

Generic classification of Asian horned toads (Anura: Megophryidae: Megophryinae) and monograph of Chinese species

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ABSTRACT

The subfamily Megophryinae, as a representative batrachian group of the Oriental Realm and one of the most diverse groups of amphibians, has attracted considerable attention due to continued conjecture regarding its generic classification and failure to reach a satisfactory consensus. China boasts the richest diversity of Asian horned toads, containing some two thirds of the total species cataloged. However, most species have a complicated taxonomic history, resulting in multiple misidentifications. As such, an overall clarification of historical records and regional checklists is required. In the current investigation, we established the phylogeny of the Asian horned toads and performed detailed examinations with redefinitions of several important morphological traits. Based on the phylogenetic relationships and morphological differences, we propose a new ten-genus classification for the Asian horned toad subfamily Megophryinae: i.e., *Brachytarsophrys*, *Atympanophrys*, *Grillitschia*, *Sarawakiphrys* **gen. nov.**, *Jingophrys* **gen. nov.**, *Xenophrys*, *Megophrys*, *Pelobatrachus*, *Ophryophryne*, and *Boulenophrys*. Revisions on the diagnosability, distribution, and content of each genus are provided. Furthermore, we present a careful review of the taxonomic history of Asian horned toad species from China and provide a monograph of congeners, including six species of *Brachytarsophrys*, four species of *Atympanophrys*, five species of *Jingophrys* **gen. nov.**, 10 species of *Xenophrys*,

two species of *Ophryophryne*, and 60 species of *Boulenophrys*. Finally, we discuss the importance of traditional morphological traits based on multiple populations in taxonomic work as well as taxonomic inflation caused by the genetic species delimitation.

Keywords: *Atympanophrys*; *Boulenophrys*; *Megophrys*; *Jingophrys* **gen. nov.**; Review; *Sarawakiphrys* **gen. nov.**; Taxonomy; *Xenophrys*

INTRODUCTION

Biodiversity plays a leading role in maintaining ecosystem functions and providing ecosystem services to humanity (Duffy, 2009; Watson et al., 1995). Due to the influence of human activities, habitat destruction, climate change, infectious disease, and biological invasion, global biodiversity is disappearing and under threat (Naeem et al., 2012). Amphibians are one of the most diverse groups of vertebrates (Pyron & Wiens, 2011) and among the most threatened, with dramatically declining diversity since the 1970s (Stuart et al., 2004). As the foundation of zoological research, accurate phylogeny and taxonomy are essential for understanding amphibian utilization and conservation (Pyron & Wiens, 2011). However, current phylogenetic and taxonomic studies on amphibians only cover part of the taxa, and many groups remain taxonomically confusing.

The subfamily Megophryinae (Bonaparte, 1850), also known as the Asian horned toads, is a representative batrachian group of the Oriental Realm and contains nearly 130 recognized species, distributed throughout southern China and the southern and eastern Himalayas, as well as

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across Indochina to the Malay Archipelago (Frost, 2022; Lyu et al., 2021). In recent decades, these toads have attracted considerable interest due to their extended taxonomic debate and substantial underestimation of diversity (Chen et al., 2017; Delorme et al., 2006; Dubois, 1987; Dubois et al., 2021; Fei & Ye, 2016; Li et al., 2020a; Liu et al., 2018; Lyu et al., 2021; Mahony et al., 2017; Qi et al., 2021; Tian & Hu, 1983). Notably, the generic recognitions of these toads have been frequently changed, based on different reasons put forward by different authors (Chen et al., 2017; Delorme et al., 2006; Dubois et al., 2021; Fei & Ye, 2016; Lyu et al., 2021; Mahony et al., 2017; summarized in Table 1). Based on morphological characteristics, Delorme et al. (2006) and Fei & Ye (2016) partitioned the subfamily Megophryinae into five and seven genera, respectively. However, Mahony et al. (2017) considered the morphological diagnosability of genus-level groups (*sensu* Delorme et al., 2006) to be ambiguous, and suggested that all Asian horned toads in Megophryinae be placed into one large genus with seven subgenera to reflect primary molecular clades. In contrast, other studies have suggested a multiple-genus taxonomy for the subfamily Megophryinae, but with disagreement on the number of genera. Chen et al. (2017) suggested a five-genus taxonomy, while Dubois et al. (2021) proposed a seven-genus taxonomy. In recent discussions, Lyu et al. (2021) and Qi et al. (2021)

proposed a new seven-genus taxonomy built upon the seven-subgenus phylogeny of Mahony et al. (2017), with this updated taxonomy widely adopted in several databases and subsequent studies (e.g., Amphibia China, 2022; AmphibiaWeb, 2022; Frost, 2022; Luong et al., 2022; Wang et al., 2022). However, regardless of the efforts to classify these toads at the generic level, no satisfactory consensus has been reached (Dubois et al., 2021; Fei, 2020; Frost, 2022). As stated by Mahony et al. (2017) and Lyu et al. (2021), despite substantial phylogenetic reconstruction of this subfamily, the main challenge in generic classification lies in morphological comparison, especially for the revision of the diagnosability of each genus. In particular, many different researchers have used different terminologies (e.g., Delorme et al., 2006; Fei et al., 2005; Mahony et al., 2018; Tian & Hu, 1983), resulting in confusion and misunderstanding of generic recognition.

Apart from generic debates, recognition of toads at the species level has also faced challenges in recent years. Several Asian horned toad species were initially described based on brief and simple diagnoses and subsequently reported with wide distributions, such as *Xenophrys major*, *X. parva*, *Boulenophrys minor*, *B. brachykolos*, and *B. kuatunensis*. However, many subsequent records have been found to be misidentifications, instead representing

Table 1 Different generic affiliations for the subfamily Megophryinae in several important revisions and this study

Genus	Authorship	Delorme et al., 2006	Fei & Ye, 2016	Chen et al., 2017	Mahony et al., 2017	Dubois et al., 2021	Lyu et al., 2021 (revised by Qi et al., 2021)	This study
<i>Megophrys</i>	Kuhl and Van Hasselt, 1822	Accepted genus	Accepted genus (by implication)	Accepted genus	Accepted genus	Accepted genus	Accepted genus	Accepted genus
<i>Xenophrys</i>	Günther, 1864	Accepted genus	Accepted genus	Accepted genus	Subgenus of <i>Megophrys</i>	Accepted genus	Accepted genus	Accepted genus
<i>Ophryophryne</i>	Boulenger, 1903	Accepted genus	Accepted genus	Accepted genus	Subgenus of <i>Megophrys</i>	Accepted genus	Accepted genus	Accepted genus
<i>Pelobatrachus</i>	Beddard, 1907	Synonymy of <i>Megophrys</i>	N/A	Synonymy of <i>Megophrys</i>	Subgenus of <i>Megophrys</i>	Synonymy of <i>Megophrys</i>	Accepted genus	Accepted genus
<i>Atympanophrys</i>	Tian and Hu, 1983	Synonymy of <i>Xenophrys</i>	Accepted genus	Accepted genus	Subgenus of <i>Megophrys</i>	Accepted genus	Accepted genus	Accepted genus
<i>Brachytarsophrys</i>	Tian and Hu, 1983	Accepted genus	Accepted genus	Accepted genus	Subgenus of <i>Megophrys</i>	Accepted genus	Accepted genus	Accepted genus
<i>Panophrys</i>	Rao and Yang, 1997	Synonymy of <i>Xenophrys</i>	Synonymy of <i>Xenophrys</i>	Subgenus of <i>Xenophrys</i>	Subgenus of <i>Megophrys</i>	Synonymy of <i>Boulenophrys</i>	Synonymy of <i>Boulenophrys</i> (revised by Qi et al., 2021)	Synonymy of <i>Boulenophrys</i>
<i>Borneophrys</i>	Delorme, Dubois, Grosjean, and Ohler, 2006	Accepted genus	N/A	Synonymy of <i>Megophrys</i>	Synonymy of <i>Pelobatrachus</i>	Synonymy of <i>Megophrys</i>	Synonymy of <i>Pelobatrachus</i>	Synonymy of <i>Pelobatrachus</i>
<i>Liuophrys</i>	Fei, Ye, and Jiang, 2016	N/A	Accepted genus	N/A	N/A	Synonymy of <i>Xenophrys</i>	Synonymy of <i>Xenophrys</i>	Synonymy of <i>Xenophrys</i>
<i>Boulenophrys</i>	Fei, Ye, and Jiang, 2016	N/A	Accepted genus	N/A	N/A	Accepted genus	Accepted genus (revised by Qi et al., 2021)	Accepted genus
<i>Grillitschia</i>	Dubois, Ohler, and Pyron, 2021	N/A	N/A	N/A	N/A, <i>sensu X. aceras</i> group	Accepted genus	Synonymy of <i>Xenophrys</i> , <i>sensu X. aceras</i> group	Accepted genus
<i>Jingophrys</i> gen. nov.	Lyu and Wang	N/A	N/A	N/A	N/A, <i>sensu X. vegrandis</i> group	N/A	N/A, <i>sensu X. vegrandis</i> group	Accepted genus
<i>Sarawakiphrys</i> gen. nov.	Lyu and Wang	N/A	N/A	N/A	N/A	N/A	N/A, <i>sensu "M." dringi</i>	Accepted genus

N/A: Nomenclature not involved in relative revision.

independent species, with some being erected as new species (see Chresonymy/Remarks on relative species below). Nevertheless, in their descriptions, many studies did not provide detailed reviews of the historic records or present the chresonymies of the proposed new species. As more new species have been described, rectifying historical records and reviewing regional checklists have become increasingly important (Mahony et al., 2018; Qi et al., 2021).

In the present study, we performed detailed morphological comparisons of Asian horned toads from different clades to revise the diagnoses of each genus and provide a new ten-genus classification within the subfamily Megophryinae. Furthermore, we carefully reviewed the taxonomic history of each species occurring in China and provided a monograph of Chinese congeners.

MATERIALS AND METHODS

Phylogenetic analyses

Various recent studies have reconstructed the phylogeny of the subfamily Megophryinae (Chen et al., 2017; Liu et al., 2018; Mahony et al., 2017). However, these studies did not include all species in the subfamily, concentrating on primary Himalayan, Indochinese, and eastern Chinese congeners, respectively. To address this, we integrated molecular data from recent studies on Asian horned toads to generate a comprehensive phylogeny, which included nine nuclear gene (nuDNA) segments and four mitochondrial gene (mtDNA) segments (Supplementary Tables S1–S3). All recognized megophryid species were included in our phylogenetic analysis, except for three congeners lacking genetic data (Table 2). We also included data on “*Megophrys*” *feii*, whose phylogenetic placement is currently uncertain (Lyu et al., 2021). DNA extraction, polymerase chain reaction (PCR) amplification, and sequencing of new sequences followed the same protocols as Liu et al. (2018).

For phylogenetic analysis of Megophryinae, all of nine nuDNA segments and four mtDNA segments were used (Supplementary Table S1). The nuDNA segments included 1 310 bp of *Rag-1*, 818 bp of *Rag-2*, 883 bp of *Disp-2*, 713 bp of *Sall-1*, 682 bp of *CXCR-4*, 711 bp of *BDNF*, 339 bp of *RHOD*, 892 bp of *TTN*, and 1 060 bp of *SACS*, while the mtDNA segments included 548 bp of *16S*, 731 bp of *12S*, 632 bp of *COI*, and 1 050 bp of *cyt b*. Each gene segment was aligned using the ClustalW algorithm with default parameters (Thompson et al., 1997), and nucleotide positions with missing data were represented by “N” in the alignments. Alignments of nuDNA and mtDNA were concatenated with seriatim into a 7 408 bp nuDNA matrix and a 2 961 bp mtDNA matrix, respectively, with the two matrices analyzed independently. PartitionFinder2 was used to test the best partitioning scheme and jModelTest v2.1.2 was used to test the best fitting nucleotide substitution models. The two matrices were analyzed using maximum-likelihood (ML) in RAxML v8.0 (Stamatakis, 2014) and Bayesian inference (BI) in MrBayes 3.2.4 (Ronquist et al., 2012). For ML analysis, a bootstrap consensus tree inferred from 1 000 replicates was used to represent the evolutionary history of the taxa analyzed. Two independent runs of 50 000 000 generations were performed for BI analysis, with four Markov Chains Monte Carlo chains, sampling every 1 000 generations, and the first 25% of samples discarded as burn-in. Convergence was confirmed based on the average standard deviation of split frequencies

below 0.01 and an effective sample size larger than 200 using Tracer v1.6. ML bootstrap support (BS) greater than 85% and Bayesian posterior probability (BPP) greater than 0.95 represented strong support.

As the two largest genera of the subfamily, the phylogenies of *Xenophrys* and *Boulenophrys* were further analyzed. Three mtDNA segments (*16S+12S+COI*) were used for intrageneric analysis (Supplementary Tables S2, S3), and downstream analysis methods followed the same protocols as used above.

Morphological comparison

For morphological comparison, a total of 1 267 museum specimens were examined in this study (see taxonomic accounts for detailed information). Morphological characters of all known Asian horned toads were additionally obtained from the original or subsequent descriptions (Table 2). Abbreviations for museums and institutes include: SYS (The Museum of Biology, Sun Yat-sen University, Guangzhou, China), CIB (Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu, China), AMNH (American Museum of Natural History, New York, USA), BMNH (British Museum Natural History, now Natural History Museum, London, UK), BNHS (Bombay Natural History Museum, Mumbai, India), FMNH (Field Museum, Chicago, USA), GZNU (Guizhou Normal University, Guiyang, China), HNNU (Hunan Normal University, Changsha, China), KIZ (Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China), LTHC (Liupanshui Normal College, Liupanshui, China), MCZ (Museum of Comparative Zoology, Harvard University, Cambridge, USA), MNHN (Muséum National d'Histoire Naturelle, Paris, France), MSNG (Museo di Storia Naturale Giacomo Doria, Genoa, Italy), NJFU (Nanjing Forestry University, Nanjing, China), NWIPB (Northwest Institute of Plateau Biology, Xining, China), TRU (Tongren University, Tongren, China), USNM (National Museum of Natural History, Washington, USA), VNMM (Vietnam National Museum of Nature, Hanoi, Vietnam), WUYI (Fujian Wuyishan National Nature Reserve, Nanping, China), and ZSI (Zoological Survey of India, Kolkata, India).

External measurements were performed with digital calipers (Neiko 01407A Stainless Steel 6-Inch Digital Caliper (China)) to the nearest 0.1 mm, following Fei et al. (2009), Lyu et al. (2020, 2021), and Wang et al. (2014, 2019a). Snout-vent length (SVL, from tip of snout to posterior margin of vent) was recorded for all examined specimens. For newly proposed species in this work, additional measurements included: head length (HDL, from tip of snout to articulation of jaw); head width (HDW, head width at commissure of jaw); snout length (SNT, from tip of snout to anterior corner of eye); internasal distance (IND, distance between nares); interorbital distance (IOD, minimum distance between upper eyelids); eye diameter (ED, from anterior corner to posterior corner of eye); tympanum diameter (TD, horizontal diameter of tympanum); tympanum–eye distance (TED, from anterior edge of tympanum to posterior corner of eye); hand length (HND, from proximal border of outer palmar tubercle to tip of digit III); radius length (RAD, from flexed elbow to proximal border of outer palmar tubercle); foot length (FTL, from distal end of shank to tip of digit IV); tibia length (TIB, from outer surface of flexed knee to heel). Sex was determined by secondary sexual characters, such as the presence of vocal sacs and nuptial pads or spines in males and their absence in females (Fei & Ye, 2016).

Table 2 Morphological references and molecular data included in this work

Species	Authorship	Reference for morphology	Molecular data
(A) genus <i>Brachytarsophrys</i> , 8 species			
(Aa) <i>Brachytarsophrys carinense</i> group, 2 species			
<i>carinense</i>	(Boulenger, 1889)	Li et al., 2020a	mtDNA
<i>intermedia</i>	(Smith, 1921)	Li et al., 2020a	mtDNA
(Ab) <i>Brachytarsophrys orientalis</i> group, 6 species			
<i>chuannanensis</i>	Fei, Ye, and Huang, 2001	Li et al., 2020a; this study	mtDNA; nuDNA
<i>feae</i>	(Boulenger, 1886)	Li et al., 2020a; this study	mtDNA; nuDNA
<i>orientalis</i>	Li, Lyu, Wang, and Wang, 2020	Li et al., 2020a; this study	mtDNA
<i>platyparietus</i>	Rao and Yang, 1997	Li et al., 2020a; this study	mtDNA
<i>popei</i>	Zhao, Yang, Chen, Chen, and Wang, 2014	Li et al., 2020a; this study	mtDNA; nuDNA
<i>qiannanensis</i>	Li, Liu, Yang, Wei, and Su, 2022	Li et al., 2022; this study	mtDNA
(B) genus <i>Atympanophrys</i> , 4 species			
<i>gigantica</i>	(Liu, Hu, and Yang, 1960)	Fei & Ye, 2016; this study	mtDNA; nuDNA
<i>nankiangensis</i>	(Liu and Hu, 1966)	Hu et al., 1966; Fei & Ye, 2016	mtDNA; nuDNA
<i>shapingensis</i>	(Liu, 1950)	Fei & Ye, 2016; this study	mtDNA; nuDNA
<i>wawuensis</i>	(Fei, Jiang, and Zheng, 2001)	Fei & Ye, 2001, 2016; this study	mtDNA; nuDNA
(C) genus <i>Grillitschia</i> , 2 species			
<i>aceras</i>	(Boulenger, 1903)	Smith, 1930; Dubois et al., 2021	mtDNA; nuDNA
<i>longipes</i>	(Boulenger, 1886)	Boulenger, 1886; Dubois et al., 2021	mtDNA
(D) genus <i>Sarawakiphrys</i> gen. nov., 1 species			
<i>dringi</i> comb. nov.	(Inger, Stuebing, and Tan, 1995)	Inger et al., 1995	mtDNA
(E) genus <i>Jingophrys</i> gen. nov., 5 species			
<i>feii</i> comb. nov.	(Yang, Wang, and Wang, 2018)	This study	mtDNA; nuDNA
<i>pachyproctus</i> comb. nov.	(Huang, 1981)	Huang & Fei, 1981; Shi et al., 2020a	mtDNA; nuDNA
<i>vegrandis</i> comb. nov.	(Mahony, Teeling, Biju, 2013)	Mahony et al., 2013	mtDNA; nuDNA
<i>yeae</i> comb. nov.	(Shi, Zhang, Xie, Jiang, Liu, Ding, Luan, and Wang, 2020)	Shi et al., 2020a; this study	mtDNA; nuDNA
<i>zhoui</i> comb. nov.	(Shi, Zhang, Xie, Jiang, Liu, Ding, Luan, and Wang, 2020)	Shi et al., 2020a	mtDNA; nuDNA
(F) genus <i>Xenophrys</i> , 28 species			
(Fa) <i>Xenophrys lekaguli</i> group, 6 species			
<i>auralensis</i>	(Ohler, Swan, and Daltry, 2002)	Ohler et al., 2002	mtDNA
<i>damrei</i>	(Mahony, 2011)	Mahony, 2011	N/A
<i>dehongensis</i> sp. nov.	Lyu and Wang	This study	mtDNA; nuDNA
<i>lekaguli</i>	(Stuart, Chuaynkern, Chan-ard, and Inger, 2006)	Stuart et al., 2006a	mtDNA; nuDNA
<i>parva</i>	(Boulenger, 1893)	Mahony et al., 2020; this study	mtDNA; nuDNA
<i>takensis</i>	(Mahony, 2011)	Mahony, 2011	mtDNA; nuDNA
(Fb) <i>Xenophrys megacephala</i> group, 8 species			
<i>ancae</i>	(Mahony, Teeling, and Biju, 2013)	Mahony et al., 2013, 2020	mtDNA; nuDNA
<i>awuh</i>	(Mahony, Kamei, Teeling, and Biju, 2020)	Mahony et al., 2020	mtDNA; nuDNA
<i>dzukou</i>	(Mahony, Kamei, Teeling, and Biju, 2020)	Mahony et al., 2020	mtDNA; nuDNA
<i>megacephala</i>	(Mahony, Sengupta, Kamei, and Biju, 2011)	Mahony et al., 2020	mtDNA; nuDNA
<i>numhumaeng</i>	(Mahony, Kamei, Teeling, and Biju, 2020)	Mahony et al., 2020	mtDNA; nuDNA
<i>oropedion</i>	(Mahony, Teeling, and Biju, 2013)	Mahony et al., 2020	mtDNA; nuDNA
<i>serchhipii</i>	Mathew and Sen, 2007	Mahony et al., 2020	mtDNA; nuDNA
<i>zunhehotoensis</i>	Mathew and Sen, 2007	Mahony et al., 2020	mtDNA; nuDNA
(Fc) <i>Xenophrys major</i> group, 14 species			
<i>flavipunctata</i>	(Mahony, Kamei, Teeling, and Biju, 2018)	Mahony et al., 2018	mtDNA; nuDNA
<i>glandulosa</i>	(Fei, Ye, and Huang, 1990)	This study	mtDNA; nuDNA
<i>himalayana</i>	(Mahony, Kamei, Teeling, and Biju, 2018)	Mahony et al., 2018	mtDNA; nuDNA
<i>lancangica</i> sp. nov.	Lyu, Wang, and Wang	This study	mtDNA; nuDNA
<i>major</i>	(Boulenger, 1908)	Mahony et al., 2018	mtDNA; nuDNA
<i>mangshanensis</i>	(Fei and Ye, 1990)	This study	mtDNA; nuDNA
<i>maosonensis</i>	(Bourret, 1937)	This study	mtDNA; nuDNA
<i>medogensis</i>	(Fei, Ye, and Huang, 1983)	This study	mtDNA; nuDNA
<i>monticola</i>	Günther, 1864	Mahony et al., 2018	mtDNA; nuDNA
<i>oreocrypta</i>	(Mahony, Kamei, Teeling, and Biju, 2018)	Mahony et al., 2018	mtDNA; nuDNA
<i>periosa</i>	(Mahony, Kamei, Teeling, and Biju, 2018)	Mahony et al., 2018; Shi et al., 2020b	mtDNA; nuDNA

Species	Authorship	Reference for morphology	Molecular data
<i>robusta</i>	(Boulenger, 1908)	Mahony et al., 2018	mtDNA; nuDNA
<i>truongsonensis</i>	Luong, Hoang, Pham, Nguyen, Orlov, Ziegler, and Nguyen, 2022	Luong et al., 2022	mtDNA
<i>zhangii</i>	(Ye and Fei, 1992)	Ye & Fei, 1992; Che et al., 2020; this study	mtDNA; nuDNA
(G) genus <i>Megophrys</i> , 5 species			
<i>acehensis</i>	Munir, Nishikawa, Hamidy, and Smith, 2021	Munir et al., 2021	mtDNA
<i>lancip</i>	Munir, Hamidy, Farajallah, and Smith, 2018	Munir et al., 2018	mtDNA; nuDNA
<i>montana</i>	Kuhl and Van Hasselt, 1822	Kuhl & Van Hasselt, 1822; Munir et al., 2021; this study	mtDNA; nuDNA
<i>parallela</i>	Inger and Iskandar, 2005	Inger & Iskandar, 2005; Munir et al., 2021	mtDNA
<i>selatanensis</i>	Munir, Nishikawa, Hamidy, and Smith, 2021	Munir et al., 2021	mtDNA
(H) genus <i>Pelobatrachus</i> , 7 species			
<i>baluensis</i>	(Boulenger, 1899)	Boulenger, 1899a; Munir et al., 2021	mtDNA; nuDNA
<i>edwardinae</i>	(Inger, 1989)	Inger, 1989; Munir et al., 2021	mtDNA; nuDNA
<i>kalimantanensis</i>	(Munir, Hamidy, Matsui, Iskandar, Sidik, and Shimada, 2019)	Munir et al., 2019, 2021; this study	mtDNA
<i>kobayashii</i>	(Malkmus and Matsui, 1997)	Malkmus & Matsui, 1997; Munir et al., 2019, 2021	mtDNA
<i>ligayae</i>	(Taylor, 1920)	Taylor, 1920; Munir et al., 2019, 2021	mtDNA; nuDNA
<i>nasutus</i>	(Schlegel, 1858)	Schlegel, 1858; Munir et al., 2019, 2021	mtDNA; nuDNA
<i>stejnegeri</i>	(Taylor, 1920)	Taylor, 1920; Munir et al., 2021	mtDNA; nuDNA
(I) genus <i>Ophryophryne</i> , 7 species			
<i>elfina</i>	(Poyarkov, Duong, Orlov, Gogoleva, Vassilieva, Nguyen, Nguyen, Nguyen, Che, and Mahony, 2017)	Poyarkov et al., 2017	mtDNA
<i>gerti</i>	(Ohler, 2003)	Ohler, 2003; Poyarkov et al., 2017	mtDNA
<i>microstoma</i>	Boulenger, 1903	Fei & Ye, 2016; Poyarkov et al., 2017; this study	mtDNA; nuDNA
<i>pachyproctus</i>	Kou, 1985	Kou, 1985; Fei & Ye, 2016	N/A
<i>poilani</i>	Bourret, 1937	Bourret, 1937; Poyarkov et al., 2017	mtDNA; nuDNA
<i>synoria</i>	Stuart, Sok, and Neang, 2006	Stuart et al., 2006b; Poyarkov et al., 2017	mtDNA; nuDNA
<i>hansi</i>	(Ohler, 2003)	Ohler, 2003; Poyarkov et al., 2017	mtDNA; nuDNA
(J) genus <i>Boulenophrys</i> , 65 species			
(Ja) <i>Boulenophrys minor</i> group, 3 species			
<i>chishuiensis</i>	(Xu, Li, Liu, Wei, and Wang, 2020)	This study	mtDNA; nuDNA
<i>jiangii</i>	(Liu, Li, Wei, Xu, Cheng, Wang, and Wu, 2020)	Liu et al., 2020; this study	mtDNA; nuDNA
<i>minor</i>	(Stejneger, 1926)	This study	mtDNA; nuDNA
(Jb) <i>Boulenophrys omeimontis</i> group, 16 species			
<i>angka</i>	(Wu, Suwannapoom, Poyarkov, Chen, Pawangkhanant, Xu, Jin, Murphy, and Che, 2019)	Wu et al., 2019	mtDNA
<i>anlongensis</i>	(Li, Lu, Liu, and Wang, 2020)	Li et al., 2020b	mtDNA
<i>binchuanensis</i>	(Ye and Fei, 1995)	This study	mtDNA; nuDNA
<i>binlingensis</i>	(Jiang, Fei, and Ye, 2009)	Fei et al., 2009; this study	mtDNA; nuDNA
<i>caobangensis</i>	(Nguyen, Pham, Nguyen, Luong, and Ziegler, 2020)	Nguyen et al., 2020b	mtDNA
<i>daweimontis</i>	(Rao and Yang, 1997)	Rao & Yang, 1997	mtDNA; nuDNA
<i>fanjingmontis</i> comb. nov.	(Zhang, Liang, Ran, and Shen, 2012)	This study	mtDNA; nuDNA
<i>jingdongensis</i>	(Fei and Ye, 1983)	This study	mtDNA; nuDNA
<i>lushuiensis</i>	(Shi, Li, Zhu, Jiang, Jiang, and Wang, 2021)	This study	mtDNA; nuDNA
<i>omeimontis</i>	(Liu, 1950)	This study	mtDNA; nuDNA
<i>palpebralespinosa</i>	(Bourret, 1937)	Liu & Hu, 1961; Fei et al., 2019	mtDNA; nuDNA
<i>qianbeiensis</i>	(Su, Shi, Wu, Li, Yao, Wang, and Li, 2020)	This study	mtDNA; nuDNA
<i>rubrimera</i>	(Tapley, Cutajar, Mahony, Chung, Dau, Nguyen, Luong, and Rowley, 2017)	Tapley et al., 2017	mtDNA; nuDNA
<i>sangzhiensis</i>	(Jiang, Ye, and Fei, 2008)	This study	mtDNA; nuDNA
<i>spinata</i>	(Liu and Hu, 1973)	Hu et al., 1973; this study	mtDNA; nuDNA
<i>wuliangshanensis</i>	(Ye and Fei, 1995)	This study	mtDNA; nuDNA
(Jc) <i>Boulenophrys boettgeri</i> group, 43 species			
<i>acuta</i>	(Wang, Li, and Jin, 2014)	This study	mtDNA; nuDNA
<i>baishanzuensis</i>	(Wu, Li, Liu, Wang, and Wu, 2020)	Wu et al., 2020	mtDNA
<i>baolongensis</i>	(Ye, Fei, and Xie, 2007)	Ye et al., 2007; Fei & Ye, 2016	mtDNA; nuDNA

Continued

Species	Authorship	Reference for morphology	Molecular data
<i>boettgeri</i>	(Boulenger, 1899)	This study	mtDNA; nuDNA
<i>brachykolos</i>	(Inger and Romer, 1961)	This study	mtDNA; nuDNA
<i>caudoprocta</i>	(Shen, 1994)	Shen et al., 2013; this study	mtDNA; nuDNA
<i>cheni</i>	(Wang and Liu, 2014)	This study	mtDNA; nuDNA
<i>congjiangensis</i>	(Luo, Wang, Wang, Lu, Wang, Deng, and Zhou, 2021)	This study	mtDNA; nuDNA
<i>daiyunensis</i>	(Lyu, Wang, and Wang, 2021)	This study	mtDNA; nuDNA
<i>daoji</i>	(Lyu, Zeng, Wang, and Wang, 2021)	This study	mtDNA; nuDNA
<i>dongguanensis</i>	(Wang and Wang, 2019)	This study	mtDNA; nuDNA
<i>fengshunensis</i>	Wang, Zeng, Lyu, and Wang, 2022	This study	mtDNA; nuDNA
<i>hungtai</i>	Wang, Zeng, Lyu, Xiao, and Wang, 2022	This study	mtDNA
<i>insularis</i>	(Wang, Liu, Lyu, Zeng, and Wang, 2017)	This study	mtDNA; nuDNA
<i>jinggangensis</i>	(Wang, 2012)	This study	mtDNA; nuDNA
<i>julianensis</i>	(Wang, Zeng, Lyu, and Wang, 2019)	This study	mtDNA; nuDNA
<i>kuatunensis</i>	(Pope, 1929)	This study	mtDNA; nuDNA
<i>leishanensis</i>	(Li, Xu, Liu, Jiang, Wei, and Wang, 2018)	This study	mtDNA; nuDNA
<i>liboensis</i>	(Zhang, Li, Xiao, Li, Pan, Wang, Zhang, and Zhou, 2017)	Zhang et al., 2017	mtDNA
<i>lini</i>	(Wang and Yang, 2014)	This study	mtDNA; nuDNA
<i>lishuiensis</i>	(Wang, Liu and Jiang, 2017)	This study	mtDNA
<i>mirabilis</i>	(Lyu, Wang, and Zhao, 2020)	This study	mtDNA; nuDNA
<i>mufumontana</i>	(Wang, Lyu, and Wang, 2019)	This study	mtDNA
<i>nankunensis</i>	(Wang, Zeng, and Wang, 2019)	This study	mtDNA; nuDNA
<i>nanlingensis</i>	(Lyu, Wang, Liu, and Wang, 2019)	This study	mtDNA; nuDNA
<i>obesa</i>	(Wang, Li, and Zhao, 2014)	This study	mtDNA; nuDNA
<i>ombrophila</i>	(Messenger and Dahn, 2019)	This study	mtDNA; nuDNA
<i>puningensis</i>	Wang, Zeng, Lyu, Xiao, and Wang, 2022	This study	mtDNA
<i>sanmingensis</i>	(Lyu and Wang, 2021)	This study	mtDNA; nuDNA
<i>shimentaina</i>	(Lyu, Liu, and Wang, 2020)	This study	mtDNA; nuDNA
<i>shuichengensis</i>	(Tian and Sun, 1995)	Tian & Sun, 1995; Tian et al., 2000; Fei & Ye, 2016	N/A
<i>shunhuangensis</i>	(Wang, Deng, Liu, Wu, and Liu, 2019)	This study	mtDNA; nuDNA
<i>tongboensis</i>	(Wang and Lyu, 2021)	This study	mtDNA; nuDNA
<i>tubero granulata</i>	(Shen, Mo and Li, 2010)	Mo et al., 2010; Fei & Ye, 2016; this study	mtDNA; nuDNA
<i>wugongensis</i>	(Wang, Lyu, and Wang, 2019)	This study	mtDNA; nuDNA
<i>wushanensis</i>	(Ye and Fei, 1995)	Ye & Fei, 1995; Fei & Ye, 2016; this study	mtDNA; nuDNA
<i>xiangnanensis</i>	(Lyu, Zeng, and Wang, 2020)	This study	mtDNA; nuDNA
<i>xianjuensis</i>	(Wang, Wu, Peng, Shi, Lu, and Wu, 2020)	This study	mtDNA; nuDNA
<i>xuefengmontis</i> sp.nov.	Lyu and Wang	This study	mtDNA; nuDNA
<i>yangmingensis</i>	(Lyu, Zeng, and Wang, 2020)	This study	mtDNA; nuDNA
<i>yaoshanensis</i>	Qi, Mo, Lyu, Wang, and Wang, 2021	This study	mtDNA; nuDNA
<i>yingdeensis</i>	Qi, Lyu, Wang & Wang, 2021	This study	mtDNA; nuDNA
<i>yunkaiensis</i>	Qi, Wang, Lyu, and Wang, 2021	This study	mtDNA; nuDNA
Uncertain sedis within <i>Boulenophrys</i> , 3 species			
<i>fansipanensis</i>	(Tapley, Cutajar, Mahony, Nguyen, Dau, Luong, Le, Nguyen, Nguyen, Portway, Luong, and Rowley, 2018)	Tapley et al., 2018	mtDNA
<i>frigida</i>	(Tapley, Cutajar, Nguyen, Portway, Mahony, Nguyen, Harding, Luong, and Rowley, 2021)	Tapley et al., 2021	mtDNA
<i>hoanglienensis</i>	(Tapley, Cutajar, Mahony, Nguyen, Dau, Luong, Le, Nguyen, Nguyen, Portway, Luong, and Rowley, 2018)	Tapley et al., 2018	mtDNA

N/A: Molecular data not available.

RESULTS

Phylogenetic relationship

For the Megophryinae subfamily phylogeny, ML and BI nuDNA-based analyses generated almost identical topologies (Figure 1A). Based on nuclear phylogeny, the subfamily was identified as a monophyletic group with nine clades. For mitochondrial analysis, ML and BI generated almost identical

topologies, revealing 10 clades within the monophyletic subfamily Megophryinae (Figure 1B). The additional clade was monotypic with "*Megophrys*" *dringi*. Except for this species, all other congeners of Megophryinae were assigned into nine clades, as revealed by nuDNA and mtDNA, although the two matrices showed differences in the subclade relationships.

Based on both nuDNA and mtDNA analyses, clades A and B were identified as two basal clades, corresponding to the

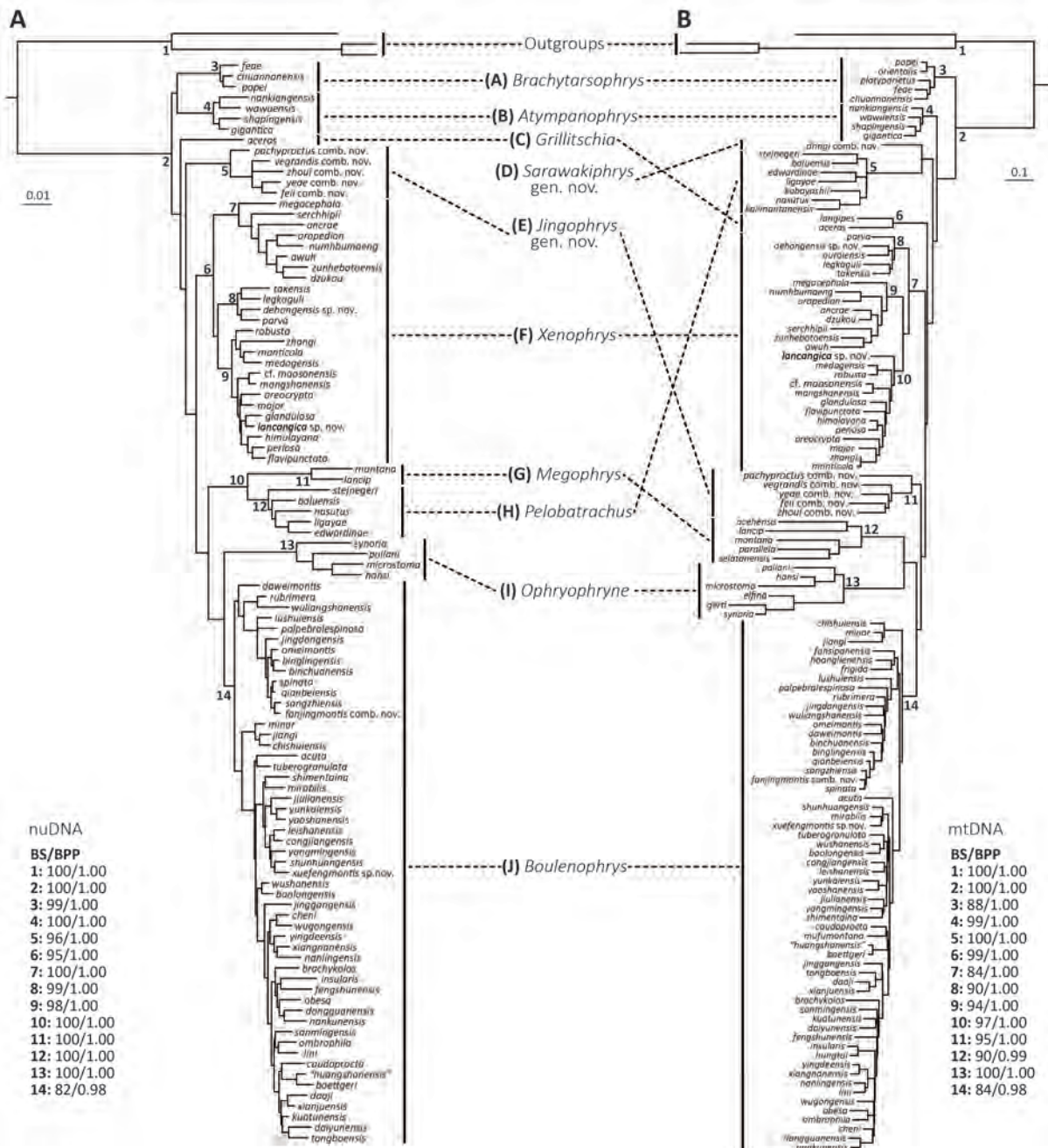


Figure 1 Phylogenetics of Asian horned frogs (Megophryinae) based on nuDNA (A) and mtDNA (B) data, respectively

Maximum-likelihood bootstrap support (BS) greater than 75% and Bayesian posterior probabilities (BPP) greater than 0.90 are labeled for major nodes.

Brachytarsophrys and *Atympanophrys* nomenclatures, respectively. Clade D was monotypic with “*Megophrys*” *dringi* and was only revealed by mtDNA phylogeny. Clades C, E, and F were placed together within the genus *Xenophrys* according to recent revision (Lyu et al., 2021; Qi et al., 2021). However, our nuDNA- and mtDNA-based analyses revealed that these clades were paraphyletic with distinct divergences, consistent with previous phylogenetic studies reporting similar patterns of divergence (Chen et al., 2017; Mahony et al., 2017). Clade C included two species from the Malay Peninsula, *X. aceras* and *X. longipes*, which were previously treated as members of the *X. aceras* group (Lyu et al., 2021; Mahony et al., 2017; Qi et al., 2021). Dubois et al. (2021) recently erected the genus *Grillitschia* for these two species, although this taxonomic change has not been widely accepted

(Frost, 2022). Clade E consisted of five species from the eastern Himalayas, i.e., *X. vegrandis*, *X. pachyproctus*, *X. yae*, *X. zhoui*, and “*Megophrys*” *feii*, for which this study provides the first genetic data (Figures 1, 2). This clade was previously suggested as a basal clade of *Xenophrys* (Chen et al., 2017; Mahony et al., 2017), named the *X. vegrandis* group (Lyu et al., 2021; Mahony et al., 2017; Qi et al., 2021). Clade F contained the remaining species of *Xenophrys* and was further divided into three subclades corresponding to three species groups, i.e., subclade Fa – *X. lekaguli* group, subclade Fb – *X. megacephala* group, and subclade Fc – *X. major* group (Figure 2; Lyu et al., 2021; Mahony et al., 2017; Qi et al., 2021).

Clades G and H corresponded to the *Megophrys* and *Pelobatrachus* nomenclatures, respectively. While these two

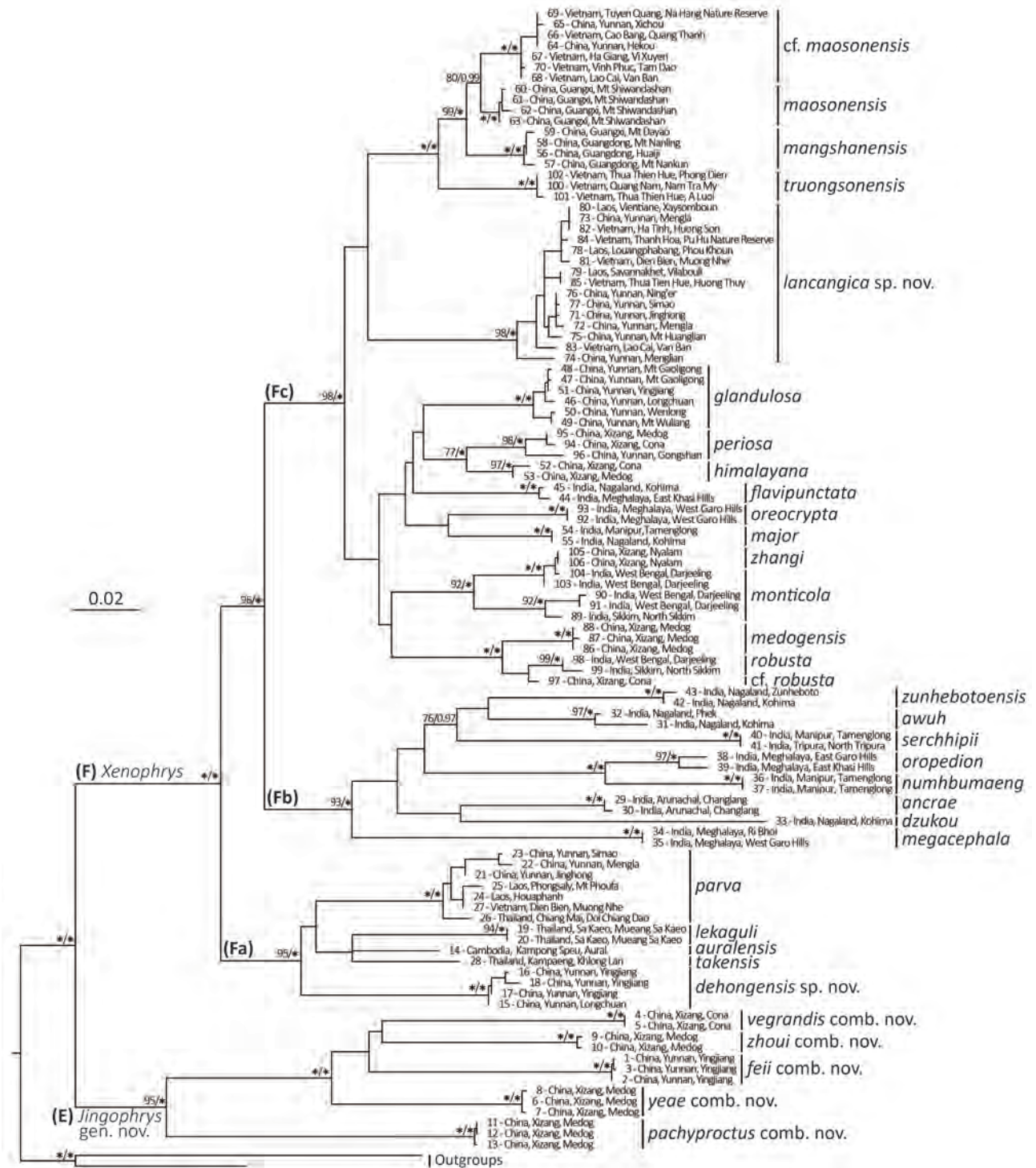


Figure 2 Phylogenetics of genera *Xenophrys* and *Jingophrys* gen. nov.

Numbers at terminal of lineage correspond to ID in Supplementary Table S2. Maximum-likelihood bootstrap support (BS) greater than 75% and Bayesian posterior probabilities (BPP) greater than 0.90 are labeled for major nodes. *: BS=100% or BPP=1.00.

clades formed a sister taxon based on nuclear phylogeny, they exhibited distinctly distant relationships based on mitochondrial phylogeny. Clades I and J were identified as relative terminal clades within the subfamily, corresponding to the *Ophryophryne* and *Boulenophrys* nomenclatures, respectively. Three strongly supported subclades were recovered within clade J (*Boulenophrys*), corresponding to three species groups, i.e., subclade Ja – *B. minor* group, subclade Jb – *B. omeimontis* group, and subclade Jc – *B. boettgeri* group (Figure 3; Qi et al., 2021). The three remaining

congeners, *B. fansipanensis*, *B. frigida*, and *B. hoanglienensis*, formed an independent subclade closely related to the *B. omeimontis* group but with relatively weak support (BS 55, BPP 0.90; Figure 3).

Morphological examination

In the course of comparing morphologies of the Asian horned toad species, we observed that different terminologies were used by various researchers, which may lead to confusion or misunderstanding. Therefore, we present updated definitions

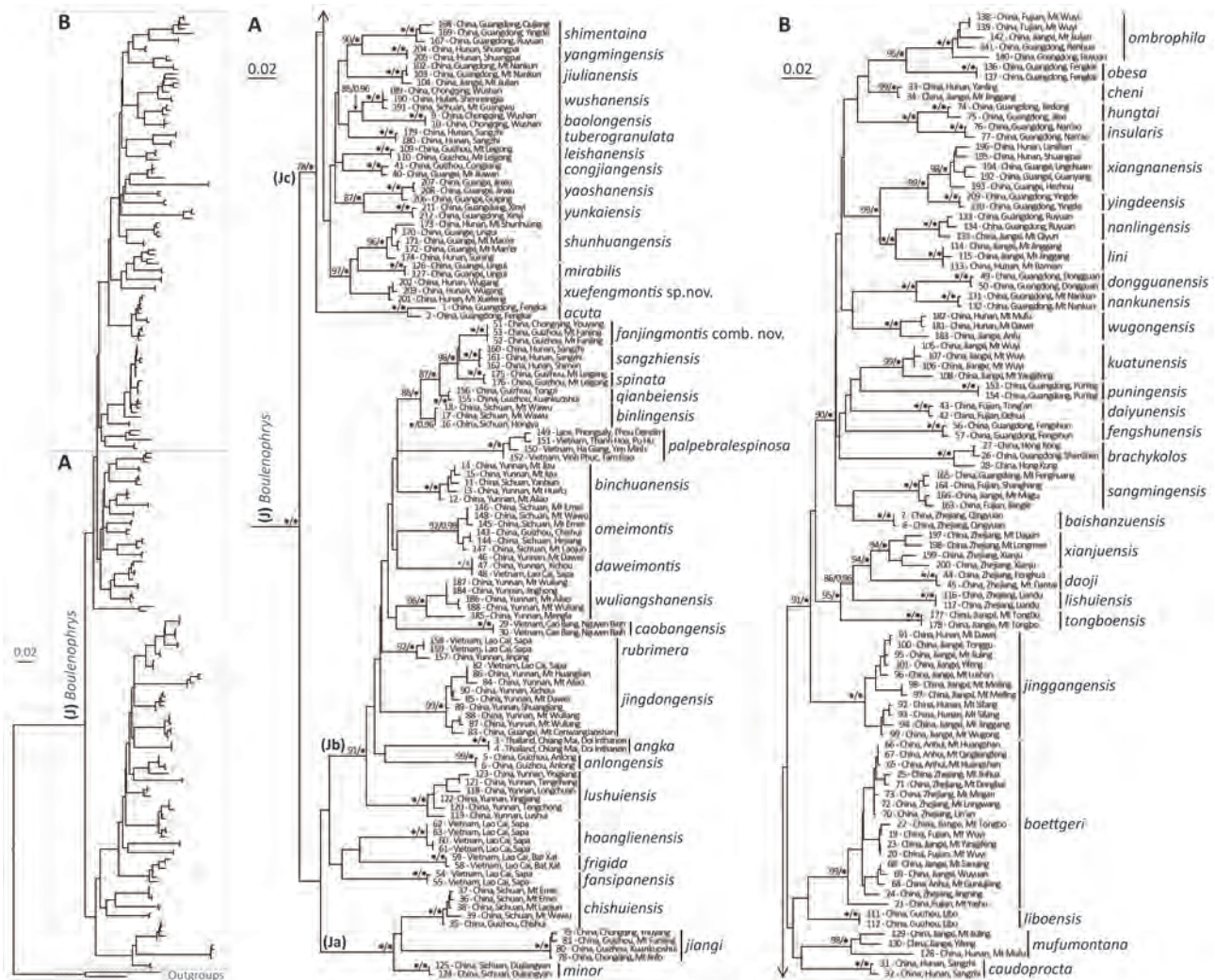


Figure 3 Phylogenetics of genus *Boulenophrys*

Numbers at terminal of lineage correspond to ID in Supplementary Table S3. Maximum-likelihood bootstrap support (BS) greater than 75% and Bayesian posterior probabilities (BPP) greater than 0.90 are labeled for major nodes. *: BS=100% or BPP=1.00.

of several important characteristics below.

I. Palpebral tubercles or appendages. Species within the subfamily Megophryinae are known as Asian horned toads in reference to their remarkable palpebral tubercles or appendages in some of the congeners. These palpebral tubercles or appendages are classified into five types: (i) outer margin of upper eyelid elongated as pointed triangular appendage, large horn-like prominent tubercle absent (Figures 4A, B, 5A) or present (Figure 4C) on tip, edge of appendage sharp and connected with canthus rostralis and supratympanic fold; (ii) weak medial bumped appendage at outer margin of upper eyelid, without horn-like tubercles, edge of appendage sharp and connected with canthus rostralis and supratympanic fold (Figures 4D, E, 5B); (iii) appendage absent, large (Figures 4F, 5C), small (Figure 4G), or tiny (Figures 4H, 5D) horn-like tubercle at outer margin of upper eyelid present, flattened tubercles around horn-like tubercle absent or present, edge of upper eyelid sharp and only connected with canthus rostralis or supratympanic fold; (iv) appendage absent, remarkable conical tubercle at outer margin of upper eyelid present, small tubercles around conical tubercle present or absent (Figures 4I, 5E); (v) upper eyelid smooth without appendages or horn-like tubercles, margin of eyelid smooth (Figures 4J, 5F).

II. Temporal region. Temporal region appearance is classified into four types: (i) temporal region elongated, tympanum small, distinct, or slightly concealed, far from posterior corner of eye, supratympanic fold narrow, distinctly or slightly curved over tympanum (Figures 4A, B, 5A); (ii) temporal region short, tympanum moderate or large, distinct or concealed, relatively close to posterior corner of eye, supratympanic fold narrow and distinctly curved over tympanum (Figures 4C–E, G, H, 5B, D); (iii) temporal region short, tympanum moderate or large, distinct or slightly concealed, relatively close to posterior corner of eye, supratympanic fold thick and slightly curved over tympanum (Figures 4F, 5C); (iv) temporal region short, tympanum concealed and invisible, supratympanic fold narrow (Figures 4I, 5E) or thick (Figures 4J, 5F), extending straightly.

III. Dorsolateral ridge. Dorsolateral ridge appearance is classified into four types: (i) single dorsolateral ridge at each side, extending continuously from shoulder to groin or mid-body (Figures 4A, D, E and 5G); (ii) based on type (i), additional lateral fold on flank, extending continuously from corner of supratympanic fold to groin or mid-body (Figures 4B, 5H); (iii) single dorsolateral ridge at each side, extending discontinuously from shoulder to groin or mid-body (Figures 4C, F, G, 5I); (iv) absent (Figures 4H–J, 5J).



Figure 4 Appearance differences among Asian horned toads

A: *Megophrys montana*; B: *Pelobatrachus kalimantanensis*; C: *Boulenophrys caudoprocta*; D: *Xenophrys zhangii*; E: *Boulenophrys jingdongensis*; F: *Ophryophryne microstoma*; G: *Jingophrys yeae* **comb. nov.**; H: *Boulenophrys wushanensis*; I: *Brachytarsophrys orientalis*; J: *Atympanophrys gigantea*. Photos by Z.T. Lyu, S. Qi, J. Wang, J. Zhao, and Y.B. Lin.

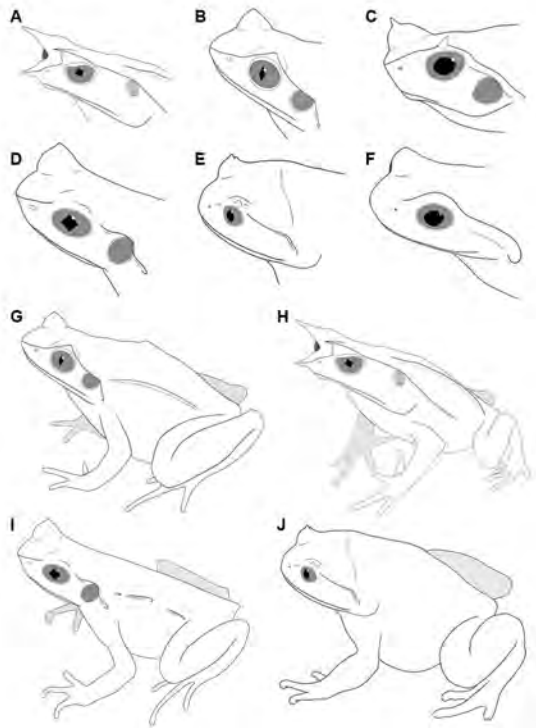


Figure 5 Line illustrations showing characteristics redefined in this work

A–F: Head showing appearance of palpebral tubercles or appendages and temporal region (see text for detailed definitions); G–J: Lateral view showing appearance of dorsolateral ridge (see text for detailed definitions). Illustrated by S. Qi.

Furthermore, during morphological examinations, we noted two characteristics that were seldom mentioned in previous studies but can be considered as key diagnostic features for two clades of the Asian horned toads (Figures 6, 7; see Remarks on *Jingophrys* gen. nov. and *Xenophrys* below). Table 3 provides a summary of the morphological differences among the 10 phylogenetic clades, which can be distinguished based on a combination of characteristics.

Generic classification

Based on phylogenetic relationships and morphological comparisons, we hereby propose a new ten-genus classification for the Asian horned toad subfamily Megophryinae: i.e., *Brachytarsophrys*, *Atympanophrys*, *Grillitschia*, *Sarawakiphrys* gen. nov., *Jingophrys* gen. nov., *Xenophrys*, *Megophrys*, *Pelobatrachus*, *Ophryophryne*, and *Boulenophrys*. These 10 genera correspond to the 10 phylogenetic clades (Figure 1) and can be diagnosed independently by a combination of morphological characteristics (see Table 3 and identification key below). Geographically, the genera show different dispersal tendencies into East Asia, the Himalayas, and maritime Southeast Asia, despite several sympatric regions in Indochina and southwestern China (Figures 8, 9).

Key to genera of subfamily Megophryinae

- 1a) Maxillary teeth absent *Ophryophryne*
- 1b) Maxillary teeth present 2
- 2a) Temporal region elongated; tympanum small, distinct, or slightly concealed, far from posterior corner of eye; supratympanic fold narrow 3
- 2b) Not possessing above combination of three characters

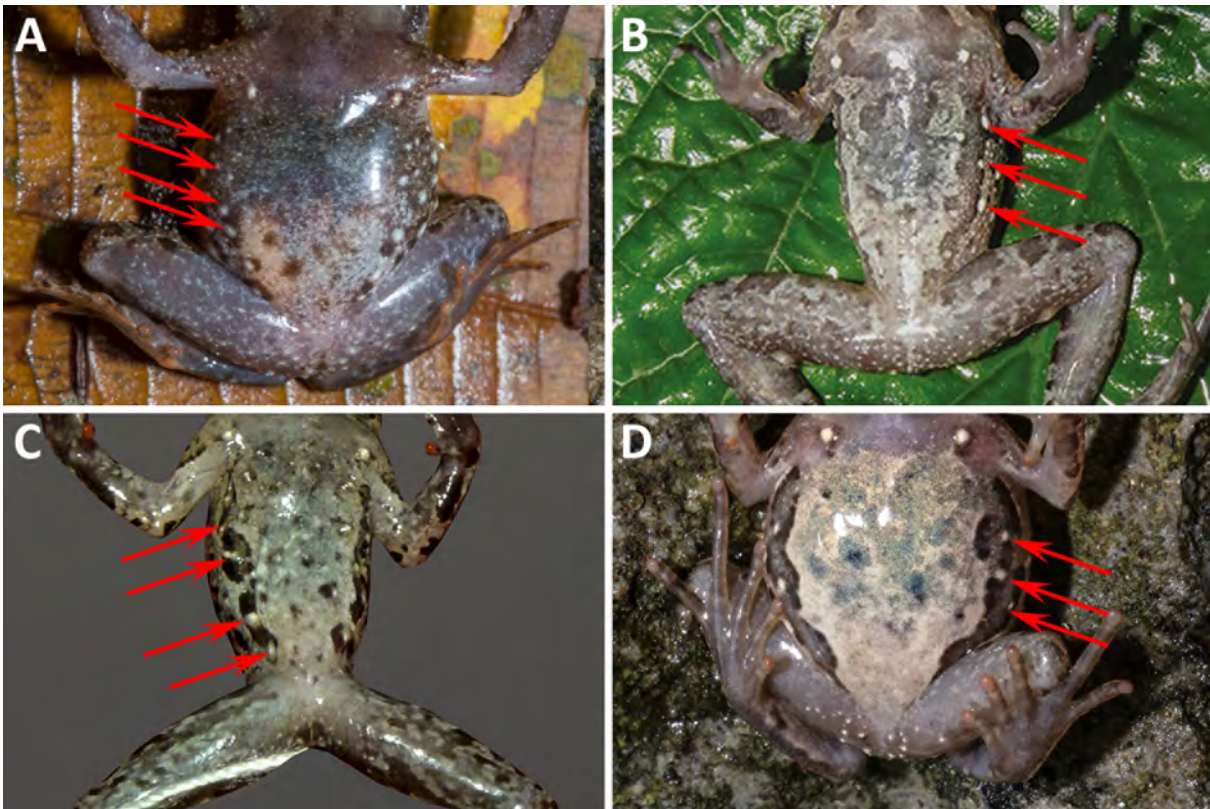


Figure 6 Seriate tubercles on both sides of belly in congeners of *Jingophrys* gen. nov.

A: Male SYS a003876 of *J. feii* comb. nov.; B: Male CIB 022017061805 of *J. pachyproctus* comb. nov. (cited from Figure 7B in Shi et al., 2020a); C: Male ZSI A11605 of *J. vegrandis* comb. nov. (cited from Figure 9D in Mahony et al., 2013); D: Male SYS a006683 of *J. yeae* comb. nov. Photos by J. Zhao and J. Wang.

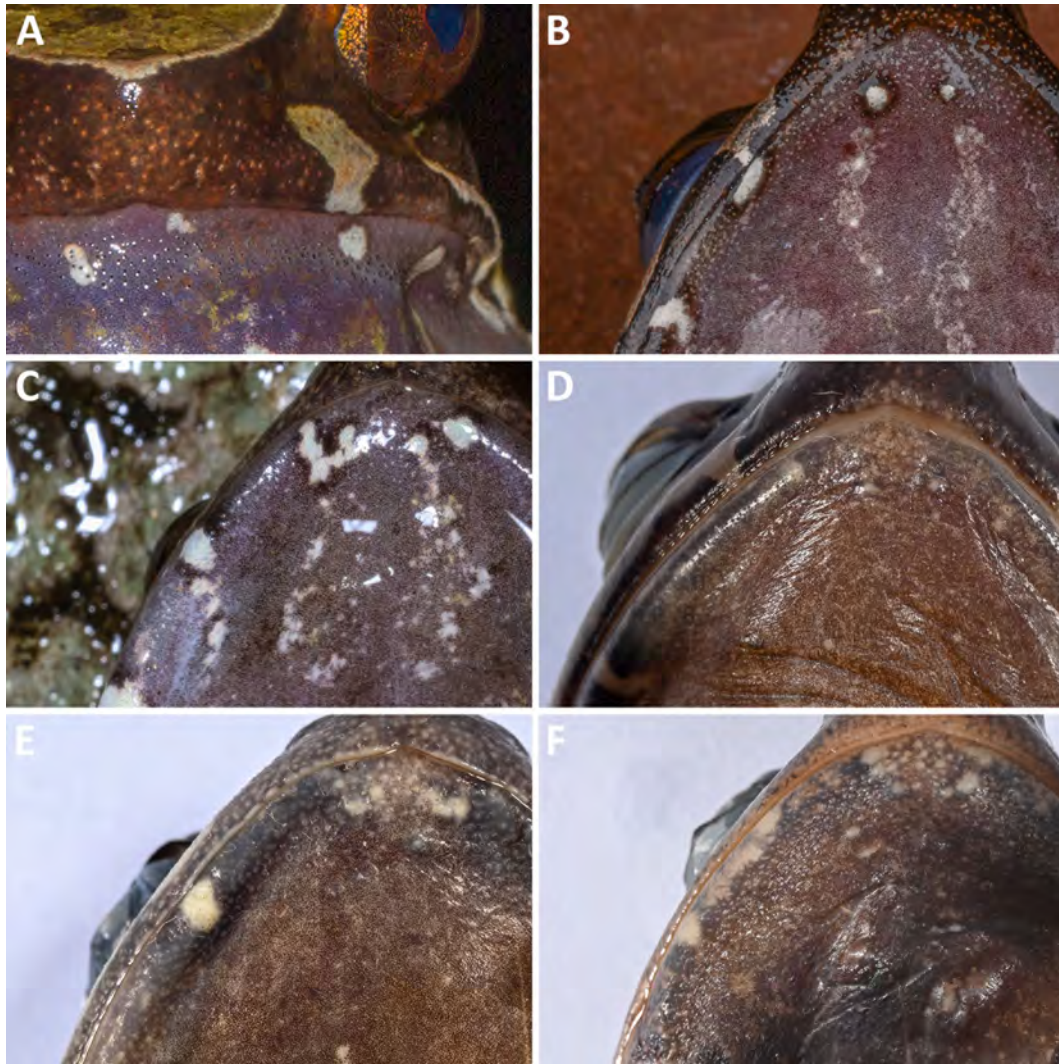


Figure 7 Asperities on lower jaw in congeners of *Xenophrys*

A: Black asperities on uncaptured *X. mangshanensis* individual *in situ*; B: White asperities on *X. maosonensis* male SYS a008766 *in life*; C: White asperities on *X. medogensis* male SYS a006634 *in life*; D: Black asperities on *X. lancangica* *sp. nov.* male SYS a002961 in preservative; E: Black asperities on *X. glandulosa* male SYS a002946 in preservative; F: White asperities on *X. glandulosa* female SYS a003762 in preservative. Photos by Z.T. Lyu, S. Qi, J. Wang, and Y.H. Zhu.

simultaneously 5
3a) X- or V-shaped dermal ridge present on center of dorsum ..
 *Grillitschia*
3b) Dermal ridge absent on center of dorsum 4
4a) Relatively smaller body size, SVL smaller than 60 mm in
 males; vomerine teeth present; with type (i) dorsolateral ridge ..
 *Megophrys*
4b) Not possessing above combination of three characters
 simultaneously *Pelobatrachus*
5a) Transverse fold behind head present; head distinctly
 enlarged and extremely depressed *Brachytarsophrys*
5b) Transverse fold behind head absent; head not enlarged
 and depressed 6
6a) Upper eyelid smooth without appendages or horn-like
 tubercles, margin of eyelid smooth *Atympanophrys*
6b) Upper eyelid with appendages or horn-like tubercles 7
7a) Subarticular tubercles on fingers present, distinct or
 indistinct *Boulenophrys*
7b) Subarticular tubercles on fingers absent 8
8a) Weak medial bumped appendage at outer margin of upper
 eyelid, without horn-like tubercles; nuptial pads/spines present

on fingers I and II in breeding males *Xenophrys*
8b) Upper eyelid without appendage, horn-like tubercle at
 outer margin of eyelid present; nuptial pads/spines absent or
 only present on finger I in breeding males 9
9a) Medium body size, SVL larger than 40 mm in males;
 tympanum mostly obscured by skin; distributed in
 Borneo..... *Sarawakiphrys* **gen. nov.**
9b) Small body size, SVL smaller than 40 mm in males;
 tympanum distinct and visible; distributed in eastern
 Himalayas *Jingophrys* **gen. nov.**

(A) *Brachytarsophrys* Tian and Hu, 1983

Short-legged toads / duǎn tuǐ chán shǔ (短腿蟾属)

Synonym: *Megophrys* (*Brachytarsophrys*) — Dubois, 1987; Mahony et al., 2017

Type species: *Leptobrachium carinensis* Boulenger, 1899.

Diagnosis: (1) Large body size, SVL>70 mm in males, body habitus thickset and stocky; (2) head distinctly enlarged and extremely depressed; snout rounded or pointed, without rostral appendage; (3) maxillary teeth present, vomerine teeth present; (4) upper eyelid without appendage, remarkable conical tubercle at outer margin of eyelid present, several

Table 3 Morphological comparisons of 10 genera within the subfamily Megophryinae

	<i>Brachytarsophrys</i>	<i>Atympanophrys</i>	<i>Grillitschia</i>	<i>Sarawakiphrys</i> gen. nov.	<i>Jingophrys</i> gen. nov.
Habitus	Large body size, SVL>70 mm in males, body thickset and stocky	Small, medium, or large body size, SVL 30–110 mm in males, body stocky	Medium body size, mean SVL>40 mm in males, body slender	Medium body size, SVL>40 mm in males, body slender	Small body size, SVL<40 mm in males, body slender
Head	Distinctly enlarged and extremely depressed	Not enlarged and depressed	Moderately enlarged and much depressed	Not enlarged and depressed	Not enlarged and depressed
Snout and rostral appendage	Rounded or pointed, without rostral appendage	Rounded, without rostral appendage	Truncated or obtusely pointed, without rostral appendage	Obtusely rounded, without rostral appendage	Rounded, without rostral appendage
Maxillary teeth	Present	Present	Present	Present	Present
Vomerine teeth	Present	Absent	Present	Absent	Present or absent
Palpebral tubercles or appendage	Type (iv)	Type (v)	Type (iii)	Type (iii)	Type (iii)
Temporal region	Type (iv)	Type (iii) or (iv)	Type (i)	Type (ii)	Type (ii)
Transverse fold behind head	Present	Absent	Present or absent	Absent	Absent
Dermal ridge on center of dorsum	Absent	Absent or present	Present, X- or V-shaped	Present, V-shaped	Present, X- or V-shaped
Dorsolateral ridge	Type (i) or (iv)	Type (iv)	Type (i)	Type (iii)	Type (iii)
Ventrolateral tubercles	Absent	Absent	Not mentioned	Not mentioned	Present
Asperities on lower jaw	Absent	Absent	Not mentioned	Absent	Absent
Subarticular tubercles on fingers	Absent	Absent	Absent	Absent	Absent
Nuptial pads/spines in breeding males	Present	Absent or present	Not mentioned	Absent	Absent or present on dorsal base of finger I

Table 3 (Continued)

	<i>Xenophrys</i>	<i>Megophrys</i>	<i>Pelobatrachus</i>	<i>Ophryophryne</i>	<i>Boulenophrys</i>
Habitus	Small, medium, or large body size, SVL 30–100 mm in males, body moderate	Small or medium body size, SVL<70 mm in males, body stocky	Medium or large body size, mean SVL>40 mm in males, body stocky	Small or medium body size, mean SVL<50 mm in males, body slender	Small, medium, or large body size, SVL 25–120 mm in males, body moderate
Head	Not enlarged and depressed (except <i>X. parva</i>)	Moderately enlarged and much depressed	Slightly enlarged and depressed	Not enlarged and depressed	Not enlarged and depressed
Snout and rostral appendage	Rounded or obtusely pointed, without rostral appendage	Pointed, with or without rostral appendage	Pointed or truncated, with or without rostral appendage	Rounded or truncated, without rostral appendage	Rounded or obtusely pointed, without rostral appendage
Maxillary teeth	Present	Present	Present	Absent	Present
Vomerine teeth	Present	Present	Present or absent	Absent	Present or absent
Palpebral tubercles or appendage	Type (ii)	Type (i)	Type (i) or (iii)	Type (iii)	Type (i), (ii), or (iii)
Temporal region	Type (ii)	Type (i)	Type (i)	Type (iii)	Type (ii)
Transverse fold behind head	Absent	Present	Present	Absent	Absent
Dermal ridge on center of dorsum	Present, weakly developed	Absent	Absent	Present, variable shaped	Present, variable shape
Dorsolateral ridge	Type (i) or (iii)	Type (i)	Type (i), (ii), (iii), or (iv)	Type (iii) or (iv)	Type (iii) or (iv)
Ventrolateral tubercles	Absent	Not mentioned	Not mentioned	Absent	Absent
Asperities on lower jaw	Present	Absent	Absent	Absent	Absent
Subarticular tubercles on fingers	Absent	Absent	Absent	Absent	Present, distinct or indistinct
Nuptial pads/spines in breeding males	Present on dorsal bases of fingers I and II	Present	Present	Present	Absent or present on dorsal bases of fingers I and II

small tubercles around conical tubercle present or absent; (5) temporal region short; tympanum concealed and invisible; supratympanic fold narrow and slightly curved over tympanic region; (6) transverse fold behind head present; (7) dermal ridges on center of dorsum absent; (8) dorsolateral ridges present or absent, distinct and continuous if present; (9) both sides of belly without seriate tubercles; (10) asperities on

lower jaw absent; (11) subarticular tubercles on fingers absent; nuptial pads/spines present in breeding males.

Distribution: Southern China (Yunnan, Sichuan, Guizhou, Guangxi, Guangdong, Hunan, Jiangxi, and Fujian) and mainland Indochina including Myanmar, Thailand, Laos, and Vietnam (Figure 8).

Content: Eight recognized species, divided into two species



Figure 8 Distributions of genera *Brachytarsophrys*, *Atympanophrys*, *Grillitschia*, *Sarawakiphrys* gen. nov., *Jingophrys* gen. nov., *Megophrys*, and *Ophryophryne*

groups: *B. carinense* group (two recognized species) and *B. orientalis* group (six recognized species) (Table 2).

Remarks: Li et al. (2020a) proposed two species groups, i.e., *B. carinense* group and *B. feae* group, for interspecific classification. However, the taxonomic review of *B. feae* by Li et al. (2020a) was primarily based on populations from China and lacked the topotypic population from Myanmar. To avoid potential confusion in the event of any future revision of phylogenetic placement of *B. feae*, Lyu et al. (2021) suggested that the name of the *B. feae* group be replaced with the *B. orientalis* group, as subsequently followed by Qi et al. (2021) and this study (Table 2).

(B) *Atympanophrys* Tian and Hu, 1983

Hidden-tympanum horned toad / wú ěr chán shǔ (无耳蟾属)

Synonym: *Megophrys* (*Atympanophrys*) — Dubois, 1987; Mahony et al., 2017

Atympanophrys (*Atympanophrys*) — Fei & Ye, 2016

Atympanophrys (*Borealophrys*) — Fei & Ye, 2016

Atympanophrys (*Gigantophrys*) — Fei & Ye, 2016

Type species: *Megophrys shapingensis* Liu, 1950.

Diagnosis: (1) Small, medium, or large body size, SVL 30–110 mm in males, body habitus stocky; (2) head not enlarged and depressed; snout rounded, without rostral appendage; (3) maxillary teeth present, vomerine teeth absent; (4) upper eyelid smooth without appendages or horn-like tubercles, margin of eyelid smooth; (5) temporal region short; tympanum concealed or distinct; supratympanic fold thick, extending straightly or slightly curved over tympanic region; (6) transverse fold behind head absent; (7) dermal ridges on center of dorsum absent or present; (8) dorsolateral ridges absent; (9) both sides of belly without seriate tubercles; (10) asperities on lower jaw absent; (11) subarticular tubercles on fingers absent; nuptial pads/spines absent or present in breeding males.



Figure 9 Distributions of genera *Xenophrys*, *Pelobatrachus*, and *Boulenophrys*

Distribution: Several isolated localities in western China (Yunnan, Sichuan, Gansu, and Shaanxi) and northernmost Vietnam (Figure 8).

Content: Four recognized species (Table 2).

Remarks: Fei & Ye (2016) did not include *A. wawuensis* within this genus which they partitioned into three monotypic subgenera, i.e., *Atymanophrys*, *Borealophrys*, and *Gigantophrys*. In this work, we suggest that it is unnecessary to partition this small genus, which contains only four species, into multiple subgenera, despite the distinct differences among the congeners. Furthermore, phylogenetic studies (Chen et al., 2017; Liu et al., 2018; this study) and morphological examinations both suggest the inclusion of *A. wawuensis* within the genus (refer to Remarks on *A. wawuensis* below). Previous diagnosis of the genus emphasized concealed and invisible tympanum as important diagnostic feature (Fei & Ye, 2016; Fei et al., 2009); however, *A. wawuensis* possesses a visible and distinct tympanum, and therefore we revise

diagnosis of this genus in the current study.

(C) *Grillitschia* Dubois, Ohler, and Pyron, 2021

Peninsular horned toad / bàn đảo jiǎo chán shǔ (半岛角蟾属)

Type species: *Megalophrys longipes* Boulenger, 1886.

Diagnosis: (1) Medium body size, mean SVL > 40 mm in males, body habitus slender; (2) head moderately enlarged and much depressed; snout truncated or obtusely pointed, without rostral appendage; (3) maxillary teeth present, vomerine teeth present; (4) upper eyelid without appendage, single large or small horn-like tubercle at outer margin of eyelid present; (5) temporal region elongated; tympanum small, distinct, or slightly concealed, far from posterior corner of eye; supratympanic fold narrow and distinctly curved over tympanum; (6) transverse fold behind head present or absent; (7) dermal ridges on center of dorsum present, V- or X-shaped; (8) single dorsolateral ridge at each side present, extending continuously from shoulder to groin or mid-body; (9) subarticular tubercles on fingers absent.

Distribution: Malay Peninsula, including southernmost Myanmar, southernmost Thailand, and West Malaysia (Figure 8).

Content: Two recognized species (Table 2).

(D) *Sarawakiphrys* gen. nov. Lyu and Wang

Sarawak horned toad / shā jiǎo chán shǔ (砂角蟾属)

Type species: *Megophrys dringi* Inger, Stuebing, and Tan, 1995.

Etymology: The generic nomen of *Sarawakiphrys* gen. nov. is derived from Sarawak in East Malaysia, the only known distributed region of this genus, and *-phrys*, the common generic root for Asian horned toads.

Diagnosis: (1) Medium body size, SVL>40 mm in males, body habitus slender; (2) head not enlarged and depressed; snout obtusely rounded, without rostral appendage; (3) maxillary teeth present, vomerine teeth absent; (4) upper eyelid without appendage, large horn-like tubercle at outer margin of eyelid present; (5) temporal region short; tympanum mostly obscured by skin; supratympanic fold narrow and curved over tympanum; (6) transverse fold behind head absent; (7) dermal ridges on center of dorsum present, V-shaped; (8) dorsolateral ridges present, discontinuous; (9) asperities on lower jaw absent; (10) subarticular tubercles on fingers absent; nuptial pads/spines absent in breeding males.

Distribution: Only known from Mt. Mulu, Sarawak in East Malaysia (Figure 8).

Content: One recognized species (Table 2).

Remarks: The only available molecular data for this genus were obtained from a short segment of the 16S gene from a single species, *Sarawakiphrys dringi* comb. nov. Mitochondrial phylogenetics revealed its independent status as a sister taxon of the genus *Pelobatrachus* (Figure 1). Morphological comparisons further support its uniqueness from all other genera (Table 3 and key presented above). As such, it is hereby erected as a distinct genus.

(E) *Jingophrys* gen. nov. Lyu and Wang

Diminutive horned toad / jìng jiǎo chán shǔ (靖角蟾属)

Type species: *Megophrys feii* Yang, Wang, and Wang, 2018.

Etymology: The generic nomen of *Jingophrys* gen. nov. is derived from the Chinese character “靖” (Pinyin: “jìng”, meaning “lilliputian” in English), referring to the small body size of this genus compared with other Asian horned toads, and *-phrys*, the common generic root for Asian horned toads.

Diagnosis: (1) Small body size, SVL<40 mm in males, body habitus slender; (2) head not enlarged and depressed; snout short, rounded, without rostral appendage; (3) maxillary teeth present, vomerine teeth present or absent; (4) upper eyelid without appendage, small or tiny horn-like tubercle at outer margin of eyelid present; (5) temporal region short; tympanum moderate or large, distinct and visible, relatively close to posterior corner of eye; supratympanic fold narrow and curved over tympanum; (6) transverse fold behind head absent; (7) dermal ridges on center of dorsum present, X- or V-shaped; (8) dorsolateral ridges present, discontinuous; (9) both sides of belly with seriate tubercles; (10) asperities on lower jaw absent; (11) subarticular tubercles on fingers absent; nuptial pads/spines absent or only present on dorsal base of finger I in breeding males.

Distribution: Only reported from Cona and Medog counties of southeastern Xizang and Yingjiang County of westernmost Yunnan in China (Figure 8).

Content: Five recognized species (Table 2).

Remarks: *Jingophrys* gen. nov. species possess seriate tubercles on both sides of the belly (Figure 6). While these tubercles may be weakly developed in certain individuals depending on their different growth stage, this character is consistently absent in all species of other genera of Asian horned toads and is therefore proposed as a diagnostic feature of *Jingophrys* gen. nov.

(F) *Xenophrys* Günther, 1864

Strange horned toad / yì jiǎo chán shǔ (异角蟾属)

Synonym: *Liuophrys* — Fei & Ye, 2016

Xenophrys (*Xenophrys*) — Fei & Ye, 2016

Megophrys (*Xenophrys*) — Mahony et al., 2017

Type species: *Xenophrys monticola* Günther, 1864.

Diagnosis: (1) Small, medium, or large body size, SVL 30–100 mm in males, body habitus moderate; (2) head not enlarged and depressed (except *X. parva* with slightly concave dorsal snout); snout rounded or obtusely pointed, without rostral appendage; (3) maxillary teeth present, vomerine teeth present; (4) weak medial bumped appendage at outer margin of upper eyelid, without horn-like tubercles, edge of appendage sharp and connected with canthus rostralis and supratympanic fold; (5) temporal region short; tympanum moderate or large, distinct or slightly concealed, relatively close to posterior corner of eye; supratympanic fold narrow and curved over tympanum; (6) transverse fold behind head absent; (7) dermal ridges on center of dorsum present but weakly developed; (8) dorsolateral ridges present, continuous or discontinuous; (9) sides of belly without seriate tubercles; (10) small black or white asperities present on lower jaw; (11) subarticular tubercles on fingers absent; nuptial pads/spines present on dorsal bases of fingers I and II in breeding males.

Distribution: Tropical mainland South, Southeast, and East Asia, including Nepal, Bhutan, northeastern India, Bangladesh, Myanmar, Thailand, Laos, Vietnam, Cambodia, and southern China (Xizang, Yunnan, Guizhou, Guangxi, Guangdong, Hunan, and Jiangxi) (Figure 9).

Content: Twenty-eight recognized species, divided into three species groups: *X. lekaguli* group (six recognized species), *X. megacephala* group (eight recognized species) and *X. major* group (14 recognized species) (Table 2).

Remarks: Based on phylogenetic results, Mahony et al. (2017) divided *Xenophrys* into five species groups, as followed by Lyu et al. (2021) and Qi et al. (2021). In this work, the *X. aceras* and *X. vegrandis* groups are recognized as two distinct genera, i.e., *Grillitschia* and *Jingophrys* gen. nov., and the *X. lekaguli*, *X. megacephala*, and *X. major* groups are retained within the genus *Xenophrys*. The division of species groups was primarily based on phylogenetic relationships, with the congener *X. damrei* remaining unassigned due to a lack of molecular data (Lyu et al., 2021; Mahony et al., 2017). Based on its close distribution and appearance to *X. auralensis* and *X. lekaguli* (Mahony, 2011), we herein place *X. damrei* in the *X. lekaguli* group.

Black or white asperities on the lower jaw were observed in several *Xenophrys* species (e.g., Delorme et al., 2006; Mahony et al., 2018, 2020), but were not recognized as a key diagnosis. During our examination, most species of the genus *Xenophrys* possessed such asperities on the lower jaw, even though these were not mentioned in previous descriptions (e.g., *X. mangshanensis* and *X. glandulosa*; Figure 7). These asperities may sometimes be invisible due to the different

growth stages among individuals or different preservative conditions among specimens, suggesting variability (Mahony et al., 2020; this work). Nonetheless, black or white asperities on the lower jaw were never observed in any species of other Asian horned toad genera, and thus we consider this character to be diagnostic of *Xenophrys*.

(G) *Megophrys* Kuhl and Van Hasselt, 1822

Indonesian horned toad / jiǎo chán shǔ (角蟾属)

Type species: *Mogophrys montana* Kuhl and Van Hasselt, 1822.

Diagnosis: (1) Small or medium body size, SVL<70 mm in males, body habitus stocky; (2) head moderately enlarged and much depressed; snout pointed, with or without rostral appendage; (3) maxillary teeth present, vomerine teeth present; (4) outer margin of upper eyelid elongated as pointed triangular appendage; (5) temporal region elongated; tympanum small, distinct, far from posterior corner of eye; supratympanic fold narrow and distinctly curved over tympanum; (6) transverse fold behind head present; (7) dermal ridges on center of dorsum absent; (8) single dorsolateral ridge at each side present, extending continuously from shoulder to groin or mid-body; (9) asperities on lower jaw absent; (10) subarticular tubercles on fingers absent; nuptial pads/spines present in breeding males.

Distribution: Sumatra and Java in Indonesia (Figure 8).

Content: Five recognized species (Table 2).

Remarks: Except for *M. montana*, the other four congeners are only reported from Sumatra (Munir et al., 2021). Previously widely reported from Indonesia, Malaysia, and Thailand (Frost, 2022), recent study has suggested that only the Java population represents true *M. montana*, and other records may be misidentifications (Munir et al., 2021). Thus, we hereby restrict the distribution of this genus to Sumatra and Java, Indonesia. Further studies are warranted to determine the diversity and biogeography of this genus.

(H) *Pelobatrachus* Beddard, 1907

Clay horned toad / dì jiǎo chán shǔ (地角蟾属)

Synonym: *Ceratophryne* — Schlegel, 1858

Borneophrys — Delorme et al., 2006

Megophrys (*Pelobatrachus*) — Mahony et al., 2017

Type species: *Ceratophryne nasuta* Schlegel, 1858.

Diagnosis: (1) Medium or large body size, mean SVL>40 mm in males, body habitus stocky; (2) head slightly enlarged and depressed; snout pointed or truncated, with or without rostral appendage; (3) maxillary teeth present, vomerine teeth present or absent; (4) outer margin of upper eyelid elongated as pointed triangular appendage, or palpebral appendage absent with horn-like tubercles at outer margin of upper eyelid present; (5) temporal region elongated; tympanum small, distinct, far from posterior corner of eye; supratympanic fold narrow, distinctly or slightly curved over tympanum; (6) transverse fold behind head present; (7) dermal ridges on center of dorsum absent; (8) dorsolateral ridges present or absent; (9) asperities on lower jaw absent; (10) subarticular tubercles on fingers absent; nuptial pads/spines present in breeding males.

Distribution: Equatorial southeastern Asia, including southernmost Thailand, Malaysia, Singapore, Brunei, southern Philippines, and Sumatra and Kalimantan in Indonesia (Figure 9).

Content: Seven recognized species (Table 2).

(I) *Ophryophryne* Boulenger, 1903

Narrow-mouth horned toad / nǐ jiǎo chán shǔ (拟角蟾属)

Synonym: *Megophrys* (*Ophryophryne*) — Dubois, 1980; Mahony et al., 2017

Diagnosis: (1) Small or medium body size, mean SVL<50 mm in males, body habitus slender; (2) head not enlarged and depressed; snout short, rounded or truncated, without rostral appendage; (3) maxillary teeth absent, vomerine teeth absent; (4) upper eyelid without appendage, single large or small horn-like tubercle at outer margin of eyelid present; (5) temporal region short; tympanum moderate or large, relatively close to posterior corner of eye; supratympanic fold thick and slightly curved over tympanum; (6) transverse fold behind head absent; (7) dermal ridges on center of dorsum present, X-, Y-, V-, or H-shaped; (8) dorsolateral ridges discontinuously present or absent; (9) asperities on lower jaw absent; (10) nuptial pads/spines present in breeding males.

Distribution: Tropical mainland southeastern Asia, including Laos, Cambodia, Vietnam, and southern China (Yunnan, Guangxi, and Guangdong), all majorly east of the Annamite Range (Figure 8).

Content: Seven recognized species (Table 2).

(J) *Boulenophrys* Fei, Ye, and Jiang, 2016

Chinese horned toad / bù jiǎo chán shǔ (布角蟾属)

Synonym: *Panophrys* — Rao & Yang, 1997; Lyu et al., 2021

Xenophrys (*Tianophrys*) — Fei & Ye, 2016

Xenophrys (*Panophrys*) — Chen et al., 2017

Megophrys (*Panophrys*) — Mahony et al., 2017

Diagnosis: (1) Small, medium, or large body size, SVL 25–120 mm in males, body habitus moderate; (2) head not enlarged and depressed; snout rounded or obtusely pointed, without rostral appendage; (3) maxillary teeth present, vomerine teeth present or absent; (4) palpebral tubercle or appendage type variable; (5) temporal region short; tympanum moderate or large, relatively close to posterior corner of eye; supratympanic fold narrow and distinctly curved over tympanum; (6) transverse fold behind head absent; (7) dermal ridges on center of dorsum present, with variable shape; (8) dorsolateral ridges present or absent; (9) both sides of belly without seriate tubercles; (10) asperities on lower jaw absent; (11) subarticular tubercles on fingers present, distinct or indistinct; nuptial pads/spines absent or present on dorsal bases of fingers I and II in breeding males.

Distribution: Subtropical and tropical mainland East Asia, mostly in southern China (Yunnan, Sichuan, Gansu, Shaanxi, Chongqing, Guizhou, Hunan, Hubei, Anhui, Zhejiang, Fujian, Jiangxi, Guangdong, Guangxi, and Hong Kong), extending south into northernmost Indochina, including Vietnam, Laos, Myanmar, and Thailand (Figure 9).

Content: Sixty-five recognized species; 62 congeners divided into three species groups: *B. minor* group (three recognized species), *B. omeimontis* group (16 recognized species), and *B. boettgeri* group (43 recognized species) (Table 2).

Remarks: Qi et al. (2021) proposed three species groups, i.e., *B. minor* group, *B. omeimontis* group, and *B. boettgeri* group, for interspecific classification of the genus. The division of species groups was primarily based on phylogenetic relationships, as well as their distributions (Supplementary Figures S5–S10). The three remaining congeners *B. fansipanensis*, *B. frigida*, and *B. hoanglienensis* formed an independent clade that was phylogenetically close to the *B. omeimontis* group but with relatively weak support (BS 55,

BPP 0.90; Figure 3). Thus, we consider their phylogenetic placement within the genus to be uncertain and they are not assigned to any current species group.

Based on detailed morphological examinations, subarticular tubercles on the fingers were consistently in the *Boulenophrys* specimens but found to be absent in all species of other genera of the subfamily. Furthermore, although previous research stated that “supernumerary tubercles absent, but skin raised on articulations of Fingers III, IV” in *B. rubrimera*, we identified indistinct supernumerary tubercles (Figure 4E, F in Tapley et al., 2017), similar to that reported in *B. shuichengensis* (Fei et al., 2012). We therefore propose that the presence of subarticular tubercles on the fingers may be a diagnostic character for *Boulenophrys*.

Monograph of Chinese species

China contains the richest diversity of Asian horned toads, with a total of 87 recognized species listed in this study. These 87 species accounts for approximately two-thirds of the total 132 species in the subfamily and are classified into six genera. The genus *Brachytarsophrys* contains six members in China and was recently reviewed in detail (Li et al., 2020a), with an additional species (*Brachytarsophrys qiannanensis*) subsequently described (Li et al., 2022). The genus *Ophryophryne* has two species in China, which have remained taxonomically stable for decades (Fei & Ye, 2016; Fei et al., 2009). Thus, species within *Brachytarsophrys* and *Ophryophryne* have not been included in this work.

The remaining four genera, i.e., *Atympanophrys*, *Jingophrys* **gen. nov.**, *Xenophrys*, and *Boulenophrys*, collectively form an integral part of *Megophrys sensu lato* (Fei et al., 2009), and have experienced similar taxonomic confusion. In this research, we present a key to distinguish all Chinese congeners in these four genera, clarify their taxonomic histories, revise their diagnoses, and further delimit their current distributions.

All four species in the genus *Atympanophrys* are distributed in China. We assigned *A. wawuensis* to the genus based on morphological similarity and phylogenetics. The newly erected genus *Jingophrys* **gen. nov.** contains five members, resulting in new combinations of nomenclatures. These species all occur in China.

Ten species of the genus *Xenophrys* are distributed in China. Among them, we redefined the concept of *X. maosonensis* based on newly collected material. Additionally, we propose two new species, i.e., *Xenophrys dehongensis* **sp. nov.** and *Xenophrys lancangica* **sp. nov.**

Boulenophrys, the largest genus within the subfamily Megophryinae, is primarily distributed in southern China. This research presents a comprehensive account of the 60 species of *Boulenophrys* from China, including redefinition of *B. minor*, new species-level proposal for *B. fanjingmontis* **comb. nov.**, synonymization of *B. huangshanensis* with *B. boettgeri*, and identification of newly described species *B. xuefengmontis* **sp. nov.**

Key to species of genus *Atympanophrys* from China (four species)

- 1a) SVL smaller than 50 mm in males; supratympanic fold slightly curving over tympanic region; breeding males bearing nuptial spines 2
- 1b) SVL larger than 65 mm in males; supratympanic fold extending straightly; breeding males without nuptial spines ... 3
- 2a) Tympanum concealed and invisible *nankiangensis*

- 2b) Tympanum distinct and visible *wawuensis*
- 3a) Subgular vocal sacs present in males; toes with 1/4 webbing *gigantica*
- 3b) Subgular vocal sacs absent in males; toes with half webbing *shapingensis*

Atympanophrys gigantea (Liu, Hu, and Yang, 1960)

Giant horned toad / dà huā jiǎo chán (大花角蟾)

Chresonymy: *Megophrys gigantea* — Liu et al., 1960

Megophrys (Megophrys) gigantea — Dubois, 1980

Megophrys gigantea — Tian & Hu, 1983; Fei et al., 2009, 2012

Atympanophrys gigantea — Rao & Yang, 1997; Chen et al., 2017; Lyu et al., 2021; Qi et al., 2021

Xenophrys gigantea — Delorme et al., 2006

Megophrys (Atympanophrys) gigantea — Mahony et al., 2017

Atympanophrys (Gigantophrys) gigantea — Fei & Ye, 2016; Fei, 2020

Holotype: CIB 24088 (formerly CIB 581539), adult female, from Xinmin Village (2 120 m a.s.l.), Jingdong County, Pu'er, Yunnan, China.

Specimens examined: Two adult males SYS a003933–3934, from Xinmin Village (N24.3664°, E100.7610°; ca. 2 150 m a.s.l.), Jingdong County; one adult male SYS a003883 from Shimexia (N23.9708°, E101.5240°; ca. 2 030 m a.s.l.), Xinping County, Yuxi, Yunnan.

Diagnosis: Based on previous description (Fei & Ye, 2016) and examined specimens: (1) adult males, SVL 80.5–107.0 mm ($n=6$; Fei & Ye, 2016) (SVL 92.4–97.2 mm, $n=3$; this study); adult females, SVL 110.4–115.4 mm ($n=2$; Fei & Ye, 2016); (2) canthus rostralis rounded; tongue notched posteriorly; (3) tympanum concealed and invisible; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin smooth without tubercles and dermal ridges; dorsolateral ridges absent; sparse small tubercles on flanks; ventral skin smooth; (6) outer margin of upper eyelid smooth without appendages or horn-like tubercles; supratympanic fold distinct, thick and raised, extending straightly to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths I<IV=II<III; subarticular tubercles absent; (8) hindlimbs relatively thickset, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes with 1/4 webbing and wide lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface dark purplish brown; irregular reddish brown or grayish yellow patches scattered on dorsum and flanks; throat and chest with dark purplish brown spots, belly creamy yellow; (11) dark brown nuptial pads on dorsal bases of fingers I and II in breeding adult males; pair of subgular vocal sacs in males (Figures 4J and 10A).

Distribution: Only known from Jingdong, Xinping, and Yongde counties in southern Yunnan in China and northernmost Vietnam at elevations of 2 100–2 400 m a.s.l. (Fei & Ye, 2016; this study) (Supplementary Figure S1).

Atympanophrys nankiangensis (Liu and Hu, 1966)

Nankiang horned toad / nán jiāng jiǎo chán (南江角蟾)

Chresonymy: *Megophrys nankiangensis* — Hu et al., 1966; Tian & Hu, 1983; Fei et al., 2009, 2012

Megophrys (Megophrys) nankiangensis — Dubois, 1980

Panophrys nankiangensis — Rao & Yang, 1997

Megophrys (Xenophrys) nankiangensis — Dubois & Ohler, 1998

Xenophrys nankiangensis — Delorme et al., 2006

Atympanophrys nankiangensis — Chen et al., 2017; Lyu et al., 2021; Qi et al., 2021

Atympanophrys (Borealophrys) nankiangensis — Fei & Ye, 2016; Fei, 2020

Megophrys (Atympanophrys) nankiangensis — Mahony et al., 2017

Holotype: CIB 24201 (formerly CIB 610588), adult female, from Kuangwu Shan (=Mt. Guangwu) (1 750 m a.s.l.), Nankiang Hsien (=Nanjiang County, Bazhong), Szechwan (=Sichuan), China.

Diagnosis: Based on previous descriptions (Fei & Ye, 2016; Hu et al., 1966): (1) adult male, SVL 39.1 mm ($n=1$); adult females, SVL 44.0–52.9 mm ($n=10$); (2) canthus rostralis rounded; tongue weakly notched posteriorly; (3) tympanum concealed and invisible; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin relatively smooth with scattered spiny granules; weak discontinuous V-shaped ridges on center of dorsum, dorsolateral ridges absent; sparse large tubercles on flanks; ventral skin smooth; (6) outer margin of upper eyelid smooth without appendages or horn-like tubercles; supratympanic fold distinct, thick and raised, slightly curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths $II < I < IV < III$; subarticular tubercles absent; (8) hindlimbs short and relatively thickset, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching posterior corner of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface light reddish brown; dark triangular marking between eyes; dark X-shaped marking on center of dorsum; dorsal limbs with transverse bands; ventral surface reddish brown; throat and chest with dark spots; (11) dark brown nuptial spines on dorsal bases of fingers I and II in breeding adult male; pair of subgular vocal sacs in male.

Distribution: Known from multiple localities in the Daba Mountains along the border of Sichuan, Shaanxi, and Gansu at elevations of 1 600–1 850 m a.s.l. (Fei & Ye, 2016) (Supplementary Figure S1).

***Atympanophrys shapingensis* (Liu, 1950)**

Shaping horned toad / shā píng jiǎo chán (沙坪角蟾)

Chresonymy: *Megophrys shapingensis*— Liu, 1950

Megophrys (Megophrys) shapingensis — Dubois, 1980

Atympanophrys shapingensis — Tian & Hu, 1983; Rao &

Yang, 1997; Chen et al., 2017; Lyu et al., 2021; Qi et al., 2021

Megophrys (Atympanophrys) shapingensis — Dubois, 1987;

Mahony et al., 2017

Xenophrys shapingensis — Delorme et al., 2006

Megophrys shapingensis — Fei et al., 2009, 2012

Atympanophrys (Atympanophrys) shapingensis— Fei & Ye,

2016; Fei, 2020

Holotype: FMNH 49405, adult male, from Shaping, Opienhsien (=Ebian County, Leshan), Szechwan (=Sichuan), China.

Specimens examined: One adult male SYS a005310, from Mt. Wawu (N29.7001°, E102.9565°; ca. 1 560 m a.s.l.), Hongya County, Meishan, Sichuan; one adult male SYS a005340 and one adult female SYS a005339, from Qiliba (N27.8872°, E102.5188°; ca. 3 100 m a.s.l.), Zhaojue County, Liangshan, Sichuan.

Diagnosis: Based on previous description (Fei & Ye, 2016)

and examined specimens: (1) adult males, SVL 65.9–84.2 mm ($n=10$; Fei & Ye, 2016) (SVL 66.2–68.0 mm, $n=2$; this study); adult females, SVL 76.6–104.0 mm ($n=10$; Fei & Ye, 2016) (SVL 85.5 mm, $n=1$; this study); (2) canthus rostralis rounded; tongue weakly notched posteriorly; (3) tympanum concealed and invisible; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin relatively smooth with scattered spiny granules; weak discontinuous V-shaped ridges on center of dorsum, dorsolateral ridges absent; sparse small tubercles on flanks; ventral skin smooth; (6) outer margin of upper eyelid smooth without appendages or horn-like tubercles; supratympanic fold distinct, thick and raised, extending straightly to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths $I < IV = II < III$; subarticular tubercles absent; (8) hindlimbs relatively thickset, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes with half webbing and wide lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface reddish brown or greenish yellow; dark triangular marking between eyes; dark X-shaped marking on center of dorsum; dorsal limbs with transverse bands; dark spots with yellow edge on ventral surface; (11) nuptial pads/spines absent in breeding adult males; vocal sacs absent in males (Figure 10B).

Distribution: Known from multiple localities on the eastern edge of the Hengduan Mountains in central Sichuan at elevations of 2 000–3 200 m a.s.l. (Fei & Ye, 2016) (Supplementary Figure S1).

***Atympanophrys wawuensis* (Fei, Jiang, and Zheng, 2001)**

Wawu horned toad / wǎ wū jiǎo chán (瓦屋角蟾)

Chresonymy: *Megophrys wawuensis* — Fei & Ye, 2001; Fei et al., 2009, 2012

Xenophrys wawuensis — Delorme et al., 2006

Boulenophrys wawuensis — Fei & Ye, 2016; Fei, 2020

Atympanophrys wawuensis — Chen et al., 2017; Lyu et al., 2021; Qi et al., 2021

Megophrys (Panophrys) wawuensis — Mahony et al., 2017

Holotype: CIB 950219, adult male, from Mt. Wawu (N29°56', E103°22'), Hongya County, Meishan, Sichuan, China.

Specimens examined: One adult female SYS a005311, from Mt. Wawu.

Diagnosis: Based on previous descriptions (Fei & Ye, 2001, 2016) and examined specimens: (1) adult males, SVL 34.4–42.8 mm ($n=4$; Fei & Ye, 2016); adult females, SVL 47.0–49.8 mm ($n=2$; Fei & Ye, 2016) (SVL 49.3 mm, $n=1$; this study); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin relatively smooth with scattered spiny granules; dorsolateral ridges absent; sparse large or elongated tubercles on flanks; ventral skin smooth; (6) outer margin of upper eyelid smooth without appendages or horn-like tubercles; supratympanic fold distinct, thick and raised, slightly curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct and flat, inner one observably enlarged; relative finger lengths $II < I < IV < III$; subarticular tubercles absent; (8) hindlimbs relatively thickset, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface dark grayish brown or yellowish brown; hollow dark triangular marking between eyes;

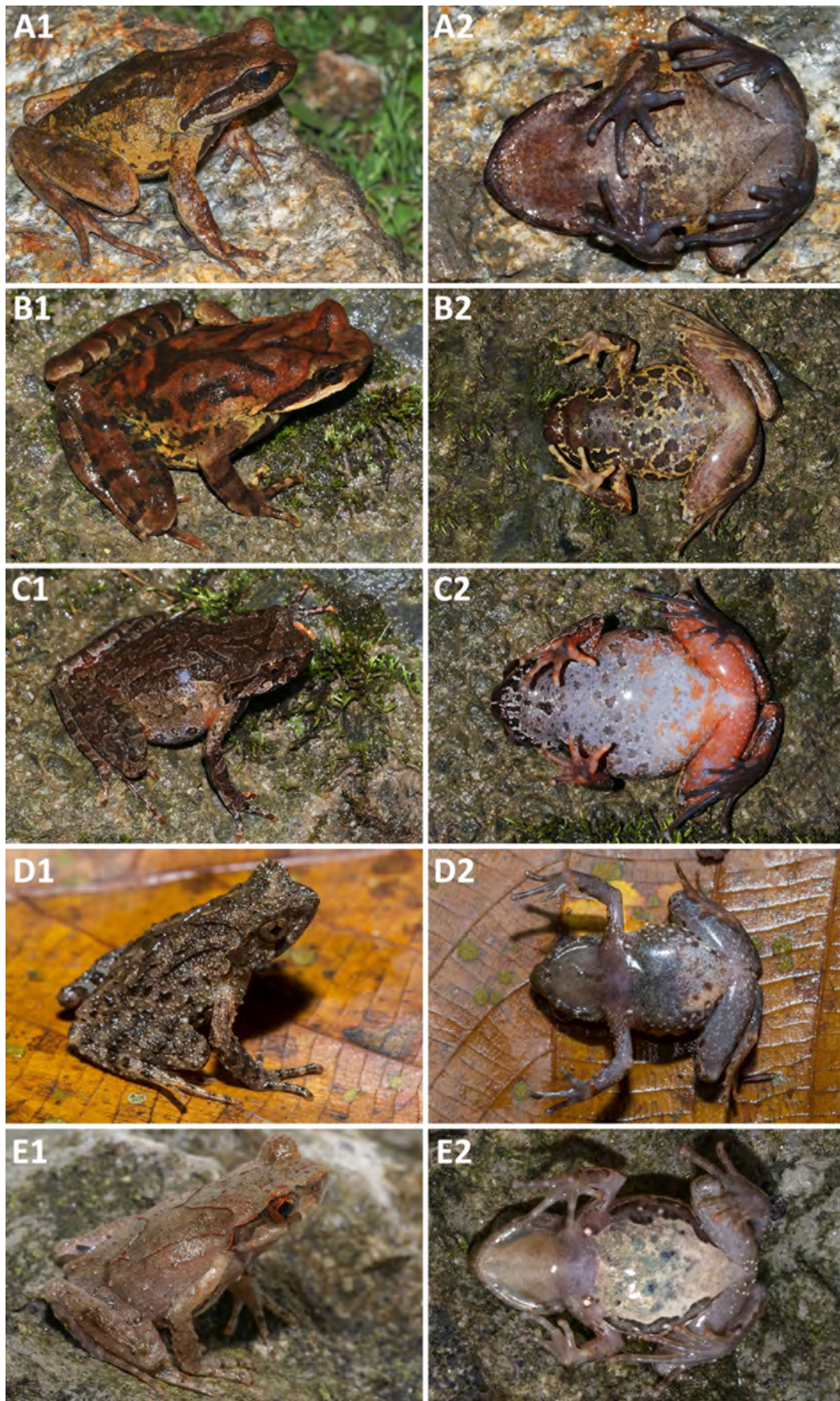


Figure 10 Species of *Atympanophrys* and *Jingophrys* gen. nov. in life

A: *A. gigantica* male SYS a003933; B: *A. shapingensis* male SYS a005310; C: *A. wawuensis* female SYS a005311; D: *J. feii* **comb. nov.** male SYS a003876. E: *J. yae* **comb. nov.** male SYS a006683. 1: Dorsolateral view; 2: Ventral view. Photos by Z.T. Lyu, J. Wang, and J. Zhao.

dark X-shaped or netlike marking on center of dorsum; dorsal limbs with transverse bands; ventral surface purplish gray with dark spots; (11) dense nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 10C).

Distribution: Known only from its type locality in Mt. Wawu at elevations over 1 800 m a.s.l. (Fei & Ye, 2016) (Supplementary Figure S1).

Remarks: Due to having distinct tympanum, this species was for a long time not associated with other congeners of the genus *Atympanophrys*, which was suggested to have a concealed tympanum (Fei & Ye, 2016; Fei et al., 2009; Mahony et al., 2017). Nonetheless, this species resembles other congeners of the genus *Atympanophrys* based on upper eyelid smooth without any appendages or horn-like tubercles, vomerine teeth absent, supratympanic fold thick, and subarticular tubercles absent. Within the genus, *A. wawuensis* is close to *A. nankiangensis* based on similar SVL, supratympanic fold slightly curving over tympanic region, and nuptial spines present in breeding adult males. These morphological similarities are supported by phylogenetics (Chen et al., 2017; Liu et al., 2018; this study).

Key to species of genus *Jingophrys* gen. nov. from China (five species)

- 1a) Vomerine teeth present; breeding males with nuptial pads and nuptial spines on finger I *pachyproctus*
- 1b) Vomerine teeth absent; breeding males without nuptial pads/spines 2
- 2a) Vomerine ridge absent 3
- 2b) Vomerine ridge present but weak 4
- 3a) Dorsal skin rough with dense tubercles *feii*
- 3b) Dorsal skin primarily smooth *vegrandis*
- 4a) Upper margin of tympanum in contact with supratympanic fold; tibiotarsal articulation reaching region between nostril and eye when leg stretched forward *yeae*
- 4b) Upper 1/3 of tympanum concealed by supratympanic fold; tibiotarsal articulation reaching center of eye when leg stretched forward *zhoui*

***Jingophrys feii* comb. nov. (Yang, Wang, and Wang, 2018)**

Fei's horned toad / fèi shì jiǎo chán (费氏角蟾)

Chresonymy: *Megophrys feii* — Yang et al., 2018

"*Megophrys*" *feii* — Lyu et al., 2021; Qi et al., 2021

Holotype: SYS a006524, adult male, from Xiaolangsu Village (N24°30'03.23", E97°34'16.75"; 700 m a.s.l.), Tongbiguan Town, Yingjiang County, Dehong, Yunnan, China.

Paratypes: Three adult males SYS a006527–6529 and two adult females SYS a006525–6526, from same locality as holotype (700–1 200 m a.s.l.).

Specimens examined: Type materials (four adult males and two adult females); one adult male SYS a008691 and one juvenile SYS a008690, from Xiaolangsu Village; seven adult males SYS a003874–3880, from Nabang Town (N24.7134°, E97.5995°; ca. 760 m a.s.l.), Yingjiang County.

Diagnosis: Based on examined specimens: (1) adult males, SVL 24.2–28.1 mm ($n=12$); adult females, SVL 28.8–38.9 mm ($n=2$); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct, upper margin slightly concealed by supratympanic fold; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin rough with dense tubercles; discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; ventral skin smooth, seriate tubercles ventrolaterally; (6) outer margin of upper

eyelid with small horn-like tubercles; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct; relative finger lengths I<II<IV<III; subarticular tubercles absent; (8) hindlimbs slender; heels overlapping when hindlimbs folded; tibiotarsal articulation reaching posterior corner of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and moderate lateral fringes; inner metatarsal tubercle ovoid but indistinct, outer one absent; (10) dorsal surface light grayish brown; dark brown triangular marking between eyes; X-shaped marking on center of dorsum; dorsal limbs with transverse bands; throat and chest dark gray; belly pale gray, two parallel dark bands ventrolaterally; (11) nuptial pads/spines absent in breeding adult males; subgular vocal sac present in males (Figures 6A and 10D).

Distribution: Known only from the vicinity of its type locality in Yingjiang County at elevations of 700–1 200 m a.s.l. (Yang et al., 2018) (Supplementary Figure S2).

***Jingophrys pachyproctus* comb. nov. (Huang, 1981)**

Convex-vented horned toad / tū gāng jiǎo chán (凸肛角蟾)

Chresonymy: *Megophrys pachyproctus* — Huang & Fei, 1981

Megophrys (Megophrys) pachyproctus — Dubois, 1987

Megophrys (Xenophrys) pachyproctus — Dubois & Ohler, 1998

Xenophrys pachyproctus — Delorme et al., 2006; Chen et al., 2017; Lyu et al., 2021; Qi et al., 2021

Xenophrys (Xenophrys) pachyproctus — Fei & Ye, 2016; Fei, 2020

Megophrys (Xenophrys) pachyproctus — Mahony et al., 2017

Megophrys cf. *pachyproctus* — Shi et al., 2020a

Holotype: NWIPB 770650, adult male, from Gelin (1 530 m a.s.l.), Medog County, Nyingchi, Xizang, China.

Allotype: NWIPB 770652, adult female, from same locality as holotype.

Paratypes: One adult male NWIPB 770651, from same locality as holotype.

Diagnosis: Based on previous descriptions (Huang & Fei, 1981; Shi et al., 2020a): (1) adult males, SVL 33.6–36.6 mm ($n=7$); adult females, SVL 35.8–42.8 mm ($n=5$); (2) canthus rostralis well developed; tongue notched posteriorly; (3) tympanum distinct, upper 1/3 part concealed by supratympanic fold; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin relatively rough with dense small granules; weak discontinuous V- or X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; dense granules and scattered large tubercles on flanks; ventral skin smooth, seriate tubercles ventrolaterally; (6) outer margin of upper eyelid with tiny tubercles; supratympanic fold distinct, curving posteroventrally to above arm; (7) two metacarpal tubercles small and ovoid; relative finger lengths I<II<IV<III; subarticular tubercles absent; (8) hindlimbs slender, tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle rounded and indistinct, outer one absent; (10) dorsal brown or dark brown; dark triangular marking between eyes; netlike marking on center of dorsum; dorsal limbs with transverse bands; ventral surface grayish white, two parallel brown bands ventrolaterally; (11) gray nuptial pad with dense nuptial spines on dorsal base of finger I in breeding adult males; subgular vocal sac present in males (Figure 6B).

Distribution: Recorded only from several localities in Medog County at elevations of 1 530–2 003 m a.s.l. (refer to Remarks below) (Supplementary Figure S2).

Remarks: This species was originally described based on three specimens collected from Gelin in Medog County. Subsequent specimens assigned to this species by Li et al. (2010), Fei & Ye (2016), and Che et al. (2020) have been suggested as misidentifications and reallocated to the congener *J. yae* **comb. nov.** based on morphological and molecular data (Shi et al., 2020a; this study).

Shi et al. (2020a) redescribed the holotype of *J. pachyproctus* **comb. nov.** and reported a population labeled as *M. cf. pachyproctus* collected from Bari and Renqingbeng Temple ca. 20 km from Gelin. Furthermore, *M. cf. pachyproctus* was suggested to differ from *J. pachyproctus* **comb. nov.** based on small protuberance beyond cloaca (vs large arc-shaped protuberance), inner metatarsal tubercle partially fused with toe I (vs separated), and several osteological differences (Shi et al., 2020a). Nevertheless, the protuberance beyond the cloaca is considered a variable character among individuals (Wang et al., 2020; Yang & Rao, 2008; this study) that may change in preservative (Yang et al., 2018; this study) and the status of the inner metatarsal tubercle is also variable among individuals. In addition, the osteological differences were only based on the examination of a single individual, introducing potential bias. Therefore, the population of *M. cf. pachyproctus* (Shi et al., 2020a) could not be reliably distinguished from the type specimens of *J. pachyproctus* **comb. nov.** morphologically. Accordingly, we regard *M. cf. pachyproctus* in Shi et al. (2020a) as a new reported population of *J. pachyproctus* **comb. nov.**

***Jingophrys vegrandis* comb. nov. (Mahony, Teeling, and Biju, 2013)**

Diminutive horned toad / xì jiǎo chán (细角蟾)

Chresonymy: *Megophrys vegrandis* — Mahony et al., 2013

Xenophrys vegrandis — Chen et al., 2017; Lyu et al., 2021; Qi et al., 2021

Megophrys (Xenophrys) vegrandis — Mahony et al., 2017

Holotype: ZSI A11605, adult male, from Cona County (N27°06.067', E92°31.642'; 1 110 m a.s.l.), Shannan, Xizang, China.

Paratypes: Two adult males ZSI A11604 and BNHS 5597, from same locality as holotype.

Diagnosis: Based on original description (Mahony et al., 2013): (1) adult males, SVL 27.5–30.6 mm ($n=4$); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct, upper margin concealed by supratympanic fold; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin primarily smooth; weak discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; small scattered tubercles on flanks; ventral skin smooth, seriate tubercles ventrolaterally; (6) outer margin of upper eyelid with small tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct; relative finger lengths I<II=IV<III; subarticular tubercles absent; (8) hindlimbs slender, heels overlapping when hindlimbs folded; (9) toes with rudimentary webbing at bases and wide lateral fringes; inner metatarsal tubercle indistinct, outer one absent; (10) dorsal surface light grayish brown; hollow brown triangular marking between eyes; brown X-shaped or netlike marking on center of dorsum; dorsal limbs

with transverse bands; ventral surface grayish yellow or pale gray, two parallel black bands ventrolaterally; (11) nuptial pads/spines absent in breeding adult males; subgular vocal sac present in males (Figure 6C).

Distribution: Only recognized from its type locality in Cona County at elevations of ca. 1 100 m a.s.l. but could also be expected from neighboring localities in southeastern Xizang (Mahony et al., 2013) (Supplementary Figure S2).

***Jingophrys yae* comb. nov. (Shi, Zhang, Xie, Jiang, Liu, Ding, Luan, and Wang, 2020)**

Ye's horned toad / yè shì jiǎo chán (叶氏角蟾)

Chresonymy: *Megophrys pachyproctus* — Li et al., 2010; Che et al., 2020

Megophrys yae — Shi et al., 2020a

Xenophrys yae — Qi et al., 2021

Holotype: CIB 201706MT02, adult male, from Beibeng Village (N29.24292°, E95.18561°; 870 m a.s.l.), Medog County, Nyingchi, Xizang, China.

Paratypes: Two adult males CIB 022017061606–07, from same locality as holotype; four adult males CIB 201706MT01, 022017061102–04, from Didong Village (N29.22508°, E95.12463°; 670 m a.s.l.), Medog County; one adult male CIB 022017061804, from Bari Village (N29.32947°, E95.36016°; 1 780 m a.s.l.), Medog County; two adult males CIB MT171065–66, from Yarang Village (N29.29485°, E95.28126°; 795 m a.s.l.), Medog County; one adult male CIB MT171064, from Yadong Village (N29.32654°, E95.34397°; 1 073 m a.s.l.), Medog County; one adult male CIB MTXC-201701-044 and two adult females CIB 201706MT03, MTXC-201701-043, from Medog urban neighborhood (N29.32213°, E95.31324°; 907 m a.s.l.), Medog County.

Specimens examined: Two adult males SYS a004519–4520, from Xirang Village (N29.1780°, E95.0221°; ca. 750 m a.s.l.), Medog County; three adult males SYS a006681–6683, from Didong Village; three adult males SYS a006684–6686, from urban neighborhood in Medog.

Diagnosis: Based on original description (Shi et al., 2020a) and examined specimens: (1) adult males, SVL 23.8–29.1 mm ($n=12$; Shi et al., 2020a) (SVL 26.2–30.3 mm, $n=8$; this study); adult females, SVL 27.9–31.3 mm ($n=2$; Shi et al., 2020a); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct, upper margin in contact with supratympanic fold; (4) vomerine ridge weak, vomerine teeth absent; (5) dorsal skin relatively smooth with scattered tubercles; weak discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; ventral skin smooth, seriate tubercles ventrolaterally; (6) outer margin of upper eyelid with distinct horn-like tubercles; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct; relative finger lengths I<II<IV<III; subarticular tubercles absent; (8) hindlimbs slender; heels overlapping when hindlimbs folded; tibiotarsal articulation reaching region between nostril and eye when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle ovoid but indistinct, outer one absent; (10) dorsal surface light brown with scattered orange tubercles; barely visible triangular marking between eyes; barely visible X-shaped marking on center of dorsum; ventral surface pale gray, two parallel dark bands ventrolaterally; (11) nuptial pads/spines absent in breeding adult males; subgular vocal sac present in males (Figures 4G, 6D, 10E).

Distribution: Currently known from multiple localities in Medog County at elevations of 670–1 780 m a.s.l. (Shi et al., 2020a; this study) (Supplementary Figure S2).

***Jingophrys zhoui* comb. nov. (Shi, Zhang, Xie, Jiang, Liu, Ding, Luan, and Wang, 2020)**

Zhou's horned toad / zhōu shì jiǎo chán (周氏角蟾)

Chresonymy: *Megophrys zhoui* — Shi et al., 2020a

Xenophrys zhoui — Qi et al., 2021

Holotype: CIB MT171053, adult male, from vicinity of Renqingbeng Temple (N29.304832°, E95.361682°; 2 003 m a.s.l.), Medog County, Nyingchi, Xizang, China.

Paratypes: Two adult females CIB MT171060, 62, from same locality as holotype.

Diagnosis: Based on original description (Shi et al., 2020a): (1) adult male, SVL 23.0 mm ($n=1$); adult females, SVL 23.5–23.9 mm ($n=2$); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct, upper 1/3 part concealed by supratympanic fold; (4) vomerine ridge weak, vomerine teeth absent; (5) dorsal skin relatively smooth scattered with tiny granules; weak discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; several small tubercles on flanks; ventral skin smooth, seriate tubercles ventrolaterally; (6) outer margin of upper eyelid with two tiny tubercles; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct; relative finger lengths $IV < II < I < III$; subarticular tubercles absent; (8) hindlimbs slender; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle long ovoid but indistinct, outer one absent; (10) dorsal surface orange brown; dark triangular marking between eyes; dark X-shaped marking on center of dorsum; throat and chest orange brown mottled with dense spots; belly white, two parallel brown bands ventrolaterally; (11) nuptial pads/spines absent in breeding adult male; subgular vocal sac present in male.

Distribution: Only recognized from its type locality in Medog County at elevations of ca. 2 000 m a.s.l. (Shi et al., 2020a) (Supplementary Figure S2).

Key to species of genus *Xenophrys* from China (10 species)

- 1a) SVL smaller than 50 mm in males 2
- 1b) SVL larger than 50 mm in males 4
- 2a) Toes without lateral fringes 3
- 2b) Toes with lateral fringes *zhangii*
- 3a) Toes without webbing; tibiotarsal articulation reaching anterior corner of eye when leg stretched forward *parva*
- 3b) Toes with rudimentary webbing at bases, tibiotarsal articulation reaching posterior corner of eye when leg stretched forward *dehongensis* sp. nov.
- 4a) Toes without webbing *mangshanensis*
- 4b) Toes with rudimentary webbing at bases 5
- 5a) Toes with wide lateral fringes *glandulosa*
- 5b) Toes without lateral fringes or with indistinct narrow lateral fringes 6
- 6a) SVL larger than 75 mm in males on average *periosa*
- 6b) SVL smaller than 75 mm in males on average 7
- 7a) Toes without lateral fringes 8
- 7b) Toes with narrow lateral fringes 9
- 8a) Larger body size; relative finger lengths $IV < II < I < III$ *himalayana*
- 8b) Smaller body size; relative finger lengths $II < I < IV < III$

..... *medogensis*

9a) Tibiotarsal articulation reaching center of eye when leg stretched forward *maosonensis*

9b) Tibiotarsal articulation reaching region between nostril and tip of snout when leg stretched forward *lancangica* sp. nov.

***Xenophrys lekaguli* group**

***Xenophrys parva* (Boulenger, 1893)**

Little Karen Hills horned toad / āo dǐng jiǎo chán (凹顶角蟾)

Chresonymy: *Leptobrachium parvum* — Boulenger, 1893

Megophrys parva — Bourret, 1942; Liu & Hu, 1961; Fei et al., 2009, 2012

Megophrys (Megophrys) parva — Dubois, 1980

Panophrys parva — Rao & Yang, 1997

Megophrys (Xenophrys) parva — Dubois & Ohler, 1998; Mahony et al., 2017

Xenophrys parva — Delorme et al., 2006; Chen et al., 2017; Lyu et al., 2021; Qi et al., 2021

Xenophrys (Xenophrys) parva — Fei & Ye, 2016; Fei, 2020

Boulenophrys parva — Dubois et al., 2021

Lectotype: MSNG 29412 A, from Karin Bia-po (now Thandaunggyi Township, Hpa-An District, Kayin), Myanmar.

Paralectotypes: Two adult males BMNH 1947.2.25.11–12 (formerly BMNH 1893.10.9.44–45) and two adult females BMNH 1947.2.25.9–10 (formerly BMNH 1893.10.9.42–43), from same locality as lectotype.

Specimens examined: One adult male SYS a002965 and one adult female SYS a002964, from Mengyang Town (N22.1676°, E100.8685°; ca. 920 m a.s.l.), Jinghong City, Xishuangbanna, Yunnan, China; one adult female SYS a006729, from Xishuangbanna; one adult male SYS a001769, from Menglun Town (N21.9089°, E101.2723°; ca. 600 m a.s.l.), Mengla County, Xishuangbanna; and eight adult males SYS a002947, 2960, 3042–3046, 3956 and one adult female SYS a002959, from Zhushihe (N22.2143°, E101.5131°; ca. 1 060 m a.s.l.), Mengla County.

Diagnosis: Based on examined specimens: (1) adult males, SVL 36.6–42.9 mm ($n=10$); adult females, SVL 41.4–52.1 mm ($n=3$); (2) canthus rostralis well developed, dorsal surface of snout slightly concave; tongue not notched or weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin smooth with sparse small granules; weak discontinuous X- or V-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; sparse large tubercles on flanks; ventral skin smooth; (6) outer margin of upper eyelid with weak medial bumped appendage; supratympanic fold distinct, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct; relative finger lengths $II < IV < I < III$; subarticular tubercles absent; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching anterior corner of eye when leg stretched forward; (9) toes without webbing and lateral fringes; inner metatarsal tubercle indistinct, outer one absent; (10) dorsal surface dark brown or olive brown; hollow dark triangular marking between eyes, dark X-shaped marking on center of dorsum; throat and chest purplish; belly pale gray; (11) dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 11A).

Distribution: Currently known from Xishuangbanna in Yunnan in China, Laos, northwestern Vietnam, northern Thailand, and southeastern Myanmar at elevations of 600–1 000 m a.s.l. (Fei & Ye, 2016; this study, refer to

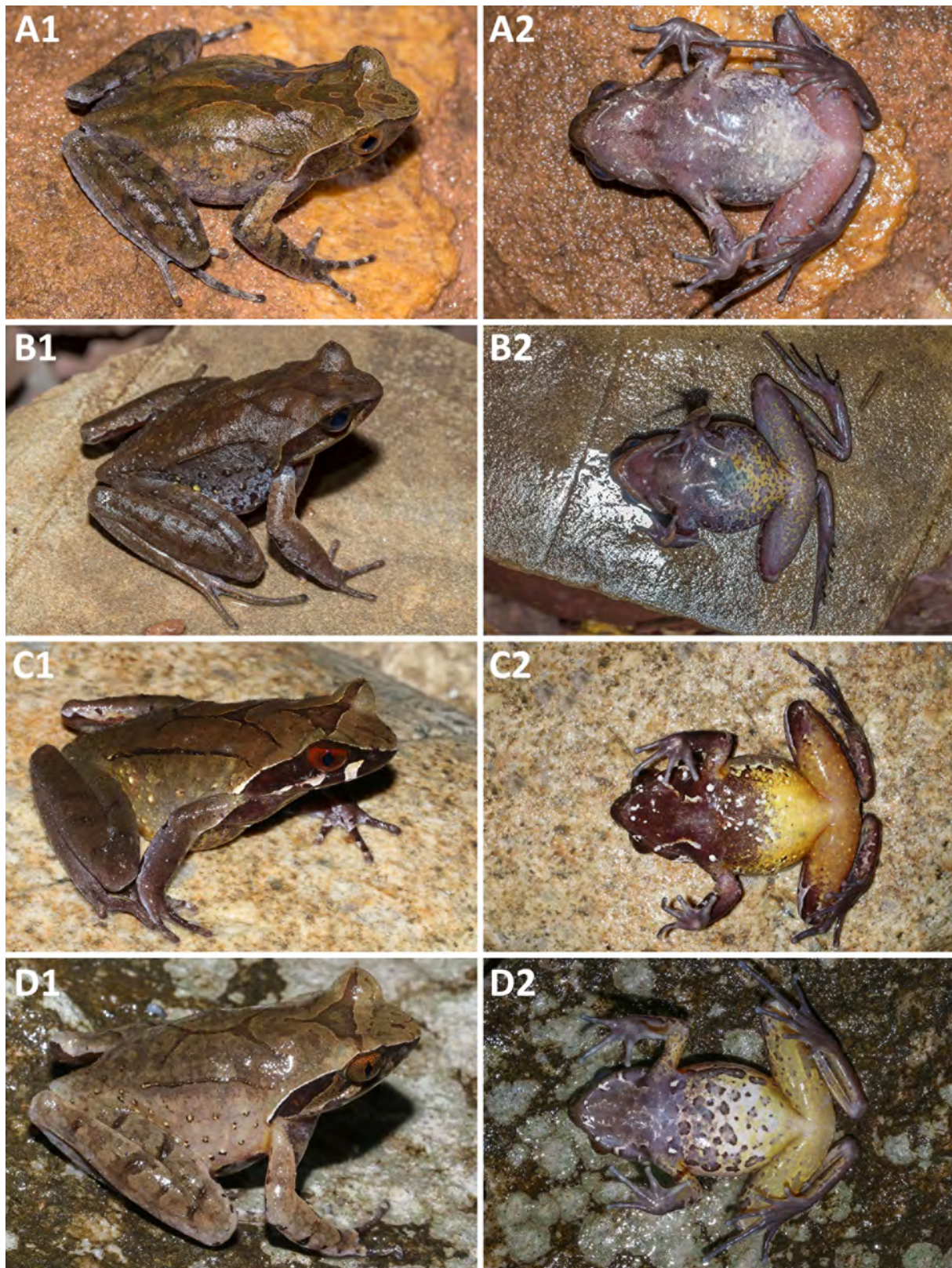


Figure 11 Species of *Xenophrys* in life

A: *X. parva* male SYS a002960; B: *X. glandulosa* male SYS a003907; C: *X. mangshanensis* male SYS a005753; D: *X. medogensis* male SYS a006634; 1: Dorsolateral view; 2: Ventral view. Photos by Z.T. Lyu, J. Wang, J. Zhao, and Z.Y. Liu.

Remarks below) (Supplementary Figure S3).

Remarks: The taxonomic validity of *X. parva* was controversial for a long time, often confused with *X. monticola* from India. This led to a complicated taxonomic history surrounding the two species and the geographic range of *X.*

parva was previously recorded across a wide region, stretching from the Himalayas to Indochina (Mahony et al., 2018, 2020). Recently, Mahony et al. (2020) restricted the distribution of this species in its type locality in southeastern Myanmar. In our analysis, the previous records of *X. parva*

from Yunnan in China, Laos, northwestern Vietnam, and northern Thailand clustered in distinct lineage representing a member of *Xenophrys* (Figure 2). The taxonomic status of this lineage suggested a reassessment in comparison to the topotypic population. Nonetheless, the currently recognized locality of this lineage includes Doi Chiang Dao, Chiang Mai, Thailand (samples 26 in Figure 2), which is ca. 230 km from the type locality of *X. parva* in southeastern Myanmar. The region including Yunnan in China, northern Laos, northern Thailand, and eastern Myanmar, also known as the Golden Triangle, is suggested to share similar amphibian fauna (e.g., *Leptobranchella pelodytoides*, *Sylvirana cubitalis*, *Limnonectes limborgi*, *Microhyla berdmorei*). Additionally, our morphological examination on specimens from Yunnan did not reveal any distinct characters to distinguish them from the type series of *X. parva* (Mahony et al., 2020). Therefore, we consider retaining *X. parva* for the lineage composed of samples from Yunnan in China, Laos, northwestern Vietnam, and northern Thailand.

***Xenophrys dehongensis* sp. nov. Lyu and Wang**

Dehong horned toad / dé hóng jiǎo chán (德宏角蟾)

Chresonymy: *Megophrys* cf. *parva* — Chen et al., 2017

Megophrys sp43 — Liu et al., 2018

Holotype: SYS a003860, adult male, collected by Jian Zhao and Jian Wang on 23 May 2015 from Nabang Town (N24.7134°, E97.5995°; ca. 760 m a.s.l.), Yingjiang County, Dehong, Yunnan, China.

Paratypes: One adult male SYS a003861, same collection data as holotype; one adult male SYS a003443 and one adult female SYS a003448, collected by Jian-Huan Yang on August 2014 from Tongbiguan Town (N24.5009°, E97.5713°; ca. 700 m a.s.l.), Yingjiang County; one adult male SYS a005822, collected by Jian-Huan Yang on 5 May 2016 from Tongbiguan Town; one adult female SYS a005823, collected by Jian-Huan Yang on 1 June 2016 from Hongbenghe (N24.4368°, E97.5387°; ca. 300 m a.s.l.), Yingjiang County; and one adult male CIB 119022, collected by De-Chun Jiang, Jin-Long Ren, and Si-Bo Su on 4 June 2018 from Qingping Town (N24.5384°, E98.0450°; ca. 1 470 m a.s.l.), Longchuan County, Dehong.

Etymology: The specific nomen *dehongensis* is derived from

Dehong, where the new species is primarily distributed.

Diagnosis: (1) Adult males, SVL 34.8–36.7 mm ($n=5$); adult females, SVL 45.7–46.8 mm ($n=2$); detailed measurements are presented in Table 4; (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin relatively rough with distinct tubercles; weak discontinuous X- or V-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; elongated tubercles on flanks; ventral skin smooth; (6) outer margin of upper eyelid with weak medial bumped appendage; supratympanic fold distinct, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct; relative finger lengths II<I<IV<III; subarticular tubercles absent; (8) hindlimbs slender, heels slightly overlapping when hindlimbs folded; tibiotarsal articulation reaching posterior corner of eye when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle indistinct, outer one absent; (10) dorsal surface orange brown or reddish brown; hollow dark triangular marking between eyes, dark X-shaped marking on center of dorsum; throat and chest dark brown; belly pale gray; (11) dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 12).

Distribution: Only known from Yingjiang and Longchuan counties in Dehong at elevations of 300–800 m a.s.l., but could be expected from neighboring localities in northern Myanmar (Chen et al., 2017; this study) (Supplementary Figure S3).

***Xenophrys major* group**

***Xenophrys glandulosa* (Fei, Ye, and Huang, 1990)**

Glandular horned toad / xiàn jiǎo chán (腺角蟾)

Chresonymy: *Megophrys glandulosa* — Fei et al., 1990

Megophrys (Xenophrys) glandulosa — Dubois & Ohler, 1998; Mahony et al., 2017

Xenophrys glandulosa — Delorme et al., 2006; Chen et al., 2017; Lyu et al., 2021; Qi et al., 2021

Liuophrys glandulosa — Fei & Ye, 2016; Fei, 2020

Holotype: CIB 24341 (formerly CIB 873112), adult male, from Mt. Wuliang (1 900 m a.s.l.), Jingdong County, Pu'er, Yunnan, China.

Table 4 Measurements (in mm) of examined specimens of *Xenophrys dehongensis* sp. nov., *X. maosonensis*, and *X. lancangica* sp. nov.

	<i>X. dehongensis</i> sp. nov.								<i>X. maosonensis</i>		<i>X. lancangica</i> sp. nov.					
	SYS a003443	SYS a003860	SYS a003861	SYS a005822	CIB 119022	SYS a003448	SYS a005823	SYS a008766	SYS a008803	SYS a002961	SYS a002962	CIB 118533	SYS a007794	SYS a007825	SYS a008339	
Sex	M	M	M	M	M	F	F	M	F	M	M	M	F	F	F	
SVL	34.8	36.7	35.9	36.1	36.0	46.8	45.7	66.2	76.9	64.5	65.4	64.0	75.0	88.6	73.0	
HDL	12.8	13.9	14.2	13.8	12.7	18.3	17.7	26.1	29.7	25.3	26.5	24.4	28.6	33.8	29.4	
HDW	11.8	13.2	13.3	13.3	12.4	15.9	15.9	24.0	29.4	23.0	24.0	21.9	26.8	30.1	25.6	
SNT	3.6	4.2	4.5	4.6	5.2	5.2	4.7	8.9	9.9	8.9	9.0	8.4	8.7	12.0	9.5	
IND	4.3	5.0	4.7	5.1	4.6	5.7	5.7	7.5	9.5	7.5	8.3	7.4	8.4	10.0	8.5	
IOD	3.1	3.5	3.3	3.5	3.6	4.4	3.7	5.7	7.3	5.5	6.1	4.7	7.1	8.3	6.2	
ED	4.0	4.2	4.4	4.4	4.7	5.8	5.5	8.3	9.0	8.1	8.1	7.6	8.6	10.4	8.3	
TD	2.2	2.2	2.3	2.4	2.6	3.1	2.9	3.9	4.2	3.4	3.5	3.8	4.0	5.4	4.7	
TED	1.5	1.5	1.5	1.5	2.1	2.5	2.4	4.6	5.4	5.2	5.1	5.6	5.1	7.0	6.4	
HND	9.2	9.5	9.2	10.4	9.1	12.5	10.9	17.0	18.6	17.4	17.8	15.3	18.3	22.8	19.5	
RAD	7.3	7.9	7.7	8.6	7.6	10.9	9.7	13.1	16.3	14.8	14.7	13.8	14.9	19.6	16.5	
FTL	22.6	23.9	23.2	25.4	23.8	31.6	31.8	44.4	54.9	49.5	48.6	46.9	56.0	65.3	56.1	
TIB	14.8	16.9	17.1	17.9	16.5	23.3	22.7	31.5	42.7	36.5	36.3	34.8	42.1	49.2	42.7	

See text for abbreviations. M: Male; F: Female.

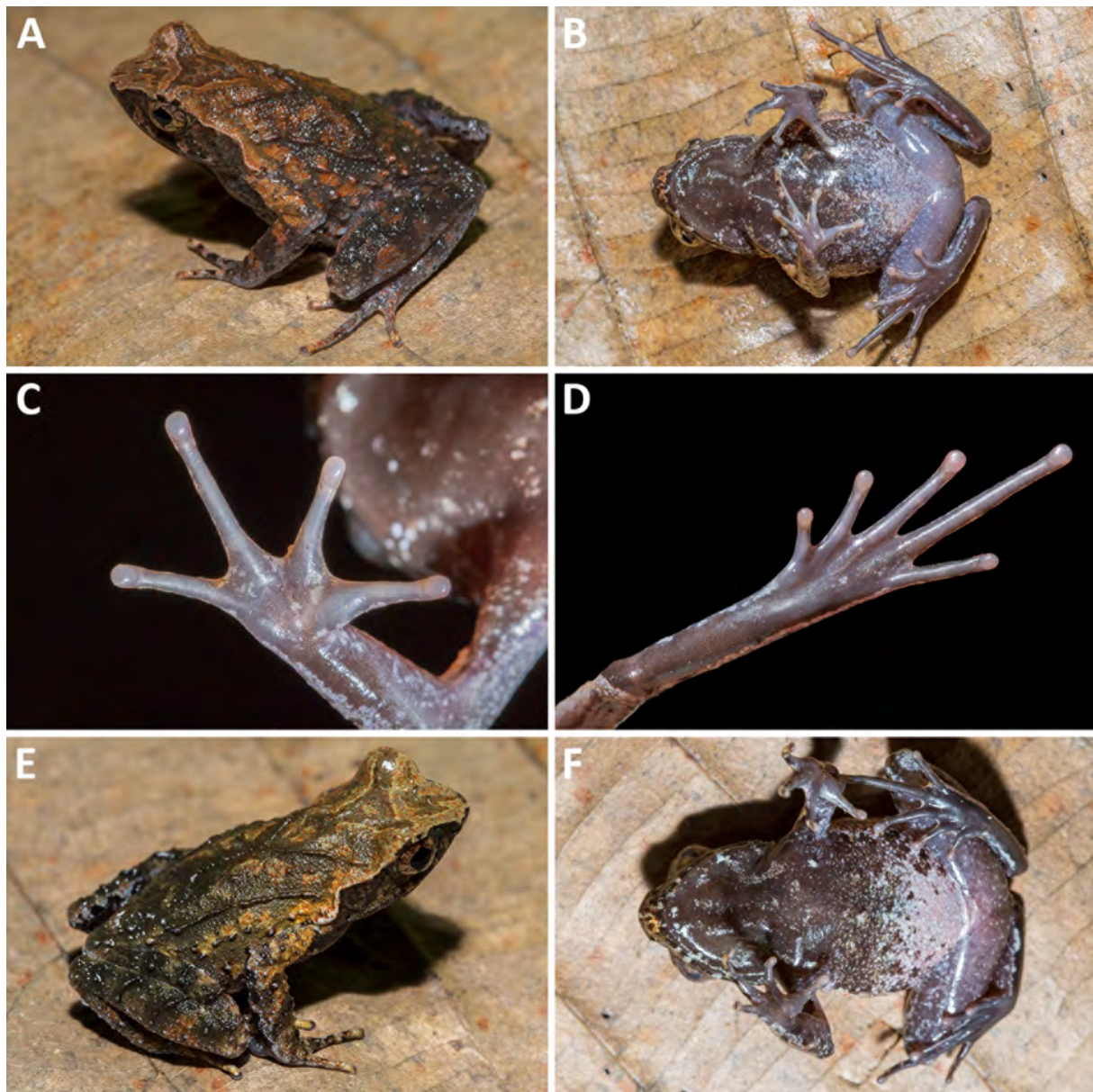


Figure 12 *Xenophrys dehongensis* sp. nov. in life

A: Dorsolateral view of male holotype SYS a003860; B: Ventral view of holotype; C: Hand of holotype; D: Foot of holotype; E: Dorsolateral view of male paratype SYS a003861; F: Ventral view of SYS a003861. Photos by J. Zhao.

Allotype: CIB 24342 (formerly CIB 873201), adult female, from Mt. Wuliang (2 100 m a.s.l.).

Paratypes: Twenty-five males and two females (voucher numbers not provided), from same locality as holotype.

Specimens examined: Two adult males SYS a003907–3908 and one adult female SYS a003923, from Mt. Wuliang (N24.3664°, E100.7610°; ca. 2 400 m a.s.l.); one adult female SYS a003442, from Longchuan County, Dehong, Yunnan; one adult male SYS a005825 and one adult female SYS a005826, from Xiaolangsu Village (N24.5009°, E97.5713°; 700 m a.s.l.), Yingjiang County, Dehong; five adult males SYS a002945–2946, 3793–3795 and five adult females SYS a002944, 3757–3758, 3762, 3792, from Mt. Gaoligong (N25.2976°, E98.7011°; ca. 2 100 m a.s.l.), Tengchong City, Baoshan, Yunnan.

Diagnosis: Based on examined specimens: (1) adult males, SVL 64.3–74.8 mm ($n=8$); adult females, SVL 73.5–93.2 mm ($n=8$); (2) canthus rostralis well developed; tongue weakly

notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin smooth with sparse small granules; weak discontinuous X- or V-shaped ridge on center of dorsum, dorsolateral ridges present; large tubercles on flanks; ventral skin smooth; small black or white dermal asperities on lower jaw; (6) outer margin of upper eyelid with weak medial bumped appendage; supratympanic fold distinct, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct; relative finger lengths $II < I < IV < III$; subarticular tubercles absent; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching region between nostril and tip of snout when leg stretched forward; (9) toes with rudimentary webbing at bases and wide lateral fringes; inner metatarsal tubercle indistinct, outer one absent; (10) dorsal surface dark brown or grayish brown; dark triangular marking between eyes, indistinct V-shaped or netlike marking on center of dorsum; throat and chest purplish brown with white patches on lower

jaw; belly yellowish with dark patches; (11) dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figures 7E, F, 11B).

Distribution: Currently known from multiple localities in western Yunnan, China, and neighboring Kachin, Myanmar, at elevations of 1 900–2 500 m a.s.l. (Fei & Ye, 2016; Mahony et al., 2018; this study) (Supplementary Figure S4).

***Xenophrys himalayana* (Mahony, Kamei, Teeling, and Biju, 2018)**

Himalayan horned toad / xǐ shān jiǎo chán (喜山角蟾)

Chresonymy: *Megophrys* cf. *major* 4 — Mahony et al., 2017

Megophrys (*Xenophrys*) *himalayana* — Mahony et al., 2018

Xenophrys himalayana — Lyu et al., 2021; Qi et al., 2021

Holotype: BNHS 6050, adult male, from Cona County (N27°04'56.52", E92°34'50.22"; 370 m a.s.l.), Shannan, Xizang, China.

Paratypes: Four adult males BNHS 6051–6054, from same locality as holotype.

Diagnosis: Based on original description (Mahony et al., 2018): (1) adult males, SVL 68.0–73.5 mm ($n=6$); adult female, SVL 83.9 mm ($n=1$); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct, upper margin concealed by supratympanic fold; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin primarily smooth with sparse small granules; weak discontinuous V- or X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; ventral skin smooth; small black or white dermal asperities on lower jaw; (6) outer margin of upper eyelid with weak medial bumped appendage; supratympanic fold distinct, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct; relative finger lengths $IV < II < I < III$; subarticular tubercles absent; (8) hindlimbs slender; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle indistinct, outer one absent; (10) dorsal surface orange brown; dark triangular marking between eyes; dark X-shaped or netlike marking on center of dorsum; dorsal limbs with transverse bands; ventral surface lighter with brown blotches; (11) nuptial pad with black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known from Cona and Medog counties in southeastern Xizang at elevations of 375–410 m a.s.l. (Mahony et al., 2018) (Supplementary Figure S3).

Remarks: In the original description of the species (Mahony et al., 2018), the number of male specimens was indicated as one holotype, four paratypes, and one referred specimen in the designation, and six males were provided in the measurements in Table 1, but “adult males, $N=7$ ” was stated in the morphological comparison, which is inconsistent. Here, we follow the designation and measurement, citing the number of examined male specimens as “ $n=6$ ”.

***Xenophrys mangshanensis* (Fei and Ye, 1990)**

Mangshan horned toad / mǎng shān jiǎo chán (莽山角蟾)

Chresonymy: *Megophrys mangshanensis* — Fei et al., 1990

Megophrys (*Xenophrys*) *mangshanensis* — Dubois & Ohler, 1998; Mahony et al., 2017

Xenophrys mangshanensis — Delorme et al., 2006; Chen et al., 2017; Lyu et al., 2021; Qi et al., 2021

Liuophrys mangshanensis — Fei & Ye, 2016; Fei, 2020

Holotype: CIB 66000 (formerly CIB 7510689), adult female,

from Mangshan Nature Reserve (1 000 m a.s.l.), Yizhang County, Chenzhou, Hunan, China.

Allotype: CIB 65999 (formerly CIB 7510907), adult male, from same locality as holotype.

Specimens examined: Two adult males SYS a005753, 8764, from Nanling Nature Reserve (N24.9171°, E113.0090°; ca. 1 160 m a.s.l.), Ruyuan County, Shaoguan, Guangdong, China; one adult male SYS a002793 and one adult female SYS a002794, from Mt. Tianjing (N24.6689°, E112.9436°; ca. 990 m a.s.l.), Ruyuan County; one adult male SYS a002767 and one adult female SYS a002752, from Mt. Longtou (N24.7127°, E113.8938°; ca. 400 m a.s.l.), Qujiang District, Shaoguan; two adult males SYS a001564, 4979, from Shimentai Nature Reserve (N24.4095°, E113.1095°; ca. 370 m a.s.l.), Yingde City, Qingyuan, Guangdong; one adult male SYS a002177, from Mt. Sanyue (N24.2242°, E111.9680°; ca. 660 m a.s.l.), Huaiji County, Zhaoqing, Guangdong; three adult males SYS a004870–4871, 4876 and three adult females SYS a004874–4875, 4877, from Dayaoshan Nature Reserve (N24.1602°, E110.2304°; ca. 1 200 m a.s.l.), Jinxiu County, Laibin, Guangxi, China.

Diagnosis: Based on examined specimens: (1) adult males, SVL 60.4–71.6 mm ($n=10$); adult females, SVL 62.0–77.9 mm ($n=5$); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin smooth with sparse small granules; weak discontinuous X- or V-shaped ridge on center of dorsum, dorsolateral ridges present; sparse tubercles on flanks; ventral skin smooth; small black dermal asperities on lower jaw; (6) outer margin of upper eyelid with weak medial bumped appendage; supratympanic fold distinct, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct; relative finger lengths $II < I < IV < III$; subarticular tubercles absent; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes without webbing and lateral fringes; inner metatarsal tubercle indistinct, outer one absent; (10) dorsal surface greenish brown, yellowish brown or reddish brown; dark triangular marking between eyes, indistinct X-shaped marking on center of dorsum; throat and chest purplish; belly yellowish; (11) dense brown nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figures 7A and 11C).

Distribution: Common from multiple localities in the Nanling Mountains and Dayao Mountains along border of Jiangxi, Hunan, Guangdong, and Guangxi at elevations of 350–1 200 m a.s.l. (Fei & Ye, 2016; this study) (Supplementary Figure S4).

***Xenophrys maosonensis* (Bourret, 1937)**

Maoson horned toad / máo sǒ jiǎo chán (茅索角蟾)

Chresonymy: *Megophrys longipes maosonensis* — Bourret, 1937

Megophrys major — Bourret, 1942; Fei et al., 2009, 2012; Mo et al., 2014

Liuophrys major — Fei & Ye, 2016; Fei, 2020

Xenophrys maosonensis — Chen et al., 2017; Lyu et al., 2021; Qi et al., 2021

Lectotype (by present designation). MNHN 1938.97, adult male, collected by R. Bourret on 1 June 1937 from Mao-Son (=Mt. Mau Son, Loc Binh District, Lang Son) (N21°51', E106°58'), Vietnam.

Specimens examined: One adult male SYS a008766 and one adult female SYS a008803, from Pinglonggou (N21.8479°, E107.8683°; ca. 670 m a.s.l.), Mt. Shiwandashan, Shangsi County, Fangchenggang, Guangxi, China.

Diagnosis: Based on examined specimens: (1) adult male, SVL 66.2 mm ($n=1$); adult female, SVL 76.9 mm ($n=1$); detailed measurements are presented in Table 4; (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct, upper margin concealed by supratympanic fold; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin relatively smooth with sparse small granules; weak discontinuous X-shaped ridge on center of dorsum, dorsolateral ridges present; sparse large tubercles on flanks; ventral skin smooth; small black or white dermal asperities on lower jaw; (6) outer margin of upper eyelid with weak medial bumped appendage; supratympanic fold distinct, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct; relative finger lengths $I < II < IV < III$;

subarticular tubercles absent; (8) hindlimbs slender, heels slightly overlapping when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle indistinct, outer one absent; (10) dorsal surface dark brown; triangular marking between eyes, X-shaped marking on center of dorsum; throat and chest purplish with white patches on lower jaw; belly pale gray with yellowish margin; (11) black nuptial pads on dorsal bases of fingers I and II in breeding adult male; subgular vocal sac present in male (Figures 7B and 13).

Distribution: Currently known from Mt. Mau Son in northeastern Vietnam, and Mt. Shiwandashan and Jingxi County in southwestern Guangxi, China, at elevations of 600–700 m a.s.l. (Mo et al., 2014; this study, refer to Remarks below) (Supplementary Figure S4).

Remarks: This species was originally coined as the subspecies *Megophrys longipes maosonensis* based on a



Figure 13 *Xenophrys maosonensis* in life

A: Dorsolateral view of male SYS a008766; B: Ventral view of SYS a008766; C: Hand of SYS a008766; D: Foot of SYS a008766; E: Dorsolateral view of female SYS a008803; F: Ventral view of SYS a008803 *in situ*. Photos by S. Qi and W.L. Xie.

series of syntypes collected from Mao-Son (=Mt. Mau Son, Loc Binh District, Lang Son) and Chapa (=Sa Pa District, Lao Cai), Vietnam (Bourret, 1937). Subsequently, Bourret (1942) synonymized it with *M. major* (currently *X. major*), which was followed by most amphibian checklists for China and Indochina. Chen et al. (2017) recently resurrected this nomenclature as *X. maosonensis* for the populations from southwestern China and northern Vietnam but did not provide any morphological examination. In the same work, they identified the population from southwestern China, Laos, and Vietnam as a cryptic species *M. sp14* (Chen et al., 2017). Mahony et al. (2018) restricted the distribution of *X. major* in northeastern India and agreed with the species-level validity of *X. maosonensis*. Nevertheless, they suggested that *X. maosonensis* requires further clarification as multiple potential species-level taxa are present in northern Vietnam, and labeled the populations previously reported from China and Indochina as *M. (X.) cf. maosonensis 1* and *M. (X.) cf. maosonensis 2*, respectively, corresponding to *X. maosonensis* and *M. sp14* in Chen et al. (2017).

In this work, we included data from Chen et al. (2017) and Mahony et al. (2018) with our samples for phylogenetic analyses. Results indicated that the populations from China and Indochina previously recorded as *X. major* or *X. maosonensis* formed three distinct lineages (Figures 1 and 2). Samples from southwestern Guangxi in China formed an independent lineage. Samples from southeastern Yunnan in China and northern Vietnam (*sensu X. maosonensis* in Chen et al., 2017) formed a second lineage, with moderate support as a sister taxon to Guangxi lineage (BS 80, BPP 0.99). Samples from southern Yunnan in China, Laos, and northern and central Vietnam (*sensu M. sp14* in Chen et al., 2017) formed a third lineage, which was distinctly separate from the other two lineages. Of note, samples from Lao Cai were included in both the second and third lineages (IDs 68 and 83 in Figure 2).

The syntypes of *M. longipes maosonensis* contain specimens from two localities. These syntypes collectively constitute the name-bearing type. However, as this species is named with *maosonensis*, we herein designate one of the individuals from Mao-Son, MNHN 1938.97 (information available at <https://science.mnhn.fr/institution/mnhn/collection/ra/item/1938.97>), as the lectotype of *M. longipes maosonensis*. Molecular data for the population from Mt. Mau Son are unavailable currently. However, this region is located at the border between Guangxi in China and Vietnam, ca. 80 km from Mt. Shiwandashan, and the two regions are suggested to share similar amphibian fauna (e.g., *Ophryophryne microstoma*, *Sylvirana maosonensis*, and *Theloderma corticale*). Thus, we consider that the lineage composed of samples from Mt. Shiwandashan, Guangxi represent the population from the vicinity of Mt. Mau Son, i.e., concept of *X. maosonensis sensu stricto*.

The second lineage (*sensu X. maosonensis* in Chen et al., 2017) formed the sister taxon of *X. maosonensis sensu stricto*, but with moderate BS support and moderate divergence between them. We only had a tadpole specimen (SYS a004527, ID 64 in Figure 2), so morphological comparison was not possible. Thus, the lineage is tentatively labeled as *X. cf. maosonensis* in this work, but further study is warranted, even though it likely should be a geographic population of *X. maosonensis sensu stricto*. The third lineage (*sensu M. sp14* in Chen et al., 2017) represents a cryptic species and is

described below.

***Xenophrys lancangica* sp. nov. Lyu, Wang, and Wang**

Lancang horned toad / lán cāng jiǎo chán (澜沧角蟾)

Chresonymy: *Megophrys longipes maosonensis* — Bourret, 1937

Megophrys major — Bourret, 1942; Fei et al., 2009, 2012; Liu et al., 2018

Liuophrys major — Fei & Ye, 2016; Fei, 2020

Megophrys sp14 — Chen et al., 2017

Megophrys (Xenophrys) cf. maosonensis 2 — Mahony et al., 2017, 2018

Holotype: SYS a002961, adult male, collected by Zu-Yao Liu on 11 July 2014 from Zhushihe (N22.2143°, E101.5131°; ca. 1060 m a.s.l.), Mengla County, Xishuangbanna, Yunnan, China.

Paratypes: One adult male SYS a002962, same collection data as holotype; one adult male CIB 118533 (formerly SYS a003955), collected by Jian Zhao on 30 May 2015 from same locality as holotype; one adult female SYS a007825, collected by Jian Wang on 7 June 2019 from Madihe (N22.4443°, E101.0341°; ca. 1100 m a.s.l.), Puwen Town, Jinghong City, Xishuangbanna; one adult female SYS a007794, collected by Jian Wang on 6 June 2019 from Dakaihe Village (N22.5947°, E101.0600°; ca. 1200 m a.s.l.), Simao District, Pu'er, Yunnan; one adult female SYS a008339, collected by Sheng Zheng and Hang Zhou on 3 May 2020 from Mt. Huanglian (N22.8079°, E102.2429°; ca. 800 m a.s.l.), Lyuchun County, Honghe, Yunnan.

Etymology: The specific nomen *lancangica* is derived from the Lancang-Mekong River Basin, where the new species is primarily distributed.

Diagnosis: (1) Adult males, SVL 64.0–65.4 mm ($n=3$); adult females, SVL 75.0–88.6 mm ($n=3$); detailed measurements are presented in Table 4; (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct, upper margin concealed by supratympanic fold; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin smooth with sparse small granules; weak discontinuous X-, Y-, or "> <"-shaped ridge on center of dorsum, dorsolateral ridges present; sparse large tubercles on flanks; ventral skin smooth; small black dermal asperities on lower jaw; (6) outer margin of upper eyelid with weak medial bumped appendage; supratympanic fold distinct, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct; relative finger lengths II<IV<I<III; subarticular tubercles absent; (8) hindlimbs slender, heels slightly overlapping when hindlimbs folded; tibiotarsal articulation reaching region between nostril and tip of snout when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle indistinct, outer one absent; (10) dorsal surface yellowish brown; triangular marking between eyes, X-shaped marking on center of dorsum; dorsal limbs with transverse bands; throat and chest purplish brown; belly creamy white; (11) brown nuptial pads on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figures 7D and 14).

Distribution: Currently known from multiple localities in southern Yunnan in China, Laos, and northern and central Vietnam at elevations of 500–1300 m a.s.l. (Fei & Ye, 2016; this study) (Supplementary Figure S4).

***Xenophrys medogensis* (Fei, Ye, and Huang, 1983)**

Medog horned toad / muò tuō jiǎo chán (墨脱角蟾)

Chresonymy: *Megophrys omeimontis medogensis* — Fei



Figure 14 *Xenophrys lancangica* sp. nov. in life

A: Dorsolateral view of male holotype SYS a002961; B: Ventral view of holotype; C: Hand of holotype; D: Foot of holotype; E: Dorsolateral view of male paratype SYS a003955; F: Dorsolateral view of female paratype SYS a007825. Photos by Z.Y. Liu and J. Wang.

et al., 1983

Megophrys medogensis — Fei et al., 1990

Megophrys (Xenophrys) medogensis — Dubois & Ohler, 1998; Mahony et al., 2017

Xenophrys medogensis — Delorme et al., 2006; Chen et al., 2017; Lyu et al., 2021; Qi et al., 2021

Xenophrys (Xenophrys) medogensis — Fei & Ye, 2016; Fei, 2020

Holotype: CIB 24350 (formerly CIB 73110015), adult male, from Muotuo (=Medog) County (1 000 m a.s.l.), Nyingchi, Xizang, China.

Paratypes: 160 adult males, one juvenile, and tadpoles (voucher numbers not provided), from same locality as holotype (850–1 350 m a.s.l.).

Specimens examined: Two adult males SYS a006623–6624 and two adult females SYS a006625–6626, from Beibeng Village (N29.24292°, E95.18561°; 870 m a.s.l.), Medog County; two adult males SYS a006634–6635, from Xirang

Village (N29.1780°, E95.0221°; ca. 750 m a.s.l.), Medog County; and two adult males SYS a002932–2933, from Medog urban neighborhood (N29.32213°, E95.31324°; 907 m a.s.l.), Medog County.

Diagnosis: Based on examined specimens: (1) adult males, SVL 56.1–62.4 mm ($n=6$); adult females, SVL 73.8–79.6 mm ($n=2$); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin smooth with sparse small granules; weak discontinuous X-shaped ridge on center of dorsum, dorsolateral ridges present; ventral skin smooth; small black or white dermal asperities on lower jaw; (6) outer margin of upper eyelid with weak medial bumped appendage; supratympanic fold distinct, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct; relative finger lengths $II < I < IV < III$; subarticular tubercles absent; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching region

between eye and tip of snout when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle indistinct, outer one absent; (10) dorsal surface brown; dark triangular marking between eyes, X marking on center of dorsum; throat and chest purplish brown with white patches on lower jaw; belly yellowish with dark patches; (11) dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figures 7C and 11D).

Distribution: Common in multiple localities in Medog County at elevations of 600–2 200 m a.s.l. (Che et al., 2020; Shi et al., 2020a; this study) (Supplementary Figure S3).

***Xenophrys periosa* (Mahony, Kamei, Teeling, and Biju, 2018)**

Giant Himalayan horned toad / zàng nán jiǎo chán (藏南角蟾)

Chresonymy: *Megophrys* cf. *major* 5 — Mahony et al., 2017

Megophrys (*Xenophrys*) *periosa* — Mahony et al., 2018; Shi et al., 2020b

Xenophrys periosa —Lyu et al., 2021; Qi et al., 2021

Holotype: BNHS 6055, adult male, from Medog County (N28°12'33.96", E94°59'10.02"; 450 m a.s.l.), Nyingchi, Xizang, China.

Paratypes: Four adult males BNHS 6057–6060, from same locality as holotype; four adult males BNHS 6061–6064 and one adult female BNHS 6056, from Cona County (N27°06'04.02", E92°31'38.52"; 1 110 m a.s.l.), Shannan, Xizang, China.

Diagnosis: Based on original description (Mahony et al., 2018): (1) adult males, SVL 71.3–93.8 mm ($n=12$); adult female, SVL 112.0 mm ($n=1$); (2) canthus rostralis well developed; tongue notched posteriorly; (3) tympanum distinct, upper margin concealed by supratympanic fold; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin primarily smooth with sparse small granules; weak discontinuous X-, Y-, V- or "> <"-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; ventral skin smooth; small black or white dermal asperities on lower jaw; (6) outer margin of upper eyelid with weak medial bumped appendage; supratympanic fold distinct, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct; relative finger lengths $IV \leq II < I < III$; subarticular tubercles absent; (8) hindlimbs slender; (9) toes with rudimentary webbing at bases, without lateral fringes or with indistinct narrow lateral fringes; inner metatarsal tubercle indistinct, outer one absent; (10) dorsal surface olive brown; dark triangular marking between eyes; indistinct X-shaped or netlike marking on center of dorsum; dorsal limbs with indistinct transverse bands; ventral surface lighter with or without dark brown blotches; (11) nuptial pad with black or brown nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known from Cona and Medog counties in southeastern Xizang, and Gongshan County in northwestern Yunnan, at elevations of 260–2 236 m a.s.l. (Mahony et al., 2018; Shi et al., 2020b) (Supplementary Figure S4).

***Xenophrys zhangii* (Ye and Fei, 1992)**

Zhang's horned toad / zhāng shì jiǎo chán (张氏角蟾)

Chresonymy: *Megophrys minor* — Hu et al., 1987

Megophrys zhangii — Ye & Fei, 1992

Megophrys (*Xenophrys*) *zhangii* — Dubois & Ohler, 1998; Mahony et al., 2017

Xenophrys zhangii — Delorme et al., 2006; Chen et al., 2017;

Lyu et al., 2021; Qi et al., 2021

Xenophrys (*Xenophrys*) *zhangii* — Fei & Ye, 2016; Fei, 2020

Holotype: CIB 750296, adult male, from Zhangmo (=Zhangmu Town) (1 000 m a.s.l., altitude in error, refer to Remark below) Nyanang=Nyalan County Shigatse Xizang China.

Paratypes: Two adult males CIB 750295, 97, from same locality as holotype (700–1 000 m a.s.l., altitude in error).

Specimens examined: One adult male SYS a008202 and two adult females SYS a008203–8204, from Lixin Village (N27.9749°, E85.9722°; ca. 2 180 m a.s.l.), Zhangmu Town.

Diagnosis: Based on previous descriptions (Che et al., 2020; Ye & Fei, 1992) and examined specimens: (1) adult males, SVL 32.5–40.0 mm ($n=7$; Che et al., 2020) (SVL 39.5 mm, $n=1$; this study); adult females, SVL 44.5–50.2 mm ($n=2$; this study); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin smooth with sparse small granules; weak discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; ventral skin smooth; (6) outer margin of upper eyelid with weak medial bumped appendage; supratympanic fold distinct, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct; relative finger lengths $I < II < IV < III$; subarticular tubercles absent; (8) hindlimbs slender, heels slightly overlapping when hindlimbs folded; tibiotarsal articulation reaching anterior corner of eye when leg stretched forward; (9) toes without webbing but with narrow lateral fringes; inner metatarsal tubercle indistinct and flat, outer one absent; (10) dorsal surface yellowish brown; dark brown triangular marking between eyes, dark V- or X-shaped marking on center of dorsum; dorsal limbs with dark transverse bands; throat and chest purplish brown, belly creamy white with dark patches; (11) dense gray nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 4D).

Distribution: Known from its type locality in Nyalam County at elevations of 1 800–2 100 m a.s.l. (Che et al., 2020; this study) (Supplementary Figure S3) but expected from neighboring areas in Nepal and India.

Remarks: In the original description of this species, the type series was collected from Zhangmo (=Zhangmu Town) at elevations of 700–1 000 m a.s.l. (Ye & Fei, 1992). However, current geographic data shows that the altitude in the vicinity of Zhangmu Town is higher than 1 500 m a.s.l., and altitudes in neighboring areas of Nepal are not lower than 1 300 m a.s.l. The altitudinal data (700–1 000 m) presented in the original description may be due to altimeter error. Based on the collected information in Che et al. (2020) and this study, *X. zhangii* is known at elevations of 1 800–2 180 m a.s.l.

Based on phylogenetic analysis, *X. zhangii* was closely related to the mid-elevation population of *X. monticola* (*sensu* Mahony et al., 2018), with minor mitochondrial gene-based divergence and distinct nuclear gene-based divergence between the two species (Figure 1). The clade consisting of *X. zhangii* and the mid-elevation population of *X. monticola* were distinctly divergent from the high-elevation population of *X. monticola* (Figure 2). The available molecular data of *X. zhangii* and *X. monticola* were only from the vicinity of their type localities, located more than 230 km from each other, but both species are reported from neighboring areas in eastern Nepal. Further study on population genetics, including all populations from the three countries, is warranted. In this work, we retain the two species in their current status.

Key to species of genus *Boulenophrys* from China (60 species)

1a) Vomerine teeth present **2**
1b) Vomerine teeth absent **22**
2a) Webbing on toes distinct and developed, 1/3 webbing or half webbing **3**
2b) Webbing on toes absent or only rudimentary at bases **5**
3a) Weak medial bumped appendage at outer margin of upper eyelid, without horn-like tubercles *jingdongensis*
3b) Upper eyelid without appendage, horn-like tubercle at outer margin of eyelid present **4**
4a) Toes with 1/3 webbing; large, conical, and sparse nuptial spines in breeding males *qianbeiensis*
4b) Toes with half webbing; tiny, dense nuptial spines in breeding males *palpebralespinosa*
5a) Larger body size, SVL larger than 50 mm in males **6**
5b) Smaller body size, SVL smaller than 45 mm in males **8**
6a) Outer margin of upper eyelid elongated as triangular appendage *caudoprocta*
6b) Upper eyelid without appendage **7**
7a) Distinct elongated horn-like tubercle on outer margin of upper eyelid; toes with narrow lateral fringes *liboensis*
7b) Small horn-like tubercle on outer margin of upper eyelid; toes with moderate lateral fringes *omeimontis*
8a) Toes without webbing **9**
8b) Toes with rudimentary webbing at bases **11**
9a) Groin, inner surface of thighs and outer surface of shanks red-orange *rubrimera*
9b) Absence of such red-orange coloration **10**
10a) Tympanum with distinct edge; SVL larger than 33 mm in males; dorsolateral ridges present *daweimontis*
10b) Anterior edge of tympanum indistinct; SVL smaller than 32 mm in males; dorsolateral ridges indistinct or absent..... *tongboensis*
11a) Toes with narrow lateral fringes **12**
11b) Toes without lateral fringes **15**
12a) Margin of tongue rounded *nanlingensis*
12b) Margin of tongue notched **13**
13a) Tiny spines on whole dorsal skin *shimentaina*
13b) Absence of tiny spines on whole dorsal skin **14**
14a) SVL smaller than 31 mm in males; discontinuous dorsolateral ridges present; nuptial pads/spines absent in breeding males *daiyunensis*
14b) SVL larger than 33 mm in males; dorsolateral ridges absent; nuptial spines present in breeding males *jinggangensis*
15a) Heels overlapping when hindlimbs folded **16**
15b) Heels not meeting when hindlimbs folded **17**
16a) Dorsal skin rough with black spines *julianensis*
16b) Dorsal skin smooth, without spines *yingdeensis*
17a) Raised tubercles bearing spines present on ventral thighs and around cloaca **18**
17b) Absence of such tubercles and spines **20**
18a) Margin of tongue notched *brachykolos*
18b) Margin of tongue rounded **19**
19a) Temporal region with tubercles bearing spines; tubercles on posterior belly without spines *fengshunensis*
19b) Temporal region with tubercles but not bearing spines; tubercles on posterior belly bearing spines *puningensis*
20a) Margin of tongue notched; tibiotarsal articulation reaching between posterior edge of tympanum when leg stretched forward *insularis*
20b) Margin of tongue rounded; tibiotarsal articulation

reaching region between tympanum and eye when leg stretched forward **21**
21a) Dorsal skin rough; discontinuous dorsolateral ridges present *dongguanensis*
21b) Dorsal skin smooth; dorsolateral ridges absent *nankunensis*
22a) Outer margin of upper eyelid elongated as triangular appendage; SVL larger than 100 mm in males *shuichengensis*
22b) Upper eyelid without appendage; SVL smaller than 70 mm in males **23**
23a) Webbing on toes distinct and developed, 1/3 webbing **24**
23b) Webbing on toes absent or only rudimentary at bases **25**
24a) Large, conical, and sparse nuptial spines in breeding males; SVL smaller than 55 mm in males; dorsal skin relatively rough with scattered spines *spinata*
24b) Tiny, sparse nuptial spines in breeding males; SVL larger than 57 mm in males; dorsal skin smooth, without spines *fanjingmontis* **comb. nov.**
25a) Toes without webbing **26**
25b) Toes with rudimentary webbing at bases **34**
26a) Tibiotarsal articulation reaching center of eye when leg stretched forward **27**
26b) Tibiotarsal articulation reaching region behind eye when leg stretched forward **28**
27a) Vomerine ridges present; toes with narrow lateral fringes *baishanzuensis*
27b) Vomerine ridges absent; toes without lateral fringes *wuliangshanensis*
28a) Heels not meeting when hindlimbs folded **29**
28b) Heels overlapping or just meeting when hindlimbs folded **31**
29a) Margin of tongue notched *kuatunensis*
29b) Margin of tongue rounded **30**
30a) Distinct enlarged tubercles on chest, belly, and around cloaca; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward *hungtai*
30b) Ventral surface smooth; tibiotarsal articulation reaching region between anterior and posterior margins of tympanum when leg stretched forward *ombrophila*
31a) Margin of tongue notched; SVL larger than 40 mm in males *baolongensis*
31b) Margin of tongue rounded; SVL smaller than 40 mm in males **32**
32a) Dorsal skin relatively smooth; dorsolateral ridges absent .. *lishuiensis*
32b) Dorsal skin rough; discontinuous dorsolateral ridges present **33**
33a) Heels distinctly overlapping when hindlimbs folded; relative finger lengths I<II<IV<III *jiangi*
33b) Heels just meeting when hindlimbs folded; relative finger lengths II<I<IV<III *xuefengmontis* **sp. nov.**
34a) Toes without lateral fringes **35**
34b) Toes with wide or narrow lateral fringes **43**
35a) Heels not meeting when hindlimbs folded **36**
35b) Heels overlapping or just meeting when hindlimbs folded **37**
36a) Ventral surface with creamy white nebulous patches; relative finger lengths II<I=IV<III *wugongensis*
36b) Ventral surface without such patches; relative finger lengths I<II<IV<III *obesa*

37a) Vomerine ridges present	38
37b) Vomerine ridges absent	40
38a) Margin of tongue notched; SVL larger than 55 mm in males	<i>sangzhiensis</i>
38b) Margin of tongue rounded; SVL smaller than 45 mm in males	39
39a) Dorsal skin rough; discontinuous dorsolateral ridges present; tiny spines present on upper lip, upper eyelid, loreal and temporal regions excluding tympanum in adult males	<i>yunkaiensis</i>
39b) Dorsal skin relatively smooth; dorsolateral ridges absent; above-mentioned tiny spines in adult males absent	<i>yaoshanensis</i>
40a) Dorsal surface with irregular netlike markings, without triangular marking between eyes and X-shaped marking on center of dorsum	<i>tubero granulata</i>
40b) Dorsal surface with triangular marking between eyes and X-shaped marking on center of dorsum, without netlike markings	41
41a) Tibiotarsal articulation reaching region between eye and tip of snout when leg stretched forward	<i>shunhuangensis</i>
41b) Tibiotarsal articulation reaching behind loreal region when leg stretched forward	42
42a) Heels distinctly overlapping when hindlimbs folded; relative finger lengths $II < IV < III$	<i>leishanensis</i>
42b) Heels just meeting when hindlimbs folded; relative finger lengths $I < II < IV < III$	<i>minor</i>
43a) Pair of light-colored, large, and semi-rounded marking usually present on shoulder regions	<i>boettgeri</i>
43b) Absence of such marking on shoulder regions	44
44a) Heels not meeting when hindlimbs folded	45
44b) Heels overlapping or just meeting when hindlimbs folded	46
45a) SVL smaller than 35 mm in females; remarkably prominent horn-like tubercle at edge of eyelid	<i>acuta</i>
45b) SVL larger than 37 mm in females; small horn-like tubercle at edge of upper eyelid	<i>daoji</i>
46a) Toes with wide lateral fringes	47
46b) Toes with narrow lateral fringes	51
47a) Margin of tongue notched	48
47b) Margin of tongue rounded	49
48a) Dorsal surface with netlike markings; tibiotarsal articulation reaching region between nostril and tip of snout when leg stretched forward	<i>cheni</i>
48b) Dorsal surface with triangular marking between eyes and X-shaped marking on center of dorsum; tibiotarsal articulation reaching posterior corner of eye when leg stretched forward	<i>sanmingensis</i>
49a) Vomerine ridges absent	<i>wushanensis</i>
49b) Vomerine ridges present	50
50a) Heels distinctly overlapping when hindlimbs folded; tibiotarsal articulation reaching anterior corner of eye when leg stretched forward	<i>lini</i>
50b) Heels just meeting when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward	<i>xiangnanensis</i>
51a) Vomerine ridges absent	52
51b) Vomerine ridges present	55
52a) Tongue small, majority attached to mandible; SVL larger than 55 mm in males	<i>mirabilis</i>
52b) Tongue large, not attached to mandible; SVL smaller than 45 mm in males	53
53a) Heels just meeting when hindlimbs folded	

.....	<i>binchuanensis</i>
53b) Heels distinctly overlapping when hindlimbs folded	54
54a) SVL larger than 33 mm in males on average	<i>chishuiensis</i>
54b) SVL smaller than 33 mm in males on average	<i>congjiangensis</i>
55a) Margin of tongue notched	56
55b) Margin of tongue rounded	57
56a) SVL larger than 45 mm in males	<i>binlingensis</i>
56b) SVL smaller than 38 mm in males	<i>lushuiensis</i>
57a) SVL smaller than 31 mm in males; dorsolateral ridges absent	<i>mufumontana</i>
57b) SVL larger than 33 mm in males; discontinuous dorsolateral ridges present	58
58a) SVL larger than 40 mm in males	<i>anlongensis</i>
58b) SVL smaller than 38 mm in males	59
59a) Tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward	<i>xianjuensis</i>
59b) Tibiotarsal articulation reaching anterior corner of eye when leg stretched forward	<i>yangmingensis</i>

***Boulenophrys minor* group**

***Boulenophrys minor* (Stejneger, 1926)**

Little horned toad / xiǎo jiǎo chán (小角蟾)

Chresonymy: *Megophrys minor* — Stejneger, 1926; Liu, 1950; Liu & Hu, 1961; Fei et al., 2009, 2012

Megophrys (Megophrys) minor — Dubois, 1980

Megophrys minor minor — Ye & Fei, 1995

Panophrys minor — Rao & Yang, 1997; Lyu et al., 2021

Megophrys (Xenophrys) minor — Dubois & Ohler, 1998

Xenophrys minor — Delorme et al., 2006; Chen et al., 2017

Boulenophrys minor — Fei & Ye, 2016; Fei, 2020; Dubois et al., 2021; Qi et al., 2021

Megophrys (Panophrys) minor — Mahony et al., 2017

Holotype: USNM 68816, male, from Kwanghsien (now Dujiangyan City, Chengdu), Szechwan (=Sichuan), China.

Specimens examined: Three adult males SYS a003211–3213 and one adult female SYS a003209, from Mt. Qingcheng (N30.9286°, E103.4768°; ca. 1 390 m a.s.l.), Dujiangyan City.

Diagnosis: Based on examined specimens: (1) adult males, SVL 34.2–37.2 mm ($n=3$); adult female, SVL 40.9 mm ($n=1$); detailed measurements are presented in Table 5; (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin relatively rough with numerous granules and sparse tubercles; weak discontinuous X-shaped or "> <"-shaped ridge on center of dorsum, discontinuous dorsolateral ridges indistinct; several large tubercles on flanks; dorsal limbs with discontinuous transverse ridges and tubercles; ventral skin smooth; (6) outer margin of upper eyelid with small horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct and flat, inner one observably enlarged; relative finger lengths $I < II < IV < III$; indistinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels just meeting when hindlimbs folded; tibiotarsal articulation reaching region between anterior margin of tympanum and anterior corner of eye when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface yellowish brown or reddish brown; dark brown triangular marking between eyes; dark X-

Table 5 Measurements (in mm) of examined specimens of *Boulenophrys minor* and *B. xuefengmontis* sp. nov..

	<i>B. minor</i>				<i>B. xuefengmontis</i> sp. nov.							
	SYS a003211	SYS a003212	SYS a003213	SYS a003209	SYS a007224	SYS a007225	SYS a007226	SYS a007227	SYS a007228	CIB 118532	SYS a007222	SYS a007223
Sex	M	M	M	F	M	M	M	M	M	M	F	F
SVL	37.2	34.2	35.1	40.9	38.1	37.4	38.0	37.6	37.0	38.3	48.9	45.3
HDL	12.8	11.7	12.4	13.3	12.4	13.2	13.6	13.3	13.4	12.7	15.2	14.5
HDW	11.0	10.3	10.7	11.6	12.4	12.4	12.8	12.8	12.3	12.3	14.1	13.8
SNT	4.4	3.9	4.0	4.0	3.7	3.6	4.3	3.9	3.8	4.5	5.3	5.1
IND	5.3	4.2	4.9	4.9	4.7	3.8	3.9	4.7	5.0	4.3	4.8	4.5
IOD	3.4	3.1	3.4	3.3	2.7	3.0	3.1	3.2	3.5	3.0	3.7	2.8
ED	3.7	3.3	3.5	3.2	3.6	3.6	3.6	3.4	3.5	3.6	4.9	4.5
TD	2.4	2.1	2.4	2.5	1.9	2.3	2.2	2.0	1.9	2.1	2.1	2.0
TED	1.3	1.1	1.2	1.6	1.1	1.2	1.3	1.3	1.2	1.2	1.3	1.2
HND	9.6	8.5	9.0	10.0	9.2	9.1	9.0	9.3	9.5	9.2	10.4	9.6
RAD	8.0	7.2	7.5	7.5	7.7	7.6	6.5	7.4	7.7	7.1	9.3	8.8
FTL	26.5	23.5	23.6	27.3	23.5	24.9	21.4	25.1	24.4	22.7	27.8	27.3
TIB	18.0	15.8	16.7	19.3	16.6	17.1	15.2	16.7	16.7	16.1	19.1	19.2

See text for abbreviations. M: Male; F: Female.

shaped or netlike marking on center of dorsum; dorsal limbs with dark transverse bands; throat and chest purplish or gray; belly pale white with dark irregular patches; (11) nuptial pads with tiny and dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 15).

Distribution: Currently recognized from its type locality in Dujiangyan City at elevations of 1 200–1 400 m a.s.l. (this study, refer to Remarks below) (Supplementary Figure S8).

Remarks: This species was originally described based on a single male specimen with a brief combination of diagnoses (Stejneger, 1926). Liu (1950) re-described the holotype in detail and suggested that the small-sized Asian horned toad from Mt. Omei (=Mt. Emei, Emeishan City, Leshan, Sichuan) is conspecific with the Kwanghsien population. Subsequently, the species was widely recorded from multiple localities in southern China (Liu, 1950; Liu & Hu, 1961; Fei & Ye, 2016; Fei et al., 2009, 2012; Ye & Fei, 1995). Ye & Fei (1992, 1995) proposed that several records of this species should be considered distinct congeners, erected as *M. zhangii* (currently *X. zhangii*), *M. wuliangshanensis* (currently *B. wuliangshanensis*), *M. wushanensis* (currently *B. wushanensis*), and *M. minor binchuanensis* (currently *B. binchuanensis*), respectively, based on morphological comparison with the population from Mt. Emei. Following Liu (1950), the population from Mt. Emei was long used as a reference for *B. minor* (Fei & Ye, 2016; Fei et al., 2009; Liu et al., 2020; Xu et al., 2020). Nonetheless, recent phylogenetic analyses have indicated that the Dujiangyan and Emeishan populations should represent two distinct and diverged taxa (Chen et al., 2017; Liu et al., 2018). Thus, we restrict the distribution of *B. minor* to Dujiangyan based on molecular data and voucher specimens. Historic records of this species from other localities are all assigned to other congeners (refer to Chresonymy/Remarks on *B. chishuiensis*, *B. jiangii*, *B. binchuanensis*, *B. leishanensis*, and *B. shunhuangensis*).

***Boulenophrys chishuiensis* (Xu, Li, Liu, Wei, and Wang, 2020)**

Chishui horned toad / chì shuǐ jiǎo chán (赤水角蟾)

Chresonymy: *Megophrys minor* — Liu, 1950; Liu & Hu, 1961; Fei et al., 2009, 2012

Megophrys minor minor — Ye & Fei, 1995

Boulenophrys minor — Fei & Ye, 2016; Fei, 2020

Megophrys sp10 — Chen et al., 2017

Megophrys sp41 — Liu et al., 2018

Megophrys chishuiensis — Xu et al., 2020

Panophrys chishuiensis — Lyu et al., 2021

Boulenophrys chishuiensis — Qi et al., 2021

Holotype: CIB CS20190518031, adult male, from Chishui Nature Reserve (N28.436708°, E105.997794°; ca. 460 m a.s.l.), Chishui City, Zunyi, Guizhou, China.

Paratypes: Two adult males CIB CS20190518019, 021, and five adult females CIB CS20190518022–023, 025, 027, 030, from same locality as holotype.

Specimens examined: Six adult males SYS a001802–1805, 5307–5308, from Mt. Emei (N29.5473°, E103.3759°; ca. 1 600 m a.s.l.), Emeishan City, Leshan, Sichuan, China; seven adult males SYS a005321–5327 and one adult female SYS a005338, from Mt. Wawu (N29.7001°, E102.9565°; ca. 1 560 m a.s.l.), Hongya County, Meishan, Sichuan; two adult males SYS a002164–2165 and one adult female SYS a002166, from Mt. Laojun (N28.6951°, E104.0527°; ca. 1 500 m a.s.l.), Pingshan County, Yibin, Sichuan; six adult females SYS a004949–4954, from Chishui Nature Reserve.

Diagnosis: Based on examined specimens: (1) adult males, SVL 33.8–41.2 mm ($n=15$); adult females, SVL 43.8–54.1 mm ($n=8$); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin rough with numerous granules and dense tubercles; weak discontinuous X-shaped or “> <”-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; several large warts on flanks; dorsal limbs with discontinuous transverse ridges and tubercles; ventral skin smooth; (6) outer margin of upper eyelid with small horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles present, distinct or indistinct; relative finger lengths II<I<IV<III; subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and tip of snout when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle ovoid, outer

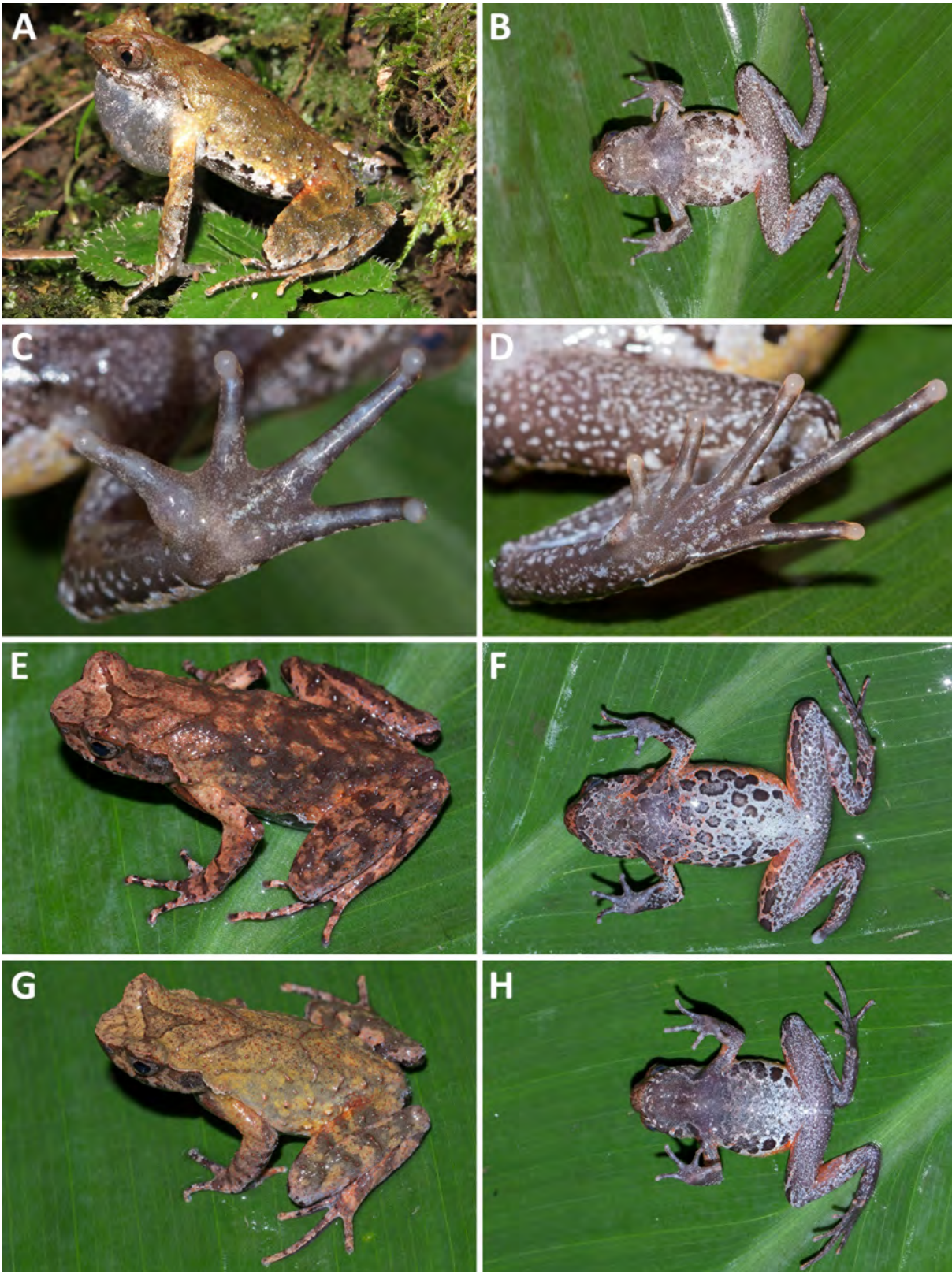


Figure 15 *Boulenophrys minor* in life

A: Dorsolateral view of male SYS a003213; B: Ventral view of SYS a003213; C: Hand of SYS a003213; D: Foot of SYS a003213; E: Dorsolateral view of female SYS a003209; F: Ventral view of SYS a003209; G: Dorsolateral view of male SYS a003212; H: Ventral view of SYS a003212. Photos by Y.Y. Wang.

one absent; (10) dorsal surface yellowish brown, reddish brown, or dark brown; dark brown triangular marking between eyes; dark brown X-shaped, "> <"-shaped, or netlike marking on center of dorsum; dorsal limbs with dark transverse bands;

throat and chest purplish; belly grayish white, two discontinuous parallel dark brown bands ventrolaterally; (11) nuptial pads with tiny and dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular

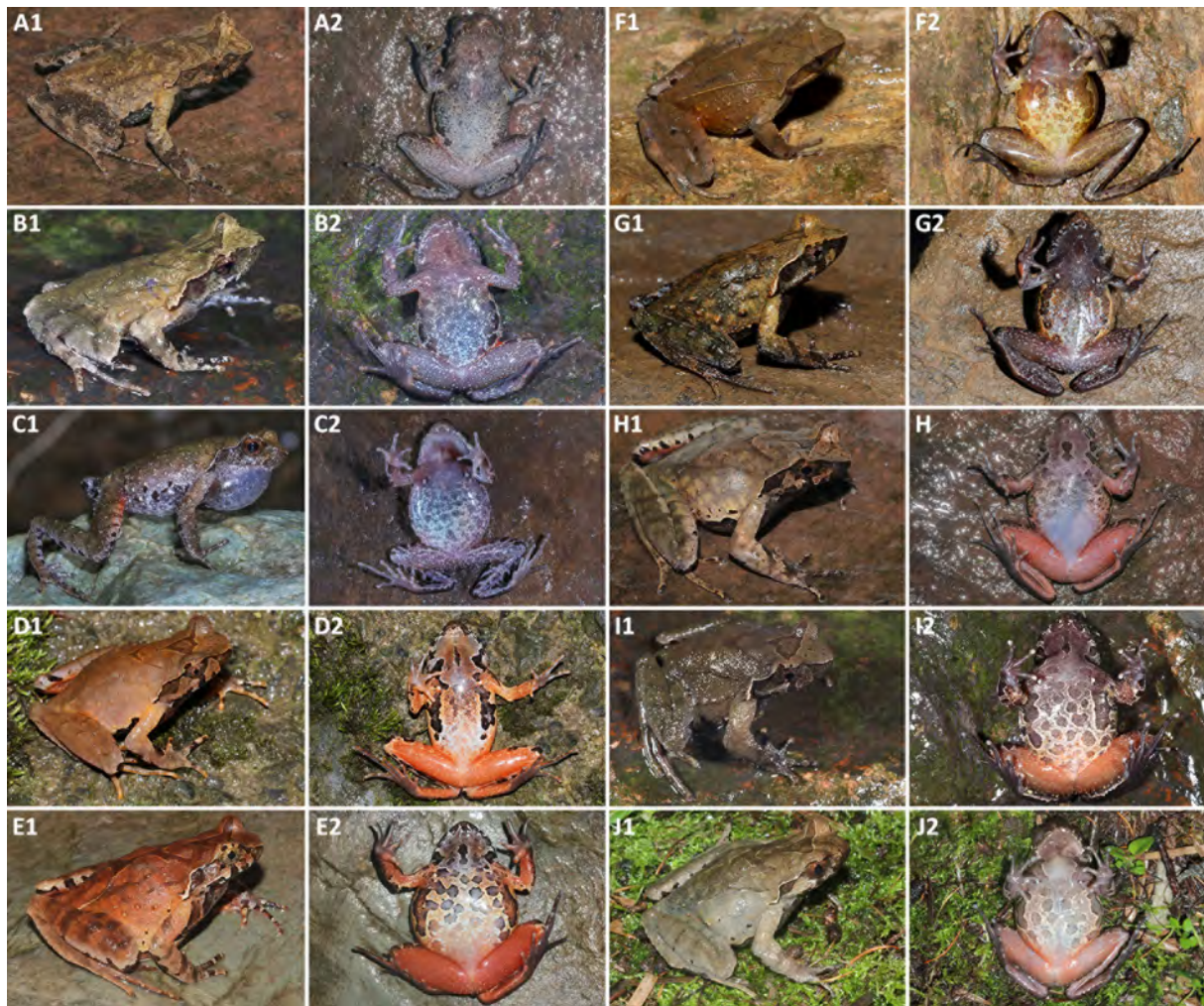


Figure 16 Species of *Boulenophrys* in life (*B. minor* group and *B. omeimontis* group)

A: *B. chishuiensis* male SYS a005308; B: *B. jiangi* male SYS a007187; C: *B. binchuanensis* male SYS a007848; D: *B. binlingensis* male SYS a005313; E: *B. fanjingmontis* comb. nov. female SYS a004349; F: *B. jingdongensis* male SYS a003903; G: *B. lushuiensis* male SYS a003755; H: *B. omeimontis* male SYS a005301; I: *B. qianbeiensis* male SYS a007184; J: *B. sangzhiensis* male SYS a004307; 1: Dorsolateral view; 2: Ventral view. Photos by Z.T. Lyu and J. Wang.

vocal sac present in males (Figure 16A).

Distribution: Currently known from multiple localities in hilly areas on the southern edge of the Sichuan Basin, including southeastern Sichuan, southwestern Chongqing, northwestern Guizhou, and northeastern Yunnan, at elevations of 270–1 600 m a.s.l. (this study, refer to Remarks below) (Supplementary Figure S6).

Remarks: The first study of this species was reported in Liu (1950), in which the population from Emeishan was designated as *B. minor*, and subsequently long used as a reference for *B. minor* (Fei et al., 2009; Fei & Ye, 2016; Liu et al., 2020; Xu et al., 2020). However, recent studies have indicated that the Emeishan population should represent a cryptic species different from the topotypic population of *B. minor* from Dujiangyan (Chen et al., 2017; Liu et al., 2018). Liu et al. (2018) also indicated that this cryptic species (labeled as *M. sp41*) included multiple populations from the southern edge of the Sichuan Basin (namely Mt. Laojun, Mt. Wawu, and Mt. Emei in Sichuan, and Chishui City in Guizhou). Subsequently, Xu et al. (2020) described the Chishui population as a new species, named *B. chishuiensis*. They also conducted phylogenetic analysis with molecular data of *B. minor* from Dujiangyan released by Chen et al. (2017) and Liu et al.

(2018), but without molecular data from Emeishan. Instead, they performed morphological comparisons of the Chishui and Emeishan populations, which were revealed as conspecific by Liu et al. (2018). This makes the diagnosis of *B. chishuiensis* problematic. In this work, we revise the diagnoses of *B. chishuiensis* based on examined specimens from multiple localities and revise the historic records of *B. minor* from Emeishan, Gulin, and Hejiang in Sichuan and Weixin in Yunnan (Fei & Ye, 2016) to *B. chishuiensis* due to biogeographical integrity.

***Boulenophrys jiangi* (Liu, Li, Wei, Xu, Cheng, Wang, and Wu, 2020)**

Jiang's horned toad / jiāng shì jiǎo chán (江氏角蟾)

Chresonymy: *Megophrys minor* — Wu et al., 1987; Fei et al., 2009, 2012

Megophrys minor minor — Ye & Fei, 1995

Boulenophrys minor — Fei & Ye, 2016; Fei, 2020

Megophrys sp11 — Chen et al., 2017

Megophrys jiangi — Liu et al., 2020

Panophrys jiangi — Lyu et al., 2021

Boulenophrys jiangi — Qi et al., 2021

Holotype: CIB KKS20180722006, adult male, from Kuankuoshui Nature Reserve (N28°13 '14 ", E107°09 '47 ";

1 521 m a.s.l.), Suiyang County, Zunyi, Guizhou, China.

Paratypes: Three adult males CIB KKS20180723001–002, 007, and one adult female CIB KKS20180723003, from same locality as holotype; five adult males CIB FJS20150719006–007, 009, FJS20150720003–004, and one adult female CIB FJS20150718005, from Mt. Fanjing, Jiangkou County, Tongren, Guizhou.

Specimens examined: Five adult males SYS a007177–7178, 7187–7188, 7191, from Taiyangshan, Kuankuoshui Nature Reserve (N28.2415°, E107.1537°; ca. 1 600 m a.s.l.); three adult males SYS a008382–8383, 8385, from Mt. Jinfo (N29.0487°, E107.1908°; ca. 1 420 m a.s.l.), Nanchuan District, Chongqing, China.

Diagnosis: Based on original description (Liu et al., 2020) and examined specimens: (1) adult males, SVL 34.4–39.2 mm ($n=9$; Liu et al., 2020) (SVL 34.5–38.6 mm, $n=8$; this study); adult females, SVL 39.5–40.4 mm ($n=2$; Liu et al., 2020); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin rough with numerous granules; weak discontinuous X-shaped or “> <”-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; several large warts on flanks; dorsal limbs relatively smooth with discontinuous transverse ridges and tubercles; ventral skin smooth; (6) outer margin of upper eyelid with small horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) inner metacarpal tubercle ovoid and enlarged, outer one indistinct and slightly separated; relative finger lengths I<II<IV<III; subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward; (9) toes without webbing and lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface olive brown; hollow dark brown triangular marking between eyes; dark brown X-shaped or “> <”-shaped marking on center of dorsum; dorsal limbs with dark transverse bands; throat and chest purplish; belly grayish white with dark irregular patches, two discontinuous parallel dark brown bands ventrolaterally; (11) nuptial pads with tiny and dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 16B).

Distribution: Currently known from multiple localities in hilly areas along the border between northern Guizhou and southern Chongqing at elevations of 1 270–1 704 m a.s.l. (Liu et al., 2020; this study) (Supplementary Figure S7).

***Boulenophrys omeimontis* group**

***Boulenophrys anlongensis* (Li, Lu, Liu, and Wang, 2020)**

Anlong horned toad / ān lóng jiǎo chán (安龙角蟾)

Chresonymy: *Megophrys anlongensis* — Li et al., 2020b

Boulenophrys anlongensis — Qi et al., 2021

Holotype: CIB AL20190531018, adult male, from Anlong County (N24.9899277°, E105.5990611°; ca. 1 290 m a.s.l.), Qianxinan, Guizhou, China.

Paratypes: Three adult males CIB AL20190531017, 19, 21, and three adult females CIB AL20190811014–15, AL20190531022, from same locality as holotype.

Diagnosis: Based on original description (Li et al., 2020b): (1) adult males, SVL 40.0–45.5 mm ($n=4$); adult females, SVL 48.9–51.2 mm ($n=3$); (2) snout obtusely pointed, canthus rostralis well developed; tongue not notched posteriorly; (3)

tympanum distinct; (4) vomerine ridges present, vomerine teeth absent; (5) dorsal skin rough; weak discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; flanks with large warts; ventral skin smooth; (6) outer margin of upper eyelid with small horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles prominent and ovoid, inner one enlarged; relative finger lengths I<II<IV<III; distinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface brown; brown triangular marking between eyes, X-shaped marking on center of dorsum; dorsal limbs with dark transverse bands; ventral surface brown with white patches on belly, two parallel dark brown bands ventrolaterally; (11) brownish nuptial pads bearing black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known only from its type locality in Anlong County at elevations of 1 400–1 600 m a.s.l. (Li et al., 2020b) (Supplementary Figure S5).

Remarks: In the original description of this species, the number of male paratypes was mentioned as “4 adult males” in the designation of type series, and the measurements in Table 1 presented data for five adult males (Li et al., 2020b). Male specimen CIB AL20190531020 appeared in Table 1 but was not listed in the designation. Thus, the number of paratypes should be corrected as three males and three females.

***Boulenophrys binchuanensis* (Ye and Fei, 1995)**

Binchuan horned toad / bīn chuān jiǎo chán (宾川角蟾)

Chresonymy: *Megophrys minor* — Liu & Hu, 1961

Megophrys minor binchuanensis — Ye & Fei, 1995

Megophrys (Xenophrys) binchuanensis — Dubois & Ohler, 1998

Xenophrys binchuanensis — Delorme et al., 2006; Chen et al., 2017

Megophrys binchuanensis — Fei et al., 2009, 2012

Boulenophrys binchuanensis — Fei & Ye, 2016; Fei, 2020; Qi et al., 2021

Megophrys (Panophrys) binchuanensis — Mahony et al., 2017

Panophrys binchuanensis — Lyu et al., 2021

Holotype: CIB 98008 (formerly CIB 580768), adult male, from Mt. Jizu (N26°00', E100°35'; 1 920 m a.s.l.), Binchuan County, Dali, Yunnan, China.

Allotype: CIB 98009 (formerly CIB 580733), adult female, from same locality as holotype (2 027 m a.s.l.).

Paratypes: Three males, two females, and tadpoles (voucher numbers not provided), from same locality as holotype (1 920–2 027 m a.s.l.); 10 males and tadpoles (voucher numbers not provided), from Mt. Yulong (=Jade Dragon Snow Mountain), Yulong County, Lijiang, Yunnan.

Specimens examined: Two adult males SYS a007847–7848 and three adult females SYS a007849–7851, from Yumen Town (N26.8807°, E101.5654°; ca. 1 730 m a.s.l.), Yanbian County, Panzhihua, Sichuan.

Diagnosis: Based on examined specimens: (1) adult males, SVL 34.4–36.3 mm ($n=2$); adult females, SVL 39.4–46.2 mm ($n=3$); (2) canthus rostralis well developed; tongue not notched or weakly notched posteriorly; (3) tympanum distinct;

(4) vomerine ridges and vomerine teeth absent; (5) dorsal skin relatively rough with dense tubercles; weak discontinuous X-shaped or "> <"-shaped ridge on center of dorsum, dorsolateral ridges present; sparse large tubercles on flanks; dorsal limbs with discontinuous transverse ridges and tubercles; ventral skin smooth; (6) outer margin of upper eyelid with small horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths $I \leq II < IV < III$; indistinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels just meeting when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface brown; dark-brown triangular marking between eyes; dorsal limbs with dark brown transverse bands; throat and chest gray, belly white with gray spot; (11) brown nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 16C).

Distribution: Occurs widely in hilly areas along the border between northern Yunnan and southernmost Sichuan at elevations of 1 700–2 800 m a.s.l. (this study) (Supplementary Figure S5).

Remarks: This species was initially proposed as the subspecies *M. minor binchuanensis*, but subsequently recognized as a full species (Dubois & Ohler, 1998; Ye & Fei, 1995). After recognition, *B. binchuanensis* was considered only from two localities, Mt. Jizu and Mt. Yulong in Yunnan, according to the type series, and other populations from northern Yunnan and southern Sichuan were retained as *B. minor* (Fei & Ye, 2016). In this study, the distribution of *B. minor* is restricted in Duijiangyan based upon molecular data and voucher specimens (refer to Remarks on *B. minor*). Furthermore, we determined that the populations previously recorded as *B. minor* from Yanbian, close to the border between Yunnan and Sichuan, should be *B. binchuanensis*. Thus, we suggest that the historic records of *B. minor* from Wuding and Qiaojia in Yunnan and Huili, Jiulong, and Muli in Sichuan (Fei & Ye, 2016) be revised to *B. binchuanensis* because of biogeographical integrity.

***Boulenophrys binlingensis* (Jiang, Fei, and Ye, 2009)**

Bingling horned toad / bǐng líng jiǎo chán (炳灵角蟾)

Chresonymy: *Megophrys binlingensis* — Fei et al., 2009, 2012

Xenophrys (Xenophrys) binlingensis — Fei & Ye, 2016; Fei, 2020

Xenophrys binlingensis — Chen et al., 2017

Megophrys (Panophrys) binlingensis — Mahony et al., 2017

Panophrys binlingensis — Lyu et al., 2021

Boulenophrys binlingensis — Qi et al., 2021

Holotype: CIB 950263, adult male, from Bingling (1 480 m a.s.l.), Wawushan Town, Hongya County, Meishan, Sichuan, China.

Paratypes: Two adult males CIB 950261–62 and 13 tadpoles, from same locality as holotype.

Specimens examined: One adult male SYS a005313 and one adult female SYS a005314, from Gufuping, Mt. Wawu (N29.7001°, E102.9565°; ca. 1 560 m a.s.l.), Wawushan Town.

Diagnosis: Based on original description (Fei et al., 2009)

and examined specimens: (1) adult males, SVL 45.1–51.0 ($n=3$; Fei et al., 2009) (SVL 44.8 mm, $n=1$; this study); adult female, SVL 59.2 mm ($n=1$; this study); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges weak, vomerine teeth absent; (5) dorsal skin relatively smooth with scattered granules; weak discontinuous V-shaped or X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; several warts on flanks; dorsal limbs relatively smooth with discontinuous transverse ridges; ventral skin smooth; (6) outer margin of upper eyelid with tiny horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) inner metacarpal tubercle ovoid, outer one indistinct; relative finger lengths $II=IV < I < III$; distinct subarticular tubercle at base of finger I, absent on other fingers; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching region between center of eye and nostril when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface grayish brown; dark brown hollow triangular marking between eyes; dark brown V-shaped or X-shaped marking on center of dorsum; dorsal limbs with distinct or indistinct dark brown transverse bands; ventral surface grayish white or reddish brown with dark spots on chest; dark brown longitudinal stripe on center of throat; two parallel dark brown bands ventrolaterally; (11) tiny and dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 16D).

Distribution: Known only from the vicinity of its type locality in Hongya County at elevations of 1 480–1 560 m a.s.l. (Fei et al., 2009; this study) (Supplementary Figure S5).

Remarks: In the original description of this species, the type locality was given as “Binling of Hongya” in the designation of type series but as “Bingling, Hongya” in Table 122, which is inconsistent (Fei et al., 2009). The correct transliteration from Chinese Pinyin into English for the type locality should be “Bingling”, and the misspelling of “Binling” may be a typographical error. The etymology of this species was mentioned as “according to the type locality” and provided as “*binlingensis*” (Fei et al., 2009), which should be preserved unaltered following Articles 32.2 and 32.5 of the Code, despite its incorrect transliteration. In contrast, the English common name for this species is revised as “Bingling horned toad” in this work according to the correct transliteration.

***Boulenophrys daweimontis* (Rao and Yang, 1997)**

Dawei horned toad / dà wéi jiǎo chán (大围角蟾)

Chresonymy: *Megophrys daweimontis* — Rao & Yang, 1997; Fei et al., 2009, 2012

Panophrys daweimontis — Rao & Yang, 1997; Lyu et al., 2021

Megophrys (Xenophrys) daweimontis — Dubois & Ohler, 1998
Xenophrys daweimontis — Delorme et al., 2006; Chen et al., 2017

Xenophrys (Xenophrys) daweimontis — Fei & Ye, 2016; Fei, 2020

Megophrys (Panophrys) daweimontis — Mahony et al., 2017

Boulenophrys daweimontis — Qi et al., 2021

Holotype: KIZ 93088, adult male, from Mt. Dawei (1 900 m a.s.l.), Pingbian County, Honghe, Yunnan, China.

Paratypes: Seventeen adult males KIZ 93069–85 and three adult females KIZ 93086–87, 89, from same locality as

holotype.

Diagnosis: Based on original description (Rao & Yang, 1997): (1) adult males, SVL 34–37 mm ($n=18$); adult females, SVL 40–46 mm ($n=3$); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin smooth; weak discontinuous V-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; small warts on flanks; ventral skin smooth; (6) outer margin of upper eyelid with small horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching tip of snout when leg stretched forward; (9) toes without webbing; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface olive brown; triangular marking between eyes, V-shaped or X-shaped marking on center of dorsum; dorsal limbs with dark transverse bands; (11) subgular vocal sac present in males.

Distribution: Recognized from Pingbian and Xichou counties of Yunnan in China and neighboring Lao Cai in northern Vietnam at elevations of ca. 1 900 m a.s.l., situated in hilly areas along the border between China and Vietnam (Chen et al., 2017; Fei & Ye, 2016) (Supplementary Figure S6).

Remarks: In the original description of this species, the nomenclature was given as *Megophrys daweimontis*, however, in the same work a new genus *Panophrys* was erected for several congeners (including *M. daweimontis*) previously placed in the genus *Megophrys*, which simultaneously created the combination *Panophrys daweimontis* (Rao & Yang, 1997).

***Boulenophrys fanjingmontis* comb. nov. (Zhang, Liang, Ran, and Shen, 2012)**

Mt. Fanjing horned toad / fàn jǐng shān jiǎo chán (梵净山角蟾)

Chresonymy: *Megophrys spinata* — Fei et al., 2009, 2012

Megophrys binlingensis fanjingmontis — Zhang et al., 2012

Xenophrys (Xenophrys) spinata — Fei & Ye, 2016; Fei, 2020

Xenophrys spinata — Chen et al., 2017

Megophrys sp37 — Liu et al., 2018

Holotype: TRU trxy01, adult male, from Heiwanhe (900 m a.s.l.), Mt. Fanjing, Jiangkou County, Tongren, Guizhou, China.

Allotype: TRU trxy02, adult female, from same locality as holotype.

Paratypes: Three adult males TRU trxy03–05, from same locality as holotype.

Specimens examined: Four adult males SYS a004348, 4350, 4353, 4355, and four adult females SYS a004349, 4351–4352, 4354, from Heiwanhe, Mt. Fanjing (N27.8685°, E108.7474°; ca. 860 m a.s.l.).

Diagnosis: Based on examined specimens: (1) adult males, SVL 58.2–63.6 mm ($n=4$); adult females, SVL 62.8–72.2 mm ($n=4$); (2) snout rounded, canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges weak, vomerine teeth absent; (5) dorsal skin smooth with scattered granules; weak discontinuous X-shaped or “> <”-shaped ridge on center of dorsum, discontinuous dorsolateral ridges distinct or indistinct; several large warts on flanks; dorsal limbs relatively smooth with discontinuous transverse ridges and tubercles; ventral skin smooth with granules on rear of hindlimbs; (6) outer margin of upper eyelid

with tiny horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) inner metacarpal tubercle ovoid, outer one indistinct; relative finger lengths II<I<IV<III; indistinct subarticular tubercle at base of finger I, absent on other fingers; (8) hindlimbs slender, heels slightly overlapping when hindlimbs folded; tibiotarsal articulation reaching region between center of eye and nostril when leg stretched forward; (9) toes with 1/3 webbing and wide lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface reddish brown or yellowish brown; hollow dark brown triangular marking between eyes; dark brown X-shaped marking on center of dorsum; dorsal limbs with dark brown transverse bands; ventral surface grayish white with dark brown irregular patches on chest; dark brown longitudinal stripe on center of throat; two discontinuous parallel dark brown bands ventrolaterally; (11) sparse tiny black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 16E).

Distribution: Known from Mt. Fanjing in northeastern Guizhou and Youyang County in southeastern Chongqing at elevations of 800–950 m a.s.l. (this study) (Supplementary Figure S6). The historic record of *B. spinata* from Xiushan County in southeastern Chongqing (Fei & Ye, 2016) is suggested to be ascribed to this species due to biogeographical integrity but further vouchers with molecular data are warranted (refer to Remarks on *B. spinata*).

Remarks: For a long time, the large-sized Asian horned toad from the vicinity of Mt. Fanjing was recorded as *M. spinata* (currently *B. spinata*) (e.g., Fei et al., 2009, 2012). Zhang et al. (2012) described the new subspecies *M. binlingensis fanjingmontis* (currently *B. fanjingmontis* **comb. nov.**) from this region, identifying it as a large-sized and morphologically close species to *M. binlingensis* (currently *B. binlingensis*), *M. spinata*, and *M. omeimontis* (currently *B. omeimontis*), but without discussion of the historic record of *B. spinata* from the same region. This subspecies was subsequently somewhat neglected. Fei & Ye (2016) and Fei (2020) both excluded the subspecies from data of *B. binlingensis* and retained the record of *B. spinata* in Mt. Fanjing (Jiangkou and Yinjiang) without mentioning the nomenclature of *M. b. fanjingmontis*. In contrast, Lv et al. (2017) and Wei et al. (2017) listed both *M. spinata* and *M. b. fanjingmontis* in their checklists for Mt. Fanjing, stating that record of *M. spinata* was based on voucher specimens while record of *M. b. fanjingmontis* was cited from the literature, unaware that these two records referred to the same large-sized Asian horned toad in the region.

Based on molecular data for species delimitation, Liu et al. (2018) suggested that the large-sized species of Asian horned toad from Mt. Fanjing may be a cryptic species (labeled as *M. sp37*), distinct from *B. spinata* and *B. binlingensis*. In this study, detailed morphological examination supported the molecular data. Hence, *Megophrys binlingensis fanjingmontis* is elevated to a full species, *Boulenophrys fanjingmontis* **comb. nov.**, in this work to accommodate the large-sized species of Asian horned toad from northeastern Guizhou and southeastern Chongqing (refer to Remarks on *B. spinata*).

***Boulenophrys jingdongensis* (Fei and Ye, 1983)**

Jingdong horned toad / jǐng dōng jiǎo chán (景东角蟾)

Chresonymy: *Megophrys omeimontis* — Liu & Hu, 1961

Megophrys omeimontis jingdongensis — Fei et al., 1983

Megophrys jingdongensis — Fei et al., 1990

Megophrys (Xenophrys) jingdongensis — Dubois & Ohler, 1998

Xenophrys jingdongensis — Delorme et al., 2006; Chen et al., 2017

Xenophrys (Xenophrys) jingdongensis — Fei & Ye, 2016; Fei, 2020

Megophrys (Panophrys) jingdongensis — Mahony et al., 2017

Panophrys jingdongensis — Lyu et al., 2021

Boulenophrys jingdongensis — Qi et al., 2021

Holotype: CIB 24345 (formerly CIB 583007), adult male, from Jingdong County (2 060 m a.s.l.), Pu'er, Yunnan, China.

Allotype: CIB 24346 (formerly CIB 581672), adult female, from same locality as holotype.

Paratypes: Two adult males CIB 581673–74, from same locality as holotype.

Specimens examined: One adult male SYS a003929 and one adult female SYS a003928, from Mt. Wuliang (N24.3664°, E100.7610°; ca. 2 400 m a.s.l.), Jingdong County; eight adult males SYS a002988–2992, 3005–3007, from Mt. Ailao (N23.9293°, E101.4981°; ca. 1 980 m a.s.l.), Zhenyuan County, Pu'er; two adult males SYS a003903–3904 from Shimexia (N23.9682°, E101.5196°; ca. 2 200 m a.s.l.), Xinping County, Yuxi, Yunnan; two adult males SYS a007335–7336 from Nanxi Village (N23.5874°, E101.7470°; ca. 2 060 m a.s.l.), Yuanjiang County, Yuxi; one adult male SYS a008340 and one adult female SYS a002739, from Mt. Huanglian (N22.8079°, E102.2429°; ca. 800 m a.s.l.), Lyuchun County, Honghe, Yunnan; one adult female SYS a008337, from Mt. Dawei (N22.9201°, E103.6991°; ca. 1 980 m a.s.l.), Pingbian County, Honghe; one adult male SYS a007833, from Daqing (N23.6578°, E99.9829°; ca. 2 000 m a.s.l.), Shuangjiang County, Lincang, Yunnan; nine adult males SYS a005160–5165, 5968–5970, from Mt. Cenwanglaoshan (N24.4863°, E106.4022°; ca. 1 700 m a.s.l.), Tianlin County, Baise, Guangxi, China.

Diagnosis: Based on examined specimens: (1) adult males, SVL 48.3–62.5 mm ($n=24$); adult females, SVL 58.6–68.2 mm ($n=3$); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin relatively smooth with granules; discontinuous V-shaped or “> <”-shaped ridge on center of dorsum, dorsolateral ridges distinct and continuous; ventral skin smooth; (6) weak medial bumped appendage at outer margin of upper eyelid, without horn-like tubercles; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) outer metacarpal tubercle indistinct, inner one observably enlarged; relative finger lengths II<I=IV<III; subarticular tubercle at base of finger I, indistinct on other fingers; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes with half webbing and wide lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface olive brown, yellowish brown or reddish brown; solid or hollow dark triangular marking between eyes; irregular markings on center of dorsum; dorsal limbs with indistinct transverse bands; ventral surface yellowish white or grayish white, with dark irregular patches on chest and belly; dark longitudinal stripe on center of throat, two parallel black bands ventrolaterally; (11) dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figures 4E and 16F).

Distribution: Occurs widely in southern Yunnan and northwestern Guangxi in China and neighboring northern Vietnam at elevations of 1 150–2 400 m a.s.l. (Fei & Ye, 2016; this study) (Supplementary Figure S7).

***Boulenophrys lushuiensis* (Shi, Li, Zhu, Jiang, Jiang, and Wang, 2021)**

Lushui horned toad / lú shuǐ jiǎo chán (泸水角蟾)

Chresonymy: *Megophrys minor* — Yang & Rao, 2008

Megophrys sp2 — Chen et al., 2017

Megophrys sp39 — Liu et al., 2018

Megophrys sp40 — Liu et al., 2018

Megophrys lushuiensis — Shi et al., 2021

Boulenophrys lushuiensis — Qi et al., 2021

Holotype: CIB YN201909290, adult male, from Gutan River (N25.977066°, E98.795983°, ca. 2 358 m a.s.l.), Luzhang Town, Lushui City, Nujiang, Yunnan, China.

Paratypes: One adult male CIB YN201909283 from Bashan (N25.953588°, E98.734431°, 1 986 m a.s.l.), Luzhang Town; two juvenile males CIB YN201909288–89, from Langbazhai Village (N25.95118°, E98.768903°, 2 006 m a.s.l.), Luzhang Town.

Specimens examined: Four adult males SYS a003755, 3760–3761, 3767, from Linjiapu (N25.2976°, E98.7011°; ca. 2 100 m a.s.l.), Qushi Town, Tengchong City, Baoshan, Yunnan; three adult males SYS a003790, 3801, 3804, and 17 adult females, SYS a003782–3789, 3791, 3802–3803, 3805–3810, from Dahaoping (N24.9786°, E98.7339°; ca. 2 090 m a.s.l.), Mangbang Town, Tengchong City; six adult males SYS a003821–3822, 3824, 3826, 3837–3838, and three adult females SYS a003825, 3827, 3839, from Zizhi (N25.7655°, E98.6242°; ca. 2 210 m a.s.l.), Mingguang Town, Tengchong City.

Diagnosis: Based on examined specimens: (1) adult males, SVL 32.3–38.0 mm ($n=13$); adult females, SVL 37.8–47.4 mm ($n=20$); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges weak, vomerine teeth absent; (5) dorsal skin relatively smooth with scattered granules and tubercles; discontinuous X-shaped or V-shape ridge on center of dorsum, discontinuous dorsolateral ridges present; ventral skin smooth; (6) outer margin of upper eyelid with remarkably prominent horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles present, inner one observably enlarged; relative finger lengths II<I<IV<III; indistinct subarticular tubercle at bases of fingers I and II, absent on other fingers; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface pale brown, grayish brown, or dark brown; hollow dark triangular marking between eyes; dark netlike markings on dorsum; dorsal limbs with dark brown transverse bands; throat and chest purplish gray or dark brown, longitudinal dark brown stripe on center of throat; belly grayish white with dark patches, two discontinuous parallel dark brown bands ventrolaterally; (11) nuptial pads bearing tiny and dense nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 16G).

Distribution: Known from multiple localities in Lushui, Tengchong, Yingjiang, and Longchuan counties in western

Yunnan at elevations between 1 900–2 400 m a.s.l., all situated in hilly areas along the border between China and Myanmar (this study) (Supplementary Figure S8).

Remarks: Based on molecular data for species delimitation, Chen et al. (2017) suggested that the populations from Yingjiang and Longchuan (labeled as *M. sp2*) may be an undescribed species, while Liu et al. (2018) suggested that the populations from northern Tengchong (labeled as *M. sp39*) and southern Tengchong (labeled as *M. sp40*) may belong to two cryptic species. Shi et al. (2021) subsequently described the population from Lushui as a new species but did not include data from Chen et al. (2017) and Liu et al. (2018). Here, molecular analysis of all above-mentioned populations revealed a monophyletic lineage comprise of *B. lushuiensis*, *M. sp2*, *M. sp39*, and *M. sp40* (Figure 3), despite small intraspecific divergence. Additionally, morphological examination of specimens from northern and southern Tengchong populations did not reveal any distinct characters to differentiate them from the type series of *B. lushuiensis* from Lushui (Shi et al., 2021). Thus, we consider the populations within this monophyletic lineage to be conspecific, and the molecular intraspecific divergence may be due to geographical isolation.

***Boulenophrys omeimontis* (Liu, 1950)**

Omei horned toad / é méi jiǎo chán (峨眉角蟾)

Chresonymy: *Megophrys omeimontis* — Liu, 1950; Liu & Hu, 1961; Fei et al., 2009, 2012

Megophrys (Megophrys) omeimontis — Dubois, 1980

Megophrys omeimontis omeimontis — Fei et al., 1983

Panophrys omeimontis — Rao & Yang, 1997; Lyu et al., 2021

Megophrys (Xenophrys) omeimontis — Dubois & Ohler, 1998

Xenophrys omeimontis — Delorme et al., 2006; Chen et al., 2017

Xenophrys (Xenophrys) omeimontis — Fei & Ye, 2016; Fei, 2020

Megophrys (Panophrys) omeimontis — Mahony et al., 2017

Boulenophrys omeimontis — Dubois et al., 2021; Qi et al., 2021

Holotype: FMNH 49406, adult male, from Mt. Omei (=Mt. Emei, Emeishan City, Leshan), Szechwan (=Sichuan), China.

Paratypes: Five males and two females (voucher numbers not provided), from Mt. Omei.

Specimens examined: Five adult males SYS a001800–1801, 1940–1941, 5301, from Mt. Emei (N29.5473°, E103.3759°; ca. 1 600 m a.s.l.); two adult females SYS a005330–5331, from Mt. Wawu (N29.7001°, E102.9565°; ca. 1 560 m a.s.l.), Hongya County, Meishan, Sichuan; two adult males SYS a002740–2741, from Mt. Laojun (N28.6951°, E104.0527°; ca. 1 500 m a.s.l.), Pingshan County, Yibin, Sichuan; five adult females SYS a004915–4919, from Zihuai Town (N28.6282°, E106.2982°; ca. 800 m a.s.l.), Hejiang County, Luzhou, Sichuan; one adult male SYS a004933, from Mt. Simian (N28.6096°, E106.3362°; ca. 920 m a.s.l.), Jiangjin District, Chongqing, China; two adult males SYS a004939–4940, from Chishui Nature Reserve (N28.4521°, E106.0003°; ca. 580 m a.s.l.), Chishui City, Zunyi, Guizhou, China.

Diagnosis: Based on examined specimens: (1) adult males, SVL 52.1–62.0 mm ($n=10$); adult females, SVL 65.7–71.2 mm ($n=7$); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin smooth with granules; discontinuous V-shaped or “> <”-shaped ridge on

center of dorsum, discontinuous dorsolateral ridges distinct; dorsal limbs rough with scattered granules; ventral skin smooth; (6) outer margin of upper eyelid with small horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths I<IV<II<III; subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching between posterior corner of eye and tip of snout when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface yellowish brown or reddish brown; solid or hollow dark triangular marking between eyes; irregular markings on center of dorsum; dorsal limbs with indistinct transverse bands; ventral surface reddish white or grayish white, with dark irregular patches on throat and chest; two parallel black bands ventrolaterally; (11) dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 16H).

Distribution: Currently recognized from multiple localities in the hilly areas on the southern edge of the Sichuan Basin, including southeastern Sichuan, southwestern Chongqing, northwestern Guizhou, and northeastern Yunnan, at elevations of 400–1 600 m a.s.l. (Fei & Ye, 2016; this study) (Supplementary Figure S8).

***Boulenophrys palpebralespinosa* (Bourret, 1937)**

Rough-skinned horned toad / cū pí jiǎo chán (粗皮角蟾)

Chresonymy: *Megophrys palpebralespinosa* — Bourret, 1937; Liu & Hu, 1961; Fei et al., 2009, 2012

Megophrys (Megophrys) palpebralespinosa — Dubois, 1980

Panophrys palpebralespinosa — Rao & Yang, 1997; Lyu et al., 2021

Megophrys (Xenophrys) palpebralespinosa — Dubois & Ohler, 1998

Xenophrys palpebralespinosa — Delorme et al., 2006; Chen et al., 2017

Megophrys latidactyla — Orlov et al., 2015

Xenophrys (Xenophrys) palpebralespinosa — Fei & Ye, 2016; Fei, 2020

Xenophrys latidactyla — Chen et al., 2017

Megophrys (Panophrys) palpebralespinosa — Mahony et al., 2017

Megophrys (Panophrys) latidactyla — Mahony et al., 2017

Boulenophrys palpebralespinosa — Qi et al., 2021

Syntypes: MNHN 1948.114–116, from Chapa (=Sa Pa District, Lao Cai) (1 500 m a.s.l.), Tokin (now northern Vietnam).

Diagnosis: Based on previous descriptions (Liu & Hu, 1961; Fei et al., 2009) on specimens from Bozhujing, Qiaotou Town, Hekou County, Honghe, Yunnan, China (detailed locality data provided in Liu et al., 1960): (1) adult males, SVL 36.2–38.0 mm ($n=2$); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin rough with large tubercles and distinct ridges; ventral skin smooth; (6) outer margin of upper eyelid with several horn-like large prominent tubercles; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct; subarticular tubercle at base of each finger; (8) hindlimbs slender, heels slightly overlapping when

hindlimbs folded; tibiotarsal articulation reaching eye when leg stretched forward; (9) toes with half webbing and wide lateral fringe; inner metatarsal tubercle flat, outer one absent; (10) in preservative, dorsal surface grayish brown with dark irregular markings; dorsal limbs with dark transverse bands; longitudinal stripe on center of throat; chest and belly with dark irregular patches; (11) dense brown nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known from Hekou and Lyuchun counties in southern Yunnan, and Jingxi City in southwestern Guangxi, China, and neighboring northern Vietnam and northeastern Laos, at elevations of 1 100–2 070 m a.s.l. (Fei & Ye, 2016; Nguyen et al., 2020a) (Supplementary Figure S8).

Remarks: This species is currently recorded from wide hilly areas encompassing northern Vietnam and northeastern Laos, extending to the border of southwestern China (Nguyen et al., 2020a; Wu et al., 2019). In China, this species is relatively rare and has only been confirmed from several localities in Yunnan and Guangxi close to the border with Vietnam (Fei & Ye, 2016). Li et al. (2011) provided a record from Mt. Tianjing in northern Guangdong, far from the main distribution of the species. According to the voucher figure presented by Li et al. (2011), we affirm that this is a misidentification of the congener *B. shimentaina* and remove the record of *B. palpebralespinosa* from Guangdong.

The description of specimens from Hekou mentioned “1 male and 1 female” and “male with a pair of vocal sacs” in Liu & Hu (1961), which was revised as “2 males” and “males with a subgular vocal sac” in Fei et al. (2009).

***Boulenophrys qianbeiensis* (Su, Shi, Wu, Li, Yao, Wang, and Li, 2020)**

Northern Guizhou horned toad / qián běi jiǎo chán (黔北角蟾)

Chresonymy: *Megophrys spinata* — Fei et al., 2009, 2012

Xenophrys (Xenophrys) spinata — Fei & Ye, 2016; Fei, 2020

Xenophrys spinata — Chen et al., 2017

Megophrys qianbeiensis — Su et al., 2020

Boulenophrys qianbeiensis — Qi et al., 2021

Holotype: CIB TZ20190608017, adult male, from Huanglian Nature Reserve (N28.498056°, E107.046944°; ca. 1 500 m a.s.l.), Tongzi County, Zunyi, Guizhou, China.

Paratypes: Four adult males CIB TZ20160715003, TZ20190608015–16, 18, from same locality as holotype; one adult male CIB KKS20180722001, from Kuankuoshui Nature Reserve (N28.21835°, E107.166388°; ca. 1 520 m a.s.l.), Suiyang County, Zunyi.

Specimens examined: Three adult males SYS a007176, 7184, 7186, and one adult female SYS a007185, from Taiyangshan, Kuankuoshui Nature Reserve (N28.2415°, E107.1537°; ca. 1 600 m a.s.l.).

Diagnosis: Based on examined specimens: (1) adult males, SVL 50.5–53.7 mm ($n=3$); adult female, SVL 65.2 mm ($n=1$); (2) snout rounded, canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin rough with dense spiny granules; weak discontinuous X-shaped, V-shaped, or “\”-shaped ridge on center of dorsum, discontinuous dorsolateral ridges distinct; scattered warts on flanks; dorsal limbs rough with dense spiny granules and indistinct discontinuous transverse ridges; ventral skin relatively smooth with dense granules; (6) outer margin of upper eyelid with small horn-like prominent tubercle;

supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths II<I<IV<III; distinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward; (9) toes with 1/3 webbing and wide lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface olive brown or reddish brown; hollow dark triangular marking between eyes; dark V-shaped, Y-shaped, or X-shaped marking on center of dorsum; dorsal limbs with indistinct transverse bands; ventral surface grayish white or grayish red with dark irregular patches on chest; dark longitudinal stripe on center of throat; two discontinuous parallel dark brown bands ventrolaterally; (11) large and sparse black conical nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 16I).

Distribution: Known from Tongzi and Suiyang counties in northern Guizhou at elevations of 1 500–1 600 m a.s.l., both situated in the Dalou Mountains along the border of Guizhou, Sichuan, and Chongqing (Su et al., 2020; this study) (Supplementary Figure S9). The historic records of *B. spinata* from northwestern Guizhou, southeastern Sichuan, and western Chongqing (Fei & Ye, 2016) are suggested to be ascribed to this species due to biogeographical integrity, but further vouchers with molecular data are warranted (refer to Remarks on *B. spinata*).

Remarks: In the original description of this species (Su et al., 2020), the collection locality of paratypes CIB TZ20160715003, TZ20190608015–16, 18 was provided in error as “from Kuankuoshui National Nature Reserve”, which was a typographical error.

***Boulenophrys rubrimera* (Tapley, Cutajar, Mahony, Chung, Dau, Nguyen, Luong, and Rowley, 2017)**

Red-thighed horned toad / hóng gǔ jiǎo chán (红股角蟾)

Chresonymy: *Megophrys* sp3 — Chen et al., 2017

Megophrys (Panophrys) rubrimera — Tapley et al., 2017

Panophrys rubrimera — Lyu et al., 2021

Boulenophrys rubrimera — Qi et al., 2021

Holotype: VNMN 2017.002, adult male, from Sa Pa District (N22.38205°, E103.78745°; 1 708 m a.s.l.), Lao Cai, Vietnam.

Paratypes: Six adult males VNMN 2017.003, AMS R177675–79, from vicinity of Sa Pa District (N22.38208°–22.39829°, E103.78545°–103.78798°; 1 400–1 722 m a.s.l.).

Diagnosis: Based on original description (Tapley et al., 2017): (1) adult males, SVL 26.7–30.5 mm ($n=7$); (2) snout rounded, canthus rostralis well developed; tongue not clearly or weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges weak, vomerine teeth present; (5) dorsal skin weakly granular; tubercles bearing dark spines on dorsum, flanks, and dorsal limbs; weak discontinuous V-shaped or X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; ventral skin smooth; (6) outer margin of upper eyelid with tiny horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) metacarpal tubercles absent; relative finger lengths I<II<IV<III; indistinct subarticular tubercle at base of each finger; (8) hindlimbs relatively short and stocky; (9) toes without webbing but with narrow lateral fringes; inner metatarsal tubercle prominent, outer one absent; (10) dorsal

surface yellowish brown; dark brown triangular marking with light edge between eyes; dorsal limbs with dark transverse bands; posterior flank and anterior thighs near groin red-orange; throat and chest grayish brown; belly light gray with dark gray blotches and white speckling; (11) nuptial pads bearing dense nuptial spines on dorsal base of finger II in breeding adult males; subgular vocal sac present in males.

Distribution: Known from Maandi Town, Jinping County, Yunnan, China, and neighboring Lao Cai and Lau Chau, northern Vietnam, at elevations of 1 400–1 722 m a.s.l., situated in hilly areas along the border between China and Vietnam (Luong et al., 2021; Tapley et al., 2017) (Supplementary Figure S9).

***Boulenophrys sangzhiensis* (Jiang, Ye, and Fei, 2008)**

Sangzhi horned toad / sāng zhí jiǎo chán (桑植角蟾)

Chresonymy: *Megophrys spinata* — Fei et al., 1990

Megophrys caudoprocta — Jiang et al., 2003

Megophrys sangzhiensis — Jiang et al., 2008; Fei et al., 2009, 2012

Xenophrys (Xenophrys) sangzhiensis — Fei & Ye, 2016; Fei, 2020

Xenophrys sangzhiensis — Chen et al., 2017

Megophrys (Panophrys) sangzhiensis — Mahony et al., 2017

Panophrys sangzhiensis — Lyu et al., 2021

Boulenophrys sangzhiensis — Qi et al., 2021

Holotype: CIB 200078, adult male, from Mt. Tianping (N29°49', E110°09'; 1 300 m a.s.l.), Sangzhi County, Zhangjiajie, Hunan, China.

Specimens examined: Two adult males SYS a004306–4307 and four adult females SYS a004313–4316, from Mt. Tianping (N29.7591°, E110.0624°; ca. 1 380 m a.s.l.).

Diagnosis: Based on examined specimens: (1) adult males, SVL 55.7–62.2 mm ($n=2$); adult females, SVL 62.2–76.3 mm ($n=4$); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges weak, vomerine teeth absent; (5) dorsal skin relatively smooth with scattered granules; weak discontinuous V-shaped, “\”-shaped, or Y-shaped ridge on center of dorsum, discontinuous dorsolateral ridges indistinct; several warts on flanks; dorsal limbs smooth with discontinuous transverse ridges; ventral skin smooth; (6) outer margin of upper eyelid with tiny horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) inner metacarpal tubercle ovoid, outer one small; relative finger lengths I<II<IV<III; distinct subarticular tubercle at bases of fingers I and II, absent on other fingers; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching anterior corner of eye when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface brown; dark brown triangular marking with light edge between eyes; dark brown V-shaped or “> <”-shaped marking with light edge on center of dorsum; dorsal limbs with distinct or indistinct dark brown transverse bands; posterior flank and anterior thighs near groin red; ventral surface grayish white with gray patches on chest; two parallel dark brown bands ventrolaterally; (11) sparse tiny black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 16J).

Distribution: Known from Mt. Tianping and Mt. Huping in northwestern Hunan at elevations of 1 300–1 400 m a.s.l. (Fei

& Ye, 2016; this study) (Supplementary Figure S9).

***Boulenophrys spinata* (Liu and Hu, 1973)**

Spiny-fingered horned toad / jí zhǐ jiǎo chán (棘指角蟾)

Chresonymy: *Megophrys spinata* — Hu et al., 1973

Megophrys (Megophrys) spinata — Dubois, 1980

Megophrys (Xenophrys) spinata — Dubois & Ohler, 1998

Xenophrys spinata — Delorme et al., 2006; Chen et al., 2017

Xenophrys (Xenophrys) spinata — Fei & Ye, 2016; Fei, 2020

Megophrys (Panophrys) spinata — Mahony et al., 2017

Panophrys spinata — Lyu et al., 2021

Boulenophrys spinata — Dubois et al., 2021; Qi et al., 2021

Holotype: CIB 24339 (formerly CIB 63II0615), adult male, from Getou Village (N25.614417°, E108.410076°; 1 100 m a.s.l.), Fangxiang Town, Leishan County, Qiandongnan, Kweichow (=Guizhou), China.

Allotype: CIB 24340 (formerly CIB 63II0617), adult female, from same locality as holotype.

Paratypes: Seventeen adult males, one adult female, and tadpoles (voucher numbers not provided), from same locality as holotype.

Specimens examined: Two adult males SYS a002226–2227, from Mt. Leigong (N26.3851°, E108.1866°; ca. 1 620 m a.s.l.), Leishan County.

Diagnosis: Based on original description (Hu et al., 1973) and examined specimens: (1) adult males, SVL 47.2–54.4 ($n=18$; Hu et al., 1973) (SVL 49.6–51.6 mm, $n=2$, this study); adult females, SVL 54.0–55.0 ($n=2$; Hu et al., 1973); (2) snout rounded, canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges weak, vomerine teeth absent; (5) dorsal skin relatively rough with scattered spiny granules; weak discontinuous V-shaped or “\”-shaped ridge on center of dorsum, discontinuous dorsolateral ridges indistinct or absent; scattered warts on flanks; dorsal limbs rough with scattered spiny granules; dense black spines on loreal and temporal regions; ventral skin smooth; (6) outer margin of upper eyelid with tiny horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths I<II<IV<III; distinct subarticular tubercle at bases of fingers I and II, absent on other fingers; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching anterior corner of eye when leg stretched forward; (9) toes with 1/3 webbing and wide lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface olive brown; hollow dark triangular marking between eyes; dark V-shaped marking on center of dorsum; dorsal limbs with indistinct transverse bands; ventral surface grayish white with dark irregular patches on chest; dark longitudinal stripe on center of throat; (11) large and sparse black conical nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Currently recognized from its type locality in Leishan County at elevations of 800–1 800 m a.s.l. (Hu et al., 1973; this study, refer to Remarks below) (Supplementary Figure S9).

Remarks: This species has been reported from multiple localities in southwestern China (Fei & Ye, 2016; Fei et al., 2009, 2012). Nonetheless, recent molecular analysis has suggested that these different populations formed a paraphyletic relationship (Chen et al., 2017). Subsequently,

the populations from northern Guizhou were erected as new species *B. qianbeiensis*, and historic records of *B. spinata* from northwestern Guizhou, southeastern Sichuan, and western Chongqing are assigned to *B. qianbeiensis* in this work due to biogeographical integrity (refer to Remarks on *B. qianbeiensis*). Furthermore, *B. fanjingmontis* **comb. nov.** is currently suggested to be a full species to accommodate the populations/records from northeastern Guizhou and southeastern Chongqing (refer to Remarks on *B. fanjingmontis* **comb. nov.**). The population in Guangxi forms an independent lineage in phylogeny (Chen et al., 2017), and its taxonomic status remains unresolved due to the lack of voucher specimens. Hereby, we restrict the distribution of *B. spinata* in Leishan County based on voucher specimens and molecular data.

***Boulenophrys wuliangshanensis* (Ye and Fei, 1995)**

Wuliangshan horned toad / wú liàng shān jiǎo chán (无量山角蟾)

Chresonymy: *Megophrys minor* — Liu & Hu, 1961

Megophrys wuliangshanensis — Ye & Fei, 1995; Fei et al., 2009, 2012

Megophrys (Xenophrys) wuliangshanensis — Dubois & Ohler, 1998

Xenophrys wuliangshanensis — Delorme et al., 2006; Chen et al., 2017

Boulenophrys wuliangshanensis — Fei & Ye, 2016; Fei, 2020; Qi et al., 2021

Megophrys (Panophrys) wuliangshanensis — Mahony et al., 2017

Panophrys wuliangshanensis — Lyu et al., 2021

Holotype: CIB 98010 (formerly CIB 890126), adult male, from Xinmin Village (N24°45', E100°75' (*sic*, should be E100°45'); 1200 m a.s.l.), Mt. Wuliang, Jingdong County, Pu'er, Yunnan, China.

Allotype: CIB 98011 (formerly CIB 890128), adult female, from same locality as holotype.

Paratypes: Eighteen males, one female, three juveniles, and tadpoles (voucher numbers not provided), from Xinmin Village and Huangcaoling Village (2 000–2 400 m a.s.l.), Mt. Wuliang.

Specimens examined: Two adult males SYS a003924–3925, from Huangcaoling Village (N24.3664°, E100.7610°; ca. 2 400 m a.s.l.), Mt. Wuliang; two adult males SYS a001796, 1798, and five adult females SYS a001797, 1799, 2983–2985, from Mt. Ailao (N23.9293°, E101.4981°; ca. 1 980 m a.s.l.), Zhenyuan County, Pu'er.

Diagnosis: Based on examined specimens: (1) adult males, SVL 25.9–28.5 mm ($n=4$); adult females, SVL 32.1–38.0 mm ($n=5$); (2) canthus rostralis well developed; tongue not notched or weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin rough with dense granules; weak discontinuous X-shaped ridge on center of dorsum, dorsolateral ridges present; sparse large tubercles on flanks; dorsal limbs with discontinuous transverse ridges and tubercles; ventral skin smooth (6) outer margin of upper eyelid with small horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths I=II<IV<III; faintly visible subarticular tubercle at base of each finger; (8) hindlimbs slender, heels slightly overlapping when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes without webbing and

lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface brown; hollow dark-brown triangular marking between eyes; indistinct or distinct X-shaped marking on center of dorsum; dorsal limbs with dark brown transverse bands; throat and chest gray, belly white with black spot; (11) brown nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Occurs in wide hilly areas of the Jingdong, Zhenyuan, Linxiang, and Jinhong counties in southwestern Yunnan at elevations of 2 000–2 400 m a.s.l. (Fei & Ye, 2016; this study) (Supplementary Figure S10).

***Boulenophrys boettgeri* group**

***Boulenophrys acuta* (Wang, Li, and Jin, 2014)**

Fengkai horned toad / fēng kāi jiǎo chán (封开角蟾)

Chresonymy: *Megophrys acuta* — Li et al., 2014

Xenophrys acuta — Chen et al., 2017

Megophrys (Panophrys) acuta — Mahony et al., 2017

Boulenophrys acuta — Fei, 2020; Qi et al., 2021

Panophrys acuta — Lyu et al., 2021

Holotype: SYS a002267, adult male, from Heishiding Nature Reserve (N23°28'27", E111°53'53"; 277.1 m a.s.l.), Fengkai County, Zhaoqing, Guangdong, China.

Paratypes: Nine adult males SYS a000165, 0169, 1957, 2159, 2266, 2268–2269, 2278, CIB 107662 (formerly SYS a002276), four adult females SYS a000168, 0187, 0517, 0521, and one juvenile SYS a002274, from same locality as holotype.

Specimens examined: Type materials (10 adult males, four adult females, and one juvenile).

Diagnosis: Based on examined specimens: (1) adult males, SVL 27.1–33.0 mm ($n=10$); adult females, SVL 28.1–33.6 mm ($n=4$); (2) snout remarkably pointed, canthus rostralis sharp, well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges weak, vomerine teeth absent; (5) dorsal skin smooth with scattered granules and several tubercles; discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; ventral skin smooth, with small granules on throat and chest; (6) outer margin of upper eyelid with horn-like, remarkably prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles well developed, inner one observably enlarged; relative finger lengths I<II≤IV<III; large subarticular tubercle at base of each finger; (8) hindlimbs moderate, slightly robust, heels not meeting when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface brown; incomplete dark triangular marking between eyes, rectangular dark marking on center of dorsum; ventral surface reddish brown; longitudinal dark brown stripe on center of throat; center of posterior belly with black and white patches, two parallel broad gray-brown bands ventrolaterally; (11) weak nuptial pads not bearing nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known only from Heishiding Nature Reserve and neighboring Qixing Nature Reserve in western Guangdong at elevations of 270–450 m a.s.l. (Li et al., 2014) (Supplementary Figure S5).

***Boulenophrys baishanzuensis* (Wu, Li, Liu, Wang, and**

Wu, 2020)

Baishanzu horned toad / bǎi shān zǔ jiǎo chán (百山祖角蟾)

Chresonymy: *Megophrys baishanzuensis* — Wu et al., 2020
Boulenophrys baishanzuensis — Qi et al., 2021

Holotype: CIB QY20200726001, adult male, from Baishanzu National Park (N27.76°, E119.18°; ca. 1 537 m a.s.l.), Qingyuan County, Lishui, Zhejiang, China.

Paratypes: Five adult males CIB QY20200719001–004, QY 20200726002, from same locality as holotype.

Diagnosis: Based on original description (Wu et al., 2020): (1) adult males, SVL 28.4–32.4 mm ($n=6$); (2) snout obtusely pointed, canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges present, vomerine teeth absent; (5) dorsal skin rough; discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; flanks with large warts; ventral skin with numerous granules; (6) outer margin of upper eyelid with small horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles prominent and ovoid, inner one enlarged; relative finger lengths I<II<IV<III; distinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes without webbing but with narrow lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface brown; brown triangular marking between eyes, X-shaped marking on center of dorsum; dorsal limbs with dark transverse bands; throat brown; belly white, gray, or brownish red, with brown spots, two parallel dark brown bands ventrolaterally; (11) nuptial pads on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known only from its type locality in Baishanzu National Park at elevations of 1 400–1 600 m a.s.l. (Wu et al., 2020) (Supplementary Figure S5).

***Boulenophrys baolongensis* (Ye, Fei, and Xie, 2007)**

Baolong horned toad / bào lóng jiǎo chán (抱龙角蟾)

Chresonymy: *Megophrys boettgeri* — Liu & Hu, 1961

Megophrys baolongensis — Ye et al., 2007; Fei et al., 2009, 2012

Boulenophrys baolongensis — Fei & Ye, 2016; Fei, 2020; Qi et al., 2021

Xenophrys baolongensis — Chen et al., 2017

Megophrys (Panophrys) baolongensis — Mahony et al., 2017

Panophrys baolongensis — Lyu et al., 2021

Holotype: CIB 572249, adult male, from Baolong Town (793 m a.s.l.), Wushan County, Chongqing, China.

Paratypes: Four adult males CIB 572243–44, 572250–51, and 13 tadpoles, from same locality as holotype.

Diagnosis: Based on previous descriptions (Ye et al., 2007; Fei & Ye, 2016): (1) adult males, SVL 41.8–45.0 mm ($n=5$); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin smooth with scattered spiny granules; discontinuous weak “> <”-shaped ridge on center of dorsum, discontinuous dorsolateral ridges absent; flanks with distinct tubercles; ventral skin smooth; (6) outer margin of upper eyelid without horn-like tubercles; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct; relative finger lengths I=II<IV<III; subarticular

tubercle at base of each finger, more distinct at fingers I and II; (8) hindlimbs slender, heels slightly overlapping or just meeting when hindlimbs folded; tibiotarsal articulation reaching posterior corner of eye when leg stretched forward; (9) toes without webbing and lateral fringes; inner metatarsal tubercle small and ovoid, outer one absent; (10) dorsal surface yellowish green; dark brown triangular marking between eyes; irregular dark brown marking on center of dorsum; dorsal limbs with transverse bands; anterior thighs near groin red; ventral surface brown; longitudinal dark brown stripe on center of throat; large irregular grayish brown patches on chest and belly; (11) brown nuptial pads bearing black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known only from its type locality in Wushan County (Fei & Ye, 2016) (Supplementary Figure S5).

***Boulenophrys boettgeri* (Boulenger, 1899)**

Pale-shouldered horned toad / dàn jiān jiǎo chán (淡肩角蟾)

Chresonymy: *Leptobrachium boettgeri* — Boulenger, 1899b

Megalophrys boettgeri — Boulenger, 1908

Megophrys boettgeri — Gee & Boring, 1929; Liu & Hu, 1961; Fei et al., 2009, 2012

Megophrys (Megophrys) boettgeri — Dubois, 1980

Panophrys boettgeri — Rao & Yang, 1997; Lyu et al., 2021

Megophrys (Xenophrys) boettgeri — Dubois & Ohler, 1998

Megophrys huangshanensis — Fei et al., 2005, 2009, 2012

Xenophrys boettgeri — Delorme et al., 2006; Chen et al., 2017

Xenophrys huangshanensis — Delorme et al., 2006; Chen et al., 2017

Boulenophrys boettgeri — Fei & Ye, 2016; Fei, 2020; Dubois et al., 2021; Qi et al., 2021

Boulenophrys huangshanensis — Fei & Ye, 2016; Fei, 2020; Dubois et al., 2021; Qi et al., 2021

Megophrys (Panophrys) boettgeri — Mahony et al., 2017

Megophrys (Panophrys) huangshanensis — Mahony et al., 2017

Panophrys huangshanensis — Lyu et al., 2021

Megophrys sp35 — Liu et al., 2018

Syntypes: BMNH 1947.2.25.4, 1899.4.24.87–91, MCZ 3790, from Kuatun, a village about 270 miles from Foochow, in the mountains in the northwest of the Province of Fokien (= Guadun Village, Wuyishan City, Nanping, Fujian), China.

Specimens examined: Four adult males SYS a004149–4151, 5927, and one adult female SYS a005928, from Guadun Village (N27.7334°, E117.6387°; ca. 1 360 m a.s.l.); three adult males SYS a004125–4127 and two adult females SYS a004123–4124, from Longhu (N27.5159°, E117.4672°; ca. 800 m a.s.l.), Shaowu City, Nanping; six adult males SYS a005839–5844, from Mt. Yashu (N26.5205°, E116.5915°; ca. 740 m a.s.l.), Ninghua County, Sanming, Fujian; three adult males SYS a006907–6909, from . Mt. Yangjifeng (N27.9180°, E117.3652°; ca. 1 300 m a.s.l.), Guixi City, Yingtan, Jiangxi, China; six adult males SYS a001671, 1673, 1683, 1700, 2475–2476, and two adult females SYS a001672, 2477, from Mt. Tongbo (N28.1154°, E118.2372°; ca. 1 100 m a.s.l.), Guangfeng District, Shangrao, Jiangxi; two adult males SYS a008076–8077, from Mt. Sanqing (N28.9062°, E118.1068°; ca. 400 m a.s.l.), Yushan County, Shangrao; 10 adult males SYS a001316–1321, 1622, 3705–3707, and two adult females SYS a001322, 1623, from Mt. Dazhang (N29.5394°, E117.7552°; ca. 1 190 m a.s.l.), Wuyuan County, Shangrao; two adult males SYS

a007926–7927, from Mt. Guniujiang (N30.1069°, E117.4569°; ca. 400 m a.s.l.), Shitai County, Chizhou, Anhui, China; six adult males SYS a002702–2707, from Mt. Huangshan (N30.1900°, E118.1615°; ca. 600 m a.s.l.), Huangshan District, Huangshan, Anhui; three adult males SYS a007959–7961, from Mt. Qingliangfeng (N30.1123°, E118.8007°; ca. 860 m a.s.l.), Jixi County, Xuancheng, Anhui; seven adult males SYS a002684–2685, 7967–7971, from Mt. Tianmu (N30.3649°, E119.4407°; ca. 700 m a.s.l.), Lin'an District, Hangzhou, Zhejiang, China; one adult male SYS a002746 and one adult female SYS a002747, from Mt. Qianligang (N29.2437°, E118.8179°; ca. 400 m a.s.l.), Qujiang District, Quzhou, Zhejiang.

Diagnosis: Based on examined specimens: (1) adult males, SVL 32.5–40.3 mm ($n=53$); adult females, SVL 41.7–45.8 mm ($n=8$); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin relatively smooth with scattered tubercles and granules; discontinuous X-shaped or “> <”-shaped ridge on center of dorsum, dorsolateral ridges absent; large tubercles on flanks; ventral skin smooth, large tubercles on posterior thigh; (6) outer margin of upper eyelid with remarkably prominent horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths $II < IV < III$; distinct subarticular tubercle at base of each finger; (8) hindlimbs moderate, heels not meeting or slightly overlapping when hindlimbs folded; tibiotarsal articulation reaching region between corner of eye and anterior margin of tympanum when leg stretched forward; (9) toes with rudimentary webbing at bases and lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsum brown, dark triangular marking between eyes; dark X-shaped or netlike marking on center of dorsum; usually pair of light-colored, large, and semi-rounded markings on shoulder

regions; dorsal limbs with distinct or indistinct dark transverse bands; ventral surface purplish with dark patches; two parallel dark brown bands ventrolaterally; (11) dense nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 17).

Distribution: Currently known from multiple localities in eastern China, including Fujian, Jiangxi, Zhejiang, and Anhui, at elevations of 200–1 400 m a.s.l. (this study, refer to Remarks below) (Supplementary Figure S6).

Remarks: This species was originally described based on specimens from Wuyishan in northwestern Fujian (Boulenger, 1899b) and was subsequently widely recorded from multiple localities in eastern China (Fei et al., 2009, 2012; Liu & Hu, 1961). The population from Mt. Huangshan was erected as *B. huangshanensis* (Fei et al., 2005). Based on molecular data for species delimitation and with recognition of *B. boettgeri* and *B. huangshanensis*, Liu et al. (2018) suggested that the Wuyuan population (labeled as *M. sp35*) may belong to a cryptic species, although these three lineages were controversially considered conspecific in the ABGD delimitation analysis.

In our phylogenetic analysis, populations recorded as *B. boettgeri* and *B. huangshanensis* were clustered in a monophyletic lineage, despite distinct intraspecific divergence (Figure 3). Morphologically, *B. huangshanensis* is suggested to differ from *B. boettgeri* based on webbing and lateral fringes on toes absent (vs present), subarticular tubercles on toes I and II present (vs absent), and coloration patterns (Fei et al., 2005). However, our morphological examination suggested that the specimens from Mt. Huangshan possessed rudimentary webbing and lateral fringes on the toes (SYS a002702–2707), although the lateral fringes were relatively narrower than in specimens from Wuyishan (SYS a004149–4151, 5927–5928). Furthermore, subarticular tubercles were present on toes I and II in the specimens from Wuyishan. Based on examination of all specimens collected



Figure 17 *Boulenophrys boettgeri* in life

A: Dorsolateral view of male SYS a005927; B: Ventral view of SYS a005927; C: Hand of SYS a005927; D: Foot of SYS a005927; E: Dorsolateral view of male SYS a002702; F: Ventral view of SYS a002702; G: Hand of SYS a002702; H: Foot of SYS a002702; I: Dorsolateral view of male SYS a005842; J: Dorsolateral view of male SYS a003906; K: Dorsolateral view of male SYS a007969; L: Dorsolateral view of female SYS a005928. Photos by Z.T. Lyu, Z.C. Zeng, and Y.Y. Wang.

from Fujian, Jiangxi, Zhejiang, and Anhui in eastern China, we determined that the width of the lateral fringes on the toes and coloration patterns varied gradually among different geographical populations, but no definitive characters distinguished the specimens from each other. Therefore, we consider that the populations within this monophyletic lineage are conspecific (*B. huangshanensis* is therefore synonymized with *B. boettgeri*), and molecular intraspecific divergence may be due to geographical isolation.

***Boulenophrys brachykolos* (Inger and Romer, 1961)**

Short-legged horned toad / duǎn zhī jiǎo chán (短肢角蟾)

Chresonymy: *Megophrys brachykolos* — Inger & Romer, 1961; Fei et al., 2009, 2012

Megophrys (Megophrys) brachykolos — Dubois, 1980

Megophrys minor brachykolos — Ye & Fei, 1995

Panophrys brachykolos — Rao & Yang, 1997; Lyu et al., 2021

Megophrys (Xenophrys) brachykolos — Dubois & Ohler, 1998

Xenophrys brachykolos — Delorme et al., 2006; Chen et al., 2017

Boulenophrys brachykolos — Fei & Ye, 2016; Fei, 2020;

Dubois et al., 2021; Qi et al., 2021

Megophrys (Panophrys) brachykolos — Mahony et al., 2017

Megophrys sp17 — Liu et al., 2018

Holotype: FMNH 69063, adult male, from The Peak, Hong Kong Island, Hong Kong, China.

Paratypes: Fourteen adults FMNH 64165, 69062, 69064–65, 109977–86, from same locality as holotype; tadpoles FMNH 190087, from Wong Nai Chung Gap, Hong Kong Island; one adult FMNH 24408 from Kuatun, Chungan Hisen, Fekien Province (=Guadun Village, Wuyishan City, Nanping, Fujian), China (refer to Remarks below).

Specimens examined: One adult female SYS a005562, from Tai Tam (N22.2554°, E114.2051°; ca. 280 m a.s.l.), Hong Kong Island; two adult males SYS a002258–2259, from Lantau Island (N22.2518°, E113.9372°; ca. 320 m a.s.l.), Hong Kong; one adult male SYS a001502 and one adult female SYS a001503, from Hong Kong; 13 adult males SYS a2051–2056, 2071–2074, 2453, 3312, 7604, and three adult females SYS a002070, 2413, 2454, 3329, 7605, from Mt. Yangtai (N22.6434°, E113.9854°; ca. 150 m a.s.l.), Longhua District, Shenzhen, Guangdong; three adult males SYS a002446–2448 and one adult female SYS a002449, from Mt. Sanzhoutian (N22.6241°, E114.2722°; ca. 580 m a.s.l.), Yantian District, Shenzhen; three adult males SYS a002410–2442, from Mt. Qiniang (N22.5413°, E114.5686°; ca. 30 m a.s.l.), Dapeng District, Shenzhen.

Diagnosis: Based on examined specimens: (1) adult males, SVL 31.5–40.1 mm ($n=22$); adult females, SVL 37.6–45.2 mm ($n=8$); (2) canthus rostralis well developed; tongue notched posteriorly; (3) tympanum distinct, conical spines on temporal region; (4) vomerine ridges present, vomerine teeth weakly developed; (5) dorsal skin relatively smooth with scattered granules and several tubercles; discontinuous X-shaped or Y-shaped ridge on center of dorsum, discontinuous dorsolateral ridges indistinct; ventral skin smooth, rear of thighs and around cloaca with tubercles bearing spines; (6) outer margin of upper eyelid with remarkably prominent horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths II<IV<I<III; distinct subarticular tubercle at base of finger I, absent on other fingers; (8) hindlimbs robust and short, heels

not meeting when hindlimbs folded; tibiotarsal articulation reaching region between anterior margin of tympanum and shoulder when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface dark brown to yellowish brown; hollow dark triangular marking between eyes; dark X-shaped or Y-shaped marking on center of dorsum, absent in some individuals; ventral surface dark gray with reddish spots and white tubercles; longitudinal stripe on center of throat; belly with black patches; (11) tiny and dense nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 18A).

Distribution: Currently recognized from Hong Kong and neighboring Shenzhen at elevations of 30–580 m a.s.l. (Inger & Romer, 1961; this study, refer to Remarks below) (Supplementary Figure S5).

Remarks: Based on molecular data for species delimitation, Liu et al. (2018) suggested that the Shenzhen population (labeled as *M. sp17*) may belong to a cryptic species different from its sister taxon from Hong Kong (labeled as *M. brachykolos*). In this study, after detailed morphological examination, we failed to discover distinct characters to distinguish the two populations, which are hence considered to be conspecific.

This species has also been reported from multiple localities in southern China and neighboring countries (Fei & Ye, 2016; Fei et al., 2009, 2012). The record from the vicinity of Jinxiu County has been revised to another species after examination of vouchers, i.e., *B. yaoshanensis* (Qi et al., 2021). However, most records from other localities lack voucher specimens (uncaptured or lost) and are therefore unavailable for re-examination and re-identification. Hereby, we consider restricting the distribution of this species to Hong Kong and Shenzhen based on voucher specimens and molecular data. Records outside this region should be deprecated and removed. In particular, a paratype from Fujian in eastern China was included in the type series of this species (Inger & Romer, 1961). This specimen may be a misidentification and should be removed from the type series of this species and assigned to another congener (possibly *B. ombrophila* due to morphological similarity) after detailed morphological re-examination.

***Boulenophrys caudoprocta* (Shen, 1994)**

Convex-tailed horned toad / wěi tū jiǎo chán (尾突角蟾)

Chresonymy: *Megophrys caudoprocta* — Shen, 1994; Fei et al., 2009, 2012

Xenophrys caudoprocta — Delorme et al., 2006; Chen et al., 2017

Xenophrys (Tianophrys) caudoprocta — Fei & Ye, 2016; Fei, 2020

Megophrys (Panophrys) caudoprocta — Mahony et al., 2017

Panophrys caudoprocta — Lyu et al., 2021

Boulenophrys caudoprocta — Qi et al., 2021

Holotype: HNNU 81-801, adult male, from Mt. Tianping (N29°23', E110°01'; 1 600 m a.s.l.), Sangzhi County, Zhangjiajie, Hunan, China.

Specimens examined: One adult male SYS a004308, from Mt. Tianping (N29.7591°, E110.0624°; ca. 1 380 m a.s.l.).

Diagnosis: Based on previous description (Shen et al., 2013) and examined specimens: (1) adult males, SVL 70.8–81.3 ($n=3$; Shen et al., 2013) (SVL 66.2 mm, $n=1$; this study); adult



Figure 18 Species of *Boulenophrys* in life (*B. boettgeri* group)

A: *B. brachykolos* female SYS a003329; B: *B. congjiangensis* male SYS a005133; C: *B. jinggangensis* male SYS a007878; D: *B. kuatunensis* male SYS a006906; E: *B. leishanensis* male SYS a002213; F: *B. lishuiensis* male SYS a008440; G: *B. ombrophila* male SYS a005756; H: *B. shunhuangensis* male SYS a002915; I: *B. tuberogranulata* male SYS a004310; J: *B. xianjuensis* male SYS a002673; 1: Dorsolateral view; 2: Ventral view. Photos by Z.T. Lyu, J. Wang, and Y.Y. Wang.

female, SVL 77.8 ($n=1$; Shen et al., 2013); (2) snout rounded, canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum indistinct, upper margin in contact with or slightly concealed by supratympanic fold; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin relatively smooth with sparse granules; discontinuous V-shaped, X-shaped, or irregular ridge on center of dorsum, discontinuous dorsolateral ridges present; sparse tubercles on flanks; ventral skin smooth; (6) outer margin of upper eyelid elongated as triangular appendage with large horn-like prominent tubercle on tip; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct, inner one observably enlarged; relative finger lengths $I < II < IV < III$; faintly visible subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes with rudimentary webbing at bases, fourth toe with narrow lateral fringe, other toes without lateral fringes; inner metatarsal tubercle indistinct, outer one absent; (10) dorsal surface gray in males, bright reddish in female; dark triangular marking between eyes, X or netlike marking with light edge on center of dorsum; ventral surface pale brown with reddish spots on throat and chest;

(11) nuptial spines on dorsal bases of fingers I and II in breeding adult males; males without subgular vocal sacs (Figure 4C).

Distribution: Known from Mt. Tianping in northwestern Hunan and neighboring Houhe Nature Reserve in southwestern Hubei at elevations of 1 100–1 600 m a.s.l. (Shen et al., 2013) (Supplementary Figure S5).

Remarks: The institute abbreviation of this species was provided as HNUL in the original description by Shen (1994) but has been officially changed to HNNU (Sheng-Chao Shi, pers. comm.). It was also given as HNU in Fei et al. (2009) and Fei & Ye (2016) to differentiate it from Henan Normal University, which is also abbreviated as HNNU.

***Boulenophrys cheni* (Wang and Liu, 2014)**

Chen's horned toad / chén shì jiǎo chán (陈氏角蟾)

Chresonymy: *Xenophrys cheni* — Wang et al., 2014; Chen et al. 2017

Megophrys cheni — Li et al., 2014

Megophrys (Panophrys) cheni — Mahony et al., 2017

Boulenophrys cheni — Fei, 2020; Qi et al., 2021

Panophrys cheni — Lyu et al., 2021

Holotype: SYS a001873, adult male, from Jingzhushan (N26°29'45.95", E114°04'45.66"; 1 210 m a.s.l.), Mt. Jinggang,

Jinggangshan City, Ji'an, Jiangxi, China.

Paratypes: Five adult males SYS a001427–1428, 1538, 1871–1872, and one adult female SYS a001429, from same locality as holotype; three adult males SYS a002125–2127 and two adult females SYS a002124, CIB 107665 (formerly SYS a002123), from Lishuzhou (N26°20'31.33"–26°20'47.70", E113°59'01.10"–113°00'34.50"; 1 480–1 530 m a.s.l.), Taoyuandong Nature Reserve, Yanling County, Zhuzhou, Hunan, China; six adult males SYS a002140–2145, from Dayuan (N26°23'16.40", E114°01'56.20"; 1 480 m a.s.l.), Taoyuandong Nature Reserve.

Specimens examined: Type materials (15 adult males and three adult females).

Diagnosis: Based on examined specimens: (1) adult males, SVL 26.2–29.5 mm ($n=15$); adult females, SVL 31.8–34.1 mm ($n=3$); (2) snout obtusely rounded, canthus rostralis well developed; tongue notched posteriorly; (3) tympanum indistinct, upper margin usually concealed by supratympanic fold; (4) vomerine ridges weak, vomerine teeth absent; (5) dorsal skin smooth with tubercles, discontinuous weak X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges indistinct; flanks smooth with tubercles; ventral skin smooth; (6) outer margin of upper eyelid with horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths I<II<IV<III; indistinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching region between nostril and tip of snout when leg stretched forward; (9) toes with rudimentary webbing at bases and wide lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface red-brown or olive-brown; dark netlike markings on dorsum; dorsal limbs with dark transverse bands; ventral surface olive with pinkish and white spots; obscure longitudinal darker stripe on center of throat; several white blotches on belly, two parallel black bands ventrolaterally; (11) nuptial pads/spines absent in breeding adult males; subgular vocal sac present in males.

Distribution: Known from Mt. Jinggang in western Jiangxi and neighboring Taoyuandong Nature Reserve in eastern Hunan at elevations of 1 200–1 530 m a.s.l. (Wang et al., 2014) (Supplementary Figure S5).

***Boulenophrys congjiangensis* (Luo, Wang, Wang, Lu, Wang, Deng, and Zhou, 2021)**

Congjiang horned toad / cóng jiāng jiǎo chán (从江角蟾)

Chresonymy: *Megophrys* sp33 — Liu et al., 2018

Panophrys congjiangensis — Luo et al., 2021

Boulenophrys congjiangensis — Qi et al., 2021

Holotype: GZNU 20200706010, adult male, from Yueliangshan Nature Reserve (N25.614417°, E108.410076°; ca. 730 m a.s.l.), Congjiang County, Qiandongnan, Guizhou, China.

Paratypes: Fourteen adult males GZNU 20200706001–009, 012–013, 20200707001–003, and four adult females GZNU 20200706011, 20200707004–006, from same locality as holotype.

Specimens examined: Three adult males SYS a005133–5134, 5147, and one adult female SYS a005949, from Mt. Jiuwan (N25.2065°, E108.6750°; ca. 1 280 m a.s.l.), Huanjiang County, Hechi, Guangxi, China.

Diagnosis: Based on examined specimens: (1) adult males,

SVL 31.7–33.9 mm ($n=3$) (SVL 28.6–33.4, $n=15$; type series); adult female, SVL 39.0 mm ($n=1$) (SVL 38.4–40.2, $n=4$; type series); (2) canthus rostralis well developed; tongue notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin rough with small granules; discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; large tubercles on flanks; ventral skin smooth; (6) outer margin of upper eyelid with small horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths II<I<IV<III; subarticular tubercle on base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching region between nostril and eye when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface reddish brown or light-brown; dark brown triangular marking between eyes; dark X-shaped marking on center of dorsum; ventral surface brown with creamy white and orange spots; (11) gray-black nuptial pad with black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 18B).

Distribution: Known from Congjiang County in southern Guizhou and Mt. Jiuwan in northern Guangxi at elevations of 1 100–1 300 m a.s.l. (Luo et al., 2021; this study) (Supplementary Figure S5).

Remarks: In the original description of this species, the number of male paratypes was mentioned as “15 males” in the designation while the total number of males in the type series (holotype and paratypes) was mentioned as “ $n=15$ ” in Table 5 (Luo et al., 2021), which is inconsistent. The correct number of male paratypes should be “14 males” as only 14 specimens were listed in the designation. The voucher numbers for three female paratypes collected on 7 July 2020 should be GZNU 20200707004–006 (provided in error as GZNU 20200706004–006 in the original description).

***Boulenophrys daiyunensis* (Lyu, Wang, and Wang, 2021)**

Daiyun horned toad / dài yún jiǎo chán (戴云角蟾)

Chresonymy: *Megophrys kuatunensis* — Ting et al., 1980

Megophrys sp18 — Liu et al., 2018

Panophrys daiyunensis — Lyu et al., 2021

Boulenophrys daiyunensis — Qi et al., 2021

Holotype: SYS a001733, adult male, from Daiyun Village (N25.6362°, E118.2139°; ca. 1 040 m a.s.l.), Daiyun Mountain Nature Reserve, Dehua County, Quanzhou, Fujian, China.

Paratypes: Three adult males SYS a001731–1732, CIB 116075, and one adult female SYS a006002, from same locality as holotype; two adult females SYS a006000, 6003, from Jiuxianshan (N25.7101°, E118.1200°; ca. 1 200 m a.s.l.), Daiyun Mountain Nature Reserve.

Specimens examined: Type materials (four adult males and three adult females); six adult males SYS a007711–7716, from Tingxi Farm (N24.8339°, E118.1220°; ca. 400 m a.s.l.), Tong'an District, Xiamen, Fujian.

Diagnosis: Based on examined specimens: (1) adult males, SVL 27.6–30.9 mm ($n=10$); adult females, SVL 33.7–35.6 mm ($n=3$); (2) canthus rostralis well developed; tongue notched posteriorly; (3) tympanum distinct, upper margin in contact with supratympanic fold; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin rough with distributed

granules and scattered tubercles; discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; throat smooth, rounded densely distributed tubercles present on chest and belly, raised densely distributed tubercles on ventral thigh; (6) outer margin of upper eyelid with small horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths $II < IV < III$; distinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping or just meeting when hindlimbs folded; tibiotarsal articulation reaching posterior corner of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface yellowish brown or reddish brown; dark triangular marking with light edge between eyes; dark X-shaped or “> <”-shaped marking with light edge on center of dorsum; ventral surface dark brown; red spots on chest and densely distributed tiny white spots on belly and ventral thigh; (11) nuptial pads/spines absent in breeding adult males; subgular vocal sac present in males.

Distribution: Known from Daiyun Mountain Nature Reserve (1 000–1 250 m a.s.l.) and Tingxi Farm (ca. 400 m a.s.l.) in southern Fujian (Lyu et al., 2021) (Supplementary Figure S6).

***Boulenophrys daoji* (Lyu, Zeng, Wang, and Wang, 2021)**

Daoji's horned toad / dào jì jiǎo chán (道济角蟾)

Chresonymy: *Megophrys* sp20 — Liu et al., 2018

Panophrys daoji — Lyu et al., 2021

Boulenophrys daoji — Qi et al., 2021

Holotype: SYS a006209, adult male, from Huading (N29.2781°, E121.0996°; ca. 680 m a.s.l.), Mt. Tiantai, Tiantai County, Taizhou, Zhejiang, China.

Paratypes: Three adult males SYS a006210–6211, CIB 116076, and two adult females SYS a006213–6214, from same locality as holotype.

Specimens examined: Type materials (four adult males and two adult females); five adult males SYS a006143–6144, 6205–6207, from Xikou Town (N29.7153°, E121.2454°; ca. 570 m a.s.l.), Fenghua District, Ningbo, Zhejiang.

Diagnosis: Based on examined specimens: (1) adult males, SVL 30.7–33.6 mm ($n=9$); adult females, SVL 37.5–41.4 mm ($n=2$); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct, edge raised, upper margin in contact with supratympanic fold; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin rough with densely distributed granules and tubercles; discontinuous X-shaped or “> <”-shaped ridge on center of dorsum, dorsolateral ridges absent, short transverse skin ridges present on dorsal shank and thigh; ventral skin smooth, with densely distributed tubercles on ventral thigh; (6) outer margin of upper eyelid with small horn-like tubercle; supratympanic fold distinct and narrow, with distinct raised tubercles, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths $II < IV < III$; distinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels not meeting when hindlimbs folded; tibiotarsal articulation reaching center of tympanum when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle rounded, outer one absent; (10) dorsal surface variable from dark gray, pale brown, yellowish brown, to reddish brown; dark brown triangular marking with light edge between eyes; dark X-

shaped or “> <”-shaped marking with light edge on center of dorsum; ventral surface variable, lighter than color of dorsum; large white patch and tiny scarlet spots on belly, two parallel black bands ventrolaterally; (11) black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known from Mt. Tiantai and neighboring Xikou Town in eastern Zhejiang at elevations of 500–700 m a.s.l. (Lyu et al., 2021) (Supplementary Figure S7).

***Boulenophrys dongguanensis* (Wang and Wang, 2019)**

Dongguan horned toad / dōng guǎn jiǎo chán (东莞角蟾)

Chresonymy: *Megophrys* sp11 — Liu et al., 2018

Megophrys (Panophrys) dongguanensis — Wang et al., 2019a

Panophrys dongguanensis — Lyu et al., 2021

Boulenophrys dongguanensis — Qi et al., 2021

Holotype: SYS a001973, adult male, from Mt. Yinping, Xiegang Town (N22°54'17.20", E114°13'23.88"; 132 m a.s.l.), Dongguan, Guangdong, China.

Paratypes: Eight adult males SYS a001492–1495, 1972, 1974–1975, CIB 110006; one adult male SYS a002007, from Mt. Yinping, Qingxi Town (N22°53'26.21", E114°10'14.82"; 277 m a.s.l.), Dongguan.

Specimens examined: Type materials (10 adult males).

Diagnosis: Based on examined specimens: (1) adult males, SVL 30.2–39.3 mm ($n=10$); (2) snout pointed, canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges strong, vomerine teeth present; (5) dorsal skin rough with numerous granules; discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; flanks with several large tubercles; ventral skin smooth with several granules present on belly and ventral and posterior thighs; (6) outer margin of upper eyelid with small horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) inner metacarpal tubercle distinct and observably enlarged, outer one indistinct; relative finger lengths $II < IV < III$, distinct subarticular tubercle at base of each finger; (8) hindlimbs short, heels not meeting when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface yellowish brown; incomplete dark brown triangular marking between eyes; X-shaped marking on center of dorsum; dorsal limbs with dark gray transverse bands; ventral surface black brown, with white spots on posterior belly; (11) nuptial pads bearing darker nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known only from the vicinity of its type locality in Dongguan at elevations of 100–300 m a.s.l. (Wang et al., 2019a) (Supplementary Figure S6).

Remarks: In the original description of this species, the number of paratypes was mentioned as “10 males” in the designation while total number in the type series (holotype and paratypes) was mentioned as “11 adult male specimens” in the diagnosis and “ $n=9$ ” in the measurements in Table 4 (Wang et al., 2019a), which is inconsistent. The correct number of paratypes should be “nine adult males” as only nine specimens were listed in the designation, and the total number in the type series should be “ $n=10$ ”. The collection localities Xiegang and Qingxi are two towns in Dongguan, not counties as mentioned in the original description.

***Boulenophrys fengshunensis* Wang, Zeng, Lyu, and Wang, 2022**

Fengshun horned toad / fēng shùn jiǎo chán (丰顺角蟾)

Chresonymy: *Megophrys* sp14 — Liu et al., 2018

Boulenophrys fengshunensis — Wang et al., 2022

Holotype: SYS a004744, adult male, from Mt. Tongguzhang (N24°10'31.12", E116°21'02.63"; ca. 1 500 m a.s.l.), Fengshun County, Meizhou, Guangdong, China.

Paratypes: Five adult males SYS a004725–4728, CIB 118528, and two adult females SYS a005220–5221, from same locality as holotype.

Specimens examined: Type materials (six adult males and two adult females).

Diagnosis: Based on examined specimens: (1) adult males, SVL 34.3–39.4 mm ($n=6$); adult females, SVL 42.5–44.9 mm ($n=2$); (2) snout pointed, canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct, tubercles bearing spines on temporal region; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin rough and granular, with sparse tubercles; tiny spines on dorsum and dorsal limbs; weak discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges indistinct; sparse large conical tubercles on flanks; throat, chest, and anterior part of belly smooth; ventral thighs and posterior part of belly with dense tubercles; skin around cloaca with dense tubercles bearing tiny spines; (6) outer margin of upper eyelid with small horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one enlarged; relative finger lengths I=II<IV<III; subarticular tubercle at base of each finger; (8) hindlimbs short, heels not meeting when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface dark brown or beige; dark brown triangular marking between eyes; X-shaped marking on center of dorsum; dorsal limbs with dark gray transverse bands; ventral surface dark brown or light orange; black longitudinal stripe on center of throat; posterior part of belly with irregular grayish white patches; ventral thighs and around cloaca light gray to dark gray; (11) nuptial pads bearing fine and dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known only from its type locality in Mt. Tongguzhang at elevations of 800–1 500 m a.s.l. (Wang et al., 2022) (Supplementary Figure S6).

***Boulenophrys hungtai* Wang, Zeng, Lyu, Xiao, and Wang, 2022**

Hung-Ta Chang's horned toad / jiē yáng jiǎo chán (揭阳角蟾)

Chresonymy: *Boulenophrys hungtai* — Wang et al., 2022

Holotype: SYS a007578, adult male, from Mt. Liwangzhang (N23°38'6.42", E115°48'51.78"; ca. 990 m a.s.l.), Jiexi County, Jieyang, Guangdong, China.

Paratypes: Eleven adult males SYS a007576–7577, 7579–7582, 7594–7597, CIB 118527, from same locality as holotype; one adult male SYS a008576, from Shuangkeng Forestry Station (N23°43'56.25", E116°21'26.4"; ca. 550 m a.s.l.), Jiedong District, Jieyang.

Specimens examined: Type materials (13 adult males).

Diagnosis: Based on examined specimens: (1) adult males, SVL 25.8–33.3 mm ($n=13$); (2) snout pointed, canthus rostralis

well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin rough and granular, with raised conical tubercles; discontinuous weak X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges indistinct; large warts on dorsal limbs and flanks; ventral skin rough with large tubercles on chest, belly, and around cloaca, tips of tubercles on posterior belly, ventral thighs, and around cloaca with tiny spines; (6) outer margin of upper eyelid with small horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths I<II<IV<III; subarticular tubercle at base of each finger; (8) hindlimbs short, heels not meeting when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward; (9) toes without webbing and lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface maroon or light brown; dark brown triangular marking between eyes; dorsal limbs with dark gray transverse bands; black longitudinal stripe on center of throat; ventral surface dark brown with white and orange mottling, two parallel black bands ventrolaterally; ventral thighs and around cloaca dark gray; (11) nuptial pads bearing fine and dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known only from two localities in Jiedong District and Jiexi County in eastern Guangdong at elevations of 500–1 000 m a.s.l. (Wang et al., 2022) (Supplementary Figure S6).

***Boulenophrys insularis* (Wang, Liu, Lyu, Zeng, and Wang, 2017)**

Nan'ao Island horned toad / nán ào dǎo jiǎo chán (南澳岛角蟾)

Chresonymy: *Megophrys minor* — Li et al., 2011

Xenophrys insularis — Wang et al., 2017a

Megophrys insularis — Wang et al., 2019a

Panophrys insularis — Lyu et al., 2021

Boulenophrys insularis — Qi et al., 2021

Holotype: SYS a002169, adult male, from Nan'ao Island (N23°26'00.09", E117°04'45.61"; 425 m a.s.l.), Nan'ao County, Shantou, Guangdong, China.

Paratypes: Four adult males SYS a002167, 2170–2171, CIB 106881, and one adult female SYS a002168, from same locality as holotype.

Specimens examined: Type materials (five adult males and one adult female).

Diagnosis: Based on examined specimens: (1) adult males, SVL 36.8–41.2 mm ($n=5$); adult female, SVL 47.1 mm ($n=1$); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct, rounded; (4) vomerine ridges strong, vomerine teeth present; (5) dorsal skin rough with numerous granules and tubercles; several large warts scattered on flanks; ventral skin smooth, with small granules on throat and chest, posterior belly and ventral and rear of thighs with dense pustules and small granules; (6) outer margin of upper eyelid with horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths II<I≤IV<III; large subarticular tubercle at base of each finger; (8) hindlimbs slightly robust, heels not meeting when hindlimbs folded;

tibiotarsal articulation reaching posterior edge of tympanum when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal long ellipsoid, outer one absent; (10) dorsal surface dark-olive in males and brownish-yellow in female; incomplete dark triangular marking between eyes; dorsal limbs with black transverse bands; throat, chest, and anterior belly grayish-brown scattered with white spots in males, while throat and chest brownish-red, belly grayish-white in female; (11) dark brown nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known only from its type locality in Nan'ao Island at elevations of 50–500 m a.s.l. (Wang et al., 2017a) (Supplementary Figure S6).

***Boulenophrys jinggangensis* (Wang, 2012)**

Jinggang horned toad / jǐng gāng jiǎo chán (井冈角蟾)

Chresonymy: *Xenophrys jinggangensis* — Wang et al., 2012; Chen et al. 2017

Megophrys jinggangensis — Li et al., 2014

Xenophrys (Xenophrys) jinggangensis — Fei & Ye, 2016; Fei, 2020

Megophrys (Panophrys) jinggangensis — Mahony et al., 2017

Megophrys sp22 — Liu et al., 2018

Megophrys sp23 — Liu et al., 2018

Panophrys jinggangensis — Lyu et al., 2021

Boulenophrys jinggangensis — Qi et al., 2021

Holotype: SYS a001430, adult female, from Mt. Jinggang (N26°33'06.30", E114°09'17.60"; 845 m a.s.l.), Jinggangshan City, Ji'an, Jiangxi, China.

Paratypes: Two adult males SYS a001414–1415 and two adult females CIB 107664 (formerly SYS a001413), SYS a001416 from same locality as holotype.

Specimens examined: Type materials (two adult males and three adult females); three adult males SYS a001533, 4028–4029, and four adult females SYS a004030–4032, 6952, from Mt. Jinggang; 16 adult males SYS a002574–2576, 2612–2613, 3130–3131, 3133–3134, 4047, 4049, 4778–4782, and seven adult females SYS a002567, 2607–2608, 2626, 2630, 3132, 4048, from Wugongshan Scenic Area (N27.5677°, E114.1746°; ca. 1 050–1 080 m a.s.l.), Anfu County, Ji'an; two adult males SYS a002638–2639, from Mt. Mengshan (N28.0605°, E114.9258°; ca. 800 m a.s.l.), Shanggao County, Yichun City, Jiangxi; six adult males SYS a007875–7880, from Mt. Meiling (N28.7709°, E115.7178°; ca. 500 m a.s.l.), Wanli District, Nanchang, Jiangxi; 10 adult males SYS a003164–3165, 3167–3169, 6967–6969, from Mt. Jiuling (N29.1078°, E115.3048°; ca. 700 m a.s.l.), Wuning County, Jiujiang, Jiangxi; two adult males SYS a006988–6989, from Mt. Taiping (N29.3850°, E114.8844°; ca. 1 020 m a.s.l.), Wuning County; one adult male SYS a006460 and four adult females SYS a005527–5528, 6461, 6490, from Mt. Dawei (N28.4250°, E114.0805°; ca. 800 m a.s.l.), Liuyang City, Changsha, Hunan, China; two adult males SYS a004825–4826 and two adult females SYS a004824, 4827, from Mt. Sifang (N26.9678°, E113.0672°; ca. 400 m a.s.l.), Hengdong County, Hengyang, Hunan; two adult males SYS a006381–6382, from Chuankou Town (N26.8836°, E113.0557°; ca. 600 m a.s.l.), Hennen County, Hengyang; one adult male SYS a002543 and one adult female SYS a002544, from Mt. Yunyang (N26.7641°, E113.4771°; ca. 500 m a.s.l.), Chaling County, Zhuzhou, Hunan; four adult males SYS a001859–1862, from Taoyuandong Nature Reserve

(N26.4988°, E114.0297°; ca. 1 020 m a.s.l.), Yanling County, Zhuzhou.

Diagnosis: Based on examined specimens: (1) adult males, SVL 33.9–48.9 mm ($n=49$); adult females, SVL 38.4–52.6 mm ($n=21$); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges weak, vomerine teeth present; (5) dorsal skin rough with scattered tubercles and granules; short irregular weak ridges on dorsum, dorsolateral ridges absent; several tubercles on flanks; ventral skin smooth; (6) outer margin of upper eyelid with horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths II<I<IV<III; distinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching region between center of eye and anterior margin of tympanum when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsum light brown, irregular dark-brown patches on dorsum; dorsal limbs and digits light brown with dark brown transverse bands; ventral surface grayish with black and brown spots; (11) dense nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 18C).

Distribution: Common from multiple localities in the Wanyang, Jiuling, and Mufu mountains along the border between Jiangxi and Hunan at elevations of 400–1 200 m a.s.l. (this study) (Supplementary Figure S6).

Remarks: Based on molecular data for species delimitation, Liu et al. (2018) suggested that populations from Mt. Jiuling (labeled as *M. sp22*) and Mt. Meiling (labeled as *M. sp23*) may differ from the topotype population from Mt. Jinggang (labeled as *M. jinggangensis*) and should be considered as two cryptic species. Nonetheless, these three populations were considered conspecific in the ABGD delimitation analysis (Liu et al., 2018). In this study, after detailed morphological examination, we failed to discover distinct characters to distinguish the specimens collected from multiple localities in the Wanyang, Jiuling, and Mufu mountains. Thus, these populations are considered to be conspecific as *B. jinggangensis*.

***Boulenophrys jiulianensis* (Wang, Zeng, Lyu, and Wang, 2019)**

Mt. Jiulian horned toad / jiū lián shān jiǎo chán (九连山角蟾)

Chresonymy: *Megophrys* sp9 — Chen et al., 2017

Megophrys sp30 — Liu et al., 2018

Megophrys (Panophrys) jiulianensis — Wang et al., 2019a

Panophrys jiulianensis — Lyu et al., 2021

Boulenophrys jiulianensis — Qi et al., 2021

Holotype: SYS a002112, adult male, from Daqitian Protection Station (N24°34'34.99", E114°26'28.53"; 560 m a.s.l.), Mt. Jiulian, Longnan City, Ganzhou, Jiangxi, China.

Paratypes: Two adult males SYS a001007, 1009, from same locality as holotype; six adult males SYS a002107–2109, 2113–2114, CIB 116076, and two adult females SYS a002110–2111, from Xiagongtang Protection Station (N24°32'16.74", E114°27'56.82"; 770 m a.s.l.), Mt. Jiulian; one adult male SYS a002031 from Mt. Nankun (N23°38'21.94", E113°50'39.49"; 610 m a.s.l.), Longmen County, Huizhou, Guangdong, China.

Specimens examined: Type materials (10 adult males and two adult females).

Diagnosis: Based on examined specimens: (1) adult males, SVL 30.4–33.9 mm ($n=10$); adult females, SVL 34.1–37.5 mm ($n=2$); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges weak, vomerine teeth present; (5) dorsal skin rough with black spines; indistinct discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges distinct, all ridges with black spines; large tubercles on flanks; ventral skin smooth, sides of belly with large tubercles; ventral thighs smooth with several small tubercles, rear of thighs and around cloaca with large tubercles bearing spines; (6) outer margin of upper eyelid with horn-like prominent tubercle bearing black spine; supratympanic fold distinct and narrow, with black spines, curving posteroventrally to above arm; (7) inner metacarpal tubercle distinct and observably enlarged, outer one indistinct; relative finger lengths $II < I < IV < III$; indistinct subarticular tubercle on base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface beige to brownish red, with indistinct light brown patches; hollow dark triangular marking between eyes; forearm with distinct black oblique band, hindlimb with indistinct transverse bands; ventral surface yellow, scattered with dense dark gray spots and black scarlet blotches, two parallel black bands ventrolaterally; (11) nuptial pads bearing darker nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Common from Mt. Jiulian in southwestern Jiangxi and Mt. Nankun in northern Guangdong at elevations of 500–800 m a.s.l. (Wang et al., 2019a) (Supplementary Figure S7).

***Boulenophrys kuatunensis* (Pope, 1929)**

Kuatun horned toad / guà dūn jiǎo chán (挂墩角蟾)

Chresonymy: *Megalophrys kuatunensis* — Pope, 1929

Megophrys kuatunensis — Liu & Hu, 1961; Fei et al., 2009, 2012

Megophrys (*Megophrys*) *kuatunensis* — Dubois, 1980

Panophrys kuatunensis — Rao & Yang, 1997; Lyu et al., 2021

Megophrys (*Xenophrys*) *kuatunensis* — Dubois & Ohler, 1998

Xenophrys kuatunensis — Delorme et al., 2006; Chen et al., 2017

Boulenophrys kuatunensis — Fei & Ye, 2016; Fei, 2020; Dubois et al., 2021; Qi et al., 2021

Megophrys (*Panophrys*) *kuatunensis* — Mahony et al., 2017

Holotype: AMNH 30126, adult male, from Kuatun, Chungan Hisen, northwest Fekien Province (=Guadun Village, Wuyishan City, Nanping, Fujian), China.

Paratypes: Thirty-one adults AMNH 30123–30124, FMNH 24406 (formerly AMNH 30230), BMNH 1985.1295 (formerly AMNH 30231, then FMNH 24407), FMNH 24408 (formerly AMNH 30232), MCZ 28297 (formerly AMNH 30233, then FMNH 24409), BMNH 1985.1294 (formerly AMNH 30234, then FMNH 24410), FMNH 24411–24413 (formerly AMNH 30235–30237), BMNH 1961.956 (formerly AMNH 30238, then FMNH 24414), and AMNH 30239–30258, from same locality as holotype.

Specimens examined: Eight adult males SYS a000640–0645, 1579, 1590, from Guadun Village (N27.7334°,

E117.6387°; ca. 1 360 m a.s.l.); two adult males SYS a008408–8409 and one adult female SYS a008410, from Mt. Wuyi (N27.8373°, E117.7295°; ca. 1 200 m a.s.l.), Yanshan County, Shangrao, Jiangxi, China; three adult males SYS a006669, 6905–6906, from Mt. Yangjifeng (N27.9180°, E117.3652°; ca. 1 300 m a.s.l.), Guixi City, Yingtan, Jiangxi.

Diagnosis: Based on examined specimens: (1) adult males, SVL 27.5–33.6 mm ($n=13$); adult female, SVL 32.3 mm ($n=1$); (2) canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin relatively smooth with granules and tubercles; discontinuous X-shaped, “> <”-shaped or Y-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; ventral skin smooth; (6) outer margin of upper eyelid with remarkably prominent horn-like tubercle; supratympanic fold distinct, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths $I \leq II < IV < III$; subarticular tubercle at base of each finger; (8) hindlimbs robust and short, heels not meeting when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward; (9) toes without webbing and lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface yellowish brown; dark triangular marking between eyes; dark X-shaped or “> <”-shaped marking on center of dorsum; throat and chest purplish, longitudinal stripe on center of throat; belly grayish white, two parallel dark brown bands ventrolaterally; (11) tiny and dense nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 18D).

Distribution: Currently only recognized from Mt. Wuyi and Mt. Yangjifeng at the border between Fujian and Jiangxi at elevations of 1 200–1 400 m a.s.l. (this study) (Supplementary Figure S7).

Remarks: This species was widely recorded from multiple localities in southern China (Fei & Ye, 2016; Fei et al., 2009, 2012; Liu & Hu, 1961). However, most records lack voucher specimens (uncaptured or lost) and are therefore unavailable for re-examination and re-identification. Hereby, we consider restricting the distribution of this species to the vicinity of its type locality, namely Mt. Wuyi and Mt. Yangjifeng situated at the border between Fujian and Jiangxi, based on voucher specimens and molecular data. Records outside this region should therefore be deprecated and removed.

***Boulenophrys leishanensis* (Li, Xu, Liu, Jiang, Wei, and Wang, 2018)**

Leishan horned toad / léi shān jiǎo chán (雷山角蟾)

Chresonymy: *Megophrys minor* — Wu et al., 1987; Ye & Fei, 1995; Fei et al., 2009, 2012; Fei & Ye, 2016

Megophrys sp8 — Chen et al., 2017

Megophrys sp34 — Liu et al., 2018

Megophrys (*Panophrys*) *leishanensis* — Li et al., 2018

Panophrys leishanensis — Lyu et al., 2021

Boulenophrys leishanensis — Qi et al., 2021

Holotype: CIB LS20160610002, adult male, from Mt. Leigong (N26.35888°, E108.19055°E; 1 571 m a.s.l.), Leishan County, Qiandongnan, Guizhou, China.

Paratypes: Nine adult males CIB LS20141004004, LS20160610001, 003–004, 006, LS20171001001, 003–005, and two adult females CIB LS20160610005, LS20171001002, from same locality as holotype.

Specimens examined: Six adult males SYS a001835–1836, 2213–2214, 2279–2280, and one female SYS a002228, from Mt. Leigong.

Diagnosis: Based on examined specimens: (1) adult males, SVL 30.9–34.7 mm ($n=6$) (SVL 30.4–38.7, $n=10$; type series); adult female, SVL 37.4 mm ($n=1$) (SVL 42.3–42.3, $n=2$; type series); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin rough with numerous granules; weak discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; dorsal limbs with discontinuous transverse ridges; large tubercles scattered on flanks; ventral skin smooth; (6) outer margin of upper eyelid with small horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) inner metacarpal tubercle ovoid and moderate, outer one smaller; relative finger lengths $II < I < IV < III$; distinct subarticular tubercle on base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface brown; dark brown triangular marking between eyes; dark brown X-shaped marking on center of dorsum; dorsal limbs with dark brown transverse bands; ventral surface brown with white blotches on belly; (11) nuptial pads bearing black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 18E).

Distribution: Known only from its type locality in Mt. Leigong at elevations of 1 200–1 750 m a.s.l. (Li et al., 2018; this study) (Supplementary Figure S7).

***Boulenophrys liboensis* (Zhang, Li, Xiao, Li, Pan, Wang, Zhang, and Zhou, 2017)**

Libo horned toad / li bō jiǎo chán (荔波角蟾)

Chresonymy: *Xenophrys liboensis* — Zhang et al., 2017

Megophrys liboensis — Yang et al. 2018

Xenophrys (Xenophrys) liboensis — Fei, 2020

Panophrys liboensis — Lyu et al., 2021

Boulenophrys liboensis — Qi et al., 2021

Holotype: GZNU 20160408008, adult male, from Libo County (N25.4731°, E108.1054°; 634 m a.s.l.), Qiannan, Guizhou, China.

Paratypes: Three adult males GZNU 20160408001, 004, 007, eight adult females GZNU 20150813002, 20160408002–003, 005–006, 009–011, and one juvenile GZNU 20150813001, from same locality as holotype.

Diagnosis: Based on original description (Zhang et al., 2017): (1) adult males, SVL 60.5–67.7 mm ($n=4$); adult females, SVL 60.8–70.6 mm ($n=8$); (2) snout obtusely pointed, canthus rostralis well developed, sharp; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin mostly smooth with scattered distinct tubercles; weak X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; ventral skin smooth; (6) outer margin of upper eyelid with distinct elongated horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) inner metacarpal tubercle moderate and elliptical, outer one small and flat; relative finger lengths $I < II < IV < III$; indistinct, rounded, and slightly protuberant subarticular tubercle at base of each

finger; (8) hindlimbs slender, heels slightly overlapping when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and moderate lateral fringes; inner metatarsal tubercle small and ovoid, outer one absent; (10) dorsal surface rust with maroon markings; brown triangular marking between eyes; brown X-shaped marking on center of dorsum; dorsal limbs with rosewood transverse bands; posterior flank and anterior thighs near groin red; two parallel black bands ventrolaterally; throat and chest carmine, belly gray, all with rosewood blotches; (11) subgular vocal sac present in males.

Distribution: Known only from its type locality in Libo County at elevations of ca. 630 m a.s.l. (Zhang et al., 2017) (Supplementary Figure S7).

Remarks: The institute abbreviation of this species was provided as GNUG in the original description (Zhang et al., 2017) but has been officially changed to GZNU (Luo et al., 2021).

***Boulenophrys lini* (Wang and Yang, 2014)**

Lin's horned toad / lín shì jiǎo chán (林氏角蟾)

Chresonymy: *Xenophrys lini* — Wang et al., 2014; Chen et al. 2017

Megophrys lini — Li et al., 2014

Megophrys (Panophrys) lini — Mahony et al., 2017

Boulenophrys lini — Fei, 2020; Qi et al., 2021

Panophrys lini — Lyu et al., 2021

Holotype: SYS a001420, adult male, from Bamianshan (N26°34'37.97", E114°06'06.43"; 1 369 m a.s.l.), Mt. Jinggang, Jinggangshan City, Ji'an, Jiangxi, China.

Paratypes: Eight adult males SYS a001419, 1421, 2382–2386, CIB 107666 (formerly SYS a002381), from same locality as holotype; six adult males SYS a002375–2380, from Jingzhushan (N26°29'48.32", E114°04'49.21"; 1 150 m a.s.l.), Mt. Jinggang; five adult males SYS a002369–2370, 2372–2374, from Nanfengmian (N26°18 '40.99 ", E114°02'26.71 "; 1 100–1 200 m a.s.l.), Suichuan County, Ji'an; five adult females SYS a001417–1418, 1422–1424, from Dabali (N26°28'12.43", E114°05'07.72"; 1 523–1 610 m a.s.l.), Mt. Jinggang; one juvenile SYS a002128 from Niushiping (N26°25'19.08", E114°02'53.21"; 1 560 m a.s.l.), Taoyuandong Nature Reserve, Yanling County, Zhuzhou, Hunan, China.

Specimens examined: Type materials (20 adult males, five adult females, and one juvenile).

Diagnosis: Based on examined specimens: (1) adult males, SVL 34.1–39.7 mm ($n=20$); adult females, SVL 37.0–39.9 mm ($n=5$); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges weak, vomerine teeth absent; (5) dorsal skin smooth with scattered granules; indistinct discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges indistinct; several tubercles on flanks; ventral skin smooth; (6) outer margin of upper eyelid with horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles substantially enlarged; relative finger lengths $II < I < IV < III$; distinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching anterior corner of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and wide lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface light brown or olive; dark triangular marking between eyes; X marking on center of

dorsum; dorsal limbs and digits with dark brown transverse bands; ventral surface reddish brown; obscure longitudinal black stripe on center of throat; several white blotches on belly, two parallel black bands ventrolaterally; (11) scattered, tiny, black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Occurs in multiple localities in the hilly areas along the border between Jiangxi and Hunan at elevations of 1 100–1 610 m a.s.l., including Mt. Jinggang and Nanfengmian in western Jiangxi and Taoyuandong Nature Reserve and Mt. Bamian in eastern Hunan (Wang et al., 2014; this study) (Supplementary Figure S8).

***Boulenophrys lishuiensis* (Wang, Liu, and Jiang, 2017)**

Lishui horned toad / lí shuǐ jiǎo chán (丽水角蟾)

Chresonymy: *Xenophrys lishuiensis* — Wang et al., 2017b

Megophrys lishuiensis — Tapley et al., 2018

Boulenophrys lishuiensis — Fei, 2020; Qi et al., 2021

Panophrys lishuiensis — Lyu et al., 2021

Holotype: CIB 106669 (formerly WYF00164), adult male, from Fengyang Forest Station (N28°11'51.72", E119°49'02.28"; 1 100 m a.s.l.), Liandu District, Lishui, Zhejiang, China.

Allotype: CIB 106670 (formerly WYF00169), adult female, from same locality as holotype.

Paratypes: Twelve adult males CIB 106671–106677 (formerly WYF00165–168, 171–173), ZMNH WYF00174–00178, and two adult females CIB 106678 (formerly WYF11011), ZMNH WYF00170, from same locality as holotype.

Specimens examined: Nine adult males SYS a008439–8440, 8442–8448, and one adult female SYS a008441, from Fengyang Forest Station.

Diagnosis: Based on examined specimens: (1) adult males, SVL 30.9–33.9 mm ($n=9$); adult female, SVL 38.3 mm ($n=1$); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin relatively smooth with sparse granules; discontinuous weak X-shaped, "><"-shaped, or V-shaped ridge on center of dorsum or absent, dorsolateral ridges absent; ventral skin smooth with several tubercles on rear of hindlimbs; (6) outer margin of upper eyelid with horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths $I=II<IV<III$; indistinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels just meeting when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward; (9) toes without webbing and lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface grayish brown, yellowish brown, or reddish brown; triangular marking with light edge between eyes; dark X-shaped, "><"-shaped, or V-shaped marking with light edge on center of dorsum; dorsal limbs with dark brown transverse bands; longitudinal dark brown stripe on center of throat; ventral surface gray, two parallel broad gray-brown bands ventrolaterally; (11) nuptial pad with dense black spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 18F).

Distribution: Known only from its type locality in Liandu District at elevations of 900–1 200 m a.s.l. (Wang et al., 2017b; this study) (Supplementary Figure S7).

***Boulenophrys mirabilis* (Lyu, Wang, and Zhao, 2020)**

Huaping horned toad / huā píng jiǎo chán (花坪角蟾)

Chresonymy: *Megophrys* sp25 — Liu et al., 2018

Megophrys (*Panophrys*) *mirabilis* — Lyu et al., 2020

Panophrys mirabilis — Lyu et al., 2021

Boulenophrys mirabilis — Qi et al., 2021

Holotype: SYS a002917, adult male, from Huaping Nature Reserve (N25.5554°, E109.9490°; ca. 1 300 m a.s.l.), Lingui District, Guilin, Guangxi, China.

Paratypes: Adult male SYS a002192 and two adult females SYS a002193, CIB 118530 (formerly SYS a002289), from same locality as holotype.

Specimens examined: Type materials (two adult males and two adult females).

Diagnosis: Based on examined specimens: (1) adult males, SVL 55.8–61.4 mm ($n=2$); adult females, SVL 68.5–74.8 mm ($n=2$); (2) canthus rostralis well developed; tongue small, majority attached to mandible, not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin smooth with sparse granules; discontinuous X-shaped ridge on center of dorsum, with several short ridges, dorsolateral ridges absent; ventral skin smooth with several tubercles on rear of hindlimbs; (6) outer margin of upper eyelid with horn-like, distinctly prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; small tubercles arranged from above nostril, along canthus rostralis, edge of upper eyelid and supratympanic fold, to posterior margin of temporal region; (7) two metacarpal tubercles indistinct, inner one observably enlarged; relative finger lengths $II<IV<III$; indistinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and distinct narrow lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface grayish brown, tinged with blue in males, but dorsal surface reddish brown in females; dark X-shaped marking with light edge on center of dorsum; dorsal limbs with dark brown transverse bands; throat and chest with grayish blue latticed patches and black spots in males, but with orange latticed patches and black spots in females; ventral hands and feet grayish white; (11) underdeveloped nuptial pad not bearing spines on dorsal bases of fingers I and II in breeding adult males; males without subgular vocal sacs.

Distribution: Known only from its type locality in Huaping Nature Reserve at elevations of 1 300–1 330 m a.s.l. (Lyu et al., 2020) (Supplementary Figure S7).

***Boulenophrys mufumontana* (Wang, Lyu, and Wang, 2019)**

Mt. Mufu horned toad / mù fù shān jiǎo chán (幕阜山角蟾)

Chresonymy: *Megophrys* (*Panophrys*) *mufumontana* — Wang et al., 2019a

Panophrys mufumontana — Lyu et al., 2021

Boulenophrys mufumontana — Qi et al., 2021

Holotype: SYS a006391, adult male, from Mt. Mufu (N28°58'18.45", E113°48'58.53"; 1 300 m a.s.l.), Pingjiang County, Yueyang, Hunan, China.

Paratypes: One adult male SYS a006392, and two adult females CIB 110012, SYS a006419, from same locality as holotype.

Specimens examined: Type materials (two adult males and two adult females); one adult male SYS a006458 and one

adult female SYS a006489, from Mt. Dawei (N28.4250°, E114.0805°; ca. 800 m a.s.l.), Liuyang City, Changsha, Hunan; two adult females SYS a006971–6972, from Mt. Jiuling (N29.1078°, E115.3048°; ca.700 m a.s.l.), Wuning County, Jiujiang, Jiangxi, China.

Diagnosis: Based on examined specimens: (1) adult males, SVL 29.9–30.8 mm ($n=3$); adult females, SVL 36.3–38.8 mm ($n=5$); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct, upper 1/4 part concealed by supratympanic fold; (4) vomerine ridges weak, vomerine teeth absent; (5) dorsal skin rough with dense granules and small tubercles; discontinuous V-shaped or X-shaped ridge on center of dorsum, dorsolateral ridges absent; flanks with tubercles; ventral skin smooth with granules; ventral thighs with dense small whitish tubercles; (6) outer margin of upper eyelid with horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) inner metacarpal tubercle distinct and observably enlarged, outer one indistinct; relative finger lengths $II=IV<I<III$; distinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching region between posterior margin of tympanum and center of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface light brown to dark brown; dark triangular marking between eyes, dorsal limbs with black transverse bands; throat and chest grayish brown with dark brown patches and creamy white spots, belly grayish white with creamy white and orange spots, two parallel black bands ventrolaterally; (11) nuptial spines present on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known from Mt. Mufu in northeastern Hunan and Mt. Jiuling and Guanshan Nature Reserve in northwestern Jiangxi at elevations of 300–1 300 m a.s.l. (Wang et al., 2019a; this study) (Supplementary Figure S8).

Remarks: Based on phylogenetic analysis of three mitochondrial segments (Figure 3), the intraspecific divergences between different populations of this species are relatively large compared with other congeners. Nonetheless, our morphological examination of specimens from different populations failed to discover distinct characters to distinguish them, and thus they are hereby considered to be conspecific. Moreover, different populations of *B. mufumontana* are distributed in the Jiuling and Mufu mountains along the border between Jiangxi and Hunan, thus molecular intraspecific divergences may be due to geographical isolation.

***Boulenophrys nankunensis* (Wang, Zeng, and Wang, 2019)**

Mt. Nankun horned toad / nán kūn shān jiǎo chán (南昆山角蟾)

Chresonymy: *Megophrys* sp10 — Liu et al., 2018

Megophrys (*Panophrys*) *nankunensis* — Wang et al., 2019a

Panophrys nankunensis — Lyu et al., 2021

Boulenophrys nankunensis — Qi et al., 2021

Holotype: SYS a004498, adult male, from Mt. Nankun (N23°38'19", E113°53'24"; 400 m a.s.l.), Longmen County, Huizhou, Guangdong, China.

Paratypes: Ten adult males SYS a002023, 2032–2033, 4499–4504, CIB 110007, and two adult females SYS a004506–4507, from same locality as holotype.

Specimens examined: Type materials (11 adult males and two adult females).

Diagnosis: Based on examined specimens: (1) adult males, SVL 29.9–34.9 mm ($n=11$); adult females, SVL 39.4–41.9 mm ($n=2$); (2) snout rounded, canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges strong, vomerine teeth present; (5) dorsal skin smooth with dense granules; discontinuous weak X-shaped ridge on center of dorsum, dorsolateral ridges absent; large tubercles on flanks; ventral skin smooth with granules on belly; (6) outer margin of upper eyelid with horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) inner metacarpal tubercle distinct and observably enlarged, outer one indistinct; relative finger lengths $II<I<IV<III$; distinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels not meeting when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface beige to dark brown, with indistinct light brown patches; incomplete triangular marking between eyes, X-shaped marking on center of dorsum; dorsal limbs with black transverse bands; throat and chest dark brown with scarlet spots, posterior of belly white with dark brown and scarlet spots; (11) dense dark villiform nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known only from its type locality in Mt. Nankun at elevations of 300–600 m a.s.l. (Wang et al., 2019a) (Supplementary Figure S8).

***Boulenophrys nanlingensis* (Lyu, Wang, Liu, and Wang, 2019)**

Nanling horned toad / nán líng jiǎo chán (南岭角蟾)

Chresonymy: *Megophrys* sp6 — Liu et al., 2018

Megophrys sp7 — Liu et al., 2018

Megophrys (*Panophrys*) *nanlingensis* — Wang et al., 2019a

Panophrys nanlingensis — Lyu et al., 2021

Boulenophrys nanlingensis — Qi et al., 2021

Holotype: SYS a001964, adult male, from Nanling Nature Reserve (N24°54'48.80", E113°01'12.34"; 1 008 m a.s.l.), Ruyuan County, Shaoguan, Guangdong, China.

Paratypes: Five adult males SYS a001959–1962, CIB 110010, from same locality as holotype; four adult males SYS a002334, 2356–2358, from Mt. Qiyun (N25°52'22.84", E114°01'52.09"; 691–1 355 m a.s.l.), Chongyi County, Ganzhou, Jiangxi, China.

Specimens examined: Type materials (10 adult males).

Diagnosis: Based on examined specimens: (1) adult males, SVL 30.5–37.3 mm ($n=10$); (2) snout rounded, canthus rostralis well developed; tongue notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin rough; head covered with small tapered granules from temporal region, upper lip, loreal region to tip of snout; discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; large tubercles on flanks; ventral skin smooth, several large granules and tubercles ventrolaterally; (6) outer margin of upper eyelid with horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths $II<I<IV<III$;

subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching region between posterior corner and center of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface brown; dark triangular marking with light edge between eyes, X marking with light edge on center of dorsum; dorsal limbs with brown transverse bands; ventral surface pale gray, indistinct longitudinal stripe on center of throat, scarlet spots on chest, belly whitish gray with dark brown marbling, two parallel black bands scattered with several white tubercles ventrolaterally; (11) nuptial pads/spines absent in breeding adult males; subgular vocal sac present in males.

Distribution: Known from Nanling Nature Reserve, Mangshan Nature Reserve, and Mt. Qiyun, at elevations of 690–1 400 m a.s.l., all situated at the border of Guangdong, Hunan, and Jiangxi (Wang et al., 2019a) (Supplementary Figure S7).

Remarks: Based on molecular data for species delimitation, Liu et al. (2018) suggested that the populations from Jiangxi (labeled as *M. sp6*) and Guangdong (labeled as *M. sp7*) may belong to two cryptic species (though considered conspecific in ABGD analysis). Further detailed morphological examination failed to discover distinct characters to distinguish these two populations, which were suggested to be conspecific (Wang et al., 2019a).

***Boulenophrys obesa* (Wang, Li, and Zhao, 2014)**

Heishiding horned toad / hēi shí dǐng jiǎo chán (黑石顶角蟾)

Chresonymy: *Megophrys obesa* — Li et al., 2014

Xenophrys obesa — Chen et al., 2017

Megophrys (Panophrys) obesa — Mahony et al., 2017

Boulenophrys obesa — Fei, 2020; Qi et al., 2021

Panophrys obesa — Lyu et al., 2021

Holotype: SYS a002275, adult male, from Heishiding Nature Reserve (N23°28'27", E111°53'53"; 399.2 m a.s.l.), Fengkai County, Zhaoqing, Guangdong, China.

Paratypes: Six adult females SYS a000164, 0178, 1956, 2271–2272, CIB 107663 (formerly SYS a002270), from same locality as holotype.

Specimens examined: Type materials (one adult male and six adult females).

Diagnosis: Based on examined specimens: (1) adult male, SVL 35.6 mm ($n=1$); adult females, SVL 37.5–41.2 mm ($n=6$); (2) snout rounded, canthus rostralis developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges present, vomerine teeth absent; (5) dorsal skin smooth with scattered granules and several tubercles; discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; several tubercles scattered on flanks and posterior dorsum; ventral skin smooth with scattered small granules; (6) outer margin of upper eyelid with horn-like, slightly prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles well developed, inner one observably enlarged; relative finger lengths I<II<IV<III; distinct subarticular tubercle at base of each finger; (8) hindlimbs robust, heels not meeting when hindlimbs folded; tibiotarsal articulation reaching posterior corner of eye when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface dark brown; dark

triangular marking between eyes; dorsal limbs with black transverse bands; ventral surface gray black; throat, chest with black spots and scattered orange spots; black longitudinal stripe on center of throat; belly mottled with white and dotted with orange red spots on center, large black bands ventrolaterally; (11) nuptial pads/spines absent in collected adult male; subgular vocal sac present in male.

Distribution: Known only from its type locality in Heishiding Nature Reserve at elevations of 399–435 m a.s.l. (Li et al., 2014) (Supplementary Figure S8).

***Boulenophrys ombrophila* (Messenger and Dahn, 2019)**

Yu Shen horned toad / yǔ shén jiǎo chán (雨神角蟾)

Chresonymy: *Megophrys sp8* — Liu et al., 2018

Megophrys sp9 — Liu et al., 2018

Megophrys ombrophila — Messenger et al., 2019

Panophrys ombrophila — Lyu et al., 2021

Boulenophrys ombrophila — Qi et al., 2021

Holotype: WUYI 2014101, adult male, from a bamboo plantation outside Guadun Village (N27.735980°, E117.640810°; 1242 m a.s.l.), Wuyishan City, Nanping, Fujian, China.

Paratypes: Four adult males WUYI 2014102–03, NJFU 2015201–02, four adult females WUYI 2014104, 2015101, NJFU 2015203–04, and one road-killed specimen of unknown sex NJFU 2015205, from vicinity of Guadun Village (N27.7317°–27.734°, E117.6366°–117.646°; 1 125–1 350 m a.s.l.).

Specimens examined: Nine adult males SYS a004612–4620 and one adult female SYS a004621, from Daqitian Protection Station (N24.5776°, E114.4432°; ca. 560 m a.s.l.), Mt. Jiulian, Longnan City, Ganzhou, Jiangxi, China; 14 adult males SYS a001976–1985, 5755–5758, from Gaoping Reservoir (N25.1999°, E113.6539°; ca. 430 m a.s.l.), Renhua County, Shaoguan, Guangdong, China; two adult males SYS a008822, 8830, from Mt. Tianjing (N24.6689°, E112.9436°; ca. 990 m a.s.l.), Ruyuan County, Shaoguan; two adult males SYS a008914–8915, from Nanshui Reservoir (N24.8646°, E113.1274°; ca. 500 m a.s.l.), Ruyuan County.

Diagnosis: Based on examined specimens: (1) adult males, SVL 28.4–37.0 mm ($n=27$); adult female, SVL 42.1 mm ($n=1$); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin relatively rough with granules and tubercles; discontinuous V-shaped or X-shaped ridge on center of dorsum, dorsolateral ridges present; flanks with tubercles; ventral skin smooth with granules; (6) outer margin of upper eyelid with horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths I<II<IV<III; distinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels not meeting when hindlimbs folded; tibiotarsal articulation reaching region between anterior and posterior margins of tympanum when leg stretched forward; (9) toes without webbing and lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface light brown to dark brown; dark triangular marking between eyes, X-, V-, or Y-shaped marking on center of dorsum; dorsal limbs with black transverse bands; throat and chest reddish, longitudinal stripe on center of throat; belly gray with white and reddish spots, two parallel black bands ventrolaterally; (11) nuptial spines present on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac

present in males (Figure 18G).

Distribution: Known from multiple localities in hilly areas along the border of Jiangxi, Guangdong, and Hunan, including Mt. Jiulian, Gaoping Reservoir, Mt. Tianjing, Nanshui Reservoir, and Mangshan Nature Reserve, at elevations of 400–990 m a.s.l., and an isolated locality in Mt. Wuyi at the border between Fujian and Jiangxi at elevations of 1 125–1 350 m a.s.l. (Messenger et al., 2019; this study) (Supplementary Figure S8).

Remarks: Based on molecular data for species delimitation, Liu et al. (2018) suggested that the populations from Longnan (labeled as *M. sp8*) and Renhua (labeled as *M. sp9*) may belong to two cryptic species (though considered conspecific in ABGD analysis). Subsequently, Messenger et al. (2019) proposed the species *B. ombrophila*, indicating the close relationship and small genetic divergences among *M. sp8*, *M. sp9*, and *B. ombrophila*. In this study, our morphological examination of specimens from the hilly areas along the border of Jiangxi, Guangdong, and Hunan failed to discover any distinct characters to distinguish them from the type series of *B. ombrophila* from Mt. Wuyi (Messenger et al., 2019). Thus, we consider these populations to be conspecific, despite their distinctly isolated distributions. Messenger et al. (2019) also presented a bioacoustic comparison between *M. sp9* and *B. ombrophila*, suggesting some differences contrary to the morphological and molecular proposals, which may be due to limited data or geographical isolation.

***Boulenophrys puningensis* Wang, Zeng, Lyu, Xiao, and Wang, 2022**

Puning horned toad / pǔ níng jiǎo chán (普宁角蟾)

Chresonymy: *Boulenophrys puningensis* — Wang et al., 2022

Holotype: SYS a005770, adult male, from Longkeng Village (N23°07'54.07", E115°51'05.28"; ca. 120 m a.s.l.), Daping Town, Puning City, Jieyang, Guangdong, China.

Paratypes: Three adult males SYS a007649–7650, CIB 118526, and two adult female SYS a007647–7648, from same locality as holotype.

Specimens examined: Type materials (four adult males and two adult females).

Diagnosis: Based on examined specimens: (1) adult males, SVL 31.7–34.6 mm ($n=4$); adult females, SVL 37.8–38.3 mm ($n=2$); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct, dense tubercles on temporal region; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin rough and granular with raised conical tubercles; discontinuous weak X-shaped or V-shaped ridge on center of dorsum, discontinuous dorsolateral ridges indistinct or absent; large tubercles on dorsal limbs and flanks; ventral skin rough with large tubercles on chest, belly, and around cloaca; tubercles on posterior belly, ventral thighs, and around cloaca bearing tiny spines; (6) outer margin of upper eyelid with small horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths $I=II<IV<III$; subarticular tubercle at base of each finger; (8) hindlimbs short, heels not meeting when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle rounded, outer one absent; (10) dorsal surface yellowish brown or light

brown; dark brown triangular marking between eyes; X- or V-shaped marking on center of dorsum; dorsal limbs with dark gray transverse bands; black longitudinal stripe on center of throat; ventral surface dark gray, two parallel black bands ventrolaterally; ventral surface of thighs and around cloaca dark gray; (11) nuptial pads bearing fine and dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known only from its type locality in Puning City at elevations of 120–300 m a.s.l. (Wang et al., 2022) (Supplementary Figure S9).

***Boulenophrys sanmingensis* (Lyu and Wang, 2021)**

Sanming horned toad / sān míng jiǎo chán (三明角蟾)

Chresonymy: *Megophrys sp15* — Liu et al., 2018

Megophrys sp16 — Liu et al., 2018

Panophrys sanmingensis — Lyu et al., 2021

Boulenophrys sanmingensis — Qi et al., 2021

Holotype: SYS a002498, adult male, from Mt. Longqi (N26.5233°, E117.2976°; ca. 700 m a.s.l.), Jiangle County, Sanming, Fujian, China.

Paratypes: Five adult males SYS a002493–2496, CIB 116077, and one adult female SYS a002500, from same locality as holotype.

Specimens examined: Type materials (six adult males and one adult female); six adult males SYS a002486–2491, from Mt. Emeifeng (N27.0058°, E117.0837°; ca. 1 500 m a.s.l.), Taining County, Sanming; one adult male SYS a004110, from Gutian Town (N25.2257°, E116.8492°; ca. 890 m a.s.l.), Shanghang County, Longyan, Fujian; three adult males SYS a001587–1588, 8713, from Mt. Fenghuang (N23.9105°, E116.6081°; ca. 1 180 m a.s.l.), Chao'an District, Chaozhou, Guangdong, China; six adult males SYS a007061–7066, from Mt. Junfeng (N27.2039°, E116.3478°; ca. 910 m a.s.l.), Nanfeng County, Fuzhou, Jiangxi, China; four adult males SYS a007057–7060 and one adult female SYS a007056, from Mt. Magu (N27.5284°, E116.5251°; ca. 910 m a.s.l.), Nancheng County, Fuzhou.

Diagnosis: Based on examined specimens: (1) adult males, SVL 26.4–32.4 mm ($n=26$); adult female, SVL 29.5–34.7 mm ($n=2$); (2) canthus rostralis well developed; tongue notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin rough with dense spiny granules and scattered raised tubercles; discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; flank with large raised conical tubercles; ventral surface smooth with tiny granules; (6) outer margin of upper eyelid with small horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths $I<II<IV<III$; subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching posterior corner of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and wide lateral fringes; inner metatarsal tubercle rounded, outer one absent; (10) dorsal surface yellowish brown or reddish brown; dark incomplete triangular marking with light edge between eyes; dark X-shaped marking with light edge on center of dorsum; ventral surface pale with densely distributed white spots, two parallel black bands ventrolaterally; (11) nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Occurs in the wide hilly areas of Fujian, Jiangxi, and Guangdong provinces at elevations of 500–1 250 m a.s.l. (Lyu et al., 2021; this study) (Supplementary Figure S9).

Remarks: Based on molecular data for species delimitation, Liu et al. (2018) suggested that the populations from Sanming (labeled as *M. sp15*) and Chaozhou (labeled as *M. sp16*) may belong to two cryptic species (though considered conspecific in ABGD analysis). Subsequently, Lyu et al. (2021) described *B. sanmingensis* based on specimens from Sanming and mentioned that its distribution included Chaozhou but did not discuss the status of *M. sp16*, as only two tadpoles were available for the Chaozhou population. In this work, newly collected adult specimens of the Chaozhou population are included, and the morphological examination failed to discover distinct characters to distinguish them from the Sanming, Longyan, and Fuzhou populations. Thus, we consider these populations to be conspecific.

***Boulenophrys shimentaina* (Lyu, Liu, and Wang, 2020)**

Shimentai horned toad / shí mén tái jiǎo chán (石门台角蟾)

Chresonymy: *Megophrys palpebralespinosa* — Li et al., 2011
Megophrys sp29 — Liu et al., 2018

Megophrys (Panophrys) shimentaina — Lyu et al., 2020

Panophrys shimentaina — Lyu et al., 2021

Boulenophrys shimentaina — Qi et al., 2021

Holotype: SYS a004710, adult male, from Shimentai Nature Reserve (N24.4095°, E113.1095°; ca. 370 m a.s.l.), Yingde City, Qingyuan, Guangdong, China.

Paratypes: Eleven adult males SYS a002077, 2081–2085, 4172–4173, 5992–5993, CIB 110015, from same locality as holotype.

Specimens examined: Type materials (12 adult males); eight adult males SYS a002819–2826, from Nanling Nature Reserve (N24.9171°, E113.0090°; ca. 1 160 m a.s.l.), Ruyuan County, Shaoguan, Guangdong; one adult female SYS a004189, from Mt. Tianjing (N24.6689°, E112.9436°; ca. 990 m a.s.l.), Ruyuan County.

Diagnosis: Based on examined specimens: (1) adult males, SVL 25.8–30.6 mm ($n=20$); adult female, SVL 34.5 mm ($n=1$); (2) snout rounded, canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges weak, vomerine teeth present; (5) dorsal skin rough; tiny, barely visible, black to dark brown spines arranged on whole dorsal skin, flanks, dorsal limbs, around cloaca, and rear of hindlimbs; discontinuous X-shaped, Y-shaped, or “\ /”-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; several large warts on flanks; ventral skin smooth with several granules bearing black spines on rear of hindlimbs and around cloaca; (6) outer margin of upper eyelid with small horn-like tubercle; supratympanic fold distinct and narrow, with or without spines, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths $I=II<IV<III$; indistinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and tip of snout when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface light brown; dark brown stripe on each upper eyelid in Yingde population, incomplete dark triangular marking between eyes in Ruyuan population; dorsal limbs with narrow dark brown transverse bands; ventral surface pale, scarlet

spots on chest; large white blotch on belly, two parallel black bands ventrolaterally; (11) weak nuptial pads bearing serrated olive nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known from Shimentai Nature Reserve, Luokeng Nature Reserve, and Nanling Nature Reserve in northern Guangdong, and Mangshan Nature Reserve in southernmost Hunan, at elevations of 210–1 200 m a.s.l. (Lyu et al., 2020; this study) (Supplementary Figure S9).

***Boulenophrys shuichengensis* (Tian and Sun, 1995)**

Shuicheng horned toad / shuǐ chéng jiǎo chán (水城角蟾)

Chresonymy: *Megophrys shuichengensis* — Tian & Sun, 1995; Tian et al., 2000; Fei et al., 2009, 2012

Xenophrys shuichengensis — Delorme et al., 2006; Chen et al., 2017

Xenophrys (Tianophrys) shuichengensis — Fei & Ye, 2016; Fei, 2020

Megophrys (Panophrys) shuichengensis — Mahony et al., 2017

Panophrys shuichengensis — Lyu et al., 2021

Boulenophrys shuichengensis — Qi et al., 2021

Holotype: LTHC 944001, adult female, from Fenghuang Town (N26°34', E104°51'; 1 850 m a.s.l.), Shuicheng County (now not Shuicheng but Zhongshan District), Liupanshui, Guizhou, China.

Paratypes: Seven males, three females, and 34 tadpoles (voucher numbers not provided), from same locality as holotype.

Diagnosis: Based on previous descriptions (Fei & Ye, 2016; Tian & Sun, 1995; Tian et al., 2000): (1) adult males, SVL 102.0–118.3 mm ($n=8$); adult females, SVL 99.8–115.6 mm ($n=7$); (2) snout rounded, canthus rostralis well developed; tongue weakly notched posteriorly; (3) tympanum distinct; (4) vomerine ridges present, vomerine teeth absent; (5) dorsal skin relatively smooth with sparse granules; discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; large tubercles on flanks; ventral skin smooth; (6) outer margin of upper eyelid elongated as triangular appendage; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) outer metacarpal tubercles absent, inner one distinct; relative finger lengths $II<IV<I<III$; indistinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels not meeting when hindlimbs folded; tibiotarsal articulation reaching posterior corner of eye when leg stretched forward; (9) toes with wide lateral fringe, fourth toe with 1/3 webbing; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface brown; hollow dark triangular marking between eyes, indistinct X-shaped marking on center of dorsum; ventral surface pale gray with dark patches on chest; longitudinal stripe on center of throat; (11) nuptial pads/spines absent in collected adult males; subgular vocal sacs in males absent.

Distribution: Currently recognized from its type locality in Shuicheng County in western Guizhou at elevations of 1 800–1 870 m a.s.l. (Tian et al., 2000) (Supplementary Figure S9). A record from Suiyang County in northern Guizhou was also provided but related voucher numbers were not given (Fei & Ye, 2016; Fei et al., 2009, 2012). This region is far from the type locality in Shuicheng County and this record is suspect, with further vouchers warranted.

Remarks: In the original description of this species, the designation of the type series was stated as one female

holotype with “7 males, 3 females, and 34 tadpoles” paratypes, but was stated as one female holotype with three female paratypes, one male allotype, and five male paratypes in the measurements in Table 2, which is inconsistent (Tian & Sun, 1995). We consider the allotype as invalid as it was not officially stated in the designation. However, the number of male paratypes is currently uncertain as the voucher numbers were not provided in the original description and the paratypes were invalidly re-designated in subsequent work (Tian et al., 2000). This species was subsequently redescribed as a “new species” by Tian et al. (2000) using the same holotype, creating an objective synonym (Ohler et al., 2015). Particularly, males were described as “with a subgular vocal sac” in Tian & Sun (1995) but revised as “without subgular vocal sacs” in Tian et al. (2000).

The phylogenetic placement of *B. shuichengensis* remains uncertain due to the current lack of available molecular data. It was placed in the genus *Boulenophrys* based on its morphological similarities with other *Boulenophrys* congeners (subarticular tubercles present on fingers). Furthermore, *B. shuichengensis* was suggested to be morphologically close to *B. caudoprocta* (as subgenus *Tianophrys*; Fei & Ye, 2016). According to information provided by two anonymous reviewers, they both collected the samples of *B. shuichengensis* and their unpublished phylogenetic results both support its close relationship with *B. caudoprocta*. Hence, we place this species within the *B. boettgeri* group in current study following suggestions from two anonymous reviewers.

***Boulenophrys shunhuangensis* (Wang, Deng, Liu, Wu, and Liu, 2019)**

Shunhuang horned toad / shùn huáng jiǎo chán (舜皇角蟾)

Chresonymy: *Megophrys minor* — Liu & Hu, 1961

Megophrys minor brachykolos — Ye & Fei, 1995

Megophrys brachykolos — Fei et al., 2009, 2012; Fei & Ye, 2016

Megophrys sp6 — Chen et al., 2017

Megophrys sp24 — Liu et al., 2018

Megophrys shunhuangensis — Wang et al., 2019b

Panophrys shunhuangensis — Lyu et al., 2021

Boulenophrys shunhuangensis — Qi et al., 2021

Holotype: HNNU 16SH02, adult male, from Mt. Shunhuang (N26.441990°, E111.013876°; 882 m a.s.l.), Xinning County, Shaoyang, Hunan, China.

Paratypes: Four adult males HNNU 16SH06–08, 16SH13, one adult female HNNU 16SH04, and one juvenile HNNU 16SH14, from same locality as holotype; five adult males HNNU 18NS01–05 from vicinity of Nanshan Town, Nanshan Forest Park (N26.148937°–26.156547°, E110.166623°–110.175120°; 1 102–1 233 m a.s.l.), Chengbu County, Shaoyang.

Specimens examined: Five adult males SYS a002196, 2198, 2914–2916, and one female SYS a002282, from Huaping Nature Reserve (N25.5554°, E109.9490°; ca. 1 300 m a.s.l.), Lingui District, Guilin, Guangxi, China; 10 adult males SYS a002292, 2294–2302, and two adult females SYS a002291, 2293, from Mt. Mao'er (N25.8621°, E110.4083°; ca. 1 600 m a.s.l.), Xing'an County, Guilin.

Diagnosis: Based on examined specimens: (1) adult males, SVL 28.9–37.1 mm ($n=15$); adult females, SVL 38.4–42.5 mm ($n=3$); (2) snout rounded, canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin

mostly smooth with scattered granules and several tubercles; discontinuous X-shaped on center of dorsum, discontinuous dorsolateral ridges present; several large warts on flanks; limbs mostly smooth with discontinuous transverse ridges; ventral skin smooth with granules on hindlimbs and posterior belly; (6) outer margin of upper eyelid with small horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) inner metacarpal tubercle ovoid and moderate, outer one smaller and flat; relative finger lengths I<II<IV<III; subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching region between eye and tip of snout when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle small ovoid, outer one absent; (10) dorsal surface brick red or grayish brown; brown triangular marking between eyes; light brown X-shaped marking on center of dorsum; dorsal limbs with dark brown transverse bands; ventral surface brown with white reticulate pattern at center of lower belly, two parallel dark brown bands ventrolaterally; (11) nuptial pads bearing tiny and dense nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 18H).

Distribution: Known from multiple localities in hilly areas along the border between Hunan and Guangxi at elevations of 880–1 600 m a.s.l., including Mt. Shunhuang, Nanshan Forest Park, and Huangsang Nature Reserve in southwestern Hunan, and Huaping Nature Reserve and Mt. Mao'er in northeastern Guangxi (Wang et al., 2019b; this study) (Supplementary Figure S8).

***Boulenophrys tongboensis* (Wang and Lyu, 2021)**

Mt. Tongbo horned toad / tóng bó shān jiǎo chán (铜拔山角蟾)

Chresonymy: *Megophrys* sp21 — Liu et al., 2018

Panophrys tongboensis — Lyu et al., 2021

Boulenophrys tongboensis — Qi et al., 2021

Holotype: SYS a003228, adult male, from Pingxi (N28.1154°, E118.2372°; ca. 1 100 m a.s.l.), Mt. Tongbo, Guangfeng District, Shangrao, Jiangxi, China.

Paratypes: Four adult males SYS a003225–3227, CIB 116078, from same locality as holotype.

Specimens examined: Type materials (five adult males).

Diagnosis: Based on examined specimens: (1) adult males, SVL 26.5–31.5 mm ($n=5$); (2) canthus rostralis well developed; tongue notched posteriorly; (3) tympanum visible, anterior edge indistinct; (4) vomerine ridges and vomerine teeth present; (5) dorsal skin relatively smooth with tiny granules; discontinuous X-shaped or “> <”-shaped ridge on center of dorsum, dorsolateral ridges indistinct or absent; ventral surface smooth with scattered tubercles on thigh; (6) outer margin of upper eyelid with small horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths II<I<IV<III; subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes without webbing and lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface beige or olive-beige; brown V-shaped or triangular marking with light edge between eyes; brown X-shaped or “> <”-shaped marking with light edge on center of dorsum; ventral surface dark brown with densely distributed

white spots, two parallel black bands ventrolaterally; (11) nuptial pads/spines absent in collected adult males; subgular vocal sac present in males.

Distribution: Known only from its type locality in Mt. Tongbo at elevations of 1 100–1 115 m a.s.l. (Lyu et al., 2021) (Supplementary Figure S9).

***Boulenophrys tuberogranulata* (Shen, Mo, and Li, 2010)**

Tianzishan horned toad / jí yóu jiǎo chán (棘疣角蟾)

Chresonymy: *Megophrys tuberogranulatus* — Mo et al., 2010; Fei et al., 2012

Boulenophrys tuberogranulatus — Fei & Ye, 2016; Fei, 2020; Qi et al., 2021

Xenophrys tuberogranulatus — Chen et al., 2017

Megophrys (Panophrys) tuberogranulatus — Mahony et al., 2017

Panophrys tuberogranulatus — Lyu et al., 2021

Holotype: HNNU 03080902, adult male, from Tianzishan Nature Reserve (N29°20′–29°50′, E110°20′–110°30′; 1 130 m a.s.l.), Sangzhi County, Zhangjiajie, Hunan, China.

Allotype: HNNU 880800853, adult female, from Simenyan, Mt. Tianping (N20°20′–29°50′, E109°50′–110°30′; 1 130 m a.s.l.), Sangzhi.

Paratypes: Six adult males HNNU 03080904, 880800851–52, 880700751–53, from same locality as holotype; two adult males HNNU 88062801–02, from Mt. Tianping.

Specimens examined: One adult male SYS a004310, from Mt. Tianping (N29.7591°, E110.0624°; ca. 1 380 m a.s.l.).

Diagnosis: Based on previous descriptions (Fei & Ye, 2016; Mo et al., 2010) and examined specimens: (1) adult males, SVL 33.2–40.3 mm ($n=9$; Fei & Ye, 2016) (SVL 44.0 mm, $n=1$; this study); adult female, SVL 50.5 mm ($n=1$; Fei & Ye, 2016); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin granulated with faint folds and tubercles; weak discontinuous X-shaped ridge on center of dorsum or absent, discontinuous dorsolateral ridges indistinct or absent; large tubercles on flanks and dorsal hindlimbs; ventral skin smooth; (6) outer margin of upper eyelid with small horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct, inner one observably enlarged; relative finger lengths $II < I = IV < III$; subarticular tubercle at base of each finger; (8) hindlimbs slender, heels slightly overlapping when hindlimbs folded; tibiotarsal articulation reaching anterior corner of eye when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle indistinct, outer one absent; (10) dorsal surface yellowish brown with irregular netlike dark brown markings; dorsal limbs with dark brown transverse bands; posterior flank and anterior thighs near groin red; ventral surface purplish brown, belly whitish netlike markings; (11) nuptial pads bearing black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 181).

Distribution: Known only from Tianzishan Nature Reserve and Mt. Tianping in northwestern Hunan at elevations of 1 000–1 380 m a.s.l. (Mo et al., 2010; this study) (Supplementary Figure S10).

Remarks: The institute abbreviation of this species was provided as HNUL in the original description by Mo et al. (2010) but has been officially changed to HNNU (Sheng-Chao Shi, pers. comm.). The gender of this species is changed to *B.*

tuberogranulata in this work.

***Boulenophrys wugongensis* (Wang, Lyu, and Wang, 2019)**

Wugongshan horned toad / wǔ gōng shān jiǎo chán (武功山角蟾)

Chresonymy: *Megophrys* sp12 — Liu et al., 2018

Megophrys (Panophrys) wugongensis — Wang et al., 2019a

Panophrys wugongensis — Lyu et al., 2021

Boulenophrys wugongensis — Qi et al., 2021

Holotype: SYS a00 2625, adult male, from Yangshimu Scenic Area (N27°34′47.93″, E114°15′07.34″; 550 m a.s.l.), Luxi County, Pingxiang, Jiangxi, China.

Paratypes: Three adult males SYS a004796, 4800, CIB 110011, and nine adult females SYS a002610–2611, 4797–4799, 4801–4804, from Wugongshan Scenic Area (N27°34′03.94″, E114°10′28.38″; 1 050–1 080 m a.s.l.), Anfu County, Ji'an, Jiangxi.

Specimens examined: Type materials (four adult males and nine adult females); three adult males SYS a005525–5526, 5529, from Mt. Dawei (N28.4250°, E114.0805°; ca. 800 m a.s.l.), Liuyang City, Changsha, Hunan, China; one adult male SYS a005510, from Mt. Mufu (N28.9750°, E113.8304°; ca. 1 200 m a.s.l.), Pingjiang County, Yueyang, Hunan.

Diagnosis: Based on examined specimens: (1) adult males, SVL 30.9–34.1 mm ($n=8$); adult females, SVL 38.5–42.8 mm ($n=9$); (2) snout rounded, canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct, upper margin in contact with supratympanic fold; (4) vomerine ridges weak, vomerine teeth absent; (5) dorsal skin rough with dense granules; discontinuous X-shaped ridge on center of dorsum, dorsolateral ridges absent; flanks with large tubercles; ventral skin smooth with granules on belly; (6) outer margin of upper eyelid with horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) inner metacarpal tubercle distinct and observably enlarged, outer one indistinct; relative finger lengths $II < I = IV < III$; distinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels not meeting when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface yellowish brown or reddish brown; incomplete dark triangular marking between eyes, X-shaped marking on center of dorsum; dorsal limbs with broad black transverse bands; ventral surface grayish brown with creamy white nebulous patches and black spots on belly, two parallel black bands ventrolaterally; (11) dark nuptial pads with dense spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known from the Wugongshan Scenic Area and neighboring Yangshimu Scenic Area, Mt. Dawei, and Mt. Mufu at elevations of 550–1 200 m a.s.l., all situated at the border between Hunan and Jiangxi (Wang et al., 2019a; this study) (Supplementary Figure S10).

Remarks: The original description of this species mentioned “males bearing nuptial pads with nuptial spines during breeding season” when performing comparisons with congeners, but “In consideration of the invisible nuptial pad and nuptial spines in all male specimens..., the breeding season of *M. wugongensis* sp. nov. still remains unknown” when stating its habits (Wang et al., 2019a). After re-examination of the type series and newly collected specimens,

this character is revised here as “dark nuptial pads with dense spines on dorsal bases of fingers I and II in breeding adult males”.

***Boulenophrys wushanensis* (Ye and Fei, 1995)**

Wushan horned toad / wū shān jiǎo chán (巫山角蟾)

Chresonymy: *Megophrys minor* — Liu & Hu, 1961

Megophrys wushanensis — Ye & Fei, 1995; Fei et al., 2009, 2012

Megophrys (Xenophrys) wushanensis — Dubois & Ohler, 1998

Xenophrys wushanensis — Delorme et al., 2006; Chen et al., 2017

Boulenophrys wushanensis — Fei & Ye, 2016; Fei, 2020; Qi et al., 2021

Megophrys (Panophrys) wushanensis — Mahony et al., 2017

Panophrys wushanensis — Lyu et al., 2021

Holotype: CIB 98012 (formerly CIB 571991), adult male, from Miaotang Town (now Wulipo Nature Reserve) (N31°27' ; E110°56'; 1 200 m a.s.l.), Wushan County, Sichuan (now not Sichuan but Chongqing), China.

Allotype: CIB 98013 (formerly CIB 571944), adult female, from Tanzigou (945 m a.s.l.), Miaotang Town.

Paratypes: Fifteen males and 45 tadpoles (voucher numbers not provided), from Miaotang Town and Dangyang Town (1 158–1 206 m a.s.l.), Wushan.

Specimens examined: Five adult males SYS a003008–3011, 3013, from Wenshui Forest Station (N31.5707°, E110.1751°; ca. 1 490 m a.s.l.), Shennongjia Forestry District, Hubei, China.

Diagnosis: Based on previous descriptions (Fei & Ye, 2016; Ye & Fei, 1995) and examined specimens: (1) adult males, SVL 30.4–35.5 mm ($n=10$; Ye & Fei, 1995) (SVL 31.4–32.9 mm, $n=5$; this study); adult female, SVL 38.4 mm ($n=1$; Ye & Fei, 1995); (2) snout rounded, canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin relatively smooth with sparse granules; short irregular weak ridges on dorsum, dorsolateral ridges absent; sparse tubercles on flanks; ventral skin smooth; (6) outer margin of upper eyelid with tiny horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles indistinct, inner one observably enlarged; relative finger lengths I<II=IV<III; indistinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels just meeting or slightly overlapping when hindlimbs folded; tibiotarsal articulation reaching center of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and relatively wide lateral fringes in males; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface brown; irregular dark-brown patches with light edge on dorsum; dorsal limbs with indistinct transverse bands; ventral surface reddish black with white patches on belly, posterior flank and anterior thighs near groin red; (11) brown nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 4H).

Distribution: Known from multiple localities in the Wushan and Daba mountains along the border of Hubei, Chongqing, Sichuan, Shaanxi, and Gansu at elevations of 900–1 500 m a.s.l. (Fei & Ye, 2016; this study) (Supplementary Figure S10).

Remarks: Previous descriptions of this species (Fei & Ye, 2016; Ye & Fei, 1995) mentioned that “toes with rudimentary

webbing at bases and relatively wide lateral fringes in males while without webbing and lateral fringes in females”. Nonetheless, only a single female specimen (allotype) was available for examination; thus, we consider such differences observed in a single specimen to be a variation rather than a diagnosis. Further study on additional female specimens is required for clarification.

***Boulenophrys xiangnanensis* (Lyu, Zeng, and Wang, 2020)**

Southern Hunan horned toad / xiāng nán jiǎo chán (湘南角蟾)

Chresonymy: *Megophrys* sp1 — Liu et al., 2018

Megophrys sp2 — Liu et al., 2018

Megophrys sp3 — Liu et al., 2018

Megophrys (Panophrys) xiangnanensis — Lyu et al., 2020

Panophrys xiangnanensis — Lyu et al., 2021

Boulenophrys xiangnanensis — Qi et al., 2021

Holotype: SYS a002875, adult male, from Mt. Yangming (N26.1177°, E111.8945°; ca. 1 360 m a.s.l.), Shuangpai County, Yongzhou, Hunan, China.

Paratypes: Ten adult males SYS a002878–2886, CIB 116072, and one adult female SYS a002874, from same locality as holotype.

Specimens examined: Type materials (11 adult males and one adult female); one adult male SYS a002870, from Suocheng Town (N25.2948°, E112.1210°; ca. 560 m a.s.l.), Lanshan County, Yongzhou; one adult male SYS a003990, from Mt. Mao'er (N25.8621°, E110.4083°; ca. 1 600 m a.s.l.), Xing'an County, Guilin, Guangxi; one adult male SYS a008504, from Dajing (N25.1431°, E110.5748°; ca. 520 m a.s.l.), Lingchuan County, Guilin; nine adult males SYS a005078–5082, 5112, 6580, 6596–9597, from Mt. Dupangling (N25.4978°, E111.2362°; ca. 500 m a.s.l.), Guanyang County, Guilin; two adult males SYS a006556, 6589, from Mt. Yangxi (N24.8511°, E111.2147°; ca. 710 m a.s.l.), Fuchuan County, Hezhou, Guangxi.

Diagnosis: Based on examined specimens: (1) adult males, SVL 33.3–42.1 mm ($n=25$); adult female, SVL 44.4 mm ($n=1$); (2) snout rounded, canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges weak, vomerine teeth absent; (5) dorsal skin smooth with sparse granules; discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; sparse tubercles on flanks; ventral skin smooth with several tubercles on posterior hindlimbs; (6) outer margin of upper eyelid with small horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths I<II<IV<III; distinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels just meeting when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward; (9) toes with rudimentary webbing at bases and relatively wide lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface yellowish brown; dark triangular marking between eyes; dark X-shaped marking with light edge on center of dorsum; dorsal limbs with dark brown transverse bands; throat and anterior chest reddish gray; large white blotch with scarlet spots on belly, two parallel black bands ventrolaterally; (11) nuptial pads/spines absent in adult males; subgular vocal sac present in males.

Distribution: Known from multiple localities in hilly areas along the border between Hunan and Guangxi at elevations of

500–1 600 m a.s.l., including Mt. Jiuyi and Mt. Yangming in southwestern Hunan, and Mt. Mao'er, Mt. Haiyang, Mt. Dupangling, and Mt. Xiling in northeastern Guangxi (this study) (Supplementary Figure S9).

Remarks: Based on molecular data for species delimitation, Liu et al. (2018) suggested that the populations from Guanyang (labeled as *M. sp1*), Shuangpai (labeled as *M. sp2*, topotype population of *B. xiangnanensis*), and Fuchuan (labeled as *M. sp3*) may be three cryptic species. After detailed morphological examination, we failed to discover any distinct characters to distinguish the different specimens collected from multiple localities along the border between Hunan and Jiangxi. Thus, these populations are considered conspecific as *B. xiangnanensis*. Based on phylogenetic analysis of three mitochondrial segments (Figure 3), the intraspecific divergences of different populations of this species are relatively large compared with other congeners, which may be due to geographical isolation and its relatively wider distributional area.

The original description of this species mentioned “presence of nuptial pads on the dorsal surface of the first and second fingers in adult males” due to a typographical error (Lyu et al., 2020). This character should be revised as “nuptial pads/spines absent in adult males”.

***Boulenophrys xianjuensis* (Wang, Wu, Peng, Shi, Lu, and Wu, 2020)**

Xianju horned toad / xiān jū jiǎo chán (仙居角蟾)

Chresonymy: *Megophrys* sp19 — Liu et al., 2018

Megophrys xianjuensis — Wang et al., 2020

Panophrys xianjuensis — Lyu et al., 2021

Boulenophrys xianjuensis — Qi et al., 2021

Holotype: CIB XJ190503, adult male, from Shenxianju Scenic Area (N28.677483°, E120.594888°; 350 m a.s.l.), Danzhu Town, Xianju County, Taizhou, Zhejiang, China.

Paratypes: Seven adult males CIB 20180514007, XJ190501, XJ20190801–05, and two adult females CIB 20180514008, XJ190505, from same locality as holotype.

Specimens examined: Four adult males SYS a002671–2674 and two adult females SYS a002668–2669, from Mt. Dapan (N28.9801°, E120.5447°; ca. 860 m a.s.l.), Pan'an County, Jinhua, Zhejiang.

Diagnosis: Based on examined specimens: (1) adult males, SVL 33.0–34.8 mm ($n=4$); adult females, SVL 42.8–45.3 mm ($n=2$); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum slightly concealed; (4) vomerine ridges present, vomerine teeth absent; (5) dorsal skin rough with numerous granules; weak discontinuous X-shaped or Y-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; large warts on flanks and dorsal hindlimbs; ventral skin with numerous granules; (6) outer margin of upper eyelid with small horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles prominent, inner one observably enlarged; relative finger lengths II<I<IV<III; distinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface brown; triangular marking between eyes; dark X-shaped or Y-shaped marking on center of

dorsum; ventral surface purplish brown; large blotch on belly, two parallel black bands ventrolaterally; (11) nuptial pads bearing black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males (Figure 18J).

Distribution: Known from multiple localities in Shenxianju Scenic Area of Xianju County, Mt. Dapan of Pan'an County, and Mt. Longmen of Fuyang District in northeastern Zhejiang at elevations between 320–900 m a.s.l. (Wang et al., 2020; this study) (Supplementary Figure S10).

Remarks: In the original description of this species, the designation of paratypes was provided with seven adult male specimens, however, the measurements for the type series in Table 3 and Supplementary Table S1 only included six male paratypes (Wang et al., 2020). Data on the male paratype CIB 20180514007 were absent in the description without discussion. However, this specimen should be treated as one of the paratypes as it was listed in the designation.

Furthermore, the description of the holotype mentioned “posterior end of the body protrudes distinct and appears as an arc-shaped swelling, upper the anal region”, but this character was not listed as one of the specific diagnoses (Wang et al., 2020) and was not observed in the examined specimens in this study either. Thus, this character is suggested to be a variation that may occur in some individuals of Asian horned toads (refer to Remarks on *J. pachyproctus* comb. nov. in this study).

***Boulenophrys xuefengmontis* sp. nov. Lyu and Wang**

Xuefengshan horned toad / xuě fēng shān jiǎo chán (雪峰山角蟾)

Chresonymy: *Megophrys* sp26 — Liu et al., 2018

Holotype: SYS a007226, adult male, collected by Zhi-Tong Lyu and Yu-Long Li on 15 June 2018 from Mt. Xuefeng (N27.3072°, E110.3995°; ca. 1 280 m a.s.l.), Hongjiang City, Huaihua, Hunan, China.

Paratypes: Five adult males SYS a007224–7225, 7227–7228, CIB 118532 (formerly SYS a007229), and two adult females SYS a007222–7223, same collection data as holotype.

Etymology: The specific nomen *xuefengmontis* refers to Mt. Xuefeng, the type locality of this new species.

Diagnosis: (1) adult males, SVL 37.0–38.3 mm ($n=6$); adult females, SVL 45.3–48.9 mm ($n=2$); detailed measurements are presented in Table 5; (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges and vomerine teeth absent; (5) dorsal skin rough with sparse granules; weak discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; elongated tubercles on flanks; ventral skin smooth with several granules on chest; (6) outer margin of upper eyelid with small horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths II<I<IV<III; distinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels just meeting when hindlimbs folded; tibiotarsal articulation reaching region between posterior margin of tympanum and posterior corner of eye when leg stretched forward; (9) toes without webbing and lateral fringes; inner metatarsal tubercle ovoid, outer one absent; (10) dorsal surface yellowish brown, reddish brown, or olive brown; hollow triangular marking with light edge between eyes; indistinct X-shaped or netlike marking on center of dorsum; throat and anterior chest

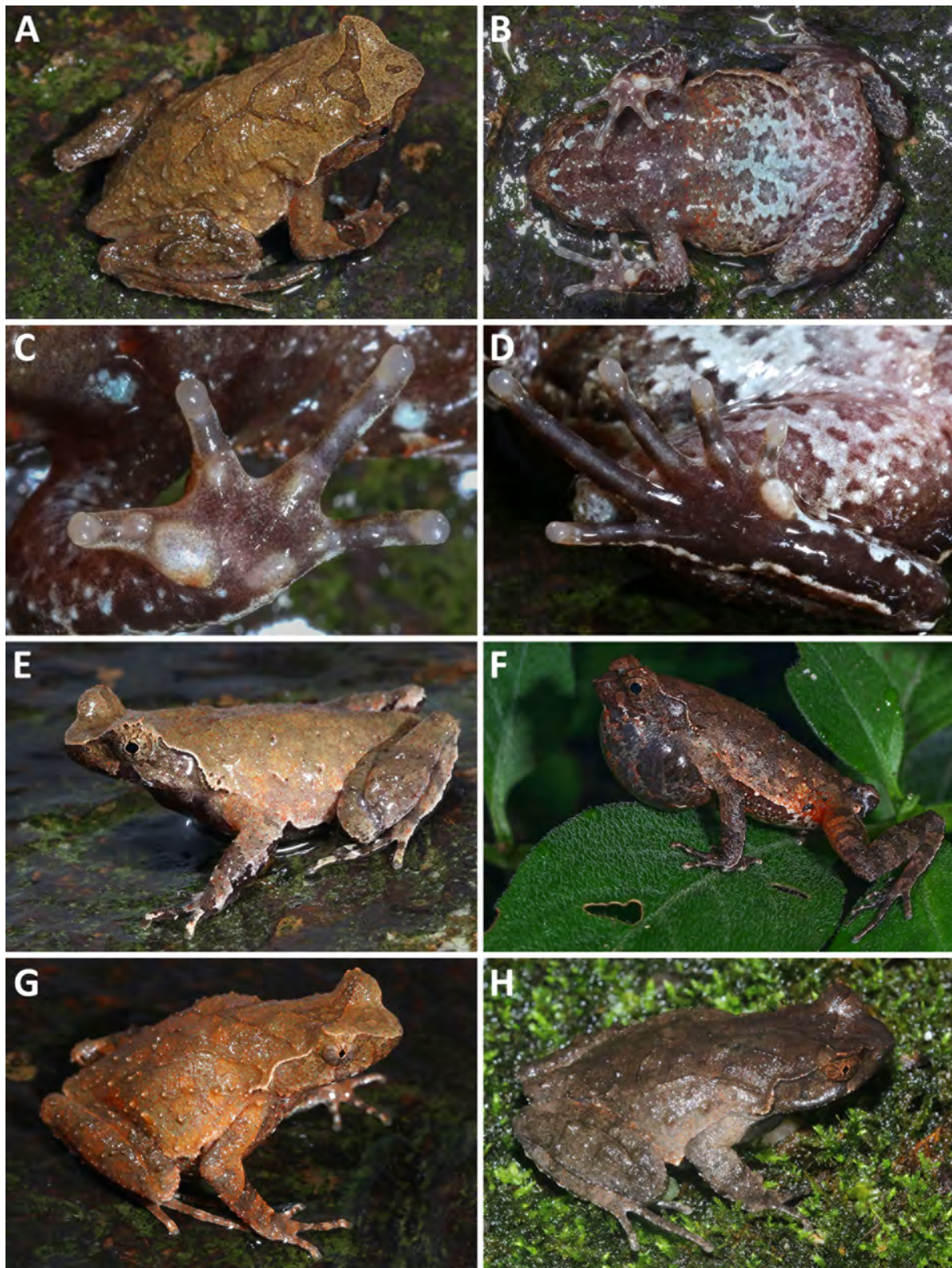


Figure 19 *Boulenophrys xuefengmontis* sp. nov. in life

A: Dorsolateral view of male holotype SYS a007226; B: Ventral view of holotype; C: Hand of holotype; D: Foot of holotype; E: Dorsolateral view of male paratype SYS a007224; F: Dorsolateral view of male paratype SYS a007225; G: Dorsolateral view of female paratype SYS a007223; H: Dorsolateral view of female SYS a004366 from Mt. Yunshan. Photos by Z.T. Lyu.

purplish with reddish spots; large white blotch on belly, two parallel black bands ventrolaterally, and contact with chest; (11) dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in

males (Figure 19).

Distribution: Currently known from Mt. Xuefeng of Hongjiang City and Mt. Yunshan of Wugang City at elevations of 1 200–1 300 m a.s.l., both situated in the Xuefeng Mountains

in western Hunan (Supplementary Figure S10).

***Boulenophrys yangmingensis* (Lyu, Zeng, and Wang, 2020)**

Mt. Yangming horned toad / yáng míng shān jiǎo chán (阳明山角蟾)

Chresonymy: *Megophrys* sp28 — Liu et al., 2018

Megophrys (*Panophrys*) *yangmingensis* — Lyu et al., 2020

Panophrys yangmingensis — Lyu et al., 2021

Boulenophrys yangmingensis — Qi et al., 2021

Holotype: SYS a002887, adult male, from Mt. Yangming (N26.1177°, E111.8945°; ca. 1 360 m a.s.l.), Shuangpai County, Yongzhou, Hunan, China.

Paratypes: Six adult males SYS a002307, 2888–2889, 2891–2892, CIB 116073, and one adult female SYS a002877, from same locality as holotype.

Specimens examined: Type materials (seven adult males and one adult female).

Diagnosis: Based on examined specimens: (1) adult males, SVL 33.2–37.1 mm ($n=7$); adult female, SVL 45.2 mm ($n=1$); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges weak, vomerine teeth absent; (5) dorsal skin rough with sparse granules; discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; sparse tubercles on flanks; ventral skin smooth with several tubercles on posterior hindlimbs; (6) outer margin of upper eyelid with small horn-like tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths $II < I < IV < III$; distinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping when hindlimbs folded; tibiotarsal articulation reaching anterior corner of eye when leg stretched forward; (9) toes with rudimentary webbing at bases and narrow lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface orange-brown; triangular marking with light edge between eyes; dark X-shaped marking with light edge on center of dorsum; throat and anterior chest purplish brown; large white blotch on belly, two parallel black bands ventrolaterally; (11) villiform black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known only from its type locality in Mt. Yangming at elevations over 1 300 m a.s.l. (Lyu et al., 2020) (Supplementary Figure S10).

***Boulenophrys yaoshanensis* Qi, Mo, Lyu, Wang, and Wang, 2021**

Mt. Dayao horned toad / yáo shān jiǎo chán (瑶山角蟾)

Chresonymy: *Megophrys minor* — Liu & Hu, 1962

Megophrys minor brachykolos — Ye & Fei, 1995

Megophrys brachykolos — Fei et al., 2009, 2012

Boulenophrys brachykolos — Fei & Ye, 2016; Fei, 2020

Megophrys sp7 — Chen et al., 2017

Megophrys sp31 — Liu et al., 2018

Boulenophrys yaoshanensis — Qi et al., 2021, 2022

Holotype: SYS a002189, adult male, from Dayaoshan Nature Reserve (originally provided as “N26.5517°, E114.1548°; ca. 845 m a.s.l.” and corrected as “N24.1602°, E110.2304°; ca. 1 200 m a.s.l.” in Qi et al., 2022), Jinxiu County, Laibin, Guangxi, China.

Paratypes: Four adult males SYS a000838, 4850, 7023, CIB 116086, and one adult female SYS a004878, from same locality as holotype; one adult female NHMG 1503016, from

Mt. Xianglu (N24.1055°, E110.2300°; ca. 1 305 m a.s.l.), Jinxiu; one adult male NHMG 201705032, from 16 km west of Jinxiu (N24.1162°, E110.2491°, ca. 1 115 m a.s.l.).

Specimens examined: Type materials (six adult males and two adult females).

Diagnosis: Based on examined specimens: (1) adult males, SVL 32.5–42.6 mm ($n=6$); adult females, SVL 46.6–47.4 mm ($n=2$); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges weak, vomerine teeth absent; (5) dorsal skin relatively smooth with small granules; weak discontinuous X-shaped ridge on center of dorsum, dorsolateral ridges absent; sparse large tubercles on flanks; ventral skin relatively smooth; (6) outer margin of upper eyelid with small horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths $II < I < IV < III$; distinct or indistinct subarticular tubercle at base of each finger; (8) hindlimbs slender, heels slightly overlapping or just meeting when hindlimbs folded; tibiotarsal articulation reaching region between anterior and posterior corners of eye when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface yellowish brown; hollow dark-brown triangular marking between eyes; X-shaped marking on center of dorsum; dorsal limbs with dark brown transverse bands; ventral surface grayish white with creamy white and orange spots, two parallel black bands ventrolaterally; (11) nuptial pads bearing fine and dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known from multiple localities in Jinxiu County, Mengshan County, and Guiping City at elevations of 1 200–1 300 m a.s.l., all situated in the Dayao Mountains in eastern Guangxi (Qi et al., 2021, 2202; this study) (Supplementary Figure S10).

***Boulenophrys yingdeensis* Qi, Lyu, Wang, and Wang, 2021**

Yingde horned toad / yīng dé jiǎo chán (英德角蟾)

Chresonymy: *Megophrys* sp4 — Liu et al., 2018

Boulenophrys yingdeensis — Qi et al., 2021

Holotype: SYS a002099, adult male, from Shimentai Nature Reserve (N24.4435°, E113.3034°; ca. 357 m a.s.l.), Yingde City, Qingyuan, Guangdong, China.

Paratypes: Three adult males SYS a005449, 7405, CIB 116084, and five adult females SYS a001563, 4721, 5447, 7406–7407, from same locality as holotype.

Specimens examined: Type materials (four adult males and five adult females).

Diagnosis: Based on examined specimens: (1) adult males, SVL 33.2–35.3 mm ($n=4$); adult females, SVL 36.3–45.8 mm ($n=5$); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges prominent, vomerine teeth present; (5) dorsal skin smooth with small granules; small conical tubercles on flanks; weak discontinuous X-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; ventral surface smooth; (6) outer margin of upper eyelid with small horn-like prominent tubercle; supratympanic fold distinct and narrow, curving posteroventrally to above arm; (7) inner metacarpal tubercle observably enlarged and outer one smaller; relative finger lengths $I < II < IV < III$; subarticular tubercle at base of each

finger; (8) hindlimbs slender, heels slightly overlapping or just meeting when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface light brown, reddish brown, olive brown, or dark brown; hollow dark brown triangular marking between eyes; X-shaped marking on center of dorsum; dorsal limbs with dark brown transverse bands; ventral surface white with brown patches, two parallel black bands ventrolaterally; (11) nuptial pads bearing fine and dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males.

Distribution: Known only from its type locality in Shimentai Nature Reserve at elevations of 300–400 m a.s.l. (Qi et al., 2021) (Supplementary Figure S10).

***Boulenophrys yunkaiensis* Qi, Wang, Lyu, and Wang, 2021**

Yunkai horned toad / yún kāi jiǎo chán (云开角蟾)

Chresonymy: *Megophrys* sp32 — Liu et al., 2018

Boulenophrys yunkaiensis — Qi et al., 2021

Holotype: SYS a004637, adult male, from Yunkaishan Nature Reserve (N22.2758°, E111.1952°; ca. 950 m a.s.l.), Xinyi City, Maoming, Guangdong, China.

Paratypes: Five adult males SYS a004636, 4638, 4986–4987, CIB 116085, and three adult females SYS a004659–4660, 4691, from same locality as holotype.

Specimens examined: Type materials (six adult males and three adult females).

Diagnosis: Based on examined specimens: (1) adult males, SVL 35.3–40.0 mm ($n=6$); adult females, SVL 45.3–46.1 mm ($n=3$); (2) canthus rostralis well developed; tongue not notched posteriorly; (3) tympanum distinct; (4) vomerine ridges weak, vomerine teeth absent; (5) dorsal skin rough, with small granules; large warts on flanks; weak discontinuous X-shaped or Y-shaped ridge on center of dorsum, discontinuous dorsolateral ridges present; ventral surface smooth; dense tubercles on ventral thigh, spiny tubercles surrounding cloaca; (6) outer margin of upper eyelid with small horn-like prominent tubercle; supratympanic fold distinct, curving posteroventrally to above arm; (7) two metacarpal tubercles distinct, inner one observably enlarged; relative finger lengths $II < IV < III$; subarticular tubercle at base of each finger; (8) hindlimbs slender, heels overlapping or just meeting when hindlimbs folded; tibiotarsal articulation reaching region between tympanum and eye when leg stretched forward; (9) toes with rudimentary webbing at bases but without lateral fringes; inner metatarsal tubercle long ovoid, outer one absent; (10) dorsal surface yellow brown; hollow dark brown triangular marking between eyes; X-shaped or Y-shaped marking on center of dorsum; dorsal limbs with dark brown transverse bands; ventral surface light salmon or yellow brown with brown patches, two parallel black bands ventrolaterally; (11) nuptial pads bearing fine and dense black nuptial spines on dorsal bases of fingers I and II in breeding adult males; subgular vocal sac present in males; tiny spines present on upper lip, upper eyelid, and loreal and temporal regions excluding tympanum in adult males.

Distribution: Known only from its type locality in Yunkaishan Nature Reserve at elevations of 900–1 400 m a.s.l. (Qi et al., 2021) (Supplementary Figure S10).

DISCUSSION

The rapid advancement and application of molecular biology techniques in taxonomic studies have led to momentous changes in species discovery and supraspecific classifications in many groups of organisms with their evolutionary history (Agung et al., 2022; Guo et al., 2022, 2023; Schram, 2004; Vences et al., 2013; Wheeler et al., 2004; Wilson, 2003, 2004; Zhang et al., 2022). However, one of the consequences of these changes is that phylogenetic conclusions often challenge previously held notions, which may lead to confusion, such as the distant relationship between lotus and water lily (The Angiosperm Phylogeny Group, 2016) and abandonment of the avian superorder Impennes (Sibley & Ahlquist, 1990) and mammalian order Insectivora (Beck et al., 2006). In addition, traditional morphological traits are sometimes questioned regarding their suitability for higher-taxon classification, with some phylogenetic researchers suggesting that genomic big data may be the only appropriate evidence for taxonomic verdicts.

Nonetheless, traditional morphological traits still remain valuable in taxonomic studies. The subfamily Megophryinae, one of the most diverse groups of amphibians, has been the subject of intense debate regarding generic classification. The main obstacle to resolving this debate is the morphological diagnosability of each proposed genus (Delorme et al., 2006; Lyu et al., 2021; Mahony et al., 2017). There are several reasons why such disputes arise, most commonly the paraphyly of previously proposed genera. The differences between *Boulenophrys* and *Xenophrys* (*sensu* Mahony et al., 2017), the two largest genera of this subfamily, are considered to be not well supported as many characteristics are shared by some species in both groups (Delorme et al., 2006; Fei & Ye, 2016; Mahony et al., 2017). However, based on our independent nuDNA and mtDNA phylogenetic analyses, we found the genus *Xenophrys* (*sensu* Mahony et al., 2017, based on concatenated nuDNA + mtDNA) to be paraphyletic. Morphologically, after the division of *Xenophrys* (*sensu* Mahony et al., 2017) into three genera, i.e., *Xenophrys*, *Grillitschia*, and *Jingophrys* **gen. nov.** in this study, these genera can be clearly differentiated from each other, as well as from *Boulenophrys* (Table 3 and generic key). Additionally, previous recognition of generic diagnosis may be improper and require revision. For instance, the placement of *A. wawuensis* in the genus *Atympanophrys* seems to reject the definition of *Atympanophrys* with concealed and invisible tympanum. However, all species of *Atympanophrys* still share a combination of characters, including upper eyelid smooth without any appendages or tubercles, maxillary teeth present, vomerine teeth absent, supratympanic fold thick, and subarticular tubercles absent, which can be diagnosed independently. In modern classifications, relying on a single or few characteristics to distinguish species/genera is insufficient and biased (Jiang et al., 2021; Li et al., 2021; Wang et al., 2021). Instead, we used a combination of multiple characters for comparison. This principle is also embodied in the identification keys. Traditional identification keys usually avoid using the same feature or character in different steps that means at least 59 characters are required in a key to 60 species (e.g., for genus *Boulenophrys*) and this is difficult to achieve. Thus, we employ the same character in different steps of an identification key — for instance, in the key for genus *Boulenophrys*, the character of toes webbing is used after both “vomerine teeth present” and “vomerine teeth

absent” to create different combinations of characters.

As a conclusion in this work, we present a ten-genus classification for Asian horned toads based on both morphological and phylogenetic support. Such classification is also corresponding to the geographic patterns of different genera. We consider this work will be an inspiration for the re-assessment of other groups of amphibians under generic controversy, such as *Rana sensu lato*, *Nanorana sensu lato*, and *Occidozyga sensu lato* (Hofmann et al., 2019; Lyu et al., 2022; Wan et al., 2020). Asian horned toads have attracted much attention because of their dramatically underestimated diversity. However, caution against taxonomic inflation within these species has been recently raised by many cases (e.g., Lyu et al., 2021; Wang et al., 2019a, 2022). For example, the molecular-based cryptic species *M. sp6* and *M. sp7* proposed by Liu et al. (2018) were suggested to be the same species and described as *B. nanlingensis* after detailed morphological examination (Wang et al., 2019a). In this study, most putative species defined from molecular analysis were suggested to be conspecific after undergoing morphological examination (e.g., *B. lushuiensis*, *B. ombrophila*, and *B. xiangnanensis*). In this molecular biology era, some researchers suggest the use of uniform criteria for species-level evaluation, such as genetic distances from specific gene markers. However, it is important to acknowledge that different species may have undergone different speciation processes, and it is not uncommon for intraspecific divergence to be distinct and relatively large in one species (e.g., *X. lancangica* sp. nov. and *B. mufumontana*) but almost absent in another. Thus, to use sole genetic data (or else such as divergent time estimated from molecular clock) for species delimitation should be vigilant and morphological comparison based on multiple populations should always be one of the important traits for taxonomic work.

NOMENCLATURE ACTS REGISTRATION

The electronic version of this article in portable document format represents a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone (see Articles 8.5–8.6 of the Code). This published work and the nomenclature acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information can be viewed through any standard web browser by appending the LSID to the prefix <http://zoobank.org/>.

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Sarawakiphrys LSID: [urn:lsid:zoobank.org:act:32737779-ED66-4242-B259-56FE57D1ECD5](http://zoobank.org/act:32737779-ED66-4242-B259-56FE57D1ECD5)

Jingophrys LSID: [urn:lsid:zoobank.org:act:BD6EBE03-5B85-409C-B78A-81B181A90C2B](http://zoobank.org/act:BD6EBE03-5B85-409C-B78A-81B181A90C2B)

Xenophrys dehongensis LSID: [urn:lsid:zoobank.org:act:F73C41C1-29A0-4846-8851-FAA0C97468F4](http://zoobank.org/act:F73C41C1-29A0-4846-8851-FAA0C97468F4)

Xenophrys lancangica LSID: [urn:lsid:zoobank.org:act:802FF820-1A0A-40AF-8E5A-36EF26FFD04A](http://zoobank.org/act:802FF820-1A0A-40AF-8E5A-36EF26FFD04A)

Boulenophrys xuefengmontis LSID: [urn:lsid:zoobank.org:act:DCEB6D12-483F-4FAA-B17F-9758DE0A5970](http://zoobank.org/act:DCEB6D12-483F-4FAA-B17F-9758DE0A5970)

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

All authors collected the specimens and data in the field. Z.T.L., S.Q., S.Y.Z., Z.C.Z., and H.W. performed experimental work and phylogenetic analyses. Z.T.L., S.Q., J.W., J.Z., J.H.Y., Y.M.M., and Y.Y.W. performed morphological examinations and comparisons. Z.T.L., S.Q., and J.W. prepared the manuscript with input from all authors. Y.Y.W. revised the manuscript. All authors read and approved the final version of the manuscript.

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