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PHYLOGENETIC RELATIONSHIPS, TAXONOMIC REVISION, AND
CONSERVATION OF MOUNTAIN DRAGONS OF THE GENUS *JAPALURA*
SENSU LATO FROM ASIA

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PHYLOGENETIC RELATIONSHIPS, TAXONOMIC REVISION, AND
CONSERVATION OF MOUNTAIN DRAGONS OF THE GENUS *JAPALURA*
SENSU LATO FROM ASIA

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余自童稚无由痴迷鳞虫，立志精研鳞甲分类。笼养异物以为好，甚有毒蛇以伴。其痴之甚，弱冠之年噬于毒蛇亦未改。遗恨国中教统老旧，学体之昧，常视以为另类尽遭耻笑。实幸家人虽不以为好，仍助稚愿，励余追梦十余载：束发之年家父置首书，滇之虫蛇尽开眼界；家母弃业离家以为余学，离乡泊夷只为创机，使吾能钻研蛇虫以为业。更幸巧遇良师益友，蒋兄提携引吾入业，耘珂、金龙、智勇一路相辅，良师车静鼎力支持，门学书院之师创机传授，同行提意指教，嵩阳院所布泉相助。今初业乃拜于此，承蒙以上之助，余不甚感激。

游离大洋两岸，研学之辛难以言表。局之所致非余所能控，迫弃人之所常，愧友诸多，殊颜由甚。结业之际且又历辛酸，悲抑难解，稠整问己。幸得师长良友疏导，思通会悟。感恩伴侣相伴之时，所伴之助，乃至相离之痛，终促蜕变成长。豆蔻之年亦能相伴，时光虽短，余之幸也。自幼寻梦，均为儿时宏愿，途中所历艰难终助完人，实为经历。

或为鳞虫，或为稚梦，勿忘初衷。

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Abstract

Mountain Dragons of the genus *Japalura sensu lato* (*sensu lato* means “in the broad sense”) are small-to-medium sized, insectivore lizards of the family Agamidae. Although similar to the Iguanaian lizards of the New World in external morphology, members of the genus *Japalura sensu lato* are found in Asia only, and have a distribution from eastern Pakistan along the Himalaya to Southwest China, and eventually reaching the Okinawa islands of Japan. Being one of the most diverse genera in the family, the genus currently consists of 34 recognized species. Such a wide-distributional range across major geological features (e.g. the Himalaya, Tibetan Plateau, and East Asian island archipelagos) and high species diversity make *Japalura sensu lato* a great potential system for evolutionary and biogeographic studies.

However, despite such great potential as a study system, little research has been done on the group, mostly due to its problematic and unresolved taxonomy. Although the genus *sensu lato* has long been recognized as paraphyletic based on limited genetic sampling, its taxonomy has not been revised, and phylogenetic relationships among the majority of congeners remain unknown. In addition, species diversity in southwest China has continued to be underestimated, where cryptic diversities are overlooked, resulting in a large species complex. Lastly, with the current problematic taxonomy, most congeners lack accurate conservation assessments, despite the great conservation threats that they face from landscape changes and habitat destruction.

For my first chapter, I utilize a densely sampled data set of both multilocus genetic and morphological data to provide the first phylogenetic inference of relationships among *Japalura sensu lato* species. My results show that members of

Japalura sensu lato are polyphyletic, consisting of four major clades that are scattered across the phylogeny of the subfamily Draconinae: the first clade from the western, central, and middle-eastern Trans-Himalaya, the second clade from the far eastern Trans-Himalaya, the third clade containing species from East Asia, and the last clade from Indochina. To address the widespread paraphyly of *Japalura sensu lato* and to stabilize the taxonomy within the family Draconinae, we revise the current taxonomy and split *Japalura sensu lato* into four genera, including two recognized generic names, *Japalura sensu stricto* and *Pseudocalotes*, one resurrected nomenclature, *Diploderma*, and one new genus. Following our revised taxonomy, we provided morphological diagnostic keys to all species of each of the four genera from *Japalura sensu lato*, and we discussed phylogenetic relationships, taxonomy at both generic and species levels, and the general biogeography of *Japalura sensu lato*.

For my second chapter, I focus on the East Asian clade of *Japalura sensu lato*, which is the genus *Diploderma* after my taxonomic revision, and I investigate the species level diversity of the genus in Southwest China, particularly along the rich fluvial systems of the Hengduan Mountain Region, east of the Tibetan Plateau. Despite being recognized as ecologically and biogeographically important, the biodiversity of the Hengduan Mountain Region, particularly along the upper Mekong and Yangtze River, remains poorly understood. Using morphological evidence, I describe three new species of Mountain Dragon in the genus *Diploderma* Hallowell, 1861 from the upper reaches of the Mekong and Yangtze Rivers in Tibet Autonomous Region, Sichuan Province, and Yunnan Province of China. These species are recognized as members of the *Diploderma flaviceps* (Barbour & Dunn 1919) complex, but they can be distinguished readily from all congeners by a suite

of distinct morphological characteristics. In addition to the descriptions of new species, I also report morphological variations and range extensions of three recently described congeners, namely *D. batangense*, *D. iadinum*, and *D. vela*. I discussed the distribution patterns of the genus and the urgent conservation priorities for protecting *Diploderma* species in the Hengduan Mountain Region. According to the best available population and habitat data from my field surveys, I provide IUCN assessments for all recognized species of the genus in the Hengduan Mountain Region and propose listings of all congeners as nationally protected under the Chinese Wildlife Protection Act.

Chapter 1: Introduction

Despite the progress that the field of biological sciences has made in the past decade, an ironic dilemma remains true: we still do not know much about the biodiversity around us (Godfray & Knapp 2004). To date, most extant biodiversity has yet to be described or cataloged; and for those taxa that have been described, we know very little about their general biology, including natural history, evolutionary relationships, and conservation status (Mace 2004; Agnarsson & Kuntner 2007; May 2011). This lack of knowledge on the most fundamental aspect of biology not only delays potential progress in various scientific fields, but also, it creates a particularly serious problem given that we are experiencing the “sixth great extinction”: how can we monitor the loss of biodiversity and protect our environments if we do not know what is out there?

Such a dilemma is particularly true for many biodiverse yet understudied regions in Asia. Although Eastern, Southern, and Southeastern Asia harbor a great number of global biodiversity hotspots (Mittermeier *et al.* 2011; Hughes 2017), the taxonomic diversity of most biota in these regions remain understudied, and they all face increasing anthropogenic pressures from regional economic growth and global climate changes (Sodhi & Liow 2000; Sodhi *et al.* 2004). To conserve the unique biodiversity in Asia, there is a stronger need for taxonomic research than ever before.

Of the vertebrate animals in Asia, lizards of the genus *Japalura sensu lato* Gray, 1831 (Reptilia: Squamata: Agamidae) represent a good example of a threatened yet poorly understood group. Commonly known as Mountain Dragons, *Japalura sensu lato* is one of the most species-rich and widespread genera in the family Agamidae. Currently containing 34 recognized species, the genus is distributed across a wide

and diverse geographic area, from the tropical forests of southern Himalaya, to deep parallel river valleys in Eastern Tibet, and finally to island archipelagos of Taiwan and Japan (Figure 1-1; Moody, 1980; Uetz & Hallermann, 2017; Wang *et al.* 2016; 2017). In response to diverse habitats, species of *Japalura* have evolved distinct ecomorphologies, varying from small, terrestrial, valley-dwelling forms, to large, arboreal, forest-specialist forms (Zhao *et al.* 1999; Figure 1-2). Particularly, most species in the Hengduan Mountain Region (HMR) of Southwest China are micro-endemic valley dwellers, where each species is closely affiliated with a specific section of the river valley, sympatric to congeners along the same river but isolated by continuous mountain peaks from allopatric congeners in nearby rivers valleys (Wang *et al.* 2016). Such high species diversity, diverse ecologies, and the close affiliation with major geological features make the group an ideal system to investigate evolutionary and biogeographic questions (Wang *et al.* 2015, 2016). Furthermore, species of *Japalura sensu lato* are exploited heavily for the global pet trade, and their native habitats overlap greatly with human developments (e.g. hydropower developments and road construction in the HMR of China) and face direct threats from global warming (e.g. oceanic island archipelagos of Taiwan and Japan) (Rahmstorf 2007).

However, despite the fact that Mountain Dragons represent an ideal system to tackle interesting biological questions, and are facing great conservation threats, none of this research has been undertaken, in large part due to the group's unresolved taxonomy and understudied phylogenetic relationships. Based on limited phylogenetic studies on five of the 34 recognized species, the genus appears to be paraphyletic with respect to other genera, containing at least two deeply divergent clades (Macey *et al.* 2000; Pyron *et al.* 2013). Yet all members of *Japalura sensu*

lato are still recognized as a single genus to date, despite the fact that the current taxonomy does not reflect the evolutionary history of its members (Rao *et al.* 2017; Wang *et al.* 2017). Furthermore, with limited active research ongoing, species-level diversity of the genus, particularly in the mountain-river systems in Southwest China, remains underestimated. Cryptic diversity has been overlooked, with several species complexes treated as a single, widespread lineage (Hu *et al.* 1987; Zhao *et al.* 1999; Manthey *et al.* 2012; Wang *et al.* 2016). Such taxonomic confusion and misidentification of endemic lineages have resulted in misleading conservation assessments (Zhao *et al.* 1999; Yu *et al.* 2005; Zhang *et al.* 2010; Manthey & Xie 2011), which in turn have led to inappropriate evaluations of the environmental impact of construction activities throughout the region (Northwest Engineering Corporation Lt. 2013).

The goal of my thesis research is to clarify the long-standing issues concerning the taxonomy of *Japalura sensu lato*, and provide informed guidelines to the conservation of Mountain Dragons and their native habitat in Southwest China. Particularly, my work aims to: (1) clarify generic-level taxonomy and phylogenetic relationships of *Japalura sensu lato* with respect to other Draconinae genera; (2) revise the species-level taxonomy of the Chinese clade in Southwest China and describe cryptic diversity of the region; and (3) assess the conservation status of species from Southwest China based on field surveys and provide conservation recommendations.

Chapter 2: Multilocus Phylogeny and Revised Classification of *Japalura sensu lato* (Reptilia: Agamidae: Draconinae) from Asia

Abstract

Although Mountain Dragons of the genus *Japalura sensu lato* have long been recognized as paraphyletic based on limited genetic sampling, its problematic taxonomy has not been revised, and phylogenetic relationships among the majority of congeners remain unknown. Here we utilize a densely sampled data set of both multilocus genetic and morphological data to provide the first phylogenetic inference of relationships among *Japalura sensu lato* species. Our results show that members of *Japalura sensu lato* are polyphyletic, consisting of four major clades that are scattered across the phylogeny of the subfamily Draconinae: the first clade from the western, central, and middle-eastern Trans-Himalaya, the second clade from the far eastern Trans-Himalaya, the third clade containing species from East Asia, and the last clade from Indochina. To address the widespread paraphyly of *Japalura sensu lato* and to stabilize the taxonomy within the family Draconinae, we revise the current taxonomy and split *Japalura sensu lato* into four genera, including two recognized generic names, *Japalura sensu stricto* and *Pseudocalotes*, one resurrecting nomenclature, *Diploderma*, and one new genus *GenusXXX* gen. nov.. Following our revised taxonomy, we provided morphological diagnostic keys to all four genera from *Japalura sensu lato*, and we discussed phylogenetics relationships, taxonomy at both generic and species levels, and the general biogeography of *Japalura sensu lato*.

Introduction

With extreme ecological and morphological variations from winged, gliding arboreal ecomorph to spiny, desert specialist, lizards of the Old World family Agamidae have long fascinated biologists (Smith, 1935; Moody, 1980). In the family Agamidae, dragon lizards of the subfamily Draconinae represent a remarkable radiation of reptiles distributed throughout Asia, with more than 214 species recognized (Pyron *et al.*, 2013; Grismer *et al.*, 2016; Uetz & Hošek, 2017). In this subfamily, *Japalura* Gray, 1853 is one of the most speciose and most widespread genera, containing 34 recognized species that are distributed from Pakistan along the foothills of the Himalaya to oceanic islands of Japan (Wang *et al.*, 2016; Ananjeva *et al.*, 2017; Rao *et al.*, 2017). Members of the genus display a diverse spectrum of species-specific, sexually-selected morphological traits, including ornamentation, coloration, crest morphology, limb length, and body size (Mahony, 2009; Manthey, 2010; Denzer *et al.*, 2016). Such common and high-levels of sexual dimorphisms among congeners were hypothesized to facilitate speciation and maintain genetic integrity of sympatric species (Wang *et al.*, 2015, 2016). Furthermore, the unique association between the microendemic distributions of congeners and the major mountains and rivers in Asia also make the genus a great system for investigating the biogeographic history of the region (Zhao *et al.*, 1999; Wang *et al.*, 2016).

Yet despite the high diversity in the genus and its importance in evolutionary and biogeographic studies, little is known about the phylogenetic relationships of *Japalura sensu lato*, both within the genus as well as with respect to other Draconinae genera. Although *Japalura* has long been suspected to be paraphyletic based on morphological traits (Schmidt, 1927), it was not until 2000 that

phylogenetic analyses using genetic data confirmed this conclusion (Macey *et al.*, 2000). Using mitochondrial (mt)DNA data only, Macey *et al.* (2000) showed that *Japalura sensu lato* has two, well-supported, deeply divergent clades: the first clade, which is represented by the type species of the genus, *Japalura variegata*, and *Japalura tricarinata*, was inferred to be closely related to members of the genus *Draco*; and the second clade, which is represented by *Japalura flaviceps* and *Japalura splendida*, was recovered as a sister group to members of the genus *Pseudocalotes* (Macey *et al.*, 2000). Subsequent studies that used the same sequence data of *Japalura* congeners as in Macey *et al.* (2000) recovered similar phylogenetic relationships among Draconinae lizards, where two clades of *Japalura* were recovered consistently in the same generic groups, adding additional support for the paraphyletic nature of *Japalura sensu lato* (Schulte *et al.*, 2004; Zug *et al.*, 2006).

Using a different mtDNA locus of a different, island endemic species, *Japalura polygonata*, Honda *et al.* (2000) also investigated the phylogenetic position of *Japalura* in the family Agamidae. Although the results of this study failed to infer the exact placement of the *Japalura* species used with strong support, Honda and colleagues showed that *J. polygonata* was more closely related to a clade containing the genera *Calotes* and *Aphaniotis* than to the clade containing the genera *Draco* and *Mantheyus* (Honda *et al.*, 2000). More recently, Pyron *et al.* (2013) conducted a higher-level study of squamate reptiles that incorporated all available mtDNA data from previous studies. Including five species of *Japalura sensu lato* (*J. flaviceps*, *J. polygonata*, *J. splendida*, *J. tricarinata*, and *J. variegata*), Pyron *et al.* (2013) not only recovered the same two divergent clades of *Japalura* observed previously by Macey *et al.* (2000), but they also recovered a third distinct clade represented by *J. polygonata*, which is sister to the Southeast Asian agamid *Gonocephalus robinsonii*

(now recognized as *Malayodracon robinsonii*). However, given the large amount of missing data and non-overlapping gene samplings among different clades, questions remain on the phylogenetic position of this third clade represented by *Japalura polygonata* (Pyron *et al.*, 2013).

Currently, most authors agree that *Japalura sensu lato* is paraphyletic, and the genus *sensu lato* represents multiple deeply divergent clades, but no one has yet revised the problematic paraphyly of the genus *sensu lato* (Macey *et al.*, 2000; Stuart-Fox & Owens, 2003; Mahony, 2010; Ananjeva *et al.*, 2011; Pyron *et al.*, 2013; Rao *et al.*, 2017). Furthermore, although authors have given names to all three clades recovered from previous phylogenetic studies (including *Japalura veriegata* species group/Himalayan Lineage, *Japalura splendida* group/Indochina Lineage, and *Japalura polygonata* group/Island Lineage), these clade names were established based on five of 34 species of the genus *sensu lato* only, leaving the exact group/lineage memberships of the remaining 29 congeners unknown (Stuart-Fox & Owens, 2003; Mahony, 2010; Ananjeva *et al.*, 2011).

Fortunately, broader genetic and morphological sampling across the genus *sensu lato* has now been amassed, allowing for a more robust phylogenetic assessment of monophyly of the genus and phylogenetic positions of different clades of the genus *sensu lato* with respect to other genera in the subfamily Draconinae. In this study, we employ a multilocus phylogenetic dataset to evaluate the monophyly of the genus *Japalura sensu lato* and to address long-standing taxonomic problems at the generic level. Specifically, we are interested in testing the monophyly of *Japalura sensu lato*, estimating the number of distinct clades within the genus *sensu lato*, and testing whether the three proposed species groups based on limited phylogenetic sampling and geographic distributions represent monophyletic clades. According to

our results, we provide a revised nomenclatural classification scheme that recognizes the species diversity of *Japalura sensu lato* as members of one of four distinct genera, revise the morphological diagnoses for each of the four genera, and present an updated key to all members of each revised genus. Finally, we point to future directions on the phylogenetic, taxonomic, and biogeographic studies of *Japalura sensu lato*.

Taxonomic History

The genus *Japalura sensu lato* has a long-lasting, convoluted taxonomic history based on morphological data. First being described by Gray in 1853, the genus *Japalura* was established based on the type species, *Japalura variegata* from Sikkim, Himalaya. Like many taxonomists early on, Gray (1853) gave a vague definition of his new genus and stated that his new genus was most similar to *Agama*, but differed by having a concealed tympanum. Ever since the initial description, different species were placed into the genus *Japalura*, and numerous authors attempted to refine the taxonomic definition of the genus based on newly included taxa. For example, Boulenger (1885) first added more diagnostic characteristics to *Japalura*, including having a compressed body shape, heterogeneous dorsal scales, a dorsal crest, a small gular pouch (or absent), an oblique fold, a feebly compressed tail, and no preanal or femoral pores. Pope (1935) diagnosed *Japalura* from other agamid genera by having a not depressed body and a hidden tympanum. In the same year, Smith (1935) provided a combined version of diagnosis from Pope (1935) and Boulenger (1885), which was much more comprehensive. However, Smith's (1935) diagnosis of *Japalura* still cannot differentiate most of its members from other Draconae genera, as many exceptions exist within the genus *sensu lato* (e.g., *Japalura dymondi*, *J. major*, *J. tricarinata*, *J. kumaonensis*, and *J. varcoae* have

exposed tympanum). Later Inger (1960) further differentiated *Japalura sensu lato* from the Southeast Asian genus *Phoxophrys* Hubrecht, 1881 by having greatly overlapping supraciliaries, a relatively long head, the presence of hair-like sense organs on the head scales, and a compressed tail at the base. However, those diagnostic characters again are not consistent among many of the congeners of *Japalura* (Ota, 1989). Later authors followed nevertheless similar diagnosis of the genus by Boulenger (1885), but these generic definitions remained ambiguous and impracticable, and failed to differentiate *Japalura sensu lato* from other Draconae genera such as *Pseudocalotes* (Zhao *et al.*, 1999; Yang & Rao, 2008; Wang *et al.*, 2015).

Such absence of practical morphological diagnoses of *Japalura sensu lato* resulted in uncertain systematic affiliation and unstable nomenclature, not only for members of the genus *sensu lato* alone, but also for species in other genera (Pope, 1935; Smith, 1935; Inger, 1960; Yang & Rao, 2008; Mahony, 2010). Species that are currently recognized as members of *Japalura sensu lato* were confused and assigned to different, recognized agamid genera, including to *Acanthosaura* Gray, 1831 (*Japalura dymondi* Boulenger, 1906; *Japalura varcoae*, Boulenger, 1918; *Japalura major*, Boulenger, 1885; *Japalura kumaonensis*; Annandale, 1907), *Calotes* Cuvier, 1817 (*Japalura tricarinata*, Blyth, 1853), and *Phoxophrys* (*J. gramahi*, Stejenger, 1924); and species that are currently recognized in other recognized agamid genera were placed into *Japalura sensu lato*, including *Aphaniotis* Boulenger, 1885 (*Aphaniotis ornata*, Lidth De Jeude, 1893), *Phoxophrys* (*Phoxophrys nigrilabris*, Boulenger, 1885; *Phoxophrys robinsoni* Boulenger, 1920) (Inger, 1960), and *Pseudocalotes* Fitzinger, 1843 [*Pseudocalotes kaulbacki*, (Smith 1937)] (Mahony, 2010).

Moreover, several generic nomenclatures were established, but later synonymized as subjective junior synonyms of *Japalura* based on morphological data alone, including *Diploderma* Hallowell, 1861 (type species *D. polygonontum*, from the Okinawa islands of Japan), *Oriotiaris* Günther, 1864 (type species *Oriotiaris tricarinata*, from northeast India), and *Oreocalotes* Jerdon, 1870 (type species *Oreocalotes major*, from the western Himalaya). Nonetheless, those nomenclatures were synonymized based on morphological data and previous vague morphological diagnoses of *Japalura*, and the evolutionary independencies of most of those genera represented were not examined specifically under a comprehensive morphological or molecular phylogenetic framework (Macey *et al.*, 2000; Pyron *et al.*, 2013; Grismer *et al.*, 2016).

To date, a total of 34 species are recognized as members of the genus *Japalura sensu lato* in the recent literature (Yang & Rao, 2008; Mahony, 2010; Manthey *et al.*, 2012; Cai *et al.*, 2015; Wang *et al.*, 2016; Ananjeva *et al.*, 2017; Rao *et al.*, 2017), including *Japalura andersoniana* Annandale, 1905, *Japalura bapoensis* (Yang, Su, Li, 1979), *Japalura batangensis* Li, Deng, Wu, Wang, 2001, *Japalura brevicauda* Manthey, Denzer, Hou, Wang, 2012, *Japalura brevipes* Gressitt, 1936, *Japalura chapaensis* Bourret, 1937, *Japalura dasi* (Shan, Kästle, 2002), *Japalura dymondi* (Boulenger, 1906), *Japalura fasiata* Mertens, 1926, *Japalura flaviceps* Barbour, Dunn, 1919, *Japalura grahami* (Stejneger, 1924), *Japalura hamptoni* Smith, 1935, *Japalura iadina* Wang, Jiang, Siler, Che, 2016, *Japalura kunmaonensis* (Annandale, 1907), *Japalura laeviventris* Wang, Jiang, Siler, Che, 2016, *Japalura luei* Ota, Chen, Shang, 1998, *Japalura major* (Jerdon, 1870), *Japalura makii* Ota, 1989, *Japalura micangshanensis* Song, 1987, *Japalura ngoclinensis* Ananjeva, Orlov, Nguyen 2017, *Japalura otai* Mahony, 2009, *Japalura planidorsata* Jerdon, 1870, *Japalura*

polygonata (Hallowell, 1861), *Japalura sagittifera* Smith, 1940, *Japalura slowinskii* Rao, Vindum, Ma, Fu, Wilkinson, 2017, *Japalura splendida* Barbour, Dunn, 1919, *Japalura swinhonis* Günther, 1864, *Japalura tricarinata* (Blyth, 1853), *Japalura varcoea* (Boulenger, 1918), *Japalura variegata* Gray, 1853, *Japalura vela* Wang, Jiang, Pan, Hou, Siler, Che, 2015, *Japalura yunnanensis* Anderson, 1878, *Japalura yulongensis* Manthey, Denzer, Hou, Wang, 2012, and *Japalura zhaoermii* Gao, Hou, 2002.

Materials and Methods

Taxon Sampling

We collected 25 out of 34 species of the genus *Japalura sensu lato* from Mainland China, Taiwan, and India (Field collection permits [Mainland China: BBCJ-2014-001; Taiwan: Forest Bureau No. 1061700632]; Wang *et al.* 2017a, b; Appendix III). Lizards were euthanized after capture in the field following the protocols of corresponding institutions in their home countries (IACUC R17-019; Taiwan: IACUC of NTNU No. 106027), and liver or muscle tissues were collected from each individual and preserved in 95% ethanol. Specimens were fixed in buffered 10% formalin and subsequently transferred to 70% ethanol for long-term preservation. Vouchered specimens were deposited in research institutions, including the Museum of Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ), National Museum of Natural Science (NMNS), and Center for Ecological Sciences, Indian Institute of Science (CESG).

Additional specimens and tissue samples were also obtained through museum loans from the California Academy of Sciences, USA (CAS), Museum of Comparative Zoology, USA (MVZ), and Sam Noble Oklahoma Museum of Natural

History (OMNH) (Appendix III). Additionally, we collected novel sequence data for six outgroup species of agamids representing four genera from Mainland China and the Philippines (Appendix III), and we incorporated existing genetic sequence data of four species of *Japalura sensu lato* and 17 species of outgroup agamids were obtained from Genbank (Appendix I).

Morphological Data Collection

We examined a total of 215 specimens of 27 species of *Japalura sensu lato* and 39 specimens of 16 species (ten genera) of outgroup agamid (Appendix II). Following previous studies (Moody 1980; Mahony 2010) and our prior knowledge on morphological characteristics of Draconinae, the following pholidosis characteristics were chosen and examined for all specimens, as they are shown to be most useful in delimiting generic level diversity (abbreviations given in parentheses): presence of modified scales on dorsal body (MDS), defined as presence of scales on dorsal body that are modified in shape, size, or texture (e.g. enlarged, keeled, flat, or raised in conical shape); degree of modification of dorsal modified scales (DMDS), defined as the level of modification compared to the ground or normal scales on dorsal body, defined as strongly modified or weakly modified; presence of dorsolateral ridges (PDR), defined as presence of regularly and closely arranged rows of enlarged, keeled dorsal scales on the body; presence of V-shaped ridges on dorsal body (PVR), defined as presence of enlarged, keeled scales that are arranged in V-shape ridges on dorsal body; and presence of head spines (PS), defined as presence of elongated spines on the post-orbital, occipital, and supratympanic regions of head.

In addition to these pholidosis characteristics, standard morphometric measurements of agamid lizards were taken by KW for a subset of male specimens only (53 specimens in 21 species of *Japalura sensu lato* and 22 specimens of 10 species in seven genera of outgroup Draconinae), which were used for statistical analyses (statistical methods see below; specimen information see Appendix II). Male specimens were chosen only for the statistical analyses, because males are generally more diverse in morphology; and by choosing one sex only, we remove the confounding impacts from sexual dimorphism from the analyses, which is evident in most Draconinae genera (Zug *et al.* 2006; Manthey 2012; Wang *et al.* 2016). The following morphological characters and their measurement methods followed Wang *et al.* (2016) and included: snout–vent length (SVL), tail length (TAL), head width (HW), head length (HL), snout–eye length (SEL), fore-limb length (FLL), hind limb length (HLL), and trunk length (TRL). In addition, length of tallest nuchal crest (CL), measured from the base to the tips of the tallest nuchal crest scale, was also recorded.

Statistical Analyses for Morphological Data

Principle Component Analysis (PCA) and Discriminant Analysis of Principle Components (DAPC) were performed to determine if *Japalura sensu lato* occupied unique morphospace with respect to morphologically similar Draconinae genera, and whether the morphological clustering coincide with the clades recovered from our molecular data set. PCA was performed on the continuous morphometric measurements (SVL, and CL) and their relative ratios (TAL/SVL, TrL/SVL, FLL/SVL, HLL/SVL, HL/SVL, HW/HL, SEL/HL, and CL/HL), using the `prcomp` command in R v. 3.2.1 (R Code Team 2015). All PCA data were natural log

transformed prior to analysis and scaled to their standard deviation in order to normalize their distribution. DAPC were performed on principle components with eigenvalues greater than one (Kaiser 1960), using R v. 3.2.1.

Molecular Data Collection

Total genomic DNA was extracted from liver or muscle tissue using Fujita's Guanidine Thiocyanate protocol (Esselstyn *et al.*, 2008). We targeted three nuclear loci, including Brain Derived Neurotrophic Factor (BDNF), Oocyte Maturation Factor (CMOS), and RNA Fingerprint Protein 35 (R35), and one mitochondrial gene, NADH Dehydrogenase Subunit 2 (ND2). As results of primer amplification of the mitochondrial gene, we also obtained a short fragment of Cytochrome C Oxidase Subunit I (COI) and components of eight flanking transfer RNA genes (tRNA^{Gln}, tRNA^{Ile}, tRNA^{Met}, tRNA^{Trp}, tRNA^{Ala}, tRNA^{Asn}, tRNA^{Cys}, and tRNA^{Tyr}). Genes were targeted and amplified using both published and newly designed primers and PCR protocols (Table 2-1).

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. All novel sequences were deposited in GenBank (Appendix III).

Alignment and Phylogenetic Analysis

Continuous gene sequences were assembled and edited using GENEIOUS v. 10.0.6. Alignments were produced initially using MUSCLE (Edgar, 2004), with minor subsequent manual adjustments. Alignments and resulting topologies are deposited in Dryad (doi:XXXXXXX). 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, we concatenated the two data sets for the final analyses.

We conducted concatenated, partitioned Bayesian analyses in the program MrBayes v. 3.2.1 (Ronquist & Huelsenbeck, 2003). All protein-coding genes were partitioned by codon positions, except for COI, which is treated as a single partition due to its short length, and the mitochondrial tRNAs were combined and treated as a single partition as well (Table 2-2). The best models of nucleotide substitution were selected for each partition by the Akaike Information Criterion (AIC), as implemented in jModelTest v. 2.1.10 (Guindon & Gascuel, 2003; Darriba *et al.* 2012). A rate multiplier model was used to allow substitution rates to vary among subsets. Default settings were used for all other model parameters. Two independent Markov chain Monte Carlo analyses were run, each with four Metropolis-coupled chains, a melting temperature of 0.02, and an exponential distribution with a rate parameter of 25 as the prior branch lengths (Marshall 2010). All Bayesian analyses were run for 6,000,000 generations, with parameters and topologies sampled every 3,000 generations. Stationarity and convergence were assessed with TRACER v. 1.6.0 (Rambaut, Suchard & Drummond, 2013), and we confirmed convergence of tree splits with AWTY (Wilgenbusch *et al.*, 2004). Although runs reached stationarity after 5 million generations, we conservatively discarded the first 15% of

samples as burn in, resulting in a total of 1,700 topologies from the posterior distribution for both runs.

Partitioned Maximum Likelihood analyses were conducted using RAXMLHPC v. 8.2.X (Stamatakis 2014) on the concatenated data set using the same partitioning strategy as for Bayesian analysis. The more complex model (GTR + Γ) was applied for all subsets (Table 2-2), with 100 replicate ML inferences run. Each inference was initiated with a random starting tree, and nodal support was assessed with 1,000 bootstrap pseudoreplicates (Stamatakis, Hoover & Rougemont, 2008).

To root the resulting phylogenetic trees, *Hydrosaurus pustulatus* (subfamily Hydrosaurinae) was chosen as the outgroup of subfamily Draconinae, based on published high-level phylogenetic studies of squamate reptiles (Pyron *et al.*, 2013).

Hypothesis Testing

We tested taxonomic hypotheses proposed in previous studies to address the following questions (1) Does our expanded data set support the previous shown relationship between *Malayodracon* and island species of *Japalura sensu lato* by Pyron *et al.* (2013)? (2) With expanded taxa sampling, does our data set support the previous shown sister relationship between the genus *Calotes* and *Salea* by Grismer JL *et al.* (2016)? (3) With the exclusion of the controversial species *Japalura bapoensis*, do congeners from each of the three general geographic regions (Himalaya, Indochina/Mainland East Asia, and East Asian Islands) form a monophyletic group, as suggested by previously proposed species groups (e.g. Himalayan Species Group, Indochinese Species Group, and Island Species Group)? (4) Does *Japalura bapoensis* form a monophyletic group with remaining species of *Japalura sensu lato* in mainland East Asia?

To do so, we estimated posterior probabilities of different topologies that correspond to each of the above question using a Bayesian approach. We constrained corresponding topologies for each hypothetical scenario and estimated the posterior probability of supporting such hypotheses using the proportion of 50% post-burn-in trees (out of a total 2000 post-burn-in trees) that are consistent with the corresponding hypothesized topology. This was accomplished by filtering the total number of post-burn-in trees for each constrained topology using PAUP* v. 4.0b10 (Swofford, 1999).

Results

Phylogenetic Results

We did not observe any incongruent clades with above 0.95 posterior probability or 70 bootstrap supports between nuclear and mitochondrial gene trees. Therefore we concatenated all data into one matrix, containing 3,388 nucleotides. Characteristics of nucleotides, as well as the best evolutionary models selected are summarized in Table 2-2.

No conflicting relationships with strong supports were observed between the two analyses, although the placements of an outgroup (*Acanthosaura lepidogaster*) are different in the two analyses (with BS=53 in RaxML analyses). For all key nodes regarding relationships of major clades in *Japalura sansu lato*, the final consensus tree using a fully-partitioned data set from both the Bayesian phylogenetic analyses and partitioned RaxML analyses yielded the same topology with strong supports (posterior probability, herein referred as PP, PP $\geq$ 0.99; and bootstrap value, herein referred as BS, BS $\geq$ 80), supporting the polyphyly of the genus *Japalura sensu lato*. Four deeply diverged clades were recovered within the *Japalura sensu lato* (Figure

2, Clades C, G, N, O): (1) *Japalura andersoniana*, *J. kumaonensis*, *J. tricarinata*, and *J. variegata* form a monophyletic group with strong support (Figure 2, Clade C; 1.00/83 for BI PP and ML BS respectively, herein noted in the same order), which form a strongly supported group with *Draco* and *Ptyctolaemus* (Figure 2, Clade A; 1.00/91); (2) *Japalura otai* and *J. planidorsata* form the second, distantly related clade (Clade G, 1.00/100) that is sister to the genus *Selea* (0.99/69; Figure. 2); (3) *Japalura bapoensis* is nested within the *Pseudocalotes* with strong support (clade L; 1.00/100); and (4) all the remaining species from Mainland China and East Asian islands form a monophyletic clade (Clade H, 1.00/100) that is sister to the genus *Pseudocalotes* (1.00/100). Furthermore, two well-supported sub-clades (sub-clade P, 1.00/100; and sub-clade Q, 1.00/100) were recovered within the Clade O (Figure 2).

Although population sampling is not the focus of this paper, we included multiple populations of the same species when samples were available. At the species level, most species are recovered as monophyletic lineages, except *J. planidorsata* and *J. flaviceps* in Clade G and Clade O respectively. The Myanmar individuals of *J. c.f. planidorsata* are paraphyletic with respect to *Japalura otai*, and the Genbank sequence of *J. c.f. flaviceps* does not form a monophyletic clade with topotypic individuals of the species, but instead forms a monophyletic lineage with topotypic *J. zhaoermii* (Figure 2).

Morphological Results

For continuous morphometric data, PCA and DAPC analyses show members of *Japalura sensu lato* occupy distinct morphological spaces comparing to other genera (Figure 3). Furthermore, four groups were recovered within *Japalura sensu lato* in morphospace, which coincide with the four major clades of the genus *sensu lato*

recovered from the genetic data (Figure 3). For PCA analysis, the first four components account for 75% of the total variance: PC1 loads most heavily on CL and CL/HL (28% of the total variance), PC2 loads most heavily on FLL/SVL and HLL/SVL (19% of total variance); PC3 loads most heavily on TrL/SVL and HL/SVL (15% of the total variance), and PC4 loads most heavily on TAL/SVL and HW/HL (13% of the total variance) (Table 2-3). The DAPC further characterizes these results and shows the visual clustering of different clades of *Japalura sensu lato* in morphospace (Figure 2-3). In addition, each of the four genetic clades/morphological clusters can also be diagnosed readily using a combination of discrete pholidosis characteristics (Figure 4; Table 2-4).

Topology Testing

Our topological test results show no supports for the monophyly of the clade containing the East Asian *Japalura sensu lato* and *Malayodracon robinsonii* (H1, PP=0.00) and the clade containing *Calotes* and *Salea* (H2, PP=0.00) (Table 2-5). For *Japalura sensu lato* species from the three geographic regions, with the exclusion of the controversial species, *Japalura bapoensis*, the Bayesian statistical tests show no support for the monophyly of Himalayan species (H3, PP=0.00) and monophyly of remaining mainland Indochinese species (H4, PP=0.00). Only the monophyly of East Asian species (together both mainland and island species) is statistically supported (H5, PP=1.00) (Table 2-5). As for the controversial species *Japalura bapoensis*, we found no statistical support for its monophyly with respect to the remaining East Asian species (H6, PP=0.00).

Discussion

New Classification of Japalura sensu lato

Our morphological and phylogenetic results both support previous studies on the polyphyletic nature of *Japalura sensu lato* (Figure 2 & 3; Table 2-4; Macey *et al.* 2000; Mahony 2010). We recover similar phylogenetic positions of the two previously recognized clades within *Japalura sensu lato* (*J. tricarinata*/*J. variegata* clade and *flaviceps*/*J. splendida* clade), and we confirm the generic placement of *Japalura bapoensis* in the genus *Pseudocalotes* as in previous studies (Macey *et al.*, 2000; Schulte *et al.*, 2004; Zug *et al.*, 2006; Pyron *et al.*, 2013; Grismer *et al.*, 2016; Figure 2). Furthermore, with the exclusion of *Japalura bapoensis*, we support the previously assumed monophyly of all East Asian species, including both mainland and island species (hypothesis test PP=1.00; Clade O, BS=100, PP=1.00; Ananjeva *et al.* 2011).

In addition to the similar results as in previous studies, our results also revealed novel findings with the expanded taxa and gene samplings. Firstly, our phylogeny recovers two distinct clades from the previously proposed Himalayan species group: Clade C, which corresponds to the previously discovered Himalayan clade by Macey *et al.* (2000) and Pyron *et al.* (2013), and the novel clade G, which is a new clade discovered here at the first time. Although species of both clades are from the Himalayan region, they are recovered in distantly related groups within Draconinae with strong supports (Figure 2). Statistical topology tests further support the phylogenetic results, rejecting the assumed monophyly of the Himalayan congeners (PP=0.00; Table 2-5; Stuart-Fox & Owens, 2003; Mahony, 2010; Ananjeva *et al.*, 2011). Secondly, we reject the previously hypothesized sister relationship between island congeners and *Malayodracon* by Pyron *et al.* (2013). The phylogenetic results show a strongly supported sister relationship between East Asian species of *Japalura sensu lato* (Mainland and Island) and *Pseudocalotes* (Figure 2, Clade L);

and topology tests reject the sister relationship between Island *Japalura sensu lato* and *Malayodracon* with statistical confidence (Table 2-5).

As recognizing all four clades of *Japalura sensu lato* as a single genus would render most genera of the subfamily Draconinae paraphyletic, thus, to stabilize this polyphyletic and problematic taxonomy and to best reflect evolutionary histories of each clade of *Japalura sensu lato* in nomenclature, we revise the taxonomy of *Japalura sensu lato* and split it into four genera that correspond to the four evolutionary clades recovered in our phylogenetic and morphological analyses.

The first clade, Clade C, includes the type species of three nomenclatures, namely *Japalura sensu stricto* Gray, 1835 (type species *Japalura variegata*), *Oriotiaris* Günther, 1864 (type species *Oriotiaris tricarinata*), and *Oreocalotes* (type species *Oreocalotes major*) (Fig. 2). For the name *Oriotiaris*, as recognizing it as a valid nomenclature would render itself and *Japalura sensu stricto* both paraphyletic (Figure 2), therefore, we recognize *Japalura*, which has the naming priority, and we treated *Oriotiaris* as a junior synonym of *Japalura sensu stricto* as in previous literature (Mahony, 2009). For the generic name *Oreocalotes*, although we did not have access to the genetic materials of its type species, because morphological characteristics of its type species *J. major* fall within the larger cluster of Clade C in the PCA and DAPC analyses (Figure 3), and since *J. major* is morphologically most similar to *Japalura kumaonensis* (Wang *et al.*, 2017c), a confirmed member of the genus *Japalura sensu stricto*, therefore, we treat *Oreocalotes* as a junior synonym of *Japalura sensu stricto* as well, pending on available genetic materials in the future.

For clade N, we followed Mahony (2010) and transfer *Japalura bapoensis* into the genus *Pseudocalotes*, and conservatively consider it as a subspecies of *Pseudocalotes kingdonwardi* (see discussion below on its species status). For

monophyletic clade O, we resurrect the only available generic name that represented this clade in the past, *Diploderma* (with its type species *Diploderma polygonatum polygonatum*). Lastly, since the newly discovered clade G has no available generic nomenclature, we describe it as a new genus, ***GenusXXX* gen. nov.** (described below).

Based on our revised taxonomy and the morphological diagnoses summarized for each of the four clades based on sampled taxa, we proposed a new classification scheme for all recognized members of *Japalura sensu lato*.

Taxonomic Accounts

Japalura sensu stricto Gray, 1853

Etymology

The Latin name “*Japalura*” may be derived from a locality name in India, and the term is feminine gender. We suggest the English common name as “Himalayan Dragon”, and the Chinese name as “攀蜥” (pronounced as “Pan-Shi”)

Type species

Japalura variegata, Gray, 1853

Diagnosis

Lizards of the genus *Japalura sensu stricto* differ from closely related genera by possessing the following morphological characteristics: (1) head width moderate, HW mostly <70% of HL; (2) nuchal and dorsal crest scales relatively low and thick, not significantly elongated into lanceolate spines; (3) post orbital and occipital spines absent; (4) gular scales mostly homogeneous in size; (5) size of scales on lateral jaw subequal in size across gular region; (6) dorsal scale significantly heterogeneous in size and shape, not regularly imbricate; (7) pair of distinctively

enlarged, conical scales absent on nape above shoulder; (8) paravertebral rows of enlarged scales present on dorsolateral body; and (9) V-shaped ridges present along dorsal midline, formed by enlarged, keeled scales.

Phylogenetic Definition

We define *Japalura sensu stricto* using the maximum crown-clade definition, which include species that share a more recent common ancestor to *Japalura variegata* than *Draco volans* or *Ptyctolaemus gularis*.

Content

Based on our phylogenetic results, we assigned the following species into the genus *Japalura sensu stricto*: *Japalura andersoniana* Annandale, 1905, *Japalura kumaonensis* (Annandale, 1907), *Japalura tricarinata* (Blyth, 1853), and *Japalura variegata* Gray, 1853. Following our morphological results and proposed morphological diagnoses, we also assign *Japalura dasi* (Shah, Kästle, 2002), *Japalura major* (Jerdon, 1870), and *Japalura sagittifera* Smith, 1940 into the genus *Japalura sensu stricto*, pending on future phylogenetic confirmations.

Distribution Range

Members of the genus are distributed along the southern foothills of the Himalaya, including northeastern Pakistan (*J. kumaonensis* and *J. major*), northern and northeastern India (*J. andersoniana*, *J. kumaonensis*, *J. major*, *J. sagittifera*, *J. tricarinata*, and *J. variegata*), Nepal (*J. dasi*, *J. tricarinata* and *J. variegata*), Bhutan (*J. andersoniana*, *J. tricarinata*, and *J. variegata*), southern parts of the Tibet Autonomous Region in China (*J. andersoniana* and *J. tricarinata*), and northern part of Myanmar (*J. sagittifera*). Congeners may also be found in northwestern Bangladesh.

GenusXXX gen. nov.

Wang, Veerappan, Aniruddha, Lin, Jiang, Che, Siler, 2017

Etymology

The Latin term “*GenusXXX*” means “ridged dorsum”, which describes the distinct, characteristic ridges on the dorsal surface of the body in the new genus. The generic name is feminine, and it consists of two parts, namely “*Cristi-*” (meaning “ridged”) and “*-dorsa*” (meaning “dorsum”).

Type species

GenusXXX otai (Mahony, 2009)

Diagnosis

Lizards of the genus *GenusXXX* differ from other closely related Draconinae genera by having the following morphological characteristics: (1) head robust and relatively wide, HW/HL mostly >70%; (2) scales of lateral head keeled; (3) nuchal and dorsal crest feeble; (4) occipital and post-orbital spines absent; (5) gular scales mostly homogeneous in size; (6) size of scales on lateral jaw subequal in size across gular region; (7) single pair of distinctively enlarged conical scales present on nape above shoulder, one scale on each side of vertebral crest; (8) dorsal scale significantly heterogeneous in sizes and shapes; (9) distinct, dorsolateral rows of enlarged, keeled scales present on dorsum; and (10) V-shaped ridges present along dorsal midline, formed by enlarged, keeled scales.

Phylogenetic Definition

We define *GenusXXX* using the maximum crown-clade definition, which include species that share a more recent common ancestor to *GenusXXX otai* than *Salea horsfieldii*.

Content

Based on our phylogenetic results, we assigned *GenusXXX otai* (Mahony, 2009) and *GenusXXX planidorsata* (Jerdon, 1870) to the genus *GenusXXX*.

Distribution Range

Members of the genus *GenusXXX* distribute on the southeast extreme of the Himalaya foothills, including northeast India (*GenusXXX otai* and *GenusXXX planidorsata*) and the northwest part of Myanmar (*GenusXXX otai*; see discussion on taxonomic status of the Myanmar population below).

Diploderma Hallowell, 1861

Etymology

The Latin generic name “*Diploderma*” consists of two parts, “*Diplo-*” means “double” or “many”, and “*-derma*” means “skin”, and the whole word is in a neutral gender. As the previous generic name “*Japalura*” and most species names of the genus *sensu lato* are feminine, most names of species that are now assigned to *Diploderma* need to change their gender to neutral (except for the neutral gender ones like *brevipes* or *flaviceps*, Latin nouns like *vela*, or peoples’ names like *dymondi*, *luei*, *makii*, *swinhonis*, *varcoae*, and *zhaoermii*). We suggest the English common name of the genus as “Mountain Dragon”, and the Chinese common name as “龙蜥” (pronounced as “Long-Shi”).

Type species

Diploderma polygonatum Hallowell, 1861

Diagnosis

Lizards of the genus *Diploderma* differs from closely related genera by having the following morphological characteristics: (1) scales of lateral head keeled; (2)

nuchal and dorsal crest scales relatively short and thick, not elongated into lanceolate spines; (3) occipital and postorbital spines absent; (4) gular scales mostly homogeneous in size, not decreasing in size toward the center; (5) scales on lateral jaw subequal in size across gular region; (6) dorsal scale significantly heterogeneous in size and shape, not regularly imbricate; (7) paravertebral dorsolateral ridges of body present in most species, formed by enlarged, keeled scales (except in *D. swinhonis* and *D. leui*); and (8) V-shaped ridges along dorsal body midline absent in all but one species (except in *D. swinhonis*).

Phylogenetic Definition

We define *Diploderma* using the maximum crown-clade definition, which include species that share a more recent common ancestor to *Diploderma polygonatum* than *Pseudocalotes tymanistriga* and *Acanthosaura lepidogaster*.

Content

Based on our phylogenetic results, we assigned the following species into the genus *Diploderma*: *Diploderma batangense* (Li, Deng, Wu, Wang, 2001), *Diploderma brevipes* (Gressitt, 1936), *Diploderma chapaense* (Bourret, 1937), *Diploderma dymondi* (Boulenger, 1906), *Diploderma flaviceps* (Barbour, Dunn, 1919), *Diploderma laeviventre* (Wang, Jiang, Siler, Che, 2016), *Diploderma luei* (Ota, Chen, Shang, 1998), *Diploderma makii* (Ota, 1989), *Diploderma micangshanense* (Song, 1987), *Diploderma polygonatum* Hallowell, 1861 (and all of its subspecies), *Diploderma slowinskii* (Rao, Vindum, Ma, Fu, Wilkinson, 2017), *Diploderma splendidum* (Barbour, Dunn, 1919), *Diploderma swinhonis* (Günther, 1864), *Diploderma varcoae* (Boulenger, 1918), *Diploderma vela* (Wang, Jiang, Pan, Hou, Siler, Che 2015), *Diploderma yulongense* (Manthey, Denzer, Hou, Wang,

2012), *Diploderma yunnanense* (Anderson, 1878), and *Diploderma zhaoermii* (Gao, Hou, 2002).

According to our proposed morphological diagnoses, we also assign *Diploderma brevicaudum* (Manthey, Denzer, Hou, Wang, 2012), *Diploderma fasciatum* (Mertens, 1926), *Diploderma grahami* (Stejneger, 1924), *Diploderma hamptoni* (Smith, 1935), and *Diploderma iadinum* (Wang, Jiang, Siler, Che, 2016) to this genus, pending on future phylogenetic confirmations.

In total, 24 species of *Japalura sensu lato* species are reclassified into the genus *Diploderma* (issue regarding taxonomic status of *D. ngoclinense* see discussion below).

Distribution Range

Members of the genus are distributed in the Mainland East Asia, East Asian Islands, and northern Indochina, including central, southern, and southwestern Mainland China (*D. batangense*, *D. brevicaudum*, *D. chapaense*, *D. dymondi*, *D. fasciatum*, *D. flaviceps*, *D. grahami*, *D. iadinum*, *D. laeviventre*, *D. micangshanense*, *D. splendidum*, *D. slowinskii*, *D. vela*, *D. yunnanense*, *D. yulongense*, and *D. zhaoermii*) and Taiwan (*D. brevipes*, *D. luei*, *D. makii*, *D. polygonatum*, and *D. swinhonis*), southern islands of Japan (*D. polygonatum*), central and eastern Myanmar (*D. hamptoni*), northern Vietnam (*D. fasciatum* and *D. chapaense*), and northern Thailand (*D. yunnanense*). Congeners such as *D. yunnanense* may also be distributed in Myanmar and northern Laos close to the Chinese border.

Pseudocalotes Fitzinger, 1843

Type species

Pseudocalotes tympanistriga (Gray, 1831)

Diagnosis

Pseudocalotes can be diagnosed from other Draconinae genera by having: (1) scales of lateral head smooth, especially loreal and subocular region; (2) scales of lateral jaw enlarged; (3) scales of central gular region distinctively smaller than others of throat; (4) sub-orbital scale row usually one, or multiple but with the middle one significantly enlarged; (5) post-orbital and post-occipital spines absent; (6) nuchal crest scales mostly elongated and tall, CL/HL mostly >10%; (7) dorsal crest scales feeble and low; (8) dorsal body scales heterogeneous in size and shape; (9) enlarged dorsal body scales not arranged in paravertebral, dorsolateral, or V-shaped ridges.

Phylogenetic definition

We define *Pseudocalotes* using the maximum crown-clade definition, which include species that share a more recent common ancestor to *Pseudocalotes tympanistriga* than *Diploderma polygonatum* and *Acanthosaura lepidogaster*.

Content

The genus contains a single species from *Japalura sensu lato*, which is *Pseudocalotes kingdonwardi bapoensis*. Currently, the genus includes 21 recognized species in total (Grismer *et al.*, 2016).

Distribution Range

The genus is distributed in Southeast Asia and Indochina, including southern Mainland China, Cambodia, Indonesia, Laos, Malaysia, Myanmar, Sumatra, Thailand, and Vietnam.

Phylogenetic Relationships of Japalura sensu lato

Generic level relationships

Being the first comprehensive phylogenetic analysis of the genus *Japalura sensu lato*, our results confirm previous observations of paraphyly among members of the genus (Figure 2; Macey *et al.*, 2000; Schulte *et al.*, 2004; Zug *et al.*, 2006; Pyron *et al.*, 2013). Although we recover four distinct genera within *Japalura sensu lato*: *Japalura sensu stricto*, *GenusXXX*, *Pseudocalotes*, and *Diploderma* (Figure 2, Clades C, G, N, and O, respectfully), and support the monophyly of *Japalura sensu stricto* with strong support (1.00/83), we cannot resolve the intergeneric relationships among *Japalura sensu stricto*, *Draco*, and *Ptyctolaemus* (Figure 2, Clade B; 0.587/45). This result is consistent with previous studies, which have recovered *Japalura sensu stricto* both as sister to *Draco* (Schulte *et al.*, 2004) or *Ptyctolaemus* (Pyron *et al.*, 2013). Therefore, at this time, no conclusion can be made with confidence regarding the intergeneric relationships among the three Himalayan genera—future studies with expanded taxonomic and genomic datasets are needed.

Without taxonomic representation of the new genus *GenusXXX*, previous genomic studies supported a sister relationship between *Calotes* and *Salea*, and together, this clade was observed to be reciprocally monophyletic with a clade consisting of *Bronchocela*, *Ceratophora*, *Cophotis*, *Gonocephalus*, and *Lyriocephalus* (Grismer JL *et al.*, 2016). In contrast, with our expanded taxon sampling, our data supports the new genus *GenusXXX* (Figure 2, Clade G) as sister group to *Salea* (Figure 2, Clade F; 0.99/69), and together with *Bronchocela*, *Calotes*, *Ceratophora*, and *Gonocephalus*, they form a monophyletic clade (Figure 2, Clade E; 0.985/53). Furthermore, our Bayesian topology tests reject the hypothesized monophyly of a *Calotes* + *Salea* clade (Table 2-5, H2; PP=0.00). We suspect that incomplete taxonomic sampling may have resulted in the relationships recovered in

previous studies (Grismer JL *et al.* 2016). However, continued research on this diverse group of agamid lizards is needed.

Using a supermatrix of 12 genetic loci, Pyron *et al.* (2013) showed that the East Asian species of *Japalura sensu lato* do not form a monophyletic group: the sampled mainland species (*D. flaviceps* and *D. splendidum*; both were recognized as *Japalura* at the time) are not the closest sister group to the island species, *D. polygonatum* (recognized as *Japalura polygonata* at the time). Instead, Pyron *et al.* (2013) showed that *D. polygonatum* was most closely related to *Malayodracon robinsonii* (recognized as *Gonocephalus robinsonii* at the time) from Southeast Asia. However, Pyron *et al.* (2013) sampled non-overlapping loci between the mainland and island species (ND2 for *D. flaviceps* and *D. splendidum*, 16S and 12S for *D. polygonatum* and *Malayodracon robinsonii*). Additionally, it is recognized that *D. polygonatum* is morphologically distinct from *Malayodracon* and distributed in distinct biogeographic regions (Denzer *et al.*, 2016; Fig. 2). Therefore, the unexpected relationships observed previously may be an artifact of incomplete gene coverage. With expanded, overlapping genetic datasets across sampled Draconinae genera, our results recover different relationships from those observed in Pyron *et al.* (2013). Although all island species of *Diploderma* from Taiwan and Japan are recovered as a monophyletic clade (Figure 2, Clade S), they are nested within a larger clade containing species from mainland East Asia (Figure 2, Clade O), and the whole group is sister to *Pseudocalotes* with strong statistical support (Figure 2; PP=1.00/100). The results also failed to support *Malayodracon* as sister to *Diploderma polygonatum*, and the hypothesis of a sister relationship is rejected with strong statistical support (Table 2-5). Our observed phylogenetic relationships are largely consistent with conclusions from previous phylogenetic (Macey *et al.*, 2000;

Zug *et al.*, 2006; Grismer JL *et al.*, 2016) and morphological studies (Mahony, 2009; 2010; Ananjeva *et al.*, 2011).

Our findings provide further clarity to some of the more contentious taxonomic issues surrounding individual species. For *Japalura bapoensis* (Yang & Su, 1978; Yang & Rao, 2008; Mahony, 2010; Cai *et al.*, 2015;), our findings support the recent generic designation of the species in the genus *Pseudocalotes* (Mahony, 2010). First, being described as a subspecies of *Pseudocalotes kingdonwardi* (considered as *Calotes kingdonwardi* at the time; Smith, 1935; Yang & Su, 1978; Zhao *et al.*, 1999), *P. k. bapoensis* was later transferred to the genus *Japalura* based on morphological characteristics and subsequently elevated to full species status as *J. bapoensis* (Yang & Rao, 2008). However, the morphological diagnoses of *Japalura* provided by Yang and Rao (2008) (e.g. heterogeneous dorsal scales, well-developed nuchal crests, presence of shoulder fold, feebly developed gular pouch, and small and exposed tympanum) are not diagnostic for *Japalura sensu lato* and cannot differentiate *Japalura sensu lato* from *Pseudocalotes* (Mahony, 2010). In contrast, the proposed morphological characteristics of *Japalura bapoensis* match the revised diagnoses of *Pseudocalotes*, including members having a single, enlarged suborbital scale row, distinctively smaller scales in the center of the throat, enlarged scales toward the lateral jaw, and distinctively large nuchal crest scales (Figure 3; Yang & Rao, 2008; Mahony, 2010). Furthermore, the results of phylogenetic analyses in this and previous studies recover *J. bapoensis* as nested within the genus *Pseudocalotes* with strong support (was even treated as *Pseudocalotes kingdonwardi* in Grismer *et al.* 2016) (Figure 2, Clade M; 1.00/100). Therefore, on the basis of morphological and phylogenetic evidence, we consider *Japalura bapoensis* as a member of the genus *Pseudocalotes*. As neither additional specimens nor genetic data of the

nominate subspecies, *Pseudocalotes kingdonwardi kingdonwardi*, are available, we cannot evaluate the validity of *P. k. bapoensis* as a distinct species from *P. k. kingdonwardi* at this time. Therefore, following previous published work (Mahony, 2010), we conservatively treat *bapoensis* as a subspecies of *P. kingdonwardi*, pending future analyses should specimens and genetic material of *P. k. kingdonwardi* become available.

Finally, it is important to note that our new classification aims to provide a suite of testable hypotheses for future phylogenetic work, with new classifications for non-sampled species representing our best attempt at a more stable taxonomic structure given all data available to date. Many species, such as *Japalura sagittifera* and *Diploderma hamptoni* are known from poorly surveyed regions, and lack vouchered specimens and genetic samples. Therefore, our new classification of these understudied taxa is based on the best available morphological data alone, which may be subject to convergence and warrants additional investigations. Additionally, future phylogenomic studies are needed to better resolve the higher-level phylogenetic relationships of the understudied agamids of *Japalura sensu lato*. To facilitate future taxonomic works, we provide the updated morphological diagnoses to each of the four genera within *Japalura sensu lato*.

Diagnostic key to genera within Japalura sensu lato

Body scale heterogeneous in size and shape; dorsal crest scales mostly low and thick, not elongated in lanceolate shape; post-tympanic and occipital spines absent; femoral pores absent; tail not markedly swallow or flattened dorsally at base-----
-----*Japalura sensu lato*

- 1a. Suborbital scale usually in single enlarged row; lateral head scales smooth, especially in loreal and subocular region; dorsal scales imbricated; enlarged scales of body not arranged in paravertebral rows; scales around center of throat distinctively smaller than others on ventral head; ventral head scales increasing in size toward lateral jaw; nuchal crest scales generally tall, elongated in spine or laceolate shape -----*Pseudocalotes*
- 1b. Suborbital scales in multiple rows, usually about same size; lateral head scales keeled; dorsal scales not imbricated; enlarged dorsal scale arranged in regular rows and/or ridges; scales around center of throat about same sizes as others on ventral head; ventral head scales not increasing in size toward lateral jaw; nuchal crest scales mostly low and thick, not in laceolate shape-----2
- 2a. Enlarged scales of dorsal body arranged in V-shaped ridges along body midline-- -----3
- 2b. Enlarged scales not arranged in “V”-shaped ridges on dorsal body along midline (except *D. swinhonis*)-----*Diploderma*
- 3a. Head robust; HW/HL mostly above 70%; single pair of distinctively enlarged conical scales on posterior nape above shoulder, one on each side of vertebral crest-- -----*GenusX*
- 3b. Head slender; HW/HL mostly below 70%; pair of distinctively enlarged conical scale absent on nape above shoulder-----*Japalura sensu stricto*

SPECIES LEVEL RELATIONSHIPS AND TAXONOMY

Japalura sensu stricto

Within *Japalura sensu stricto*, relationships of sampled taxa are largely resolved (Figure 2). Interestingly, despite morphological similarity between *J. kumaonensis*

and *J. tricarinata* (Wang *et al.* 2017c), *Japalura kumaonensis* is most closely related to *J. variegata* (Figure 2; 0.986/69). As many of the Himalayan regions lack detailed surveys for *Japalura* diversity, including in northeast India, Bhutan, Nepal, and northwestern Bangladesh, many congeners are still poorly studied. In fact, several recognized species are known from a few vouchered specimens only and no genetic samples (e.g. *J. dasi*, *J. hamptoni*, *J. major*, and *J. sagittifera*). Not only may these remote regions harbor undescribed diversity, but also, given the wide variation in ornamentation observed among populations (Bhosale, Das, Manthey, 2013; Wang *et al.* 2017c), understudied taxa such as *J. andersoniana*, *J. kumaonensis*, *J. tricarinata*, and *J. variegata* may represent species complexes and contain cryptic diversity. Future research should focus on the collection of additional, vouchered genetic data of these poorly studied lineages and close examination of *Japalura* populations across the Himalaya region.

GenusXXX

For the congeners from Myanmar, both our morphological and molecular data support the previous suspicion that Myanmar populations of *GenusXXX* c.f. *planidorsata* were misidentified, and are in fact *GenusXXX otai*. When discussing the taxonomy of Myanmar populations of *GenusXXX. planidorsata* (considered as *Japalura planidorsata* in the paper), Mahony (2009) stated specifically that the only available specimen (juvenile) of *GenusXXX planidorsata* examined from Myanmar resembled the morphology of *GenusXXX otai*. However, given the lack of access to adult specimens from Myanmar, Mahony (2009) conservatively treated the Myanmar population as *GenusXXX* c.f. *planidorsata*, but he calls for further investigation on the taxonomic status of these populations. Based on our data, the

individuals of previously identified *GenusXXX planidorsata* from Myanmar are not monophyletic with respect to the topotypic *GenusXXX planidorsata*, but instead, form a monophyletic clade with topotypic *GenusXXX otai* from northeast India (Figure 2, Clade G). In addition, the morphological characteristics of the Myanmar populations match the diagnoses of *GenusXXX otai* and differ from *GenusXXX planidorsata*, including having flattened and posteriorly pointing conical scales on the temporal region of the head, shorter body lengths TrL 41.8–47.4% SVL, longer tails TAL 154.6–190.8% SVL, and shorter lip-stripes ending anterior to shoulders (Mahony, 2009). Therefore, we diagnose the Myanmar populations of *GenusXXX* c.f. *planidorsata* as *GenusXXX otai*, and recommend that records of the former species in Myanmar be corrected to represent the latter.

Diploderma

Recently, Ananjeva *et al.* (2007) described a new species of *Japalura*, *J. ngoclinensis* on the basis of three female specimens collected from the central highland of Vietnam, far outside of the known range of *Japalura sensu lato* at the time. Although there are no genetic data available for the species, we can assign it to the genus *Diploderma* based on our revised morphological diagnosis. The issue that remains is in regard to the taxonomic validity of *D. ngoclinense*. Despite the fact that the type specimens of the species are morphologically most similar to *D. splendidum*, a brief comparison was made to the latter species using one morphological characteristic only (Ananjeva *et al.*, 2017). The authors argued that the new species differs from *D. splendidum* by the absence of a transverse gular fold (Ananjeva *et al.*, 2017). However, based on the photographs of the type series in the original description, all type specimens of *D. ngoclinense* do have a shallow

transverse gular fold (particularly distinct on the paratype, VNMH 3110) (Ananjeva *et al.*, 2017:figs. 2–4), which are identical to what specimens of *D. splendidum* have in preservation (USNM 35522 [holotype], CIB 2588, 2591, 2596, 72468, 72469 from Chongqin, China). Based on the available data, the only differentiating characteristic between *D. ngoclinense* from *D. splendidum* is the middorsal scale count, which is higher in *D. ngoclinense* (54–56 vs. 44–52 in *J. splendidum*; Ananjeva *et al.* 2017). However, such a difference is based on a small sample size of three specimens of *D. ngoclinense*, and middorsal scale counts are known to vary in *Diploderma* (Ota, 1989; Manthey *et al.*, 2012; Wang *et al.*, 2016, 2017b). In addition to the suspicious distribution of *D. ngoclinense* (isolated and 1,000 km south of the most southern known range of the genus; Ananjeva *et al.*, 2017), we question the taxonomic validity of *D. ngoclinense* and have chosen to exclude it from our diagnostic key. Future field confirmation, detailed morphological comparisons, and phylogenetic analyses are needed to validate the taxonomic status of this species.

Historically, almost all *Diploderma* diversity in central and southwest China were thought to be a single species, *D. flaviceps* (Zhao *et al.*, 1999). Although numerous new species have been described from the *Diploderma flaviceps* complex, including *D. batangense*, *D. brevicaudum*, *D. flaviceps*, *D. iadinum*, *D. laeviventre*, *D. micangshanense*, *D. vela*, *D. yulongense*, and *D. zhaoermii* (Song, 1987; Li *et al.*, 2001; Gao & Hou, 2002; Manthey *et al.*, 2012; Wang *et al.*, 2015, 2016), many outlier records of *D. flaviceps* in southwest China have not been examined, some of which may represent cryptic diversity in the genus (Wang *et al.*, 2016). For example, the genetic sequence data of an MVZ specimen from Wenchuan, northwest Sichuan Province, China (MVZ 216622) was recorded as *D. flaviceps*

upon deposition in GenBank, and subsequently has been used for numerous phylogenetic studies (GenBank accession no. AF128500; Macey *et al.*, 2000; Schulte *et al.*, 2004; Zug *et al.*, 2006; Pyron *et al.*, 2013; Grismer JL *et al.*, 2016). However, according to the museum record, the collection locality of this specimen is East of Wenchuan, Sichuan Province, China, which is geographically proximate to the type locality of a different congener, *D. zhaoermii* (Gao & Hou, 2002). Furthermore, we were able to examine topotypic material of true *D. flaviceps* and *D. zhaoermii*, and access genetic data for both, and our phylogenetic analyses recover this individual of *D. cf. flaviceps* as nested within topotypic material of *D. zhaoermii* (Figure 2). Additionally, *D. flaviceps* is not recognized to occur outside the upper Dadu River Valley and its direct tributaries (Manthey *et al.*, 2012; Wang *et al.*, 2016). Therefore, we suspect that the specimen of *Diploderma* in question (MVZ 216622) and its associated genetic sequence on GenBank (AF128500) was misidentified, and represents the species *D. zhaoermii*. Poorly studied groups and continuous taxonomic revisions create problems such as this for museum and online databases. Numerous changes to the taxonomy of the *D. flaviceps* complex in China are no exception.

Biogeography

The historical recognition of four unique clades of distinct agamid lizards as a single genus, *Japalura sensu lato*, has resulted in an unusual distribution across multiple biogeographic regions, which has troubled biologists and posed problems for biogeographic inferences (Moody, 1980; Ananjeva *et al.*, 2017). With our revised taxonomy and classification of the genus *sensu lato*, the distributions of each of the four clades correspond well with the major recognized biogeographic regions: 1)

Japalura sensu stricto is distributed along the foothills of Himalaya from Pakistan to northeast India; 2), *GenusXXX* follows *Japalura sensu stricto* on the east and is distributed in the far eastern extension of the Himalaya in northeast India and northern Myanmar; 3), *Pseudocalotes* is distributed further to the south and east into the Indochinese region and Southeast Asia from southern China to Indonesia; and 4), and *Diploderma* is distributed in the far east, including East Asia and northern Indochina, from southwest Mainland China to Japan and northern Thailand (Figure 5). Relationships among congeners of each of the four genera within *Japalura sensu lato* may be useful in inferring biogeographic hypotheses of each distinct region, including the formation of Himalaya, the raising of the Tibetan plateau, and the formation of the Hengduan Mountain Region (Grismer JL *et al.*, 2016; Wang *et al.*, 2016).

Conclusion

Utilizing multi-locus and morphological datasets, we have addressed a long-standing issue concerning the paraphyletic nature of *Japalura sensu lato*, reclassifying the genus *sensu lato* into four genera. Revision of this widespread group further clarifies the phylogenetic relationships among Draconinae genera and sheds light on the biogeographic patterns of fauna across the Himalaya, Indochina, and East Asia. However, several questions remain that fall outside of the scope of this study. First, interspecific phylogenetic relationships of each of the four genera within *Japalura sensu lato* are still not well understood. Second, without a fully resolved phylogeny of these major clades within *Japalura sensu lato*, it will remain difficult to test finer-scale biogeographic hypotheses concerning some of the most interesting landscapes on earth, including the Himalaya Mountains and the

Hengduan Mountain Region in Southwest China. Third, genetic samples continue to be unavailable for many genera of Draconinae lizards (e.g. *Harpesaurus*, *Mictopholis*, *Oriocalotes*, and *Pseudocophotis*, etc.), and as results of such limited taxa sampling, phylogenetic relationships among some Draconinae genera (e.g. *Acanthosaura*, *Malayodracon*, and *Sitana*) remain poorly understood and in need of future study. Lastly, many species rich Draconinae genera such as *Acanthosaura* and *Pseudocalotes* have yet to be the focus of a comprehensive phylogenetic studies, leaving questions about interspecific relationships and the taxonomic validity of some species currently recognized. As such, dragon lizards of Asia continue to represent an enigmatic vertebrate radiation in need of a broad spectrum of studies aimed at better understanding everything from species-level diversity to evolutionary patterns of diversification.

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Chapter 3: Taxonomic Revisions and Conservation of *Diploderma* (Agamidae: Draconinae) in Southwest China

Abstract

Despite being recognized as ecologically and biogeographically important, the biodiversity of the Hengduan Mountain Region, particularly along the upper Mekong River, remains poorly understood. Here we describe a new species of Mountain Dragon of the genus *Diploderma* Hallowell, 1861 from the headwater region of the Mekong River in Chamdo, Tibet Autonomous Region, PR China. The species is recognized as a member of the *Diploderma flaviceps* (Barbour & Dunn 1919) complex, and it can be distinguished readily from all congeners by a suite of morphological characteristics, including its dwarf appearance (small body size and disproportionally short tails and short hind limbs), smooth or weakly keeled ventral scales, feebly developed vertebral crests in males, and by the absence of distinct gular spots in males and females. In addition to the description of the new species, we also reported morphological variations and range extensions of three recently described congeners along the same river, namely *D. batangense*, *D. iadinum*, and *D. vela*. We discussed the distribution patterns of the genus in the Hengduan Mountain Region and the urgent conservation priorities for protecting *Diploderma* species along the Mekong River. According to our best available data, we provided the IUCN assessments of the three species and proposed to list them as nationally protected under Chinese Wildlife Protection Act

Introduction

The historical continental collision between India and Asia resulted in dramatic changes to the landscape of southwest China, including the formation of the Hengduan Mountain Region (HMR) on the eastern edge of the Tibetan Plateau (Yang *et al.* 1982, 1983). Representing a major ecological transition zone along the sharp elevational gradients between the Tibet Plateau (over 4000 m) and lower Southwest China (less than 1000 m), the HMR possesses a unique topography of mountains and rivers. Not only do five of the major rivers of Asia (Irrawaddy, Mekong, Red, Salween, and Yangtze River) pass through this relatively small geographic region, but also, three of the five rivers (Mekong, Salween, and Yangtze) run parallel to each other in close proximity down this elevational gradient. This geography creates a parallel river system containing isolated valleys separated by north-south trending, continuous mountain ranges.

Of the five major rivers in the HMR, the Yangtze and Mekong Rivers are of particular interest. The two rivers differ substantially in their general topography: the Yangtze River has dramatic changes in flow directions, and its entire course is restricted within China only, while the Mekong flows consistently to the southeast and passes through six countries in Southeast Asia (Ren *et al.* 1959; Gu *et al.* 2016). Despite such differences, the upper reaches of both rivers in China stretch across similar environmental gradients in southwest China, moving from high-elevation grasslands, to deep and arid shrub valleys, and eventually to coniferous and subtropical forests in the far south (Ren *et al.* 1959; Yang *et al.* 1982, 1983). Recent work has suggested that the unique geography of these rivers in the HMR may have served as a source for refugial habitats during the Quaternary Ice Age, possibly contributing significantly to species diversification for many lineages across the

region (Fu *et al.* 2005; Che *et al.* 2010; López-Pujol *et al.* 2011; Yu *et al.* 2013; Lei *et al.* 2015).

Unfortunately, the general paucity of modern organismal studies across the HMR has impeded efforts to better understand the unique biogeographic history of this region in Southwest China. To date, vertebrate diversity, particularly amphibians and reptiles, remains understudied throughout the HMR—partly as a result of the general belief that the high-elevation and arid environments are unsuitable for many species (Hu *et al.* 1987; Zhao & Yang 1997; Li *et al.* 2010). As a result of this misconception, limited herpetofaunal surveys have been conducted along the upper Yangtze and Mekong rivers, and few studies have focused on species diversity along the river valleys (Hu *et al.* 1977; Zhao & Yang 1997; Zhao *et al.* 1999; Yang & Rao 2008). Interestingly, recent surveys and taxonomic studies have revealed significant cryptic diversity in multiple groups of endemic reptiles from the northern part of the HMR, suggesting an underestimated endemic reptilian diversity in this region (Huang *et al.* 2012; Manthey *et al.* 2012; Peng *et al.* 2014; Wang *et al.* 2015, 2016). One example of an overlooked group is the Mountain Dragons of the genus *Diploderma* Hallowell, 1861.

Historically, only a single species of *Diploderma*, *Diploderma flaviceps* (Barbour, Dunn, 1919) was recognized in the HMR, distributed across multiple isolated river valleys, including the upper Mekong, Salween, and upper Yangtze Rivers (Hu *et al.* 1987; Zhao *et al.* 1999; Yang & Rao 2008; Manthey *et al.* 2012). With renewed survey efforts, newly available vouchered specimens, and closer examination of published literature, recent taxonomic works have revised the morphological diagnoses of *D. flaviceps*, and the nomenclature of the species is restricted now to individuals with faint radial stripes around the eyes (or an absence

of stripes altogether), an absence of gular spots, and a presence of distinct dark rhombus-shaped patterns with light centers along the dorsal midline of the body (Manthey *et al.* 2012; Wang *et al.* 2015, 2016). Additionally, the range of *D. flaviceps* is restricted to the upper reaches of the Dadu River valleys only (Wang *et al.* 2016).

Following the revised taxonomic definition, re-examination of previously recognized specimens of *D. flaviceps* have revealed surprising endemic, cryptic diversity along major river valleys in Tibet and Yunnan provinces of China. In the past five years alone, five new species have been described from the *D. flaviceps* complex, including *D. iadinum* (Wang, Jiang, Siler, Che, 2016) and *D. vela* (Wang, Jiang, Che, 2015) from the upper Mekong River, *D. laeviventre* (Wang, Jiang, Siler, Che, 2016) from the upper Salween River, and *D. brevicaudum* (Manthey, Denzer, Hou, Wang, 2012) and *D. yulongense* (Manthey, Denzer, Hou, Wang, 2012) from the upper Yangtze River (Manthey *et al.* 2012; Wang *et al.* 2015, 2016, 2017a; Figure 3-1).

However, despite the recent discoveries of new congeners, many questionable records of *D. flaviceps* outside its current recognized range in the HMR remain unexamined by herpetologists, and herpetological diversity of many reaches of major rivers in the HMR were poorly understood. For example, in Yunnan Province, Yang and Rao (2008) reported a questionable record of *D. flaviceps* from the Upper Yangtze River valley in Shangri-La County (=Xianggelila), between the type localities of *D. batangense* and *D. yulongense*. Based on their description, the Shangri-La populations possess distinct morphological characteristics such as dark radial stripes around the eyes and colorful gular spots (Yang & Rao 2008), which contradict the original description of true *D. flaviceps* (Manthey *et al.* 2012; Wang *et*

al. 2016). In Sichuan Province, Zhao (2003) recorded *D. flaviceps* from Ganzi Prefecture, without referencing which specific river valleys the species was observed in. Although Garzê Prefecture does overlap with the currently recognized range (e.g. the Dadu River Valley) of true *D. flaviceps*, the prefecture also comprises many other isolated river valleys, including the upper Yangtze River Valley at the Sichuan-Tibet border in the far west. In Tibet, Hu *et al.* (1987) described a population of *D. flaviceps* from Chamdo, which also possesses conflicting characteristics such as distinct radial stripes around the eyes and colorful gular spots. As species of *Diploderma* across the HMR are recognized to be restricted and endemic to specific reaches of disparate river valleys (Zhao & Yang 1997; Manthey *et al.* 2012; Wang *et al.* 2016, 2017), these records of *D. flaviceps* with distinct morphological characteristics along upper Yangtze and Mekong Rivers in Yunnan, Sichuan, and Tibet may represent cryptic diversity. Therefore, it is likely that the diversity of *Diploderma* across the HMR remains underestimated (Wang *et al.* 2015, 2016, 2017).

In addition to poorly understood species diversity, most of the recently described congeners from the HMR lack basic natural history data (Li *et al.* 2001; Manthey *et al.* 2012; Wang *et al.* 2015, 2016). In particular, since their original descriptions, no study has been published regarding the morphological variation, distribution range, or conservation status of *D. batangense* along the upper Yangtze River and *D. iadinum* or *D. vela* along the upper Mekong River. Such an absence of basic biological data not only limits ecological and evolutionary studies of the group, but also prevents effective conservation assessments and environmental policy reform. With rapid, ongoing human developments along major rivers in the norther HMR, particularly along the upper Mekong and upper Yangtze rivers (Gu *et al.* 2016),

understanding vertebrate species diversity and basic natural history of endemic lineages across this region is of critical importance for effective conservation measures to be taken.

During herpetological surveys from 2015 to 2017, we collected specimens of previously identified *D. flavipes* populations along the upper Mekong River and upper Yangtze River in Yunnan, and Sichuan, and Tibet of China. Subsequent morphological comparisons reveal that the populations in Chamdo (Tibet), Shangri-La (Yunnan), and Baiyu (Sichuan) represent distinct, evolutionary lineages of *Diploderma* that have not been documented before, which we describe here as three new species. Furthermore, the *Diploderma* populations from the upper reaches of Yangtze River in Yunnan Province resemble *D. batangense*, and populations from the upper Mekong River in Tibet and Yunnan match the morphological diagnoses of *D. vela* and *D. iadinum*. Therefore, we discuss morphological variation observed for these newly discovered populations of *D. batangense*, *D. iadinum*, and *D. vela*, and extend their recognized ranges along the upper Yangtze and Mekong rivers. Based on all survey data to date, we comment on the natural history of *Diploderma* congeners in the HMR, assess their conservation status based on IUCN criteria, and provide conservation recommendations for all focal species. Lastly, with the addition of the new species described here, we provide an updated diagnostic key to all members of the genus *Diploderma*.

Methods

Taxa Samplings

Collections of all animals used for this present study obey the Wildlife Protection Act of PR China. Collection permits were issued by the Kunming Institute of

Zoology, Chinese Academy of Sciences (BBCJ-2014-001), and permissions for collections and surveys were granted by the Forestry Department and National Reserves of China. IACUC protocols (IACUC R17-019) and relevant protocols of the Animal Care and Ethics Committee at the Kunming Institute of Zoology were followed for the proper treatment of animals in the field.

Individuals of recognized *Diploderma* species were collected along the upper Yangtze and Mekong Rivers in Yunnan, Sichuan, and Tibet of China (Figure 2-1). In addition, eight specimens of the first new species were collected from the river valley near the headwaters of the Mekong River in Chamdo, Tibet, including one female from Karuo, Chamdo, Tibet in 2015 and two males and five females from Chaya, Chamdo, Tibet in 2016; 10 specimens of the second new species from upstream of the Jinsha River Valley in the Baiyu County, northwest Sichuan Province; and seven specimens of the third new species from lower Jinsha River Valley in Shangri-La County, northwest Yunnan Province (Figure 3-1; Appendix IV, V).

Following euthanasia, 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 specimens were deposited in the Museum of Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ).

Morphological Data

Measurements were made with digital slide calipers by KW to the nearest 0.01 mm. Focal characters and character definitions follow Wang *et al.* (2016), including: snout–vent length (SVL); tail length (TAL); head width (HW); snout–eye length (SEL); fore-limb length (FLL); hind limb length (HLL); Finger IV length (F4L);

Toe IV length (T4L); trunk length (TRL); supralabial count (SL); infralabial count (IL); number of scales between nasal and first supralabials (NSL); and number of scale rows between supralabials and orbit circle (SOR); enlarged post-occipital scale count (POS); enlarged post-tympanic scale count (PTY); enlarged post-riotal scale count (PRS); Finger IV subdigital lamellae count (F4S); Toe IV subdigital lamellae count (T4S); and middorsal scale count (MD). In addition, texture of ventral scales (TVS) (distinctively keeled vs. feebly keeled or smooth), presence of skin fold under nuchal crest (SNC) (present vs. absent), presence of skin fold under dorsal crest (SDC) (present vs. absent), presence of gular spot (GS) (present vs. absent), and status of crest scales (SCS) (erected and serrated vs. not erected or serrated) were also examined. Values for paired characters (SL, IL, NSL, SOR) were recorded from both sides of the body, with counts provided in left/right order. Comparisons of coloration in life were based on photographs of live specimens and type descriptions (Zhao *et al.* 1999; Manthey 2010; Wang *et al.* 2016).

In addition to the morphometric data, we also collected coloration and ornamentation data of both live and preserved specimens, which are standardized using terminology and codes in Köhler (2012). We recorded the following coloration and ornamentation data: (1) presence or absence of gular-spot; (2) coloration of gular spot; (3) shape of dorsolateral stripe of body (jagged vs. smooth); (4) coloration of dorsolateral stripes; (5) presence or absence of distinct vermiculated stripes on ventral head; (6) shape of vermiculated stripes on ventral head if present (reticulated vs. scattered); (7) coloration of inner lips; (8) coloration of oral cavity and tongue; and (9) coloration of ventrolateral body.

Whenever possible, morphological data for congener species were taken from type specimens or topotypic material, or secondarily from specimens collected

within close proximity to the type locality. Summaries of specimens examined are presented in Appendix V. In addition to vouchered specimens examined, morphological data of congeners were also obtained from the literature (Manthey *et al.* 2012). For maximum comparability and consistency, terminology in color descriptions follow Köhler (2012). Museum abbreviations for specimens examined follow Sabaj (2016) and include: Chengdu Institute of Biology, Chinese Academy of Sciences (CIB); Museum für Naturkunde Berlin, Berlin, Germany (ZMB); and National Museum of Natural History (NMNH), Washington D.C., USA.

Results

Morphological Variations of Recognized Congeners

Detailed morphometric data of the newly collected specimens of *Diploderma batangense*, *D. iadinum*, and *D. vela* are summarized in Appendix IV. For *D. batangense*, while individuals from the Tibetan sides of the upper Yangtze River match diagnoses of the topotypic and the type specimens, individuals from relatively lower reaches of Yangtze River Valley in Yunnan Province possess fainter yellow coloration on the ventral body surface in males (Figure 3-2). For *D. iadinum*, the newly collected specimens resemble the type series closely, although males (KIZ 027702 and 027704) possess distinct skin folds beneath crest scales, which differ from the type series.

Lastly, although morphological characteristics of the southern populations of *D. vela* in Yunnan Province matches the morphological data of type series, the northern populations of the species, which are in higher elevation habitats in the upper reaches of the Mekong River, possess noticeable morphological variation from the type series (Appendix IV). Specifically, the most northern populations have

relatively shorter tails (TAL 174.58–175.11% SVL in males, 159.82–161.62% in females) and shorter hind limbs (HLL 72.47–73.56% SVL in males, 65.67–67.67% in females) when compared to type specimens and other newly discovered southern populations (TAL 180.64–238.11% SVL in males, 177.37–202.17% in females; HLL 67.53–85.64% SVL in males, 71.45–81.62% in females). In addition, the T4S of newly discovered populations show greater variation than the type series (20–25 vs. 24 or 25).

With respect to color and ornamentation variation, males of the newly discovered *D. vela* populations of both species are largely consistent with the original description. However, the northern populations of *D. vela* from Rumei and Tongsha are observed to have more faint, dark vermiculate stripes on the ventral surfaces of the head (or the stripes are absent) and a lighter dorsal coloration.

Taxonomic Account

***Diploderma A* sp. nov.**

Wang, Ren, Jiang, Zou, Che, Siler (Figure 3-3-3-6)

Synonyms

Japalura flaviceps Hu *et al.* 1987; Zhao & Yang 1997; Li *et al.* 2010

Japalura cf. *flaviceps* Wang *et al.* 2015, 2016

Holotype. KIZ 027616, adult male from Chaya County, Chamdo, Tibet, PR China (30.7294° N, 97.3808° E, elevation 3,310 m; WGS 84), collected by Kai WANG on 19 June 2016 (Figures 3-3).

Paratopotypes. KIZ 027617–19, 027629–30, adult females collected by Kai WANG and Gadeng NIMA on 19 June 2016; KIZ 027628, adult male collected by Kai WANG and Gadeng NIMA on 21 June 2016.

Paratypes. KIZ 016486, adult female from Kanuo, Chamdo, Tibet, PR China (31.0433° N, 97.2239° E, elevation 3,245 m; WGS 84), collected by Dahu ZOU and Fang YAN on 13 May 2015.

Diagnosis. *Diploderma A* sp. nov. can be distinguished from all congeners by a combination of the following morphological characteristics: (1) adult body size small, SVL 49.85–58.93 mm; (2) head moderate, HW 66.31–75.16%; (3) HD limbs short, FLL 37.52–45.40% SVL, HLL 58.18–63.75% SVL; (4) tail short, TAL 153.01–154.40% SVL in males, 132.84–143.95% SVL in females; (5) transverse gular fold present, well developed; (6) tympanum concealed; (7) MD 43–56; (8) T4S 18–25; (9) ventral head and body scales feebly keeled or smooth; (10) nuchal and dorsal crest scales feebly developed, not distinctively erected or raised on skin folds; (11) dorsal enlarged scales relatively flat; (12) gular spots absent in both sexes; and (13) dorsolateral stripes present in both sexes, jagged, bright sulphur yellow in males, medium chrome orange in females.

Description of holotype. Adult male. Body size small, SVL 49.85 mm, moderately compressed dorsally, dwarf looking; tail short, TAL 154.40% SVL; hind limbs short, HLL 63.75% SVL. Head moderate, HL 33.16% SVL, HW 65.94% HL, HD 73.21% HD. Rostral rectangular, four times wider than long; nasal oval in shape, separated from rostral and first supralabial by single small scale; supralabials 9/10 (Left/Right), weakly keeled; suborbital scale rows 4/4, scales roughly equal in size, keeled; infralabials 10/9, smooth; post-riotal scales roughly homogeneous in size, except single moderately enlarged, keeled, post-riotal scale present on each side of head; enlarged scales spanning posterior orbit to dorsal anterior tympanum, 6/7; tympanum concealed beneath small scales; single enlarged, conical scale post-superior to tympanum. Supraciliaries 6/6, overlapping more than one third of lengths

with succeeding ones posteriorly. Dorsal head scales heterogeneous in size, distinctively keeled; dorsal snout surface with raised, keeled ridge, Y-shaped, running from snout tip to point in line with anterior edge of eyes on dorsal side; interparietal sub-rectangular, with distinct pineal eyespot; enlarged, conical scales present on occipital region, 4/4.

Ground scales of dorsal body small, keeled, intermixed with enlarged, keeled scales; enlarged keeled scales mostly flat; two paravertebral ridges present on each side of vertebral crest dorsolaterally, composed of enlarged scales, spanning distance from neck to pelvis; scales of medial dorsolateral ridge smaller than distal ridge, spreading further apart along ridge, less regularly aligned; nuchal and dorsal crest feebly developed, nuchal crest scales slightly raised comparing to dorsal, not erected; skin folds along crest absent; antehumeral fold present, distinct; axillary fold present. Scales of dorsal limbs keeled, roughly homogeneous in size on fore-limbs, heterogeneous in size on hind limbs, with enlarged scales scattered on posterior thighs; ventral scales of fore-limbs and lower hind limbs distinctively keeled, ventral scales of thigh feebly keeled. Tail slender and short, covered with keeled scales.

Ventral head scales largely homogeneous in size, smooth or feebly keeled; mental triangular, in contact with single pair of enlarged chin shields; gular pouch present in life, well developed, indistinct after preservation; transverse gular fold present, distinct; scales under gular fold smaller than other ventral scales. Ventral body scales homogeneous in size and shape, smooth or weakly keeled.

Coloration of holotype in life. Color name and code conventions follow Köhler (2012). The dorsal surface of the head is Smoke Gray (Code 264), with a single, distinct Raw Umber (Code 280) transverse band present between the eyes.

The band forms a “V-shaped” point medially, with the tip pointing posteriorly. Lateral surface of head is Pale Buff (Code 1). Distinct, Sepia (Code 286) radial stripes are present around the eyes, with the posterior stripes on each side of the head the broadest. These broad posterior stripes extend posteriorly to about two scales above the corner of the mouth. Oral cavity is uniform Light Flesh Color (Code 250).

Background coloration of the dorsal surface of the body is Raw Umber (Code 280) to Jet Black (Code 300). A Sulphur Yellow (Code 80) dorsolateral strip is present on each side of the vertebral crest from the occipital region of the head to the pelvis, both of which are strongly jagged. Nine Sulphur Yellow (Code 80), narrow transverse bands are distributed evenly between the two dorsolateral stripes from the neck to the base of the tail, separating the background coloration of the dorsal surfaces of the body into nine rectangular-shaped patches of pigmentation. Irregularly scattered, enlarged, Sulphur Yellow (Code 80) scales are distributed along the lateral surface of the body, ventral to the dorsolateral stripes. The background coloration of the dorsal surfaces of the forelimbs is Jet Black (Code 300), where it is Drab (Color 19) to Olive Brown (Code 278) on the hind limbs. Numerous narrow, Pale Buff (Code 1), transverse bands are present on the dorsal surfaces of the limbs, with fore-limb bands more distinct than hind limb bands. Coloration and ornamentation patterns gradually fade posteriorly towards the base of the tail, and the coloration of the tail eventually becomes Beige (Code 254).

Background coloration of the ventral surface of head is Pale Buff (Code 1). Distinct Jet Black (Code 300) vermiculate stripes are present, but they do not reach the center of the gular pouch, resulting in a triangular empty space in background coloration. The anterior and medial part of the ventral surface of the body is Pale

Sulphur Yellow (Code 92), with no distinct ornamentation patterns. The posterior part of the ventral body is white (Figure 3-3).

Coloration of holotype in preservative. In preservation, most color, pigmentation, and ornamentation patterns remain consistent with those in live specimens, with only a few exceptions. First, Sulphur Yellow (Code 80) coloration of dorsolateral stripes, transverse bands across dorsal body, and irregular spots of lateral surfaces of body fade into Pale Buff (Code 1) or white in preservation. Second, the Pale Sulphur Yellow (Code 92) of ventral surfaces of the body fade to Pale Buff (Code 1) (Figure 3-4).

Variation. Morphological variation among the type series is summarized in Table 3-1. Even though our sample size is small, sexual dimorphism is evident in the new species, with males possessing a smaller adult body size (SVL 49.85–51.48 mm in males vs. 51.05–58.01 mm in females), relatively longer tails (TAL 153.01–154.40% SVL in males vs. 132.84–143.95% in females), and relatively shorter trunk length (TRL 40.4–45.3% SVL in males vs. 51.7–52.4% in females). Furthermore, males have distinct coloration patterns from females, including the background body coloration (Raw Umber [Code 280] to Jet Black [Code 300] in males vs. Olive Horn Color [Code 16] or Drab [Code 19] in females), dorsal ornamentation patterns (solid, Jet Black [Code 300] rectangular patches separated by Sulphur Yellow [Code 80] bands along body midline in males vs. triangular, Olive Horn Color [Code 16] or Drab [Code 19] patches or zigzag stripes separated by Pale Buff [Code 1] transverse bands in females), throat patterns (conspicuous vermiculate stripes in males vs. more faded stripes in females), and shapes and coloration of dorsolateral stripes (distinct, Sulphur Yellow [Code 80] stripes in males vs. somewhat faded, Medium Chrome Orange [Code 75] stripes in females) (Figure 3-5). In one male

individual (KIZ 016486), the center of the throat is Pale Sulphur Yellow (Code 92), but nevertheless the coloration has faded edges and does not form a clear gular spot.

Comparisons. Although populations of *D. A* sp. nov. have been confused historically with *D. flaviceps*, the former can be distinguished readily from the latter by having a smaller adult body size (SVL 49.85–58.93 mm vs. 64.35–75.35 mm), shorter hind limbs (HLL 58.18–63.75% SVL in males, 59.69–62.82% in females vs. 64.93–70.86% SVL in males, 61.61–74.09% in females), shorter tails (TAL 153.01–154.40% SVL in males, 132.84–143.95% SVL in females vs. 170.08–191.26% SVL in males, 167.18–181.98% SVL in females), less distinctive crests in males (slightly raised nuchal crest scales, flat dorsal crest scales, with no skin fold underneath vs. distinctively erected crest scales along skin fold), distinct gular pigmentation patterns (vermiculated stripes not reaching the center of the throat vs. highly reticulated, mosaic patterns occupying the center of the throat), as well as by the absence of strongly differentiated conical, post-riatal scales (vs. presence), absence of dark rhomb-shaped patterns with yellow centers along the midline of the body (vs. presence), and presence of distinct radial stripes around the eyes (vs. absence or faded and indistinct) (Figure 3-13; Table 3-5).

The new species is phenotypically most similar to *D. laeviventre* and *D. brevicaudum*, from the upper Salween and middle Jinsha river valleys, respectfully. However, *Diploderma A* sp. nov. can be differentiated from *D. laeviventre* by having a smaller adult body size (SVL 49.85–58.93 mm vs. 64.00–71.60 mm), shorter hind limbs (HLL 58.18–63.75% SVL in males, 59.69–62.82% in females vs. 70.42%–74.33% SVL in males, 64.43%–74.06% in females), shorter tails (TAL 153.01–154.40% SVL in males, 132.84–143.95% SVL in females vs. 197.22–198.51% SVL in males, 168.57–184.38% SVL in females), fewer MD (43–56 vs.

57–59), feebly developed nuchal crest in males without strongly erected crest scales or skin fold (vs. distinctively erected crest scales on skin fold), and by the absence of distinct gular spots in both sexes (vs. presence), absence of M-shaped pigmentation patterns along body midline in males (vs. presence), and absence of distinct, dense dark speckles on all surfaces of head and dorsal and lateral surfaces of body (vs. presence) (Figure 3-13); and from *D. brevicaudum* by having relatively longer tails in males (TAL 153.01–154.40% SVL in males, 132.84–143.95% SVL in females vs. 140% in males, 125–145% in females), a greater number of MD (43–56 vs. 34–40), and smooth or weakly keeled ventral scales (vs. distinctively keeled) (Figure 3-13).

Diploderma A sp. nov. can be differentiated from *D. vela* by having shorter hind limbs (HLL 58.18–63.75% SVL vs. 65.67–85.64% SVL), shorter tails (TAL 153.01–154.40% SVL in males, 132.84–143.95% SVL in females vs. 174.58–238.11% SVL in males, 159.8–202.17% SVL in females), feebly developed crests in males without strongly erected crest scales or skin fold (vs. distinctively erected crest scales on continuous, well developed skin fold), weakly keeled or smooth ventral scales of head and body (vs. strongly keeled), flat and relatively less enlarged scales on dorsal body (vs. distinctly keeled, raised, and relatively large), and faint yellowish ventral coloration in live males (vs. uniform white) (Figure 3-4, 3-5).

The new species differs from all remaining congeners in Tibet and adjacent areas (*D. batangense*, *D. dymondi*, *D. iadinum*, *D. micangshanense*, *D. splendidum*, *D. yulongense*, *D. varcoae*, and *D. zhaoermii*) by having a shorter tail (TAL 153.01–154.40% SVL in males, 132.84–143.95% SVL in females vs. >160.00% SVL in males, >150.00% SVL in females), shorter hind limbs (HLL 58.18–63.75% SVL in

males, 59.69–62.82% in females vs. >64.00% SVL), and smooth or feebly keeled ventral scales (vs. distinctively keeled). Furthermore, from *D. batangense*, *D. iadinum*, and *D. yulongense*, the new species differs by the absence of gular spots in both sexes (vs. presence); from *D. batangense*, *D. dymondi*, *D. iadinum*, *D. micangshanense*, *D. splendida*, *D. yulongense*, and *D. zhaoermii* by the presence of narrow, orange dorsolateral stripes in females (vs. absence); from *D. andersoniana*, *D. batangense*, *D. iadinum*, *D. micangshanense*, *D. yulongense*, and *D. zhaoermii* by having feebly developed crests in males without strongly erected crest scales or skin fold (vs. distinctively erected crest scales on well developed skin fold); and from *D. dymondi*, *D. tricarinata*, and *D. varcoae* by having a concealed tympanum (vs. exposed).

Natural history. *Diploderma A* sp. nov. is terrestrial and inhabits high-elevation mountains (> 3,130m) in warm-and-dry valleys near the headwaters of the Mekong River in Chamdo, Tibet (Figure 3-6). Habitat throughout the areas includes mostly spiky shrubs (e.g. *Caragana* sp. and *Selaginella* sp.). The new species was observed to be most active in the morning and at dusk in the summer, and with individuals appearing to stay around the entrances to shelters (rock crevices and rodent/insect borrows) or in the shade of vegetation during hot afternoons. Predation may come from snakes observed at the type locality, such as the Plateau Viper, *Gloydius strauchii*, which was quite common in the area. Currently, *D. A* sp. nov. is known only from the valleys near the headwaters of the Mekong River in Karuo and Chaya Counties of Chamdo, Tibet, PR China. We believe the species may be a micro-endemic to this area based on our extensive field surveys of the surrounding region.

***Diploderma B* sp. nov.**

Wang, Che, Siler (Figure 3-7-3-9)

Synonyms. *Japalura flaviceps* Zhao 2003

Holotype. KIZ 032694, adult male from Yebatan, Gaiyu County, northwest Sichuan Province, China (98.9717 E, 30.7376 N, elevation 2756 m). Collected by Kai WANG on May 27th, 2017.

Paratopotypes. KIZ 032692, 032693, adult males; KIZ 032695–032699, KIZ 032730, adult females; all collected from the same locality as the holotype by Kai WANG on May 28, 2017.

Diagnosis. The new species can be diagnosed from congeners by a combination of the following morphological characteristics: (1) body size small, SVL 50.84–55.20 mm in males, 64.22–72.93 mm in females; (2) tail short, TAL 172.82–179.26% SVL in males, 140.19–152.19% in females; (3) head wide, HW 70.07–73.01% HL, HD 68.65–75.13% HW; (4) hind limb short, HLL 72.66–74.83% SVL in males, 61.66–63.85% in females; (5) tympanum concealed; (6) transverse gular fold present, well developed; (7) MD 39–43; (8) T4S 19–22; (9) nuchal and dorsal crest well developed in males with well developed skin folds; (10) ventral head scales smooth or feebly keeled; (11) ventral body scales distinctively keeled; (12) inner lips bright spectrum yellow in both sexes in life, distinct from background coloration of oral cavity; (13) oral cavity and tongue flesh color in both sexes in life; (13) gular spots present in both sexes, pale emerald green to light turquoise green in life; (14) ventral body greenish yellow to faint yellow in live males.

Description of holotype. Small sized agamid, SVL 50.84 mm, dwarf looking. Tail short, TAL 172.82% SVL. Limbs short, FLL 48.27% SVL, HLL

74.82% SVL. Head wide, HW 71.24% HL, HD 70.15% HW; 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 about equal size, irregularly arranged, keeled; suborbital scale rows 5/4, 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 scales 6/8 post-tympanic, one of which distinctively taller on each side; enlarged conical scales 2/6 post-rectal, 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 post orbit dorsally on each side; enlarged conical scales 4/4 post occipital.

Dorsal body scale heterogeneous, strongly keeled; axillary scales much smaller than other dorsals, granular shaped; enlarged, sub-pyramidal scales, each with single distinct medial keel, scattered across dorsum; enlarged scales mostly irregularly arranged, with some arranged in single paravertebral row close to vertebral crest on each side. Middorsal scale count 41; nuchal crest scales serrated, erected, much larger than neighboring dorsal scales; dorsal crest scales less erected, serrated; both crests on distinct skin fold 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. F4S 16/16, T4S 20/20.

Ventral head scales homogeneous in size and shape, regularly arranged, smooth or feebly keeled; gular pouch present in life, well developed yet not forming strong lateral gular fold; distinct transverse gular fold present across neck; scales under gular fold smaller than ones from central gular region.

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 (Code 261). A single V-shaped, Jet Black (Code 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 (Code 56) transverse bands with distinct Dark Neutral Gray (Code 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 (Code 266), with irregular ornamentation patterns of Ducky Brown (Code 285) to Jet Black (Code 300).

Lateral surface of head is white to Light Buff (Code 2). Distinct Jet Black (Code 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.

Background coloration of the dorsal surface of the body is Jet Black (Code 300). A distinct Pale Horn Color (Code 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 (Code 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 (Code 34) in the center and gradually transition to Jet Black (Code 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 (Code 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 (Code 300) coloration into thin reticulated patterns on ventrolateral sides of body. Dorsal surfaces of limbs are Jet Black (Code 300). Distinct Pale Buff (Code 1) to Pale Pinkish Buff (Code 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.

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 (Code 141) in coloration. Jet Black (Code 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 (Code 141) as in the gular spot. This Pale Emerald Green coloration gradually fades into Pale Greenish Yellow (Code 86) as moving posteriorly to the chest and abdomen; and coloration continues to fade, where it eventually becomes Pale Buff (Code 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 (Code 1), which becomes darker and transitions to Pale Pinkish Buff (Code 3) on ventral hands and feet.

Background coloration of the tail is Pale Pinkish Buff (Code 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 (Code 298) at the proximal end to Salmon Color (Code 58) at the distal end (Figure 3-7).

Coloration of holotype in preservation. While the ornamentation patterns remain the same after preservation, coloration of the holotype fades for the most parts. Specifically, the Pale Horn Colored (Code 11) dorsolateral stripes, the Pale Pinkish Buff (Code 3) irregular spots of dorsal body, and the Spectrum Yellow (Code 79) of inner lips fade into white; the Mahogany Red (Code 34) coloration of the dorsal body becomes Burnt Umber (Code 48); the Pale Emerald Green (Code 141) gular spot fades into Pale Cyan (Code 157); and the Pale Greenish Yellow (Code 86) of anterior ventral body fades into Cyan White (Code 156) or white (Figure 3-8)

Variations. Variations in measurements and scale counts are summarized in Table 3-2. Although the sample size is small, it is evident that the new species is sexually dimorphic. Males possess relatively longer tails (TAL 172.82–179.26% SVL in males vs. 140.19–152.19% in females), relatively longer hind limbs (HLL 66.94–74.82% SVL in males vs. 61.66–65.60% in females), raised crest on skin fold (vs. not raised, no skin fold). Furthermore, males of the new species differ from females in coloration and ornamentation patterns, including having distinct background coloration of dorsum (Jet Black [Code 300] to Mahogany Red [Code 34] in males vs. Tawny Olive [Code 17] to Clay Color [Code 18] in females), presence of distinct Pale Horn Color (Code 11) dorsolateral stripes in males (vs. absent or in faint Sulphur Yellow [Code 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 (Code 71); the same specimen also has irregular Darb-Gray (Code 256) patterns on the anterior and central abdomen, and its gular spot is Greenish Turquoise (Code 166). KIZ 032699 has the most faint vermiculated stripes on the ventral head. KIZ 032700 has Grayish Horn Colored (Code 268), irregular stripes and patches on the chest region of ventral body (Figure 3-7).

Comparisons. The new species is considered as part of the *Diploderma flaviceps* complex, but it can be distinguished from *D. flaviceps* readily by having a smaller adult body size and reversed sexual dimorphism in body size (SVL 50.84–55.20 mm in males, 64.22–72.93 mm in females vs. 71.65–82.06 mm in males, 64.35–73.25 mm in females), a relatively shorter tail (TAL 172.82–179.26% SVL in males, 140.19–152.19% in females vs. 170.08–193.26%

in males, 167.18–181.98% in females), 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 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 brown rhomb-shaped patterns with distinct yellow centers along dorsal midline (vs. presence).

Diploderma B sp. nov. is morphologically most similar to *D. batangense* and *D. vela*, in which all three species possess distinct black radial stripes around eyes and blackish dorsal background coloration, raised nuchal and dorsal crests on skin folds. However, the new species can be differentiated from *D. batangense* by having a shorter tail (TAL 172.82–179.26% SVL in males, 140.19–152.19% in females vs. 187.34–206.54% in males, 171.77–203.07% in females), relatively wider head (HW 70.07–73.01% HL vs. 65.45%–71.54%), and distinct spectrum yellow coloration of inner lips in life for both sexes (vs. same flesh color as the rest of oral cavity); and from *D. vela* by having a wider head (HW 70.07–73.01% HL vs. 65.22–69.79%), discontinuous skin folds between nuchal and dorsal sections in males (vs. continuous), distinct spectrum yellow coloration of inner lips in life for both sexes (vs. same flesh color as the rest of oral cavity), coloration of dorsolateral stripes in females (orange vs. sulphur yellow), and as well as by the presence of gular spots in both sexes (vs. absent in both sexes) (Figure 3-12).

For remaining closely distributed congeners in the northern HMR, the new species can be differentiated from all species by the distinct 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. laevis* and *D. A*

by having distinctively keeled ventral scales (vs. smooth or feebly keeled); from *D. slowinskii* by a smaller body size (SVL 50.84–55.20 mm in males, 64.22–72.93 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. brevicaudum* by having a longer tail (TAL 172.82–179.26% SVL in males, 140.19–152.19% in females vs. 140% in male, 125–145% in females) and by the presence of distinct gular spots in both sexes (vs. absent); from *D. yulongense* by having a much shorter tail (TAL 172.82–179.26% SVL in males, 140.19–152.19% in females vs. 211.3–247.6% in males, 182.1–227.3% in females), as well as by the presence of distinct black radial stripes below eyes (vs. absent), and by the absence of greenish yellow ventrolateral patches of body (vs. present); and from *D. iadinum* by the distinct body coloration in males (white to pale greenish yellow ventral body, jet black dorsal body with pale pinkish buff dorsolateral stripes in males vs. bluish white ventral body and emerald black dorsal body with emerald green speckles and dorsolateral stripes in males), shape of dorsolateral stripes in males (strongly jagged vs. smooth edged), and fewer dorsolateral ridges on body in females (one regular row on each side vs. two or more).

For the remaining congeners in the mainland East Asia, in addition to the distinct spectrum yellow coloration of inner lips (vs. same coloration as in oral cavity), the new species differs from *D. varcoae* and *D. dymondi* by having a concealed tympanum; from *D. chapaense*, *D. grahami*, *D. fasciatum*, *D. micangshanense*, and *D. yunnanense* by having a distinct transverse gular fold (vs. absent or feeble); from *D. splendidum* by much smaller adult body size (SVL 50.84–55.20 mm in males, 64.22–72.93 mm in females vs. >80 mm in both sexes) and much shorter tail (TAL <180% SVL in males, <153% in females

vs. >200% in both sexes); and from *D. zhaoermii* by a smaller adult body size in males (SVL < 55.20 mm vs. > 64 mm) and more T4S (T4S 19–22 vs. 23–27).

Lastly, for the island congeners (*D. brevipes*, *D. luei*, *D. makii*, *D. polygonatum*, and *D. swinhonis*), the new species differs from all by having a terrestrial lifestyle (vs. arboreal), presence of distinct transverse gular fold (vs. absent), and much wider head (HW >70% HL vs. <65%).

Natural History. The overall habitat of the new species is warm, semi-arid valley with considerable amount of vegetation coverage (moss, shrubs, and trees), which is much moister than habitat of congeners in lower reaches of the river (e.g. *D. batangense*) (Figure 3-9). Individuals were observed inhabiting rock piles among shrubs and forest edges. Females and juveniles seem to be less selective for weather conditions and were active even in during cloudy weather, where as males were only observed during the hottest time of sunny days. All observed females, including ones that were collected, were gravid, suggesting June may be the peak breeding-season of the species. Diet of the new species includes arthropods in the region, especially ants, as considerable amount of ant remains were found in the feces of collected individuals. Possible predations are likely from birds, and snakes (*Orthriophis taeniurus*).

***Diploderma C* sp. nov.**

Wang, Ren, Che, Siler (Figure 3-8, 3-10–3-11)

Synonyms. *Japalura flaviceps* Yang & Rao, 2008

Holotype. KIZ 028332, adult male, from Wujing, Shangri-La County, northwest Yunnan Province, China (27.7017 N, 99.4563 E, elevation 1982m, WGS 84). Collected by Kai Wang on July 9th, 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 028338, 028339, adult females from Shangjiang, Shangri-La County, northwest Yunnan Province, China (27.3689 N, 99.6659 E, elevation 2028m, WGS 84). Collected by Kai Wang and Jinlong Ren on July 10th, 2016.

Diagnosis. The new species can be diagnosed from congeners by a combination of the following morphological characteristics: (1) body length moderate SVL 55.94–63.44 mm; (2) tail long, TAL 202.03–208.63% SVL in males, 174.30–199.67% in females; (3) hindlimbs moderate HLL/SVL 70.02–76.75%; (4) head relatively wide and robust, HW 68.12–74.76% HL, HD 74.39–82.72% HW; (4) MD 39–43; (5) T4S 19–25; (6) tympanum concealed; (7) transverse gular fold present, distinct; (8) ventral scales of head and body distinctively keeled; (9) gular spots present in males only, light sulphur yellow; (10) oral cavity uniformly light flash color; (11) dorsolateral stripes present, jagged, always in males, sometimes in females, sulphur yellow in males, pale buff in females; (12) ventrolateral body light sulphur yellow in males; (13) ventral body white or pale buff in both sexes.

Description of holotype. Body size moderate, SVL 55.94mm; tail slender, TAL 208.63% SVL; limbs moderate, FLL 46.44% SVL, HLL 75.76% SVL. Head wide and robust, HW 68.12% HL, HD 80.43% HW; 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 rectal modified scales 5/7, mostly in sub-conical shape. 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, much larger than neighboring dorsal scales; middorsal scale count 41. Nuchal and dorsal crests erected on weak skin fold in life, 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 homogeneous, distinctively keeled; transverse gular fold present, distinct; gular pouch well developed 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-Darb (Code 50). Single Warm Sepia (Code 40) transverse band stretches across the forehead between eyes. Loreal and suborbital regions of the head are Pale Buff (Code 1). Warm Sepia (Code 40) radial stripes are present around eyes, of

which the inferior ones are faint and indistinct. The stripe from posterior corner of eye to rictus is the broadest. The lateral postorbital region is Beige (Code 254). Oral cavity and inner lips are uniform Light Flash Color (Code 250).

The background coloration of dorsum is True Cinnamon (Code 260). The background coloration is darker and become Brunt Umber (Code 48) when it is close to the edge of dorsolateral stripes. A strongly jagged, light Sulphur Yellow (Code 80) dorsolateral stripe is present on each side of the body from neck to pelvis. In between the two dorsolateral stripes, five Brunt Umber (Code 48), somewhat-rectangular patches are equally spaced along dorsal midline of body from neck to pelvis. Irregular Cream Color (Code 12) to Sulphur Yellow (Code 80) spots are present inferior of dorsolateral stripes. Dorsal surfaces of limbs are Pale Buff (Code 1) to pale Cinnamon-Darb (Code 50), with broad Beige (Code 254) to Burnt Umber (Code 48) transverse bands scattered from proximal to distal ends. Ventral lateral surfaces of the body are light Sulphur Yellow (Code 80). Dorsal and lateral surfaces of tail are mostly uniform Beige (Code 254).

The background coloration of the ventral surface of the head is Pale Buff (Code 1). Reticulated, Darb-Gray (Code 256) vermiculate stripes are present on ventral surface of head. A light Sulphur Yellow (Code 80) gular spot is present on the center of gular pouch. Ventral surfaces of the body, limbs, and the tail are mostly uniform Pale Buff (Code 1). Coloration of the ventral body is slightly yellowish towards the most anterior parts and towards the lateral sides (Figure 3-10)

Coloration of holotype in preservation. Coloration and ornamentations remain mostly the same after preservation, except the followings: (1) the light Sulphur Yellow (Code 80) of the gular spot, dorsolateral stripes, and irregular

spots of dorsum fades into white; and (2) the remaining dark coloration of dorsal body become slightly darker (Figure 3-8).

Variations. Morphometric and pholidosis variations are summarized in Table 3-3. 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 than females (TAL 202.03–208.63% SVL in males vs. 174.30–199.67% in females), relatively larger head (HL 30.56–31.23% vs. 27.95–28.74%), relatively longer hind limbs (HLL 75.76–76.75% SVL vs. 70.02–74.23%), and relatively shorter trunk (TrL 47.50–47.81% SVL vs. 50.47–56.92%). For ornamentations and coloration, males possess light Sulphur Yellow (Code 80) dorsolateral stripes that differ from background coloration, where as in females, such dorsolateral stripes are either indistinct (as in KIZ 028336) or in the same coloration as the background of dorsum, which is True Cinnamon (Code 260); the somewhat rectangular Brunt Umber (Code 48) patches along dorsal midline of body between dorsolateral stripes are in rectangular shape in females (the tips pointing at the posterior direction); and Sulphur Yellow (Code 80) gular spots are absent in females. On one female individual (KIZ 028336), the Warm Sepia (Code 40) transverse bands on dorsal head and the True Cinnamon (Code 260) dorsolateral stripes are absent, and the Brunt Umber (Code 48) patches along dorsal midline of body are indistinct; instead, its dorsal head is uniform Peach Red (Code 70), and this coloration continues posteriorly as a vertebral stripe until the base of the tail (Figure 3-10)

Comparisons. The new species was similar and confused as *D. flaviceps*, but it can be differentiated from the latter by having a smaller adult body size

(SVL 55.94–58.57mm in males, 56.77–63.44 mm in females vs. >70 mm in males, > 64 mm in females), weakly developed skin fold of crest (vs. strongly developed and raised in both sexes), tendency toward longer hind limbs (HLL 70.02–76.75% SVL vs. 61.61–70.00%), less developed post-occipital conical scales (sub-pyramidal shape vs. tall conical shape), as well as by the presence of gular spots in males (vs. absent), presence of distinct radial stripes around eyes (vs. absent), and the absence of dark rhomb-shaped patterns with distinct light centers on dorsal body along dorsal midline (vs. present).

For closely distributed congeners along the upper Yangtze River, *D. C* differs from *D. brevicauda* by having longer tail (TAL >174% SVL vs. <145%) and longer hind limbs (HLL >70% of SVL vs. <64%); from *D. yulongense* by having different coloration of gular spots in males (Sulphur Yellow [Code 80] vs. Opaline Green [Code 106]), as well as by the absence of gular spots in females (vs. present), and the absence of Greenish Yellow (Code 88) ventrolateral patches of body (vs. present); from *D. batangense* by having more PRS (3–7 vs. 0–3), different gular coloration ((light Sulphur Yellow [Code 80] vs. Pale Cyan [Code 157]), different coloration of ventral body in males (Pale Buff [Code 1] vs. Spectrum Yellow [Code 79]), and by the absence of gular spots in females (vs. mostly present); from *D. B* sp. nov. by having a longer tail (TAL >200% SVL in males, > 174% in females vs. <179 in males, <152% in females), more robust head (HD 74.39–82.72% HW vs. 68.65–72.91%), different gular coloration in males (Sulphur Yellow [Code 80] vs. Pale Emerald Green [Code 141]), different lip coloration (Light Flesh Color [Code 250] vs. Spectrum Yellow [Code 79]), as well as by the absent of gular spots in females (vs. present).

For congeners distributed in nearby river valleys, *D. C* sp. nov. differs from *D. A* sp. nov. by having a longer tail (TAL > 174% vs. <154%), longer hind limbs (HLL >70% SVL vs. <63%), better developed crest scales in males (erected and serrated on skin folds vs. not erected or serrated, skin fold absent), distinctively keeled ventral scales (vs. feebly keeled or smooth), and by the presence of gular spots in males (vs. absent); from *D. vela* by weaker and discontinuous skin fold under crests in males (vs. sail-like, continuous skin fold under crest), a tendency toward more robust head (HD 74.39–82.72% HW vs. 64.79–76.73%), and by the presence of gular spots in males (vs. absent); from *D. iadinum* by having relatively wider head (HW 68.12–74.76% HL vs. 63.15–69.55%), distinct body coloration (Emerald Green [Code 143] vs. True Cinnamon [Code 260] to Burnt Umber [Code 48]), and different coloration of gular spot (Sulphur Yellow [Code 80] in males, no gular spots in females vs. Light Caribbean Blue [Code 163] in males, Medium Greenish Yellow [Code 88] in females); from *D. laeviventre* by distinctively keeled ventral scales (vs. smooth or feebly keeled), fewer MD (39–45 vs. 57–59), and different coloration of gular spots (Sulphur Yellow [Code 80] in males, no gular spots in females vs. Dark Spectrum Yellow [Code 78] to Light Chrome Orange [Code 76] in both sexes); from *D. slowinskii* by 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 (Sulphur Yellow [Code 80] vs. Light Grass Green [Code 109]), and by the presence of gular spots in males (vs. absent).

For the remaining congeners, *D. C* sp. nov. differs from *D. dymondi* and *D. varcoae* by a concealed tympanum (vs. exposed); from *D. chapaense*, *D.*

fasciata, *D. micangshanense*, *D. splendidum*, *D. yunnanense*, and all species from islands (*D. brevipes*, *D. makii*, *D. luei*, *D. polygonatum*, and *D. swinhonis*) by having a transverse gular fold (vs. absent or feeble); from *D. zhaoermii* by a longer tail (TAL >200% SVL in males, > 174% in females vs. <190% in males, <160% in females) and different coloration of gular spots (Sulphur Yellow [Code 80] vs. Yellow Green [Code 103]) (Figure 3-12)

Natural History. The new species inhabits mix-forests along the upper Yangtze River Valley (Figure 3-11). Although living in a forested environment, *D. C* is terrestrial, basking and seeking shelters in rock piles and crevices on the hills. Lizard-eating snakes are common at the site (including *Elaphe carinata*, *Ptyaus nigromarginata*, and *Sibynophis collaris*), which may be the main source of predation of the new species. Locals believe meet of the new species has certain medical properties, and it is known as “Shan Pi Hou” by locals.

Discussion

Distribution of Diploderma in the HMR

Previous authors have suggested that the out-ranged records of *Diploderma flaviceps* in the unsurveyed river valleys in the HMR may represent cryptic diversity within the genus (Manthey *et al.* 2012; Wang *et al.* 2015, 2016), including populations from the headwaters of the Mekong River and much of the upper Yangtze River (Hu *et al.* 1977; Zhao *et al.* 1999; Yang & Rao 2008). Our discovery of the three new species within the *D. flaviceps* complex along the river valleys of Mekong and Yangtze River further supports this hypothesis and indicates that the diversity of the genus in the HMR may still be underestimated. In addition to the fact that many areas in the HMR, particularly along the major tributaries of upper

Yangtze River (e.g. Anning River and Yalong River), remained nearly untouched by herpetologists, it is likely that additional lineages await discovery.

Mekong River. Most recently, Rao *et al.* (2017) stated that *D. laeviventre* and *D. vela* occur in Yunnan Province; however, no reference to vouchered material or new data was provided. In the original description of *D. laeviventre*, the species was reported from the type locality in Basu, Markam County, Tibet only, which is about 224 km linear distance north from the Yunnan border along the Salween River (Wang *et al.* 2016), and to date there are no other published studies about the distribution of *D. laeviventre*. Furthermore, given the fact that we did not observe the species during our extensive field surveys along the Salween River Valley in northwest Yunnan Province in 2016, even at the Yunnan-Tibet border in Gongshan County of Yunnan Province, we feel it is unlikely that the distribution of *D. laeviventre* extends into Yunnan Province. As for *D. vela*, Wang *et al.* (2015) noted that the species might also occur in the adjacent reaches of the Mekong River; however, no other vouchered information has been presented to re-evaluate the species' geographic distribution prior to the present study. Near the northern range limits of *D. vela*, we discovered two new localities along the Mekong River close to Chamdo, in the Tongsha Village and the Rumei Township, which expand the distribution range of the species northward by 114 km in linear distance (type locality at Quzika, Markam, Tibet; Wang *et al.* 2015). Additionally, at the southern limits of *D. vela*'s range, our surveys resulted in observations of the species at three new localities in Yunnan Province: Foshan, Xilu, and Xidang villages, which expand the distribution of the species southward by 78 km linear distance (Figure 3-1). Those three southern localities fall between the type locality of *D. vela* and the type locality of *D. iadinum* (Wang *et al.* 2015, 2016). With no observations of *D.*

vela at the type locality of *D. iadinum* in Ninong, Deqin County based on the previous study and our recent surveys (Wang *et al.* 2016), we suspect that the southern range limit of *D. vela* does not extend beyond Ninong, Deqin County in Yunnan Province. Furthermore, Xidang Village in Deqin County may represent the southern range limit for the species. Therefore, we conclude that *D. vela* is distributed along the upper Mekong River Valley from Markam County, Tibet to Deqin County, Yunnan, with a total of about 192 km linear distance between the northern and southern distributional limits, and provide vouchered confirmation of the record of *D. vela* in Yunnan Province for the first time.

Finally, concerning *D. iadinum*, the results of our survey efforts indicate the species may possess a much more restricted range than its neighboring species, *D. vela*. Although we did discover a more southern population of *D. iadinum* in Yunling, Deqin County, the linear distance between the northern and southern range limits of the species remains less than 20 km only (Figure 3-1). Interestingly, the newly observed population of *D. iadinum* extends the species' range into more forested habitats that are quite different from the arid bushy habitats present at the type locality. Future studies on the life history and ecology of *D. iadinum* are needed to better understand the species' microhabitat preferences and ecological requirements.

Yangtze River. Prior to this present study, all congeners along the upper Yangtze River are known from the type localities and nearby areas only (Wang *et al.*, 2017). Through our consecutive field surveys since 2015, we were able to fill the gap of knowledge on the distribution pattern of *Diploderma* along the upper Yangtze River and get a better understanding of the ecology and conservation statuses of each individual species. From the upper reaches of the Yangtze River

(Baiyu County of Sichuan Province to Lijiang of Yunnan Province), *Diploderma B*, *D. batangense*, *D. C*, *D. yulongense*, and *D. brevicaudum* occupy consecutive sections of valleys north to south (Figure 3-1). Such continuous turnover pattern of congeners along the Yangtze River consists with patterns observed in nearby Rivers of the HMR (Wang *et al.* 2015, 2016; Rao *et al.* 2017), and similar patterns may also be observed in less-surveyed or un-surveyed tributaries of the Yangtze River in the HMR, including the Dadu River and Yalong River.

In conclusion, a total of 12 species of *Diploderma sensu lato* are recorded from Yunnan Province at present, including *D. brevicaudum* (Manthey *et al.*, 2012), *D. chapaense* (Wang *et al.*, 2017) *D. dymondi* (Zhao *et al.*, 1999; Yang & Rao 2008), *D. fasciatum* (Yang & Rao 2008), *D. iadinum* (Wang *et al.*, 2016), *D. C* (present study), *D. slowinskii* (Rao *et al.*, 2017), *D. splendidum* (Yang & Rao 2008), *D. varcoae* (Zhao *et al.*, 1999; Yang & Rao 2008), *D. vela* (present study), *D. yulongense* (Manthey *et al.*, 2012; Wang *et al.*, 2017), and *D. yunnanense* (Zhao *et al.*, 1999; Yang & Rao 2008); five species are recorded from Tibet, including *D. batangense*, *D. A* (present study), *D. B* (present study), *D. laeviventre* (Wang *et al.*, 2016), and *D. vela* (Wang *et al.*, 2015); and nine species were recorded from Sichuan Province, including *D. batangense*, *D. dymondi*, *D. fasciatum*, *D. flaviceps*, *D. sp. B*, *D. grahami*, *D. micangshanense*, *D. splendidum*, and *D. zhaoermii* (Zhao 2003; present study). Of such diversity, four species are from the Mekong River Valley (*D. A*, *D. iadinum*, *D. vela*, and *D. yunnanense*), five species are from the adjacent upper Yangtze River Valleys (*D. batangense*, *D. brevicaudum*, *D. B*, *D. C*, and *D. yulongense*), and two species are from the Salween River Valley (*D. laeviventre* and *D. slowinskii*) (Figure 3-1).

Conservation of Diploderma in the HMR

Like most congeners from the HMR, the three new species described here and *D. iadinum*, and *D. vela* are all restricted to valley habitats below 3400m of elevation along the valley habitats. Unfortunately, these valley habitats overlap greatly with human development, and habitat destruction poses the greatest threats to the conservation of these endemic lizards. During our survey efforts, large-scale construction projects were observed along these valley habitats along the upper Mekong River and Yangtze River in Yunnan, Sichuan, and Tibet, including expansion of local townships and agricultural lands, construction of tourist sites, development of National Highway G214, and construction of hydropower stations (Figure 3-13). Sadly, limited attention is paid to the impact of these landscape modifications on the conservation of terrestrial vertebrate species inhabiting the valleys, and current proposed conservation actions are far from effective (Northwest Engineering Corporation Lt. 2013; Shanshui Conservation Center 2016). Furthermore, many construction activities do not comply with approved environmental regulations or abide by environmental protection laws. During our field surveys, construction waste stemming from the development of National Highway were being disposed of into the valleys directly adjacent to the construction activities, instead of being transported to designated disposal areas. This has resulted in significant damage to native plant communities and physical structures of these important valley habitats (Figure 3-13). Similar kinds of illegal activities have impacted endemic *Diploderma* species in the region already. For example, road construction has destroyed much of the type locality of *D. iadinum* at Ninong, Deqin County within just a few months after the original description. Furthermore, expansions of agricultural land and tourism-associated construction

activities at the type locality of *D. vela* have reduced the available habitat dramatically since 2015 (Figure 3-13). Lastly and most unfortunately, for one of the new species we describe here, *D. sp. B*, its type locality was already under massive destructions from construction of a hydropower station when we first discovered the species in the wild in 2017.

Therefore, according to the IUCN criteria (IUCN, 2012), we recommend *D. vela* be considered Vulnerable (VU) based on the following criteria: VU B2 ab (area of occupancy estimated less than 2,000 km², and continuing decline of area and quality of habitat), *D. A*, *D. B*, and *D. C* as Vulnerable (VU) based on the following criteria: VU B2 ab (Area of occupancy estimated less than 500km²; continue decline observed in quality of habitats), and *Diploderma iadinum* as Endangered (EN) based on the following criteria: EN B2 ab (Area of occupancy estimated less than 500km²; continue decline observed in area, extent and quality of habitat; known to exist at no more than five locations). Additionally, due to their status as regional endemic vertebrate species, and close geographic association with the iconic world-heritage sites, The Three Parallel Rivers and Meili Snow Mountains, we recommend listing *D. A*, *D. B*, *D. C*, and *D. vela* as Class II nationally protected species, and *D. iadinum* as a Class I nationally protected species in China. Lastly, we urge the regional ministry of the environment to re-evaluate the impact of road construction activities on all endemic species in China and apply conservation actions accordingly. Furthermore, we recommend greater legal enforcement of environmental laws to ensure that all such activities comply with approved environmental guidelines and regulations.

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Table 1. Primers used for the PCR amplification and sequencing.

Gene	Primer Name	Primer Sequence
ND2	L4160	CGATTCCGATATGACCARCT
	H4980	ATTTTTCGTAGTTGGGTTTGRTT
	Jap_264F	GGGCCCATACCCCRAAAAC
	Jap_1559R	GGATTAATGCCCTCTGGATT
	Jap_L4437b_F	AAGCAGTTGGGCCCATACC
	Jap_H5540_R	TTTAGGGCTTTGAAGGC
	Jap_70F	CCACCAAACAACCTACACCTA
	Jap_1559R	GGATTAATGCCCTCTGGATT
BDNF	BDNF.F	CCCCAATGAAAGAAGTGASCCTC
	BDNF.R	TGGGTAGTTCGGCACTGAGAATTCC
CMOS	cmosG73.1	GGCTR TAAARCARGTGAAGAAA
	cmosG74.1	GARCWTCCAAAGTCTCCAATC
R35	R35.F	GACTGTGGAYGAYCTGATCAGTGTGG
	R35.R	GCCAAAATGAGSGAGAARCGCTTCTG

Table 2. Models of evolution selected by Akaike Information Criterion (AIC) using jModeltest.

Genes	Codon Position	AIC Model	Number of Characters
BDNF	1st codon	GTR+G	176
	2nd codon	HKY	176
	3rd codon	HKY+G	175
CMOS	1st codon	JC+G	181
	2nd codon	HKY+G	180
	3rd codon	HKY	180
R35	1st codon	HKY+G	213
	2nd codon	GTR	213
	3rd codon	HKY+G	213
tRNA	/	GTR+G	613
ND2	1st codon	GTR+G	345
	2nd codon	GTR+G	345
	3rd codon	GTR+G	345
COI	/	GTR+G	33

Table 2-3. Summary statistics and principle component scores for continuous morphometric measurements and their ratios. SVL: snout–vent length; TAL: tail length; HW: head width; HL: head length; SEL: snout–eye length; FLL: fore-limb length; HLL: hind limb length; TrL: trunk length; and CL: tallest nuchal crest length.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Standard dev	1.6799404	1.38498686	1.23092167	1.13589668	0.92048378	0.87762345	0.66128538	0.46187126	0.36432226	0.23089997
Proportion o	0.28222	0.19182	0.15152	0.12903	0.08473	0.07702	0.04373	0.02133	0.01327	0.00533
Cumulative F	0.28222	0.47404	0.62556	0.75458	0.83931	0.91633	0.96006	0.9814	0.99467	1
eigen	2.82219974	1.91818861	1.51516814	1.29026127	0.84729039	0.77022293	0.43729835	0.21332506	0.13273071	0.0533148
SVL	-0.4917849	0.04087374	-0.26865	0.08239617	-0.1881123	0.2505404	-0.0950231	0.71348213	0.15815908	-0.190415
CrestLength	-0.5584681	-0.1197189	-0.0464356	0.15107179	0.08173051	-0.0245183	-0.1387804	-0.1405807	-0.3310525	0.70206993
CrestLength/	-0.5545613	-0.0656303	0.06496267	0.14974939	-0.0550056	-0.0155952	-0.0714165	-0.5513857	0.01764441	-0.5905952
HL/SVL	-0.0159065	-0.221483	-0.5112704	0.08560606	0.21052439	-0.7628006	0.14778137	0.12099399	-0.0564109	-0.1269645
TrL/SVL	-0.1530909	0.17047253	0.60132876	0.05312366	-0.3664867	-0.4038633	0.38130233	0.25129971	-0.2748549	-0.0397185
SEL/HL	-0.162364	-0.0774553	0.42148373	-0.4035759	0.65441001	-0.1226466	-0.3283038	0.23854247	-0.023502	-0.136322
TAL/SVL	-0.0411345	-0.1344092	-0.0996815	-0.6677583	-0.5589583	-0.2254482	-0.382565	-0.0925843	0.044157	0.06531198
HW/HL	0.25178598	-0.2256223	0.2132461	0.56206863	-0.1772668	-0.1677042	-0.6683769	0.11788531	-0.0337631	-0.0546863
FLL/SVL	-0.0905683	-0.6411483	0.25310224	0.04366724	-0.0421936	-0.0141236	0.26751169	0.00182183	0.63809529	0.18451968
HLL/SVL	0.12401661	-0.6446178	-0.0365712	-0.1058782	-0.0488315	0.31180371	0.16416464	0.09994174	-0.612816	-0.2108368

Table 2-4. Comparisons of discrete morphological characters among the four clades of *Japalura sensu lato* and morphologically similar Draconinae genera. Abbreviations are the followings: HT: heterogeneous; HM: homogeneous; DLR: dorsolateral rows; VR: V-shaped rows; A: absent; P: present; K: keeled; S: smooth; TS: tall-spine shape; TT: tall triangular shape; LT: low triangular shape; FB: feeble; WD: well developed; DWL: dewlap.

Genus/Clades	Shape of Dorsal Scales	ments of Enlarged Scales	of Enlarged Conical Scales on Nape
<i>Acanthosaura</i>	HT	Irregular	A
<i>Calotes</i>	HM	/	A
Clade C	HT	DLR and VR	A
Clade G	HT	DLR and VR	P
Clade N	HT	DLR	A
Clade O	HT	Irregular	A
<i>Malayodracon</i>	HT	Irregular	A
<i>Pseudocalotes</i>	HT	Irregular	A
<i>Salea</i>	HM	/	A

Table 2-4. Continue.

Genus/Clades	Keel Status of Loreal Scales of Head	Head Spines	Shape of Crest Scales	Gular Pouch
<i>Acanthosaura</i>	K	P	TS	WD as Large DWL
<i>Calotes</i>	K	P	TS	WD, sometimes as DWL
Clade C	K	A	LT	FB or WD, sometimes as DWL
Clade G	K	A	LT	FB
Clade N	K	A	LT	FB or WD, sometimes as Dwelap
Clade O	S	A	TT	WD, sometimes as DWL
<i>Malayodracon</i>	K	A	TS	WDas Large DWL
<i>Pseudocalotes</i>	S	A	TT or TS	WD, sometimes as DWL
<i>Salea</i>	S	A	TS	WDas Large DWL

Table 2-5. Bayesian hypothesis testing.

	Hypothesis	Description of Constraint	Posterior Probability
H1	Does <i>Malayodracon</i> form monophyletic group with East Asian <i>Japalura sensu lato</i> ? Monophyly of island <i>Japalura</i> and <i>Malayodracon</i>	All sampled Island <i>Japalura</i> and <i>Malayodracon robinsonii</i>	0.00
H2	Does <i>Calotes</i> form sister clade with <i>Salea</i> ? Monophyly of the clade containing <i>Calotes</i> and <i>Salea</i>	All sampled <i>Calotes</i> and <i>Salea</i> species	0.00
H3	With exclusion of <i>Japalura bapoensis</i> , do congeners from each of three regions form a monophyletic clade?	All sampled species from the Himalayan region	0.00
H4	Monophyly of Himalayan species group	All sampled species from mainland East Asia	0.00
H5	Monophyly of Indochinese species + island species	All sampled species from mainland East Asia and Taiwan	1.00
H6	Does <i>Japalura bapoensis</i> belong to <i>Japalura sensu lato</i> or <i>Pseudocalotes</i> ? Monophyly of <i>Japalura bapoensis</i> and remaining Indochinese+island	All sampled species from mainland East Asia including <i>J. bapoensis</i>	0.00

Table 3-1. Morphological and pholidosis characteristics of the type series of *Diploderma A* sp. nov. Abbreviations are listed in methods. Paired characteristics such as supralabial scale counts are presented in left/right order; “-” indicates missing data (KIZ 016486 has an incomplete tail).

Museum Catalog Number	KIZ 027616	KIZ 027628	KIZ 026729	KIZ 027619	KIZ 027630	KIZ 027018	KIZ 027617	KIZ 016486
Type Status	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
Sex	M	M	F	F	F	F	F	F
SVL	49.85	51.48	58.93	51.79	51.05	55.91	58.01	50.24
TAL	76.97	78.77	78.28	71.23	71.57	80.48	78.46	—
HL	16.53	13.98	17.57	14.63	14.20	16.22	16.38	15.16
HW	10.90	9.33	11.66	10.10	10.24	11.59	11.81	10.91
SEL	6.26	5.43	6.64	5.56	5.12	6.46	5.72	5.36
FLL	22.63	19.49	24.84	19.52	19.45	20.98	24.69	19.32
HLL	31.78	29.95	37.02	31.74	31.75	33.37	33.84	30.31
T4L	8.24	8.17	7.59	8.41	6.99	7.85	8.63	7.63
TRL	22.59	20.81	30.46	26.83	26.73	29.08	30.44	25.01
TAL/SVL	154.40%	153.01%	132.84%	137.54%	140.20%	143.95%	135.25%	—
HL/SVL	33.16%	27.16%	29.82%	28.25%	27.82%	29.01%	28.24%	30.18%
HW/HL	65.94%	66.74%	66.36%	69.04%	72.11%	71.45%	72.10%	71.97%
SEL/HL	37.87%	38.84%	37.79%	38.00%	36.06%	39.83%	34.92%	35.36%
FLL/SVL	45.40%	37.86%	42.15%	37.69%	38.10%	37.52%	42.56%	38.46%
HLL/SVL	63.75%	58.18%	62.82%	61.29%	62.19%	59.69%	58.33%	60.33%
TRL/SVL	45.32%	40.42%	51.69%	51.81%	52.36%	52.01%	52.47%	49.78%
SL	9/10	10/10	9/10	10/9	9/9	8/7	9/10	10/9
IL	10/9	11/11	10/11	10/10	11/11	9/9	10/12	12/10
NSL	1/1	1/1	1/2	2/2	1/2	1/1	2/1	1/1
MD	47	50	49	45	46	43	49	56
F4S	15/16	16/17	16/15	15/16	16/15	15/13	14/16	15/15
T4S	18/19	21/23	22/23	22/21	18/19	18/22	21/22	19/19
SOR	4/4	4/4	4/3	4/4	4/4	4/4	4/4	3/3
PTS	3/3	3/2	2/2	4/5	3/3	2/1	5/5	1/2
PTY	1/2	1/1	3/3	4/4	3/2	2/3	2/1	2/2
PRS	2/0	1/0	2/2	2/3	1/0	3/2	1/1	2/2

Table 3-2. Morphological and pholidosis characteristics of the type series of *Diploderma B* sp. nov.. Abbreviations are listed in methods. Paired characteristics such as supralabial scale counts are presented in left/right order; “-” indicates missing data (KIZ 032730 has missing 4th toe). KIZ 032692 has an incomplete tail.

Museum Catalog Number	KIZ 032692	KIZ 032694	KIZ 032693	KIZ 032696	KIZ 032695	KIZ 032698	KIZ 032697	KIZ 032730	KIZ 032699
Type Status	Paratopotype	Paratopotype	Holotype	Paratopotype	Paratopotype	Paratopotype	Paratopotype	Paratopotype	Paratopotype
Sex	M	M	M	F	F	F	F	F	F
SVL	54.50	55.20	50.84	64.22	67.08	72.93	67.65	67.36	66.01
TAL	81.56	98.95	87.86	92.89	100.22	102.24	98.52	98.56	100.46
HL	17.56	17.20	16.03	18.84	19.14	19.80	19.38	19.28	19.27
HW	12.82	12.16	11.42	13.51	13.49	14.21	14.13	13.51	13.69
HD	9.19	8.53	8.62	9.35	9.82	10.36	9.70	10.15	9.54
SEL	6.90	6.44	5.95	6.63	7.15	7.46	7.16	6.83	6.74
FLL	23.50	25.37	24.54	26.78	26.88	29.56	29.45	26.99	27.10
HLL	36.48	40.11	38.04	40.13	41.59	44.97	44.38	42.03	42.15
T4L	9.87	10.09	9.46	9.30	9.54	9.71	10.22	10.06	9.50
TRL	25.30	25.01	21.33	34.63	33.01	39.67	36.52	34.82	35.00
TAL/SVL	149.65%	179.26%	172.82%	144.64%	149.40%	140.19%	145.63%	146.32%	152.19%
HL/SVL	32.22%	31.16%	31.53%	29.34%	28.53%	27.15%	28.65%	28.62%	29.19%
HW/HL	73.01%	70.70%	71.24%	71.71%	70.48%	71.77%	72.91%	70.07%	71.04%
SEL/HL	39.29%	37.44%	37.12%	35.19%	37.36%	37.68%	36.95%	35.43%	34.98%
HW/HD	71.68%	70.15%	75.48%	69.21%	72.79%	72.91%	68.65%	75.13%	69.69%
FLL/SVL	43.12%	45.96%	48.27%	41.70%	40.07%	40.53%	43.53%	40.07%	41.05%
HLL/SVL	66.94%	72.66%	74.82%	62.49%	62.00%	61.66%	65.60%	62.40%	63.85%
TRL/SVL	46.42%	45.31%	41.96%	53.92%	49.21%	54.39%	53.98%	51.69%	53.02%
SL	9/8	8/9	9/8	9/9	8/9	8/10	9/9	9/8	9/8
IL	9/10	9/9	10/8	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	43	43	41	41	39	39	41	43	40
F4S	14/16	16/16	16/16	13/14	16/15	14/15	16/15	14/15	16/15
T4S	22/22	21/22	20/20	19/19	21/22	20/19	19/21	19/-	22/22
SOR	4/4	4/5	4/4	4/4	4/4	4/4	4/4	4/4	4/4
PTS	4/4	4/4	7/5	3/3	4/3	3/3	5/6	5/5	3/5
PTY	5/7	6/7	6/6	5/4	6/5	4/4	3/5	6/7	4/5
PRS	7/6	6/5	8/8	6/9	8/6	5/5	4/4	5/6	4/6

Table 3-3. Morphological and pholidosis characteristics of the type series of *Diploderma C* sp. nov.. Abbreviations are listed in methods. Paired characteristics such as supralabial scale counts are presented in left/right order; “-” indicates missing data (KIZ 028338 has an incomplete tail)

Museum Catalog Number	KIZ 028333	KIZ 028332	KIZ 028335	KIZ 028334	KIZ 028336	KIZ 028338
Type Status	Paratopotype	holotype	Paratopotype	Paratopotype	Paratopotype	Paratype
Sex	M	M	F	F	F	F
SVL	58.57	55.94	61.65	59.78	56.77	63.44
TAL	118.33	116.71	114.78	119.36	98.95	-
HL	17.90	17.47	17.38	17.18	15.87	18.07
HW	13.02	11.90	12.10	12.41	11.17	13.51
HD	10.77	9.57	9.73	9.50	8.46	10.05
SEL	6.96	6.53	6.62	6.41	5.81	6.58
FLL	28.42	25.98	29.23	27.24	25.89	27.54
HLL	44.95	42.38	44.75	43.35	42.14	44.42
T4L	11.33	10.58	10.56	11.38	11.00	10.74
TRL	28.00	26.57	35.09	30.69	28.65	33.16
TAL/SVL	202.03%	208.63%	186.18%	199.67%	174.30%	-
HL/SVL	30.56%	31.23%	28.19%	28.74%	27.95%	28.48%
HW/HL	22.23%	21.27%	19.63%	20.76%	19.68%	21.30%
SEL/HL	38.88%	37.38%	38.09%	37.31%	36.61%	36.41%
HD/HW	82.72%	80.42%	80.41%	76.55%	75.74%	74.39%
FLL/SVL	48.52%	46.44%	47.41%	45.57%	45.61%	43.41%
HLL/SVL	76.75%	75.76%	72.59%	72.52%	74.23%	70.02%
TRL/SVL	47.81%	47.50%	56.92%	51.34%	50.47%	52.27%
SL	10/9	10/10	9/10	8/8	8/8	9/9
IL	10/10	12/13	11/12	9/10	11/11	10/9
NSL	1/1	1/1	2/2	1/1	1/1	1/1
MD	39	41	40	42	45	43
F4S	16/16	16/17	17/19	18/18	15/17	14/15
T4S	21/21	23/23	21/24	25/25	21/22	19/19
SOR	3/4	5/5	4/4	5/5	3/3	3/3
PTS	3/3	4/4	4/4	5/5	4/4	3/4
PTY	6/7	7/8	4/5	3/5	5/6	3/2
PRS	4/4	5/7	3/3	4/6	4/3	3/5

Table 3-4. Ranges and averages of morphological and pholidosis comparisons among *Diploderma* A sp. nov., *D. B* sp. nov., *D. C* sp. nov., *D. brevicaudum*, *D. flaviceps*, *D. laeviventre*, and *D. vela*. Abbreviations are listed in methods. Data of *D. brevicaudum* was taken from Manthey *et al.* (2012) thus have different significant figures. Average values for each characteristic are given in parentheses. For the pholidosis characteristics (SL, IL, MD, T4S), data of males and females are grouped together for each species, as sexual dimorphism in those characteristics is not evident. "/" and "?" indicates missing data (either the actual head length or the HL/SVL ratio was not reported in the original description of *D. brevicaudum*; and live coloration of *D. brevicaudum* is unknown); "+" : presence; "-" : absence; "W" : weak or feeble; "S" : strong or distinct

Species	sex	Diploderma A sp. nov.			Diploderma B sp. nov.			Diploderma C sp. nov.		
		M	2	F	M	3	F	M	2	F
Keel status of ventral scale (TVS)	sample size									
	SVL									
	HL/SVL	49.85–51.48 (50.67)	50.24–58.93 (54.32)		50.84–55.20 (53.51)	64.22–72.93 (67.54)	55.94–58.57 (57.26)		56.77–63.44 (60.41)	
	TAL/SVL	27.16–33.16 (30.16)	27.82–30.18 (28.88)		31.16–32.22 (31.64)	27.15–29.34 (28.58)	30.56–31.23 (30.90)		27.95–28.74 (28.34)	
	FLU/SVL	153.01–154.40 (153.71)	132.84–143.95 (137.95)		172.82–179.26 (176.04)	140.19–152.19 (146.40)	202.03–208.63 (205.33)		174.30–199.67 (186.72)	
Crest Scale erect and serrated (SCS)	HLU/SVL	37.86–45.40 (41.63)	37.52–42.56 (39.41)		43.12–48.27 (45.78)	40.07–43.53 (41.16)	46.44–48.52 (47.48)		43.41–47.41 (45.50)	
	HLU/SVL	58.18–63.75 (60.96)	59.69–62.82 (60.78)		66.94–74.82 (71.47)	62.00–65.60 (63.00)	75.76–76.75 (76.25)		70.02–74.23 (72.34)	
	gular spot (GS)	W	W		S	S	S		S	
	skin fold of nuchal crest (SNC)	-	-		+	+	+		-	
	skin fold of dorsal crest (SDC)	-	-		+	+	+		-	
Inner Lip Coloration	Crest Scale erect and serrated (SCS)	-	-		+	+	+		+	
	Inner Lip Coloration	Flesh Color	Flesh Color		Spectrum Yellow	Spectrum Yellow	Flesh Color		Flesh Color	

Table 3-4. Continue.

Species	<i>Diploderma vella</i>	<i>Diploderma flaviceps</i>	<i>Diploderma laeviventre</i>	<i>J. batangense</i>	
sex	M	M	M	M	F
sample size	10	5	2	6	5
SVL	51.62–64.52 (58.23)	71.65–75.35 (74.01)	66.70–71.60 (69.15)	55.48–62.81 (59.31)	54.66–63.11 (59.98)
HU/SVL	30.48–32.84% (31.43%)	30.43%–31.95% (31.21%)	31.53%–31.79% (31.66%)	28.77–32.18% (30.93%)	28.51–31.69% (30.16%)
TAL/SVL	174.58–238.11% (199.26%)	170.08%–191.26% (182.58%)	197.22%–198.51% (197.86%)	187.34–206.54% (194.63%)	171.77–203.07% (186.88%)
FLI/SVL	43.52–53.09% (47.92%)	39.02–43.95% (41.07%)	44.44%–45.67% (45.06%)	45.98–49.80% (47.93%)	46.21–51.18% (48.37%)
HLL/SVL	67.53–85.64% (75.60%)	64.93%–70.86% (68.36%)	70.42%–74.33% (72.37%)	74.71–79.83% (76.36%)	73.42–79.22% (76.94%)
Keel status of ventral scale	S	S	W	S	S
gular spot	-	-	+	+	+
skin fold of nuchal crest	+	+	+	+	-
skin fold of dorsal crest	+	+	-	+	-
Crest Scale erect and serrated	+	+	+	+	+
Inner Lip Coloration	Flesh Color	Flesh Color	Flesh Color	Flesh Color	Flesh Color

Table 3-4. Continue.

Species sample size	<i>Diploderma A</i> sp. nov. 8	<i>Diploderma B</i> sp. nov. 9	<i>Diploderma C</i> sp. nov. 6	<i>Diploderma brevicaudum</i> 4
SL	7-10 (9.21)	8-10 (8.67)	8-10 (9.00)	6-9 (7.80)
IL	9-12 (10.28)	8-10 (9.33)	9-13 (10.67)	7-10 (8.5)
T4S	18-23 (20.44)	19-22 (20.59)	19-25 (22.00)	16-20 (18.40)
MD	43-56 (48.13)	39-43 (41.11)	39-45 (41.67)	34-40 (37.3)

Table 3-4. Continue.

Species Sample Size	<i>Diploderma vela</i> 20	<i>Diploderma flaviceps</i> 8	<i>Diploderma laeviventre</i> 5	<i>Diploderma batangense</i> 11
SL	7-10 (8.88)	9-11 (9.63)	7-9 (8.10)	7-11 (9.27)
IL	9-12 (10.15)	10-11 (10.64)	7-11 (8.80)	9-13 (10.55)
T4S	20-25 (21.90)	22-24 (23.50)	23-25 (23.80)	18-24 (21.14)
MD	40-50 (44.47)	43-48 (44.75)	57-59 (58.20)	41-53 (43.91)

Figure 1-1. Distribution range and general habitat types of *Japalura sensu lato* in Asia.

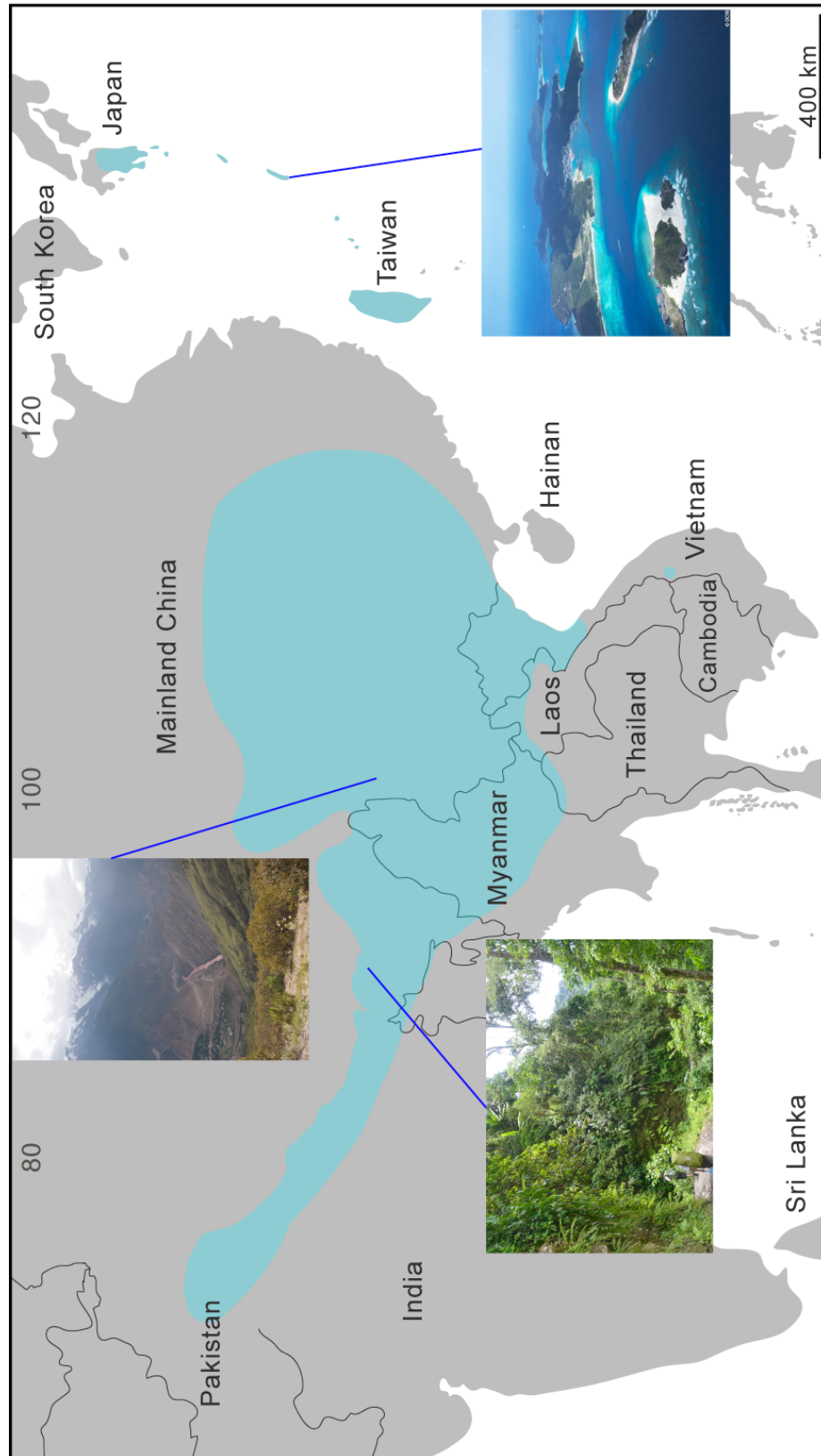
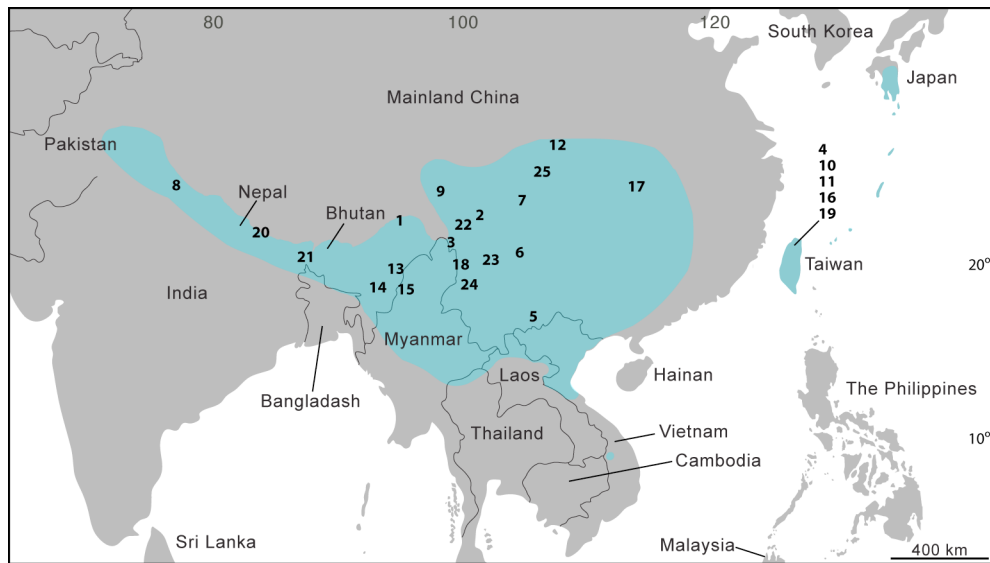


Figure 1-2. Examples of different eco-morphs of *Japalura sensu lato* in Asia. A: arboreal type (*Japalura polygonata*); B: semi-arboreal type (*Japalura yulongensis*); C: leaf litter type (*Japalura otai*); D: terrestrial type (*Japalura vela*). Photos by Kai Wang, V. Deepak, and Hang Zhou.



Figure 2-1. Taxonomic sampling of *Japalura sensu lato* in Asia.



Species of *Japalura sensu lato*

- | | | |
|--------------------------------|-------------------------------------|--------------------------------|
| 1 <i>Japalura andersoniana</i> | 9 <i>Japalura laeviventris</i> | 17 <i>Japalura splendida</i> |
| 2 <i>Japalura batangensis</i> | 10 <i>Japalura luei</i> | 18 <i>Japalura slowinskii</i> |
| 3 <i>Japalura bapoensis</i> | 11 <i>Japalura makii</i> | 19 <i>Japalura swinhonis</i> |
| 4 <i>Japalura brevipes</i> | 12 <i>Japalura micangshanensis</i> | 20 <i>Japalura tricarinata</i> |
| 5 <i>Japalura chapaensis</i> | 13 <i>Japalura otai</i> | 21 <i>Japalura variegata</i> |
| 6 <i>Japalura dymondi</i> | 14 <i>Japalura planidorsata</i> | 22 <i>Japalura vela</i> |
| 7 <i>Japalura flaviceps</i> | 15 <i>Japalura cf. planidorsata</i> | 23 <i>Japalura yulongensis</i> |
| 8 <i>Japalura kumaonensis</i> | 16 <i>Japalura polygonata</i> | 24 <i>Japalura yunnanensis</i> |
| | | 25 <i>Japalura zhaoermii</i> |

Figure 2-2. Phylogenetic relationships of *Japalura sensu lato* inferred from mitochondrial and nuclear DNA using both maximum likelihood and Bayesian analyses. Bayesian supports and bootstraps values are shown for each node, except for node I and J, which differs between two types of analyses (either are strongly supported).

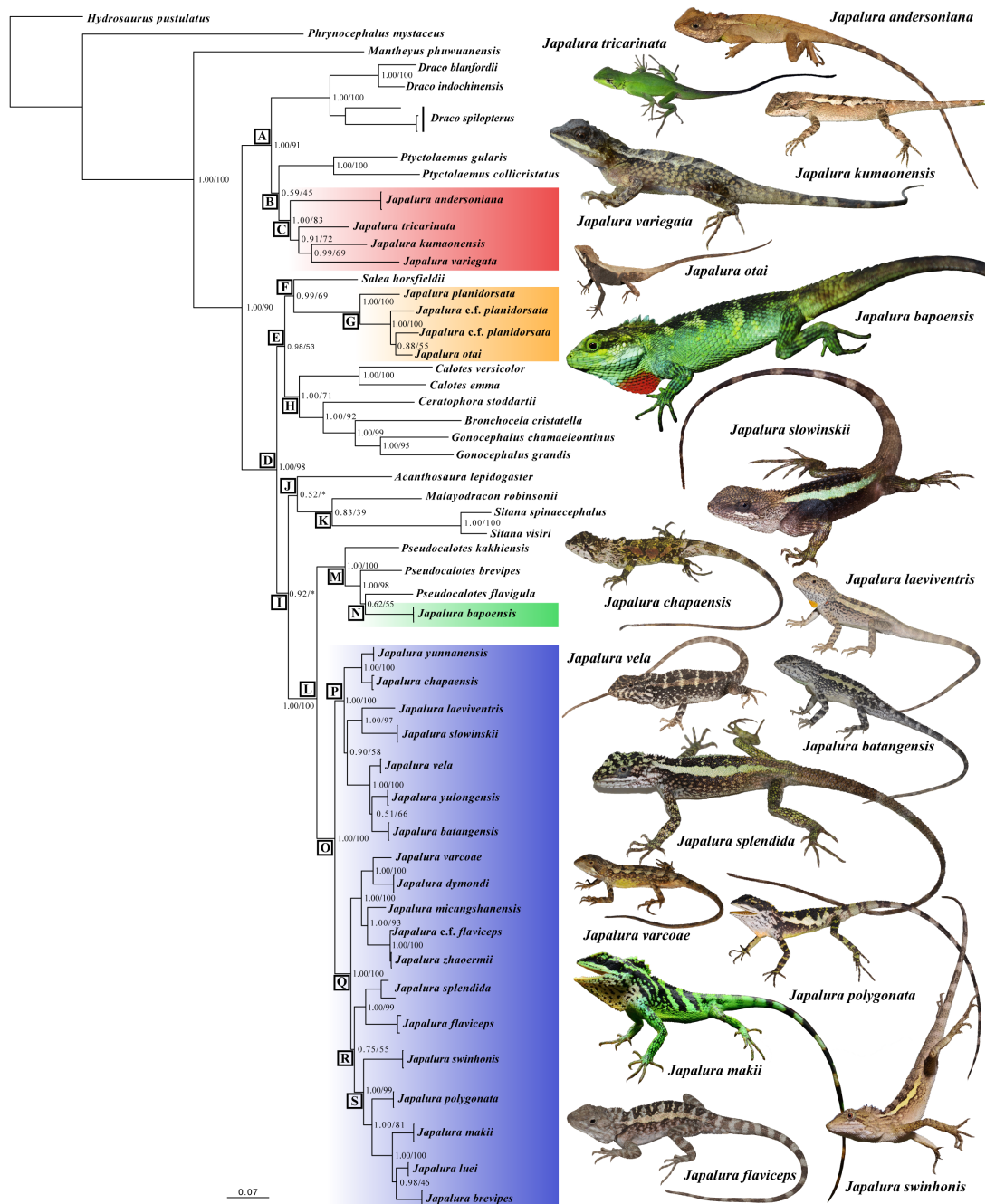


Figure 2-3. Principle component analysis (PCA) (left) and discriminant analysis of principle component (DAPC) (right) of continuous morphometric measurements and ratios of *Japalura sensu lato* and morphologically-similar genera.

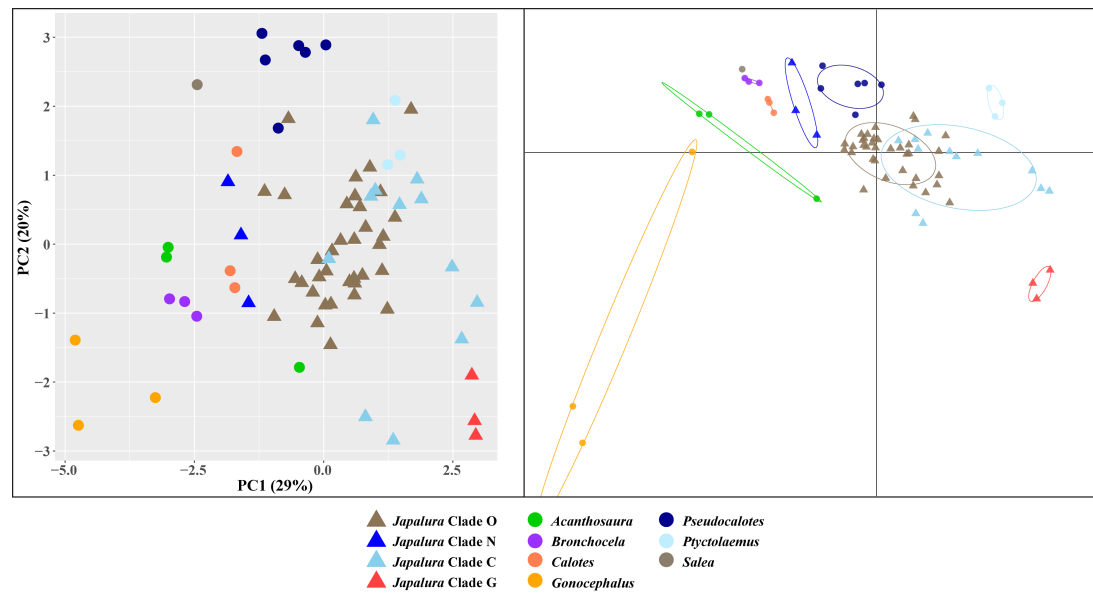


Figure 2-4. Discrete pholidosis characteristics of the four clades recovered within *Japalura sensu lato*. A: Clade C (*Japalura andersoniana*); B: Clade G (*J. otai*); C: Clade O (*J. polygonata*); D: Clade N (*J. bapoensis*).

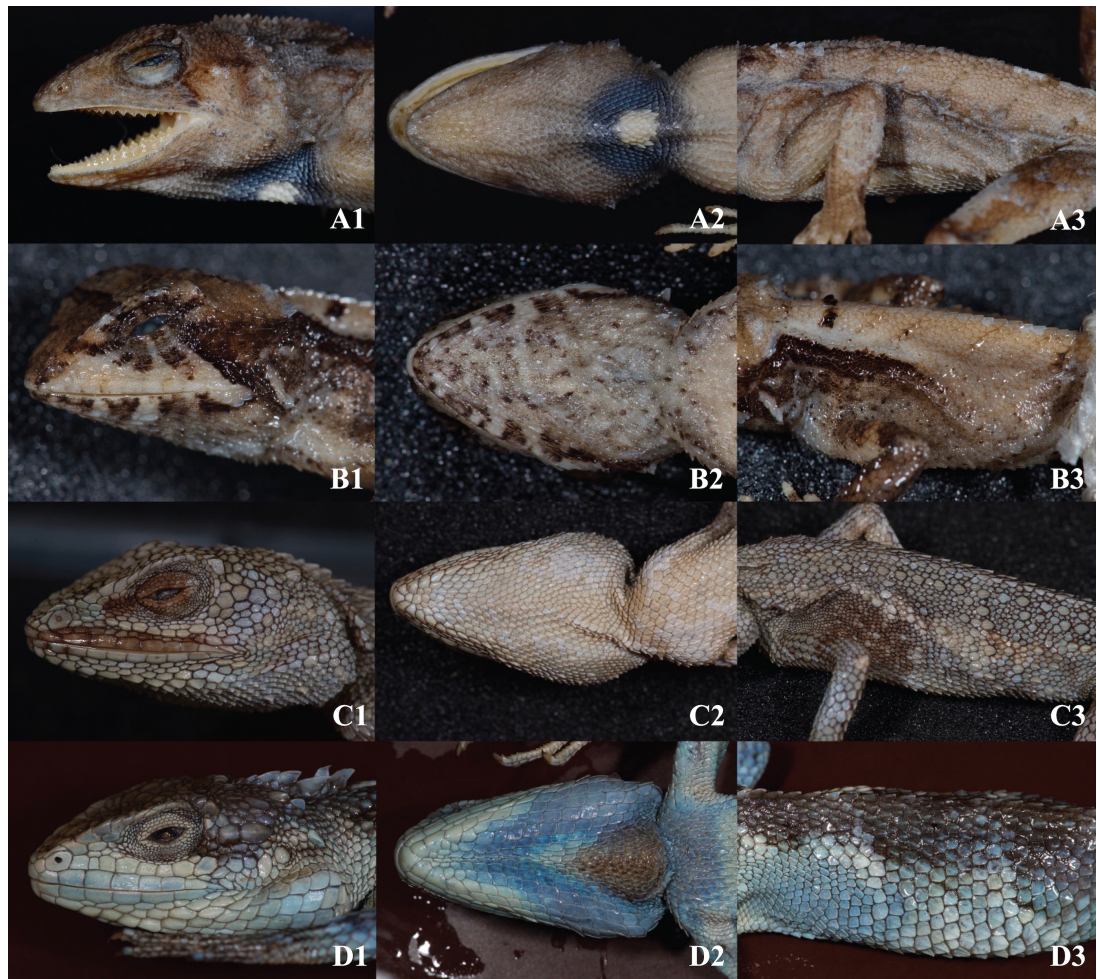


Figure 2-5. Revised classification of *Japalura sensu lato* and the new distribution ranges of each genus.

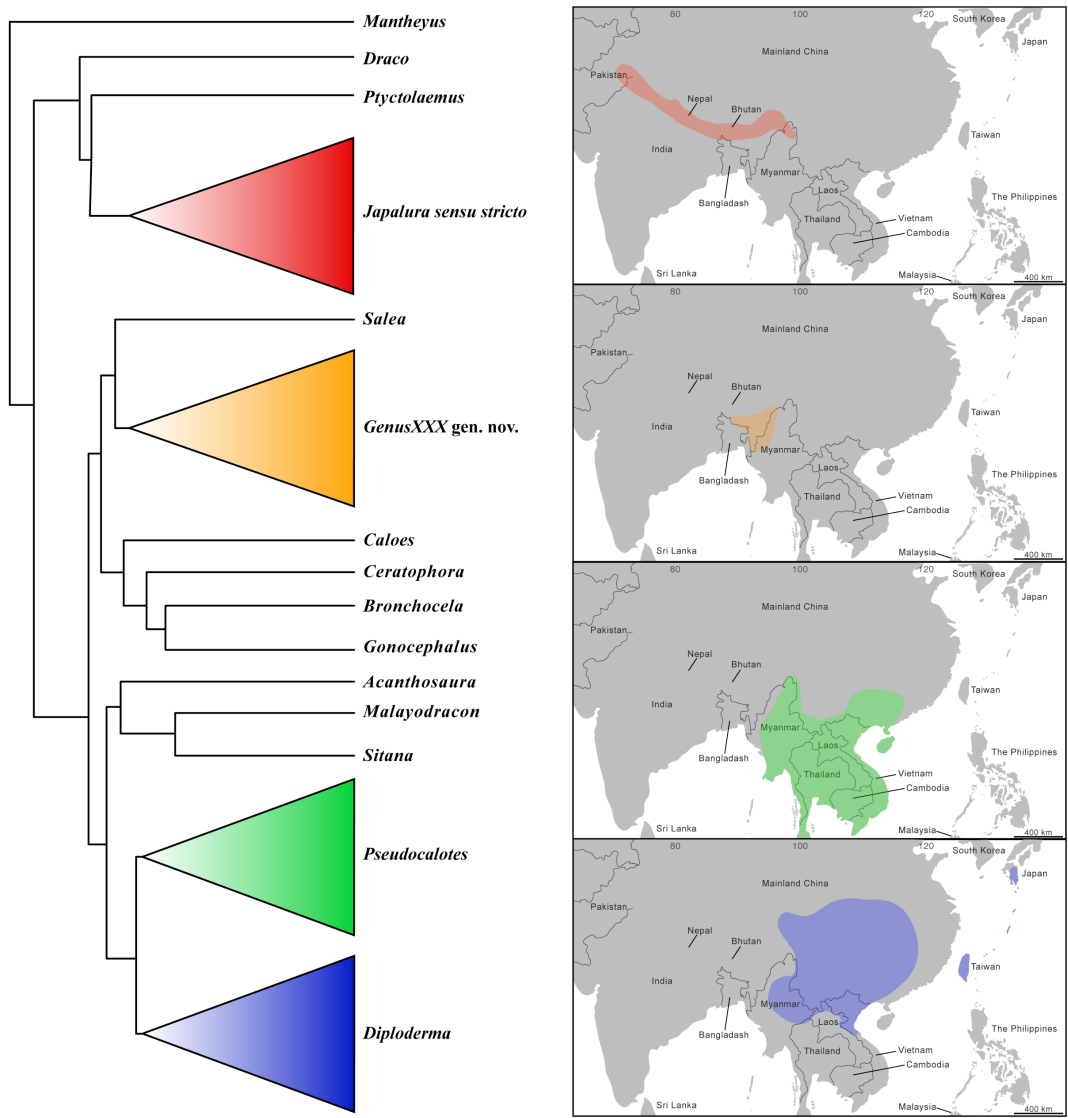


Figure 3-1. Distribution of *Diploderma* and sampling cites in the Hengduan Mountain Region of China. Different species are color-coded on map. Numbered locality represent newly recorded population of congeners.

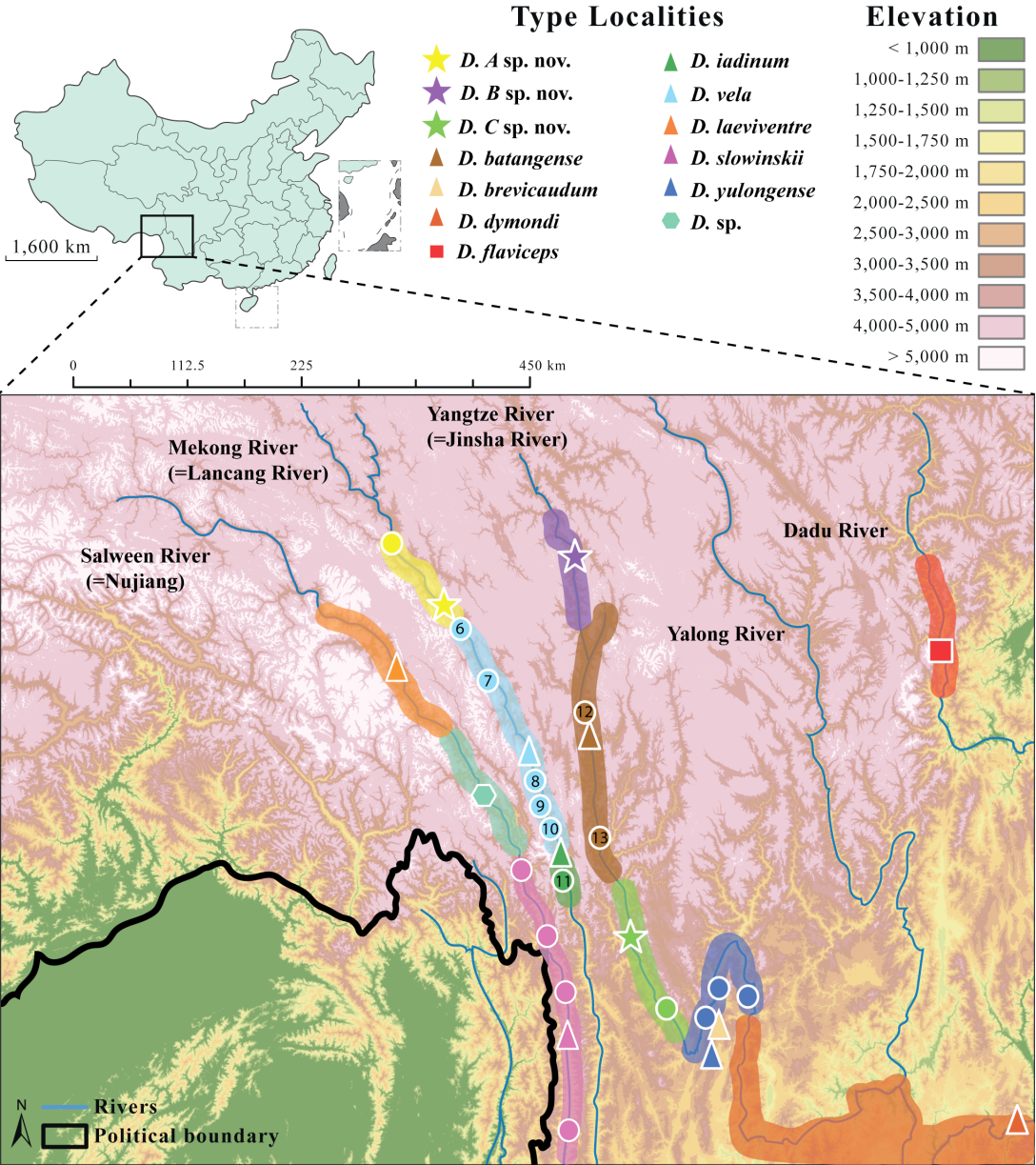


Figure 3-2. Males (1) and females (2) of newly discovered populations of *D. batangense* (A), *D. iadinum* (B), and *D. vela* (C) from Benzilan, Yunling, and Foshan of Yunnan province, respectively.

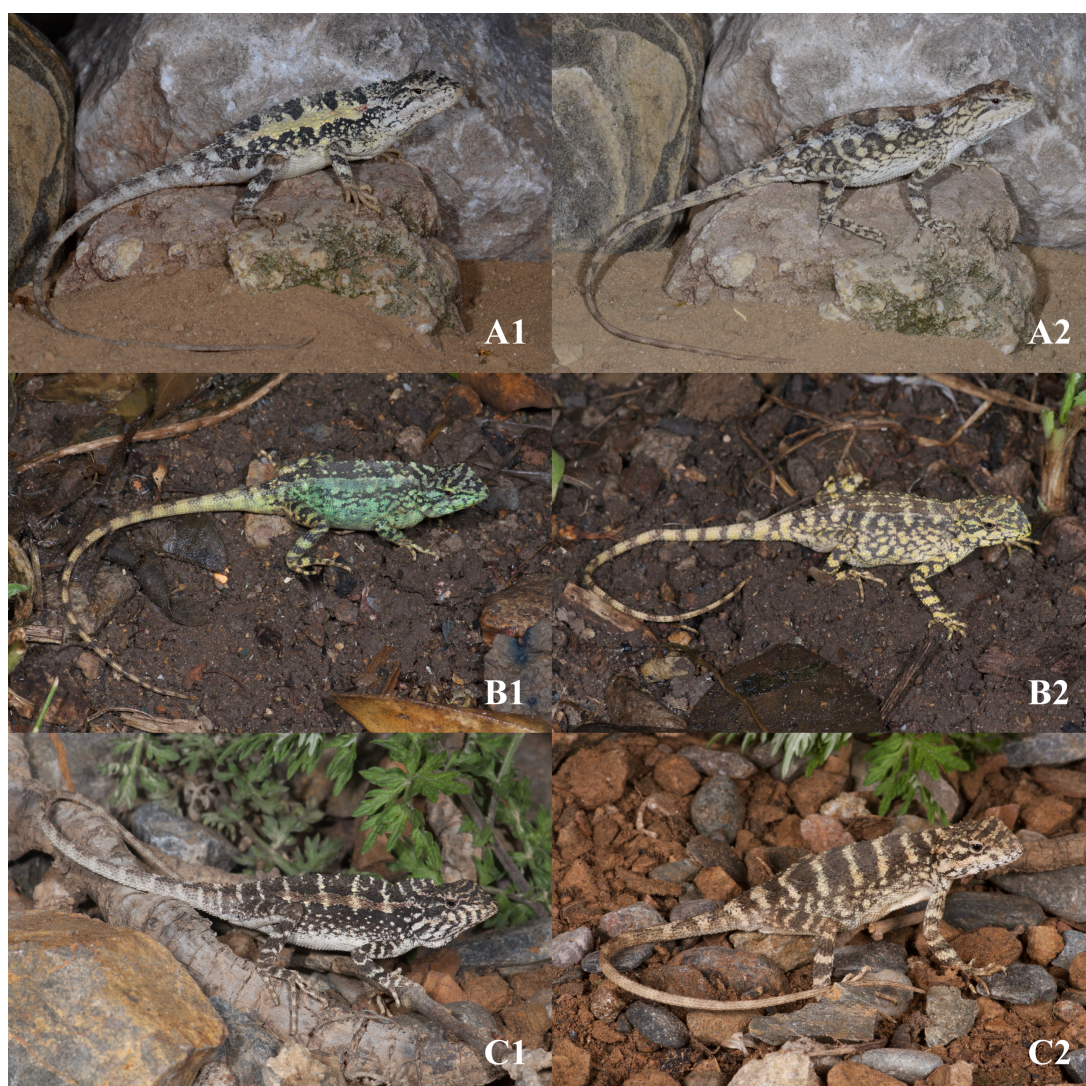


Figure 3-3. Live holotype male KIZ 027619 (left) and paratopotype female KIZ 027617 (right) of *Diploderma A* sp. nov..



Figure 3-4. Comparisons of preserved male specimens of *Diploderma A* sp. nov. (A) and *D. vela* (B).

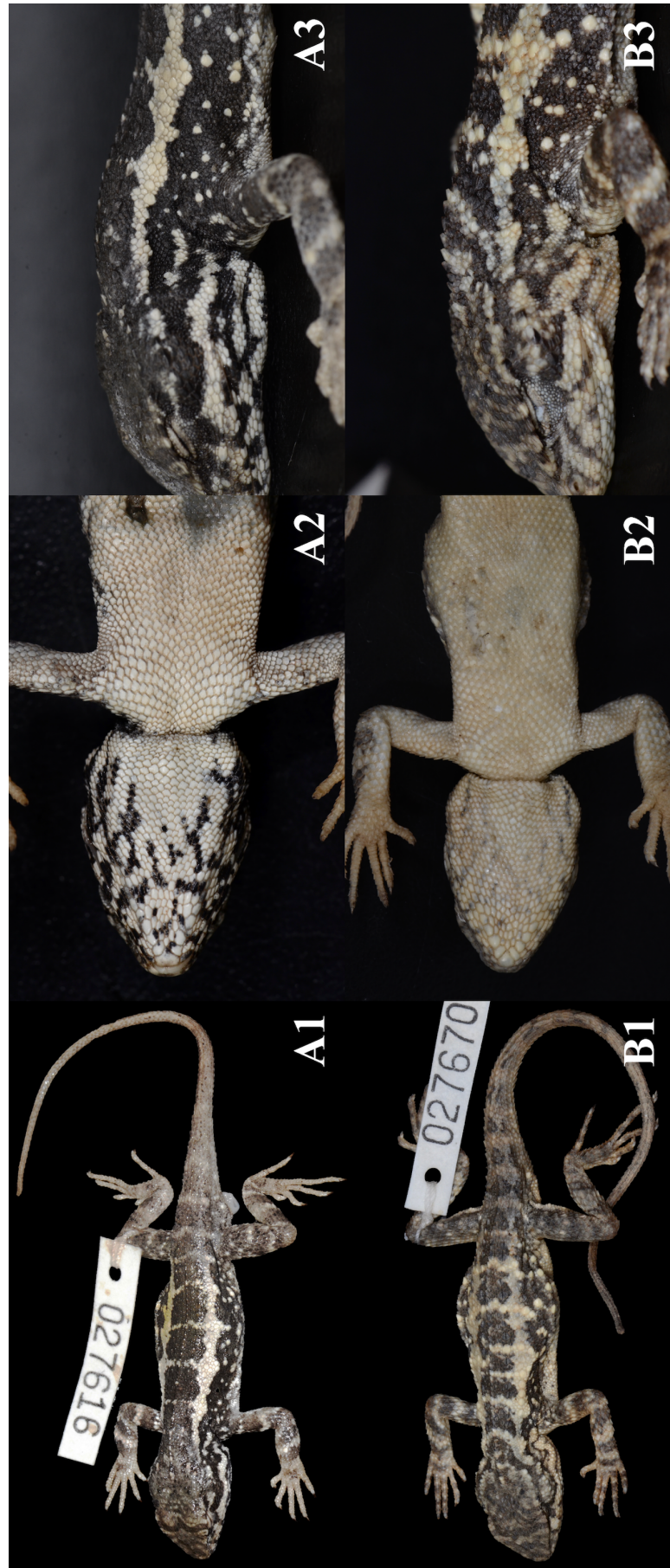


Figure 3-5. Comparisons of preserved female specimens of *Diploderma A* sp. nov. (A), *D. vela* (B), and *D. brevicaudum* (C).

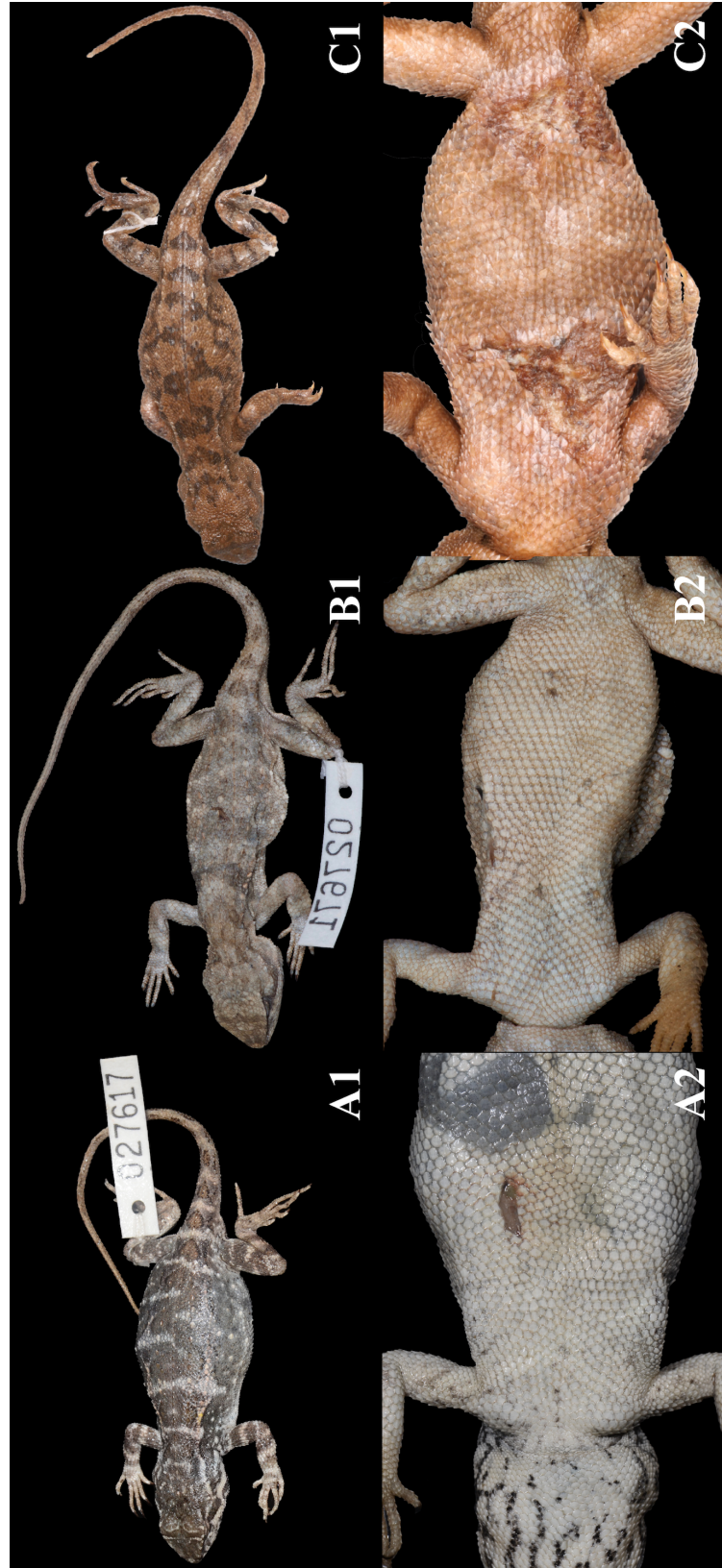


Figure 3-6. Habitats of *Diploderma A* sp. nov. at its type localities. A and B: Chaya, Chamdo; C and D: Karuo, Chamdo.



Figure 3-7. Live holotype male (KIZ 032694) (A) and paratopotype female (KIZ 032695) (B) of *Diploderma B* sp. nov. in life.

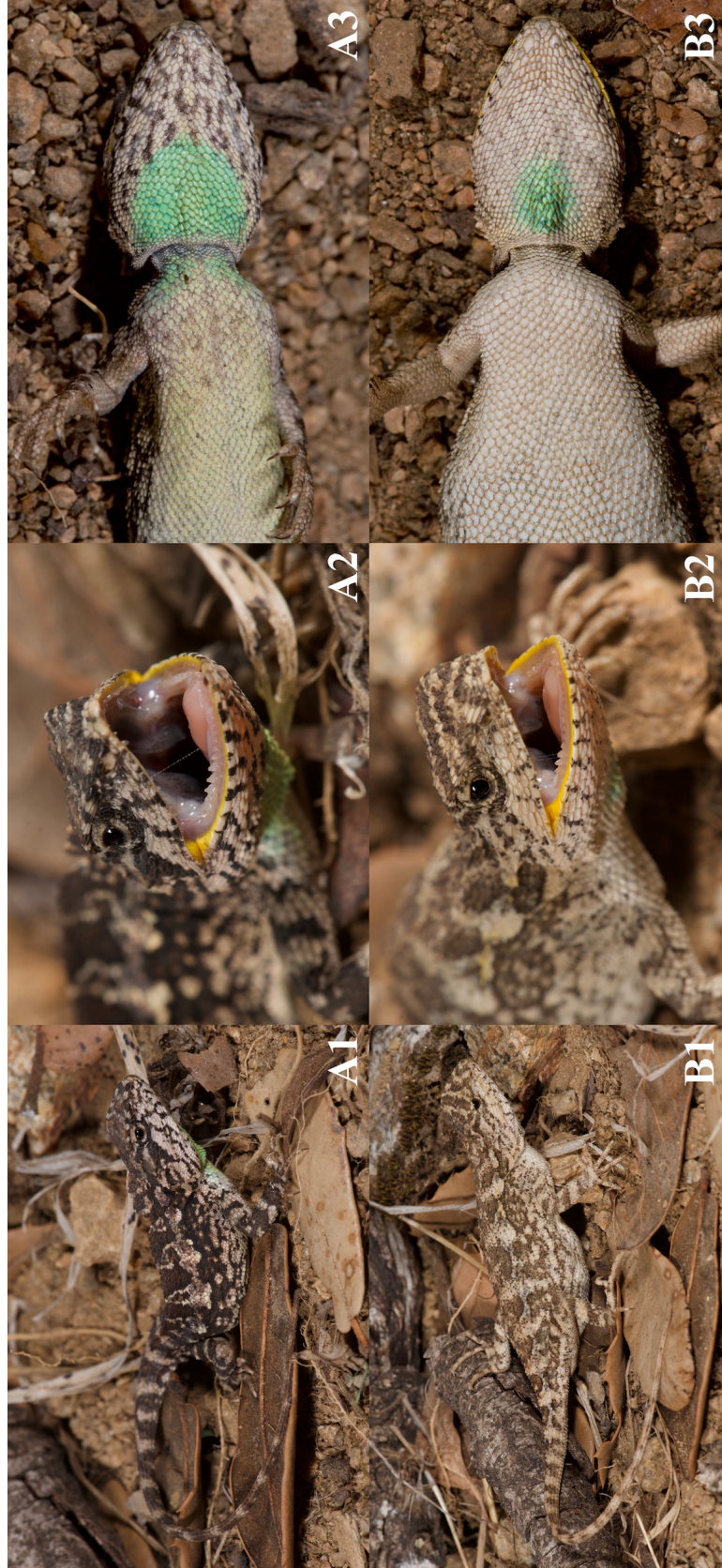


Figure 3-8. Preserved holotype males (A and C) and paratopotype females (B and D) of *Diploderma B* sp. nov. (A and B) and *D. C* sp. nov. (C and D).

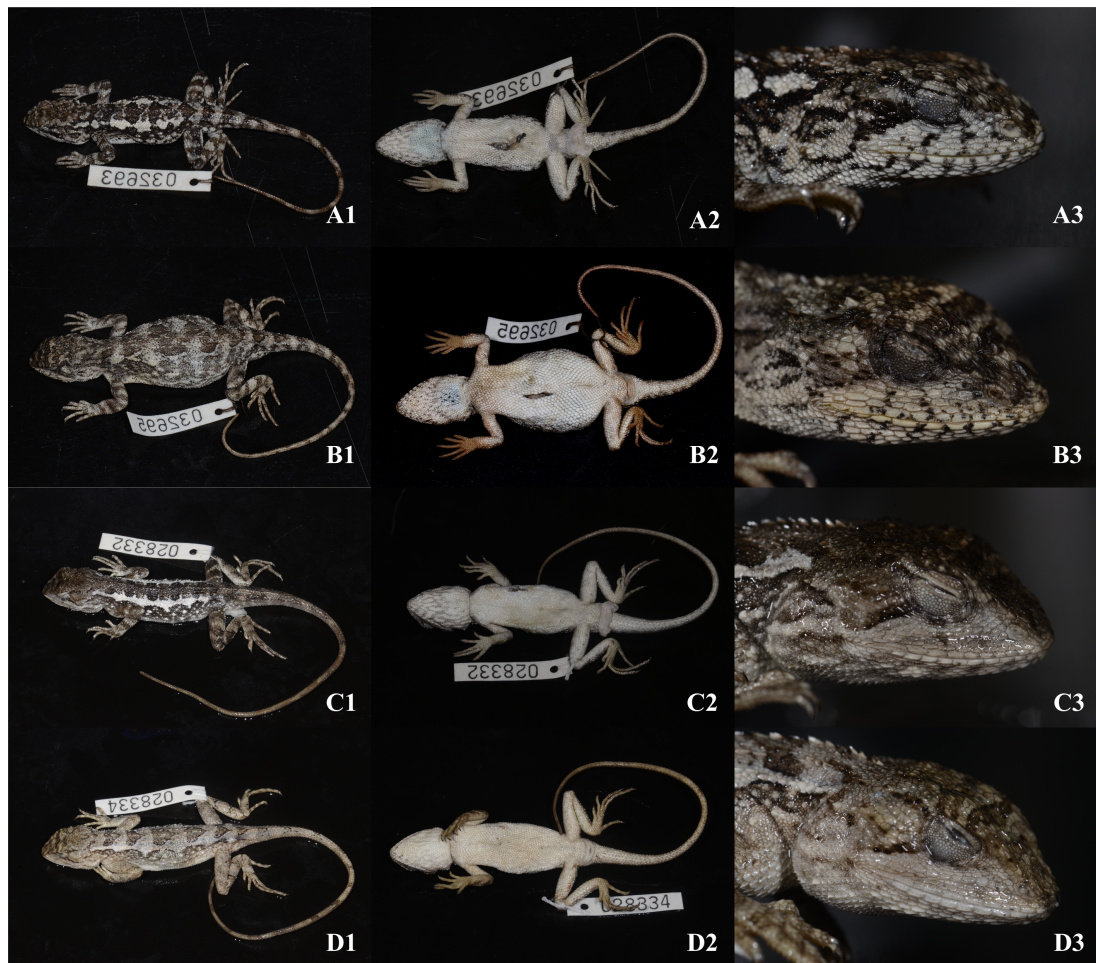


Figure 3-9. Habitat of *Diploderma B* sp. nov. at its type locality of Gaiyu, Sichuan, China.



Figure 3-10. Live holotype male KIZ 028332 (A) and paratype female KIZ 028335 (B) of *Diploderma* C sp. nov..



Figure 3-11. Habitat of *Diploderma C* sp. nov. at Wujing, Shangrila County, Yunnan Province, China.



Figure 3-12. Comparisons of coloration among live males (1 and 2) and females (3 and 4) of *Diploderma* congeners from the Hengduan Mountain Region. A: *Diploderma A* sp. nov.; B: *D. batangense*; C: *D. vela*; D: *D. laeviventre*; E: *D. flaviceps*; F: *D. C* sp. nov.; and G: *D. B* sp. nov.. Photos by Kai Wang and Xu Zhang.

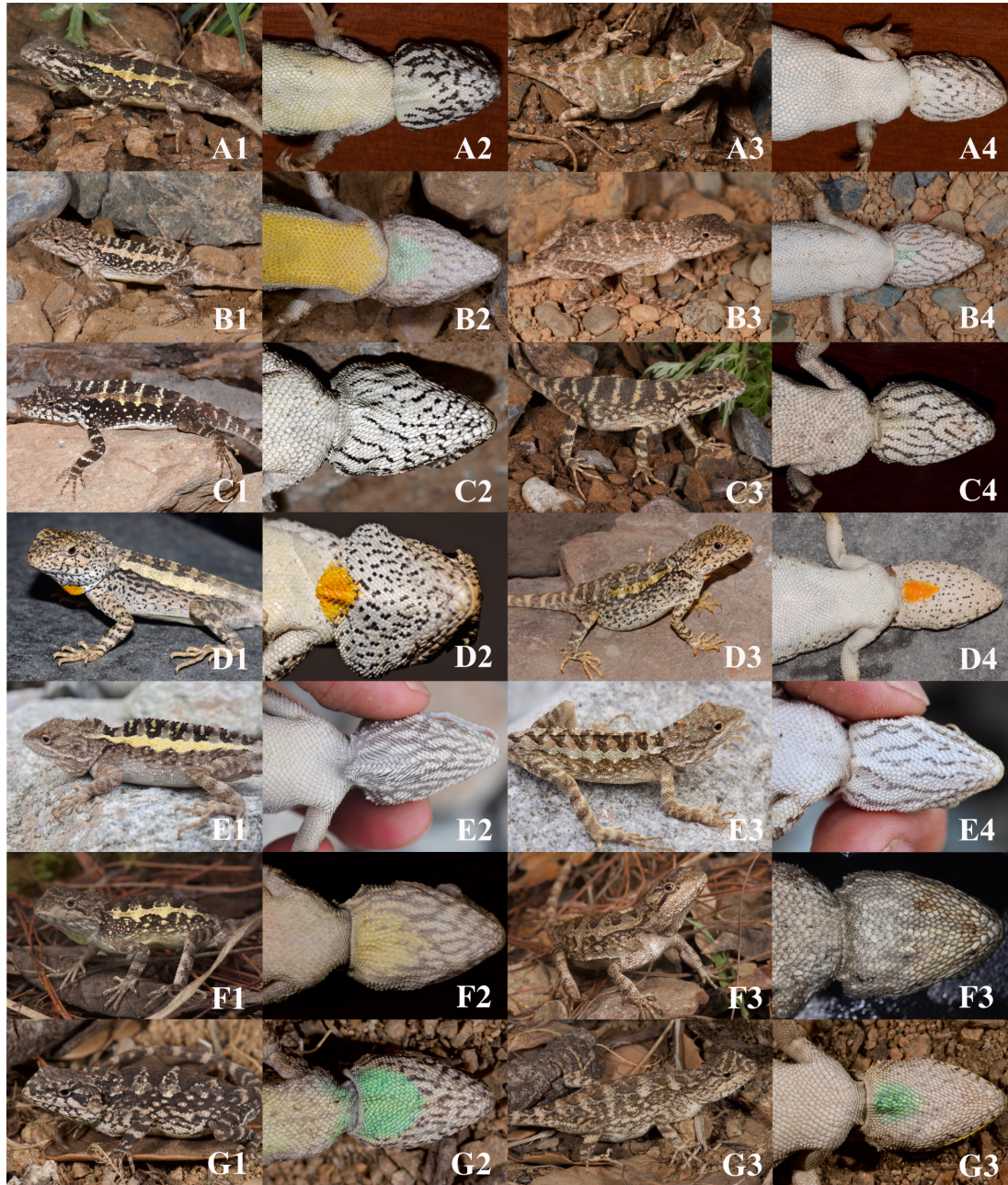


Figure 3-13. Destructions of habitat of *Diploderma* congeners in the Hengduan Mountain Region of China. A: Construction of township at type locality of *D. vela*; B: agricultural expansions near type locality of *D. vela*; C: road constructions near type locality of *D. vela*; D: construction of hydropower station at the type locality of *D. B* sp. nov..



Appendices

Appendix I. Genbank sequences used for phylogenetic study.

Genus	Species	Catlog #	Locality	Genes	Genbank Accession Number
<i>Japalura</i>	<i>flaviceps</i>	MVZ 216622	East of Wenchuan, Sichuan Province, China	ND2	AF128500.1
<i>Japalura</i>	<i>splendida</i>	CAS HERP 194476	Ya'an, Sichuan Province, China	ND2	AF128501.1
<i>Japalura</i>	<i>tricarinata</i>	CAS HERP 177397	Zhangmu, Tibet Autonomous Region, China	ND2	AF128478.1
<i>Japalura</i>	<i>variegata</i>	ZISP 20922	Sikkim, India	ND2	AF128479.1
<i>Calotes</i>	<i>versicolor</i>	CIB 091468	Hainan Province, China	ND2	KC875820.1
<i>Calotes</i>	<i>emma</i>	CAS 223062	Taung Gok, Rakhine State, Myanmar	ND2	DQ289460.1
		CAS 230941	Taunggyi, Shan State, Myanmar	BDNF	JF806005
		CAS 230941	Taunggyi, Shan State, Myanmar	R35	JF804581.1
<i>Acanthosaura</i>	<i>lepidogaster</i>	MVZ 224090	Vinh Phuc, Vietnam	ND2	AF128499.1
<i>Pseudocalotes</i>	<i>flavigula</i>	TNHC 58040	Perak, Malaysia	ND2	AF128503.1
	<i>brevipes</i>	MVZ 224106	Vinh Phuc, Vietnam	ND2	AF128502.1
<i>Ceratophora</i>	<i>stoddartii</i>	WHT 1512	Sri Lanka	ND2	AF128492
<i>Salea</i>	<i>horsfieldii</i>	BNHS-AMB 5739	Tamil Nadu, India	ND2	AF128490
<i>Bronchocele</i>	<i>crisatella</i>	TNHC 56517	Sarawak, Malaysia	ND2	AF288229.1
<i>Stiana</i>	<i>visiri</i>	CES 13656	India	R35	KT831293.1
		CES 13656	India	ND2	KT831340.1
<i>Sitana</i>	<i>spinaecephalus</i>	CES 14654	India	R35	KT831291.1
		CES 14654	India	ND2	KT831337.1
<i>Draco</i>	<i>blandfordii</i>	TNHC 5631	Perlis, Malaysia	ND2	AF 288242.1
		CAS 221153	Bago Division, Myanmar	BDNF	JF806010.1
		CAS 221153	Bago Division, Myanmar	R35	JF804589.1
<i>Draco</i>	<i>indochinensis</i>	MVZ 222156	Gia Lai, Vietnam	ND2	AF128477.1
<i>Draco</i>	<i>spilonotus</i>	LSUMZ 81375	Sulawesi Utara Province, Indonesia	ND2	AF288282.1
<i>Ptyctolaemus</i>	<i>collicristatus</i>	USNM 559811	Chin State, Myanmar	ND2	AY555837.1
<i>Mantheyus</i>	<i>phuwanensis</i>	FMNH 255495	Blikhamxay Province, Laos	ND2	AY555836.1
<i>Hydrosaurus</i>	<i>pustulatus</i>	KU 314943	Zamboanga City, Pasanonca Natural Park, Philippines	ND2	KF875294.1
<i>Phrynocephalus</i>	<i>mystaceus</i>	CAS 228621	Semnan Province, Iran	BDNF	JF806014.1
		NMVD 74190	Kapchagay District, Almaty Region, Kazakhstan	ND2	GQ242191.1
		MVZ 245941	Semnan Province, Iran	CMOS	JX838987.1

Appendix II. Specimens measured for PCA and DAPC.

Genus	species	Museum Catalog #	Sex
<i>Acanthosaura</i>	<i>lepidogaster</i>	KIZ 030164	M
<i>Acanthosaura</i>	<i>capra</i>	OMNH XXXX	M
<i>Acanthosaura</i>	<i>capra</i>	OMNH XXXX	M
<i>Bronchocela</i>	<i>marmorata</i>	OMNH 044841	M
<i>Bronchocela</i>	<i>marmorata</i>	OMNH 044838	M
<i>Bronchocela</i>	<i>marmorata</i>	OMNH 044939	M
<i>Calotes</i>	<i>bachae</i>	OMNH 045345	M
<i>Calotes</i>	<i>emma</i>	KIZ 024005	M
<i>Calotes</i>	<i>emma</i>	KIZ 024006	M
<i>Christidorsa</i>	<i>otaii</i>	CAS 234842	M
<i>Christidorsa</i>	<i>otaii</i>	CAS 240147	M
<i>Christidorsa</i>	<i>otaii</i>	CAS 240141	M
<i>Diploderma</i>	<i>batangense</i>	KIZ 019276	M
<i>Diploderma</i>	<i>batangense</i>	KIZ 032736	M
<i>Diploderma</i>	<i>batangense</i>	KIZ 019314	M
<i>Diploderma</i>	<i>chapaense</i>	KIZ 034922	M
<i>Diploderma</i>	<i>dymondi</i>	KIZ 040647	M
<i>Diploderma</i>	<i>dymondi</i>	KIZ 040648	M
<i>Diploderma</i>	<i>dymondi</i>	KIZ 040640	M
<i>Diploderma</i>	<i>fasciatum</i>	CIB 2620	M
<i>Diploderma</i>	<i>fasciatum</i>	CIB 2622	M
<i>Diploderma</i>	<i>flaviceps</i>	KIZ 820050	M
<i>Diploderma</i>	<i>flaviceps</i>	KIZ 820052	M
<i>Diploderma</i>	<i>flaviceps</i>	CIB 72138	M

Appendix II. Continue.

Genus	species	Museum Catalog #	Sex
<i>Diploderma</i>	<i>iadunum</i>	KIZ 027702	M
<i>Diploderma</i>	<i>iadunum</i>	KIZ 027703	M
<i>Diploderma</i>	<i>iadunum</i>	KIZ 027704	M
<i>Diploderma</i>	<i>makii</i>	MCZ R-181443	M
<i>Diploderma</i>	<i>micangshanense</i>	KIZ 040306	M
<i>Diploderma</i>	<i>micangshanense</i>	KIZ 040307	M
<i>Diploderma</i>	<i>micangshanense</i>	KIZ 040308	M
<i>Diploderma</i>	<i>polygonatum</i>	CAS 21215	M
<i>Diploderma</i>	<i>polygonatum</i>	CAS 21243	M
<i>Diploderma</i>	<i>polygonatum</i>	MCZ 55863	M
<i>Diploderma</i>	<i>slowinskii</i>	KIZ 027596	M
<i>Diploderma</i>	<i>slowinskii</i>	KIZ 027577	M
<i>Diploderma</i>	<i>slowinskii</i>	KIZ 027579	M
<i>Diploderma</i>	<i>splendidum</i>	CIB 86480	M
<i>Diploderma</i>	<i>splendidum</i>	CIB 86481	M
<i>Diploderma</i>	<i>splendidum</i>	CIB 86483	M
<i>Diploderma</i>	<i>swinhonis</i>	CAS 18098	M
<i>Diploderma</i>	<i>swinhonis</i>	CAS 18099	M
<i>Diploderma</i>	<i>varcoae</i>	KIZ 8510006	M
<i>Diploderma</i>	<i>varcoae</i>	KIZ 015691	M
<i>Diploderma</i>	<i>varcoae</i>	KIZ 8510009	M
<i>Diploderma</i>	<i>yulongensis</i>	KIZ 028296	M
<i>Diploderma</i>	<i>yulongensis</i>	KIZ 028298	M
<i>Diploderma</i>	<i>yunnanense</i>	KIZ 74110240	M
<i>Diploderma</i>	<i>yunnanense</i>	KIZ 791469	M
<i>Diploderma</i>	<i>zhaoermii</i>	CIB 2690	M
<i>Gonocephalus</i>	<i>sp</i>	OMNH 045456	M
<i>Gonocephalus</i>	<i>sp</i>	OMNH 045457	M
<i>Gonocephalus</i>	<i>sp</i>	OMNH 045958	M

Appendix II. Continue.

Genus	species	Museum Catalog #	Sex
<i>Japalura</i>	<i>andersoniana</i>	KIZ 011147	M
<i>Japalura</i>	<i>andersoniana</i>	KIZ 011156	M
<i>Japalura</i>	<i>kumaonensis</i>	KU 180693	M
<i>Japalura</i>	<i>kumaonensis</i>	KU 180691	M
<i>Japalura</i>	<i>kumaonensis</i>	KU 180694	M
<i>Japalura</i>	<i>major</i>	FMNH 256413	M
<i>Japalura</i>	<i>major</i>	FMNH 256414	M
<i>Japalura</i>	<i>major</i>	FMNH 256412	M
<i>Japalura</i>	<i>tricarinata</i>	CAS 177403	M
<i>Japalura</i>	<i>tricarinata</i>	CAS 177391	M
<i>Japalura</i>	<i>tricarinata</i>	CAS 177405	M
<i>Japalura</i>	<i>variegata</i>	FMNH 190842	M
<i>Pseudocalotes</i>	<i>kakhienensis</i>	KIZ 027575	M
<i>Pseudocalotes</i>	<i>kakhienensis</i>	KIZ 027585	M
<i>Pseudocalotes</i>	<i>kakhienensis</i>	KIZ 027558	M
<i>Pseudocalotes</i>	<i>kindonwardii bapoensis</i>	CAS 241965	M
<i>Pseudocalotes</i>	<i>kindonwardii bapoensis</i>	CAS 242629	M
<i>Pseudocalotes</i>	<i>kindonwardii bapoensis</i>	CAS 242628	M
<i>Pseudocalotes</i>	<i>microlepis</i>	KIZ 040631	M
<i>Pseudocalotes</i>	<i>microlepis</i>	KIZ 010916	M
<i>Pseudocalotes</i>	<i>microlepis</i>	KIZ 00214	M
<i>Ptyctolaemus</i>	<i>gularis</i>	KIZ 016452	M
<i>Ptyctolaemus</i>	<i>gularis</i>	KIZ 016453	M
<i>Ptyctolaemus</i>	<i>gularis</i>	KIZ 06654	M
<i>Salea</i>	<i>anamallayana</i>	CAS 104247	M

Appendix III. Vouchered numbers and Genbank accession numbers of samples used for the phylogenetic study.

Genus	Species	Catlog #	Locality	BDNF	Genbank Accession Number CMOS	R35	ND2+tRNA+COI
<i>Christidorsa</i>	<i>otai</i>	CAS 234833	Mintatt District, Chin State, Myanmar				
<i>Christidorsa</i>	<i>otai</i>	CAS 233296	Phalum District, Chin State, Myanmar				
<i>Christidorsa</i>	<i>otai</i>	CES XXXXXX	India				
<i>Christidorsa</i>	<i>planidorsata</i>	CES XXXXXX	India				
<i>Diploderma</i>	<i>batangense</i>	KIZ 09404	Markam, Tibet, China				
<i>Diploderma</i>	<i>batangense</i>	KIZ 019276	Batang, Sichuan, China				
<i>Diploderma</i>	<i>brevipes</i>	NMNS 19607	Taiwan				
<i>Diploderma</i>	<i>brevipes</i>	NMNS 19608	Taiwan				
<i>Diploderma</i>	<i>chapaense</i>	KIZ 034923	Lvchun, Yunnan, China				
<i>Diploderma</i>	<i>chapaense</i>	KIZ 034921	Lvchun, Yunnan, China				
<i>Diploderma</i>	<i>dymondi</i>	KIZ 040639	Dongchuan, Yunnan, China				
<i>Diploderma</i>	<i>dymondi</i>	KIZ 040640	Dongchuan, Yunnan, China				
<i>Diploderma</i>	<i>flaviceps</i>	KIZ 05181	Luding, Sichuan, China				
<i>Diploderma</i>	<i>flaviceps</i>	KIZ 01852	Luding, Sichuan, China				
<i>Diploderma</i>	<i>laeviventre</i>	KIZ 014037	Basu, Tibet, China				
<i>Diploderma</i>	<i>luei</i>	NMNS 19604	Taiwan				
<i>Diploderma</i>	<i>luei</i>	NMNS 19605	Taiwan				
<i>Diploderma</i>	<i>makii</i>	NMNS 19609	Taiwan				
<i>Diploderma</i>	<i>makii</i>	NMNH 19610	Taiwan				
<i>Diploderma</i>	<i>micangshanense</i>	KIZ 06850	Longnan, Gansu, China				
<i>Diploderma</i>	<i>polygonatum</i>	NMNS 19598	Taiwan				
<i>Diploderma</i>	<i>polygonatum</i>	NMNS 19599	Taiwan				

Appendix III. Continue.

Genus	Species	Catalog #	Locality	BDNF	Genbank Accession Number		
					CMOS	R35	ND2+tRNA+COI
<i>Diploderma</i>	<i>slowinskii</i>	CAS 214906	Gongshan, Yunnan, China				
<i>Diploderma</i>	<i>slowinskii</i>	CAS 214954	Gongshan, Yunnan, China				
<i>Diploderma</i>	<i>splendidum</i>	WK-JK 001	Yichang, Hubei, China				
<i>Diploderma</i>	<i>splendidum</i>	WK-JK 006	Yichang, Hubei, China				
<i>Diploderma</i>	<i>swinhonis</i>	NMNS 19592	Taiwan				
<i>Diploderma</i>	<i>swinhonis</i>	NMNS 19593	Taiwan				
<i>Diploderma</i>	<i>varcoe</i>	KIZ 026132	Mengzi, Yunnan, China				
<i>Diploderma</i>	<i>vela</i>	KIZ 019299	Markam, Tibet, China				
<i>Diploderma</i>	<i>vela</i>	KIZ 034925	Markam, Tibet, China				
<i>Diploderma</i>	<i>yulongense</i>	KIZ 09399	Xianggella, Yunnan, China				
<i>Diploderma</i>	<i>yulongense</i>	KIZ 43196	Xianggella, Yunnan, China				
<i>Diploderma</i>	<i>yunnanense</i>	CAS 242183	Baoshan, Yunnan, China				
<i>Diploderma</i>	<i>yunnanense</i>	CAS 242271	Baoshan, Yunnan, China				
<i>Diploderma</i>	<i>zhaoermii</i>	KIZ 019564	Wenchuan, Sichuan, China				
<i>Diploderma</i>	<i>zhaoermii</i>	KIZ 019565	Wenchuan, Sichuan, China				
<i>Pseudocalotes</i>	<i>kingdonwardi bapoensis</i>	CAS 241966	Dulongjiang, Yunnan, China				
<i>Pseudocalotes</i>	<i>kingdonwardi bapoensis</i>	CAS 242628	Dulongjiang, Yunnan, China				
<i>Pseudocalotes</i>	<i>kakhiensis</i>	WK-JK 010	Gaoligongshan, Yunnan, China				
<i>Japalura</i>	<i>andersoniana</i>	KIZ 06776	Medog, Tibet, China				
<i>Japalura</i>	<i>andersoniana</i>	KIZ 016411	Medog, Tibet, China				
<i>Japalura</i>	<i>kumaonensis</i>	CES XXXXX	India				
<i>Japalura</i>	<i>tricarinata</i>	KIZ 011133	Nielamu, Tibet, China				
<i>Japalura</i>	<i>variegata</i>	CES XXXXX	India				
<i>Gonocephalus</i>	<i>chamaeleontinus</i>	LSUHC 3788	Philippines				
<i>Gonocephalus</i>	<i>grandis</i>	LSUHC 4545	Philippines				
<i>Malayodracon</i>	<i>robinsonii</i>	LSUHC 5873	Malaysia				
<i>Draco</i>	<i>spilopterus</i>	KU 308069	Philippines				
<i>Draco</i>	<i>spilopterus</i>	KU 308070	Philippines				

Appendix IV . Detailed measurements of *Diploderma batangense*, *D. iadinum*, and *D. vela*.

Species	Catalog number	Sex	Locality code	SVL	TAL	HL	HW	SEL	FLL	HLL	F4L	T4L	TRL	
<i>Diploderma vela</i>	27693	M		4	61.68	135.83	20.21	13.18	7.67	31.24	50.29	6.75	12.16	28.13
	27667	M		4	58.99	/	18.09	12.38	7.05	28.88	44.39	6.96	11.57	25.55
	27680	M		3	57.17	136.13	18.06	11.66	6.76	30.35	48.96	7.77	11.64	25.54
	27682	M		5	62.27	126.46	18.98	13.15	7.22	30.69	50.37	7.93	12.44	30.08
	27647	M		2	64.52	/	20.3	13.81	7.71	28.08	43.57	7.17	10.35	29.69
	27646	M		2	59.44	120.72	18.21	12.02	6.63	28.32	44.74	6.93	11.28	28.03
	27645	M		2	61.66	111.38	18.89	12.83	6.74	28.24	44.46	7.06	11.33	27.7
	27668	M		1	52.92	92.67	17.38	11.35	6.37	26.35	38.35	7.01	9.05	23.16
	27670	M		1	51.62	90.12	16.3	11.25	6.15	23.59	37.97	5.7	9.99	23.82
	27669	M		1	52.07	/	16.48	11.38	6.26	23.3	37.35	6.02	8.96	27.38
	27694	F		4	61.8	114.25	18.28	12.58	7.14	29.23	45.08	6.78	12.19	28.1
	27695	F		4	58.5	118.27	16.79	11.69	6.35	26.78	41.8	6.76	10.58	29.08
	27681	F		3	60.43	121.55	18.32	11.95	6.95	31.28	49.32	7.1	10.99	27.13
	27684	F		5	64.24	114.1	18.11	12.35	6.9	31.94	49.62	6.41	10.86	32.22
	27641	F		2	61.21	106.74	18.25	12.02	6.81	26.92	43.92	6.74	10.45	29.95
	27649	F		2	59	106.72	17.54	11.58	6.41	28.44	44.95	7.16	10.76	27.71
	27648	F		2	59.66	105.82	18.14	12.66	6.91	28.56	44.21	7.35	9.52	30.05
<i>Diploderma iadinum</i>	27671	F		1	60.18	96.18	18.29	12.51	6.76	26.09	39.52	6.25	8.73	28.19
	27672	F		1	54.07	87.39	16.13	11.04	6.06	24.09	36.53	5.4	9.1	25.5
	27673	F		1	54.14	/	15.3	11.36	5.91	24.63	37.98	5.13	9.52	28.99
	27703	M		6	52.79	105.48	16.76	11.26	6.48	24.92	39.47	6.24	10.08	27.33
	27702	M		6	58.7	113.63	19.17	12.43	7.04	29.32	45.31	7.15	11.01	29.2
	27704	M		6	53.28	110	17.64	11.52	6.59	27.78	43.41	6.94	11.72	27.31
	27705	F		6	54.46	95.91	16.42	10.37	6.23	26.68	40.91	6.41	9.14	28.77
	32737	M		7	58.44	126.77	17.04	12.14	6.74	25.56	43.05	6.03	9.34	27.92
	32736	M		7	61.23	135.41	18.03	12.60	7.08	29.97	48.64	7.85	12.19	29.02
	32734	M		7	60.52	128.31	18.00	12.99	7.07	28.05	45.94	6.08	10.13	29.20
	32735	F		7	64.88	132.24	18.64	13.13	7.08	29.19	46.60	7.23	10.91	30.87

Appendix.V. Specimens examined for Chapter 3. Museum abbreviations see methods of Chapter 3. (All coordinates are in WGS 84 datum format).

Diploderma batangense (n=20): CIB 1902–1908, 2227, 2233, 2243, KIZ 84011, 801081, Batang, Sichuan, China; KIZ 09404, 019311, 019312, KIZ 019314, Mangkang, Tibet, China. KIZ 32734–32737, Deqin, Yunnan, China.

Diploderma A (n=8): KIZ 027616 (holotype), KIZ 027618, 027619, 027628–027630 (paratopotypes), Chaya, Chamdo, Tibet, PR China; KIZ 016486 (paratype), Karuo, Chamdo, Tibet, China (31.0433° N, 97.2239° E, elevation 3,245 m).

Diploderma dymondi (n=7): CIB 1869, 87234, Panzhihua, Sichuan, PR China; KIZ 95I1001, 1002, 1016, 1018, 1022, Dayao, Yunnan, China.

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

Diploderma 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 (28.2312° N, 98.8578° E, 1,990 m).

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

Diploderma micangshanense (n=9): CIB 86348, 86351, Xianyang, Shaanxi, PR China; CIB 86356, 86357, 86360, 86361, Luonan, Shaanxi, PR China; CIB 2572, 2578, 2582, Wenxian, Gansu, China.

Diploderma flaviceps (n=13): CIB 2234, 2332, 2333, 2341, 2354, 2355, 2549, 2554, 2556, 2561, 2567; KIZ 05181, 05182; Luding, Sichuan, China.

Diploderma B (n=9): KIZ 032692 (holotype), KIZ 032693–99, 032730 (paratopotypes), Gaiyu, Sichuan, China.

Diploderma C (n=6): KIZ 028332 (holotype), 028333–36 (paratopotype), Wujing, Shangrila, Yunnan, China; 028338 (paratypes), Shangjiang, Shangrila, Yunnan, China.

Diploderma splendidum (n=6): USNM 35522 (holotype), Yichang, Hubei, PR China; CIB 2588, 2591, 2596, 72468, 72469, Chongqing, China.

Diploderma varcoae (n=3): CIB 2650, 2651, KIZ 85II0006, Kunming, Yunnan, China.

Diploderma vela (n=31): KIZ 013801 (holotype), KIZ 013802, 013813, 013800, 013805–013811 (paratopotypes), Jerkalo, Tibet, China. KIZ 027641, 027645–49, Rumei, Markam, Tibet, China (29.6817° N, 98.3821° E, elevation 3,000 m); KIZ 027668, 027670–73, Tongsha, Markam, Tibet, China (29.9852° N, 98.0763° E, elevation 3,300 m); KIZ 027667, 027693–695, Foshan, Deqin, Yunnan, China (28.7906° N, 98.6652° E, elevation 2,200 m); KIZ 027680, 027681, Xilu, Deqin, Yunnan, China (28.9533° N, 98.6402° E, elevation 2,430 m); KIZ 027682, 027684, Xidang, Deqin, Yunnan, China (29.9852° N, 98.0763° E, elevation 2,260 m).

Diploderma yulongense (n=15): KIZ 09399, 09400, 028291–028293, 028294, 028296–028298, 028299, 028300, 028303, 028342–028344, Xianggelila County, Yunnan, China.

Diploderma yunnanense (n=8): CIB 2684, 2686, 2687, 2689, KIZ 82081, Longling, Yunnan, China; KIZ 74II0240, 0248, 79I469, Tengchong, Yunnan, China.

Diploderma zhaoermii (n=14): CIB 2690 (holotype), 86432, 86435, 85721, 85722, 86433, 86434, 86436, Wenchuan, Sichuan, PR China; CIB 2232, 2244, 2240, KIZ 84032, 85030, Lixian, Sichuan, China.