleo-Red River on late Oligocene/early Miocene (about 24 Ma; Node 83 in Fig. 7), and the capture time of remaining major rivers from the paleo-Red River in early Miocene (about 17 Ma; Node 61 in Fig. 7), which are all consistent with estimations from geological studies (Clark et al. 2004; Clift et al. 2008; Hoang et al. 2009; McPhillips et al. 2016).

In addition to the previously hypothesized paleo-connections, our data show much more complex drainage-wide species assemblages along the Jinsha and Yalong Rivers, which suggest the possibility of additional novel drainage reorganizations further upstream in the northern HMR. Most previous studies show that species assemblages along the Jinsha and Yalong Rivers are monophyletic (He & Chen 2006; Peng et al. 2006; Yang et al. 2012; Li et al. 2016; Ren et al. 2018); and for the few that did show paraphyletic assemblages, only two groups were recovered along the Jinsha River (Zhang et al. 2010, 2019; Qi et al. 2014). Our ancestral range reconstruction shows a series of dispersal events among the upper Mekong, upper Jinsha, and upper Yalong valleys from late Miocene to Pleistocene, and all three rivers have paraphyletic species assemblages, particularly the Jinsha and Yalong (Node 45–57 in Fig. 7 and 8). Because the mountain ranges surrounding these valleys are dispersal barriers to ectothermic lizards today (over 4000 m of elevation with snow caps), these dispersal events could only be explained

through historical connections among these valleys, either through paleo-river channels that were overlooked, or through paleo-, low-elevation terrestrial valleys. As most previous geological studies on drainage evolution have focused on the middle and lower reaches of rivers south of 29° N (Zhang et al. 2019), the fine-scale geological history and connectivity patterns among upstream major rivers remained unexamined. In the late Miocene and Pliocene, the Hengduan Mountain Region experienced another wave of intense tectonic movements known as the Hengduan Movements (Zhang & Li 2016). These intense tectonic movements could easily have led to landfalls in river valleys, which could have altered the landscape drastically in a short period of time, creating and removing temporary cuts on the mountain ranges (Zeng 2002; Hoke et al. 2014). Furthermore, the climatic fluctuations of the Pliocene and Pleistocene likely facilitated this dispersal-isolation process by creating and removing additional distributional constraints on elevation through temperature change, promoting species diversifications in the ridge-gorge system (Flantua & Hooghiemstra 2018). Future geological studies are needed to examine our hypotheses on river captures further north in the HMR.

Regarding the controversial connection between paleo-Salween River and paleo-Red River (Clark et al. 2004; Clift et al. 2008; Zheng et al. 2013; Zhang et al. 2019), unfortunately, we cannot reach a confident conclusion. While two of the best fit drainage evolution models (DEM 1 and 2) show paleo-Salween had connected to paleo-Red River prior to early Miocene, the competing model (DEM 5) that is statistically close support the opposite conclusion, where there was no connections between the paleo-Salween and the Paleo-Red River drainage. This uncertainty can be explained by the possible location of capture event and the natural history of the study organism. Unlike fish that are completely restricted to the waterways themselves, lizards in the HMR were only tied to the waterways due to the sandwiching mountain ranges on

both sides. Therefore, as the mountain topography reduces elevation toward the southern periphery of the HMR, the distribution of lizards is no longer tied to the waterways, and other biogeographic factors might begin to dominate the evolution of organisms in these regions. Because the proposed capture location between paleo-Salween and paleo-Red River drainage is in the peripheral edge of HMR (between 28° and 29°N; Clark et al. 2004), and given the lower terrains in the adjacent lower sections in Southwest Yunnan Province allow free dispersal of lizards among valleys, the biogeographic signal of river capture may be very minimal, if it indeed happened. This could also explain the contradictory conclusion from a previous amphibian biogeographic study as well, where species from the southern terrains show no signals of paleo-river drainage (Yu et al. 2013). Future studies using fully aquatic organisms are needed to better assess the connectivity between paleo-upper Salween and paleo-Red River drainage.

Impacts of Biogeographic Lines on Terrestrial Fauna

Both TKL and MSD are well known as phytogeographic lines that delimit plant distribution patterns and population genetic structures, and both lines have been tested explicitly using plants (Gao et al. 2007; Fan et al. 2013; Tian et al. 2015; Zhao & Zhang, 2015; Luo et al. 2017; Zhao et al. 2018). Although these two lines have only been mentioned briefly in a few zoogeographic literature (Thinh et al. 2010; Geissmann et al. 2011), recent zoological studies have shown that species turnover pattern and genetic structures of animals in the HMR are congruent with one or both biogeographic lines (Bain & Hurley 2011; Liedigk et al. 2012; Yuan et al. 2016; Zhuang et al. 2018; Lyu et al. 2020). Nevertheless, no zoogeographic studies have tested the impacts of both lines explicitly. Our study provides the first explicit test of both lines using an animal system, and our results show that both biogeographic lines acted as the main dispersal barrier to

animals in the HMR, as they are to plants. For the MSD, Salween River (upper and middle reaches) is the only major river in the HMR that shows a monophyletic drainage-wide species assemblage (Fig. 3, 7): extant species of the Salween valley are decedents of a single MRCA migrating from the south, with no additional contributions from cross-valley dispersals; and the subsequent northward dispersals and vicariance along the Salween valley led to the current diversity today (possibly due to ecological divergence along the elevation gradient) (Fig. 7). For the TKL, it delimits the distribution of the two main clades of *Diploderma*, and it associates with the vicariations between the upper and lower reaches of Jinsha and Yalong Rivers (see discussion below; Fig. 3). Future zoogeographic studies in the HMR should take both biogeographic lines into consideration when interpreting their results.

Tectonic Mechanism and Linkage between Biogeographic Lines, Drainage Reorganization, and Active Tectonic Faults

Our results support the Nu Mountain Range as the driver for the MSD (Ward 1921; Geissmann et al. 2010; Luo et al. 2017), which had arisen prior to Miocene (Hoke et al. 2006; Botsyun et al. 2019a). Additionally, unlike other mountain ranges in the HMR (i.e. Ningjing-Yunling Mountain, Shalili Mountain; Fig. 1) that have experienced major falls and permitted cross-valley dispersals (discussed above), the Nu Mountain have persisted through the tectonic movements and continued to be a major dispersal barrier to *Diploderma* since Oligocene/early Miocene.

For the TKL, our results support the previously speculated link between TKL and paleo-drainage evolution in the HMR (Zhao& Zhang 2015). Even with a dense geographic sampling, the TKL still delimits the two major clades of *Diploderma*, which also correspond to the paleo-Red River and paleo-Yangtze River drainages (Fig. 3). Additionally, we found the seemingly

non-structured TKL overlays on top of two major tectonic fault systems in Southwest China, namely the Longmenshan-Xianshuihe Fault Belt and the Ailao-Red River Fault Belt (Li et al. 2000; Chen 2014; Zhang & Li 2016; Yi et al. 2020; Fig. 3C). These tectonic belts are known as potential driver for drainage reorganizations (Zeng 2002; Hoke et al. 2016). Additionally, since our inferred divergence of *Diploderma* along the TKL in late Oligocene/early Miocene is consistent with both the hypothesized time of drainage captures (Clark et al. 2004; Clift et al. 2008; Hoang et al. 2009; McPhillips et al. 2016) and the most active periods of both fault systems (Chen 2014; Wang et al. 2016a; Yi et al. 2020), it is evident that the “arbitrarily drawn” TKL is linked to the tectonic movements in the region, which also led to the drainage reorganizations in the HMR. These associations bring the biogeographic lines, reorganization of paleo-drainages, and tectonic movements along faults together as a cohesive set of factors that influenced organismal biogeography in the HMR. Future biogeographical studies should consider all three factors when interpreting their results.

All previous biogeographic studies on plants, fish, and amphibians all estimated a much younger time for their observed biogeographic divergences, and the younger time frame has led them to attribute the cause of observed biogeographic patterns to either the hypothesized recent uplift of Tibetan Plateau in late Miocene/Pliocene or the Quaternary climatic oscillations (He & Cheng 2006; Peng et al. 2006; Zhang et al. 2011, 2012, 2019; Yue et al. 2012; Fan et al. 2013; Yang et al. 2012; Tian et al. 2015; Zhao & Gong, 2015; Jiang et al. 2018; Ren et al. 2018; Zhao et al. 2018; Wang et al. 2020; Sun et al. 2021). These contradictory younger time estimations (i.e., late Miocene and onwards, mostly Pliocene and Pleistocene) of major phylogenetic divergences can be explained by the known issues associated with their calibration methods. Nearly all previous biogeographic studies used secondary calibration from past molecular studies (He &

Cheng 2006; Peng et al. 2006; Zhang et al. 2011, 2012, 2019; Yue et al. 2012; Fan et al. 2013; Yang et al. 2012; Tian et al. 2015; Zhao & Gong, 2015; Jiang et al. 2018; Ren et al. 2018; Zhao et al. 2018), and such calibration method is known to produce drastically younger estimation results (Sauquet et al. 2012). Remaining studies either used geological events that are directly related to the objective hypothesis (i.e. using hypothesized time of river capture itself to date other river captures in the HMR; Li et al. 2016), which poses risk of conducting circular arguments, or they only used a single fossil calibration, which also increase errors in the divergence estimation (Gaur & Martin 2004). As the more recent geological studies have dated the uplift of HMR to a much older time (i.e. Miocene and earlier; Zheng et al. 2013; Hoke et al. 2016; Botsyun et al. 2019a), consistent with our inferences using independent fossil records, we are confident that the younger divergence time (hence the younger time of geological events) from previous studies are the results of underestimation due to calibration issues.

Nevertheless, some of these younger estimations might be accurate and reflect a more recent colonization in the HMR, with the younger divergences and biogeographic patterns being explained by the climatic factors that reinforced the pattern created by previous tectonic factors. Future biogeographic studies with robust molecular calibrations in other taxonomic groups are needed to verify the results from previous studies.

Acrodont Evolution and Revision on Age of Major Taxonomic Groups

Similar to the recent biogeographic study using Fossilized Birth-Death model (Grismer et al. 2016), our age estimations for the age of Acrodont lizards (109.5 Ma) and age of the family Agamidae (103.4 Ma) are older than studies using other divergence estimation methods: about 84 Ma for Acrodont (Amer & Kumazawa 2005; Hugall et al. 2007; Yang et al. 2018), and about

75 Ma for Agamidae (Yang et al. 2018). On the other hand, our estimation on the age of the subfamily Draconinae (72.6 Ma) and within the genus *Diploderma* (MRCA between *D. splendidum* and *D. zhaoermii* 18.9 Ma) is younger than the most recent estimation (92 Ma for Draconinae, 23.3 Ma for MRCA between *D. splendidum* and *D. zhaoermii*, Grismer et al. 2016). These time differences could be explained by the differential calibration method used and fossil choice. Most previous studies used either MCMC or Yule process in BEAST, which greatly limit the number of fossils that they can use (i.e. only the oldest fossil). On the other hand, the recent FBD analyses on Draconinae used only a very small subset of available fossils (eight fossils in Grismer et al. 2016 vs. 21 fossils in current study), and many of the chosen fossils in Grismer et al. (2016) were problematic in terms of their phylogenetic positions (i.e. †*Mimeosaurus crassus*, †*Priscagama* spp., †*Rhampholeon* sp., and †*Tinosaurus* spp.; Smith 2011; Smith et al. 2011; Čerňanský et al. 2020), which can lead to overestimation of divergences (Matschiner 2019; O'Reilly & Donoghue 2020). We recommend future biogeographic studies of the family Agamidae use analysis methods that can utilize a wide spectrum of fossil data (i.e. FBD in BEAST or CladeAge), and studies should include all available Acrodont fossils with reliable phylogenetic placements.

Cryptic Diversity, Evolution, and Conservation of *Diploderma*

The taxonomy of the genus *Diploderma* has progressed considerably in the past 20 years, with more than 18 new species described from the HMR since 2000, constituting more than 50% of the recognized diversity (Uetz et al. 2021). Although previous taxonomic works have largely focused on the *D. flaviceps* complex in northwestern HMR (Gao & Hou 2002; Manthey et al. 2012; Wang et al. 2015, 2016, 2019a, 2021a, 2021b), our dense sampling still revealed several

large distribution gaps along the Anning and upper Yalong Rivers in Sichuan Province (Fig. 3). These gaps may harbor additional undescribed diversity because previously studies have shown consistent species turn-over pattern along major river valleys in the northwest HMR (Wang et al. 2019a, 2021a, 2021b). Furthermore, until today, the *D. splendidum* complex in lower Jinsha River remains largely overlooked (Ananjeva et al. 2017). Our results highlight a rich, undescribed diversity of the *D. splendidum* complex in the lower Jinsha and Yangtze River (sp. 1–7), particularly along the main course of Jinsha in northeastern Yunnan Province and nearby Sichuan Province (Fig. 3). Because the *D. splendidum* complex experience over-exploitation by illegal pet trade (unpublished data), it is crucial to resolve its taxonomy soon, so that proper protection and regulations can be applied accordingly. Future taxonomic studies should focus survey efforts on these target regions and further resolve the standing taxonomy issues.

The complex geological processes and climatic conditions have produced a rich diversity of *Diploderma* in the HMR. Our ancestral range reconstructions suggest that the genus *Diploderma* originated in the southern subtropical regions most likely in the southeast, and then species underwent multiple northward dispersals into the northern HMR. Such a reconstruction aligns with the known ecology of the close relatives of the genus *Diploderma*, all of which are forestry groups inhabiting subtropical/tropical Southeast Asia (i.e. *Acanthosaura*, *Calotes*, and *Pseudocalotes*; Wang et al. 2019a). Additionally, our results suggest that the northward dispersals are associated with the multiple independent evolution of rocky terrestrial ecotype. Most recent physiological study has already shown that *D. vela* shows high-elevation adaptations on physiology and gut microbiology (Zhu et al. 2021). Future comparative studies are needed to fully understand this unique evolutionary radiation of agamids on the edge of Tibetan plateau.

The rich diversity of *Diploderma* not only holds the key to understand some of the most fascinating issues in organismal evolution, but also is an essential part of the fragile valley ecosystem in the HMR. Unfortunately, despite the endangered conservation assessments and their important values for advancing biological studies, these unique lizards are facing urgent threats from habitat destructions (Wang et al. 2019a, 2021a, 2021b; Zhang et al. 2021). Additionally, China's conservation legislation is still far behind recent taxonomic updates, and most members of the genus *Diploderma* are still left out of national protections (Wang et al. 2021c). We continue to call for attentions on the urgent conservation issues of *Diploderma* in Southwest China. Specifically, we echo the suggestions by Wang et al. (2021a) in listing the entire genus as Class II protected in China and increase protection efforts on their fragile valley habitats in the HMR.

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Table 1. Competing geological hypotheses on the paleo-drainage evolution in the Hengduan Mountain Region (HMR).

Evidence	Conclusion on paleo-river connectivity	Suggested mechanism of river captures and reversals	Capture time away from Red River	Literature
River topologies	Paleo-upper Mekong, Yalong, both upper and middle Yangtze with Red River (possibly Salween as well)	Overall due to broad scale tectonic uplift; locally due to Tertiary activities along thrust belts	Oligocene to mid Miocene (~13.82–33.9 Ma)	Clark et al. 2004
Detrital zircon U-Pb age spectra	Paleo-upper Mekong, Salween, and both upper and middle Yangtze with Red River	Not specified	Prior to late Miocene (>5.3 Ma)	Wang et al. 2014; Su et al. 2019
Shifts in ϵ Nd values in the Hanoi Basin	Paleo-upper Yangtze and paleo-Red River	Strike-slip motion along ASRR shear zone, or combination of volcanic activity and rising magmas	Prior to 36 Ma	Gourbet et al. 2016
Detrital zircon U-Pb age distributions from fluval sands in paleo-Yangtze	Paleo-upper Yangtze, Yalong, and paleo-Red River	Activation of Dali fault system and initiation of crustal deformation	Pleistocene, <1.7 Ma	Kong et al. 2012
Ircon U-Pb dating and Hf isotope composition	No connection between paleo-Red River and upper Yangtze, Mekong, and Salween post late Miocene	Surface uplift of Tibet/Yunnan-Vietnam	Middle Miocene or earlier (≥ 13.82 Ma)	Hoang et al. 2009
Shifts in ϵ Nd values in the Hanoi Basin	Support connection between Paleo-middle Yangtze and Red River	Progressive surface uplift of eastern Tibet	Oligocene, between 31–35 Ma	Clift et al. 2006
Major trace element proxies, bulk Nd and single K-feldspar grain Pb isotope ion probe isotope analyses	No connection between paleo-Red River and upper Yangtze, Mekong, and Salween, middle Yangtze was lost from Red River prior to 24 Ma	Progressive surface uplift of eastern Tibet	Prior to 24 Ma	Clift et al. 2008

Detrital zircon U-Pb ages and paleocurrents in sedimentary basin deposits	No Cenozoic connection between paleo-Red River and upper Yangtze Jinsha achieved its modern course in late Pliocene, no connection between upper Yalong and upper Jinsha, and no connection between lower Jinsha and Red River since Eocene	Not specified	Cretaceous (prior to 66 Ma)	Wissink et al. 2016
Detrital detrital K-feldspar Three nuclide burial age	Upper Jinsha and paleo-Red River	Surface uplift of HMR Not specified	Eocene prior to middle Miocene (≥ 9 Ma)	Zhang et al. 2017 McPhillips et al. 2016
River topologies and rock types	Paleo-upper jinsha and paleo-Red River	Magmatic activity from fault belts in Laojun Mountain area	Eocene (about 35 Ma)	Zeng 2002

Table 2. Biogeographic division used for ancestral range reconstruction analyses.

Name	Description
Upper Salween Drainage	Between Nu Mt. and Gaoligong Mt., upstream of Yunnan-Tibet border
Middle Salween Drainage	Between Nu Mt. and Gaoligong Mt., between Yunnan-Tibet border and Lushui Township, Gongshan Prefecture, Yunnan Province; upstream of Yunnan-Tibet border
Upper Mekong Drainage	Between Nu Mt. and Mangkang Mt./Yunling, upstream of Deqin Township, Diqing Prefecture, Yunnan Province
Middle Mekong Drainage	Between Nu Mt. and Mangkang Mt./Yunling, between Deqin Township and Weixi County, Diqing Prefecture, Yunnan Province
Upper Jinsha Drainage	Between Mangkang Mt./Yunling and Shaluli Mt., upstream of Shangjiang Village, Shangrila County, Yunnan Province
Upper Jinsha Drainage	Between Mangkang Mt./Yunling and Shaluli Mt., between Shangjiang Village and Lijiang City, Yunnan Province
Lower Tropical Red River Drainage	Red River Drainage, remaining lowerstreams of Salween and Mekong, and the land regions in between
Upper Yalong Drainage	Between Shaluli Mt. and Daxue Mt., upstream (and inclusion) of Jinpin Mt., Liangshan Prefecture, Sichuan Province
Lower Yalong Drainage	Between Jinpin Mt. and Panzhihua City, Sichuan Province
Lower Yangtze Drainage	Lowerstream of Yangtze (lowerstream and exclusion of Lijiang, including tributeries such as Dadu, Min, and Jialing) and East Asian islands

Table 3. Dispersal probabilities of *Diploderma* across various landscape scenarios in the ancestral range reconstruction analyses.

Condition	Dispersal Probability
Landmass over 3400m elevation	0
Landmass between 3000–3400m elevation	0.5
Secondary connection through a different region	0.5
Tectonic fault and structure zone in T0	0
Tectonic fault and structure zone in T1	0.5
Tectonic fault and structure zone in T2	1
Any direct connection through river valley	1

Table 4. Time stratification and the associated geological events used in the ancestral range reconstruction analyses. All times are in the unit of million years ago (Ma).

Intervals	Time	Major Geological Event	Major geographic barrier	Citation
T0	30–23	First rapid exhumation and mountain building in the HMR	Longmenshan-Xiaojinhe Fault	Wang et al. 2012
T1	23–5	Second rapid exhumation and mountain building in the HMR Hengduan Movements (second rapid uplift of HMR), rearrangements of upper fluvial systems	Ailao Mt.-Red River shear zone/Fault	Leloup et al. 1995, 2001; Hoang et al. 2009; Wang et al. 2016a; Su et al. 2019
T2	5–0		Modern HMR ranges	Wang et al. 2012; Hoke et al. 2014

Table 5. Statistical model test of the eight proposed drainage evolution models (DEM) and the null model (DEM 9, no dispersal constrains) using DEC (dispersal-extinction-cladogenesis), dispersal-vicariance analysis (DIVALIKE), and Bayesian inference of historical biogeography for discrete areas (BAYAREALIKE) with and without the founder dispersal free parameter (j). Higher the Log-Likelihood (LnL), model confers a higher probability on the data. AICc and AICc_wt are the second order of Akaike Information Criterion (AIC) and weighted second order of AIC, respectively. Smaller the AICc value, better fit the model to the data; and larger the AICc_wt value, better fit the model. Likelihood Ratio Test compares the results of the paired nested models (i.e. same model with and without j), and a statistically significant P value (<0.05) indicates the results from the two nested models are statistically different. The best fit model is highlighted in bold font, which is the DEM2 using DIVALIKE.

Biogeographic Model	DEM	LnL	K	d	e	j	AICc	AICc_wt	Likelihood Ratio Test
DEC	1	-106.1	2	0.021	0.029	0	216.6	6.50E-21	
	2	-105.7	2	0.021	0.029	0	215.7	9.40E-21	
	3	-108	2	0.021	0.03	0	220.3	2.50E-20	
	4	-107.3	2	0.022	0.03	0	218.8	1.10E-20	
	5	-105.7	2	0.021	0.029	0	215.7	9.30E-21	
	6	-107.3	2	0.022	0.03	0	218.8	1.20E-20	
	7	-107.3	2	0.022	0.03	0	218.8	1.10E-20	
	8	-107.5	2	0.019	0.03	0	219.3	1.80E-20	
	9	-76.09	2	0.0032	0.0069	0	156.5	8.60E-08	
DEC+ j	1	-59.44	3	0.0014	1.00E-12	0.045	125.5	0.39	4.30E-22
	2	-59.32	3	0.0013	1.00E-12	0.048	125.3	0.4	6.00E-22
	3	-62.73	3	0.0012	1.00E-12	0.049	132.1	0.37	1.80E-21
	4	-61.23	3	0.0011	1.00E-12	0.046	129.1	0.35	8.40E-22
	5	-59.32	3	0.0013	1.00E-12	0.048	125.3	0.4	6.00E-22

DIVALIKE	6	-61.4	3	0.001	1.00E-12	0.04	129.4	0.31	9.90E-22
	7	-61.21	3	0.0013	1.00E-12	0.047	129	0.35	8.20E-22
	8	-61.85	3	0.0012	1.00E-12	0.043	130.3	0.36	1.30E-21
	9	-59.53	3	0.0004	1.00E-12	0.021	125.7	0.42	8.70E-09
	1	-104.2	2	0.02	0.022	0	212.8	4.40E-20	
	2	-103.7	2	0.021	0.022	0	211.7	7.00E-20	
	3	-106.1	2	0.021	0.023	0	216.5	1.80E-19	
	4	-105.3	2	0.021	0.023	0	214.8	8.40E-20	
	5	-103.7	2	0.021	0.022	0	211.7	6.90E-20	
DIVALIKE+j	6	-105.3	2	0.021	0.023	0	214.8	8.90E-20	
	7	-105.3	2	0.021	0.023	0	214.8	8.30E-20	
	8	-105.7	2	0.019	0.023	0	215.6	1.10E-19	
	9	-74.64	2	0.0037	1.00E-12	0	153.6	3.60E-07	
	1	-59.06	3	0.0014	1.00E-12	0.046	124.7	0.57	2.00E-21
	2	-59	3	0.0015	1.00E-12	0.046	124.6	0.55	3.30E-21
	3	-62.27	3	0.0015	1.00E-12	0.047	131.2	0.58	8.00E-21
	4	-60.69	3	0.0015	1.00E-12	0.047	128	0.6	3.70E-21
	5	-58.98	3	0.0015	1.00E-12	0.046	124.6	0.56	3.20E-21
BAYAREALIKE	6	-60.69	3	0.0015	1.00E-12	0.047	128	0.63	3.70E-21
	7	-60.68	3	0.0015	1.00E-12	0.047	128	0.6	3.70E-21
	8	-61.4	3	0.0014	1.00E-12	0.041	129.4	0.57	5.10E-21
	9	-59.21	3	0.0004	1.00E-12	0.021	125	0.57	2.80E-08
	1	-119.4	2	0.028	0.07	0	243.2	1.10E-26	
	2	-119	2	0.029	0.07	0	242.3	1.50E-26	
	3	-120.7	2	0.028	0.069	0	245.8	7.50E-26	
	4	-120.2	2	0.029	0.07	0	244.7	2.70E-26	
	5	-119	2	0.029	0.07	0	242.3	1.50E-26	
	6	-120.2	2	0.029	0.07	0	244.7	2.80E-26	
	7	-120.2	2	0.029	0.069	0	244.7	2.70E-26	

BAYAREALIKE+ <i>j</i>	8	-120.2	2	0.027	0.071	0	244.7	5.40E-26	
	9	-94.35	2	0.0047	0.055	0	193	1.00E-15	
	1	-61.51	3	0.0011	1.00E-07	0.05	129.7	0.048	5.10E-27
	2	-61.48	3	0.0011	1.00E-07	0.051	129.6	0.046	7.70E-27
	3	-64.71	3	0.0011	1.00E-07	0.051	136.1	0.051	3.50E-26
	4	-63.17	3	0.0011	1.00E-07	0.052	133	0.05	1.20E-26
	5	-61.46	3	0.0011	1.00E-07	0.051	129.6	0.047	7.50E-27
	6	-63.16	3	0.0011	1.00E-07	0.052	132.9	0.054	1.20E-26
	7	-63.15	3	0.0011	1.00E-07	0.052	132.9	0.05	1.20E-26
	8	-63.59	3	0.001	1.00E-07	0.045	133.8	0.064	2.00E-26
	9	-63.38	3	0.0002	1.00E-07	0.036	133.4	0.0089	3.50E-15

Appendix I. GenBank info. for outgroup samples used.

Genus	Species	Rag1	GenBank Accession Number			
			BDNF	CMOS	R35	ND2
<i>Acanthosaura</i>	<i>lepidogaster</i>	MG599024	MK001552	MK001490	MK001455	MG599024
<i>Agama</i>	<i>agama</i>	KJ363479	KJ363400	MK328157	–	AF128504
<i>Agama</i>	<i>anchietae</i>	GQ242239	–	JX838907	JX839094	GQ242169
<i>Amphibolurus</i>	<i>muricatus</i>	KF871767	KF871530	–	–	KF871706
<i>Bufoniceps</i>	<i>laungwalaensis</i>	KJ195946	–	–	–	DQ008214
<i>Calotes</i>	<i>emma</i>	MG599026	JF806005	–	–	DQ289460
<i>Calotes</i>	<i>versicolor</i>	JN979993	DQ340705	JX838985	JX839165	DQ289478
<i>Calumma</i>	<i>parsonii</i>	FJ984190	–	HK570657	–	AB474915
<i>Chamaeleo</i>	<i>calyptratus</i>	HQ876433	GU457847	HF570667	HQ876323	AF448744
<i>Chamaeleo</i>	<i>Chamaeleon</i>	FJ984184	–	–	–	AF448745
<i>Chamaeleo</i>	<i>dilepis</i>	HQ130625	–	HF570668	–	NC_012436
<i>Chlamydosaurus</i>	<i>kingii</i>	HQ662437	KX786741	–	JF804584	KX786824
<i>Cophotis</i>	<i>ceylanica</i>	MG599025	–	–	–	AF128493
<i>Diporiphora</i>	<i>australis</i>	JN815263	–	–	–	GU556023
<i>Draco</i>	<i>blanfordi</i>	MG599027	JF806010	–	JF804589	AF288242
<i>Gonocephalus</i>	<i>grandis</i>	LC469927	–	–	LC549230	MK015640
<i>Hydrosaurus</i>	<i>sp</i>	AY662583	JF806011	–	JF804591	AF128476
<i>Hypsilurus</i>	<i>boydii</i>	JF806196	DQ340727	–	JF804592	AY133013
<i>Hypsilurus</i>	<i>nigrigularis</i>	HQ662413	–	–	–	AY133016
<i>Japalura</i>	<i>tricarinata</i>	AY662585	MK001560	MK001491	MK001480	AF128478
<i>Kinyongia</i>	<i>fischeri</i>	GQ221960	KC507660	HF570685	–	EF222188
<i>Laudakia</i>	<i>lehmanni</i>	GQ242235	–	–	–	GQ242229
<i>Laudakia</i>	<i>stellio</i>	KJ363483	KJ363403	JX838986	JX839166	AF128516
<i>Leiolepis</i>	<i>belliana</i>	FJ356734	AY987965	AB516971	HQ876324	AB537554
<i>Mantheyus</i>	<i>phuwanensis</i>	FJ356735	–	–	–	AY555836

<i>Otocryptis</i>	<i>beddomei</i>	MG641363	—	—	MG641324	MG650165
<i>Phrynocephalus</i>	<i>guttatus</i>	KJ195978	—	—	—	KJ195938
<i>Phrynocephalus</i>	<i>mystaceus</i>	GQ242268	JF806014	JX838987	JX839167	KF691656
<i>Physignathus</i>	<i>cocincinus</i>	FJ356737	DQ340736	—	HQ876322	U82690
<i>Pogona</i>	<i>barbata</i>	HQ662419	—	—	—	AF128474
<i>Pogona</i>	<i>vitticeps</i>	JF806200	DQ340739	—	JF804600	AY133026
<i>Pseudocalotes</i>	<i>brevipes</i>	MG599031	—	—	—	AF128502
<i>Pseudocalotes</i>	<i>kakhiensis</i>	—	MK001549	MK001489	MK001447	MK001435
<i>Pseudocalotes</i>	<i>kingdonwardi</i>	—	MK001551	MK001504	MK001454	MK001437
<i>Pseudocalotes</i>	<i>kingdonwardi</i>	—	MK001550	MK001503	MK001453	MK001436
<i>Pseudotrapelus</i>	<i>sinaitus</i>	KP994929	—	JX838988	JX839168	AF128507
<i>Ptyctolaemus</i>	<i>collicriistatus</i>	MG599030	—	—	—	AY555837
<i>Ptyctolaemus</i>	<i>gularis</i>	—	MK001558	MK001488	MK001481	MK001393
<i>Rhampholeon</i>	<i>platyceps</i>	AY524954	KC507662	—	—	AY524917
<i>Rieppeleon</i>	<i>kerstenii</i>	AY524965	—	HQ130537	—	AB474918
<i>Saara</i>	<i>hardwickii</i>	GU457972	GU457849	—	HQ876325	AB113803
<i>Salea</i>	<i>horsfieldii</i>	MG599032	—	—	—	AF128490
<i>Sitana</i>	<i>visiri</i>	KT831311	—	—	KT831293	KT831340
<i>Trapelus</i>	<i>agilis</i>	KJ363480	JF806016	—	JF804606	MN427875
<i>Trapelus</i>	<i>runderatus</i>	FJ356736	—	MW204543	—	AF128508
<i>Uromastyx</i>	<i>acanthinurus</i>	AY662588	AY987979	—	—	U71325
<i>Uromastyx</i>	<i>benti</i>	FJ356733	—	—	—	AB113821
<i>Xenagama</i>	<i>taylori</i>	KP994938	—	JX838994	JX839174	DQ008215

Appendix II. GenBank information for the ingroup samples (43 species of *Diploderma*) used in this chapter. New sequences were indicated by placeholders (i.e. XXXX).

Locality Labels	Species	Locality	Voucher Number	Rag1	GenBank Accession Numbers			
					BDNF	CMOS	R35	ND2
33	<i>Diploderma anguetelinea</i>	Maidilong, Muli, Sichuan, China	KIZ 044772	XXXX	XXXX	XXXX	XXXX	XXXX
33	<i>Diploderma anguetelinea</i>	Maidilong, Muli, Sichuan, China	KIZ 044792	XXXX	XXXX	XXXX	XXXX	XXXX
33	<i>Diploderma angustelinea</i>	Maidilong, Muli, Sichuan, China	KIZ 029704	XXXX	MT57799 3	MT65904 9	MT65909 3	MT57793 0
18	<i>Diploderma aorun</i>	Rongzong, Deqin, Yunnan, China	KIZ 044432	XXXX	XXXX	XXXX	XXXX	XXXX
19	<i>Diploderma aorun</i>	Bengzilan, Yunnan, China	KIZ 032733	XXXX	MT57798 9	MT65905 2	MT65909 6	MT57793 8
19	<i>Diploderma aorun</i>	Bengzilan, Yunnan, China	KIZ 032737	XXXX	–	MT65905 4	MT65909 8	MT57794 0
19	<i>Diploderma aorun</i>	Bengzilan, Yunnan, China	KIZ 044433	XXXX	XXXX	XXXX	XXXX	XXXX
20	<i>Diploderma aorun</i>	Pengnanshou Bridge, Shangrila, Yunnan, China	KIZ 044819	XXXX	XXXX	XXXX	XXXX	XXXX
15	<i>Diploderma batangense</i>	Xisuoduo village, Markam, Tibet, China	KIZ 019314	XXXX	XXXX	XXXX	XXXX	MT57793 5
15	<i>Diploderma batangense</i>	Zhubalong, Markarm, Tibet	KIZ 09404	XXXX	MK00154 1	–	–	MK00141 2
15	<i>Diploderma batangense</i>	Batang township, Sichuan, China	KIZ 032714	XXXX	XXXX	XXXX	XXXX	XXXX
16	<i>Diploderma batangense</i>	Qiongde Village, Batang, Sichuan, China	KIZ 044732	XXXX	XXXX	XXXX	XXXX	XXXX
16	<i>Diploderma batangense</i>	Qiongde Village, Batang, Sichuan, China	KIZ 044731	XXXX	XXXX	XXXX	XXXX	XXXX

32	<i>Diploderma bowoense</i>	Bowo, Muli, Sichuan, China	KIZ 044757	—	—	—	—	MW506020
32	<i>Diploderma bowoense</i>	Bowo, Muli, Sichuan, China	KIZ 044758	—	—	—	—	MW506019
22	<i>Diploderma brevicauda</i>	Lijiang, Yunnan, China	KIZ 044305	—	—	—	—	MW506021
22	<i>Diploderma brevicauda</i>	Lijiang, Yunnan, China	KIZ 044306	—	—	—	—	MW506022
73	<i>Diploderma brevipes</i>	Taiwan, China	NMNS 19607	—	—	MK001506	MK001464	MK001429
73	<i>Diploderma brevipes</i>	Taiwan, China	NMNS 19608	—	—	MK001507	MK001465	MK001430
38	<i>Diploderma chapaense</i>	Yongping, Dali, Yunnan, China	KIZ 040145	XXXX	—	—	—	MK578667
39	<i>Diploderma chapaense</i>	Huangcaoling, Jingdong, Yunnan, China	KIZ 046970	XXXX	5	MK00152	—	MT659118
41	<i>Diploderma chapaense</i>	Lvchun, Honghe Prefecture, Yunnan, China	KIZ 034923	XXXX	6	MK001524	MK001494	MK001474
41	<i>Diploderma chapaense</i>	Lvchun, Honghe Prefecture, Yunnan, China	KIZ 034921	XXXX	5	MK001522	MK001502	MK001475
42	<i>Diploderma chapaense</i>	Chapa, Vietnam	ZMMU-NAP 01911	XXXX	—	—	—	MG214262
6	<i>Diploderma drukdaypo</i>	Chamdo City, Tibet, China	KIZ 016486	XXXX	5	MT57799	—	MT659102
7	<i>Diploderma drukdaypo</i>	Jinduo County, Chamdo, Tibet, China	KIZ 027627	XXXX	—	—	—	MT577951
48	<i>Diploderma dymondi</i>	Yongren, ChuXiong, Yunnan, China	KIZ 011302	XXXX	XXXX	XXXX	XXXX	XXXX
57	<i>Diploderma dymondi</i>	Qiaojia, Yunnan, China	KIZ 044193	XXXX	XXXX	XXXX	XXXX	XXXX

57	<i>Diploderma dymondi</i>	Qiaojia, Yunnan, China	KIZ 040147	XXXX	—	—	—	MT57789 9
58	<i>Diploderma dymondi</i>	Dongchuan, Yunnan, China	KIZ 040640	XXXX	MK00154 4	MK00151 4	MK00147 8	MK00142 3
58	<i>Diploderma dymondi</i>	Dongchuan, Yunnan, China	KIZ 040639	XXXX	MK00152 8	MK00151 3	MK00147 7	MK00142 2
56	<i>Diploderma fasciatum</i>	Daguan, Zhaotong, Yunnan, China	KIZ 044133	—	—	—	—	XXXX
61	<i>Diploderma fasciatum</i>	Daweishan, Honghe, Yunnan, China	KIZ 040192	—	—	—	—	XXXX
63	<i>Diploderma fasciatum</i>	Peng County, Sichuan, China	SYS r001847	—	—	—	—	XXXX
69	<i>Diploderma fasciatum</i>	Jinggangshan, JiangXi, China	SYS r000988	—	—	—	—	XXXX
70	<i>Diploderma fasciatum</i>	Nanling Forest Park, Shaoguan, Guangdong, China	SYS r002050	—	—	—	—	XXXX
71	<i>Diploderma fasciatum</i>	Daming Mt., Wuming County, Nanning, GuangXi, China	SYS r002175	—	—	—	—	XXXX
72	<i>Diploderma fasciatum</i>	Xinyi, Maoming, Guangdong, China	SYS r002145	—	—	—	—	XXXX
49	<i>Diploderma flaviceps</i>	Luding County, Ganzi, Sichuan, China	KIZ 01581	XXXX	XXXX	XXXX	XXXX	XXXX
50	<i>Diploderma flaviceps</i>	Kangding, Ganzi, Sichuan, China	KIZ 019576	XXXX	MT57796 9	MT65906 2	MT65910 8	MT57789 7
14	<i>Diploderma flavilabre</i>	Baiyu County, Ganzi, Sichuan	KIZ 032695	XXXX	MT57800 7	MT65903 9	MT65908 1	MT57791 8
14	<i>Diploderma flavilabre</i>	Baiyu, Ganzi, Sichuan, China	KIZ 032697	XXXX	MT57798 7	MT65903 6	MT65907 8	MT57791 5
16	<i>Diploderma formosgula</i>	Yangla, Deqin, Yunnan, China	KIZ 044420	XXXX	XXXX	XXXX	MW5060 24	

16	<i>Diploderma formosgula</i>	Yangla, Deqin, Yunnan, China	KIZ 044421	XXXX	XXXX	XXXX	MW5060 25	
12	<i>Diploderma iadinum</i>	Ninong, Deqin County, Yunnan, China	KIZ 09398	XXXX	XXXX	XXXX	XXXX	XXXX
13	<i>Diploderma iadinum</i>	Degong bridge, WeiXi, Yunnan, China	KIZ 027702	XXXX	MT57796 5	MT65903 5	MT65907 7	MT57795 7
13	<i>Diploderma iadinum</i>	Degong bridge, WeiXi, Yunnan, China	KIZ 027706	XXXX	MT57796 6	MT65903 3	MT65907 5	MT57795 5
13	<i>Diploderma iadinum</i>	Degong bridge, WeiXi, Yunnan, China	KIZ 027702	XXXX	MT57796 5	MT65903 5	MT65907 7	MT57795 7
1	<i>Diploderma laeviventre</i>	Basu, Tibet, China	KIZ 014037	XXXX	MK00153 3		MK00146 6	MK00140 7
1	<i>Diploderma laeviventre</i>	Basu, Tibet, China	KIZ 027692	XXXX	MT57798 2	MT65903 2	MT65907 4	MT57789 3
73	<i>Diploderma luei</i>	Taiwan, China	NMNS 19604	—	XXXX	XXXX	XXXX	MK00143 3
73	<i>Diploderma luei</i>	Taiwan, China	NMNS 19605	—	XXXX	XXXX	XXXX	MK00143 4
73	<i>Diploderma makii</i>	Taiwan, China	NMNS 19609	—	XXXX	XXXX	XXXX	MK00143 1
73	<i>Diploderma makii</i>	Taiwan, China	NMNS 19610	—	XXXX	XXXX	XXXX	MK00143 2
40	<i>Diploderma menghaiense</i>	Menghai, Xishuangbanna, Yunnan, China	L0031	—	—	—	—	MT59865 6
40	<i>Diploderma menghaiense</i>	Menghai, Xishuangbanna, Yunnan, China	L0033	—	—	—	—	MT59865 8
64	<i>Diploderma micangshanense</i>	WenXian, Gansu, China	KIZ 06850	XXXX	—	—	MK00145 2	MK00142 4
64	<i>Diploderma micangshanense</i>	WenXian, Gansu, China	WK-JK 038	XXXX	MK00153 9	—	—	MK57866 3

65	<i>Diploderma micangshanense</i>	ZhuXi County, Shiyan, Hubei, China	KIZ 032802	XXXX	—	—	—	MK578666
65	<i>Diploderma micangshanense</i>	ZhuXi County, Shiyan, Hubei, China	KIZ 032801	XXXX	9	—	0	MK578665
68	<i>Diploderma micangshanense</i>	Nanyang, XiXia County, Henan, China	KIZ 023231	XXXX	5	—	—	MK578664
31	<i>Diploderma panchi</i>	Yajiang, Ganzi, Sichuan, China	KIZ 032715	XXXX	1	6	0	MT577946
31	<i>Diploderma panchi</i>	Yajiang, Ganzi, Sichuan, China	KIZ 032717	XXXX	—	7	1	MT577947
31	<i>Diploderma panchi</i>	Yajiang, Sichuan, China	KIZ 032729	XXXX	—	—	—	MT577945
43	<i>Diploderma panlong</i>	Kuiduo, Jiulong County, Ganzi, Sichuan, China	KIZ 044781	XXXX	XXXX	XXXX	XXXX	XXXX
43	<i>Diploderma panlong</i>	Kuiduo, Jiulong County, Ganzi, Sichuan, China	KIZ 044782	XXXX	XXXX	XXXX	XXXX	XXXX
44	<i>Diploderma panlong</i>	Miansha Village, Mianning County, Sichuan, China	KIZ 040140	XXXX	—	—	—	MT577905
44	<i>Diploderma panlong</i>	Miansha Village, Mianning County, Sichuan, China	KIZ 040139	XXXX	—	—	—	MT577908
73	<i>Diploderma polygonatum</i>	Taiwan, China	NMNS 19598	XXXX	—	5	8	MK001427
73	<i>Diploderma polygonatum</i>	Taiwan, China	NMNS 19599	XXXX	—	6	9	MK001428
21	<i>Diploderma qilin</i>	Wujing, Shangrila County, Yunnan, China	KIZ 028332	XXXX	6	—	—	MT577941
21	<i>Diploderma qilin</i>	Wujing, Shangrila County, Yunnan, China	KIZ 028335	XXXX	3	—	—	MT577943

21	<i>Diploderma qilin</i>	Wujing, Shangrila County, Yunnan, China	KIZ 028333	XXXX	MK00152 6	—	—	MT57794 2
3	<i>Diploderma slowinskii</i>	Qiunatong, Gongshan, Yunnan, China	KIZ 027572	XXXX	MT57797 2	MT65902 9	MT65907 1	MT57791 2
4	<i>Diploderma slowinskii</i>	Pengdang Village, Gongshan County, Yunnan, China	CAS 214906	XXXX	MK00152 2	—	—	MK00140 5
4	<i>Diploderma slowinskii</i>	Puladi, Gongshan, Yunnan, China	KIZ 027577	XXXX	XXXX	XXXX	XXXX	XXXX
5	<i>Diploderma slowinskii</i>	Fugong, Gongshan County, Yunnan, China	CAS 214954	XXXX	MK00153 4	—	—	MK00140 6
5	<i>Diploderma slowinskii</i>	Fugong, Gongshan County, Yunnan, China	KIZ 027543	XXXX	MT57795 9	MT65902 7	MT65906 9	MT57791 0
5	<i>Diploderma slowinskii</i>	Fugong, Gongshan County, Yunnan, China	KIZ 027542	XXXX	XXXX	XXXX	XXXX	XXXX
5	<i>Diploderma slowinskii</i>	Fugong, Gongshan County, Yunnan, China	KIZ 027546	XXXX	XXXX	XXXX	XXXX	XXXX
66	<i>Diploderma sp1</i>	Chongqing, China	KIZ 040643	XXXX	XXXX	XXXX	XXXX	XXXX
66	<i>Diploderma sp1</i>	Chongqing, China	KIZ 040644	XXXX	XXXX	XXXX	XXXX	XXXX
25	<i>Diploderma sp8</i>	Fengke, Lijiang, Yunnan, China	KIZ 044355	XXXX	XXXX	XXXX	XXXX	XXXX
25	<i>Diploderma sp8</i>	Wanmai, Lijiang, Yunnan, China	KIZ 044337	XXXX	XXXX	XXXX	XXXX	XXXX
26	<i>Diploderma sp8</i>	Shanjiang, Village, Lijiang, Yunnan, China	KIZ 044339	XXXX	XXXX	XXXX	XXXX	XXXX
26	<i>Diploderma sp8</i>	Shanjiang, Village, Lijiang, Yunnan, China	KIZ 044342	XXXX	XXXX	XXXX	XXXX	XXXX
27	<i>Diploderma sp8</i>	Dadong Village, Lijiang, Yunnan, China	KIZ 028302	XXXX	XXXX	XXXX	XXXX	XXXX
28	<i>Diploderma sp8</i>	Li-ning Rd, Lijiang, Yunnan, China	KIZ 044281	XXXX	XXXX	XXXX	XXXX	XXXX
28	<i>Diploderma sp8</i>	Li-ning Rd, Lijiang, Yunnan, China	KIZ 044283	XXXX	XXXX	XXXX	XXXX	XXXX

25	<i>Diploderma sp8</i>	Liyuan Power Station, Yulong, Lijiang, Yunnan, China	KIZ 044358	XXXX	XXXX	XXXX	XXXX	XXXX
30	<i>Diploderma sp9</i>	Donglang, Muli, Sichuan, China	KIZ 044480	XXXX	XXXX	XXXX	XXXX	XXXX
30	<i>Diploderma sp9</i>	Donglang, Muli, Sichuan, China	KIZ 044481	XXXX	XXXX	XXXX	XXXX	XXXX
54	<i>Diploderma sp2</i>	Yongshan, Zhaotong, Yunnan	KIZ 044200	XXXX	XXXX	XXXX	XXXX	XXXX
54	<i>Diploderma sp2</i>	Yongshan, Zhaotong, Yunnan	KIZ 044202	XXXX	XXXX	XXXX	XXXX	XXXX
54	<i>Diploderma sp2</i>	Yongshan, Zhaotong, Yunnan	KIZ 044203	XXXX	XXXX	XXXX	XXXX	XXXX
54	<i>Diploderma sp2</i>	Yongshan, Zhaotong, Yunnan	KIZ 044204	XXXX	XXXX	XXXX	XXXX	XXXX
54	<i>Diploderma sp2</i>	Yongshan, Zhaotong, Yunnan, China	KIZ 044201	XXXX	XXXX	XXXX	XXXX	XXXX
53	<i>Diploderma sp3</i>	Mohong Village, Leibo, Liangshan, Sichuan, China	KIZ 044241	XXXX	XXXX	XXXX	XXXX	XXXX
53	<i>Diploderma sp3</i>	MohongzhongXin Village, Leibo, Sichuan, China	KIZ 044242	XXXX	XXXX	XXXX	XXXX	XXXX
53	<i>Diploderma sp3</i>	MohongzhongXin Village, Leibo, Sichuan, China	KIZ 044249	XXXX	XXXX	XXXX	XXXX	XXXX
53	<i>Diploderma sp3</i>	MohongzhongXin Village, Leibo, Sichuan, China	KIZ 044251	XXXX	XXXX	XXXX	XXXX	XXXX
53	<i>Diploderma sp3</i>	MohongzhongXin Village, Leibo, Sichuan, China	KIZ 044252	XXXX	XXXX	XXXX	XXXX	XXXX

55	<i>Diploderma sp4</i>	Jinyang County, Liangshan, Sichuan	KIZ 044254	XXXX	XXXX	XXXX	XXXX	XXXX
55	<i>Diploderma sp4</i>	Jinyang County, Liangshan, Sichuan	KIZ 044253	XXXX	XXXX	XXXX	XXXX	XXXX
55	<i>Diploderma sp4</i>	Jinyang, Liangshan, Sichuan, China	KIZ 044255	XXXX	XXXX	XXXX	XXXX	XXXX
51	<i>Diploderma sp5</i>	Yaan, Sichuan, China	KIZ 032686	XXXX	XXXX	XXXX	XXXX	XXXX
51	<i>Diploderma sp5</i>	Yaan, Sichuan, China	KIZ 032725	XXXX	XXXX	XXXX	XXXX	XXXX
51	<i>Diploderma sp5</i>	Yaan, Sichuan, China	CAS 194476	—	—	—	—	AF12850 1
51	<i>Diploderma sp5</i>	Yaan, Sichuan, China	KIZ 032728	XXXX	XXXX	XXXX	XXXX	XXXX
51	<i>Diploderma sp5</i>	Yaan, Sichuan, China	KIZ 032687	XXXX	XXXX	XXXX	XXXX	XXXX
51	<i>Diploderma sp5</i>	Yaan, Sichuan, China	KIZ 032727	XXXX	XXXX	XXXX	XXXX	XXXX
51	<i>Diploderma sp5</i>	Yaan, Sichuan, China	KIZ 032726	XXXX	XXXX	XXXX	XXXX	XXXX
52	<i>Diploderma sp6</i>	Jinkouhe, Ebian, Sichuan, China	KIZ 040158	XXXX	XXXX	XXXX	XXXX	XXXX
52	<i>Diploderma sp6</i>	Jinkouhe, Ebian, Sichuan, China	KIZ 040159	XXXX	XXXX	XXXX	XXXX	XXXX
52	<i>Diploderma sp6</i>	Jinkouhe, Ebian, Sichuan, China	KIZ 040160	XXXX	XXXX	XXXX	XXXX	XXXX
45	<i>Diploderma sp7</i>	Xichang, Sichuan, China	KIZ 019581	XXXX	XXXX	XXXX	XXXX	XXXX
29	<i>Diploderma sp8</i>	Lugu Lake, Sichuan, China	KIZ 032488	XXXX	MT57800 0	MT65904 5	MT65908 8	MT57792 5
29	<i>Diploderma sp8</i>	Lugu Lake, Sichuan, China	KIZ 032489	XXXX	MT57799 2	MT65904 6	MT65908 9	MT57792 6
35	<i>Diploderma sp8</i>	Qingtongping, Muli, Sichuan, China	KIZ 044801	XXXX	XXXX	XXXX	XXXX	XXXX
35	<i>Diploderma sp8</i>	Qingtongping, Muli, Sichuan, China	KIZ 044802	XXXX	XXXX	XXXX	XXXX	XXXX
35	<i>Diploderma sp8</i>	Muli, Sichuan, China	KIZ 044804	XXXX	XXXX	XXXX	XXXX	XXXX

29	<i>Diploderma sp8</i>	Lugu Lake, Yanyuan, Sichuan, China	KIZ 032486	XXXX	XXXX	XXXX	XXXX	XXXX
29	<i>Diploderma sp8</i>	Lugu Lake, Yanyuan, Sichuan, China	KIZ 032487	XXXX	XXXX	XXXX	XXXX	XXXX
35	<i>Diploderma sp8</i>	Qingtongping, Muli, Sichuan, China	KIZ 044803	XXXX	XXXX	XXXX	XXXX	XXXX
67	<i>Diploderma splendidum</i>	Yiling District, Yichang, Hubei, China	WK-JK 006	XXXX	XXXX	XXXX	XXXX	XXXX
46	<i>Diploderma swild</i>	Yanbian, Panzhihua, Sichuan, China	KIZ 034914	XXXX	MT57796 2	MT65906 6	MT65911 3	MN26629 9
46	<i>Diploderma swild</i>	Yanbian, Panzhihua, Sichuan, China	KIZ 034895	XXXX	MT57797 4	MT65906 5	MT65911 2	MN26629 8
73	<i>Diploderma swinhonis</i>	Taiwan, China	NMNS 19592	–	MK00152 3	MK00149 5	MK00145 6	MK00141 9
73	<i>Diploderma swinhonis</i>	Taiwan, China	NMNS 19593	–	MK00153 1	MK00149 6	MK00145 7	MK00142 0
73	<i>Diploderma swinhonis</i>	Taiwan, China	NMNS 19594	–	XXXX	XXXX	XXXX	XXXX
73	<i>Diploderma swinhonis</i>	Taiwan, China	NMNS 19595	–	XXXX	XXXX	XXXX	XXXX
73	<i>Diploderma swinhonis</i>	Taiwan, China	NMNS 19596	–	XXXX	XXXX	XXXX	XXXX
73	<i>Diploderma swinhonis</i>	Taiwan, China	NMNS 19597	–	XXXX	XXXX	XXXX	XXXX
73	<i>Diploderma swinhonis</i>	Taiwan, China	WK-JK 007	XXXX	XXXX	XXXX	XXXX	XXXX
47	<i>Diploderma varcoae</i>	Dali, Yunnan, China	KIZ 029711	XXXX	MT57801 0	MT65906 8	MT65911 6	MT57790 2
59	<i>Diploderma varcoae</i>	YuXi, Yunnan, China	KIZ 040301	XXXX	XXXX	XXXX	XXXX	XXXX
60	<i>Diploderma varcoae</i>	Mengzi, Yunnan, China	WK-JK 011	XXXX	–	–	–	MT57790 3

8	<i>Diploderma vela</i>	Tongsha, Markam, Tibet	KIZ 027672	XXXX	MT57797 9	MT65905 9	MT65910 4	MT57794 9
9	<i>Diploderma vela</i>	Rumei, Markam, Tibet	KIZ 027643	XXXX	XXXX MK00154	XXXX MK00149	XXXX MK00144	XXXX MK00141
10	<i>Diploderma vela</i>	Quzika, Markam, Tibet	KIZ 019299	XXXX	3	9	8	4
11	<i>Diploderma vela</i>	Foshan, Deqin, Yunnan, China	KIZ 027686	XXXX	XXXX	XXXX	XXXX	XXXX
11	<i>Diploderma vela</i>	Foshan, Deqin, Yunnan, China	KIZ 027696	XXXX	XXXX	XXXX	XXXX	XXXX
12	<i>Diploderma vela</i>	Feilai Tempel, Deqin, Yunnan, China	KIZ 027684	XXXX	XXXX	XXXX	XXXX	XXXX
2	<i>Diploderma yangi</i>	SWFU Zayu, Tibet, China	005411	XXXX	XXXX	XXXX	XXXX	XXXX
23	<i>Diploderma yulongense</i>	Tiget Leaping Gorge, Shangrila County, Yunnan, China	KIZ 09399	XXXX	–	MK00149 8	MK00145 0	MK00141 0
23	<i>Diploderma yulongense</i>	Tiget Leaping Gorge, Shangrila County, Yunnan, China	KIZ 028292	XXXX	–	MT65904 3	MT65908 5	MT57792 2
23	<i>Diploderma yulongense</i>	Tiget Leaping Gorge, Shangrila County, Yunnan, China	KIZ 028344	XXXX	XXXX	XXXX	XXXX	XXXX
23	<i>Diploderma yulongense</i>	Tiget Leaping Gorge, Shangrila County, Yunnan, China	KIZ 028343	XXXX	XXXX	XXXX	XXXX	XXXX
24	<i>Diploderma yulongense</i>	Baishuitai, Shangrila, Yunnan, China	KIZ 028300	XXXX	MT57801 3	MT65904 2	MT65908 4	MT57792 3
36	<i>Diploderma yunnanense</i>	Xima, Yingjian, Yunnan, China	KIZ 040193	XXXX	MT57801 2	–	–	MT57791 4
37	<i>Diploderma yunnanense</i>	Baoshan, Yunnan, China	CAS 242183	XXXX	MK00154 8	MK00151 8	MK00147 0	MK00140 9
37	<i>Diploderma yunnanense</i>	Baoshan, Yunnan, China	CAS 242271	XXXX	MK00154 7	MK00151 7	MK00146 9	MK00140 8

62	<i>Diploderma zhaoermii</i>	Wenchuan, Sichuan, China	KIZ 019564	XXXX	MK00154 9	MK00150 0	MK00146 7	MK00142 5
62	<i>Diploderma zhaoermii</i>	Wenchuan, Sichuan, China	KIZ 019565	XXXX	MK00155 0	MK00150 1	MK00146 8	MK00142 6
62	<i>Diploderma zhaoermii</i>	Wenchuan, Sichuan, China	MVZ 216622	XXXX	—	—	—	AF12850 0

Appendix III. Fossils used for the FBD calibration analyses. Fossil date ranges were taken either from Fossilwork or original publication.

Genus	species	Phylogenetic position	Minimum Age	Maximum Age	Reference
<i>Agama</i>	sp1	Crown member of the genus <i>Agama</i>	2.6	5.3	Delfino, M., Kotsakis, T., Arca, M., Tuveri, C., Pitruzzella, G., & Rook, L. (2008). Agamid lizards from the Plio-Pleistocene of Sardinia (Italy) and an overview of the European fossil record of the family. <i>Geodiversitas</i> 30(3):641–656
<i>Agama</i>	sp2	Crown member of the genus <i>Agama</i>	0	0.8	Abbazzi, L., Angelone, C., Arca, M., Barisone, G., Bedetti, C., Delfino, M., ... & Wilkens, B. (2004). Plio-Pleistocene fossil vertebrates of Monte Tuttavista (Orosei, E. Sardinia, Italy), an overview. <i>Rivista Italiana di Paleontologia e Stratigrafia</i> 110(3):681-706
<i>Amphibolurus</i>	sp	Crown member of the genus <i>Amphibolurus</i>	0.012	0.126	Wagler, J. (1830). <i>Natürliches System der Amphibien mit vorangehender Classification der Säugethiere und Vögel. Ein Beitrag zur vergleichenden Zoologie</i>
<i>Brevidensilacerta</i>	<i>xichuanensis</i>	Stem to Leiolepidinae	37.2	48.6	Li, J. (1991). Fossil reptiles from Hetaoyuan Formation, Xichuan, Henan. <i>Vertebrata Palasiatica</i> , 29,190–203
<i>Calumma</i>	<i>benovskyi</i>	Crown member of the genus <i>Calumma</i>	15.97	20.44	Čerňanský, A., Herrel, A., Kibii, J.M. <i>et al.</i> (2020). The only complete articulated early Miocene chameleon skull (Rusinga Island, Kenya) suggests an African origin for Madagascar's endemic chameleons. <i>Scientific Report</i> 10, 109. https://doi.org/10.1038/s41598-019-57014-5

<i>Chamaeleo</i>	<i>caroliquarti</i>	Crown member of the genus <i>Chamaeleo</i>	16	20	Černanský, A. (2010). A revision of chamaeleonids from the Lower Miocene of the Czech Republic with description of a new species of <i>Chamaeleo</i> (Squamata, Chamaeleonidae). <i>Geobios</i>, 43, 605–613 Alifanov, V. R. (2009). New acrodont lizards (Lacertilia) from the Middle Eocene of southern Mongolia. <i>Paleontological Journal</i>, 43, 675–684 Mead, J. I., Moscato, D., Wang, Y., Jin, C., & Yan, Y. (2014). Pleistocene lizards (Squamata, Reptilia) from the karst caves in Chongzuo, Guangxi, southern China. <i>Quaternary International</i>, 354, 94–99. Simões, T. R., Wilner, E., Caldwell, M. W., Weinschütz, L. C., & Kellner, A. W. A. (2015). A stem acrodontan lizard in the Cretaceous of Brazil revises early lizard evolution in Gondwana. <i>Nature Communications</i> 6:8149:1-8 Rana, R. S., Augé, M., Folie, A., Rose, K. D., Kumar, K., Singh, L., Sahni, L., & Smith, T. (2013). High diversity of acrodontan lizards in the early Eocene Vastan lignite mine of India. <i>Geologica Belgica</i>, 16, 290–301 Covacevich, J., Couper, P., Molnar, R. E., Witten, G., & Young, W. (1990). Miocene dragons from Riversleigh: new data on the history of the family Agamidae (Reptilia: Squamata) in Australia. <i>Mem Queensland Mus</i>, 29, 339–360
<i>Creberidentat</i>	<i>henanensis</i>	stem to Uromastycinae	37.2	48.6	
<i>Draco</i>	sp	Crown member of the genus <i>Draco</i>	0.1	1.2	
<i>Gueragama</i>	<i>sulamericana</i>	stem to Uromastycinae	70.6	94.3	
<i>Heterodontagama</i>	<i>borsukae</i>	Stem to Leiolepidinae	48.6	55.8	
<i>Physignathus</i>	sp	Crown member of the genus <i>Physignathus</i>	15.97	23.03	

<i>Pogona</i>	sp	Crown member of the genus <i>Pogona</i>	0	0.781	Reed, E. H., & Bourne, S. J. (2009). Pleistocene fossil vertebrate sites of the South East region of South Australia II. <i>Transactions of the Royal Society of South Australia</i> 133, 30–40
<i>Pogona</i>	sp2	Crown member of the genus <i>Pogona</i>	0	2.6	Storr, G. M. (1982). Revision of the Bearded Dragons (Lacertilia: Agamidae) of Western Australia with Notes on the Dismemberment of the Genus <i>Amphibolurus</i> . <i>Records of the Western Australian Museum</i> 10, 199–214
<i>Protodraco</i>	<i>monocoli</i>	Stem to Agamidae	98.17	99.41	Wagner, P., Stanley, E. L., Daza, J. D., & Bauer, A. M. (2021). A new agamid lizard in mid-Cretaceous amber from northern Myanmar. <i>Cretaceous Research</i> , 124, 104813.
<i>Qianshanosaurus</i>	<i>huangpuensis</i>	Stem to Uromastycinae	59.2	66	Dong, L., Evans, S. E., & Wang, Y. (2016). Taxonomic revision of lizards from the Paleocene deposits of the Qianshan Basin, Anhui, China. <i>Vertebrata Palasiatica</i> 54, 243–268
<i>Uromastix</i>	<i>europaeus</i>	Crown member of Uromastycinae	28.4	33.9	Rage J. C., & Augé, M. (2015). Valbro: A new site of vertebrates from the early Oligocene (MP 22) of France (Quercy). III - Amphibians and squamates. <i>Annales de Paléontologie</i> , 101, 29–41

Appendix IV. Time stratified dispersal matrices for the nine different drainage evolution models (DEMs). The graphic illustrations for all DEMs are in Fig. 5. T2: 23–30 Ma; T1: 5–23 Ma; T0: present–5 Ma. A: upper Salween River; B: middle Salween River; C: upper Mekong River; D: middle Mekong River; E: upper Jinsha River; F: Red River and subtropical lower Salween/Mekong River; G: upper Yalong River; H: lower Yalong River; I: middle Jinsha River; and J: lower Jinsha, Pearl, Yangtze, major tributaries of Yangtze River, and East Asian Islands.

DEM1											
T2	A	B	C	D	E	F	G	H	I	J	
A	1	1	0.125	0.25	0.125	0.5	0.0625	0.125	0.25	0.25	0.25
B	1	1	0.25	0.5	0.25	1	0.125	0.25	0.5	0.5	
C	0.25	0.25	1	1	0.125	0.5	0.0625	0.125	0.25	0.25	0.25
D	0.5	0.5	1	1	0.25	1	0.125	0.25	0.5	0.5	
E	0.125	0.25	0.125	0.25	1	0.5	0.25	0.25	1	0.5	
F	0.5	1	0.5	1	0.5	1	0.25	0.5	1	1	
G	0.0625	0.125	0.0625	0.125	0.25	0.25	1	1	0.5	0.5	
H	0.125	0.25	0.125	0.25	0.25	0.5	1	1	0.25	1	
I	0.25	0.5	0.25	0.5	1	1	0.5	0.25	1	1	
J	0.25	0.5	0.25	0.5	0.5	1	0.5	1	1	1	
T1	A	B	C	D	E	F	G	H	I	J	
A	1	1	0.25	0.5	0.0625	0.5	0.0625	0.0625	0.125	0.125	
B	1	1	0.5	1	0.125	1	0.125	0.125	0.25	0.25	
C	0.25	0.5	1	1	0.0625	0.5	0.0625	0.0625	0.125	0.125	
D	0.5	1	1	1	0.125	1	0.125	0.125	0.25	0.25	
E	0.0625	0.125	0.0625	0.125	1	0.25	0.5	0.5	1	0.5	
F	0.5	1	0.5	1	0.25	1	0.25	0.25	0.5	0.5	

G	0.0625	0.125	0.0625	0.125	0.5	0.25	1	0.5	1	0.5
H	0.0625	0.125	0.0625	0.125	0.5	0.25	0.5	1	0.5	1
I	0.125	0.25	0.125	0.25	1	0.5	1	0.5	1	1
J	0.125	0.25	0.125	0.25	0.5	0.5	0.5	1	1	1

T0	A	B	C	D	E	F	G	H	I	J
A	1	1	0.25	0.5	0.125	0.5	0.125	0.0625	0.25	0.125
B	1	1	0.5	1	0.25	1	0.25	0.125	0.5	0.25
C	0.25	0.5	1	1	0.25	0.5	0.25	0.125	0.5	0.125
D	0.5	1	1	1	0.5	1	0.5	0.25	1	0.25
E	0.125	0.25	0.25	0.5	1	0.5	0.5	0.25	1	0.5
F	0.5	1	0.5	1	0.5	1	0.5	0.25	1	0.5
G	0.125	0.25	0.25	0.5	0.5	0.5	1	0.5	1	0.5
H	0.0625	0.125	0.125	0.25	0.25	0.25	0.5	1	0	1
I	0.25	0.5	0.5	1	1	1	1	0	1	0.5
J	0.125	0.25	0.125	0.25	0.5	0.5	0.5	1	0.5	1

DEM2

T2	A	B	C	D	E	F	G	H	I	J
A	1	1	0.125	0.25	0.125	0.5	0.0625	0.125	0.25	0.25
B	1	1	0.25	0.5	0.25	1	0.125	0.25	0.5	0.5
C	0.125	0.25	1	1	0.125	0.5	0.0625	0.125	0.25	0.25
D	0.25	0.5	1	1	0.25	1	0.125	0.25	0.5	0.5
E	0.125	0.25	0.125	0.25	1	0.5	0.25	0.25	1	0.5
F	0.5	1	0.5	1	0.5	1	0.25	0.5	1	1
G	0.0625	0.125	0.0625	0.125	0.25	0.25	1	1	0.5	0.5
H	0.125	0.25	0.125	0.25	0.25	0.5	1	1	0.25	1
I	0.25	0.5	0.25	0.5	1	1	0.5	0.25	1	1
J	0.25	0.5	0.25	0.5	0.5	1	0.5	1	1	1

T1	A	B	C	D	E	F	G	H	I	J
A	1	1	0.125	0.25	0.0625	0.5	0.0625	0.0625	0.125	0.125
B	1	1	0.25	0.5	0.125	1	0.125	0.125	0.25	0.25
C	0.125	0.25	1	1	0.0625	0.5	0.0625	0.0625	0.125	0.125
D	0.25	0.5	1	1	0.125	1	0.125	0.125	0.25	0.25
E	0.0625	0.125	0.0625	0.125	1	0.25	0.5	0.5	1	0.5
F	0.5	1	0.5	1	0.25	1	0.25	0.25	0.5	0.5
G	0.0625	0.125	0.0625	0.125	0.5	0.25	1	0.5	1	0.5
H	0.0625	0.125	0.0625	0.125	0.5	0.25	0.5	1	0.5	1
I	0.125	0.25	0.125	0.25	1	0.5	1	0.5	1	1
J	0.125	0.25	0.125	0.25	0.5	0.5	0.5	1	1	1

T0	A	B	C	D	E	F	G	H	I	J
A	1	1	0.25	0.5	0.125	0.5	0.125	0.0625	0.25	0.125
B	1	1	0.5	1	0.25	1	0.25	0.125	0.5	0.25
C	0.25	0.5	1	1	0.25	0.5	0.25	0.125	0.5	0.125
D	0.5	1	1	1	0.5	1	0.5	0.25	1	0.25
E	0.125	0.25	0.25	0.5	1	0.5	0.5	0.25	1	0.5
F	0.5	1	0.5	1	0.5	1	0.5	0.25	1	0.5
G	0.125	0.25	0.25	0.5	0.5	0.5	1	0.5	1	0.5
H	0.0625	0.125	0.125	0.25	0.25	0.25	0.5	1	0	1
I	0.25	0.5	0.5	1	1	1	1	0	1	0.5
J	0.125	0.25	0.125	0.25	0.5	0.5	0.5	1	0.5	1

DEM3

T2	A	B	C	D	E	F	G	H	I	J
A	1	1	0.125	0.25	0.125	0.5	0.0625	0.125	0.25	0.25
B	1	1	0.25	0.5	0.25	1	0.125	0.25	0.5	0.5

	C	0.125	0.25	1	1	0.125	0.5	0.0625	0.125	0.25	0.25
	D	0.25	0.5	1	1	0.25	1	0.125	0.25	0.5	0.5
	E	0.125	0.25	0.125	0.25	1	0.5	0.25	0.25	1	0.5
	F	0.5	1	0.5	1	0.5	1	0.25	0.5	1	1
	G	0.0625	0.125	0.0625	0.125	0.25	0.25	1	1	0.5	0.5
	H	0.125	0.25	0.125	0.25	0.25	0.5	1	1	0.25	1
	I	0.25	0.5	0.25	0.5	1	1	0.5	0.25	1	1
	J	0.25	0.5	0.25	0.5	0.5	1	0.5	1	1	1
T1		A	B	C	D	E	F	G	H	I	J
	A	1	1	0.25	0.5	0.0625	0.5	0.03125	0.0625	0.125	0.125
	B	1	1	0.5	1	0.125	1	0.0625	0.125	0.25	0.25
	C	0.25	0.5	1	1	0.0625	0.5	0.03125	0.0625	0.125	0.125
	D	0.5	1	1	1	0.125	1	0.0625	0.125	0.25	0.25
	E	0.0625	0.125	0.0625	0.125	1	0.25	0.125	0.5	1	0.5
	F	0.5	1	0.5	1	0.25	1	0.125	0.25	0.5	0.5
	G	0.03125	0.0625	0.03125	0.0625	0.125	0.125	1	1	0.25	0.5
	H	0.0625	0.125	0.0625	0.125	0.5	0.25	1	1	0.5	1
	I	0.125	0.25	0.125	0.25	1	0.5	0.25	0.5	1	1
	J	0.125	0.25	0.125	0.25	0.5	0.5	0.5	1	1	1
T0		A	B	C	D	E	F	G	H	I	J
	A	1	1	0.25	0.5	0.125	0.5	0.03125	0.0625	0.25	0.125
	B	1	1	0.5	1	0.25	1	0.0625	0.125	0.5	0.25
	C	0.25	0.5	1	1	0.25	0.5	0.0625	0.125	0.5	0.125
	D	0.5	1	1	1	0.5	1	0.125	0.25	1	0.25
	E	0.125	0.25	0.25	0.5	1	0.5	0.125	0.25	1	0.25
	F	0.5	1	0.5	1	0.5	1	0.125	0.25	1	0.5

	G	0.03125	0.0625	0.0625	0.125	0.125	0.125	1	1	0	0.5
	H	0.0625	0.125	0.125	0.25	0.25	0.25	1	1	0.5	1
	I	0.25	0.5	0.5	1	1	1	0	0.5	1	0.5
	J	0.125	0.25	0.125	0.25	0.25	0.5	0.5	1	0.5	1
	DEM4										
T2	A	B	C	D	E	F	G	H	I	J	
	A	1	1	0.125	0.25	0.125	0.5	0.0625	0.125	0.25	0.25
	B	1	1	0.25	0.5	0.25	1	0.125	0.25	0.5	0.5
	C	0.125	0.25	1	1	0.125	0.5	0.0625	0.125	0.25	0.25
	D	0.25	0.5	1	1	0.25	1	0.125	0.25	0.5	0.5
	E	0.125	0.25	0.125	0.25	1	0.5	0.25	0.25	1	0.5
	F	0.5	1	0.5	1	0.5	1	0.25	0.5	1	1
	G	0.0625	0.125	0.0625	0.125	0.25	0.25	1	1	0.5	0.5
	H	0.125	0.25	0.125	0.25	0.25	0.5	1	1	0.25	1
	I	0.25	0.5	0.25	0.5	1	1	0.5	0.25	1	1
	J	0.25	0.5	0.25	0.5	0.5	1	0.5	1	1	1
T1	A	B	C	D	E	F	G	H	I	J	
	A	1	1	0.125	0.25	0.0625	0.5	0.03125	0.0625	0.125	0.125
	B	1	1	0.25	0.5	0.125	1	0.0625	0.125	0.25	0.25
	C	0.125	0.25	1	1	0.0625	0.5	0.03125	0.0625	0.125	0.125
	D	0.25	0.5	1	1	0.125	1	0.0625	0.125	0.25	0.25
	E	0.0625	0.125	0.0625	0.125	1	0.5	0.25	0.25	1	0.5
	F	0.5	1	0.5	1	0.5	1	0.125	0.25	0.25	0.5
	G	0.03125	0.0625	0.03125	0.0625	0.25	0.125	1	1	0.5	0.5
	H	0.0625	0.125	0.0625	0.125	0.25	0.25	1	1	0.25	1
	I	0.125	0.25	0.125	0.25	1	0.25	0.5	0.25	1	1
	J	0.125	0.25	0.125	0.25	0.5	0.5	0.5	1	1	1

T0	A	B	C	D	E	F	G	H	I	J
A	1	1	0.25	0.5	0.125	0.5	0.03125	0.0625	0.25	0.125
B	1	1	0.5	1	0.25	1	0.0625	0.125	0.5	0.25
C	0.25	0.5	1	1	0.25	0.5	0.0625	0.125	0.5	0.125
D	0.5	1	1	1	0.5	1	0.125	0.25	1	0.25
E	0.125	0.25	0.25	0.5	1	0.5	0.125	0.25	1	0.25
F	0.5	1	0.5	1	0.5	1	0.125	0.25	1	0.5
G	0.03125	0.0625	0.0625	0.125	0.125	0.125	1	1	0	0.5
H	0.0625	0.125	0.125	0.25	0.25	0.25	1	1	0.5	1
I	0.25	0.5	0.5	1	1	1	0	0.5	1	0.5
J	0.125	0.25	0.125	0.25	0.25	0.5	0.5	1	0.5	1

DEM5

T2	A	B	C	D	E	F	G	H	I	J
A	1	1	0.125	0.25	0.125	0.5	0.0625	0.125	0.25	0.25
B	1	1	0.25	0.5	0.25	1	0.125	0.25	0.5	0.5
C	0.125	0.25	1	1	0.125	0.5	0.0625	0.125	0.25	0.25
D	0.25	0.5	1	1	0.25	1	0.125	0.25	0.5	0.5
E	0.125	0.25	0.125	0.25	1	0.5	0.25	0.25	1	0.5
F	0.5	1	0.5	1	0.5	1	0.25	0.5	1	1
G	0.0625	0.125	0.0625	0.125	0.25	0.25	1	1	0.5	0.5
H	0.125	0.25	0.125	0.25	0.25	0.5	1	1	0.25	1
I	0.25	0.5	0.25	0.5	1	1	0.5	0.25	1	1
J	0.25	0.5	0.25	0.5	0.5	1	0.5	1	1	1

T1	A	B	C	D	E	F	G	H	I	J
A	1	1	0.125	0.25	0.0625	0.5	0.0625	0.0625	0.125	0.125
B	1	1	0.25	0.5	0.125	1	0.125	0.125	0.25	0.25

	C	0.125	0.25	1	1	0.0625	0.5	0.0625	0.0625	0.125	0.125
	D	0.25	0.5	1	1	0.125	1	0.125	0.125	0.25	0.25
	E	0.0625	0.125	0.0625	0.125	1	0.25	0.5	0.5	1	0.5
	F	0.5	1	0.5	1	0.25	1	0.25	0.25	0.5	0.5
	G	0.0625	0.125	0.0625	0.125	0.5	0.25	1	0.5	1	0.5
	H	0.0625	0.125	0.0625	0.125	0.5	0.25	0.5	1	0.5	1
	I	0.125	0.25	0.125	0.25	1	0.5	1	0.5	1	1
	J	0.125	0.25	0.125	0.25	0.5	0.5	0.5	1	1	1
T0	A		B	C	D	E	F	G	H	I	J
	A	1	1	0.125	0.25	0.125	0.5	0.125	0.0625	0.25	0.125
	B	1	1	0.25	0.5	0.25	1	0.25	0.125	0.5	0.25
	C	0.125	0.25	1	1	0.25	0.5	0.25	0.125	0.5	0.125
	D	0.25	0.5	1	1	0.5	1	0.5	0.25	1	0.25
	E	0.125	0.25	0.25	0.5	1	0.5	0.5	0.25	1	0.25
	F	0.5	1	0.5	1	0.5	1	0.5	0.25	1	0.5
	G	0.125	0.25	0.25	0.5	0.5	0.5	1	0.5	1	0.25
	H	0.0625	0.125	0.125	0.25	0.25	0.25	0.5	1	0	1
	I	0.25	0.5	0.5	1	1	1	1	0	1	0.5
	J	0.125	0.25	0.125	0.25	0.25	0.5	0.25	1	0.5	1
	DEM6										
T2	A		B	C	D	E	F	G	H	I	J
	A	1	1	0.125	0.25	0.125	0.5	0.0625	0.125	0.25	0.25
	B	1	1	0.25	0.5	0.25	1	0.125	0.25	0.5	0.5
	C	0.125	0.25	1	1	0.125	0.5	0.0625	0.125	0.25	0.25
	D	0.25	0.5	1	1	0.25	1	0.125	0.25	0.5	0.5
	E	0.125	0.25	0.125	0.25	1	0.5	0.25	0.25	1	0.5
	F	0.5	1	0.5	1	0.5	1	0.25	0.5	1	1
	G	0.0625	0.125	0.0625	0.125	0.25	0.25	1	1	0.5	0.5

H	0.125	0.25	0.125	0.25	0.25	0.5	1	1	0.25	1
I	0.25	0.5	0.25	0.5	1	1	0.5	0.25	1	1
J	0.25	0.5	0.25	0.5	0.5	1	0.5	1	1	1

T1	A	B	C	D	E	F	G	H	I	J
A	1	1	0.125	0.25	0.0625	0.5	0.03125	0.0625	0.125	0.125
B	1	1	0.25	0.5	0.125	1	0.0625	0.125	0.25	0.25
C	0.125	0.25	1	1	0.0625	0.5	0.03125	0.0625	0.125	0.125
D	0.25	0.5	1	1	0.125	1	0.0625	0.125	0.25	0.25
E	0.0625	0.125	0.0625	0.125	1	0.5	0.25	0.25	1	0.5
F	0.5	1	0.5	1	0.5	1	0.125	0.25	0.25	0.5
G	0.03125	0.0625	0.03125	0.0625	0.25	0.125	1	1	0.5	0.5
H	0.0625	0.125	0.0625	0.125	0.25	0.25	1	1	0.25	1
I	0.125	0.25	0.125	0.25	1	0.25	0.5	0.25	1	1
J	0.125	0.25	0.125	0.25	0.5	0.5	0.5	1	1	1

T0	A	B	C	D	E	F	G	H	I	J
A	1	1	0.125	0.25	0.125	0.5	0.125	0.0625	0.25	0.125
B	1	1	0.25	0.5	0.25	1	0.25	0.125	0.5	0.25
C	0.125	0.25	1	1	0.25	0.5	0.25	0.125	0.5	0.125
D	0.25	0.5	1	1	0.5	1	0.5	0.25	1	0.25
E	0.125	0.25	0.25	0.5	1	0.5	0.5	0.25	1	0.25
F	0.5	1	0.5	1	0.5	1	0.5	0.25	1	0.5
G	0.125	0.25	0.25	0.5	0.5	0.5	1	0.5	1	0.25
H	0.0625	0.125	0.125	0.25	0.25	0.25	0.5	1	0	1
I	0.25	0.5	0.5	1	1	1	1	0	1	0.5
J	0.125	0.25	0.125	0.25	0.25	0.5	0.25	1	0.5	1

DEM7

T2	A	B	C	D	E	F	G	H	I	J
A	1	1	0.125	0.25	0.125	0.5	0.0625	0.125	0.25	0.25
B	1	1	0.25	0.5	0.25	1	0.125	0.25	0.5	0.5
C	0.125	0.25	1	1	0.125	0.5	0.0625	0.125	0.25	0.25
D	0.25	0.5	1	1	0.25	1	0.125	0.25	0.5	0.5
E	0.125	0.25	0.125	0.25	1	0.5	0.25	0.25	1	0.5
F	0.5	1	0.5	1	0.5	1	0.25	0.5	1	1
G	0.0625	0.125	0.0625	0.125	0.25	0.25	1	1	0.5	0.5
H	0.125	0.25	0.125	0.25	0.25	0.5	1	1	0.25	1
I	0.25	0.5	0.25	0.5	1	1	0.5	0.25	1	1
J	0.25	0.5	0.25	0.5	0.5	1	0.5	1	1	1

T1	A	B	C	D	E	F	G	H	I	J
A	1	1	0.125	0.25	0.0625	0.5	0.03125	0.0625	0.125	0.125
B	1	1	0.25	0.5	0.125	1	0.0625	0.125	0.25	0.25
C	0.125	0.25	1	1	0.0625	0.5	0.03125	0.0625	0.125	0.125
D	0.25	0.5	1	1	0.125	1	0.0625	0.125	0.25	0.25
E	0.0625	0.125	0.0625	0.125	1	0.5	0.25	0.25	1	0.5
F	0.5	1	0.5	1	0.5	1	0.125	0.25	0.25	0.5
G	0.03125	0.0625	0.03125	0.0625	0.25	0.125	1	1	0.5	0.5
H	0.0625	0.125	0.0625	0.125	0.25	0.25	1	1	0.25	1
I	0.125	0.25	0.125	0.25	1	0.25	0.5	0.25	1	1
J	0.125	0.25	0.125	0.25	0.5	0.5	0.5	1	1	1

T0	A	B	C	D	E	F	G	H	I	J
A	1	1	0.125	0.25	0.125	0.5	0.03125	0.0625	0.25	0.125
B	1	1	0.25	0.5	0.25	1	0.0625	0.125	0.5	0.25
C	0.125	0.25	1	1	0.25	0.5	0.0625	0.125	0.5	0.125

D	0.25	0.5	1	1	0.5	1	0.125	0.25	1	0.25
E	0.125	0.25	0.25	0.5	1	0.5	0.125	0.25	1	0.25
F	0.5	1	0.5	1	0.5	1	0.125	0.25	1	0.5
G	0.03125	0.0625	0.0625	0.125	0.125	0.125	1	1	0	0.5
H	0.0625	0.125	0.125	0.25	0.25	0.25	1	1	0.5	1
I	0.25	0.5	0.5	1	1	1	0	0.5	1	0.5
J	0.125	0.25	0.125	0.25	0.25	0.5	0.5	1	0.5	1

DEM8

T2	A	B	C	D	E	F	G	H	I	J
A	1	1	0.125	0.25	0.125	0.5	0.0625	0.125	0.25	0.25
B	1	1	0.25	0.5	0.25	1	0.125	0.25	0.5	0.5
C	0.25	0.25	1	1	0.125	0.5	0.0625	0.125	0.25	0.25
D	0.5	0.5	1	1	0.25	1	0.125	0.25	0.5	0.5
E	0.125	0.25	0.125	0.25	1	0.5	0.25	0.25	1	0.5
F	0.5	1	0.5	1	0.5	1	0.25	0.5	1	1
G	0.0625	0.125	0.0625	0.125	0.25	0.25	1	1	0.5	0.5
H	0.125	0.25	0.125	0.25	0.25	0.5	1	1	0.25	1
I	0.25	0.5	0.25	0.5	1	1	0.5	0.25	1	1
J	0.25	0.5	0.25	0.5	0.5	1	0.5	1	1	1

T1	A	B	C	D	E	F	G	H	I	J
A	1	1	0.125	0.25	0.125	0.5	0.0625	0.125	0.25	0.25
B	1	1	0.25	0.5	0.25	1	0.125	0.25	0.5	0.5
C	0.25	0.25	1	1	0.125	0.5	0.0625	0.125	0.25	0.25
D	0.5	0.5	1	1	0.25	1	0.125	0.25	0.5	0.5
E	0.125	0.25	0.125	0.25	1	0.5	0.25	0.25	1	0.5
F	0.5	1	0.5	1	0.5	1	0.25	0.5	1	1
G	0.0625	0.125	0.0625	0.125	0.25	0.25	1	1	0.5	0.5

	H	0.125	0.25	0.125	0.25	0.25	0.5	1	1	0.25	1
	I	0.25	0.5	0.25	0.5	1	1	0.5	0.25	1	1
	J	0.25	0.5	0.25	0.5	0.5	1	0.5	1	1	1
T0		A	B	C	D	E	F	G	H	I	J
	A	1	1	0.125	0.25	0.125	0.5	0.0625	0.125	0.25	0.25
	B	1	1	0.25	0.5	0.25	1	0.125	0.25	0.5	0.5
	C	0.25	0.25	1	1	0.125	0.5	0.0625	0.125	0.25	0.25
	D	0.5	0.5	1	1	0.25	1	0.125	0.25	0.5	0.5
	E	0.125	0.25	0.125	0.25	1	0.5	0.25	0.25	1	0.5
	F	0.5	1	0.5	1	0.5	1	0.25	0.5	1	1
	G	0.0625	0.125	0.0625	0.125	0.25	0.25	1	1	0.5	0.5
	H	0.125	0.25	0.125	0.25	0.25	0.5	1	1	0.25	1
	I	0.25	0.5	0.25	0.5	1	1	0.5	0.25	1	1
	J	0.25	0.5	0.25	0.5	0.5	1	0.5	1	1	1
		DEM9									
T2		A	B	C	D	E	F	G	H	I	J
	A	1	1	1	1	1	1	1	1	1	1
	B	1	1	1	1	1	1	1	1	1	1
	C	1	1	1	1	1	1	1	1	1	1
	D	1	1	1	1	1	1	1	1	1	1
	E	1	1	1	1	1	1	1	1	1	1
	F	1	1	1	1	1	1	1	1	1	1
	G	1	1	1	1	1	1	1	1	1	1
	H	1	1	1	1	1	1	1	1	1	1
	I	1	1	1	1	1	1	1	1	1	1
	J	1	1	1	1	1	1	1	1	1	1
T1		A	B	C	D	E	F	G	H	I	J

A	1	1	1	1	1	1	1	1	1	1
B	1	1	1	1	1	1	1	1	1	1
C	1	1	1	1	1	1	1	1	1	1
D	1	1	1	1	1	1	1	1	1	1
E	1	1	1	1	1	1	1	1	1	1
F	1	1	1	1	1	1	1	1	1	1
G	1	1	1	1	1	1	1	1	1	1
H	1	1	1	1	1	1	1	1	1	1
I	1	1	1	1	1	1	1	1	1	1
J	1	1	1	1	1	1	1	1	1	1

T0	A	B	C	D	E	F	G	H	I	J
A	1	1	1	1	1	1	1	1	1	1
B	1	1	1	1	1	1	1	1	1	1
C	1	1	1	1	1	1	1	1	1	1
D	1	1	1	1	1	1	1	1	1	1
E	1	1	1	1	1	1	1	1	1	1
F	1	1	1	1	1	1	1	1	1	1
G	1	1	1	1	1	1	1	1	1	1
H	1	1	1	1	1	1	1	1	1	1
I	1	1	1	1	1	1	1	1	1	1
J	1	1	1	1	1	1	1	1	1	1

Appendix V. Area adjacency matrix used for the nine time-stratified drainage evolution models (DEMs). The graphic illustrations for all DEMs are in Fig. 5. T2: 23–30 Ma; T1: 5–23 Ma; T0: present–5 Ma. A: upper Salween River; B: middle Salween River; C: upper Mekong River; D: middle Mekong River; E: upper Jinsha River; F: Red River and subtropical lower Salween/Mekong River; G: upper Yalong River; H: lower Yalong River; I: middle Jinsha River; and J: lower Jinsha, Pearl, Yangtze, major tributaries of Yangtze River, and East Asian Islands.

		DEM1										
T2		A	B	C	D	E	F	G	H	I	J	
	A		1	1	0	0	0	0	0	0	0	0
	B		1	1	0	0	0	1	0	0	0	0
	C		0	0	1	1	0	0	0	0	0	0
	D		0	0	1	1	0	1	0	0	0	0
	E		0	0	0	0	1	0	0	0	1	0
	F		0	1	0	1	0	1	0	0	1	1
	G		0	0	0	0	0	0	1	1	1	0
	H		0	0	0	0	0	0	1	1	1	1
	I		0	0	0	0	1	1	1	1	1	1
	J		0	0	0	0	0	1	0	1	1	1
T1		A	B	C	D	E	F	G	H	I	J	
	A		1	1	0	1	0	0	0	0	0	0
	B		1	1	1	1	0	1	0	0	0	0
	C		0	1	1	1	0	0	0	0	0	0
	D		1	1	1	1	0	1	0	0	0	0
	E		0	0	0	0	1	0	0	0	1	0
	F		0	1	0	1	0	1	0	0	1	1

G	0	0	0	0	0	0	1	1	1	0
H	0	0	0	0	0	0	1	1	1	1
I	0	0	0	0	1	1	1	1	1	1
J	0	0	0	0	0	1	0	1	1	1

T0

	A	B	C	D	E	F	G	H	I	J
A	1	1	0	1	0	0	0	0	0	0
B	1	1	1	1	0	1	0	0	0	0
C	0	1	1	1	0	0	0	0	0	0
D	1	1	1	1	0	1	0	0	1	0
E	0	0	0	0	1	0	0	0	1	0
F	0	1	0	1	0	1	0	0	1	1
G	0	0	0	0	0	0	1	1	1	0
H	0	0	0	0	0	0	1	1	1	1
I	0	0	0	1	1	1	1	1	1	1
J	0	0	0	0	0	1	0	1	1	1

DEM2

T2

	A	B	C	D	E	F	G	H	I	J
A	1	1	0	0	0	0	0	0	0	0
B	1	1	0	0	0	1	0	0	0	0
C	0	0	1	1	0	0	0	0	0	0
D	0	0	1	1	0	1	0	0	0	0
E	0	0	0	0	1	0	0	0	1	0
F	0	1	0	1	0	1	0	0	1	1
G	0	0	0	0	0	0	1	1	1	0
H	0	0	0	0	0	0	1	1	0	1
I	0	0	0	0	1	1	1	0	1	1
J	0	0	0	0	0	1	0	1	1	1

T1		A	B	C	D	E	F	G	H	I	J
	A	1	1	0	0	0	0	0	0	0	0
	B	1	1	0	0	0	1	0	0	0	0
	C	0	0	1	1	0	0	0	0	0	0
	D	0	0	1	1	0	1	0	0	0	0
	E	0	0	0	0	1	0	0	0	1	0
	F	0	1	0	1	0	1	0	0	1	1
	G	0	0	0	0	0	0	1	1	1	0
	H	0	0	0	0	0	0	1	1	1	1
	I	0	0	0	0	1	1	1	1	1	1
	J	0	0	0	0	0	1	0	1	1	1
T0		A	B	C	D	E	F	G	H	I	J
	A	1	1	0	1	0	0	0	0	0	0
	B	1	1	1	1	0	1	0	0	0	0
	C	0	1	1	1	0	0	0	0	0	0
	D	1	1	1	1	0	1	0	0	1	0
	E	0	0	0	0	1	0	0	0	1	0
	F	0	1	0	1	0	1	0	0	1	1
	G	0	0	0	0	0	0	1	1	1	0
	H	0	0	0	0	0	0	1	1	1	1
	I	0	0	0	1	1	1	1	1	1	1
	J	0	0	0	0	0	1	0	1	1	1
DEM3											
T2		A	B	C	D	E	F	G	H	I	J
	A	1	1	0	0	0	0	0	0	0	0
	B	1	1	0	0	0	1	0	0	0	0
	C	0	0	1	1	0	0	0	0	0	0
	D	0	0	1	1	0	1	0	0	0	0

	E	0	0	0	0	1	0	0	0	1	0
	F	0	1	0	1	0	1	0	0	1	1
	G	0	0	0	0	0	0	1	1	1	0
	H	0	0	0	0	0	0	1	1	0	1
	I	0	0	0	0	1	1	1	0	1	1
	J	0	0	0	0	0	1	0	1	1	1
T1		A	B	C	D	E	F	G	H	I	J
	A	1	1	0	0	0	0	0	0	0	0
	B	1	1	0	1	0	1	0	0	0	0
	C	0	0	1	1	0	0	0	0	0	0
	D	0	1	1	1	0	1	0	0	0	0
	E	0	0	0	0	1	0	0	0	1	0
	F	0	1	0	1	0	1	0	0	1	1
	G	0	0	0	0	0	0	1	1	1	0
	H	0	0	0	0	0	0	1	1	1	1
	I	0	0	0	0	1	1	1	1	1	1
	J	0	0	0	0	0	1	0	1	1	1
T0		A	B	C	D	E	F	G	H	I	J
	A	1	1	0	1	0	0	0	0	0	0
	B	1	1	1	1	0	1	0	0	0	0
	C	0	1	1	1	0	0	0	0	0	0
	D	1	1	1	1	0	1	0	0	1	0
	E	0	0	0	0	1	0	0	0	1	0
	F	0	1	0	1	0	1	0	0	1	1
	G	0	0	0	0	0	0	1	1	1	0
	H	0	0	0	0	0	0	1	1	1	1
	I	0	0	0	1	1	1	1	1	1	1

T2	J	0	0	0	0	0	1	0	1	1	1
		DEM4									
		A	B	C	D	E	F	G	H	I	J
	A	1	1	0	0	0	0	0	0	0	0
	B	1	1	0	0	0	1	0	0	0	0
	C	0	0	1	1	0	0	0	0	0	0
	D	0	0	1	1	0	1	0	0	0	0
	E	0	0	0	0	1	0	0	0	1	0
	F	0	1	0	1	0	1	0	0	1	1
	G	0	0	0	0	0	0	1	1	1	0
	H	0	0	0	0	0	0	1	1	0	1
	I	0	0	0	0	1	1	1	0	1	1
	J	0	0	0	0	0	1	0	1	1	1
T1		A	B	C	D	E	F	G	H	I	J
	A	1	1	0	0	0	0	0	0	0	0
	B	1	1	0	0	0	1	0	0	0	0
	C	0	0	1	1	0	0	0	0	0	0
	D	0	0	1	1	0	1	0	0	0	0
	E	0	0	0	0	1	0	0	0	1	0
	F	0	1	0	1	0	1	0	0	1	1
	G	0	0	0	0	0	0	1	1	1	0
	H	0	0	0	0	0	0	1	1	1	1
	I	0	0	0	0	1	1	1	1	1	1
	J	0	0	0	0	0	1	0	1	1	1
		A	B	C	D	E	F	G	H	I	J
T0	A	1	1	0	1	0	0	0	0	0	0
	B	1	1	1	1	0	1	0	0	0	0

C	0	1	1	1	0	0	0	0	0	0
D	1	1	1	1	0	1	0	0	1	0
E	0	0	0	0	1	0	0	0	1	0
F	0	1	0	1	0	1	0	0	1	1
G	0	0	0	0	0	0	1	1	1	0
H	0	0	0	0	0	0	1	1	1	1
I	0	0	0	1	1	1	1	1	1	1
J	0	0	0	0	0	1	0	1	1	1

DEM5

T2

	A	B	C	D	E	F	G	H	I	J
A	1	1	0	0	0	0	0	0	0	0
B	1	1	0	0	0	1	0	0	0	0
C	0	0	1	1	0	0	0	0	0	0
D	0	0	1	1	0	1	0	0	0	0
E	0	0	0	0	1	0	0	0	1	0
F	0	1	0	1	0	1	0	0	1	1
G	0	0	0	0	0	0	1	1	1	0
H	0	0	0	0	0	0	1	1	0	1
I	0	0	0	0	1	1	1	0	1	1
J	0	0	0	0	0	1	0	1	1	1

T1

	A	B	C	D	E	F	G	H	I	J
A	1	1	0	0	0	0	0	0	0	0
B	1	1	0	0	0	1	0	0	0	0
C	0	0	1	1	0	0	0	0	0	0
D	0	0	1	1	0	1	0	0	0	0
E	0	0	0	0	1	0	0	0	1	0
F	0	1	0	1	0	1	0	0	1	1
G	0	0	0	0	0	0	1	1	1	0

T0	H	0	0	0	0	0	0	1	1	1	1
	I	0	0	0	0	1	1	1	1	1	1
	J	0	0	0	0	0	1	0	1	1	1
		A	B	C	D	E	F	G	H	I	J
	A	1	1	0	0	0	0	0	0	0	0
	B	1	1	0	0	0	1	0	0	0	0
	C	0	0	1	1	0	0	0	0	0	0
	D	0	0	1	1	0	1	0	0	1	0
	E	0	0	0	0	1	0	0	0	1	0
	F	0	1	0	1	0	1	0	0	1	1
T2	G	0	0	0	0	0	0	1	1	1	0
	H	0	0	0	0	0	0	1	1	1	1
	I	0	0	0	1	1	1	1	1	1	1
	J	0	0	0	0	0	1	0	1	1	1
		DEM6									
		A	B	C	D	E	F	G	H	I	J
	A	1	1	0	0	0	0	0	0	0	0
	B	1	1	0	0	0	1	0	0	0	0
	C	0	0	1	1	0	0	0	0	0	0
	D	0	0	1	1	0	1	0	0	0	0
T1	E	0	0	0	0	1	0	0	0	1	0
	F	0	1	0	1	0	1	0	0	1	1
	G	0	0	0	0	0	0	1	1	1	0
	H	0	0	0	0	0	0	1	1	0	1
	I	0	0	0	0	1	1	1	0	1	1
	J	0	0	0	0	0	1	0	1	1	1
		A	B	C	D	E	F	G	H	I	J

A	1	1	0	0	0	0	0	0	0	0	0
B	1	1	0	0	0	1	0	0	0	0	0
C	0	0	1	1	0	0	0	0	0	0	0
D	0	0	1	1	0	1	0	0	0	0	0
E	0	0	0	0	1	0	0	0	0	1	0
F	0	1	0	1	0	1	0	0	0	1	1
G	0	0	0	0	0	0	1	1	1	1	0
H	0	0	0	0	0	0	1	1	1	1	1
I	0	0	0	0	1	1	1	1	1	1	1
J	0	0	0	0	0	1	0	1	1	1	1

T0

	A	B	C	D	E	F	G	H	I	J
A	1	1	0	0	0	0	0	0	0	0
B	1	1	0	0	0	1	0	0	0	0
C	0	0	1	1	0	0	0	0	0	0
D	0	0	1	1	0	1	0	0	1	0
E	0	0	0	0	1	0	0	0	1	0
F	0	1	0	1	0	1	0	0	1	1
G	0	0	0	0	0	0	1	1	1	0
H	0	0	0	0	0	0	1	1	1	1
I	0	0	0	1	1	1	1	1	1	1
J	0	0	0	0	0	1	0	1	1	1

DEM7

T2

	A	B	C	D	E	F	G	H	I	J
A	1	1	0	0	0	0	0	0	0	0
B	1	1	0	0	0	1	0	0	0	0
C	0	0	1	1	0	0	0	0	0	0
D	0	0	1	1	0	1	0	0	0	0
E	0	0	0	0	1	0	0	0	1	0

	F	0	1	0	1	0	1	0	0	1	1
	G	0	0	0	0	0	0	1	1	1	0
	H	0	0	0	0	0	0	1	1	0	1
	I	0	0	0	0	1	1	1	0	1	1
	J	0	0	0	0	0	1	0	1	1	1
T1		A	B	C	D	E	F	G	H	I	J
	A	1	1	0	0	0	0	0	0	0	0
	B	1	1	0	0	0	1	0	0	0	0
	C	0	0	1	1	0	0	0	0	0	0
	D	0	0	1	1	0	1	0	0	0	0
	E	0	0	0	0	1	0	0	0	1	0
	F	0	1	0	1	0	1	0	0	1	1
	G	0	0	0	0	0	0	1	1	1	0
	H	0	0	0	0	0	0	1	1	1	1
	I	0	0	0	0	1	1	1	1	1	1
	J	0	0	0	0	0	1	0	1	1	1
T0		A	B	C	D	E	F	G	H	I	J
	A	1	1	0	0	0	0	0	0	0	0
	B	1	1	0	0	0	1	0	0	0	0
	C	0	0	1	1	0	0	0	0	0	0
	D	0	0	1	1	0	1	0	0	1	0
	E	0	0	0	0	1	0	0	0	1	0
	F	0	1	0	1	0	1	0	0	1	1
	G	0	0	0	0	0	0	1	1	1	0
	H	0	0	0	0	0	0	1	1	1	1
	I	0	0	0	1	1	1	1	1	1	1
	J	0	0	0	0	0	1	0	1	1	1

		DEM8									
T2		A	B	C	D	E	F	G	H	I	J
	A	1	1	0	0	0	0	0	0	0	0
	B	1	1	0	0	0	1	0	0	0	0
	C	0	0	1	1	0	0	0	0	0	0
	D	0	0	1	1	0	1	0	0	0	0
	E	0	0	0	0	1	0	0	0	1	0
	F	0	1	0	1	0	1	0	0	1	1
	G	0	0	0	0	0	0	1	1	1	0
	H	0	0	0	0	0	0	1	1	1	1
	I	0	0	0	0	1	1	1	1	1	1
	J	0	0	0	0	0	1	0	1	1	1
T1		A	B	C	D	E	F	G	H	I	J
	A	1	1	0	0	0	0	0	0	0	0
	B	1	1	0	0	0	1	0	0	0	0
	C	0	0	1	1	0	0	0	0	0	0
	D	0	0	1	1	0	1	0	0	0	0
	E	0	0	0	0	1	0	0	0	1	0
	F	0	1	0	1	0	1	0	0	1	1
	G	0	0	0	0	0	0	1	1	1	0
	H	0	0	0	0	0	0	1	1	1	1
	I	0	0	0	0	1	1	1	1	1	1
	J	0	0	0	0	0	1	0	1	1	1
T0		A	B	C	D	E	F	G	H	I	J
	A	1	1	0	0	0	0	0	0	0	0
	B	1	1	0	0	0	1	0	0	0	0
	C	0	0	1	1	0	0	0	0	0	0

D	0	0	1	1	0	1	0	0	0	0
E	0	0	0	0	1	0	0	0	1	0
F	0	1	0	1	0	1	0	0	1	1
G	0	0	0	0	0	0	1	1	1	0
H	0	0	0	0	0	0	1	1	1	1
I	0	0	0	0	1	1	1	1	1	1
J	0	0	0	0	0	1	0	1	1	1

DEM9

T2		A	B	C	D	E	F	G	H	I	J
A	1	1	1	1	1	1	1	1	1	1	1
B	1	1	1	1	1	1	1	1	1	1	1
C	1	1	1	1	1	1	1	1	1	1	1
D	1	1	1	1	1	1	1	1	1	1	1
E	1	1	1	1	1	1	1	1	1	1	1
F	1	1	1	1	1	1	1	1	1	1	1
G	1	1	1	1	1	1	1	1	1	1	1
H	1	1	1	1	1	1	1	1	1	1	1
I	1	1	1	1	1	1	1	1	1	1	1
J	1	1	1	1	1	1	1	1	1	1	1

T1		A	B	C	D	E	F	G	H	I	J
A	1	1	1	1	1	1	1	1	1	1	1
B	1	1	1	1	1	1	1	1	1	1	1
C	1	1	1	1	1	1	1	1	1	1	1
D	1	1	1	1	1	1	1	1	1	1	1
E	1	1	1	1	1	1	1	1	1	1	1
F	1	1	1	1	1	1	1	1	1	1	1
G	1	1	1	1	1	1	1	1	1	1	1
H	1	1	1	1	1	1	1	1	1	1	1

T0	I	1	1	1	1	1	1	1	1	1	1
	J	1	1	1	1	1	1	1	1	1	1
		A	B	C	D	E	F	G	H	I	J
	A	1	1	1	1	1	1	1	1	1	1
	B	1	1	1	1	1	1	1	1	1	1
	C	1	1	1	1	1	1	1	1	1	1
	D	1	1	1	1	1	1	1	1	1	1
	E	1	1	1	1	1	1	1	1	1	1
	F	1	1	1	1	1	1	1	1	1	1
	G	1	1	1	1	1	1	1	1	1	1
	H	1	1	1	1	1	1	1	1	1	1
	I	1	1	1	1	1	1	1	1	1	1
	J	1	1	1	1	1	1	1	1	1	1

Figure 1. Modern topography, biogeographic lines, and habitat types in Southwest China. Major drainages were in blue lines; major mountain ranges of the Hengduan Mountain Region are shown in solid white lines; and biogeographic lines are depicted in purple dashed lines. Each yellow letter in the map corresponds to the photos on the side, which shows the typical habitat in each location.

Photos by Kai Wang.

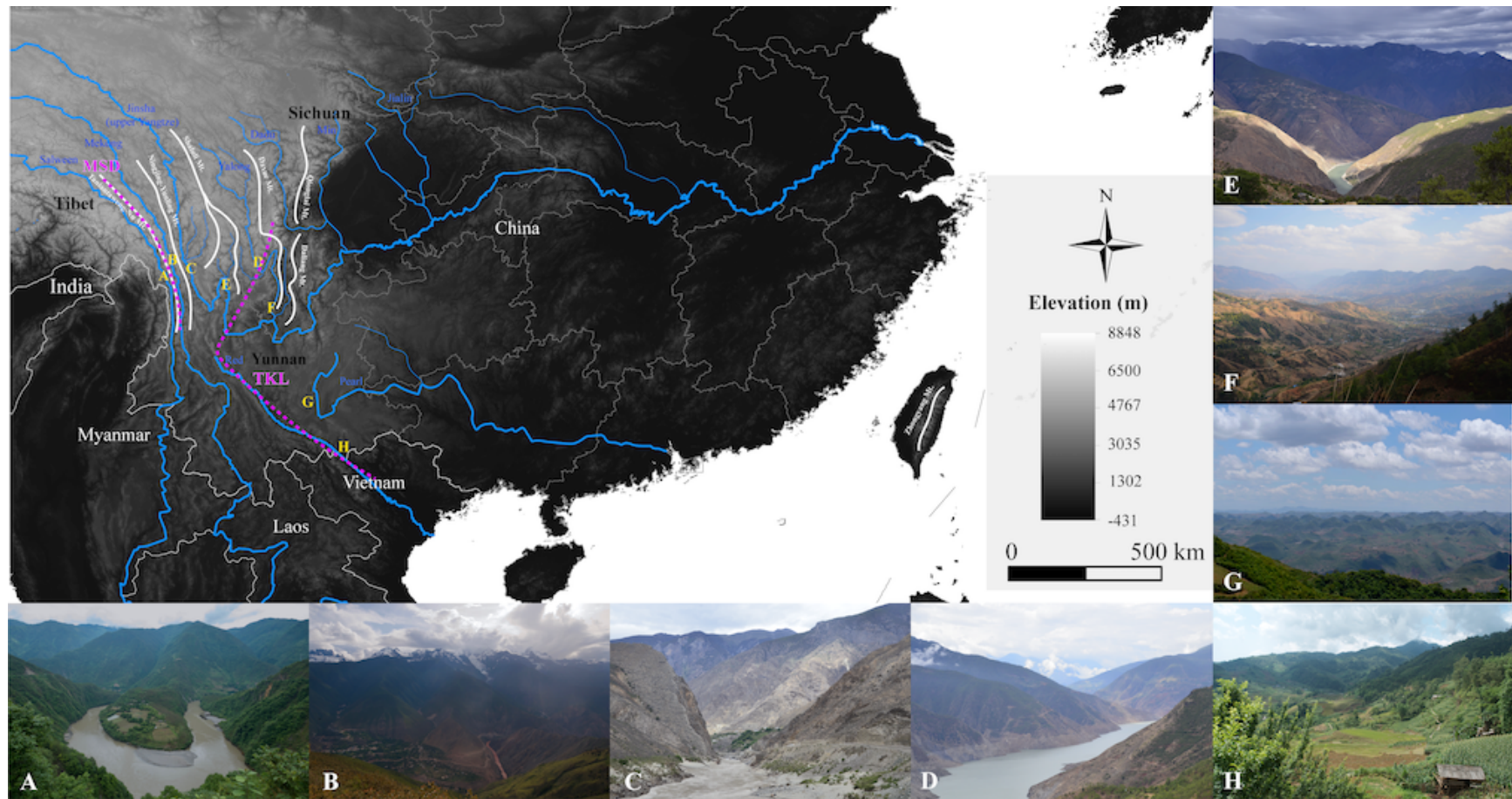


Figure 2. Hypothesized paleo-Red River drainage (A) and modern drainage system today (B). Images modified from Qi et al. 2015.

Relevant river abbreviations include R: Red; S: Salween; M: Mekong; J: Jinsha; A: Yalong; D: Dadu; and Y: Yangtze.

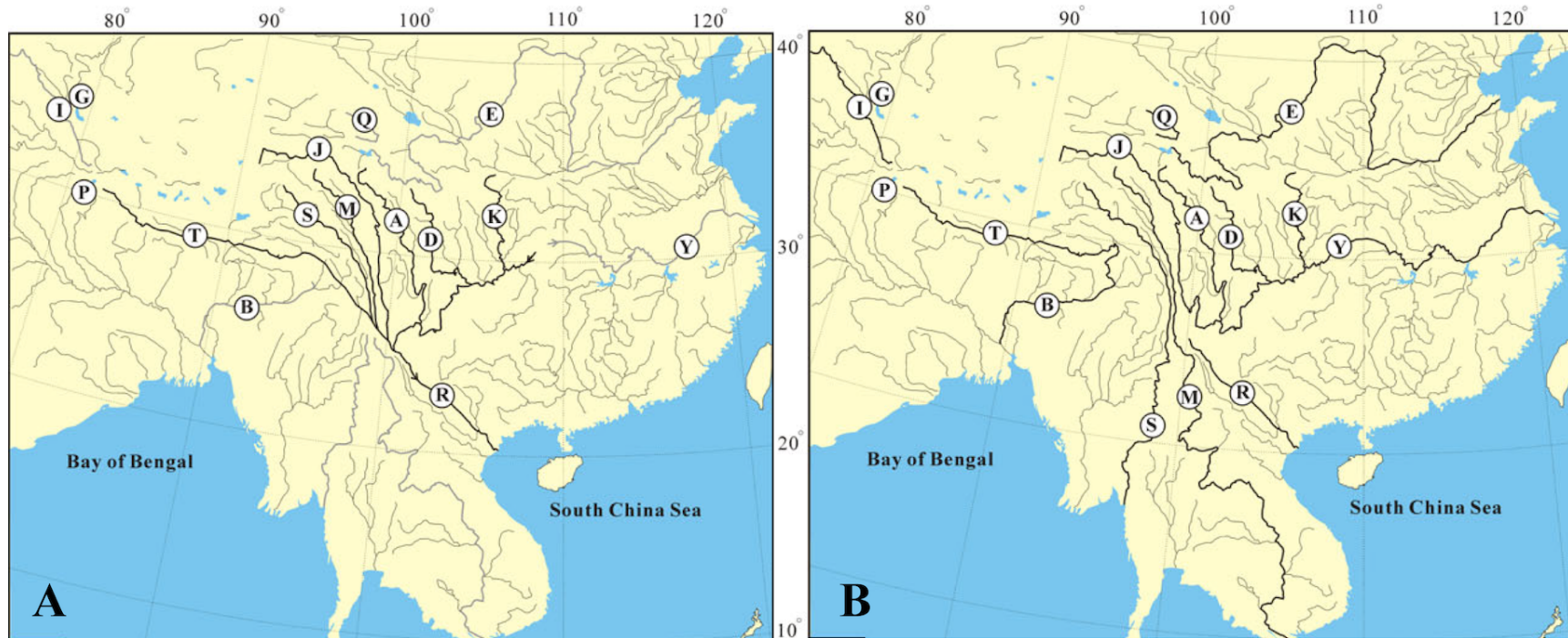


Figure 3. Phylogenetic relationships of *Diploderma* inferred from Bayesian analyses (A) and geographic distributions of samples used, showing the biogeographic lines (Mekong-Salween Divide [MSD] and Tanaka-Kaiyong Line [TKL]) (B) and the paleo-river drainage (Red River drainage and paleo-Yangtze River drainage) and tectonic fault belts (Gaoligongshan Fault (GLGSF), Longmenshan-Xianshuihe Fault [LM-XSHF], and Red River Fault [RRF]) (C). Numbers on the phylogeny correspond to the sampling localities on map. The color on the phylogeny also corresponds to the ones used on maps.

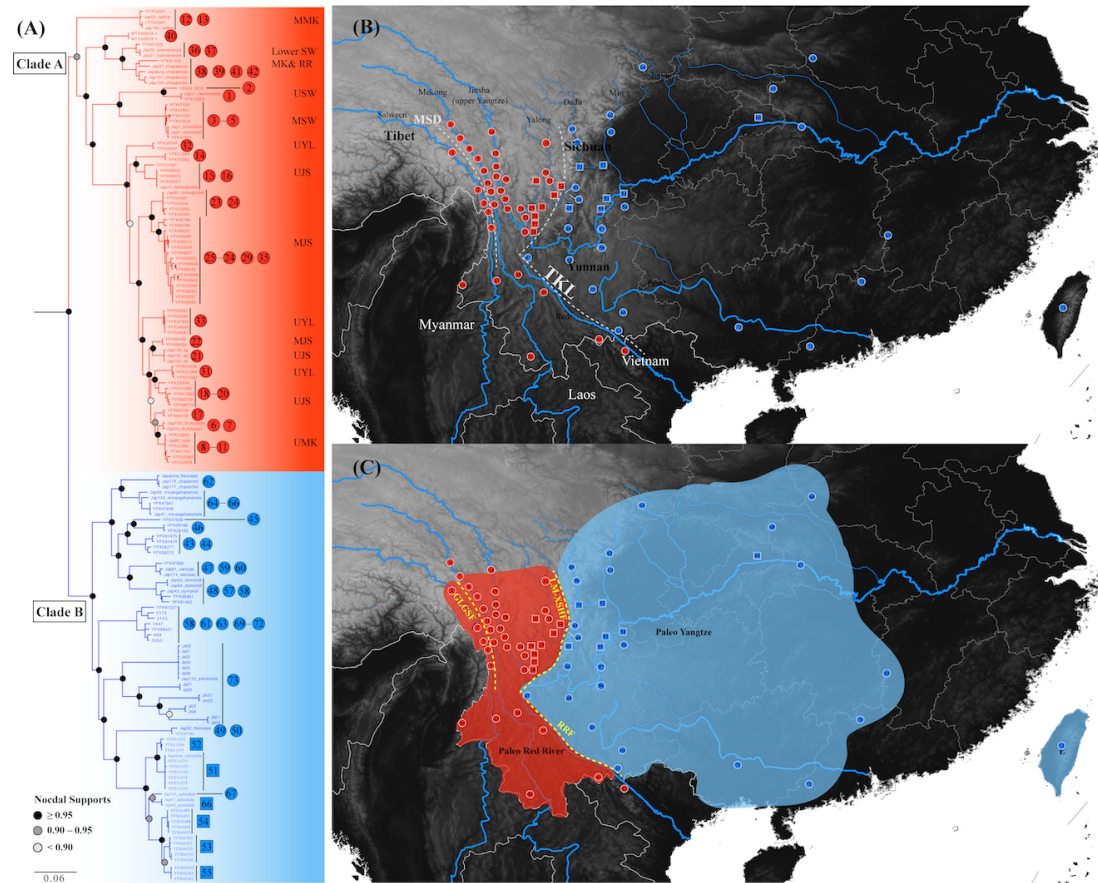


Figure 4. Biogeographic division of the Hengduan Mountain Region (HMR). A: upper Salween River; B: middle Salween River; C: upper Mekong River; D: middle Mekong River; E: upper Jinsha River; F: Red River and subtropical lower Salween/Mekong River; G: upper Yalong River; H: lower Yalong River; I: middle Jinsha River; and J: lower Jinsha, Pearl, Yangtze, major tributaries of Yangtze River, and East Asian Islands.

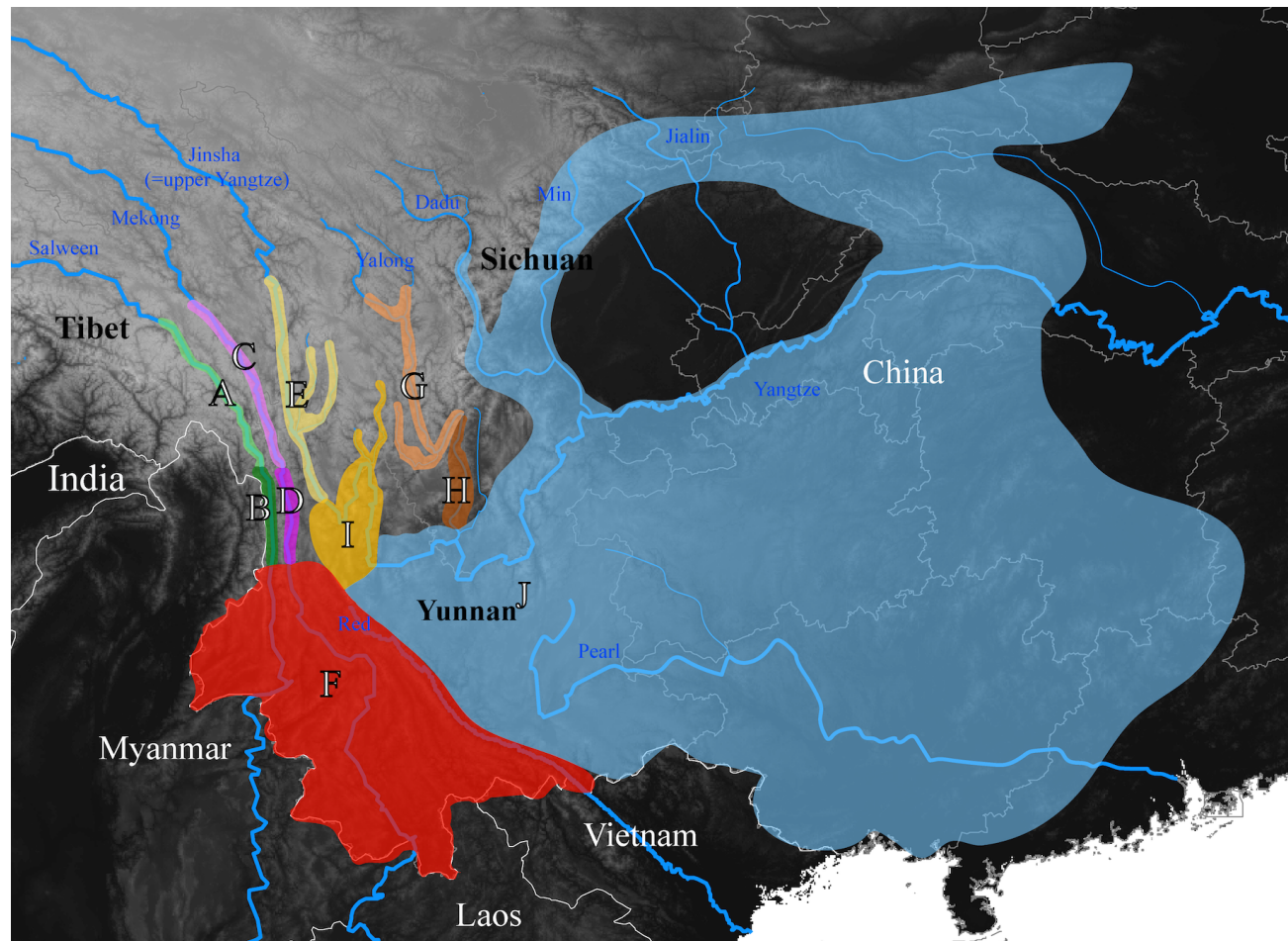


Figure 5. Simplified illustration of possible drainage evolution scenarios based on geological literature. T0: 23–30 Ma; T1: 5–23 Ma; T2: 0–5 Ma. A: upper Salween River; B: middle Salween River; C: upper Mekong River; D: middle Mekong River; E: upper Jinsha River; F: Red River and subtropical lower Salween/Mekong River; G: upper Yalong River; H: lower Yalong River; I: middle Jinsha River; and J: lower Jinsha, Pearl, Yangtze, major tributaries of Yangtze River, and East Asian Islands.

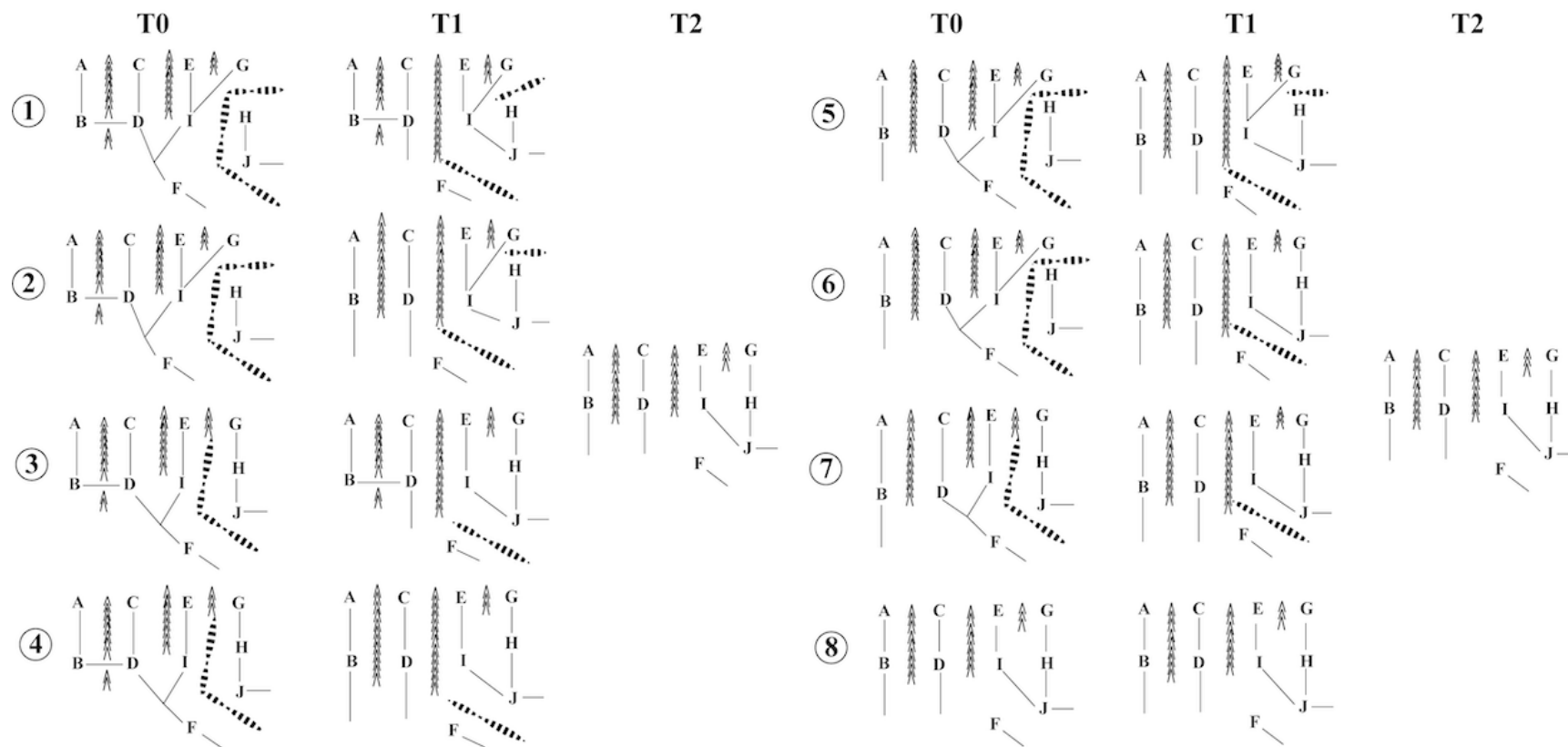


Figure 6. Time calibrated phylogeny of the genus *Diploderma* inferred from Fossilized Birth-Death Model using BEAST. The phylogeny is part of the larger tree of Acrodont lizards, which is shown in Supplementary Figure S1. The transparent blue bar at each node indicates the 95% confident interval of its time estimation, where the number above each node represent the mean time estimation (in unit of Ma). Major clades are color coded by the relative location to the paleo-drainages and to the Tanaka-Kaiyong Line (TKL). Photo of *Diploderma fasciatum* is by Hang Zhou.

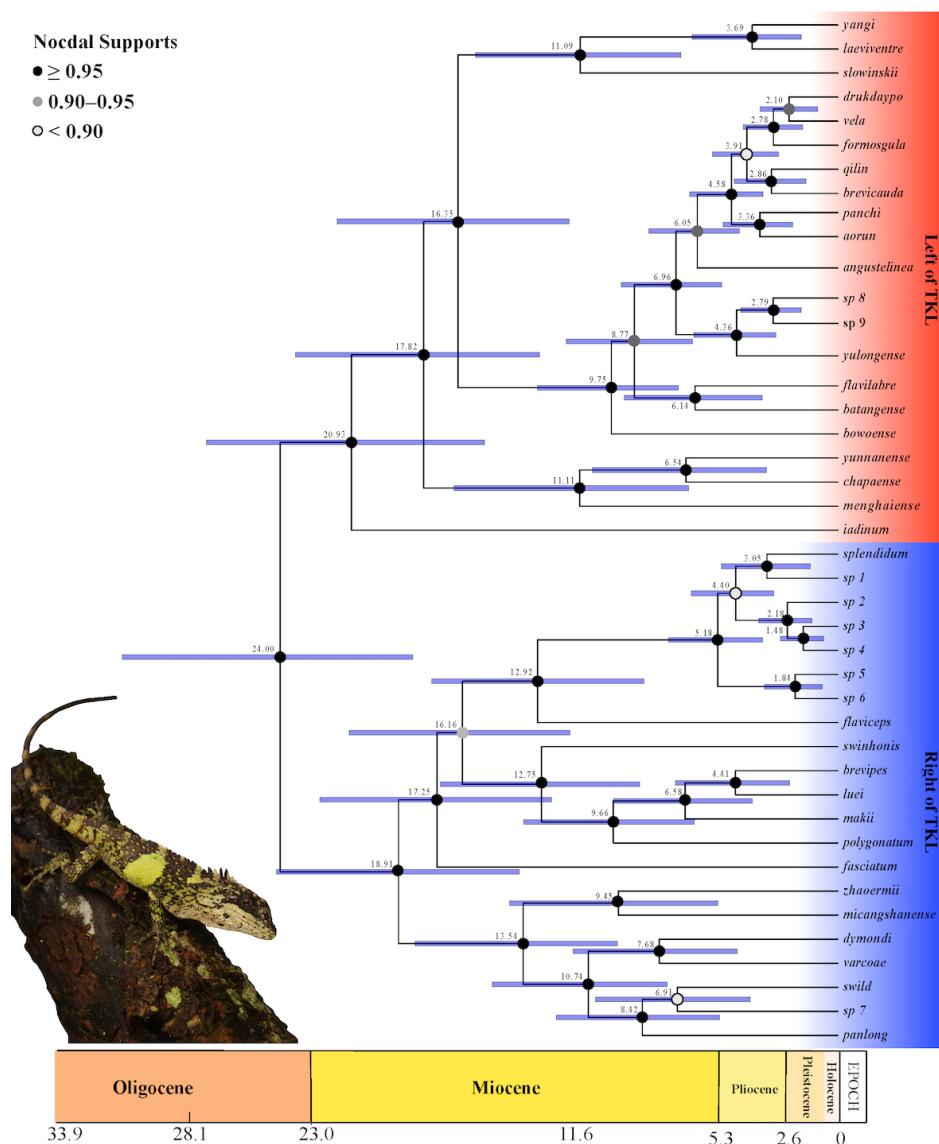


Figure 7. Ancestral range reconstruction of the genus *Diploderma* using drainage evolution model 5 (DEM 5) and DIVALIKE+*j* model using BioGEOBEARS (left) and the dispersal illustrations (right) in T0 (top), T1 (middle), and T2 (bottom). Pie chart at each node indicates the probability distribution of possible ancestral ranges, and the letter on the central of each pie chart represents the most probable ancestral range at the given node. “*” indicates areas with less than 5%. Numbers on the right of each node represents the node number. On the phylogeny, the black vertical bar indicates a vicariance event, the triangle with a horizontal bar indicates a dispersal following with a vicariance, and the triangle alone indicate a dispersal only. On the maps, the dashed white line indicates vicariance, the white arrow with a cross bar represent a dispersal following with vicariance, and the white arrow alone represents dispersal only.

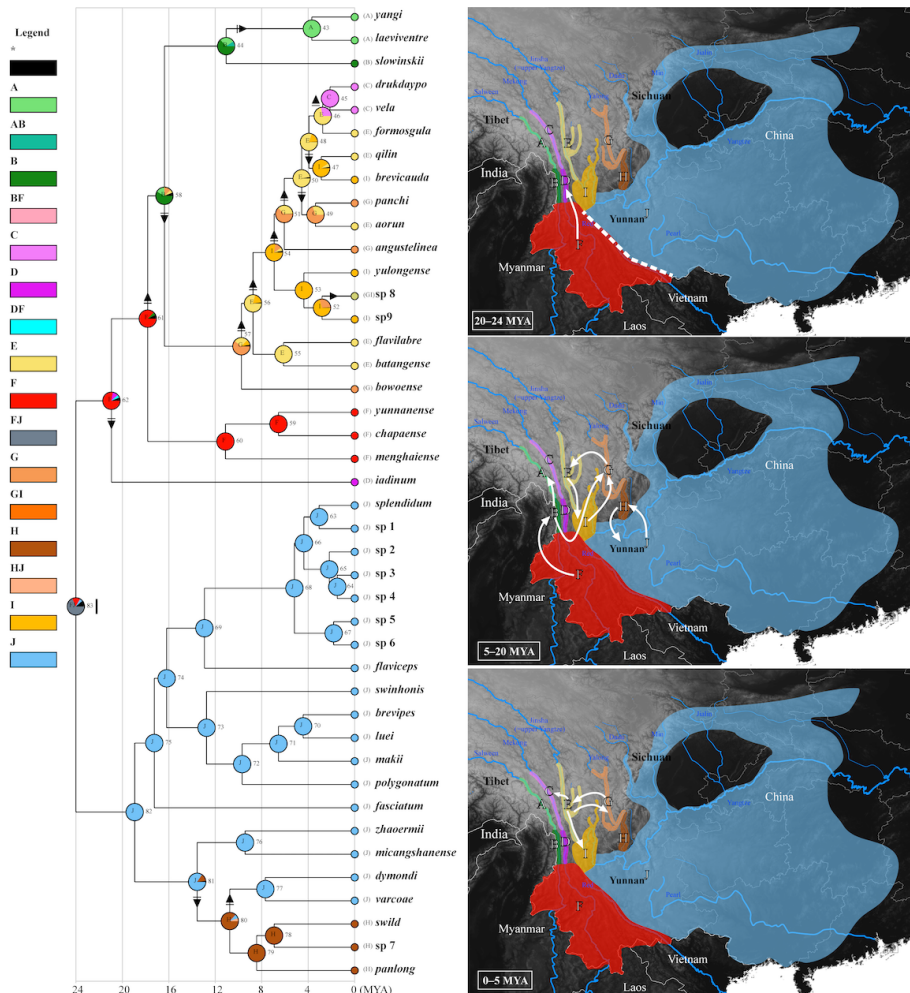
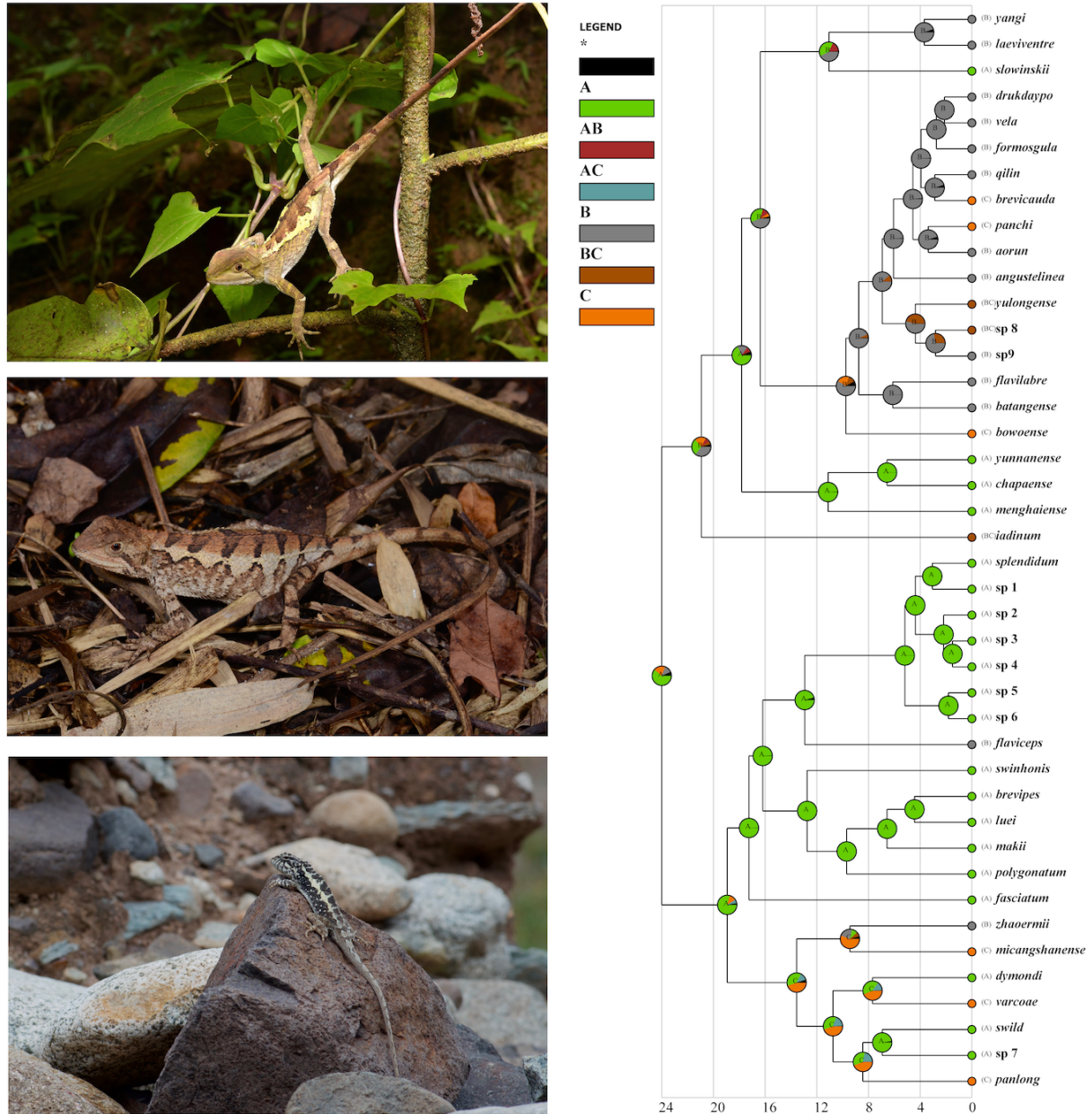


Figure 8. Ancestral state reconstruction on the three ecotypes (arboreal [A], rocky terrestrial [B], and forestry terrestrial [C]) of the genus *Diploderma* using Bayesian Binary MCMC (BBM) method. Images on the left show the representative species of each of the three general ecotypes, which are from top to bottom *D. yunnanense* (arboreal), *D. varcoae* (forestry terrestrial), and *D. vela* (rocky terrestrial). Photos by Kai Wang and Tao Zhang.



Chapter 4: Herpetofauna Pet Trades of China: Extent, Characteristics, Potential Impacts, and Recommendations

Abstract

A sustainable trade of wildlife is beneficial to both local human communities as well as to habitat conservation, but to achieve these goals and minimize the negative impacts of trade, accurate trade statistics (e.g., traded diversity, traded volume, and trade routes), scientifically guided legislation, and effective law enforcements are all required. Herpetofauna are the one of the most traded groups of exotic pets across the globe, and understanding their trade is particularly important due to the high conservation threats and implications for animal infectious diseases. Despite the well-recognized importance, very little is known about the global herpetofauna pet trade to date, particularly from the fast-developing countries in Asia such as China. Previous studies have already suggested that China has already engaged in global herpetofauna pet trade and might be a major trader, but no quantitative, comprehensive estimations have been made of the extent of China's trade, nor has any study examined the detailed characteristics of China's herpetofauna pet trade at the national scale. To fill this gap of knowledge, I integrate comprehensive datasets from multiple sources to evaluate China's herpetofauna pet trade over the last 20 years, including available international trade databases, online social medias and questionnaire surveys in China, records of customs confiscations, and all published literature to date. My results show that China's herpetofauna pet trade has a long history, and that China is a major consumer and supplier to the global herpetofauna pet trade. A rich diversity of herpetofauna have been traded by China, with a distinct preference on Testudines in its consumption trade and Sauria in its supply trade. Large volumes have been traded by China, but

these volumes are biased toward a small subgroup of commonly traded species and towards Testudines in general. Distinct regional patterns are evident in China's trade, with Mainland China and Hong Kong being the dominant importers and exporters. China's trade has a complex mixture of legal and illegal trades, with a high level of trafficking both into and out of the country. Most trafficking has occurred among major political units of China, particularly between the Mainland and Hong Kong. Based on the results, I provide specific recommendations on the conservation legislation and law enforcements in China.

Introduction

Wildlife trade, which is defined as the sales and exchanges of wild animals or plants, can be traced back early in human history, and it has become one of the main types of trade that reaps millions of dollars both legally and illegally (Sas-Rolfes et al. 2019). With the rapid growth of human population and the internationalization of trade, the demands for wildlife have grown rapidly in the past few decades (United Nation Office of Drugs and Crime, 2020), which has raised major conservation challenges on the global biodiversity (Oldfield 2003; Sodhi et al. 2004; Scheffers et al. 2019). Moreover, the growing trade of wildlife also increased the probability of environmental issues such as exotic invasion (Souviron-Priego et al. 2018) and outbreaks of infectious diseases (Kareesh et al. 2005; Martel et al. 2014; Roe et al. 2020). On the other hand, if monitored and managed closely, sustainable trade of wildlife could be beneficial to both local human communities as well as to habitat conservation (Hutton & Leader-Williams, 2003; Damania & Bulte, 2007; Luiselli et al. 2011; Robinson et al. 2018).

To minimize the negative impacts and ensure sustainable trade of wildlife, accurate trade statistics (e.g., trade diversity, trade volume, and trade routes), scientifically guided legislation, and effective law enforcements are all essential (Martin et al. 2005; Damania & Bulte, 2007; Chan et al. 2015). However, despite the major implications of wildlife trade and the well-recognized importance of trade statistics, little is known about the global wildlife trade to date (Nuno et al. 2017; Scheffers et al. 2019), and the related monitoring structures and legislation are still lacking (Chen et al. 2015; Sas-Rolfes et al. 2019). While these issues of data/structure deficiency are common for all traded species, it is particularly prominent for the traditionally neglected and difficult species groups in conservation, particularly reptiles and amphibians (Schlaepfer et al. 2005; Rowley et al. 2009; Tingley et al. 2016). Because reptiles and

amphibians are one of the most threatened vertebrate groups due to their specialized biology and restricted distributions (Stuart et al. 2004; Roll et al. 2017) such un-monitored, expanding trade causes more serious conservation concerns than for other animal groups (Tingley et al. 2016; Marshall et al. 2020).

Like any other animal groups, reptiles and amphibians (together referred as herpetofauna) have been traded substantially for a long time, with the main purpose of such trade has been consumptions (i.e. leather, meat, or traditional medicine; Klemens & Thorbjarnarson, 1995; Chen et al. 2009; Jiang et al. 2013). It is only in recent years that herpetoculture (i.e., keeping of herpetofauna pets) has become a major driver for the international herpetofauna trade (Luiselli et al. 2011; Natusch et al. 2012; Marshall et al. 2020). In fact, herpetofauna has become one of the most heavily exploited group of exotic pets globally (Bush et al. 2014; Auliya et al. 2016; Marshall et al. 2020). Because of the contemporary nature and close connection with online platforms of the herpetofauna pet trade (Harrison et al. 2016; Lavorgna, 2015; Jensen et al. 2019; Siriwat & Nijman, 2020), this recent shift of trade driver further amplified the existing issue of data/structure deficiencies and pose major challenges to trade monitoring and regulations (Marshall et al. 2020). In addition to the rapid declines and urgent conservation needs of herpetofauna globally (Gibbons et al. 2000; Beebee & Griffiths, 2005; Collins et al. 2010), it is crucial to fill this gap of knowledge soon so that effective monitoring and conservation actions can be enacted.

Although efforts have been made in characterizing the global herpetofauna pet trade, most comprehensive studies that provide both taxonomic inventory and quantitative estimation of trade volumes have focused on developed countries such as the U.S. (Schlaepfer et al. 2005; Collis & Fenili 2011; Herrel & Meijden, 2014) and the European Union (Nijman & Shepherd

2009; Auliya et al. 2016; Marshall et al. 2020). For the remaining studies, most of them focused on a few developing countries in Southeast Asia such as Indonesia (Nijman & Shepherd 2010; Lyons et al. 2011, 2013; Natusch & Lyons 2012; Nijman et al. 2012; Jassen & Shepherd 2018; Morgan & Chng 2018) and Thailand (Van Dijk & Palasuwan 2000; Nijman & Shepherd 2010, 2011, 2015; D'Cruze et al. 2015). Even with these limited studies, existing data have pointed out that developing countries in Asia have strong trade connections with the developed countries, and the Asian countries have played more and more significant roles in the pet trade of herpetofauna, both as consumers, suppliers, and transitional traders (Nijman & Shepherd, 2010; Bush et al. 2014; Herrel et al. 2014; Robinson et al. 2015; Kitade & Naruse, 2020; Koo et al. 2020). Therefore, understanding the dynamics of herpetofauna pet trade in Asia is essential to tackling and monitoring the global herpetofauna pet trade.

In spite of the importance of Asian countries in understanding global herpetofauna pet trade, substantial knowledge gaps still exist, especially for major economic entities such as China. With the world's second largest economy, a large population size, and a fast-growing pet industry (Ding et al. 2008; Tian 2020), China has all the factor of being a major contributor to the global herpetofauna pet trade. In addition to the fact that a diverse group of exotic herpetofauna has already appeared in the China's domestic markets (Feng et al. 2002; Gong et al. 2009; Wang et al. 2017, 2018; Zeng et al. 2017; Ji et al. 2020), and China's endemic species have long been sought after and appeared regularly in the international markets across the globe (Lee et al. 1999; Stuart et al. 2006; Gong et al. 2013; Schlaepfer et al. 2005; Herrel & Meijden, 2014; Rowley et al. 2016; Canlas et al. 2017), there is no doubt that China has already engaged actively in the international pet-trade of herpetofauna. However, the questions remain on the the extent and

characteristics of China's trade at the national scale and the effectiveness of current legislation and law enforcements in China.

The majority of the past studies on China's herpetofauna pet trade focused on documenting the taxonomic diversity on the consumption end in China's domestic markets (Lau & Shi, 2000; Feng et al. 2002; Wu et al. 2007; Shi et al. 2008; Gong et al. 2009; Hu et al. 2010; Ling, 2014; Meng et al. 2017; Wang et al. 2017, 2018; Zeng et al. 2017). Although together these studies have expanded across a long time frame since early 2000, most of these individual studies are based on short, opportunistic market surveys (in the units of days or weeks) in limited geographic locations, and the individual results are far too sporadic without any systematic summary at the national scale. To date, there is still no comprehensive list of the herpetofauna diversity in China's consumption trade of herpetofauna pets at the national scale, and the detailed characteristics of the trade such as taxonomic preference, geographic origins of species, commonality of species, and breeding extents in country remain unknown. Furthermore, fewer studies provided meaningful quantitative data of trade volumes in China. For the few that did provide meaningful quantitative estimates, all of them focused on two specific taxonomic groups only: Caudata (Rowley et al. 2007) and Testudines (Shi et al. 2008; Zhou et al. 2016, 2018). Because the current data already suggest a much more diverse taxonomic composition in China's trade, particularly for squamate reptiles (i.e. lizards and snakes) (Ling 2014; Auliya et al. 2016; Wang et al. 2017, 2018; Zeng et al. 2017), the existing data on the consumption volume are far from the real extent. Without comprehensive, quantitative data on the trade volumes, it is impossible to assess the impacts of the pet trade on the traded species, which prevents effective managements and regulations.

In contrast to the above-mentioned literature on China's consumption trade of herpetofauna pets, even far fewer studies examined China's supply trade of herpetofauna pets to the global herpetoculture markets (Rowley et al. 2007, 2016; Herrel et al. 2014; Auliya et al. 2016). Of these limited studies, only two examined the detail characteristics of China's supply trade from Hong Kong, and both focused on amphibians alone (Rowley et al. 2007, 2016). To date, no information is available regarding the supply aspects of most herpetofauna pet trade from most parts of China (i.e. Mainland China, Taiwan, and Macao), and the level of exploitation of China's native species by the international market, particularly those that are not listed by CITES, remain unknown.

Moreover, the majority of the past studies neglected the online component of China's herpetofauna pet trade. Since the only two studies on China's online pet trade (Sung & Fong, 2018; Ji et al. 2020) have revealed additional taxa that have not been documented in previous market surveys, the online herpetofauna pet trade in China are certainly substantial, and the extent of the total herpetofauna pet trade in China may be much larger than previously thought based on market surveys alone. Without more data from the cyberspace, it is impossible to assess the actual extent of China's herpetofauna pet trade.

Finally, the knowledge gap on the above-mentioned aspects of China's herpetofauna pet trade have caused misconceptions of the extent and impacts of herpetoculture, both by the Chinese government as well as by the international regulatory bodies of wildlife trade (e.g., CITES). With no detailed trade statistics from a potential major trader such as China, it is not only impossible to assess the impacts of the global trade on threaten herpetofauna species, making CITES legislation and enforcements difficult, but it also leads to potentially outdated, flawed domestic legislation and ineffective regulations within China, which could waste valuable

conservation resources and could lead to major conservation consequences such as neglect of endangered native species. Although numerous studies have examined the wildlife confiscations and related regulations in China (Li et al. 2010; Chen 2016; Wang et al. 2017b, 2019), none of them have evaluated the actual effectiveness of the legislation/law enforcements on regulating China's herpetofauna pet trade based on scientific data. Without such objective evaluation, it is impossible to improve the regulations and solve the underlining problems.

To fill this knowledge gap, we integrate comprehensive datasets from multiple sources to evaluate China's herpetofauna pet trade over the last 20 years, including available international trade databases, online social medias and questionnaire surveys in China, records of custom confiscations, and published literature to date. Specifically, we aim to (1) estimate the extent of China's herpetofauna pet trade at the national scale, (2) examine the overall temporal and regional patterns of China's herpetofauna pet trade in the past 20 years, and (3) provide recommendations for the current legislation and law enforcements on regulating China's herpetofauna pet trade.

Methods

Determination of Native Status, Geographic Origins, and Conservation Status

The native status of taxa was determined based on the most recent checklist of herpetofauna of China (Wang et al. 2020), and all species that were not included in the checklist were considered as exotic. The taxonomy of the native species followed China's checklist of native herpetofauna (Wang et al. 2020), while the taxonomy of exotic species followed The Reptile Database (Uetz et al. 2020) and Amphibian Species of the World (Frost 2021). For data that were only specific to the higher taxonomic level (e.g., genus or family), if the corresponding higher

taxonomic ranks were recorded from China based on the checklist, then the entrances were considered as native. All data were specified to the species level only when possible, and subspecies was not considered. If multiple similar species were present in the trade and the taxonomic identifications of specific taxa were impossible based on available evidence (i.e., photos), then taxa were identified to the generic level only.

For native species, their geographic origins were determined based on available literature (Zhao et al. 1998, 1999; Fei et al. 2013) and were further categorized in five major regions, including (1) Northwestern China (including Gansu, Ningxia, Qinghai, Shaanxi, and Xingjiang), (2) Southwestern China (including Chongqing, Guizhou, Sichuan, Tibet, and Yunnan), (3) Southern China (including Guangxi, Guangdong, Hainan, Hong Kong, and Macao), (4) Central-Eastern China (including Anhui, Fujian, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Taiwan, Zhejiang), and (5) Northern China (including Beijing, Hebei, Heilongjiang, Inner Mongolia, Jilin, Liaoning, Shandong, Shanxi, and Tianjin). For species that occur in more than three major geographic regions, its distribution was noted as “wide-spread”. If a species occur in multiple major regions, then each region would be counted separately for the frequency calculation.

For the exotic species, their geographic origins were determined based on online databases (Uetz et al. 2020; Frost 2021) and were categorized by eight major regions, including (1) Southeast Asia [including South Asia and all Asian countries east of India], (2) West Asia (all remaining countries that are west and north of India), (3) Continental Africa, (4) Madagascar, (5) Europe, (6) North America, (7) South America (including Central America), and (8) Oceania. For exotic species that occur in multiple adjacent regions, the more common and likely source of animals was chosen.

The conservation statuses of the identified taxonomic units are based on IUCN Red List (IUCN 2021). Furthermore, for species that are native to China, their in-country conservation statuses were also assessed based on the most recent China's Red List of vertebrate animals (CRL) (Jiang et al. 2016). For both IUCN and CRL conservation assessments, if the taxonomic units were identified to higher taxonomic levels only (e.g., genera or family), then the conservation status was considered as undetermined (noted as “—”). For China's native species, their in-country protection status was determined based on both the old and the most recent versions of the List of Nationally Protected Wildlife of China (http://www.forestry.gov.cn/html/main/main_5461/20210205122239482485322/file/20210205122347636743107.pdf). CITES appendix listing was based on the CITES database (<https://cites.org/eng/disc/species.php>). For CITES-listed species that have had recent changes in their listing status, the final states as by the end of 2020 were used.

Literature Review and Trafficking Records

Studies concerning China's herpetofaunal pet trade were searched using combinations of key words in both simplified Chinese and English through Google Scholar, National Knowledge Infrastructure of China (CNKI), and Baidu (Appendix I). As results, a total of 53 relevant papers and books were reviewed. For each study/book, the survey methods (online survey vs. market survey vs. national survey), time of data collection, location of surveys (if it was a market survey, identified to the province level), taxonomic diversity, and quantity/commonality of animals (if available) were recorded.

For trafficking records, data were gathered through the official website of the General Administration of Customs of P.R. China

(<http://jckspj.customs.gov.cn/customs/xwfb34/302263/index.html>) by searching using Chinese key word of “活体 查获” (= “live confiscation”). Additionally, results were also gathered on Google using a series of combination of the combination of Chinese key words “活体 海关 查获 + 类群名称” (= “live custom confiscation + taxonomic group name”).

Online Surveys

Firstly, online posts of the formerly largest Chinese herpetoculture forum (<http://bbs.www.pctx.com>) were surveyed manually in 2015 before its closure. Taxonomic diversity of reptiles and amphibians were documented. Additionally, the commercial breeding statuses of the recorded species in Mainland China were assessed based on eight experienced herpetoculturists, which were assigned to one of six categories: (1) no captive breeding, (2) commercial breeding-large scale, (3) commercial breeding-moderate scale, (4) commercial breeding-small scale, (5) commercial breeding-occasional, and (6) hobbyist breeding only.

Secondly, WeChat advertisement posts of 11 domestic sellers were surveyed up to two years between June 2018 and December 2020, including over 3000 posts in total. Data were recorded in the unit of month, including taxonomic information of the animals and any additional information available (e.g., price, quantity, source, wholesale vs. individual sale, ect.).

Thirdly, two anonymous online questionnaires (in simplified Chinese) were conducted. The first one was done using the online questionnaire platform (<http://www.wjx.cn>) to assess: (1) history of the herpetoculture trade in China; (2) the distribution and population characteristics of herpetoculturists; (3) characteristics on the animals kept by herpetoculturists; (4) level and effectiveness of current regulation, and (5) willingness to accept regulation if legal herpetofauna pet-trade is legitimized. Results from 2,264 participants were collected. The second one was

done through individual questionnaires with commercial breeders in Mainland China, which was to assess the timing and extent of captive breeding of reptile and amphibian pets in Mainland China. Results from 44 breeders were collected.

Lastly, to estimate the size of herpetoculture population and extent of herpetoculture in Mainland China, the number of Chinese herpetoculture forums and the number of their followers were surveyed in the social media platform, Baidu Tieba, using a combination of Chinese key words (Appendix II).

International Trade Databases

Trade statistics were obtained from two major sources: the CITES Trade Database (CTD) and the USFW's Law Enforcement Management Information System (LEMIS). For CTD, all import and export records of live reptiles and amphibians to and from China (including Mainland China, Hong Kong, Macau, and Taiwan) for personal (purpose code "P"), commercial purposes (purpose code "C"), and confiscation (purpose code "I") were downloaded from CTD (<https://trade.cites.org>).

For LEMIS data, trade statistics of live herpetofauna between the U.S. and China (including Mainland China, Hong Kong, Macau, and Taiwan) were obtained through two ways: the import records between 2000 and 2014 were filtered and extracted from the larger dataset by Eskew et al. (2020), and remaining data remaining import data from 2015 to 2019 and the export data from 2000 to 2019 were requested directly from USFW through separate Freedom of Information Act (FOIA) requests.

Most Soft-shell Turtles (*Pelodiscus sinensis*, *Pelodiscus maackii*, *Pelodiscus* sp., *Apalone ferox*, *Apalone spinifera*, and *Aspinderetes nigricans*), Bullfrogs (*Lithobates catesbianus*), and

Chinese Bullfrogs (*Hoplobatrachus rugulosus*) are traded mainly for consumption purposes rather than for pets. For the LEMIS dataset, given that their import numbers far exceed other taxonomic groups, their import/export records were excluded from analyses, as were those of *Rana* sp. that most likely represented Bullfrogs. In addition, all vague entrances (e.g., non-CITES reptiles, non-CITES amphibians, Sauria, ect.) were excluded.

Similarly, for the CTD data, because certain species—*Amyda cartilaginea*, *Apalone ferox*, *Apalone spinifera*, *Crocodylus porosus*, *Crocodylus siamensis*, *Crocodylus novaeguineae*, *Crocodylus niloticus*, *Crocodylus hybrid*, *Coelognathus radiata*, *Homalopsis buccata*, *Haplobatrachus tigerinus*, *Naja naja*, *Naja kaouthia*, *Naja sputatrix*, *Pelodiscus sinensis*, *Pelodiscus maackii*, *Ptyas korros*, and *Ptyas mucosus*—are mainly traded for food or leather (Marshall et al. 2000), and because their volumes overshadow other taxa, data for all of these species were also excluded from analyses. However, for the export trade from China, because *Coelognathus radiata*, *Homalopsis buccata*, and *Ptyas korros* were sold as exotic pets in the international market outside of China, records of these species were retained in the CTD export data from China. If the quantities were reported from both importer and exporter and the numbers did not match, and then the larger number was used for that entrance.

Entrances of taxonomic synonyms were combined, and the apparent misidentifications at genus level in the LEMIS export data from China were corrected based on a combination of historical taxonomic synonym relationship (Uetz & Hošek 2020; Frost 2021) and likelihood of having exports of certain exotic taxa from China, including the records of *Agkistrodon* sp. (corrected as *Deinagkistrodon* sp.), *Bothrops* sp. (corrected as *Protobothrops* sp.), *Opheodrys* sp. (corrected as *Cyclophiops* sp.), *Triturus hongkongensis* (corrected as *Paramesotriton hongkongensis*), and *Triturus* sp. (corrected as *Paramesotriton* sp.). Although the genus *Coluber*

is restricted to North America, multiple genera of snakes in China were once considered as *Coluber* (e.g., *Hemorrhois* and *Orientocoluber*) (Uetz & Hošek 2020). Therefore, we cannot identify the exact taxonomic identity of the actual taxa entering under the name “*Coluber* sp.”, and it was excluded from the analyses. Because the species *Hyla arborea* used to be considered as a widespread species complex that contains all of the current eight species of Hylidae in China, and given the true *Hyla arborea* is restricted to Europe (Frost 2021) and were not known in the international pet trade, its records were corrected as “*Hyla* sp.”. Because the taxonomy of the Chinese populations of “*Daboia russelii*” has been changed to *Daboia siamensis* (Cai et al. 2015; Wang et al. 2020), the records of *Daboia russelii* in the dataset were updated accordingly. The invalid species names of hybrids (e.g., *Mauremys iversoni*) were corrected as “hybrid” of the corresponding genus. The single CTD import entrance of *Phelsuma gigas* of Taiwan, which was extinct long before the import date, was corrected as “*Phelsuma* sp.”.

Determination of Commonality of Species in Trades

For literature review, if a species satisfied any of the following four criteria, it was considered as “common” in the trade: (1) noted specifically as common by authors; (2) the recorded volume ≥ 100 individuals in a given study, if volume data were available; (3) annual nation-wide breeding volume $\geq 10,000$ individuals, if breeding data were available; and (4) frequency of occurrence $\geq 50\%$ in the unit of individual study in literature review. For online surveys, the commonality was determined by the assessors. For the WeChat survey data, if a given taxon was noted as for wholesale, or it was sold by 50% or more of the surveyed sellers, it was considered as common. For the international trade data, commonality was determined by the

total trade volume in the past 20 years, with a total trade volume greater than 10,000 individuals considered as common.

3. Results

3.1 Extent of China's Herpetofauna Pet Trades

China's modern herpetoculture has a long history that can be traced back to 1975 (Fig. 1). Herpetoculturists represented a large and expanding group in China: a total of 389 Chinese herpetoculture discussion groups were found online, 24 of which had more than 100,000 registered users, and 88 groups had more than 10,000 registered users (Table 2). The majority of the surveyed population of herpetoculturists are young adults between the age of 18 and 29, and herpetoculturists are found in all administrative regions except Tibet (Appendix III).

China has engaged in active and major international trade of herpetofauna pets at the global scale, both as a consumer and as a supplier. A total of 91 countries has legal trade records with China based on CITES database, in which 41 countries import herpetofauna pets from China, and 79 countries export to China (Fig. 2). A total of 1,237 species of reptiles and 386 species of amphibians in all major taxonomic orders except Rhynchocephalia and Amphisbaenia were traded by China as herpetofauna pets, both as a consumer and a supplier (Fig. 3). The traded diversity constituted 10.9% and 4.7% of the global diversity of reptiles and amphibians, respectively, and China's traded native species represented 51.9% and 16.1% of the total native diversity of China's reptiles and amphibians, respectively. When categorizing by the trade directions, the consumption trade comprised more species than the supply trade (Fig. 3). Based on available data, high volumes of herpetofauna pets have been traded by China between 2000 and 2019, particularly for the consumption of reptiles and supply of amphibians (Table 3).

Although retail herpetofauna pet stores have a long history and appeared as early as 1980 in Mainland China (Fig. 1), a major portion of China's domestically trade were conducted online in recent years. About 52.0% and 38.1% of the consumed reptile and amphibian diversity, respectively, were present in the online trade, and about 16% of the consumed reptile and amphibian diversity were unique to the online trade (Fig. 3). Additionally, most surveyed herpetoculturists communicated with others through online platforms (e.g., Wechat, QQ, forums/discussion groups), and 80.5% of the surveyed population acquired their herpetofauna pets through online purchases (Appendix III).

3.2 Temporal Characteristics

China's herpetoculture continued to expand since 1975, which was reflected by the growing population of herpetoculturists, the increasing number of herpetofauna pet shops, and the number of domestic breeders and the number of species being bred (Fig. 1, A and C). Such developments of herpetoculture in China were also reflected by China's consumption volume of herpetofauna pets in CITES database (Fig. 4). However, all consumption volumes of China based on LEMIS records showed the opposite, decreasing trends through time, and the traded diversity in remaining records remained mostly constant with no statistically significant trend between 2000 and 2019 (Fig. 4). In particular, the LEMIS supply trade of amphibians from China underwent dramatic declines since 2008, which decreased to only 6% of the initial volume in 2000.

Growing along with the extent of herpetoculture, the extent of trafficking also increased. The number of confiscation cases entering China, the number of species involved, and the number of foreigner countries involved were all higher in recent years (Fig 1, B).

3.3 Legality of China's Herpetofauna Pet Trades

China's trade of herpetofauna pets consisted of a complex mixture of legal status (Fig. 5). For the CITES-listed species specifically, although 309 species of reptiles and 54 species of amphibians have legal records entering China, another 79 species of CITES-listed exotic reptiles and 10 species of exotic amphibians that were present in China's domestic markets did not have any legal records of entering China since 2000, and none of them had commercial breeding in China based on our surveys (Fig. 5, B; Appendix IV, V). In addition, 47 species of CITES-listed, exotic reptile and five species of CITES-listed, exotic amphibians had both legal import records and confiscation records, suggesting a much higher trafficking trade. For all the recorded CITES species in China's trade, species in CITES Appendix I had the highest percentage of trafficked species among all three CITES Appendices (Fig. 5, B). On the other hand, a few native, CITES-listed species have been trafficked back to China, including those that were endangered and protected (e.g., *Cuora* spp., *Platysternon megacephalum*, *Python bivittatus*, *Testudo horsfieldii*, and *Varanus salvator*).

In addition to the documented illegal trade of CITES listed animals above, illegal trade of native, nationally protected species were evident in both domestic and international markets. Based on the old List of Wild Animals under Special State Protection, 14 species of protected reptiles and six species of protected amphibians were present in the domestic trade in China. For the international supply trade, 11 species and five species of nationally protected reptiles and amphibians, respectively, have been exported out of China "legally".

For native species that were not under special protection but still regulated, majority of the diversity was exported through Hong Kong based on LEMIS data (126 species of reptiles, 86% of total supplied native reptile diversity; 34 species of amphibians, 92% of the total supplied

amphibian diversity); and of these native species exported from Hong Kong, majority of them (90 spp. of reptiles [71.4%] and 27 spp. of amphibians [79.4%]) were not native to Hong Kong but only found in Mainland China. Considering Hong Kong's own wildlife protection laws, three Hong Kong's protected native species (i.e. *Cuora trifasciata*, *Platysternon megacephalum*, and *Paramesotriton hongkongensis*) were exported from Hong Kong "legally" in large volume.

Questionnaire surveys revealed a high level of "gray" practice of herpetoculture in Mainland China (Fig. 5, A). Only 35% of the herpetoculturists acquired their pets from legal sellers, 14% purchased from illegal sellers without selling permits, and 51% were unclear about the legal status of sellers. While majority of surveyed herpetoculturists claimed they kept legal species, only 76% of them were aware of the related regulations, and only 27% knew the details of relevant regulations. Furthermore, 43% of the total surveyed population had no intention in applying for legal possession permits, 54% considered but either failed applying or did not try, and only 3% had obtained the possession permits successfully. For those who did not have possession permits, 41% were unaware of the existence of such permit, 37% had issues with the application (e.g., application was too complicated, or its requirements were too high), and 23% failed because the relevant government agencies were unable to perform their duties.

3.4 Regional Characteristics

Major political regions of China showed distinct regional patterns in herpetofauna pet trade (Fig. 6). For the legal trade, although all four major regions of China (Mainland China, Hong Kong, Macao, and Taiwan) consume considerable diversity of herpetofauna pets, only Mainland China and Hong Kong consumed considerable volumes of reptiles based on available data, and only Hong Kong and Taiwan consumed high volumes of amphibians. For the supply trade, Hong

Kong exported the most species for both reptiles and amphibians and most volume for amphibians among all four regions based on LEMIS data; Taiwan only exported a minimal portion of diversity and volumes for reptiles; and Mainland China dominated the volume exports for all reptiles and CITES amphibians.

The most common origins of 1 CITES animals in the legal consumption trade were Europe (22 countries), Africa (20 countries), and South America (16 countries) (Fig. 2; Appendix VI). The majority of the export countries for CITES reptiles (63 countries, 79.7%) and half of the export countries for CITES amphibians (six countries, 50.0%) were developing countries, and developing countries exported the majority of the volume to China (78.5% and 55.4% of total consumed reptile and amphibian volume by China) (Table 4). In contrast, for the legal supply trade of CITES animals, the most common destination regions were Europe (18 countries), Southeast Asia (nine countries), and West Asia (seven countries) (Fig. 2). In contrast to the exporting countries of the consumption trade, a higher percentage of the importing countries for both reptiles (48.8%) and amphibians (66.7%) was developed countries (Table 4; Appendix VI).

For illegal trade, domestic trafficking among major political regions of China were the leading source of illegal trade, constituting 35% of all documented trafficking cases (Fig. 7). Particularly, trafficking from Hong Kong and Taiwan to Mainland China were the two most common trafficking routes. Subsequently, Guangdong and Fujian Provinces of Mainland China, which are adjacent to Hong Kong and Taiwan, respectively, were the main entrance port for trafficked animals, particularly Guangdong Province. Additionally, Guangdong Province also had the highest number of herpetoculturists in China based on our surveys.

For international trafficking, 18 countries had trafficking records into China. The U.S., Thailand, and Vietnam were the top three countries in terms of both number of confiscation

cases as well as number of species involved (Fig. 7). In terms of major geographic regions, Southeast Asia, South America, and North America were the top three geographic origins of trafficked species. Additionally, when counting each species in each individual recorded trafficking case, more than half of them (54.1%) were trafficked from a secondary transitional site rather than from their native geographic origin (26.4%; and remaining 19.5% with unknown trafficking origins).

Majority of the traded species by China were exotic origins (970 species of reptiles, 303 species of amphibians, 78.5% of total traded species of each corresponding group; Fig. 3). In the questionnaire surveys, for the seven predefined major species groups that had options between exotic and native counterparts, more than half of the groups showed preferences on the exotic options over their native counterparts (Appendix III). For traded exotic reptiles, Continental Africa (180 species) and North America (178 species) were the top two origins with the most species, which were followed by Southeast Asia (154 species), South America (151 species), Oceania (148 species) as the top five individual geographic origins; and for exotic amphibians, on the other hand, South America (110 species), North America (57 species), and Continental Africa (45 species) were the top three origins with the most species (Fig. 8).

For all the traded native species, Southwest China was the most common geographic origin for species in both consumption and supply trade (125 species of native reptile, 34 species of native amphibian), which was followed by Southern China (116 species of reptile, 25 species of amphibian) and Central-Eastern China (88 species of reptiles, 24 species of amphibian) (Fig. 8).

3.5 Conservation Impacts

Although overall China's trade comprised a diverse group of herpetofauna in high volumes, the exploitation levels were different among geographic regions and major taxonomic orders. Overall, only a small subset of the total diversity was commonly traded in both consumption (9.7% and 11.1% of total consumed reptile and amphibian diversity, respectively) and supply trade (4.5% and 27.4% of total supplied reptile and amphibian diversity, respectively) (Table 5; Appendix VII, VIII), and an even smaller subset of the total traded diversity constituted most of the trade volumes based on the available datasets (Table 6). Trade volumes were more concentrated taxonomically in reptiles than in amphibians (Table 6).

China's native species faced much greater conservation pressure from the herpetofauna pet trade than exotic species. A much higher percentage of traded native species were threatened than their exotic counterparts, especially for the commonly traded native species that were traded in large volumes (Fig. 3, 9). Furthermore, a much higher percentage of the exported non-CITES individuals was wild-caught, particularly native reptiles (Fig. 10).

Taxonomically, Testudines in general and native Sauria faced the greatest conservation pressure from herpetofauna pet trade among traded reptiles, and native Caudata faced the greatest pressure among traded amphibians. For Testudines, China's trade covered the highest percentage of the global Testudines diversity among all traded reptilian orders (260 species of Testudines, 72.2% of global Testudines diversity) (Fig. 11), and among all the commonly traded species, Testudines was the most common taxonomic order (65 species, 47.7% of total commonly traded reptile species). For IUCN assessments, traded Testudines was the most threatened group (40.0% threatened) (Fig. 9). In terms of trade volume, Testudines dominated the trade of reptiles except for LEMIS supply trade (83.9% of China's total CITES import volume; 99.2% of China's total CITES export volume; and 99.4% of total China's import

volume) (Fig. 12). Moreover, Testudines was also the most trafficked taxonomic group, constituting 43% of total trafficked diversity and 52% of total recorded trafficking cases into China (Table 7). On the other hand, native Sauria was the most exploited group among all non-CITES reptiles, constituting 62.2% of China's total supply volume of non-CITES reptiles (Fig. 12), and majority of them had commercial breeding in China based on survey records (Appendix IV, VII, VIII). Except Gymnophiona (single species), traded native Caudata constituted the highest percentage of the total native diversity among amphibians (41.5%; Fig. 11), had the highest percentage of threatened species among all amphibian groups (38.2% threatened according to IUCN, 44.1% according to China's Red List; Fig. 9), and had the highest percentage of wild-caught individuals in the supply trade (49.0% for LEMIS data, 11.3% for CITES data) (Fig. 10).

4. DISCUSSION

4.1 Overlooked Leading Trader of Herpetofauna Pets

Our results reveal a long history and a surprisingly large extent of the herpetofauna pet trade in China. Even with limited data, the recorded taxonomic diversity in China's herpetofauna trade (1,161 species of reptiles, 357 species of amphibians) bypasses the documented diversity in traditionally believed major traders of herpetofauna pets in Asia such as Japan (543 species of reptiles in Japan; Wakao et al. 2018) and South Korea (555 species of reptiles, 122 species of amphibians; Koo et al. 2020). Furthermore, the estimated extent of China's trade already matches the extent of the U.S. trade: not only in term of the consumed diversity (1,518 total species of reptiles and amphibians in China's trade, 1,800 species in U.S. trade; Herrel & Meijden 2014), but also in terms of the number of herpetoculturists estimated from online forums (over

700,000 individuals on China's largest forum vs. about 152,000 individuals in the largest U.S. forum). Because the U.S. was considered as the leading trader of herpetofauna pets in the world (Hoover 1998; Herrel& Meijden 2014), and because our data also indicate a continuous growing pattern of China's herpetoculture (i.e., growing number of herpetoculturists, increasing volume of legal imports for certain groups, increasing number of trafficking, and increasing extent of domestic breeding; Fig. 1, 4), China's herpetofauna pet trade are certainly substantial at the global scale. By overlooking China's trade, previous studies all severely underestimate the extent of global herpetofauna pet trade (Mohanty& Measey, 2019; Marshall et al. 2020). For example, when comparing the diversity in China's trade against the species list in most recent estimate of global reptile trade (Marshall et al. 2020), 314 species of reptiles were unique to China's trade and absent from the previous global estimation, which is about 10% of the total recorded diversity in Marshall et al. (2020).

While available data already suggest that China's herpetofauna pet trade are comparable to the global leading traders such as the U.S., our current results are still an underestimation on China's trade, particularly for the trade of non-CITES species and domestic online trade. Currently, China's customs only provide records of herpetofauna trade post 2017, and such data only provide a total annual trade volume with no taxonomic resolution (i.e. as live reptiles; <http://online.customs.gov.cn/static/pages/mySearch.html>). With no global database of non-CITES species or detailed records from China's customs, our data still underestimate the traded diversity and volumes of non-CITES species. For example, we are still unable to quantify the trade with the exporters from Southeast Asia (i.e. Indonesia; Nijman& Shepherd 2009; USDA 2011), despite the signs indicating large-scaled trade in China (e.g., common trafficking and presence of common wholesale of non-CITES species such as *Hydrosaurus* spp.; Appendix VII).

Because non-CITES species usually constitute majority of the international trade in terms of both diversity and volume (Jassen& Shepherd, 2018; Janssen& Leupen, 2019), the actual extent of China's trade might be much larger than we estimated here. Additionally, our data support the previous conclusion on the growing extent of online trade of exotic pets in China (Ji et al. 2020; Sung et al. 2021). As the online trade in China have become more diversified in terms of platforms/channels used, our current data are far from comprehensive, and it remains difficult to quantify the volume of China's online trade (Sung et al. 2021).

Like the overlooked trade in China, our data show that other developing countries, particularly ones in Southeast Asia (i.e. Indonesia, Vietnam, Malaysia, Thailand, and Philippines), also have considerable amount of both legal (Fig. 2; Appendix VI) and illegal (Fig. 7) trade records, indicating similar neglect of major herpetofauna pet trade in these countries. Given that endemic species from these countries appear frequently in international trade (Siler et al. 2014; Jassen et al. 2018; Gewiss et al. 2020; Heinrich et al. 2021), and since published survey records have already indicated the presence of diverse, exotic herpetofauna in the domestic markets in many of these developing countries (Nijman et al. 2012; Nijman & Shepherd, 2015; Sy 2014, 2015; Pragatheesh et al. 2021), it is likely these developing counties have also engaged in active and major herpetofauna pet trade that have been under-documented, similar to China. We echo the previous call for better and publicly available trade statistic data of live herpetofauna across the globe (Chan et al., 2015; Jassen& Shepherd, 2018), and we further stress the urgent need for monitoring and regulations of online wildlife trade, particularly for growing developing countries across the world.

4.2 Biased Trades and Differential Conservation Pressures

Overall, the percentage of threatened species in China's consumption trade (about 16% for both reptiles and amphibians) is similar to the comparable data in Asia (Japan: 18.0% in 2007, 17.8% in 2017; Wakao *et al.* 2018), and China's trade volumes are biased towards a small subset of traded diversity, similar to available data of the U.S. (Herrel & Meijden, 2014). Specifically, China's herpetofauna pet trade are heavily biased for Testudines (Fig. 11, 12). Despite the large scale of domestic turtle farming (Shi *et al.* 2008a), China still imports a high volume of wild-caught Testudines: not only for exotic species mainly from Southeast Asia and North America (Fig. 8), but also for its own native species that have been captive bred already at a massive scale (e.g., *Mauremys reevesii* and *Mauremys mutica*; Appendix IV). Our results support the conservation concerns raised by previous studies (Gong *et al.* 2009; Shi *et al.* 2007, 2008a) and show that China's herpetofauna pet trade indeed pose major conservation pressure on the global Testudines diversity.

Furthermore, our results show that China's native species, particularly native Sauria and Caudata, face much greater conservation threats from China's herpetofauna pet trade than their exotic counterparts. On one hand, China's native species have higher conservation threat levels than the exotic species, regardless of the type of conservation assessments chosen (IUCN vs. China's Red List; Fig. 9). Further, most traded native species have not been bred in captivity in Mainland China (Appendix V), but many of them were traded in large volumes both domestically and internationally based on available data, suggesting wild-sourcing for most of the current trade on native species. Because there is no detailed quantitative volume data of international trade of non-CITES species outside of the U.S., the actual impacts of the pet trade on China's native species might be much more severe than our current data suggest. Coupled with the known demands for China's native, rare Sauria and Caudata in the international

herpetofauna pet trade (Stuart et al. 2006; Hou et al. 2014; Altherr & Lameter 2020) and the limited protection coverage of these species by China's current Wildlife Protection Act (Wang et al. 2021), China's native herpetofauna, particularly those micro-endemic Sauria and Caudata from Southern and Southwest China, are most vulnerable to the herpetofauna pet trade and require serious conservation attention.

4.3 Regional Political Discrepancies Create Legal Loopholes

Hong Kong has long been recognized as the center of wildlife trade in Asia (Kurland & Pires, 2017; Sung et al., 2021). Similarly, our data show that despite the small geographic area and population size, Hong Kong plays an essential role in the herpetofauna pet trade in China, particularly as the transitional port for China's consumption and supply trade (Fig. 6). For China's consumption trade, Hong Kong serves as the first stop for large portion of imports (Fig. 6). In addition to the legal imports from Hong Kong to Mainland China, animals have been often trafficked into Mainland China through various methods (Fig. 7). The relatively easy and common trafficking of exotic herpetofauna from Hong Kong to the adjacent Guangdong Province most likely explains the disproportionately fast development of herpetoculture in Guangdong Province, as reflected by the population of surveyed herpetoculturists (Fig. 7). For China's supply trade, Hong Kong is the leading exporter for herpetofauna diversity from China, particularly for China's native species (Fig. 6, S1). Additionally, our data reveal that Taiwan was an important consumer for exotic amphibian diversity (Fig. 6, S1), and Taiwan also plays a major role in the trafficking of herpetofauna pets into Mainland China, mostly entering through nearby Fujian Province (Fig. 7).

The fundamental differences in political systems between Mainland China and remaining parts of China have lead to mismatches on wildlife legislation, which in return creates loopholes for wildlife trafficking. While belonging to the same political entity, each region holds a high level of political autonomy, which allows each region to legislate its own constitution and all other laws. Although major parts of the political discrepancies have been worked out through legislation, such as The Basic Laws of the Hong Kong and Macao Special Administrative Regions (Ministry of Foreigner Affairs of the People's Republic of China, 1990), other more specific aspects of legal discrepancies have been largely overlooked, particularly about wildlife conservation.

For wildlife legislation, special administrative regions do not recognize the one from Mainland China, and their regional legislation do not consider any of the protection status listed by the Mainland's law (Hong Kong e-Legislation, 2012; Laws& Regulation Database of the Republic of China, 2013). As such, nationally protected, endangered, non-CITES mainland species lose their legal protections once they enter the territories of Hong Kong, Macao, and Taiwan. Such discrepancies in protection coverage between the wildlife legislation of Mainland China and special administrative regions creates a major loophole for wildlife laundry: illegally collected, native, non-CITES species from Mainland China can become "legalized" if they were transported across the border, and the crossed-over individuals can now be exported "legally" to foreigner countries with export permits from the special administrative regions. Particularly, Hong Kong has been used as the alternative export location for most of China's native species (Fig. 6), including rare and protected species such as Asian Box Turtles *Cuora* spp. (Ernst& McCord 1987) and Crocodile Newts *Tylototriton* (Rowley et al. 2016).

For CITES related legislation, the discrepancy in the requirements for the legal possession of CITES II species causes additional issues. In Hong Kong, Macao, and Taiwan, if individual keeper can prove CITES II animals had captive origins and were legally acquired, no additional permits are required (Hong Kong e-Legislation, 2006; Laws& Regulations Database of the Republic of China 2013). However, the criterion on captive origin is rarely checked, which has led to wide-spread wildlife “laundering” of wild-caught, trafficked individuals (pers. comm. with Dr. Simin Lin; Sung et al. 2021). On the other hand, in Mainland China, individual keepers are required to obtain additional Possession Permit of Endangered Species, regardless the origins of animals (National Forestry and Grassland Administration 2017). However, such possession permits were designed for commercial breeding and keeping only, and its requirements on facility size and specialized staff preclude all personal pet-keeping, making legal pet-keeping of CITES II species practically impossible in Mainland China. Such an issue of a possession permit in Mainland China lumps all pet keeping of CITES II species as illegal, which confounds law enforcements and provide the perfect environment for illegal trafficking.

Increasing Possibility of Exotic Invasion

Because China’s trade of herpetofauna pets have been largely neglected, no specific regulations on health inspection/quarantine are in place for the international trade, and makes China’s large extent of herpetofauna pet trade a great threat for the invasion of exotic species and infectious diseases. Our surveys reveal the presence of several highly invasive herpetofauna species in the domestic markets in China, and even more concerning, some of them have already been bred commercially for herpetoculture at large scale, particularly the Marine Toads, *Rhinella marina* (Appendix IV). In addition to the common Buddhist practice of wildlife release and the lack of

awareness of exotic invasion in the older generations (Liu et al., 2011), the commonality of these invasive species in China's domestic market is particularly concerning. As exotic invasion from herpetofauna pets have already happened in Taiwan and Hong Kong (To, 2005; Lee et al., 2019), it is very possible that similar issues will happen in Mainland China soon if no further actions are taken. Moreover, the international trade of amphibians without specific screening and monitoring protocols greatly increase the probability of introduction of amphibian pathogens (e.g., chytrid fungus and *Ranavirus*), which cause serious conservation concerns for both China's endemic amphibian fauna and the amphibian fauna across the globe (Fisher & Garner, 2007; Wombwell et al. 2016). In particular, because pathogens are environmentally robust and can be easily transmitted through water (Brunner & Yarber 2018), the spread of these amphibian pathogens is much easier than the invasive species themselves, as untreated wastewater from daily water changes can be a sufficient source of the infection.

Recommendations

The long-term neglect of China's herpetofauna pet trade has resulted in major issues in biological conservation, biosafety, and legislation on wildlife managements. Therefore, confronting the existing and fast-growing herpetofauna pet trade and existing issues/loopholes are a crucial first step.

To stop the loophole of protection coverage between Mainland China and the special administrative regions, a unified protection coverage of China's wildlife must be adjusted in the legislation of special administrative regions. Until these proposed legislation pass, it is important for all countries to stop recognizing regional export permits for Mainland China's endemic species, unless additional paperwork from the mainland authorities is presented. Specifically,

USFW needs to stop recognizing Hong Kong's export permits for Mainland China's species, as they all violate the Lacey Act (<https://www.fws.gov/international/laws-treaties-agreements/us-conservation-laws/lacey-act.html>) regarding their legality at the country of natal origin.

For the issues of legal possessions of herpetofauna pets in Mainland China, we recommend recognizing the legitimacy of the legal practice of herpetoculture and regulating the legal trade accordingly. The current flawed application for possession permit needs to be updated, so that the legal practice of pet keeping can be practical and properly regulated. Such an effort will also help better isolate the illegal trading community, so that efforts can be focused on combating the prevalent illegal trafficking in China. Because the sudden opening of legal possession for all herpetofauna pets may result in a chaos transition that provides additional opportunities for trafficking, we recommend taking a gradual approach. Specifically, a "White List" regulatory approach might be the best starting point: legal individuals of species with certain captive origins and easy diagnosis (such as albino or leucistic snakes) are allowed for the application of personal possession permit first, while all other species remain ineligible for personal possession. After enough experience in practice for the law enforcements has accumulated, then the list can be expanded towards more challenging species such as the ones with mixed origins but still low conservation threats (e.g., *Iguana iguana*). For certain invasive species that can pose major environmental threats, they should be completely banned. Focused law enforcement should be placed on the hotspot of trafficking entrance in Guangdong and Fujian Provinces. Additionally, regions with high population of herpetoculturists such as Beijing, Shanghai, and Sichuan should also be the focus of law enforcement for herpetofauna trafficking.

For the legal possession issues in the special administrative regions, local authorities could probably also consider the "White List Approach" and reduce the current list of species for the

exemption of possession permits. For species with complex origins (such as various South American and African tortoises), a possession permit is required, and a more rigorous vetting processes should be in place.

As China's trade displays distinct patterns and preferences, specific measures can be taken to minimize the negative impacts of trade and ensure sustainable trade. Specifically, policy changes need to be in place to guide the current herpetoculture away from wild-caught Testudines. In addition, we echo the previous calls on the conservation of China's native herpetofauna (Wang et al. 2021), increasing protection levels for the highly exploited species, particularly native Sauria and native Caudata species. Lastly, for the prevalent trafficking of CITES species, better training in taxonomic identification for law enforcement and forensic supports from academic institutions are urgently needed. Different cost-effective, reliable methods of taxonomic and origin differentiation should be explored, including but not limited to genetic barcode (Bunholi et al. 2018), micro-chip identifications (Hellebuyck et al. 2013), and stable isotope differentiation (van Schingen et al. 2016).

For China's Customs, in addition to improving the statistic records mentioned above, for legal imports of live herpetofauna pets, protocols of specific pathogen screening are urgently needed, including but not limited to *Batrachochytrium dendrobatidis*, *Batrachochytrium salamandrivorans*, and *Ranavirus* for amphibians, and *Ranavirus* and snake fungal disease for reptiles.

Summary

China represents an overlooked major trader of herpetofauna pets, with extent matching if not surpassing the U.S.. China's trade is heavily biased toward turtles taxonomically, and China's

trades pose higher threats to the conservation of China's own native species than exotic species, particularly for native turtles and lizards. Within China, Mainland China and Hong Kong contributed the most in terms of consumed volume and diversity. Illegal trafficking of herpetofauna pets was prevalent in China, particularly among major political regions of such as between Mainland and Hong Kong. The current regulations in Mainland and in Hong Kong are ineffective, and the incompatible wildlife legislation between these two regions has led to loophole for wildlife "laundering" of Mainland native species in Hong Kong. Better information system of China's Customs is needed, a "white list" approach for pet trade regulation should be tested in Mainland China, and the legal loophole of wildlife "laundering" in Hong Kong must be stopped through joint efforts by China and the international community.

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Table 1. Summary of different data sources.

Data Sources	Taxonomic Group	Number of Import/Export Records		
		Total	Supply Trades of China	Consumption Trades of China
LEMIS	Amphibian	13,974	12,539	1,435
	Reptile	9,815	2,701	7,114
CITES	Amphibian	577	22	555
	Reptile	8,311	1,643	6,668
Literature	Total Number of Literature found	Number of Literature on Amphibian Trades	Number of Literature on Reptile Trades	
	54	19	41	
Online Survey	Total Number of Total Recorded Species	Number of Amphibian Species	Number of Reptile Species	
		82	489	
	571	Total Number of Forums Found	389	
Wechat Survey	Total Number of Posts Documented	Seller Code	Monitoring Start Time	Monitoring End Time
		A	Mar-19	Jan-20
		B	Aug-19	Nov-19
		C	Mar-19	Nov-20
		D	Jun-19	Jun-19
		E	Aug-19	May-20
		F	Sep-19	Nov-20
		G	Mar-19	Jun-20
		H	Jul-20	Nov-20
		I	Jun-20	Nov-20
		J	Sep-19	Nov-20
		K	Mar-19	Nov-20
Online Questionnaire	Number of Completed Surveys	Number of Responded Breeders		
	2,264	43		
	Number of Cases Entering China		Number of Cases Leaving China	

Trafficking Records from
Chinese Custom

115

5

Table 2. Summary results of online surveys.

Taxonomic Groups Involved	Number of Corresponding Online Forums
Reptiles and amphibians in general	113
General amphibians	1
General reptiles	2
Testudines	94
Serpentes	68
Sauria	81
Crocodylia	3
Anura	13
Caudata	13
Gymnophiona	1
Total	389
Range of Registered Users	
>500,000	2
100,000–500,000	22
10,000–99,999	64
1,000–9,999	131
<1,000	170

Table 3 Trade volume summery (LEMIS and CITES)

Trade type	Volume				Total Number of species			
	Reptiles		Amphibians		Reptiles		Amphibians	
	LEMIS	CITES	LEMIS	CITES	LEMIS	CITES	LEMIS	CITES
Consumption	99,640,383	9,794,037	329,200	34,917	635	309	203	54
Supply	609,735	2,749,454	16,033,433	2,954	285	164	71	8

Table 4. Regional trade statistics of China's CITES herpetofauna pet trade. Trade volumes are in the unit of individual animal.

Country developing status were taken from United Nation data. DING: developing; DD: developed.

	Consumption Trades				Supply trade			
	Reptiles		Amphibians		Reptiles		Amphibians	
Developing Status of Import/Export countries	Total Volume	Total Number of Species	Total Volume	Total Number of Species	Total Volume	Total Number of Species	Total Volume	Total Number of Species
DING	7,692,801	211	19,358	46	246,927	130	88	8
DD	2,100,929	250	15,559	24	2,502,220	89	2,856	1
Geographic Regions								
North America	1,764,420	164	7,732	42	22,659	113	3	1
Southeast Asia	2,298,923	136	297	7	318,479	84	108	1
South America	4,568,617	26	10,275	4	1,580	62	0	0
Africa	631,228	120	8,928	17	8	23	0	0
Europe	406,934	144	7,645	35	2,398,569	1	2,825	6
West Asia	123,381	20	40	1	7,850	4	8	1
Oceania	227	4	0	0	2	1	0	0

Table 5. Conservation status of commonly traded species in China's herpetofauna pet trade.

Trade Type	Categories	Reptiles	Amphibians
Consumption	Total Number of Species	120	43
	Number of Threatened Species based on IUCN	35	6
	Percentage of Threatened Species based on IUCN	29%	14%
	Total Number of Native Species	29	17
	Number of Threatened Native Species based on China's Red List	19	4
	Percentage of Threatened Native Species to Total Commonly Traded Native Species	66%	24%
Supply	Total	17	20
	Threatened Species based on IUCN	3	0
	% All Threatened Species based on IUCN	18%	0%
	Total Number of Native Species	12	12
	Number of Threatened Native Species based on China's Red List	5	1
	Percentage of Threatened Native Species to Total Commonly Traded Native Species	42%	8%

Table 6. Taxonomically concentrated volumes of herpetofauna pets based on LEMIS and CITES data.

Type of Trade	Taxonomic Group	Data Source	Number of Species that Constitute More than 90% of Trade Volume of Its Trade Category	Percentage to the Total Number of Species of Its Trade Category	Number of Individuals Traded
Consumption	Reptile	LEMIS	3	0.5%	94,150,724
		CITES	16	5.2%	297,232
	Amphibian	LEMIS	14	6.9%	8,846,906
		CITES	20	37.0%	31,408
Supply	Reptile	LEMIS	24	8.4%	550,511
		CITES	3	1.8%	14,603,692
	Amphibian	LEMIS	8	11.3%	2,559,452
		CITES	5	62.5%	2,805

Table 7. Taxonomic composition of the recorded 115 trafficking confiscations entering China between 2008 and 2020. Each confiscation case may contain multiple taxonomic orders.

Taxonomic Orders	Number of Species	Percentage to Total Number of Species Confiscated	Number of Cases	Percentage to Total Cases
Anura	11	9.5%	13	11.3%
Crocodylia	3	2.6%	4	3.5%
Sauria	23	19.8%	33	28.7%
Serpentes	26	22.4%	30	26.1%
Testudines	50	43.1%	60	52.2%
Unknown	3	2.6%	3	2.6%

Appendix I. List of key words used for the literature search. “+” indicates combination of multiple key words.

Chinese key words: 爬宠贸易, 异宠贸易, 异宠, 爬行动物+宠物, 两栖动物+宠物, 爬行动物+贸易, 两栖动物+贸易, 观赏龟, 观赏+蛇, 观赏+蜥, 观赏+两栖, 宠物贸易+爬行动物, 宠物贸易+两栖动物

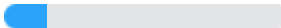
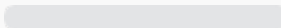
English key words: pet trade+China, exotic pets+China, reptile trade+ China, amphibian trade+China

Appendix II. List of Chinese key words used for online forum search on Baidu

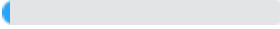
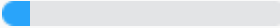
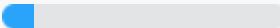
蛙, 蟾, 爬宠, 爬虫, 蜥蜴, 蛇, 龟, 大鲵, 娃娃鱼, 蜥, 蟒, 蚺, 蝮, 竹叶青, 蝥, 鬣蜥, 守宫, 睑虎, 变色龙, 避役, 石龙子, 泰加, 鳄, 六角恐龙, 蝶蜥, 锦蛇, 王蛇, 赤练, 赤链蛇, 环蛇, 鹰嘴, 地龟, 锯缘, 眼斑, 齿缘, 四爪, 草蜥, 巨蜥, 游蛇, 水蛇, 黄额, 黄缘, 凹甲, 缅甸, 鲛, 爬宠, 爬虫, 异宠

Appendix III. Results of online questionnaire surveys of herpetoculturists in China.

1 Age [Multiple choice question]

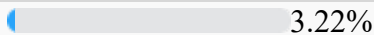
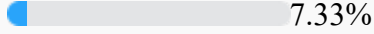
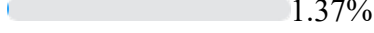
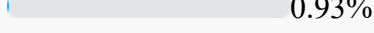
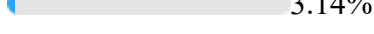
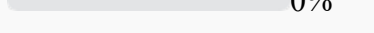
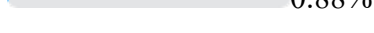
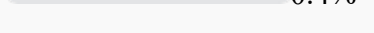
option	Count	Percentage
17 or younger	163	 7.2%
18-29	1731	 76.46%
30-49	365	 16.12%
50 and older	5	 0.22%
Sample size for this question	2264	

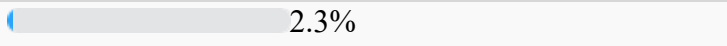
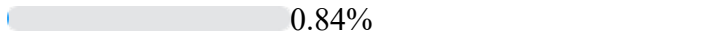
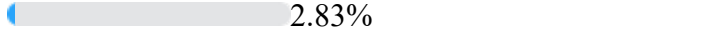
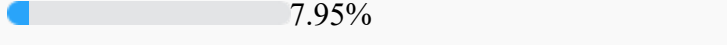
2 Education background (highest education level) [Multiple choice question]

Options	Counts	Percentages
Compulsory education (middle school)	79	 3.49%
Highschool	238	 10.51%
Undergraduate (College or University)	1689	 74.6%
Graduate degree	258	 11.4%
Sample size for this question	2264	

3 Province of residency [Multiple choice question]

Options	Counts	Percentages
Anhui	66	2.92%
Beijing	227	10.03%
Chongqin	54	2.39%
Fujian	81	3.58%
Gansu	12	0.53%
Guangdong	346	15.28%
Guangxi	63	2.78%
Guizhou	27	1.19%
Hainan	13	0.57%
Hebei	60	2.65%
Heilongjiang	27	1.19%
Henan	45	1.99%
Hong Kong	2	0.09%

Hubei	73	 3.22%
Hunan	48	 2.12%
Jiangsu	166	 7.33%
Jiangxi	31	 1.37%
Jilin	21	 0.93%
Liaoning	71	 3.14%
Macao	0	 0%
Inner Mongolia	20	 0.88%
Ningxia	9	 0.4%
Qinghai	2	 0.09%
Shandong	103	 4.55%
Shanghai	191	 8.44%
Shanxi	26	 1.15%
Shaanxi	50	 2.21%
Sichuan	114	 5.04%
Taiwan	1	 0.04%

Tianjin	52	 2.3%
Xinjiang	19	 0.84%
Tibet	0	 0%
Yunnan	64	 2.83%
Zhejiang	180	 7.95%
Sample size for this question	2264	

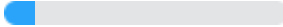
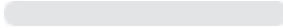
4 Earliest time when exposed to herpetoculture (year) [Filling the blank]

Year	197	197	198	198	198	198	198	198	199	199	199	199	199	199	199	199	199	199	200	200
	5	8	0	2	4	5	6	9	0	1	2	3	4	5	6	7	8	9	0	1
Coun ts	1	1	1	1	1	2	1	2	10	2	3	2	1	22	5	5	17	17	69	13

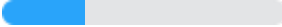
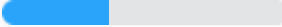
Year	200	200	200	200	200	200	200	200	201	201	201	201	201	201	201	201	201	201	201	202
	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	

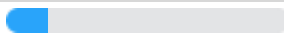
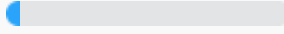
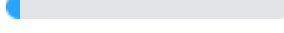
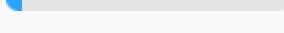
Count																			
s	20	33	39	61	68	54	126	70	178	30	109	110	148	197	189	172	208	120	85

5 If you have or you are still selling live herpetofauna pets, when did you first start? [Multiple choice question]

Options	Counts	Percentages
Yes I have this experience, and the year was _____	269	 11.88%
Not applicable	1981	 87.5%
Not answered and skipped	14	 0.62%
Sample size for this question	2264	

6 How did you first heard about herpetoculture? [Multiple choice question]

Options	Counts	Percentages
Accidental exposure in pet markets	678	 29.95%
Internet forum or discussion boards	855	 37.77%

Referred by others	337	 14.89%
TV shows or radios	126	 5.57%
Magazines or books	125	 5.52%
Others (please specify)	135	 5.96%
Not answered and skipped	8	 0.35%
Sample size for this question	2264	

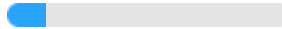
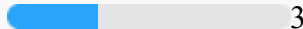
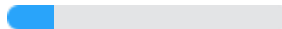
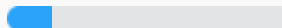
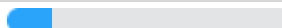
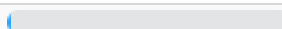
7 When did you first started to keep herpetofauna pets? (year) [Filling the blank]

Year	197	197	198	198	198	198	198	198	198	199	199	199	199	199	199	199	199	199	200	200
	5	8	0	2	4	5	6	8	9	0	1	2	4	5	6	7	8	9	0	1
Coun ts	1	1	1	1	1	3	1	1	2	9	4	5	4	20	10	6	15	20	44	13

Year	200	200	200	200	200	200	200	200	201	201	201	201	201	201	201	201	201	201	201	202
	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9		0

Count																			
s	23	34	25	54	77	44	119	61	134	46	82	95	109	151	152	189	195	186	189

8 How long in total have it been since you first started to keep herpetofauna pets? [Multiple choice question]

Options	Counts	Percentages
Less than one year	334	 14.75%
1-3 years	747	 32.99%
4-5 years	385	 17.01%
6-10 years	380	 16.78%
Longer than 10 years	379	 16.74%
Not answered and skipped	39	 1.72%
Sample size for this question	2264	

9 How many species have you kept since you first started? (species only, no morphs) [Multiple choice question]

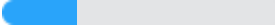
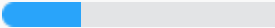
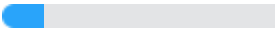
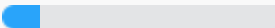
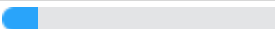
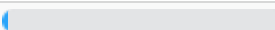
Options	Counts	Percentages
1-5 species	1382	 61.04%
6-10 species	410	 18.11%
11–20 species	185	 8.17%
More than 20 species	239	 10.56%
Not answered and skipped	48	 2.12%
Sample size for this question	2264	

10 How many individuals have you kept since you started? [Multiple choice question]

Options	Counts	Percentages
1-5 individuals	786	 34.72%
6-10 individuals	426	 18.82%
11-20 individuals	327	 14.44%
21-50 individuals	290	 12.81%
50–100 individuals	148	 6.54%
More than 100 individuals	239	 10.56%

Not answered and skipped	48	 2.12%
Sample size for this question	2264	

11 For the species that you have kept, what is the ratio between native species and exotic species? [Multiple choice question]

Options	Counts	Percentages
No native species, only keep exotic species	614	 27.12%
Native species less than one third of total species kept	642	 28.36%
Native species between one third to one half of total species kept	343	 15.15%
Native species more than one half of total species kept	317	 14%
No exotic species, only keep native species	288	 12.72%
Not answered and skipped	60	 2.65%
Sample size for this question	2264	

12 Are there/have there been any specialized herpetofauna pet shops in your city/area? [Multiple choice question]

Options	Counts	Percentages
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Yes, and they are currently open	1078	 47.61%
Yes, but they have been shut down	544	 24.03%
Never have any	181	 7.99%
Uncertain/unknown	440	 19.43%
Not answered and skipped	21	 0.93%
Sample size for this question	2264	

13 If there are any specialized herpetofauna pet shops, when did they first appear? [Multiple choice question]

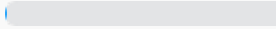
Options	Counts	Percentages
First appear in _____	491	 29.87%
Uncertain/unknown	1133	 68.92%
Not answered and skipped	20	 1.22%
Sample size for this question	1644	

14 If there are any specialized herpetofauna pet shops, how many are there? [Multiple choice question]

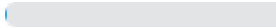
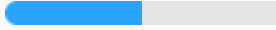
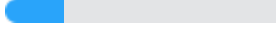
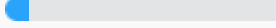
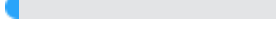
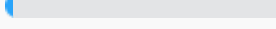
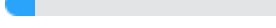
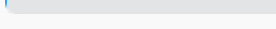
Options	Counts	Percentages
1-5	1071	 65.15%
6-10	205	 12.47%
More than 10	275	 16.73%
Not answered and skipped	93	 5.66%
Sample size for this question	1644	

15 According to what you have seen, which of the following taxonomic group had the most diversity in the specialized herpetofauna pet shops? [Multiple choice question]

Options	Counts	Percentages
Crocodylia	6	 0.36%
Testudines	961	 58.45%
Sauria	364	 22.14%
Serpentes	150	 9.12%
Anura	28	 1.7%
Caudata/Gymnophiona	17	 1.03%

Uncertain/unknown	96	 5.84%
Not answered and skipped	22	 1.34%
Sample size for this question	1644	

16 According to what you have seen, which of the following taxonomic group had the most individuals in the specialized herpetofauna pet shops? (not considering Red Eared Sliders) [Multiple choice question]

Options	Counts	Percentages
Crocodylia	13	 0.79%
Testudines	788	 47.93%
Sauria	358	 21.78%
Serpentes	147	 8.94%
Anura	84	 5.11%
Caudata/Gymnophiona	56	 3.41%
Uncertain/unknown	177	 10.77%
Not answered and skipped	21	 1.28%
Sample size for this question	1644	

17 Are there any generalized pet shops or fish stores that also carry herpetofauna pets? (excluding the ones that only carry Red Eared Sliders) ? [Multiple choice question]

Options	Counts	Percentages
Yes, and they are still carrying herps	1063	 46.95%
Yes there have been, but not anymore	371	 16.39%
Never seen any	155	 6.85%
Uncertain/unknown	647	 28.58%
Not answered and skipped	28	 1.24%
Sample size for this question	2264	

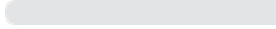
18 If there are any generalized pet shops that carry herps, when did they first started carrying herps? [Multiple choice question]

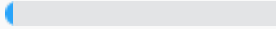
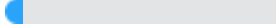
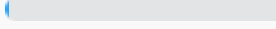
Options	Counts	Percentages
They first started carrying in _____	292	 19.97%
Uncertain/unknown	1139	 77.91%
Not answered and skipped	31	 2.12%
Sample size for this question	1462	

19 How many generalized pet shops in your city or region that carry herpetofauna pets? [Multiple choice question]

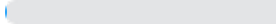
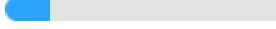
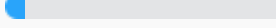
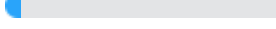
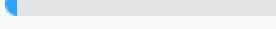
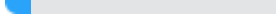
Options	Counts	Percentages
1-5	842	 57.59%
6-10	171	 11.7%
More than 10	230	 15.73%
Uncertain/unknown	183	 12.52%
Not answered and skipped	36	 2.46%
Sample size for this question	1462	

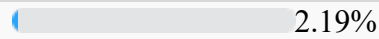
20 In these generalized pet shops, which of the following taxonomic group had the highest species diversity? [Multiple choice question]

Options	Counts	Percentages
Crocodylia	7	 0.48%
Testudines	863	 59.03%
Sauria	280	 19.15%
Serpentes	76	 5.2%

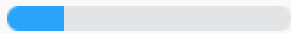
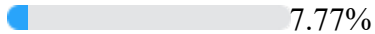
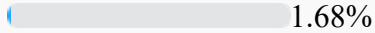
Anura	72	 4.92%
Caudata/Gymnophiona	42	 2.87%
Uncertain/unknown	94	 6.43%
Not answered and skipped	28	 1.92%
Sample size for this question	1462	

21 In these generalized pet shops, which of the following taxonomic group had the highest number of individuals? (excluding Red Eared Sliders) [Multiple choice question]

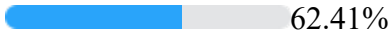
Options	Counts	Percentages
Crocodylia	14	 0.96%
Testudines	776	 53.08%
Sauria	247	 16.89%
Serpentes	106	 7.25%
Anura	83	 5.68%
Caudata/Gymnophiona	65	 4.45%
Uncertain/unknown	139	 9.51%

Not answered and skipped	32	 2.19%
Sample size for this question	1462	

22 Do you keep contact with other herpetoculturists ? [Multiple choice question]

Options	Counts	Percentages
Yes, joined online herp communities/social media groups, actively discussing and sharing with others	1581	 69.83%
Not in any online herp communities/social media groups, do not communicate much with others	469	 20.72%
Do not know any online herp communities yet, but would like to join if present	176	 7.77%
Not answered and skipped	38	 1.68%
Sample size for this question	2264	

23 What is your main reason for keeping herpetofauna pets ? [Multiple choice question]

Options	Counts	Percentages
Personal hobby/pets, never considered breeding	1413	 62.41%

Personal hobby/pets, breed species, but not breeding for sale	489	 21.6%
Personal hobby/pets, breed species, and also breeding for sale	299	 13.21%
Commercial breeding for profits	18	 0.8%
Not answered and skipped	45	 1.99%
Sample size for this question	2264	

24 If you have bred herpetofauna pets, how many animals did you produce annually? [Multiple choice with multiple answers]

Taxonomic groups	Less than 50	50–100	101–500	501–1000	1001–3000	>30000	Not answered and skipped
Crocodylia	89(10.47%)	7(0.82%)	1(0.12%)	3(0.35%)	2(0.24%)	3(0.35%)	753(88.59%)
Testudines	266(31.29%)	33(3.88%)	20(2.35%)	7(0.82%)	7(0.82%)	4(0.47%)	523(61.53%)
Serpentes	266(31.29%)	62(7.29%)	36(4.24%)	10(1.18%)	4(0.47%)	3(0.35%)	483(56.82%)
Sauria	324(38.12%)	46(5.41%)	24(2.82%)	7(0.82%)	2(0.24%)	3(0.35%)	458(53.88%)
Anura	139(16.35%)	17(2%)	7(0.82%)	2(0.24%)	3(0.35%)	1(0.12%)	684(80.47%)
Caudata/Gymnophiona	129(15.18%)	12(1.41%)	6(0.71%)	3(0.35%)	2(0.24%)	0(0%)	700(82.35%)

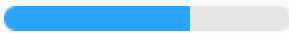
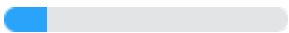
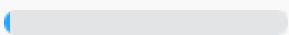
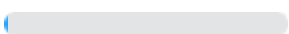
25 What is the source of your animals ? [Multiple choice with multiple answers]

Options	Counts	Percentages
Self collection from the wild	150	17.65%
Bought from retail stores	454	53.41%
Bought from online stores	684	80.47%
Others (specify)	60	7.06%
Not answered and skipped	41	4.82%
Sample size for this question	850	

26 If you bought animals from sellers, does the seller has legal permits or documentations for selleing these animals? ? [Multiple choice question]

Options	Counts	Percentages
Yes	277	34.71%
No	114	14.29%
Uncertain	402	50.38%
Not answered and skipped	5	0.63%
Sample size for this question	798	

27 Which of the following option best describe your investment level in herpetoculture? [Multiple choice question]

Options	Counts	Percentages
No special investments (using equipment designed for other purposes, i.e. fish keeping), did not purchase specialized herpetoculture equipment	313	 13.83%
Invested and purchased some specialized equipment (i.e. heat lamp, UVB lights, Calcium food supplement, ect.)	1490	 65.81%
Dedicated and expert investment level (i.e. building biotope, trying to breed species)	361	 15.95%
Commercial keeping and breeding (dedicated spaces for commercial operation and breeding)	54	 2.39%
Not answered and skipped	46	 2.03%
Sample size for this question	2264	

28 What is the highest price for the individual animal that you kept or currently keeping? [Multiple choice question]

Options	Counts	Percentages
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1-100 Yuan	346	15.28%
101-500 Yuan	607	26.81%
501-1000 Yuan	413	18.24%
1001-5000 Yuan	531	23.45%
5000–10000 Yuan	149	6.58%
More than 10000 Yuan	168	7.42%
Not answered and skipped	50	2.21%
Sample size for this question	2264	

29 How important are the following criteria when it comes to your purchase choice? (1=least concern, 7=very important)

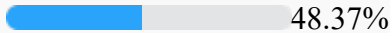
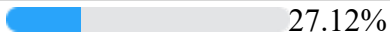
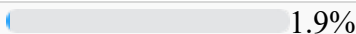
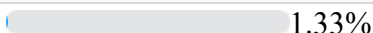
Options	1	2	3	4	5	6	7	Not answered and skipped	Average score
Price	136(6.01%)	91(4.02%)	280(12.37%)	579(25.57%)	466(20.58%)	251(11.09%)	415(18.33%)	46(2.03%)	4.42

Captive origin	212(9.37%)	58(2.56%)	90(3.98%)	222(9.81%)	230(10.16%)	325(14.36%)	1078(47.64%)	48(2.12%)	4.99
Protecting status of the species	131(5.79%)	37(1.63%)	60(2.65%)	153(6.76%)	137(6.05%)	175(7.73%)	1523(67.3%)	47(2.08%)	5.36
Geographic origins of the species (native vs. exotic)	574(25.36%)	176(7.78%)	218(9.63%)	450(19.89%)	176(7.78%)	144(6.36%)	469(20.72%)	56(2.47%)	3.6
Rarity of the species	502(22.18%)	168(7.42%)	201(8.88%)	408(18.03%)	215(9.5%)	150(6.63%)	564(24.92%)	55(2.43%)	3.82

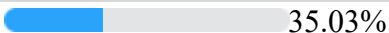
Difficulty level in husbandry	98(4.33%)	51(2.25%)	89(3.93%)	358(15.81%)	338(14.93%)	432(19.08%)	838(37.01%)	60(2.65%)	5.09
Other aspects of the species (i.e. brightness of coloration, personality, ect.)	78(3.45%)	39(1.72%)	48(2.12%)	257(11.35%)	337(14.89%)	435(19.21%)	1023(45.19%)	47(2.08%)	5.3

Counts	1731(10.93 %)	620(3.91 %)	986(6.22%)	2427(15.32 %)	1899(11.99 %)	1912(12.07 %)	5910(37.3%)	359(2.27 %)	4.65
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30 Are you familiar with the relevant laws and regulations about herpetoculture? [Multiple choice question]

Options	Counts	Percentages
Interested, but not familiar	482	 21.29%
Familiar superficially, but not knowing the specifics	1095	 48.37%
Familiar, and have searched and learned about specifics of relevant laws	614	 27.12%
Do not care	43	 1.9%
Not answered and skipped	30	 1.33%
Sample size for this question	2264	

31 As a herpetofauna pet keeper, have you worried about your pet ownership being illegal, or concerned being punished because of having illegal animals? [Multiple choice question]

Options	Counts	Percentages
My pets are legal, so I do not worry	793	 35.03%

My pets are legal, but still worry	1079	47.66%
My pets are illegal, but I am not worried	92	4.06%
My pets are illegal, and I do worry	161	7.11%
Not sure about the legality of my animals	98	4.33%
Not answered and skipped	41	1.81%
Sample size for this question	2264	

32 As a herpetoculturists, have you tried to apply for relevant legal permits? [Multiple choice question]

Options	Counts	Percentages
Never thought about it	949	41.92%
Thought about it, and have successfully gotten one	62	2.74%
Thought about it, but did not actually apply, or fail to secure one	1195	52.78%
Not answered and skipped	58	2.56%
Sample size for this question	2264	

33 If you have thought about it but did not apply or fail to secure one, what are the possible reasons that prevent you doing so?

[Multiple choice question]

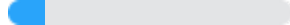
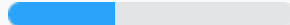
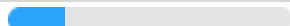
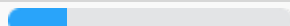
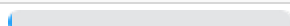
Options	Counts	Percentages
Do not know the application process or how to apply	497	 37.82%
Application process is too complicated	93	 7.08%
Application requirements are too strict to meet	356	 27.09%
Issues due to the incapability of the responsible government branch	290	 22.07%
Not answered and skipped	78	 5.94%
Sample size for this question	1314	

34 If in the near future the application become clear and reasonable, will you be willing to apply and register your pets (i.e. species info. and number of individuals) ? [Multiple choice question]

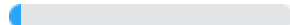
Options	Counts	Percentages
Yes, willing to support scientific management of herpetoculture trade	1842	 81.36%
No, do not believe the authority can make right decisions based on scientific data	240	 10.6%
No, because it is too complicated to apply for permits	86	 3.8%
No, because that way some species will be impossible to keep	51	 2.25%
Not answered and skipped	45	 1.99%

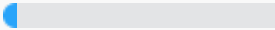
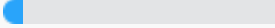
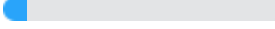
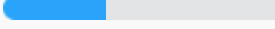
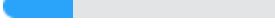
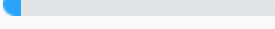
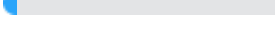
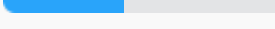
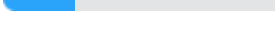
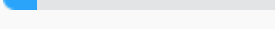
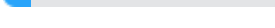
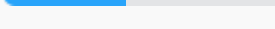
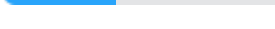
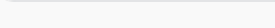
Sample size for this question	2264	
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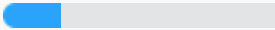
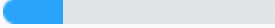
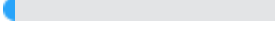
35 Have you kept pets other than herpetofauna ? [Multiple choice with multiple answers]

Options	Counts	Percentages
Have not kept any other pets	313	 13.83%
Terrestrial invertebrates (insects, spiders, scorpions, centipedes, ect.)	853	 37.68%
Fish and aquatic invertebrates	1192	 52.65%
Cats and dogs	1066	 47.08%
Mammals species other than cats and dogs (hedgehog, sugar-gliders, ect.)	476	 21.02%
Avians	488	 21.55%
Not answered and skipped	41	 1.81%
Sample size for this question	2264	

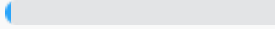
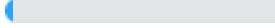
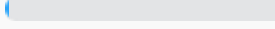
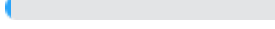
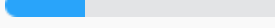
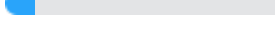
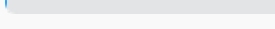
36 Which of the following groups of herpetofauna have you kept in the past? [Multiple choice with multiple possible answers]

Options	Counts	Percentages
Crocodylia	110	 4.86%

Venomous snake (exotic)	117	 5.17%
Venomous snake (native)	191	 8.44%
Pythons and boas (natural forms)	167	 7.38%
Pythons and boas (morphs)	192	 8.48%
Other non-venomous snakes (exotic)	825	 36.44%
Other non-venomous snakes (native)	558	 24.65%
Monitor lizards or Tegus	148	 6.54%
Chameleons	124	 5.48%
Other lizards (exotic)	970	 42.84%
Other lizards (native)	582	 25.71%
Tortoises (exotic)	283	 12.5%
Tortoises (native)	228	 10.07%
Turtles (native)	981	 43.33%
Turtles (exotic)	902	 39.84%
Seaturtles	28	 1.24%
Frogs and toads (exotic)	589	 26.02%

Frogs and toads (native)	464	 20.49%
Newts, salamanders, caecilians (exotic)	346	 15.28%
Newts, salamanders, caecilians (native)	487	 21.51%
Not answered and skipped	96	 4.24%
Sample size for this question	2264	

37 Species that you are currently keeping [Multiple choice with multiple answers]

Options	Counts	Percentages
Crocodylia	27	 1.19%
Venomous snake (exotic)	63	 2.78%
Venomous snake (native)	74	 3.27%
Pythons and boas (natural forms)	33	 1.46%
Pythons and boas (morphs)	58	 2.56%
Other non-venomous snakes (exotic)	639	 28.22%
Other non-venomous snakes (native)	244	 10.78%
Monitor lizards or Tegu	20	 0.88%

Chameleons	22	0.97%
Other lizards (exotic)	683	30.17%
Other lizards (native)	178	7.86%
Tortoises (exotic)	90	3.98%
Tortoises (native)	70	3.09%
Turtles (native)	632	27.92%
Turtles (exotic)	554	24.47%
Sea turtles	6	0.27%
Frogs and toads (exotic)	249	11%
Frogs and toads (native)	111	4.9%
Newts, salamanders, caecilians (exotic)	112	4.95%
Newts, salamanders, caecilians (native)	89	3.93%
Not answered and skipped	267	11.79%
Sample size for this question	2264	

Appendix IV. List of herpetofauna pet species that have been bred in mainland China. Breeding volumes are given as either actual volume estimation (in number of individual animals), estimated extent of breeding (commercial small, medium, or large extent), or both. L: literature; O: online forum surveys; W: Wechat monitoring; and Q: questionnaire survey.

Taxonomic Order	Species	Breeding Volume	Data Source
Crocodylia	<i>Crocodylus siamensis</i>	Commercial-L	O
Sauria	<i>Calotes</i> sp.	unknown	W
Sauria	<i>Calotes versicolor</i>	unknown	W
Sauria	<i>Chamaeleo calyptratus</i>	500, Commercial-S	O, Q
Sauria	<i>Chlamydosaurus kingii</i>	<100	Q
Sauria	<i>Correlophus ciliatus</i>	250, Commercial-S	O, W, Q
Sauria	<i>Diplodactylus pulcher</i>	unknown	W
Sauria	<i>Eublepharis macularius</i>	7800, Commercial-M	O, Q
Sauria	<i>Gekko gekko</i>	Commercial-S	O
Sauria	<i>Iguana iguana</i>	<100, Commercial-S	O, Q
Sauria	<i>Nephrurus amya</i>	Commercial-S	O
Sauria	<i>Nephrurus levis</i>	Commercial-S	O

Sauria	<i>Nephrurus</i> sp.	600	Q
Sauria	<i>Pogona vitticeps</i>	500, Commercial-M	O, Q
Sauria	<i>Rhacodactylus auriculatus</i>	<100,	Q
Sauria	<i>Rhacodactylus leachianus</i>	unknown	W
Sauria	<i>Tiliqua gigas</i>	100	Q
Sauria	<i>Timon lepidus</i>	unknown	W
Sauria	<i>Varanus glauerti</i>	<10	Q
Sauria	<i>Varanus primordius</i>	<10	Q
Sauria	<i>Varanus salvator</i>	Commercial-S	O
Serpentes	<i>Boa constrictor</i>	<50, Commercial-M	O, Q
Serpentes	<i>Boaedon capensis</i>	Commercial-S	O
Serpentes	<i>Boaedon fuliginosus</i>	2000	Q
Serpentes	<i>Boiga cyanea</i>	<50	Q
Serpentes	<i>Coelognathus radiatus</i>	Commercial-S	O
Serpentes	<i>Deinagkistrodon acutus</i>	Commercial-M	O
Serpentes	<i>Elaphe anomala</i>	Commercial-S	O

Serpentes	<i>Elaphe carinata</i>	<100, Commercial-S	O, Q
Serpentes	<i>Elaphe dione</i>	<50	Q
Serpentes	<i>Elaphe schrenckii</i>	Commercial-S	O
Serpentes	<i>Elaphe taeniura</i>	700, Commercial-M	O, Q
Serpentes	<i>Gloydus brevicaudus</i>	Commercial-M	O
Serpentes	<i>Gonyosoma boulengeri</i>		Q
Serpentes	<i>Heterodon nasicus</i>	3000, Commercial-S	O, Q
Serpentes	<i>Hypsiglossus plumbea</i>	Commercial-S	O
Serpentes	<i>Lampropeltis abnorma</i>	1200	Q
Serpentes	<i>Lampropeltis alterna</i>	<50, Commercial-S	O, Q
Serpentes	<i>Lampropeltis californiae</i>	3000	Q
Serpentes	<i>Lampropeltis calligaster</i>	Commercial-S	O
Serpentes	<i>Lampropeltis getula</i>	600, Commercial-M	O, Q
Serpentes	<i>Lampropeltis mexicana</i>	Commercial-S	O
Serpentes	<i>Lampropeltis polyzona</i>	<100	Q
Serpentes	<i>Lampropeltis pyromelana</i>	Commercial-S	O

Serpentes	<i>Lampropeltis</i> sp.	5000	Q
Serpentes	<i>Lampropeltis triangulum</i>	<100, Commercial-S	O, Q
Serpentes	<i>Lycodon rufozonatus</i>	<100, Commercial-S	O, Q
Serpentes	<i>Myrrophis chinensis</i>	Commercial-M	O
Serpentes	<i>Naja annulifera</i>	<20	Q
Serpentes	<i>Naja atra</i>	Commercial-M	O
Serpentes	<i>Naja kaouthia</i>	Commercial-M	O
Serpentes	<i>Oreocryptophis porphyraceus</i>	<50	Q
Serpentes	<i>Pantherophis guttatus</i>	10000, Commercial-M	O, Q
Serpentes	<i>Pantherophis obsoletus</i>	700	Q
Serpentes	<i>Pantherophis</i> sp.	250	Q
Serpentes	<i>Pituophis catenifer</i>	2000	Q
Serpentes	<i>Pituophis melanoleucus</i>	1100	Q
Serpentes	<i>Pituophis</i> sp.	900	Q
Serpentes	<i>Ptyas dhumnades</i>	Commercial-M	O
Serpentes	<i>Ptyas korros</i>	Commercial-M	O

Serpentes	<i>Ptyas mucosa</i>	Commercial-M	O
Serpentes	<i>Python bivittatus</i>	Commercial-L	O
Serpentes	<i>Python regius</i>	Commercial-S	O
Serpentes	<i>Xenodon pulcher</i>	300	Q
Testudines	<i>Aldabrachelys gigantea</i>	<1000	L
Testudines	<i>Apalone ferox</i>	Commercial-L	O
Testudines	<i>Apalone spinifera</i>	Commercial-L	O
		500 ~ 5000Commercial-	
Testudines	<i>Centrochelys sulcata</i>	M	L, O
Testudines	<i>Chelodina oblonga</i>	30000 ~ 50000	L
Testudines	<i>Chelodina rugosa</i>	Commercial-L	O
Testudines	<i>Chelonoidis carbonarius</i>	≤500, Commercial-S	L, O
Testudines	<i>Chelonoidis denticulatus</i>	< 500, Commercial-S	L, O
Testudines	<i>Chelydra serpentina</i>	≤100000, Commercial-L	L, O
		10000 ~ 20000,	
Testudines	<i>Chrysemys picta</i>	Commercial-L	L, O

Testudines	<i>Claudius angustatus</i>	≤500	L
		500 ~ 5000Commercial-	
Testudines	<i>Clemmys guttata</i>	S	L, O
Testudines	<i>Cuora amboinensis</i>	Commercial-S	O
Testudines	<i>Cuora aurocapitata</i>	≤500	L
		30000–50000,	
Testudines	<i>Cuora flavomarginata</i>	Commercial-L	L, O
Testudines	<i>Cuora galbinifrons</i>	≤500	L
Testudines	<i>Cuora mccordi</i>	≤500	L
Testudines	<i>Cuora mouhotii</i>	≤500	L
Testudines	<i>Cuora pani</i>	≤500	L
		20000 ~ 30000,	
Testudines	<i>Cuora trifasciata</i>	Commercial-L	L, O
Testudines	<i>Cuora yunnanensis</i>	≤500	L
Testudines	<i>Cuora zhoui</i>	≤500	L
Testudines	<i>Cyclemys tcheponensis</i>	Commercial-S	O

		5000 ~ 10000,	
Testudines	<i>Emydura subglobosa</i>	Commercial-L	L, O
Testudines	<i>Geochelone elegans</i>	Commercial-S	O
		10000 ~ 20000,	
Testudines	<i>Geoclemys hamiltonii</i>	Commercial-M	L, O
Testudines	<i>Geoemyda spengleri</i>	≤500	L
Testudines	<i>Glyptemys insculpta</i>	≤500	L
Testudines	<i>Graptemys nigrinoda</i>	Commercial-S	O
		500 ~ 5000,	
Testudines	<i>Graptemys ouachitensis</i>	Commercial-S	L, O
		50000 ~ 100000,	
Testudines	<i>Graptemys pseudogeographica</i>	Commercial-L	L, O
Testudines	<i>Heosemys annandalii</i>	Commercial-S	O
		10000 ~ 20000,	
Testudines	<i>Heosemys grandis</i>	Commercial-M	L, O

Testudines	<i>Indotestudo elongata</i>	< 1500	L
		500 ~ 5000,	
Testudines	<i>Kinosternon leucostomum</i>	Commercial-M	L, O
Testudines	<i>Kinosternon scorpioides</i>	Commercial-M	O
Testudines	<i>Macrochelys temminckii</i>	≤500, Commercial-L	L, O
		5000 ~ 10000,	
Testudines	<i>Malaclemys terrapin</i>	Commercial-S	L, O
Testudines	<i>Manouria emys</i>	≤500, Commercial-S	L, O
		20000 ~ 30000,	
Testudines	<i>Mauremys annamensis</i>	Commercial-L	L, O
Testudines	<i>Mauremys japonica</i>	Commercial-S	O
Testudines	<i>Mauremys mutica</i>	≤100000, Commercial-L	L, O
		20000 ~ 30000,	
Testudines	<i>Mauremys nigricans</i>	Commercial-L	L, O
Testudines	<i>Mauremys reevesii</i>	≤100000, Commercial-L	L, O
Testudines	<i>Mauremys sinensis</i>	≤100000, Commercial-L	L, O

Testudines	<i>Orlitia borneensis</i>	Commercial-S	O
Testudines	<i>Palea steindachneri</i>	Commercial-L	O
Testudines	<i>Pangshura tecta</i>	Commercial-S	O
Testudines	<i>Pelodiscus sinensis</i>	Commercial-L	O
Testudines	<i>Phrynops geoffroanus</i>	Commercial-M	O
		500 ~ 5000,	
Testudines	<i>Phrynops hilarii</i>	Commercial-M	L, O
Testudines	<i>Platysternon megacephalum</i>	≤500	L
Testudines	<i>Podocnemis erythrocephala</i>	Commercial-S	O
Testudines	<i>Podocnemis unifilis</i>	Commercial-M	O
Testudines	<i>Pseudemys alabamensis</i>	5000 ~ 10000	L
		30000 ~ 50000,	
Testudines	<i>Pseudemys concinna</i>	Commercial-L	L, O
Testudines	<i>Pseudemys nelsoni</i>	Commercial-L	O
Testudines	<i>Rhinoclemmys pulcherrima</i>	≤500, Commercial-S	L, O
Testudines	<i>Sacalia quadriocellata</i>	≤500, Commercial-S	L, O

		10000 ~ 20000,	
Testudines	<i>Sternotherus carinatus</i>	Commercial-L	L, O
		10000 ~ 20000,	
Testudines	<i>Sternotherus odoratus</i>	Commercial-L	L, O
Testudines	<i>Stigmochelys pardalis</i>	<1800, Commercial-M	L, O
Testudines	<i>Terrapene carolina</i>	≤500	L
Testudines	<i>Terrapene ornata</i>	≤500	L
Testudines	<i>Testudo graeca</i>	Commercial-S	O
Testudines	<i>Trachemys scripta</i>	Commercial-L, ≤100000	L, O

Appendix V. CITES listed species that were present in Mainland China's domestic market but had no legal import records.

Taxonomic Groups	Species	Origin	Appendix Listig	IUCN
Crocodylia	<i>Crocodylus siamensis</i>	SE Asia	I	CR
Crocodylia	<i>Tomistoma schlegelii</i>	SE Asia	I	VU
Sauria	<i>Brookesia perarmata</i>	Madagascar	I	EN
Sauria	<i>Cyclura cornuta</i>	S America	I	EN
Sauria	<i>Cyclura lewisi</i>	S America	I	EN
Sauria	<i>Cyclura nubila</i>	S America	I	VU
Sauria	<i>Lygodactylus williamsi</i>	Africa	I	CR
Sauria	<i>Varanus bengalensis</i>	SE Asia	I	LC
Sauria	<i>Varanus flavescens</i>	SE Asia	I	LC
Sauria	<i>Varanus griseus</i>	Oceania	I	NA
Sauria	<i>Varanus komodoensis</i>	SE Asia	I	VU
Testudines	<i>Astrochelys yniphora</i>	Madagascar	I	CR
Testudines	<i>Chitra vandijki</i>	SE Asia	I	NA
Testudines	<i>Cuora bourreti</i>	SE Asia	I	CR

Testudines	<i>Cuora picturata</i>	SE Asia	I	CR
Testudines	<i>Geochelone yniphora</i>	Madagascar	I	CR
Testudines	<i>Melanochelys tricarinata</i>	SE Asia	I	EN
Testudines	<i>Morenia ocellata</i>	SE Asia	I	VU
Testudines	<i>Pangshura tecta</i>	SE Asia	I	VU
Sauria	<i>Abronia deppeii</i>	S America	II	EN
Sauria	<i>Abronia graminea</i>	S America	II	EN
Sauria	<i>Abronia mixteca</i>	S America	II	VU
Sauria	<i>Abronia taeniata</i>	S America	II	VU
Sauria	<i>Brookesia spectrum</i>	Madagascar	II	LC
Sauria	<i>Ceratophora stoddartii</i>	SE Asia	II	NA
Sauria	<i>Chamaeleo namaquensis</i>	Africa	II	LC
Sauria	<i>Chamaeleo tempeli</i>	Africa	II	LC
Sauria	<i>Cordylus mossambicus</i>	Africa	II	LC
Sauria	<i>Goniurosaurus kuroiwae</i>	SE Asia	II	VU
Sauria	<i>Goniurosaurus orientalis</i>	SE Asia	II	EN

Sauria	<i>Goniurosaurus splendens</i>	SE Asia	II	EN
Sauria	<i>Goniurosaurus yamashinae</i>	SE Asia	II	CR
Sauria	<i>Lyriocephalus scutatus</i>	SE Asia	II	NT
Sauria	<i>Naultinus elegans</i>	Oceania	II	VU
Sauria	<i>Paroedura androyensis</i>	Madagascar	II	VU
Sauria	<i>Phelsuma cepediana</i>	Madagascar	II	LC
Sauria	<i>Phelsuma ornata</i>	Madagascar	II	NA
Sauria	<i>Phrynosoma cornutum</i>	N America	II	LC
Sauria	<i>Smaug depressus</i>	Africa	II	LC
Sauria	<i>Uromastyx acanthinurua</i>	Africa	II	NA
Sauria	<i>Uromastyx nigriventris</i>	Africa	II	NA
Sauria	<i>Varanus cerambonensis</i>	SE Asia	II	NA
Sauria	<i>Varanus cumingi</i>	SE Asia	II	LC
Sauria	<i>Varanus ornatus</i>	Africa	II	VU
Sauria	<i>Varanus primordius</i>	Oceania	II	LC
Serpentes	<i>Acrantophis dumerili</i>	Madagascar	II	LC

Serpentes	<i>Bothrochilus albertisii</i>	SE Asia	II	LC
Serpentes	<i>Corallus batesii</i>	S America	II	NA
Serpentes	<i>Epicrates angulifer</i>	S America	II	NT
Serpentes	<i>Epicrates striatus</i>	S America	II	LC
Serpentes	<i>Eunectes beniensis</i>	S America	II	LC
Serpentes	<i>Naja naja</i>	SE Asia	II	NA
Serpentes	<i>Naja samarensis</i>	Africa	II	LC
Serpentes	<i>Naja siamensis</i>	SE Asia	II	VU
Serpentes	<i>Simalia amethystina</i>	Oceania	II	NA
Testudines	<i>Amyda cartilaginea</i>	SE Asia	II	VU
Testudines	<i>Batagur trivittata</i>	SE Asia	II	CR
Testudines	<i>Chitra indica</i>	SE Asia	II	EN
Testudines	<i>Cyclemys atripons</i>	SE Asia	II	NA
Testudines	<i>Cyclemys tcheponensis</i>	SE Asia	II	NA
Testudines	<i>Emys blandingii</i>	N America	II	EN
Testudines	<i>Geoemyda japonica</i>	SE Asia	II	EN

Testudines	<i>Hardella thurjii</i>	SE Asia	II	VU
Testudines	<i>Heosemys depressa</i>	SE Asia	II	CR
Testudines	<i>Kinixys natalensis</i>	Africa	II	VU
Testudines	<i>Lissemys scutata</i>	SE Asia	II	DD
Testudines	<i>Nilssonina formosa</i>	SE Asia	II	EN
Testudines	<i>Pangshura sylhetensis</i>	SE Asia	II	EN
Testudines	<i>Pangshura tentoria</i>	SE Asia	II	LC
Testudines	<i>Podocnemis expansa</i>	S America	II	CR
Testudines	<i>Siebenrockiella leytensis</i>	SE Asia	II	CR
Sauria	<i>Anolis equestris</i>	S America	III	NA
Sauria	<i>Anolis porcus</i>	S America	III	NA
Sauria	<i>Hoplodactylus africanus</i>	Africa	III	NA
Sauria	<i>Sphaerodactylus torrei</i>	S America	III	EN
Testudines	<i>Graptemys caglei</i>	N America	III	EN
Testudines	<i>Graptemys ernsti</i>	N America	III	NT
Testudines	<i>Graptemys geographica</i>	N America	III	LC

Testudines

Graptemys versa

N America

III

LC

Appendix VI. Trading partners of China based on CITES dataset. DING: Developing; DD: Developed. “—” indicates no trade.

Developing Status	Major	Country	Country Abbreviations	Reptiles		Amphibians	
	Geographic Region			Total	Total		
				Number of Species	Number of Species		
Consumption Trades of China							
DING	S America	Peru	PE	3,739,265	5	—	—
DD	N America	United States	US	1,744,907	142	3,762	24
DING	SE Asia	Malaysia	MY	954,520	28	—	—
DING	SE Asia	Viet Nam	VN	744,270	17	—	—
DING	S America	El Salvador	SV	559,801	5	—	—
DING	SE Asia	Indonesia	ID	341,927	70	—	—
DING	Africa	Zambia	ZM	220,470	4	—	—
DING	SE Asia	Bangladesh	BD	171,000	1	—	—
DING	Africa	Ghana	GH	145,366	17	—	—
DD	Europe	Slovenia	SI	138,761	4	—	—

DING	S America	Brazil	BR	119,634	3	—	—
DING	Africa	Kenya	KE	96,413	8	—	—
DING	S America	Venezuela, Bolivarian Republic of Macedonia, the Former Yugoslav Republic of	VE	92,902	6	—	—
DING	Europe		MK	66,360	3	—	—
DD	SE Asia	Japan	JP	58,691	46	182	5
DING	Africa	Togo	TG	54,860	18	—	—
DD	Europe	Italy	IT	54,567	32	—	—
DD	Europe	Czech Republic	CZ	52,881	18	3,322	14
DING	Europe	Ukraine	UA	47,318	37	—	—
DING	W Asia	Jordan	JO	43,634	16	—	—

DING	W Asia	Uzbekistan	UZ	41,577	1	—	—
DING	W Asia	Syrian Arab Republic	SY	29,034	6	40	1
DING	Africa	Mali	ML	26,871	19	—	—
DD	Europe	Germany	DE	24,763	89	983	6
DING	Africa	Tanzania, United Republic of	TZ	23,257	19	—	—
DING	Africa	Madagascar	MG	23,092	47	8,928	17
DD	N America	Canada	CA	19,191	75	3,970	39
DING	S America	Colombia	CO	16,790	4	—	—
DING	SE Asia	Lao People's Democratic Republic	LA	15,400	5	—	—
DING	S America	Guyana	GY	15,329	13	—	—
DING	SE Asia	Thailand	TH	11,216	36	115	4

DING	Africa	Sudan	SD	10,931	5	—	—
DING	S America	Argentina	AR	10,407	5	—	—
DING	Europe	Russian Federation	RU	10,000	1	—	—
DING	Africa	Seychelles	SC	8,742	1	—	—
DING	Africa	Mozambique	MZ	7,664	11	—	—
DING	S America	Uruguay	UY	5,602	8	—	—
DING	W Asia	United Arab Emirates	AE	5,278	8	—	—
DING	S America	Barbados	BB	4,412	2	—	—
DD	Europe	Netherlands	NL	3,684	26	3,340	26
DING	Africa	South Africa	ZA	3,614	18	—	—
DING	Africa	Benin	BJ	3,602	10	—	—
DING	W Asia	Kuwait	KW	3,138	1	—	—
DING	S America	Suriname	SR	2,487	7	23	1
DING	Europe	Serbia	RS	1,600	1	—	—

DING	Africa	Mauritius	MU	1,572	2	—	—
DD	Europe	Slovakia	SK	1,554	1	—	—
DING	Africa	Uganda	UG	1,493	4	—	—
DING	Africa	Egypt	EG	1,403	5	—	—
DING	S America	Nicaragua	NI	1,278	2	8,530	3
DING	Europe	Switzerland	CH	1,258	21	—	—
DING	Europe	Ethiopia	ET	1,230	2	—	—
DING	SE Asia	Singapore	SG	950	1	—	—
DING	SE Asia	Korea, Republic of	KR	912	3	—	—
DING	Europe	United Kingdom	GB	869	13	—	—
DD	Europe	Bulgaria	BG	866	9	—	—
DING	Africa	Guinea	GN	791	5	—	—
DING	W Asia	Oman	OM	720	2	—	—
DD	Europe	Hungary	HU	706	5	—	—

DING	Africa	Libya	LY	500	1	—	—
DING	S America	Guatemala	GT	400	1	—	—
DING	Africa	Cameroon	CM	381	7	—	—
DING	N America	Mexico	MX	322	3	—	—
DD	Europe	Belgium	BE	200	3	—	—
DING	S America	Paraguay	PY	200	2	—	—
DING	Oceania	Solomon Islands	SB	177	4	—	—
DD	Europe	Austria	AT	116	9	—	—
DING	Africa	Congo, the Democratic Republic of the	CD	104	3	—	—
DING	Europe	Sint Maarten (Dutch part)	SX	103	2	—	—

DING	Africa	Equatorial Guinea	GQ	102	4	—	—
DING	S America	Honduras	HN	100	1	—	—
DING	Europe	Turkey	TR	56	3	—	—
DING	Oceania	Vanuatu	VU	50	2	—	—
DING	SE Asia	Philippines	PH	37	1	—	—
DD	Europe	Spain	ES	32	3	—	—
DING	S America	Costa Rica	CR	10	1	—	—
DD	Europe	France	FR	9	2	—	—
DD	Europe	Denmark	DK	1	1	—	—
DING	S America	Panama	PA	0	0	1,722	2
Supply Trades of China							
DD	Europe	Germany	DE	971,971	34	2,625	6
DD	Europe	Italy	IT	743,379	23	—	—
DD	Europe	Portugal	PT	254,358	5	—	—

DING	SE Asia	Korea, Republic of	KR	202,165	66	80	1
DD	Europe	Czech Republic	CZ	155,624	13	—	—
DD	Europe	Spain	ES	132,466	18	200	1
DD	SE Asia	Japan	JP	76,738	69	28	1
DD	Europe	Luxembourg	LU	75,000	4	—	—
DD	N America	United States	US	22,009	83	3	1
DD	Europe	Belgium	BE	20,075	7	—	—
DING	SE Asia	Malaysia	MY	15,022	38	—	—
DD	Europe	Slovakia	SK	15,000	1	—	—
DD	Europe	Netherlands	NL	11,400	3	—	—
DING	SE Asia	Viet Nam	VN	10,095	6	—	—
DING	SE Asia	Indonesia	ID	8,548	27	—	—
DD	Europe	Hungary	HU	8,080	2	—	—
DD	Europe	Denmark	DK	5,721	4	—	—

DD	W Asia	Cyprus	CY	5,000	1	—	—
DD	Europe	Poland	PL	4,964	4	—	—
DING	SE Asia	Thailand	TH	3,043	34	—	—
DING	SE Asia	Singapore	SG	1,724	4	—	—
DING	W Asia	Kuwait	KW	1,235	16	—	—
DING	SE Asia	Philippines	PH	1,141	22	—	—
DING	S America	Argentina	AR	1,080	3	—	—
DING	W Asia	United Arab Emirates	AE	767	8	8	1
DING	W Asia	Iran, Islamic Republic of	IR	540	3	—	—
DING	N America	Mexico	MX	510	6	—	—
DING	S America	El Salvador	SV	500	1	—	—
DING	W Asia	Israel	IL	229	5	—	—
DD	Europe	Sweden	SE	150	1	—	—
DD	N America	Canada	CA	140	11	—	—

DING	Europe	United Kingdom	GB	129	7	—	—
DD	Europe	France	FR	129	6	—	—
DING	Europe	Switzerland	CH	109	8	—	—
DING	W Asia	Lebanon	LB	72	1	—	—
DD	Europe	Austria	AT	12	4	—	—
DING	Africa	South Africa	ZA	8	1	—	—
DING	W Asia	Qatar	QA	7	3	—	—
DING	SE Asia	Cambodia	KH	3	1	—	—
DD	Oceania	Australia	AU	2	1	—	—
DD	Europe	Finland	FI	2	1	—	—

Appendix VII. Commonly traded reptiles and amphibians in China's consumption trade.

Class	Taxonomic Order	Species	Native Status	IUCN	China's Red List	Geographic Origin	CITES Appendix Listig
Amphibia	Anura	<i>Ceratobatrachus guentheri</i>	Exotic	LC		Oceania	
Amphibia	Anura	<i>Ceratophrys aurita</i>	Exotic	LC		S America	
Amphibia	Anura	<i>Ceratophrys calcarata</i>	Exotic	LC		S America	
Amphibia	Anura	<i>Ceratophrys cornuta</i>	Exotic	LC		S America	
Amphibia	Anura	<i>Ceratophrys cranwelli</i>	Exotic	LC		S America	
Amphibia	Anura	<i>Ceratophrys hybrid</i>	Exotic	–		S America	
Amphibia	Anura	<i>Ceratophrys ornata</i>	Exotic	NT		S America	
Amphibia	Anura	<i>Dendrobates auratus</i>	Exotic	LC		S America	II
Amphibia	Anura	<i>Dendrobates tinctorius</i>	Exotic	LC		S America	II
Amphibia	Anura	<i>Hyla annectans</i>	Native	LC	LC	CN	
Amphibia	Anura	<i>Hyla chinensis</i>	Native	LC	LC	CN	
Amphibia	Anura	<i>Hyla</i> sp.	Native	–	–	CN	
Amphibia	Anura	<i>Incilius alvarius</i>	Exotic	LC		N America	

Amphibia	Anura	<i>Kaloula pulchra</i>	Native	LC	LC	CN
Amphibia	Anura	<i>Lepidobatrachus laevis</i>	Exotic	LC		S America
Amphibia	Anura	<i>Lepidobatrachus llanensis</i>	Exotic	LC		S America
Amphibia	Anura	<i>Lithobates catesbeianus</i>	Exotic	LC		N America
Amphibia	Anura	<i>Litoria caerulea</i>	Exotic	LC		Oceania
Amphibia	Anura	<i>Megophrys nasuta</i>	Exotic	LC		SE Asia
Amphibia	Anura	<i>Phyllomedusa bicolor</i>	Exotic	LC		S America
Amphibia	Anura	<i>Phyllomedusa sauvagii</i>	Exotic	LC		S America
Amphibia	Anura	<i>Pyxicephalus adspersus</i>	Exotic	LC		Africa
Amphibia	Anura	<i>Ranoidea caerulea</i>	Exotic	LC		Oceania
Amphibia	Anura	<i>Rhinella marinus</i>	Exotic	LC		S America
		<i>Trachycephalus</i>				
Amphibia	Anura	<i>resinificatrix</i>	Exotic	LC		S America
Amphibia	Anura	<i>Xenopus laevis</i>	Exotic	LC		Africa
Amphibia	Caudata	<i>Ambystoma mavortium</i>	Exotic	LC		N America
Amphibia	Caudata	<i>Ambystoma mexicanum</i>	Exotic	CR		N America II

Amphibia	Caudata	<i>Ambystoma opacum</i>	Exotic	LC			N America	
Amphibia	Caudata	<i>Ambystoma tigrinum</i>	Exotic	LC			N America	
Amphibia	Caudata	<i>Cynops cyanurus</i>	Native	LC	NT		CN	
Amphibia	Caudata	<i>Cynops orientalis</i>	Native	LC	NT		CN	
Amphibia	Caudata	<i>Pachytriton brevipes</i>	Native	LC	LC		CN	
Amphibia	Caudata	<i>Pachytriton granulosus</i>	Native	NA	DD		CN	
Amphibia	Caudata	<i>Paramesotriton chinensis</i>	Native	LC	NT		CN	II
Amphibia	Caudata	<i>Tylototriton asperrimus</i>	Native	NT	NT		CN	II
		<i>Tylototriton</i>						
Amphibia	Caudata	<i>kweichowensis</i>	Native	VU	VU		CN	II
Amphibia	Caudata	<i>Tylototriton lizhengchangi</i>	Native	NA	VU		CN	II
Amphibia	Caudata	<i>Tylototriton pulcherrima</i>	Native	NA	NT		CN	II
Amphibia	Caudata	<i>Tylototriton shanjing</i>	Native	VU	NT		CN	II
Amphibia	Caudata	<i>Tylototriton taliangensis</i>	Native	VU	VU		CN	II
Amphibia	Caudata	<i>Tylototriton wenxianensis</i>	Native	VU	VU		CN	II
Amphibia	Caudata	<i>Tylototriton yangi</i>	Native	EN	NT		CN	II

Reptilia	Crocodylia	<i>Crocodylus siamensis</i>	Exotic	CR		SE Asia	I
Reptilia	Sauria	<i>Anolis barbatus</i>	Exotic	NA		N America	
Reptilia	Sauria	<i>Anolis carolinensis</i>	Exotic	LC		N America	
Reptilia	Sauria	<i>Basiliscus basiliscus</i>	Exotic	LC		S America	
Reptilia	Sauria	<i>Basiliscus plumifrons</i>	Exotic	LC		S America	
Reptilia	Sauria	<i>Broadleysaurus major</i>	Exotic	NA		Africa	
Reptilia	Sauria	<i>Calotes mystaceus</i>	Native	NA	LC	CN	
Reptilia	Sauria	<i>Calotes versicolor</i>	Native	NA	LC	CN	
Reptilia	Sauria	<i>Chamaeleo calyptratus</i>	Exotic	LC		W Asia	II
Reptilia	Sauria	<i>Chlamydosaurus kingii</i>	Exotic	LC		Oceania	
Reptilia	Sauria	<i>Correlophus ciliatus</i>	Exotic	NA		Oceania	
Reptilia	Sauria	<i>Crotaphytus collaris</i>	Exotic	LC		N America	
Reptilia	Sauria	<i>Ctenosaura similis</i>	Exotic	LC		S America	II
Reptilia	Sauria	<i>Cyclodomorphus gerrardii</i>	Exotic	LC		Oceania	
Reptilia	Sauria	<i>Diploderma splendidum</i>	Native	NA	LC	CN	
Reptilia	Sauria	<i>Eremias argus</i>	Native	LC	LC	CN	

Reptilia	Sauria	<i>Eublepharis macularius</i>	Exotic	LC		W Asia
Reptilia	Sauria	<i>Furcifer pardalis</i>	Exotic	LC		Madagascar II
Reptilia	Sauria	<i>Gastropholis prasina</i>	Exotic	NT		Africa
Reptilia	Sauria	<i>Gekko vittatus</i>	Exotic	NA		SE Asia
		<i>Hemitheconyx</i>				
Reptilia	Sauria	<i>caudicinctus</i>	Exotic	LC		Africa
Reptilia	Sauria	<i>Hydrosaurus amboinensis</i>	Exotic	NA		SE Asia
Reptilia	Sauria	<i>Hydrosaurus pustulatus</i>	Exotic	VU		SE Asia
Reptilia	Sauria	<i>Hydrosaurus weberi</i>	Exotic	NA		SE Asia
Reptilia	Sauria	<i>Iguana iguana</i>	Exotic	LC		S America II
Reptilia	Sauria	<i>Intellagama lesueurii</i>	Exotic	LC		Oceania
Reptilia	Sauria	<i>Nephrurus levis</i>	Exotic	LC		Oceania
Reptilia	Sauria	<i>Paroedura picta</i>	Exotic	NA		Madagascar
Reptilia	Sauria	<i>Physignathus cocincinus</i>	Native	VU	EN	CN
Reptilia	Sauria	<i>Plestiodon chinensis</i>	Native	LC	LC	CN
Reptilia	Sauria	<i>Pogona vitticeps</i>	Exotic	LC		Oceania

Reptilia	Sauria	<i>Rhacodactylus auriculatus</i>	Exotic	LC		Oceania	
Reptilia	Sauria	<i>Rhacodactylus leachianus</i>	Exotic	LC		Oceania	
Reptilia	Sauria	<i>Sauromalus ater</i>	Exotic	LC		N America	
Reptilia	Sauria	<i>Sceloporus malachiticus</i>	Exotic	LC		S America	
Reptilia	Sauria	<i>Scincus scincus</i>	Exotic	NA		W Asia	
		<i>Takydromus</i>					
Reptilia	Sauria	<i>septrionalis</i>	Native	LC	LC	CN	
Reptilia	Sauria	<i>Tarentola mauritanica</i>	Exotic	LC		Africa	
Reptilia	Sauria	<i>Teratoscincus przewalskii</i>	Native	LC	NT	CN	
Reptilia	Sauria	<i>Tiliqua gigas</i>	Exotic	NA		Oceania	
Reptilia	Sauria	<i>Tiliqua rugosa</i>	Exotic	LC		Oceania	
Reptilia	Sauria	<i>Timon lepidus</i>	Exotic	NT		Europe	
Reptilia	Sauria	<i>Tribolonotus gracilis</i>	Exotic	LC		Oceania	
Reptilia	Sauria	<i>Varanus exanthematicus</i>	Exotic	LC		Africa	II
Reptilia	Serpentes	<i>Boa constrictor</i>	Exotic	NA		S America	II
Reptilia	Serpentes	<i>Boaedon capensis</i>	Exotic	NA		Africa	

Reptilia	Serpentes	<i>Coelognathus radiatus</i>	Native	LC	EN	CN
Reptilia	Serpentes	<i>Cyclophiops major</i>	Native	LC	LC	CN
Reptilia	Serpentes	<i>Elaphe carinata</i>	Native	NA	EN	CN
Reptilia	Serpentes	<i>Elaphe dione</i>	Native	LC	LC	CN
Reptilia	Serpentes	<i>Elaphe taeniura</i>	Native	NA	EN	CN
Reptilia	Serpentes	<i>Euprepiophis mandarinus</i>	Native	LC	VU	CN
Reptilia	Serpentes	<i>Heterodon nasicus</i>	Exotic	LC		N America
Reptilia	Serpentes	<i>Lampropeltis californiae</i>	Exotic	LC		N America
Reptilia	Serpentes	<i>Lampropeltis getula</i>	Exotic	LC		N America
Reptilia	Serpentes	<i>Lampropeltis mexicana</i>	Exotic	LC		S America
Reptilia	Serpentes	<i>Lampropeltis triangulum</i>	Exotic	LC		N America
Reptilia	Serpentes	<i>Oocatochus rufodorsatus</i>	Native	LC	LC	CN
Reptilia	Serpentes	<i>Pantherophis emoryi</i>	Exotic	LC		N America
Reptilia	Serpentes	<i>Pantherophis guttatus</i>	Exotic	LC		N America
Reptilia	Serpentes	<i>Pantherophis obsoletus</i>	Exotic	LC		N America
Reptilia	Serpentes	<i>Pituophis catenifer</i>	Exotic	LC		N America

Reptilia	Serpentes	<i>Python regius</i>	Exotic	LC		Africa	II
Reptilia	Serpentes	<i>Thamnophis radix</i>	Exotic	LC		N America	
Reptilia	Testudines	<i>Apalone ferox</i>	Exotic	LC		N America	
Reptilia	Testudines	<i>Astrochelys radiata</i>	Exotic	CR		Madagascar	I
Reptilia	Testudines	<i>Carettochelys insculpta</i>	Exotic	EN		Oceania	II
Reptilia	Testudines	<i>Centrochelys sulcata</i>	Exotic	VU		Africa	II
Reptilia	Testudines	<i>Chelodina oblonga</i>	Exotic	NT		Oceania	
Reptilia	Testudines	<i>Chelodina rugosa</i>	Exotic	NT		Oceania	
Reptilia	Testudines	<i>Chelonoidis carbonarius</i>	Exotic	NA		S America	II
Reptilia	Testudines	<i>Chelus fimbriata</i>	Exotic	NA		S America	
Reptilia	Testudines	<i>Chelydra serpentina</i>	Exotic	LC		N America	III
Reptilia	Testudines	<i>Chrysemys picta</i>	Exotic	LC		N America	
Reptilia	Testudines	<i>Clemmys guttata</i>	Exotic	EN		N America	II
Reptilia	Testudines	<i>Cuora amboinensis</i>	Exotic	EN		SE Asia	II
Reptilia	Testudines	<i>Cuora flavomarginata</i>	Native	EN	CR	CN	II
Reptilia	Testudines	<i>Cuora galbinifrons</i>	Native	CR	CR	CN	II

Reptilia	Testudines	<i>Cuora mouhotii</i>	Native	CR	CR	CN	II
Reptilia	Testudines	<i>Cuora trifasciata</i>	Native	CR	CR	CN	II
Reptilia	Testudines	<i>Cyclemys dentata</i>	Exotic	NT		SE Asia	II
Reptilia	Testudines	<i>Emydura subglobosa</i>	Exotic	LC		Oceania	
Reptilia	Testudines	<i>Geochelone elegans</i>	Exotic	VU		SE Asia	II
Reptilia	Testudines	<i>Geochelone platynota</i>	Exotic	CR		SE Asia	I
Reptilia	Testudines	<i>Geoclemys hamiltonii</i>	Exotic	EN		SE Asia	I
Reptilia	Testudines	<i>Geoemyda spengleri</i>	Native	EN	EN	CN	II
Reptilia	Testudines	<i>Graptemys</i>	Exotic	LC		N America	III
		<i>pseudogeographica</i>					
Reptilia	Testudines	<i>Heosemys annandalii</i>	Exotic	EN		SE Asia	II
Reptilia	Testudines	<i>Heosemys grandis</i>	Exotic	VU		SE Asia	II
Reptilia	Testudines	<i>Heosemys spinosa</i>	Exotic	EN		SE Asia	II
Reptilia	Testudines	<i>Indotestudo elongata</i>	Native	CR	CR	CN	II
Reptilia	Testudines	<i>Kinosternon leucostomum</i>	Exotic	NA		S America	
Reptilia	Testudines	<i>Kinosternon scorpioides</i>	Exotic	NA		S America	

Reptilia	Testudines	<i>Macrochelys temminckii</i>	Exotic	VU		N America	III
Reptilia	Testudines	<i>Malaclemys terrapin</i>	Exotic	VU		N America	II
Reptilia	Testudines	<i>Malayemys subtrijuga</i>	Exotic	VU		SE Asia	II
Reptilia	Testudines	<i>Manouria impressa</i>	Native	VU	CR	CN	II
Reptilia	Testudines	<i>Mauremys annamensis</i>	Exotic	CR		SE Asia	III
Reptilia	Testudines	<i>Mauremys mutica</i>	Native	EN	EN	CN	II
Reptilia	Testudines	<i>Mauremys nigricans</i>	Native	EN	CR	CN	II
Reptilia	Testudines	<i>Mauremys reevesii</i>	Native	EN	EN	CN	III
Reptilia	Testudines	<i>Mauremys sinensis</i>	Native	EN	EN	CN	III
Reptilia	Testudines	<i>Melanochelys tricarinata</i>	Exotic	EN		SE Asia	I
Reptilia	Testudines	<i>Melanochelys trijuga</i>	Exotic	LC		SE Asia	II
Reptilia	Testudines	<i>Pelodiscus sinensis</i>	Native	VU	EN	CN	
Reptilia	Testudines	<i>Pelusios castaneus</i>	Exotic	NA		Africa	
Reptilia	Testudines	<i>Phrynops hilarii</i>	Exotic	NA		S America	
Reptilia	Testudines	<i>Platysternon megacephalum</i>	Native	EN	CR	CN	I

Reptilia	Testudines	<i>Podocnemis unifilis</i>	Exotic	VU		S America	II
Reptilia	Testudines	<i>Pseudemys alabamensis</i>	Exotic	EN		N America	
Reptilia	Testudines	<i>Pseudemys concinna</i>	Exotic	LC		N America	
Reptilia	Testudines	<i>Pseudemys peninsularis</i>	Exotic	LC		N America	
Reptilia	Testudines	<i>Sacalia bealei</i>	Native	EN	EN	CN	II
Reptilia	Testudines	<i>Staurotypus salvinii</i>	Exotic	NT		S America	
Reptilia	Testudines	<i>Sternotherus carinatus</i>	Exotic	LC		N America	
Reptilia	Testudines	<i>Sternotherus odoratus</i>	Exotic	LC		N America	
Reptilia	Testudines	<i>Stigmochelys pardalis</i>	Exotic	LC		Africa	II
Reptilia	Testudines	<i>Testudo graeca</i>	Exotic	VU		Europe	II
Reptilia	Testudines	<i>Testudo hermanni</i>	Exotic	NT		Europe	II
Reptilia	Testudines	<i>Trachemys elegans</i>	Exotic	LC		N America	

Appendix VIII. Commonly traded reptiles and amphibians in China's supply trade.

Class	Taxonomic Order	Species	Native Status	IUCN	China's Red List	Geographic Origin	CITES Appendix Listig
Amphibia	Anura	<i>Bombina bombina</i>	Exotic	LC		Europe	
Amphibia	Anura	<i>Bombina orientalis</i>	Native	LC	LC	CN	
Amphibia	Anura	<i>Bombina sp.</i>	Native	–	–	CN	
Amphibia	Anura	<i>Hyla sp.</i>	Native	–	–	CN	
Amphibia	Anura	<i>Hymenochirus boettgeri</i>	Exotic	LC		Africa	
Amphibia	Anura	<i>Hymenochirus boulengeri</i>	Exotic	DD		Africa	
Amphibia	Anura	<i>Hymenochirus curtipes</i>	Exotic	LC		Africa	
Amphibia	Anura	<i>Hymenochirus sp.</i>	Exotic	–		Africa	
Amphibia	Anura	<i>Xenopus laevis</i>	Exotic	LC		Africa	
Amphibia	Anura	<i>Xenopus sp.</i>	Exotic	–		Africa	
Amphibia	Caudata	<i>Cynops orientalis</i>	Native	LC	NT	CN	
Amphibia	Caudata	<i>Cynops pyrrhogaster</i>	Exotic	LC		SE Asia	
Amphibia	Caudata	<i>Cynops sp.</i>	Native	–	–	CN	

Amphibia	Caudata	<i>Pachytriton brevipes</i>	Native	LC	LC	CN	
Amphibia	Caudata	<i>Pachytriton sp.</i>	Native	–	–	CN	
Amphibia	Caudata	<i>Paramesotriton chinensis</i>	Native	LC	NT	CN	II
		<i>Paramesotriton</i>					
Amphibia	Caudata	<i>hongkongensis</i>	Native	NT	NT	CN	II
Amphibia	Caudata	<i>Paramesotriton labiatus</i>	Native	N	VU	CN	
Amphibia	Caudata	<i>Paramesotriton sp.</i>	Native	–	–	CN	II
Amphibia	Caudata	<i>Tylototriton verrucosus</i>	Native	LC	NT	CN	II
Reptilia	Sauria	<i>Diploderma sp.</i>	Native	–	–	CN	
Reptilia	Sauria	<i>Diploderma splendidum</i>	Native	N	LC	CN	
Reptilia	Sauria	<i>Eremias sp.</i>	Native	–	–	CN	
Reptilia	Sauria	<i>Lacerta sp.</i>	Native	–	–	CN	
Reptilia	Sauria	<i>Takydromus sp.</i>	Native	–	–	CN	
Reptilia	Sauria	<i>Teratoscincus scincus</i>	Native	LC	EN	CN	
Reptilia	Serpentes	<i>Elaphe taeniura</i>	Native	N	EN	CN	
Reptilia	Serpentes	<i>Oocatochus rufodorsatus</i>	Native	LC	LC	CN	

		<i>Graptemys</i>					
Reptilia	Testudines	<i>pseudogeographica</i>	Exotic	LC		N America	III
Reptilia	Testudines	<i>Graptemys</i> sp.	Exotic	–		N America	III
Reptilia	Testudines	<i>Graptemys versa</i>	Exotic	LC		N America	III
Reptilia	Testudines	<i>Mauremys reevesii</i>	Native	EN	EN	CN	III
Reptilia	Testudines	<i>Mauremys sinensis</i>	Native	EN	EN	CN	III
Reptilia	Testudines	<i>Palea steindachneri</i>	Native	EN	EN	CN	II
Reptilia	Testudines	<i>Stigmochelys pardalis</i>	Exotic	LC		Africa	II
Reptilia	Testudines	<i>Testudinidae</i> sp.	Exotic	–	–	NA	II
Reptilia	Testudines	<i>Trachemys scripta</i>	Exotic	LC		N America	

Figure 1. Temporal development of herpetoculture in China. (A) Number of herpetoculturists and herpetofauna pet shops in China based on questionnaire surveys; (B) number of confiscation cases entering China based on CITES database and online survey; (C) number of breeders and species being bred in Mainland China based on questionnaire survey. Photos of animals by Pingzhao Luo, Yuchao Ji, and Xijing Cao. Photos of reptile expo taken from WeChat post by rly 的自然世界.

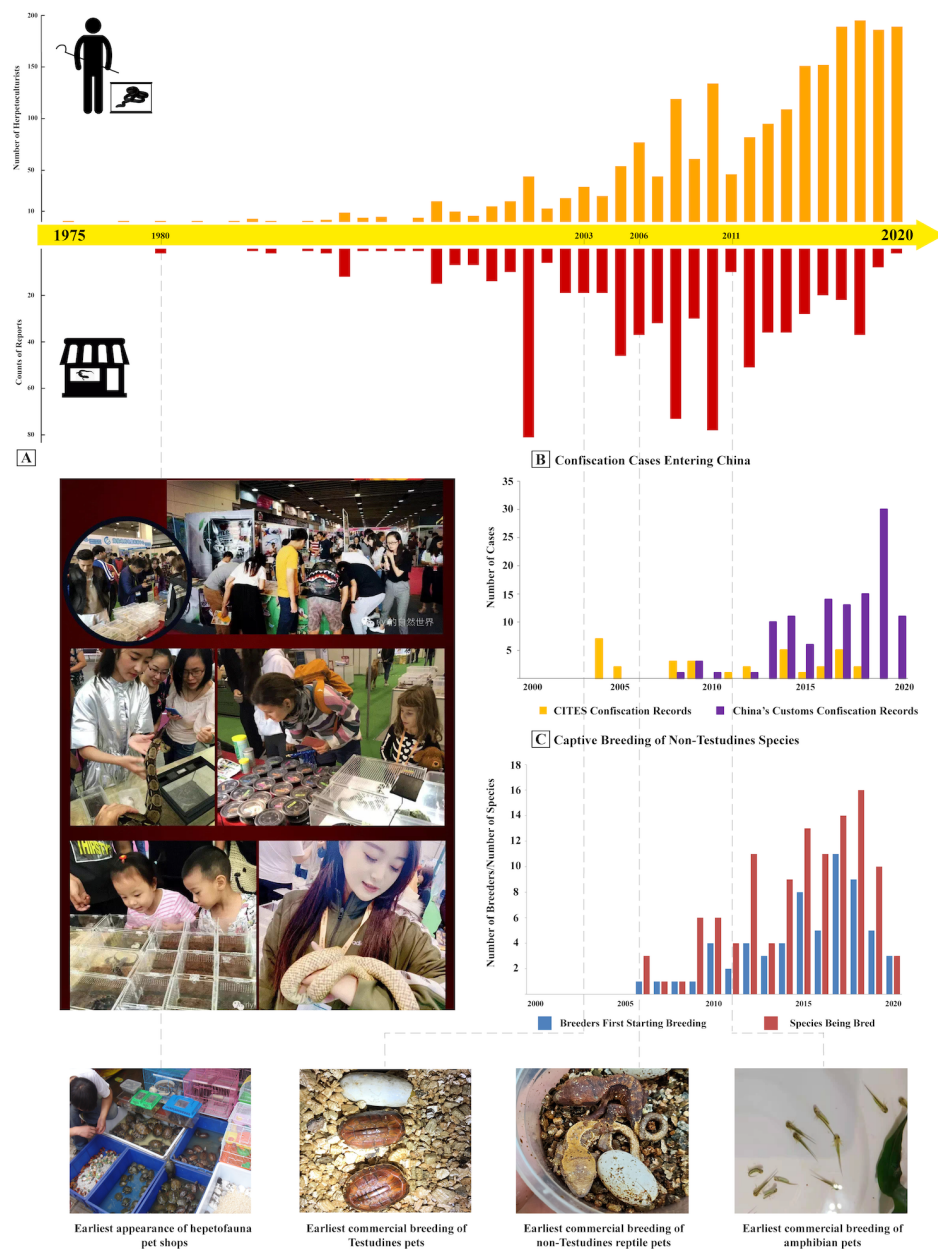


Figure 2. Global distribution and trade statistics of trading partners of China on herpetofauna pet trade based on CITES database between 2000 and 2019. Figure only depicts international trade and does not include domestic trade among major regions of China.

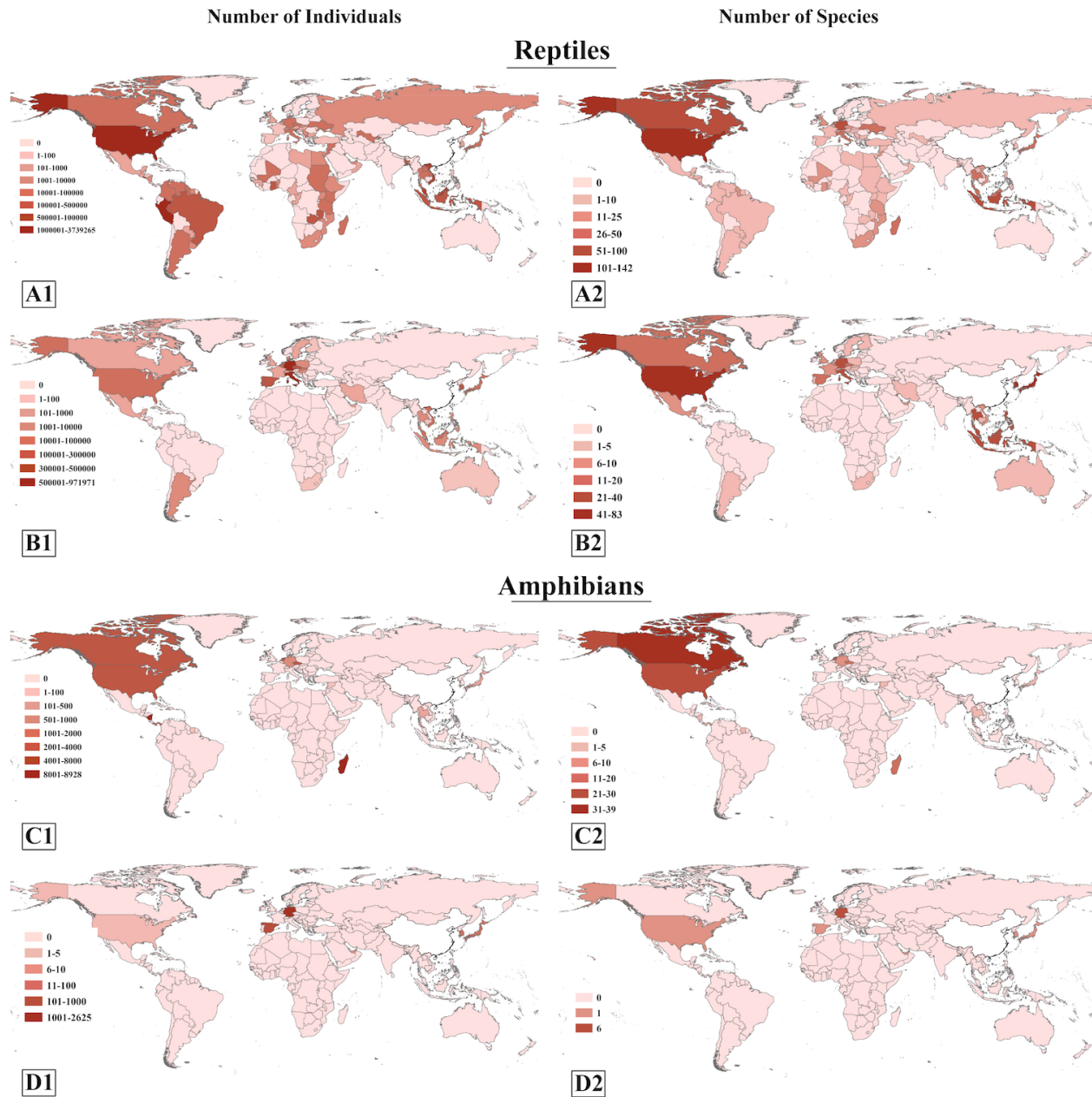


Figure 3. Taxonomic diversity in China's herpetofauna pet trade. Relative size of the Venn diagram indicates relative number of species in each category.

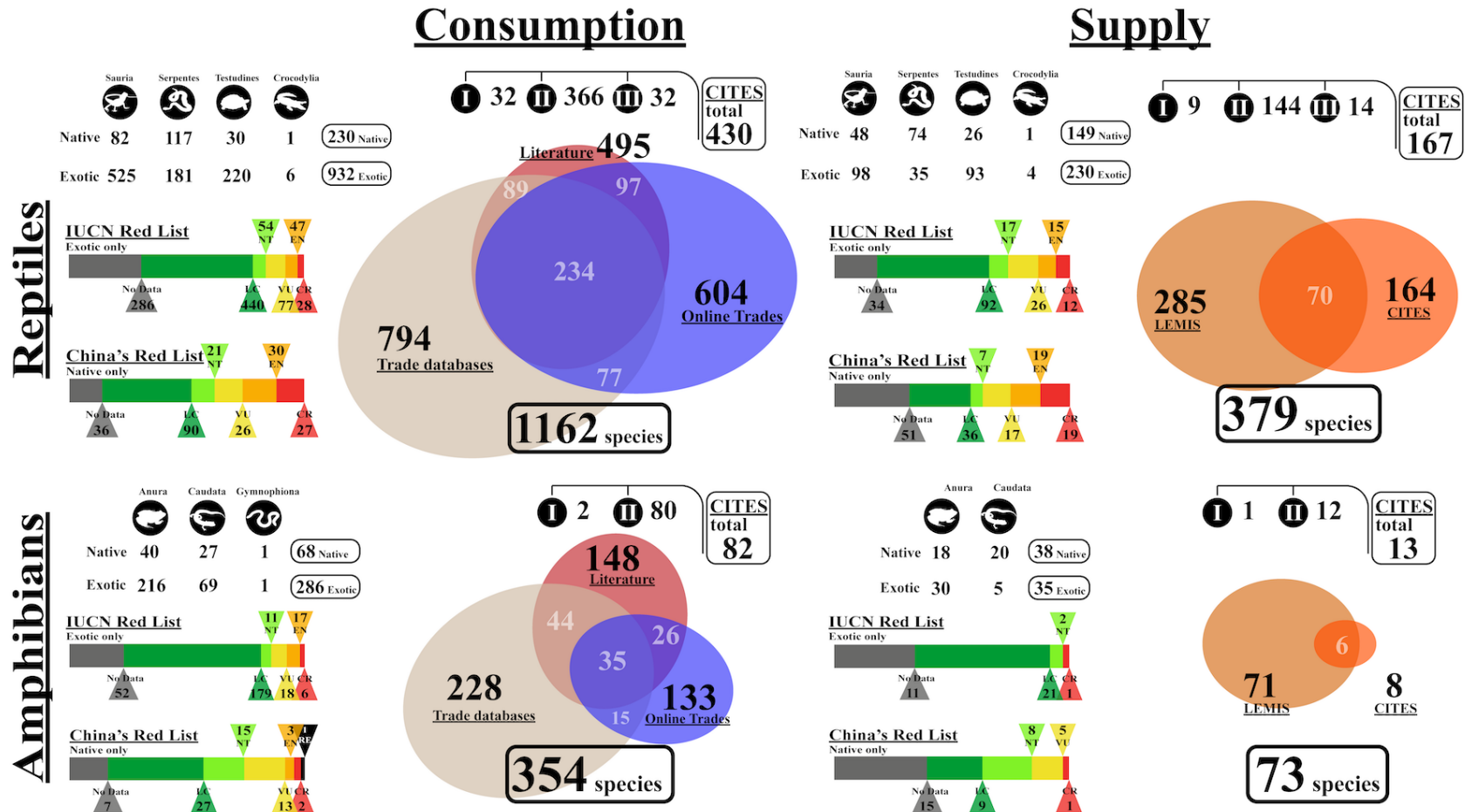


Figure 4. Temporal changes of China's international herpetofauna pet trade based on LEMIS and CITES database. For the data on diversity, star symbols indicate a regression slope that is significantly different from zero.

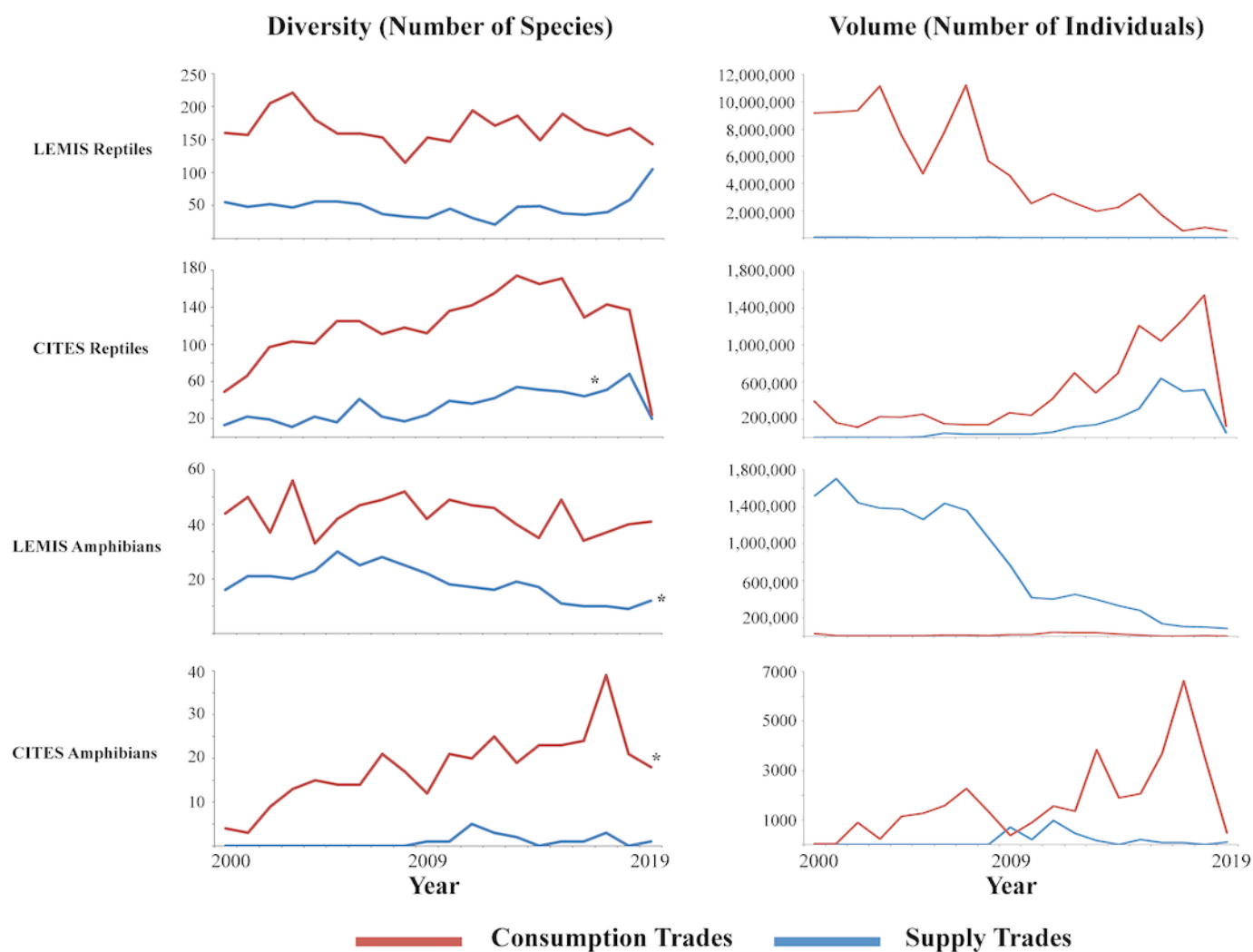


Figure 5. Legality of China’s herpetofauna pet trade. (A) Results from questionnaire surveys on the legality of herpetoculture practice in Mainland China; (B) prevalence of trafficking on CITES exotic species in China’s consumption trade based on the comparison between CITES legal import records, confiscation records, and diversity present in China’s domestic trade; (C) prevalence of trafficking of protected native species in in China.

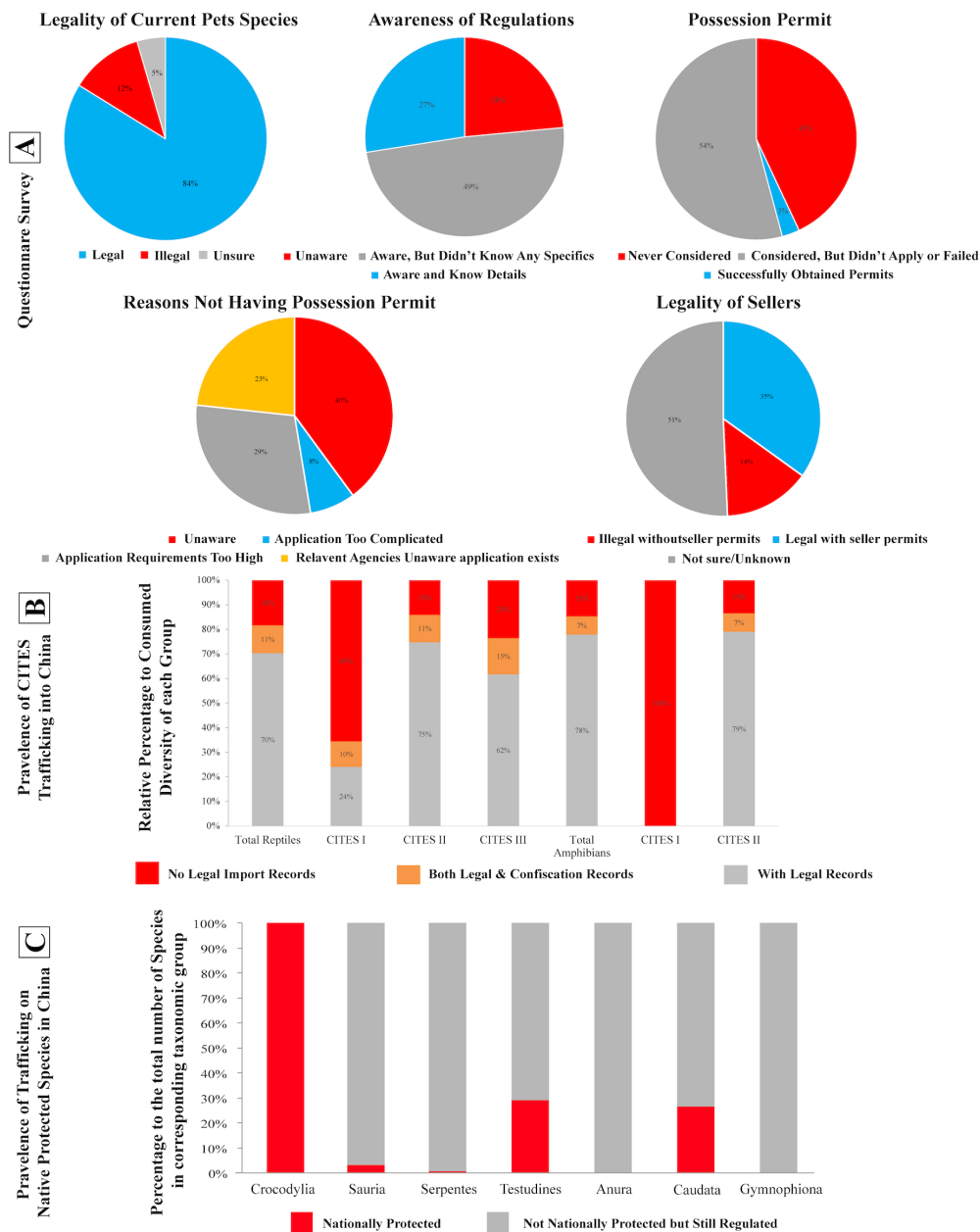


Figure 6. Regional differences in the international trade of herpetofauna pets among the major political regions of China. MC: Mainland China; HK: Hong Kong; TW: Taiwan; MO: Macao.

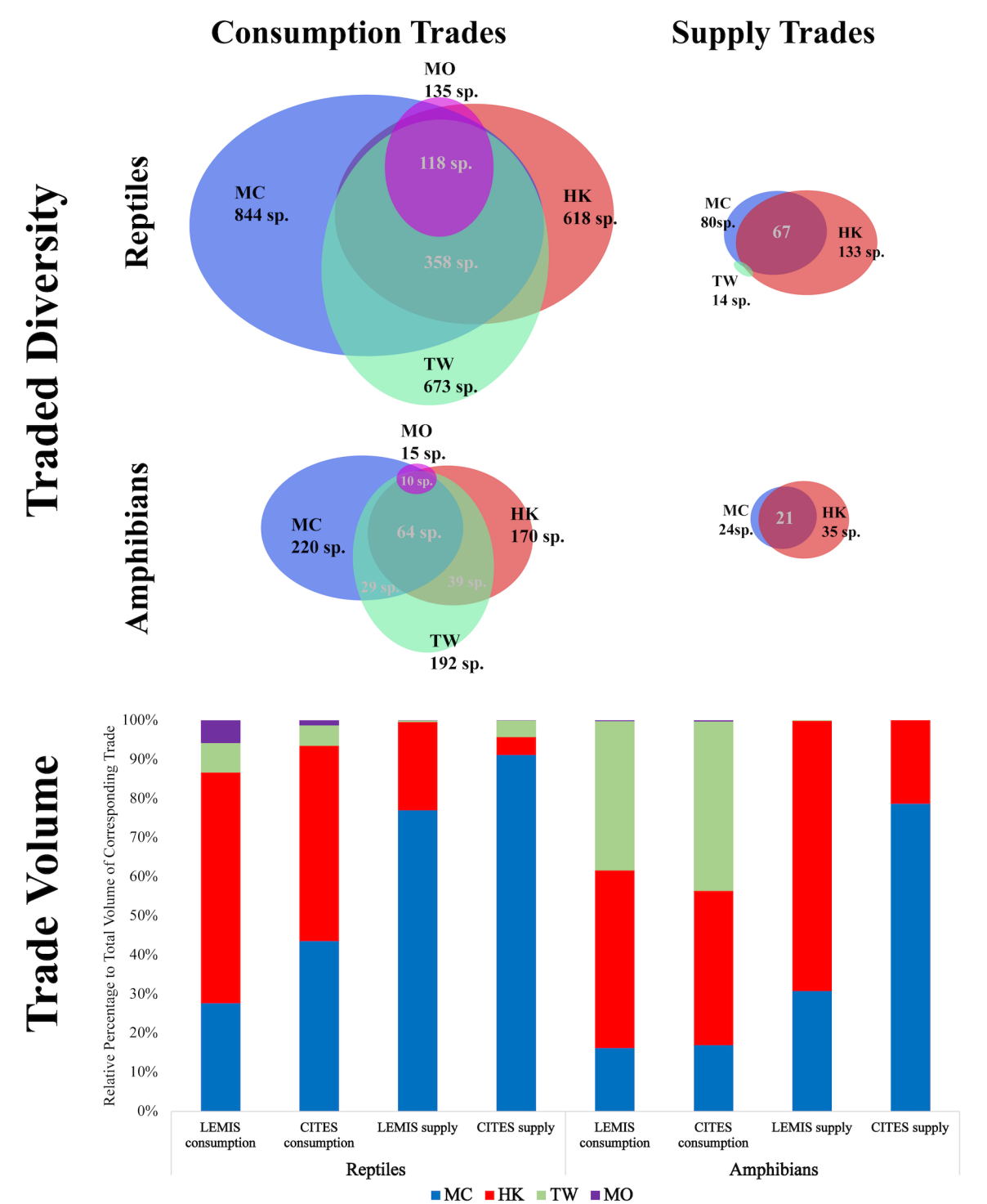


Figure 7. Characteristics of herpetofauna trafficking into China. Trafficking data were from online survey (2008–2020) and international trade databases (CITES and LEMIS, 2000–2019). Distribution of herpetoculturists were based of online questionnaire of 2,248 people.

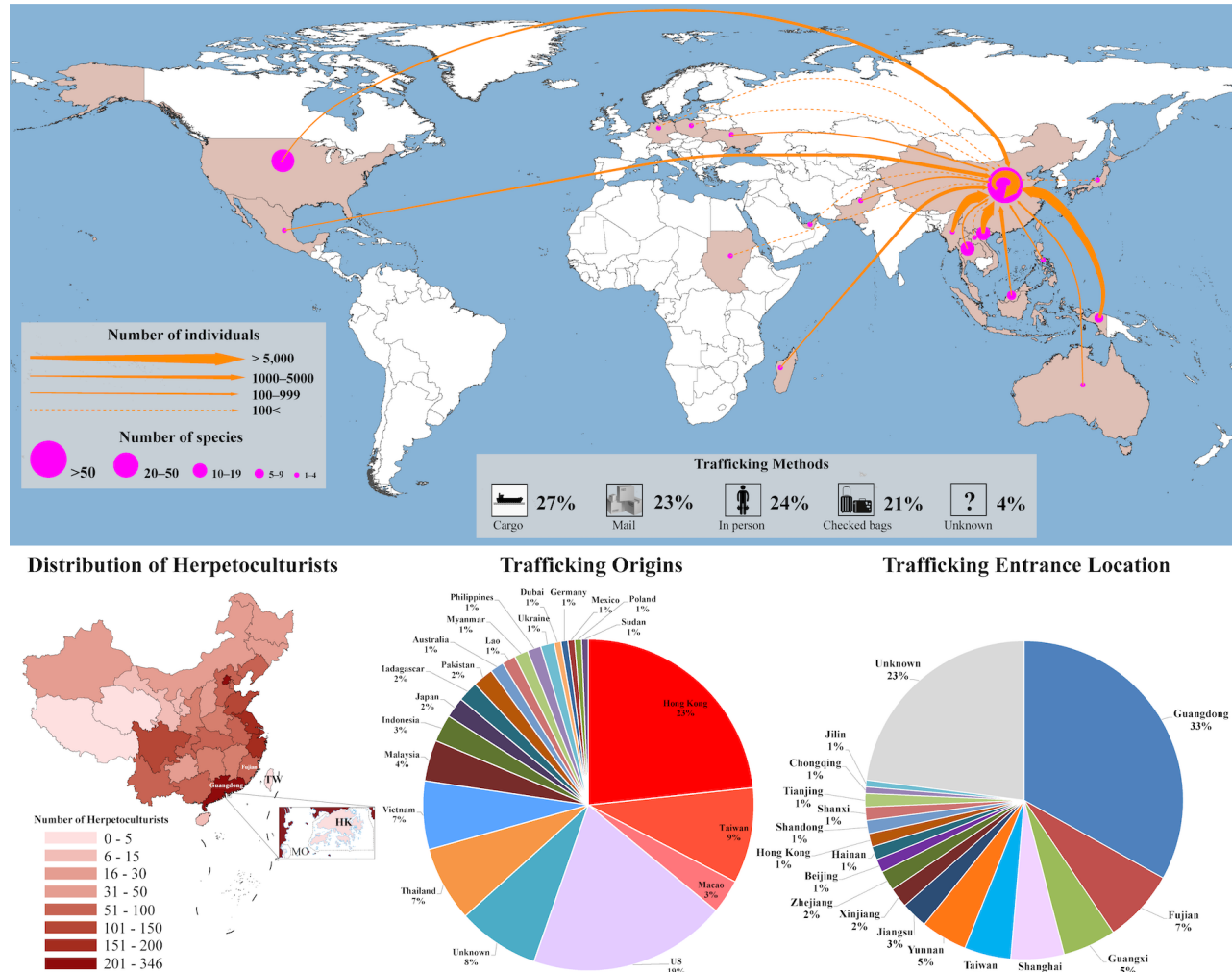


Figure 8. Geographic origins of traded exotic and native species in China's herpetofauna pet trade.

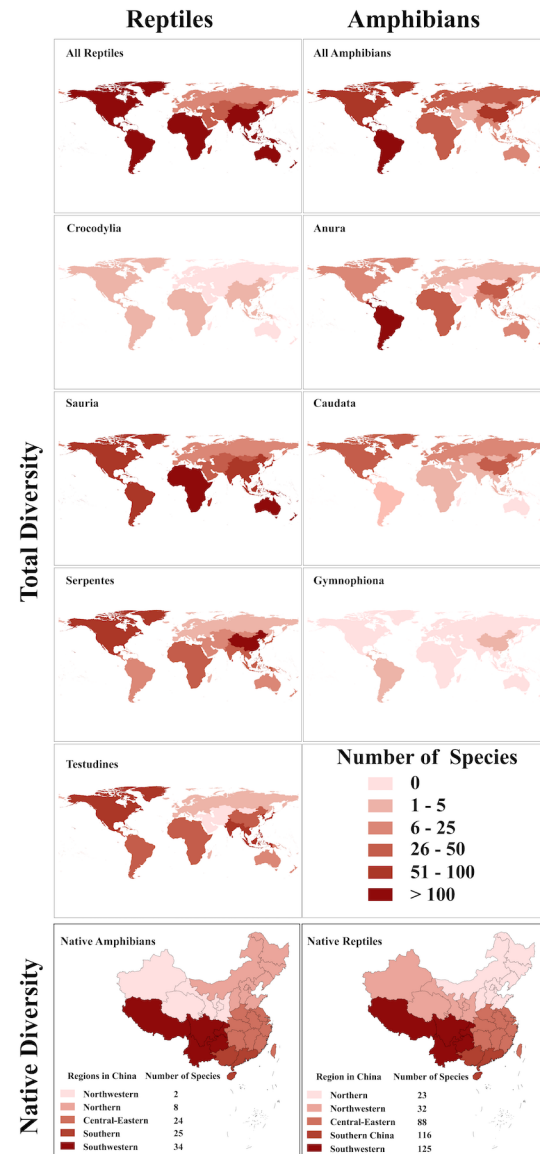


Figure 9. Conservation Statuses of traded species in China's herpetofauna pet trade by major taxonomic orders. Specific of commonly traded species see Appendix VII and VIII.

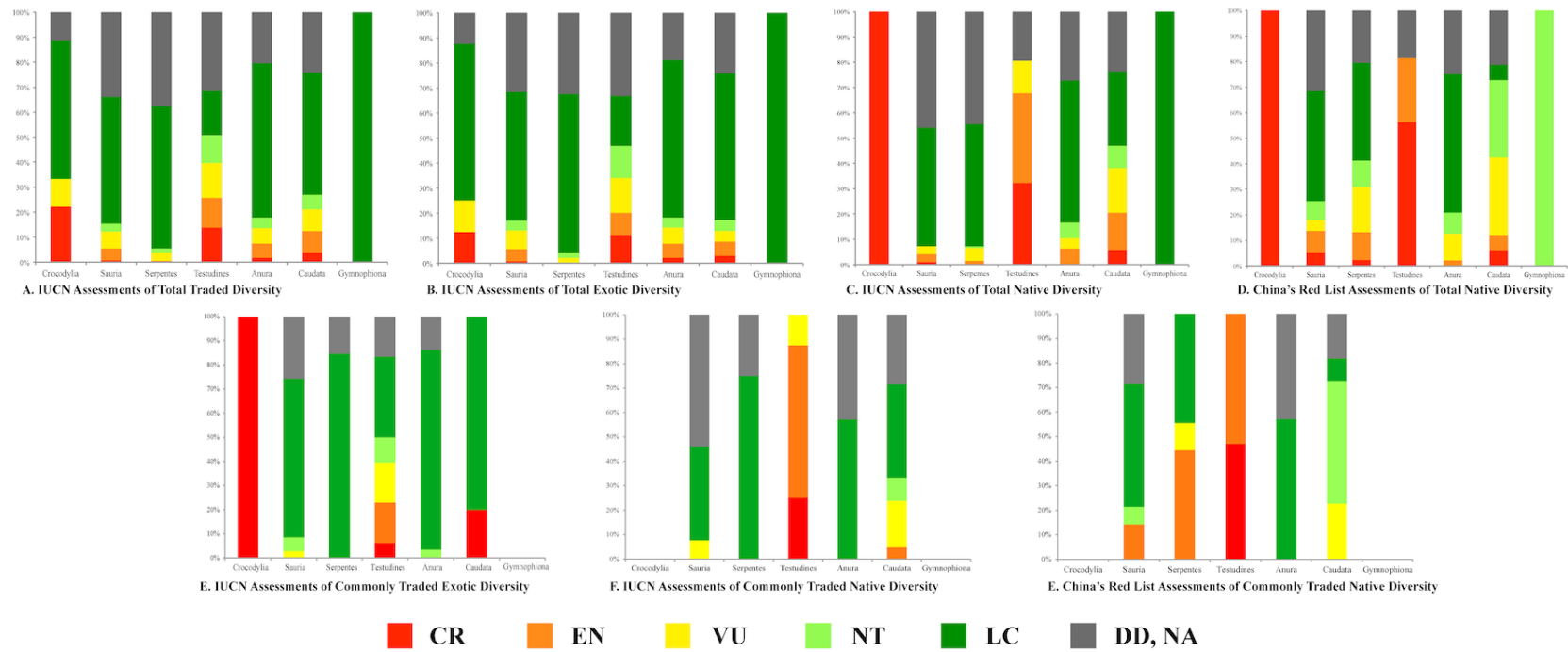


Figure 10. Origins of traded herpetofauna species based on international traded databases. Relative size of rectangles in treemap indicate the relative number of individuals belong to each category of origin. C: captive born; D: commercially bred; F: farmed; I: confiscation; R: ranched; NA: not available; O: pre-CITES convention; U: unknown; W: wild caught.

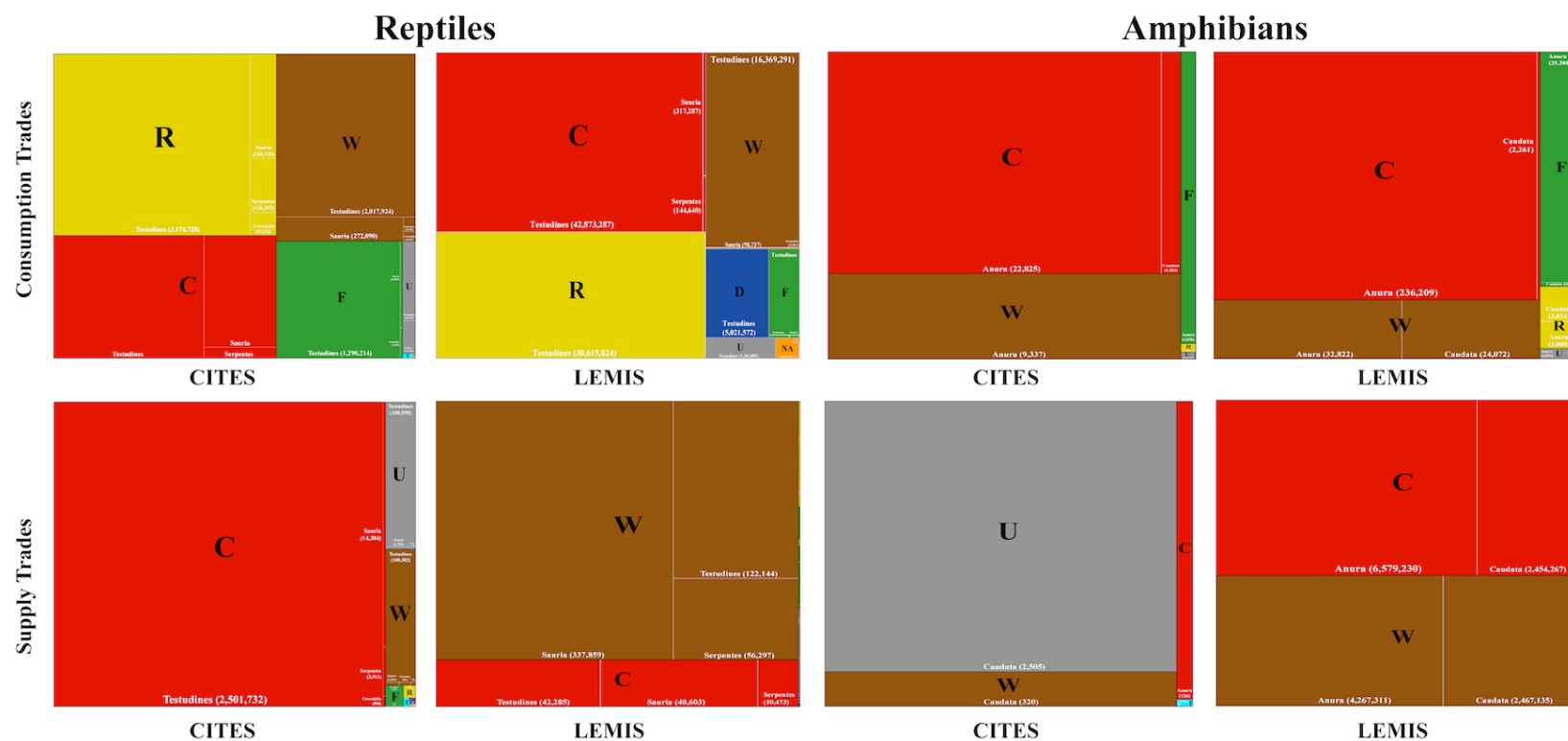


Figure 11. Taxonomic coverage of major orders in China's herpetofauna pet trade to the world's total diversity and to China's total native diversity.

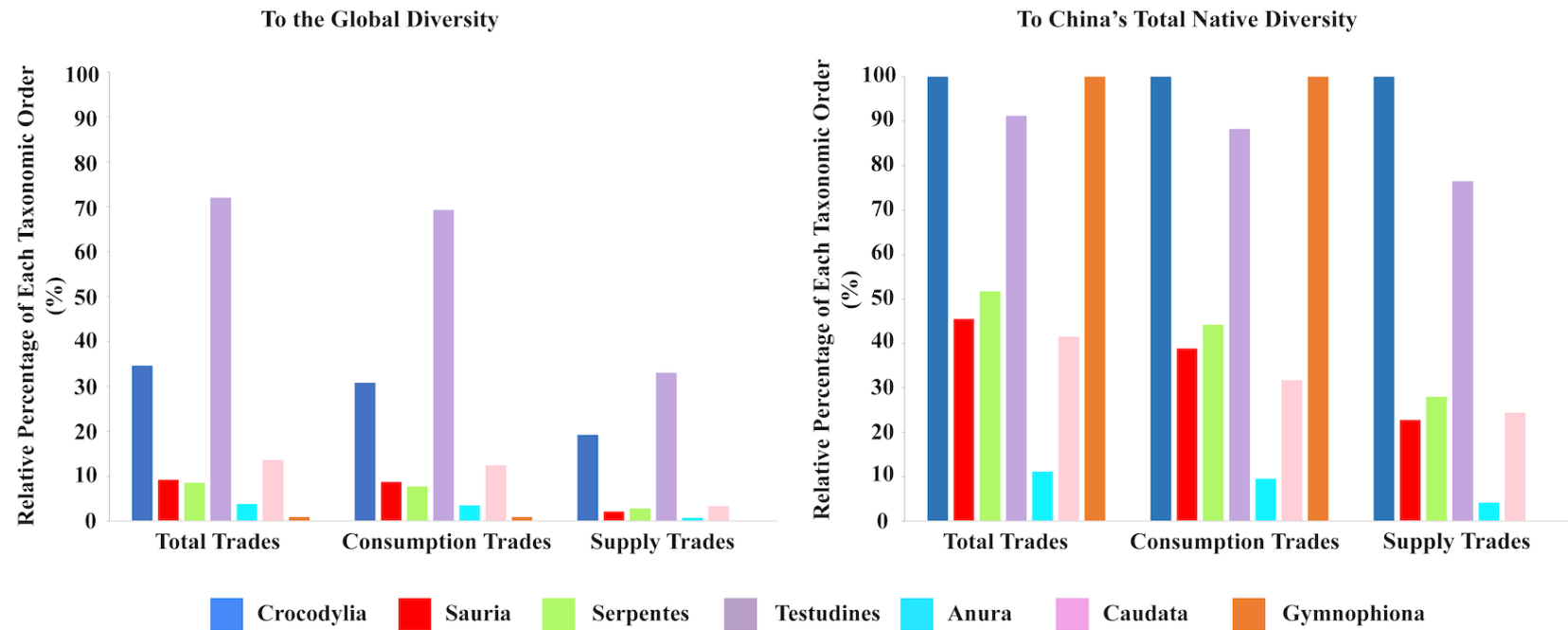


Figure 12. Volumes of major taxonomic orders in China's international pet trade based on LEMIS and CITES databases.

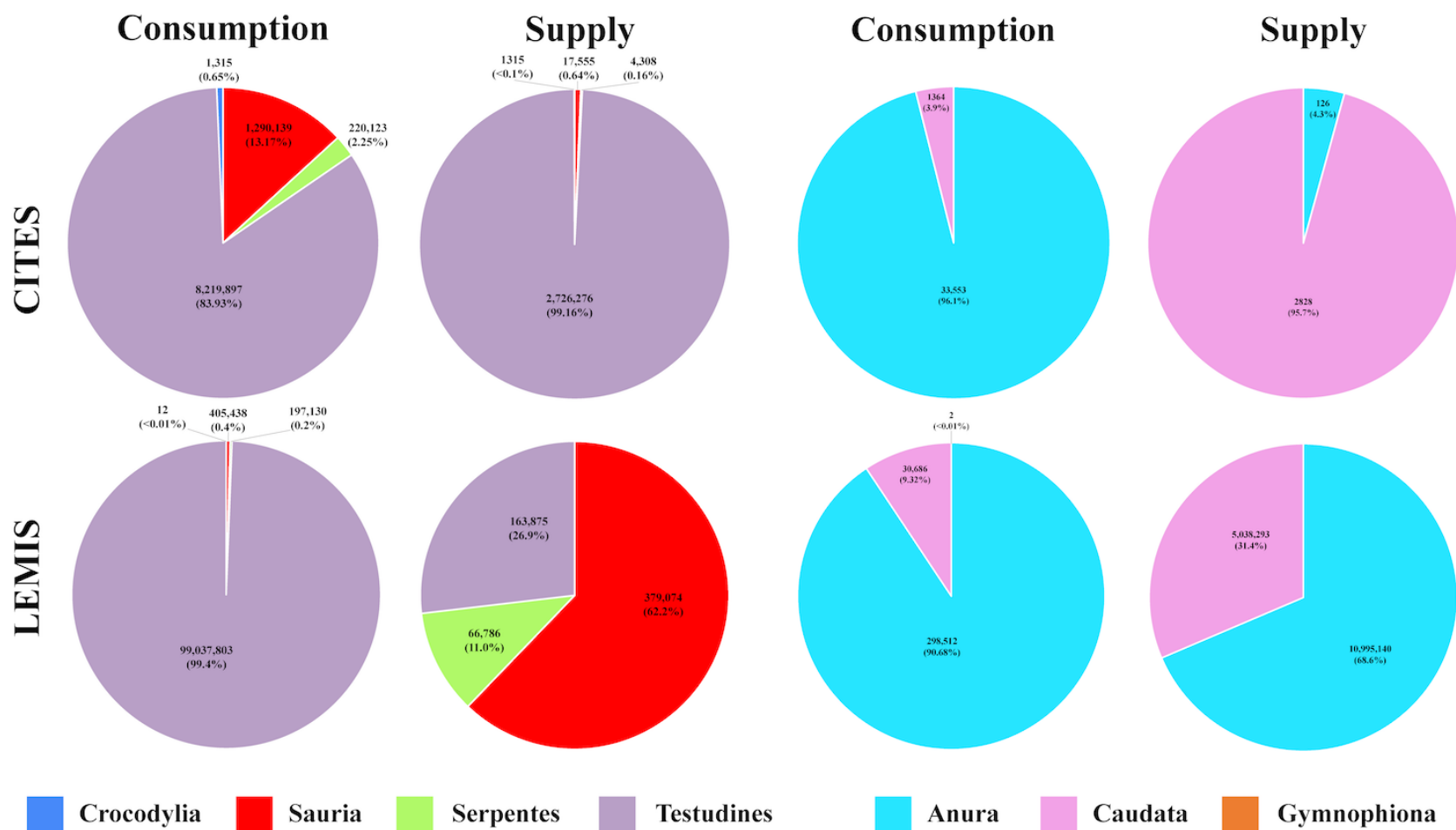


Figure S1. Temporal changes of the international herpetofauna pet trade by major political regions of China based on LEMIS and CITES database.

