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Taxonomic revision of *Amolops chunganensis* (Pope, 1929) (Amphibia: Anura) and description of a new species from southwestern China, with discussion on *Amolops monticola* group and assignment of species groups of the genus *Amolops*

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ABSTRACT

Amolops chunganensis is a species complex and reported widely from eastern, southern, and southwestern China. Based on molecular data of 19 populations of *A. chunganensis sensu lato* from China, including the population from Mt. Wuyi (type locality), we recognize *A. chunganensis sensu stricto* and provide an expanded description based on the topotypic specimens. Combining morphological and molecular data, we describe a new species, *Amolops chaochin* **sp. nov.**, from southwestern China, which was previously identified as *A. chunganensis*. The new species is distinguished from all other species in the *A. monticola* group by: (1) moderate body size, SVL 35.3–39.2 mm in males (*n*=7), and 50.5–54.4

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mm in females (n=7); (2) distinct tympanum, larger than half of eye diameter; (3) small tooth-like projection on anteromedial edge of mandible; (4) circummarginal groove on all fingers; (5) white tubercles on dorsal side of posterior body in both sexes; (6) distinct tubercles on dorsal thigh and white

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spinose tubercles on dorsal tibia in both sexes; (7) white tubercles on posterior region of tympanum in males; (8) toe webbing reaching disk by dermal fringe on inner side of toe II; (9) vomerine teeth present; (10) transverse bands on dorsal limbs; (11) external vocal sacs present in males. We further reviewed the assignment of *Amolops* groups, with an overall revision of membership and diagnosis of all species groups.

Keywords: Amolops chaochin sp. nov.; Complex; Distribution; Amolops gerbillus; Amolops chayuensis group; Amolops spinapectoralis group

INTRODUCTION

The genus Amolops Cope, 1865 currently contains 69 species distributed from Nepal, northern India, western and southern China to Malaya (Frost, 2021). At least eight species groups have been suggested to accommodate these species (Fei et al., 2009b; Lyu et al., 2019b; Wu et al., 2020; Zeng et al., 2020): A. daiyunensis group, A. hainanensis group, A. larutensis group, A. mantzorum group, A. marmoratus group, A. monticola group, A. ricketti group, and A. viridimaculatus group. Nevertheless, several species are unassigned to any group, and the membership of certain groups remains controversial. For example, Wu et al. (2020) recently proposed the A. viridimaculatus and A. larutensis groups, with the former containing two recognized species, A. medogensis and A. viridimaculatus, transferred from the A. marmoratus and A. mantzorum groups, respectively (Fei et al., 2009b; Lyu et al., 2019b). Although the morphological characters of the A. viridimaculatus group are provided in the literature, morphological revisions of the latter two groups are still lacking (Wu et al., 2020).

The A. monticola group contains 21 species, diagnosed with smooth skin, dark lateral side of head, light-colored upper lip stripe extending to shoulder, and distinct dorsolateral folds (Che et al., 2020; Gan et al., 2020a, 2020b; Jiang et al., 2016; Yu et al., 2019). The species include A. aniqiaoensis Dong, Rao & Lü, 2005, A. akhaorum Stuart, Bain, Phimmachak & Spence, 2010, A. archotaphus (Inger & Chanard, 1997), A. bellulus Liu, Yang, Ferraris & Matsui, 2000, A. chakrataensis Ray, 1992, A. chunganensis (Pope, 1929), A. compotrix (Bain, Stuart & Orlov, 2006), A. cucae (Bain, Stuart & Orlov, 2006), A. chayuensis Sun, Luo, Sun & Zhang, 2013, A. daorum (Bain, Lathrop, Murphy, Orlov & Ho, 2003), A. deng Jiang, Wang & Che, 2020, A. gerbillus (Annandale, 1912), A. iriodes (Bain & Nguyen, 2004), A. mengyangensis Wu & Tian, 1995, A. monticola (Anderson, 1871), A. mengdingensis Yu, Wu & Yang, 2019, A. nyingchiensis Jiang, Wang, Xie, Jiang & Che, 2016, A. putaoensis Gan, Qin, Lwin, Li, Quan, Liu & Yu, 2020, A. tuanjieensis Gan, Yu & Wu, 2020, A. vitreus (Bain, Stuart & Orlov, 2006), and A. wenshanensis Yuan, Jin, Li, Stuart & Wu, 2018. Within this group, the assignment of two species is disputed. Both A. gerbillus and A. chayuensis were placed in this group due to the presence of dorsolateral folds (Fei et al., 2005, 2009b; Sun et al., 2013). Nevertheless, the addition of A. gerbillus to the A. monticola group was questioned by Stuart et al. (2010) due to its divergent morphology from other

species within the group, e.g., presence of large compressed longitudinal tubercles on dorsum and lack of dark side of head and light-colored upper lip stripe. At present, however, most studies still include *A. gerbillus* in the *A. monticola* group (Gan et al., 2020a, 2020b; Jiang et al., 2016; Wu et al., 2020; Yu et al., 2019; Yuan et al., 2018). *Amolops chayuensis* was phylogenetically separated from other species within the *A. monticola* group based on mitochondrial sequencing data (Che et al., 2020; Gan et al., 2020a, 2020b; Jiang et al., 2016; Lyu et al., 2019b; Zeng et al., 2020) and was suggested to represent a new species group but without formal establishment (Zeng et al., 2020). Additionally, according to the original species description, *A. kohimaensis* Biju, Mahony & Kamei, 2010 should be a member of the *A. monticola* group based on morphological characteristics.

Amolops chunganensis was originally described from Kuatun (now spelled as Guadun), a small village in Mt. Wuyi located at the border between Fujian and Jiangxi (Pope, 1929), and was reported in Sichuan by Liu (1940, 1941). It has since been widely recorded in Anhui, Chongqing, Gansu, Guangdong, Guangxi, Guizhou, Hunan, Jiangxi, Shaanxi, Yunnan, and Zhejiang (AmphibiaChina, 2021; Fei et al., 2009b). Based on molecular phylogenetic analyses, Wu et al. (2020) revealed that A. chunganensis shows relatively high genetic divergence and may contain several undescribed cryptic species.

In the present study, we reconstructed the phylogenetic relationships within the A. monticola group based on 19 populations of A. chunganensis sensu lato from China, including the population close to its type locality in Mt. Wuyi. Phylogenetic evidence indicated that A. chunganensis sensu lato forms three distinct clades, as reported in Wu et al. (2020), which likely contain at least two undescribed species. Based on the specimens from Mt. Wuyi, we confirmed and redescribed the phylogenetic position of A. chunganensis sensu stricto and described a new species previously misidentified as A. chunganensis from Sichuan, southwestern China. Additionally, we reviewed the assignment of species groups in the genus. We established the A. chayuensis and A. spinapectoralis groups, revised membership and diagnostic characters for all species groups, and provided a speciesgroup key and new species key of the A. monticola group in China.

MATERIALS AND METHODS

Sampling

A total of 18 specimens were collected, including 14 specimens from Chengdu (Sichuan) and four specimens from Mt. Wuyi (Yanshan county, Jiangxi). Following euthanasia, all specimens were fixed in 10% formalin solution after liver tissue sampling (95% ethanol). All specimens were transferred to 75% ethanol after fieldwork and were deposited in the Herpetological Museum, Chengdu Institute of Biology (CIB), Chinese Academy of Sciences.

Morphological data

All measurements were carried out with slide calipers to the nearest 0.1 mm. Morphological characters and measurements

of adults followed Fei et al. (2009a, 2009b) and Jiang et al. (2016), morphological characters and measurements of tadpoles followed Fei et al. (2009a) and McDiarmid & Altig (1999). Morphological characters and their abbreviations include: SVL, snout-vent length; HL, head length; HW, head width; SL, snout length; INS, internarial distance; IOS, interorbital distance; EHD, eye horizontal diameter; UEW, maximum width of upper eyelid; TD, tympanum diameter; FAHL, forelimb and hand length; LAW, width of lower arm; HAL, hand length; F3W, width of finger III disk; FML, femur (thigh) length; TBL, tibia (shank) length; TFL, length of tarsus and foot; FOL, foot length; T4W, width of disk of toe IV; TAL, tail length (for tadpoles); TOL, total length (for tadpoles); TH, tail height (for tadpoles).

Morphological data of congeners were obtained from voucher specimens (Supplementary Materials) and previously published literature (Annandale, 1912; Bain et al., 2006; Bain & Nguyen, 2004; Boulenger, 1920; Che et al., 2020; Fei et al., 2009b; Gan et al., 2020a, 2020b; Jiang et al., 2016; Stuart et al., 2010; Wang et al., 2020; Yu et al., 2019; Yuan et al., 2018).

Molecular data and analyses

For specimens sequenced in this study, genomic DNA was

extracted from ethanol-preserved liver tissue samples using an Ezup Column Animal Genomic DNA Purification Kit (Sangon Biotech, China) following the protocols of the manufacturer. Two mitochondrial loci, 1 036 bp of 16S ribosomal RNA (16S) and 637 bp of cytochrome c oxidase subunit I (COI), were selected for phylogenetic reconstruction. The 16S and COI fragments were amplified using primer pairs: 16Sar-L (5'-GCCTGTTTATCAAAAACAT-3')/16Sbr-H (5'-CCGGTCTGAACTCAGATCACGT-3') (Yu et al., 2009) and Chmf4 (5'-TYTCWACWAAYCAYAAAGAYATCGG-3')/Chmr4 (5'-ACYTCRGGRTGRCCRAARAATCA-3') (Che et al., 2012), respectively. Amplification of the 16S fragments was performed in a 25 µL volume reaction. Initial denaturation step: 3 min at 94 °C (COI: 5 min at 95 °C), 40 cycles (COI: 35 cycles): denaturation 60 s at 94 °C (COI: 60 s at 95 °C), annealing for 60 s at 51 °C (COI: 60 s at 46 °C), extension for 1 min at 72 °C; final extension: 10 min at 72 °C. The polymerase chain reaction (PCR) products were purified and then sequenced in both forward and reverse directions using an ABI 3730xL sequencer (Applied Biosystems, USA) by Sangon Biotech Co., Ltd (China). All new sequences were deposited in GenBank under accession Nos. MZ702011-MZ702029 and MZ706954-MZ706971 (Table 1; Figure 1).

Table 1 Information on voucher numbers, GenBank accession Nos., and localities of samples used in this study

Species	Localities	Voucher No.	16S	COI	ID
A. akhaorum	Laos: Luang Namtha: Vieng Phou Kha	FMNH 271355	FJ417158	MN961350	48
A. akhaorum	Laos: Luang Namtha: Vieng Phou Kha	FMNH 271406	FJ417159	MN961351	49
A. aniqiaoensis	China: Tibet: Mêdog	SYNU 04II6015	MN953655	MN961352	52
A. aniqiaoensis	China: Tibet: Mêdog	SYNU 04II6016	MN953656	MN961353	53
A. archotaphus	Thailand: Chiang Mai: Amphoe Chom Thong	FMNH 271708	MN953659	MN961356	42
A. archotaphus	Thailand: Chiang Mai: Doi Inthanon	KIZ 030948	MN953661	MN961358	43
A. bellulus	China: Yunnan: Tengchong	CAS 233991	FJ417127	MN961361	54
A. bellulus	China: Yunnan: Tengchong	KIZ YPX9037	MN953664	KU243078	55
A. cf. chunganensis	China: Hubei: Fangxian	KIZ 03756	MN953671	MN961365	7
A. chaochin sp. nov.	China: Sichuan: Mt.Qingcheng	070104	KU840605	-	1
A. chaochin sp. nov.	China: Sichuan: Anxian	SCUM 045818HX	MN953669	MN961363	2
A. chaochin sp. nov.	China: Sichuan: Anxian	SCUM 045820HX	MN953668	-	3
A. chaochin sp. nov.	China: Sichuan: Mt. Emei	KUHE 27699	AB211477	_	4
A. chaochin sp. nov.	China: Gansu	CIB XM5526	KX645666	KX645666	5
A. chaochin sp. nov.	China: Guizhou: Bijie	KIZ YPX4947	MN953767	MN961468	6
A. chaochin sp. nov.	China: Sichuan: Dayi	CIB 116971	MZ702027	MZ706968	62
A. chaochin sp. nov.	China: Sichuan: Dayi	CIB 116977	MZ702026	MZ706969	63
A. chaochin sp. nov.	China: Sichuan: Dayi	CIB 116980	MZ702028	MZ706970	64
A. chaochin sp. nov.	China: Sichuan: Dayi	CIB 116979	MZ702029	MZ706971	65
A. chayuensis	China: Tibet: Baxoi	KIZ 014022/016	MN953667	KU243074	56
A. chayuensis	China: Tibet: Baxoi	SYS a007512	MK604877	MK605635	57
A. chunganensis	China: Jiangxi: Mt. Wuyi	SYS a008411	MZ702021	MZ706964	8
A. chunganensis	China: Jiangxi: Mt. Wuyi	SYS a008412	MZ702022	MZ706965	9
A. chunganensis	China: Jiangxi: Mt. Wuyi	SYS a008413	MZ702023	MZ706966	10
A. chunganensis	China: Jiangxi: Mt. Wuyi	SYS a008414	MZ702024	MZ706967	11
A. chunganensis	China: Zhejiang: Mt. Baishanzu	SYS a008301	MZ702019	MZ706962	12
A. chunganensis	China: Zhejiang: Mt. Baishanzu	SYS a008302	MZ702020	MZ706963	13
A. chunganensis	China: Jiangxi: Mt. Jinggang	SYS a004212	MK263263	MG991914	14
A. chunganensis	China: Jiangxi: Mt. Jinggang	SYS a004213	MK263264	MG991915	15
A. chunganensis	China: Jiangxi: Mt. Wugong	SYS a003136	MZ702025	KX507330	16

Species	Localities	Voucher No.	16S	COI	ID
A. chunganensis	China: Guangdong: Mt. Nanling	SYS a005778	MZ702015	MZ706958	17
A. chunganensis	China: Guangdong: Mt. Nanling	SYS a005779	MZ702016	MZ706959	18
A. chunganensis	China: Guangxi: Longsheng	SYS a004897	MZ702013	MZ706956	19
A. chunganensis	China: Hunan: Mt.Tianping	SYS a004304	MZ702011	MZ706954	20
A. chunganensis	China: Hunan: Mt.Tianping	SYS a004305	MZ702012	MZ706955	21
A. chunganensis	China: Chongqing: Wulong	SYS a008263	MZ702017	MZ706960	22
A. chunganensis	China: Chongqing: Wulong	SYS a008264	MZ702018	MZ706961	23
A. chunganensis	China: Chongqing: Chengkou	KIZ YPX18652	MN953670	MN961364	24
A. chunganensis	China: Hubei: Shennongjia	QLY313	KF771285	KF771328	25
A. chunganensis	China: Sichuan: Mt. Guangwu	SYS a005407	MZ702014	MZ706957	26
A. chunganensis	China: Sichuan: Nanjiang	KIZ C93116	DQ204476	_	27
A. compotrix	Laos: Khammouan: Nakai	FMNH 256500	FJ417141	MN961366	28
A. compotrix	Vietnam: Kon Tum: Dak Glei	ZISP A7367	FJ417142	MN961367	29
A. cucae	Vietnam: Lao Cai: Van Ban	AMNH 168727	FJ417144	MN961373	30
A. cucae	Vietnam: Lao Cai: Van Ban	AMNH 168729	FJ417145	MN961372	31
A. daorum	China: Yunnan: Jingdong	KIZ 047048	MN953678	MN961377	40
A. daorum	China: Yunnan: Jingdong	KIZ 047049	MN953679	MN961378	41
A. iriodes	Vietnam: Ha Giang: Vi Xuyen	AMNH 163926	FJ417152	MN961400	36
A. iriodes	Vietnam: Ha Giang: Vi Xuyen	AMNH 163928	FJ417153	MN961401	37
A. mantzorum	China: Sichuan: Baoxing	SYS a005365	MK573808	MK568323	58
A. mantzorum	China: Sichuan: Baoxing	SYS a005366	MK604862	MK605620	59
A. mengdingensis	China: Yunnan: Gengma	KIZ 20160265	MK501808	MK501811	46
A. mengdingensis	China: Yunnan: Gengma	KIZ 20160266	MK501809	MK501812	47
A. mengyangensis	Vietnam: Lao Cai: Sa Pa	1999.5811	KR827703	KR087618	38
A. mengyangensis	Vietnam: Lao Cai: Sa Pa	1999.5812	KR827704	KR087619	39
A. nyingchiensis	China: Tibet: Medog	KIZ 016415	MN953718	KU243069	50
A. nyingchiensis	China: Tibet: Lhünzê	SYS a007508	MK573815	MK568330	51
A. ricketti	China: Fujian: Mt. Wuyi	SYS a004141	MK263259	MG991927	66
A. ricketti	China: Fujian: Mt. Wuyi	SYS a004142	MK263260	MG991928	67
A. tuanjieensis	China: Yunnan: Gengma	GXNU YU110003	MN832772	MN832750	44
A. tuanjieensis	China: Yunnan: Gengma	GXNU YU110005	MN832773	MN832751	45
A. viridimaculatus	China: Yunnan: Mt. Gaoligong	SYS a003753	MK573793	MK568310	60
A. viridimaculatus	China: Yunnan: Mt. Gaoligong	SYS a003754	MK573794	MK568311	61
A. vitreus	Laos: Phongsaly: Phongsaly	FMNH 258183	FJ417163	-	34
A. vitreus	Laos: Phongsaly: Phongsaly	FMNH 258187	FJ417164	MN961439	35
A. wenshanensis	China: Yunnan: Xichou	KIZ 021426	MN953725	MN961427	32
A. wenshanensis	China: Guangxi: Jingxi	KU 292045	FJ417129	MN961425	33

For collections and abbreviations, see Materials and Methods. -: Not available.

Amolops ricketti was selected as the outgroup based on previous phylogenies (Wu et al., 2020; Zeng et al., 2020). Additional sequences of Amolops species and outgroup taxa were obtained from GenBank. The DNA sequences were aligned and manually adjusted using MEGA 6.0 (Tamura et al., 2013) with default parameters. Maximum-likelihood (ML) and Bayesian inference (BI) analyses were used for the 1 673 bp concatenated 16S+COI dataset. The ML analyses were conducted using RAxML v8.2.10 (Stamatakis, 2014) and bootstrap proportions (BSP) were calculated with 1 000 non-parametric bootstrap replicates. The BI analyses were performed in MrBayes v.3.2.6 (Ronquist & Huelsenbeck, 2003) with the GTR+G model, as determined using Akaike Information Criterion (AIC) in PartitionFinder v2 (Lanfear et al.,

2017). The dataset was run for 10 000 000 generations and Markov chains were sampled every 100 generations. After convergence among runs was verified by examining the likelihood plots using Tracer v1.6 (Rambaut et al., 2013) and effective sample sizes (ESSs) were confirmed to exceed 200, the first 25% of trees were discarded as burn-in. Tree topology confidence was evaluated by Bayesian posterior probability (BPP).

Bioacoustic analysis

Advertisement calls of *A. chunganensis* from Longsheng, Guangxi, China, were recorded in the field using a SONY PCM D100 digital sound recorder on 24 May 2010. Advertisement calls of the new species from Mt. Qingcheng, Chengdu, Sichuan, China, were recorded in the lab using a



Figure 1 Sampling localities of species from *A. monticola* group used in this study (colored circles)

Red: Amolops chaochin **sp. nov.**; blue: A. chunganensis; green: A. cf. chunganensis; yellow circles: other species in A. monticola group from China. Numbers correspond to IDs in Table 1. Yellow square (d): type locality of A. deng; yellow square (m): type locality of A. mengyangensis.

SONY PCM ICD-PX470 digital sound recorder on 30 May 2021. The sound files in wave format were sampled at 44.1 kHz with a depth of 24 bits. Praat v6.0.27 (Boersma, 2001) was used to obtain the oscillogram, sonogram, and power spectrum (window length=0.015 s).

Abbreviations: CIB, Herpetological Museum Herpetology, Chengdu Institute of Biology, Chinese Academy of Sciences; KIZ, Kunming Institute of Zoology, Chinese Academy of Sciences; LAB, Dr. Jia-Tang Li's lab collections in CIB; AMNH, American Museum of Natural History; CAS, California Academy of Science; FMNH, Field Museum of Natural History; GXNU, Guangxi Normal University; KU, University of Kansas Museum of Natural History; KUHE, Graduate School of Human and Environmental Studies, Kyoto University; SCUM, Zoological Museum, Sichuan University; SYNU, Shenyang Normal University, SYS, Museum of Biology, Sun Yat-sen University, ZISP, Zoological Institute, Russian Academy of Sciences.

RESULTS

Phylogenetic analyses

The ML and BI analyses yielded highly similar topologies and strong support for the monophyly of the ingroup (Clade A; BSP=100/BPP=1.00), largely coinciding with the A. monticola group, except for A. chayuensis (Figure 2). BI analysis strongly supported three highly divergent A. chunganensis sensu lato (Clade B) lineages (BPP=0.99), but ML bootstrap support was low (BSP=48). Specimens from the type locality of A. chunganensis (Mt. Wuyi, located at the Fujian and Jiangxi border; ID: 8-11) as well as other localities from Zhejiang, Guangdong, Guangxi, Hunan, Hubei, Chongging, and Sichuan (ID: 12-27) were recovered as a strongly supported monophyletic group (Clade BSP=100/BPP=1.00), identified as A. chunganensis sensu stricto. Clade D, which incorporated specimens from Guizhou, Gansu, and Sichuan (ID: 1-6, 62-65; 1BSP=100/BPP=1.00), was weakly clustered with Clade C (A. chunganensis sensu stricto) (BSP=54/BPP=0.57), which represented a new species (*Amolops chaochin* **sp. nov.**), as described herein. Additionally, the specimen from Fangxian (Hubei) was identified as sister taxon to Clade C+Clade D with weak support (clade B; BSP=48/BPP=0.99) and was identified as *A. cf. chunganensis* (ID: 7).

Morphological comparisons

In the *Amolops monticola* group, our newly collected specimens from Chengdu (Sichuan) were most similar to the specimens of *A. chunganensis sensu stricto* from Mt. Wuyi, e.g., body size moderate, dorsal side brown, circummarginal groove on all fingers, tibiotarsal articulation beyond snout, transverse bands on dorsal limbs, and external vocal sacs present. However, the specimens differed from *A. chunganensis* by white tubercles on dorsal side of posterior body, distinct tubercles on dorsal thigh, white spinose tubercles on dorsal tibia, white tubercles on temporal region, toe webbing not reaching disk on inner side of toe II, and outer metatarsal tubercle small but distinct (Figure 3).

Bioacoustics

The calls of the two species differed significantly in spectral and temporal characteristics, especially in call repertoire. The calling behavior of the new species (Figure 4G-I) is more complex than that of *A. chunganensis* (Figure 4A-C). The male of the new species can produce extremely complex compound calls (Figure 4H, I).

Systematic accounts

Re-description of *Amolops chunganensis* (Pope, 1929) based on topotypic specimens (Figures 5, 6A)

Rana chunganensis Pope, 1929, Am. Mus. Novit., 352: 3. Type locality: Kuatun, northwestern Chungan Hsien (=Wuyishan City), Fukien (=Fujian) Province, China, 4500–5000 feet altitude. Holotype: AMNH 30479, 3, by original designation.

Staurois chunganensis: Liu, 1940, J. West China Border Res. Soc., 12 (B): 32; Liu, 1941, Peking Nat. Hist. Bull., 15(4): 291 (in part).

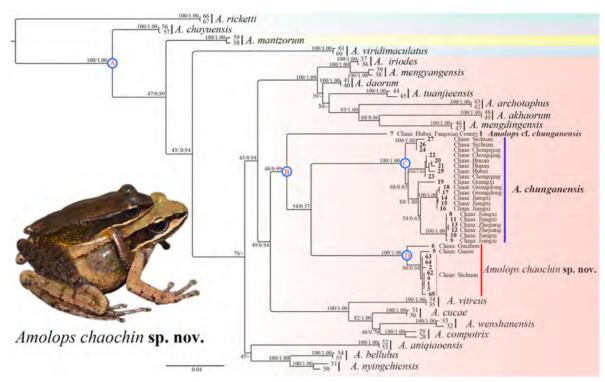


Figure 2 Phylogeny of *Amolops* frogs represented by selected species and constructed using mitochondrial sequences from 16S and COI fragments

Support values (ML bootstrap/Bayesian posterior probability) are indicated at nodes. Bayesian posterior probabilities are given as "-" where those phylogenies conflict with ML phylogeny. Photo by Jin-Long Ren.



Figure 3 Comparisons of morphological characteristics between male holotype (CIB 116971) of *Amolops chaochin* **sp. nov.** (left, A1, B1, C1) and male topotype (SYS a008411) of *A. chunganensis* (right, A2, B2, C2)

A: White tubercles on temporal region present (A1, see arrows) vs. absent (A2); B: White tubercles on dorsal side of posterior body, dorsal thigh, and dorsal tibia present (B1, see arrows) vs. absent (B2); C: Toe webbing not reaching disk on inner side of toe II (C1) vs. toe webbing reaching disk on inner side of toe II (C2). Photos by Jin-Long Ren (left) and Zhi-Tong Lyu (right).

Amolops chunganensis: Inger, 1966, Fieldiana, Zool., 52: 256, by implication; Fei, Hu, Ye & Huang, 2009, Fauna Sinica, Amph. 3: 1514.

Referred specimens: Five male specimens, including one male (CIB 33536) from Miaowan, Mt. Wuyi, Wuyishan City, Fujian; four males (CIB 116985–88) from Huanggang (N27.813344°, E117.719879°, at 1 100 m a.s.l.), Mt. Wuyi, Yanshan County, Jiangxi; and one female specimen (CIB 118077) from Guwangkeng (N27.701737°, E117.688498°, at 941 m a.s.l.), Mt. Wuyi, Wuyishan City, Fujian.

Remark: Mt. Wuyi is located on the border between southeastern Jiangxi and northwestern Fujian. Due to the close geographical distance between Kuatun, Miaowan, Guwangkeng, and Huanggang, the specimens from Miaowan, Guwangkeng, and Huanggang can be regarded as topotypic specimens of *A. chunganensis*.

Diagnosis: (1) skin smooth; (2) lateral side of head dark, with light-colored upper lip stripe extending to shoulder; (3) distinct dorsolateral folds; (4) moderate body size, SVL 37.2–41.5 mm in males (n=5), SVL 52.6 mm in female (n=1); (5) tympanum distinct, slightly larger than half of eye diameter; (6) small tooth-like projection on anteromedial edge of mandible; (7) circummarginal groove on all fingers; (8) white tubercles on dorsal side of posterior body absent; (9) distinct tubercles on dorsal thigh and white spinose tubercles on dorsal tibia absent; (10) white tubercles on temporal region absent; (11) toe webbing reaching disk on inner side of toe II; (12) vomerine teeth present; (13) transverse bands on dorsal limbs; (14) external vocal sacs present in males.

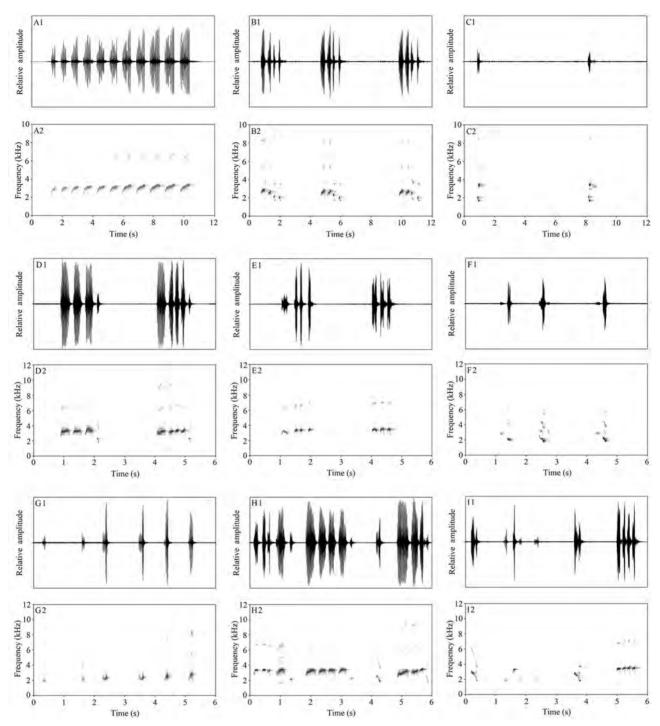


Figure 4 Amplitude-modulated waveforms (1) and spectrograms (2) of three call types in *A. chunganensis* (A–C) and *Amolops chaochin* **sp. nov.** (D–I)

FFT (fast Fourier transformation) frame is 1 024.

Description: Moderate body size, SVL 37.2-41.5 mm in males, SVL 52.6 mm in female (other known female specimen was recorded to 58.0 mm by Pope (1929)), slightly compressed on vertical direction. Head slightly longer than wide (HL/HW ratio 1.10 in males, 1.02 in female); snout projecting forward, rounded at tip; nostril lateral, slightly closer to eye than tip of snout; canthus rostralis distinct; loreal region

concave and oblique; eye relatively large (EHD/HL ratio 0.34 in males, 0.35 in female); interorbital distance larger than width of upper eyelid; tympanum distinct, tympanum diameter slightly larger than half eye diameter (TD/EHD ratio 0.54 in males, 0.59 in female), tympanic rim elevated; vomerine teeth present; tongue pyriform, deeply notched posteriorly; vocal sac openings present.



Figure 5 Adult male specimen (CIB 116985) of *A. chunganensis* sensu stricto from Mt. Wuyi, Jiangxi, in life

A: Dorsolateral view; B: Dorsal view; C: Ventral view; D: Ventral view of hand; E: Ventral view of foot. Photos by Zhi-Tong Lyu.



Figure 6 Adult male specimen of *A. chunganensis sensu stricto* (CIB 116988) (A) from Mt. Wuyi, Jiangxi, and adult male holotype of *Amolops chaochin* **sp. nov.** (CIB 116971) (B) in preservative

1: Dorsal view; 2: Ventral view; 3: Close-up view of head and temporal region, right side; 4: Close-up view of dorsal skin; 5: Ventral view of hand; 6: Ventral view of foot. Scale bar: 5 mm. Photos by Jin-Long Ren.

Forearm robust. Tips of all four fingers expanded into small discs, finger III disc much smaller than diameter of tympanum; circummarginal grooves present on tips of all fingers, but indistinct on first finger; relative finger length I<II<IV<III; one subarticular tubercle on fingers I and II, two on fingers III and IV; supernumerary tubercles below bases of all fingers; dermal fringe absent; three metacarpal tubercles present; nuptial pad developed, swollen, located on inner side of first finger.

Hindlimb slender, tibiotarsal articulation beyond snout, heels overlapped when hindlimbs flexed and held perpendicular to body. Tips of all five toes expanded into small discs, width of toe IV disc slightly smaller than finger III disc; relative toe length I<II<VIV; toes entirely webbed, webbing formula: I 0-0 II 0-1* III 0-1. IV 1-0 V; inner metatarsal tubercle oval; outer metatarsal tubercle small and indistinct.

Dorsal surface relatively smooth, without any distinct warts on dorsal head, body, or limbs; lateral surface smooth, except very small white warts below dorsolateral folds, especially near crotch; supratympanic fold indistinct, temporal region without any tubercles; dorsolateral fold distinct, from rear of upper eyelid to near vent; ventral surfaces smooth except flat tubercles on ventral surface of basal thigh; one low rictal gland, continuous with upper lip.

Coloration of holotype in life: Dorsal side pale brown, with dark brown spots on dorsal head and body; irregular transverse dark brown bands on forelimbs, distinct transverse dark brown bands on hindlimbs. Lateral head black, upper lip white, with black line below; lateral body above half grayish brown, below half pale brown, with indistinct yellow pigmentation on crotch, without distinct spots. Ventral head and body white, throat and chest with brownish black spots, sides of belly with brownish black spots or not; ventral side of limbs brownish yellow. Upper one fourth of iris golden with small brown spots, lower part red brown.

Coloration of holotype in preservative: Dorsal color pale brownish gray, spots or bands black; lateral side, yellow pigmentation changed to white; ventral color cream white, spots pale gray.

Secondary sexual characters: Males with pair of developed external subgular vocal sacs; inner side of first finger with developed, velvety nuptial pad; forearm strong.

Variation: Measurements of referred specimens are summarized in Table 2. Specimens show some differences in coloration on ventral side (in preservative), two male specimens (CIB 116 986–87) without spots on sides of belly.

Distribution and habitat: *Amolops chunganensis* is currently known from Fujian, Jiangxi, Chongqing, Guangdong, Guangxi, Guizhou (Leishan), Hubei (Shennongjia), Hunan, Sichuan (Mt. Daba), and Zhejiang, China (Fei et al., 2009b; Yang, 1991; this study).

The A. chunganensis population inhabits mountain streams at 950 to 1 150 m a.s.l. in Huanggang, Mt. Wuyi, China. The streams are ~10 m wide and surrounded by moist subtropical evergreen broadleaved forests. Males were observed calling actively on leaves or twigs of bushes at the bank of streams from dusk to midnight during our investigation in early July 2020. Nevertheless, we did not find any individuals of this population during our investigation of the same locality in late July 2019. Thus, the breeding season of this Huanggang

Table 2 Measurements of five adult male specimens and one adult female specimen of *A. chunganensis sensu stricto* from Mt. Wuyi (in mm)

Characters	CIB 33536	CIB 116985	CIB 116986	CIB 116987	CIB 116988	Range	Mean± <i>SD</i>	Ratio to SVL (%)	CIB 118077	Ratio to SVL (%)
Sex	Male	Male	Male	Male	Male	_	_	_	Female	_
SVL	37.2	39.3	38.6	41.5	38.1	37.2-41.5	38.9±1.6	-	52.6	-
HL	14.0	15.1	14.4	15.1	14.0	14.0-15.1	14.5±0.6	37.3	18.2	34.6
HW	12.5	13.5	13.1	13.9	13.0	12.5-13.9	13.2±0.5	33.9	17.8	33.8
NL	3.2	3.2	3.1	3.6	3.2	3.1-3.6	3.3±0.2	8.5	3.8	7.2
NE	2.3	2.8	2.8	2.6	2.4	2.3-2.8	2.6±0.2	6.7	3.2	6.1
SL	6.1	6.2	5.7	6.3	6.2	5.7-6.3	6.1±0.2	15.7	7.9	15.0
INS	4.5	4.7	4.5	4.8	4.4	4.4-4.8	4.6±0.2	11.8	5.7	10.8
IOS	3.7	4.3	3.9	4.3	3.7	3.7-4.3	4.0±0.3	10.3	5.3	10.1
UEW	3.5	3.6	3.6	3.8	3.8	3.5-3.8	3.7±0.1	9.5	4.9	9.3
EHD	4.8	5.2	5.2	5.0	5.0	4.8-5.2	5.0±0.2	12.9	6.4	12.2
TD	2.7	2.6	2.7	3.0	2.4	2.4-3.0	2.7±0.2	6.9	3.8	7.2
TE	1.3	1.4	1.2	1.6	1.5	1.2-1.6	1.4±0.2	3.6	1.7	3.2
FAHL	19.0	19.7	19.0	20.4	19.8	19.0-20.4	19.6±0.6	50.4	25.5	48.5
LAW	4.4	5.2	4.8	5.5	5.0	4.4-5.5	5.0±0.4	12.9	4.7	8.9
HAL	12.1	12.4	11.3	12.2	12.1	11.3-12.4	12.0±0.4	30.8	14.1	26.8
F3W	1.8	2.0	1.8	2.1	1.9	1.8-2.1	1.9±0.1	4.9	1.8	3.4
FML	21.0	21.5	18.9	20.8	20.1	18.9-21.5	20.5±1.0	52.7	26.6	50.6
TBL	23.1	23.2	21.2	23.0	21.8	21.2-23.2	22.5±0.9	57.8	30.4	57.8
TFL	31.8	32.8	29.1	32.7	31.4	29.1-32.8	31.6±1.5	81.2	39.9	75.9
FOL	19.9	21.5	19.2	21.0	20.3	19.2-21.5	20.4±0.9	52.4	25.6	48.7
T4W	1.4	1.6	1.5	1.5	1.6	1.4-1.6	1.5±0.1	3.9	1.6	3.0

For abbreviations, see Materials and Methods. -: Not available.

population may end before mid-July.

In the same microhabitat from Huanggang, Mt. Wuyi, *A. wuyiensis* (Liu & Hu, 1975), *Odorrana huanggangensis* Chen, Zhou & Zheng, 2010, *Quasipaa spinosa* (David, 1875), and *Trimeresurus stejnegeri* Schmidt, 1925 were commonly observed during the survey period in 2020. For further details on the life history of the type locality population see Pope (1931)

Amolops chaochin sp. nov. Jiang, Ren, Lyu, and Li (Figures 6B, 7)

Staurois chunganensis Liu, 1940, J. West China Border Res. Soc., 12 (B): 32–35; Liu, 1941, Peking Nat. Hist. Bull., 15(4): 291–295.

Amolops chunganensis Fei et al. 2009, Fauna Sinica Amphibia, vol.3: 1514–1519.

Holotype: CIB 116971 (field no. LAB 2020130), adult male, collected from Jiguanshan (E103.351094°, N30.782583°, 1179 m a.s.l.), Chongzhou City (county-level city), Chengdu City, Sichuan, China, on 20 June 2020 by Jin-Long Ren and Xin-Yu Li.

Allotype: CIB 116972 (field no. LAB 2020133), adult female, collected from Sanlang (E103.460097°, N30.826772°, 920 m a.s.l.), Chongzhou City (county-level city), Chengdu City, Sichuan, China, on 20 June 2020 by Jin-Long Ren and Xin-Yu Li.

Paratypes: CIB 116974, CIB 116978 (two males), collected from the same locality and date as holotype; CIB 116973, CIB 116975–77 (four males), CIB 116979–84 (six females),



Figure 7 General and close-up views of *Amolops chaochin* **sp. nov.** in life, showing color variation among individuals and features in amplexus

A: Adult male from Jiguanshan, Chongzhou, Chengdu, Sichuan; B-C: Adult males from Xiling Snow Mountain, Dayi, Chengdu, Sichuan; D: General view of mating pairs in amplexus in axillary amplectic positions, upper: male, lower: female; E: Close-up view of pair of developed external subgular vocal sacs in male (see arrows); F: Close-up views of male forelimbs in axillary amplectic positions. Photos by Jin-Long Ren.

collected from the same locality and date as allotype.

Referred specimens: CIB 118027 (vouchered bottle number, contains 12 tadpoles numbered CIB 118027–1 to 118027–12, including 10 tadpoles at stage 31, one at stage 30, and one at stage 28), collected from Qingyin'ge, Mt. Emei, Sichuan, China, on 3 October 2020 by K. Jiang.

Etymology: Specific epithet "chaochin" is named after Prof. Ch'eng-Chao Liu (1900-1976) and his wife Prof. Shu-Chin Hu (1914-1992), combining the last words of their given names "Chao" and "Chin". Prof. Liu and Prof. Hu both greatly contributed to Chinese herpetology and established the Herpetological Museum at the Chengdu Institute of Biology, Chinese Academy of Sciences. During their fieldwork in Mt. Emei, Prof. Liu and Prof. Hu found the first pair of specimens of this new species. Furthermore, based on field observations from 1938 to 1940, Prof. Liu published the detailed life history of this new species under the name "Staurois chunganensis" (Liu 1941), and the specimens collected by Prof. Liu are still preserved in CIB (Figure 8A). We suggest the English common name as "Chaochin's torrent frog" and the Chinese common name as "钊琴湍蛙 (in Chinese Pinyin: Zhāo Qín Tuān Wā)".

Diagnosis: According to the morphological characters of the *A. monticola* group stated by Stuart et al. (2010), *Amolops chaochin* sp. nov. is placed in the *A. monticola* group based

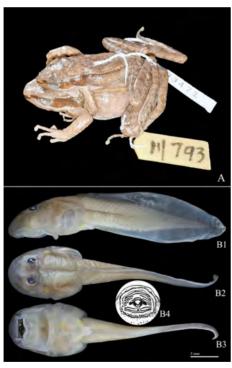


Figure 8 Paired specimens (A) (CIB 33471; field number: JII 793) of *Amolops chaochin* **sp. nov.** collected by Prof. Cheng-Chao Liu from Mt. Emei, Sichuan, on 21 July 1940, photo by Ke Jiang, and tadpole (B) of *Amolops chaochin* **sp. nov.** from Mt. Emei, Sichuan, in preservative

B1: Lateral view; B2: Dorsal view; B3: Ventral view (in preservative), photos by Jin-Long Ren. B4: Ventral view of mouth (drawing), cited from Liu (1941).

on the following diagnosis: (1) skin relatively smooth; (2) dorsolateral fold distinct; (3) lateral side of head black, upper lip stripe yellowish white extending to shoulder.

Amolops chaochin **sp. nov.** is distinguished from all other congeners in the *A. monticola* group by the following combination of characters: (1) moderate body size, SVL 35.3-39.2 mm in males (n=7) and 50.5-54.4 mm in females (n=7); (2) tympanum distinct, larger than half of eye diameter; (3) small tooth-like projection on anteromedial edge of mandible; (4) circummarginal groove on all fingers; (5) white tubercles on dorsal side of posterior body in both sexes; (6) distinct tubercles on dorsal thigh and white spinose tubercles on dorsal tibia in both sexes; (7) white tubercles on posterior region of tympanum in males; (8) toe webbing reaching disk by dermal fringe on inner side of toe II; (9) vomerine teeth present; (10) transverse bands on dorsal limbs; (11) external vocal sacs present in males.

Description of holotype. Moderate body size, SVL 37.3 mm, slightly compressed in vertical direction. Head slightly longer than wide (HL/HW 1.03); snout projecting forward, rounded at tip; nostril lateral, slightly closer to eye than tip of snout; canthus rostralis distinct; loreal region concave and oblique; eye relatively large (EHD/HL ratio 0.35); interorbital distance larger than width of upper eyelid; tympanum distinct, tympanum diameter about two thirds of eye diameter (TD/EHD ratio 0.63), tympanic rim elevated; vomerine teeth present; tongue pyriform, deeply notched posteriorly; vocal sac openings present.

Forearm robust. Tips of all four fingers expanded into small discs, finger III disc much smaller than diameter of tympanum; circummarginal grooves present on tips of all fingers, but indistinct on first finger; relative finger length I<II<V<III; one subarticular tubercle on fingers I and II, two on fingers III and IV; supernumerary tubercles below bases of outer three fingers; dermal fringe absent; three metacarpal tubercles present; nuptial pad developed, swollen, located on inner side of first finger.

Hindlimb slender, tibiotarsal articulation beyond snout, heels overlapped when hindlimbs flexed and held perpendicular to body. Tips of all five toes expanded into small discs, width of toe IV disc slightly smaller than finger III disc; relative toe length I<II<VIIV; toes webbed two thirds, webbing formula: I 0-1⁺ II 0-1 III 0-1⁻ IV 1-0 V; inner metatarsal tubercle oval; outer metatarsal tubercle small but distinct.

Dorsal surface relatively smooth, small warts present on dorsal head and body, white tubercles present on dorsal side of posterior body, distinct tubercles on dorsal thigh and white spinose tubercles on dorsal tibia; lateral surface smooth, very small white warts below dorsolateral folds, especially near crotch; supratympanic fold indistinct, temporal region with small white tubercles; dorsolateral fold distinct, from rear of upper eyelid to near vent; ventral surfaces smooth except flat tubercles on ventral surface of basal thigh; one low rictal gland, continuous with upper lip.

Coloration of holotype in life: Dorsal side brown, with black spots on dorsal head and body; irregular transverse black bands on forelimbs, distinct transverse black bands on hindlimbs. Lateral head black, upper lip white, with black line below; lateral body gray with large black spots, and yellow

pigmentation on crotch. Ventral head and body yellowish white, throat and chest with dark gray spots; ventral side of limbs yellow. Upper one fourth of iris golden with small brown spots, lower part red brown.

Coloration of holotype in preservative: Dorsal color brownish gray, spots or bands grayish black; lateral side, yellow pigmentation changed to white; ventral color cream white, spots pale gray.

Sexual dimorphism: Males with pair of developed external subgular vocal sacs; inner side of first finger with developed, velvety nuptial pad; forearm of males stronger than females, and snout-vent length of males smaller than females; white tubercles on dorsal side of posterior body, tubercles on dorsal thigh and white spinose tubercles on dorsal tibia of males more distinct than that of females.

Variation: Measurements of type series and referred specimens are summarized in Tables 3, 4. Specimens show some differences in coloration on ventral side (in preservative). Two male specimens (CIB 116973 and CIB 116977) and three female specimens (CIB 116981–82, CIB116984) with dark gray spots on throat and chest, other five male specimens (CIB 116971, CIB 116974–76, CIB 116978) and three female specimens (CIB 116979–80, CIB 116983) with pale gray spots on throat and chest.

Tadpoles in preservative (based on 10 tadpoles at stage 31): SVL 12.4–14.2 mm (mean 13.2 mm), TAL 21.4–25.3 mm (mean 23.7 mm), TOL 33.9–39.2 mm (mean 36.9 mm) (Table 5; Figure 8B). Body vertically flattened; eyes on dorsal head; pair of rounded yellow glands behind gills, same size as eyes; spiraculum on left side, spiracular tube present; large "U" shaped sucker behind mouth on ventral side; pair of rounded

yellow glands at base of hindlimb buds, smaller than eyes; medial vent tube small, opening at end; tail horizontally flattened, tail length about 1.8 times body length, tail muscle developed, tail tip blunt. Single row of regular papillae on each side of lateral mouth, single row of regular papillae on edge of lower lip; keratodont formula III: 4+4/1+1: II, some specimens III: 3+3/1+1: II in Fei et al. (2009b). Dorsal and lateral sides brownish gray, caudal fins with small dark gray spots and tiny lines; ventral side grayish white.

Distribution and habitat: Amolops chaochin **sp. nov.** is known from mountainous regions at the edge of the Sichuan Basin, including Chengdu City (Chongzhou, Dayi, and Dujiangyan), Leshan City (Mt. Emei), Mianyan City (Anxian) and Ya'an City (Tianquan) (Liu, 1941), Sichuan. Based on molecular data, it is also distributed in Bijie (Guizhou) and Wenxian (Gansu).

The new species seems to be both diurnal and nocturnal. During our field investigations in May 2019 and June 2020 at Chengdu, both males and females were rather active across daytime and nighttime, especially on rainy days. Males were found energetically calling on leaves or twigs of bushes, rocks, and even on roads adjacent to the banks of the mountain streams (Figure 9). All females were found paired with males, and the mating pairs were mostly found floating with the stream currents. Local population density appears quite large, with Liu (1941) collecting 123 males and 87 females from Mt. Emei, Sichuan, on 20 July 1940. Although we found no eggs in the field, Liu (1941, 1950) recorded egg masses attached to the under surface of stones in deep water, with a clutch size of 417–448. For further details on life history, see Liu (1941, 1950).

Table 3 Measurements of seven adult male specimens (type series) of Amolops chaochin sp. nov. (in mm)

Characters	CIB 116971*	CIB 116973	CIB 116974	CIB 116975	CIB 116977	CIB 116978	CIB 116976	Range	Mean±SD	Ratio to SVL (%)
SVL	37.3	38.3	37.5	37.4	39.2	35.3	37.6	35.3-39.2	37.5±1.2	_
HL	13.1	13.9	13.4	14.5	14.3	13.3	13.8	13.1-14.5	13.8±0.5	36.8
HW	12.7	12.7	12.6	13.3	13.0	12.4	12.8	12.4-13.3	12.8±0.3	34.1
NL	2.7	2.8	2.8	3.5	3.2	2.9	3.1	2.7-3.5	3.0±0.3	8.1
NE	2.3	2.1	1.9	2.0	2.3	1.9	2.2	1.9-2.3	2.1±0.2	5.6
SL	5.4	5.4	5.6	5.3	5.9	5.3	5.4	5.3-5.9	5.5±0.2	14.7
INS	4.1	4.4	4.2	4.3	4.2	4.0	4.2	4.0-4.4	4.2±0.1	11.2
IOS	3.4	3.5	3.5	3.8	3.8	3.6	2.7	2.7-3.8	3.4±0.4	9.2
UEW	3.3	3.1	3.4	3.6	3.4	3.3	3.3	3.1-3.6	3.3±0.2	8.9
EHD	4.6	4.8	4.5	4.8	4.7	4.6	4.4	4.4-4.8	4.6±0.1	12.4
TD	2.9	3.1	3.0	3.2	3.0	2.9	3.1	2.9-3.2	3.0±0.1	8.1
TE	0.9	1.1	0.9	0.8	0.9	0.8	1.0	0.8-1.1	0.9±0.1	2.4
FAHL	19.8	20.6	19.6	19.4	20.3	18.6	19.8	18.6-20.6	19.7±0.6	52.5
LAW	4.9	5.1	5.1	4.8	5.0	4.8	5.3	4.8-5.3	5.0±0.2	13.4
HAL	11.2	12.2	11.6	11.8	11.8	10.5	11.8	10.5-12.2	11.5±0.6	30.7
F3W	1.5	1.6	1.7	1.6	1.7	1.7	1.7	1.5-1.7	1.6±0.1	4.3
FML	19.7	18.7	20.1	19.0	19.5	17.7	19.9	17.7-20.1	19.2±0.8	51.1
TBL	23.0	22.1	23.2	22.0	22.1	20.9	23.0	20.9-23.2	22.3±0.8	59.5
TFL	31.5	31.6	29.8	30.3	32.1	29.0	32.6	29.0-32.6	30.9±1.3	82.6
FOL	19.5	20.9	19.0	20.3	21.5	19.1	21.7	19.0-21.7	20.3±1.1	54.2
T4W	1.3	1.4	1.6	1.3	1.6	1.6	1.4	1.3-1.6	1.5±0.1	3.8

^{*:} Holotype. For abbreviations, see Materials and Methods. -: Not available.

Table 4 Measurements of seven adult female specimens (type series) of Amolops chaochin sp. nov. (in mm)

Characters	CIB 116972#	CIB 116979	CIB 116980	CIB 116981	CIB 116982	CIB 116983	CIB 116984	Range	Mean± <i>SD</i>	Ratio to SVL (%)
SVL	51.3	51.8	54.4	50.5	52.7	54.0	53.1	50.5-54.4	52.5±1.4	_
HL	18.0	17.9	18.0	17.5	18.1	18.5	18.6	17.5-18.6	18.1±0.4	34.4
HW	16.7	16.9	16.9	17.0	16.8	18.4	17.2	16.7-18.4	17.1±0.6	32.8
NL	3.8	3.6	3.5	4.1	4.1	4.4	5.1	3.5-5.1	4.1±0.5	7.9
NE	3.1	3.0	3.2	2.6	2.9	3.1	3.2	2.6-3.2	3.0±0.2	5.7
SL	7.4	7.0	7.0	7.2	7.2	7.0	7.3	7.0-7.4	7.2±0.2	13.6
INS	5.5	5.2	5.5	5.5	5.6	5.8	5.4	5.2-5.8	5.5±0.2	10.5
IOS	4.6	4.6	4.6	4.6	5.1	4.7	4.7	4.6-5.1	4.7±0.2	9.0
UEW	3.7	4.7	4.5	4.3	4.0	4.2	4.2	3.7-4.7	4.2±0.3	8.1
EHD	5.2	5.7	5.4	5.4	5.7	5.6	5.6	5.2-5.7	5.5±0.2	10.4
TD	3.3	3.2	3.6	3.1	3.3	3.2	3.3	3.1-3.6	3.3±0.2	6.3
TE	1.9	2.1	1.7	2.0	1.8	2.4	1.6	1.6-2.4	1.9±0.3	3.7
FAHL	26.8	27.1	26.6	26.8	26.6	26.8	24.9	24.9-27.1	26.5±0.7	50.3
LAW	4.2	4.4	4.6	4.4	4.3	4.6	4.6	4.2-4.6	4.4±0.2	8.5
HAL	15.2	16.4	15.0	15.0	14.8	14.8	14.7	14.7-16.4	15.1±0.6	29.0
F3W	2.0	2.3	2.2	2.0	1.8	2.1	2.0	1.8-2.3	2.1±0.2	3.9
FML	26.8	27.6	26.1	26.6	27.1	27.1	24.8	24.8-27.6	26.6±0.9	50.4
TBL	30.4	30.9	29.9	30.0	30.3	30.8	28.4	28.4-30.9	30.1±0.8	57.1
TFL	42.5	43.8	41.5	43.0	42.6	41.6	39.4	39.4-43.8	42.1±1.4	79.9
FOL	28.4	28.8	26.4	28.8	26.8	27.4	26.0	26.0-28.8	27.5±1.2	52.3
T4W	1.9	1.7	1.8	1.7	1.8	1.8	2.0	1.7-2.0	1.8±0.1	3.5

^{#:} Allotype. For abbreviations, see Materials and Methods. -: Not available.

Table 5 Measurements of 10 tadpoles (at stage 31) of *Amolops chaochin* sp. nov. (in mm)

		•		
Number	SVL	TAL	TOL	TH
1	13.3	24.7	38.0	7.9
2	14.2	24.9	39.0	7.7
3	13.3	24.4	37.7	8.8
4	12.5	21.4	33.9	7.8
5	13.9	24.4	38.3	8.3
6	14.0	25.3	39.2	8.1
7	12.4	23.7	36.1	7.2
8	12.6	22.7	35.3	7.8
9	12.5	23.1	35.7	8.3
10	13.1	23.1	36.1	7.4
Range	12.4-14.2	21.4-25.3	33.9-39.2	7.2-8.8
Mean± <i>SD</i>	13.2±0.7	23.7±1.2	36.9±1.8	7.9±0.5

For abbreviations, see Materials and Methods.

In the same microhabitat in Chengdu, *Bufo gargarizans* (Cantor, 1842), *A. mantzorum* (David, 1871), *Odorrana* cf. *margaretae* (Liu, 1950), *Zhangixalus omeimontis* (Stejneger, 1924), and *Hebius metusia* (Inger, Zhao, Shaffer & Wu, 1990) were commonly observed during the survey period in 2019.

Comparison: Amolops chaochin sp. nov. differs from all other species, except the A. monticola species group, by smooth skin, lateral side of head dark, with light-colored upper lip stripe extending to shoulder, and distinct dorsolateral folds. In the A. monticola species group, Amolops chaochin sp. nov. differs from A. bellulus, A. compotrix, A. cucae, A. nyingchiensis, A. deng, A. putaoensis, and A. akhaorum based on the following characters: pair of external subgular



Figure 9 Habitat of *Amolops chaochin* **sp. nov.** at 1 179 m a.s.l. on Jiguanshan, Chongzhou, Chengdu, Sichuan, China

Type series were found across rocky, flowing streams (A) and adjacent pools (B, mating pair *in situ* on stones), ditches, and shrubs. Photos by Jin-Long Ren.

vocal sacs present (vs. absent in *A. bellulus*, *A. deng*, and *A. nyingchiensis*; internal vocal sacs present in *A. akhaorum*, *A. compotrix*, *A. cucae*, and *A. putaoensis*). *Amolops chaochin* **sp. nov.** differs from *A. archotaphus* by presence of circummarginal groove on all fingers (vs. circummarginal

groove absent at first finger), differs from A. chakrataensis by tibiotarsal articulation beyond snout (vs. tibiotarsal articulation not reaching snout); differs from A. daorum, A. iriodes, A. mengdingensis, A. vitreus, and A. wenshanensis by dorsal side brown (vs. dorsal side green); differs from A. mengyangensis by smaller body size (SVL 35.3-39.2 mm in males and 50.5-54.4 mm in females vs. SVL 39.0-40.0 mm in males and 60.0 mm in females) and tubercles and warts on dorsal surface present (vs. absent); differs from A. tuanjieensis by tympanum diameter greater than half of eye diameter (vs. tympanum diameter less than half of eye diameter); differs from A. monticola by smaller body size (SVL 35.3-39.2 mm in males and 50.5-54.4 mm in females vs. SVL 41.0 in male and 65.0 in female) and larger tympanum (TD/ED 0.60-0.65 vs. 0.33-0.50); differs from A. anigiaoensis by smaller body size (SVL 35.3-39.2 mm in males and 50.5-54.4 mm in females vs. SVL 51.6 mm in males and 69.5-71.7 mm in females) and "/ \" shaped pattern on throat absent (vs. present); differs from A. kohimaensis by smaller body size (SVL 35.3-39.2 mm in males vs. SVL 42.8-48.6 mm in males) and patch covered by microgranules on chest absent (vs. present).

Amolops chaochin **sp. nov.** is most similar to *A. chunganensis* but differs by presence of white tubercles on dorsal side of posterior body, distinct tubercles on dorsal thigh, white spinose tubercles on dorsal tibia, white tubercles on temporal region, toe webbing not reaching disk but reaching disk by dermal fringe on inner side of toe II, outer metatarsal tubercle small but distinct (vs. absence of above tubercles, toe webbing reaching disk of inner side of toe II, and outer metatarsal tubercle small and indistinct).

DISCUSSION

Cryptic diversity in Amolops chunganensis complex

Amolops chunganensis is widely reported from Fujian, Jiangxi, Chongqing, Gansu, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Shaanxi, Sichuan, Yunnan, and Zhejiang, China (AmphibiaChina, 2021; Fei et al., 2009b, 2012; Frost, 2021). Both Wu et al. (2020) and this study suggest that A. chunganensis may contain three clades with relatively high levels of intraspecific divergence. According to molecular and morphological data, the records of A. chunganensis from the northern, western, and southern edges of the Sichuan Basin (including Chengdu, Emei, and Mianyang in Sichuan; Wenxian in Gansu; Bijie in Guizhou; Figure 1, red circle) should be revised to Amolops chaochin sp. nov., but the records from the northeastern edge of the Sichuan Basin (including Nanjiang in Sichuan; and Chongqing City; Figure 1, blue circle) should remain as A. chunganensis. In addition, the historic records of A. chunganensis in eastern and southern China (Fujian, Jiangxi, Guangdong, Guangxi, Hunan, and Zhejiang; Figure 1, blue circle) are correctly identified. However, another clade previously identified as "A. chunganensis" should be further discussed. Although the single sample collected from Fangxian, northwestern Hubei (Figure 1, green circle) is geographically close to the localities of A. chunganensis sensu stricto from western Hubei and northern Chongqing, it formed a sister taxon to the A.

chunganensis+Amolops chaochin **sp. nov.** clade based on phylogeny (Figure 2; BSP=48/BPP=0.99). Consequently, the northwestern Hubei population likely represents a cryptic species, and further study is needed.

Problematic records of *Amolops chunganensis* in Yunnan. China

Amolops chunganensis is also recorded from Yunnan (Fei et al., 2009b; Yang, 1991; Yang & Rao, 2008). However, our results indicate that *A. chunganensis sensu stricto* is not distributed in this region and these problematic records should be clarified.

Amolops mengyangensis is described from Mengyang, Jinghong City, Xishuangbanna Prefecture, southern Yunnan (Wu & Tian, 1995), but was synonymized with A. chunganensis by Yang & Rao (2008) and Fei et al. (2009b), it is the reason why remained the record of A. chunganensis in this region. Although molecular data of A. mengyangensis from the type locality are not available, molecular samples from Vietnam do not cluster with A. chunganensis from the type locality (Mt. Wuyi) or other localities (Stuart et al., 2010; Wu et al., 2020; this study), and A. mengyangensis morphologically differs from A. chunganensis by its smaller tympanum (tympanum diameter less than half eve diameter vs. tympanum diameter larger than eye diameter). As the validity of A. mengyangensis is widely accepted (Frost, 2021; Nguyen et al., 2009; Ohler, 2007; Stuart et al., 2010), the A. chunganensis record from Xishuangbanna (Jinghong), southern Yunnan (Fei et al., 2009b; Yang & Rao, 2008) should be revised to its original identification, i.e., A. mengyangensis.

Yang (1991) also reported *A. chunganensis* from Menglian County, southwestern Yunnan. We re-examined the Menglian specimens (information given in the Supplementary Materials) used in Yang (1991), and their morphological characters are consistent with the original description of *A. tuanjieensis* (Gan et al., 2020b), especially in regard to living coloration, i.e., "dorsal side brown-red with irregular gray and black spots, upper part of flanks green with dark blotches, lower part white with large dark blotches", which is distinguished from *A. chunganensis* and other species of the *A. monticola* group in Yunnan. Therefore, the record of *A. chunganensis* from Menglian, Yunnan, should be provisionally revised to *A. tuanjieensis*, with further molecular confirmation required.

Revision on Amolops species groups

Group re-assignment of A. gerbillus: Amolops gerbillus was placed in the A. monticola group by Fei et al. (2005). Although this placement was doubted by Stuart et al. (2010), it has been retained in most studies (Gan et al., 2020a, 2020b; Jiang et al., 2016; Yu et al., 2019; Yuan et al., 2018). According to the original description (Annandale, 1912), A. gerbillus has "a distinct glandular laterodorsal fold". Combined with the figure (Annandale, 1912: plate II, Figure 1), the "glandular laterodorsal fold" is distinguished from the true dorsolateral folds of other species in the A. monticola group, but is consistent with species in the A. marmoratus group, e.g., "raised tubercles ...along dorsolateral row but distinct dorsolateral fold absent (A. marmoratus (Blyth, 1855); Dever et al., 2012)", "dorsolateral glands forming incomplete series on each side of dorsum (A. nepalicus Yang, 1991; Wang et

al., 2020)", and "dorsolateral fold very weakly developed with warty granules (A. mahabharatensis Khatiwada, Shu, Wang, Zhao, Xie & Jiang, 2020; Khatiwada et al., 2020)". On the other hand, A. gerbillus also has "large compressed longitudinal tubercles" on the dorsum and lacks a dark lateral head with a light-colored upper lip stripe extending to the shoulder (Annandale, 1912), in contrast with species in the A. monticola group (i.e., smooth skin, lateral side of head dark, with light-colored upper lip stripe extending to shoulder) but consistent with species in the A. marmoratus group (Dever et al., 2012; Khatiwada et al., 2020; Wang et al., 2020). Furthermore, Wang et al. (2020) suggested that A. gerbillus may be conspecific with Ixalus argus Annandale, 1912, a nomenclature synonymized with A. marmoratus in the A. marmoratus group. Therefore, we propose that A. gerbillus be moved from the A. monticola group to the A. marmoratus group, with further vouchers required for confirmation.

Establishment of A. chayuensis group and A. spinapectoralis group: Amolops chayuensis was placed into the A. monticola group by Sun et al. (2013) based on the presence of dorsolateral folds only, but it did not cluster phylogenetically with other species in the A. monticola group based on mitochondrial sequencing data (Che et al., 2020; Gan et al., 2020a, 2020b; Jiang et al., 2016; Lyu et al., 2019b; Zeng et al., 2020). Zeng et al. (2020) proposed that a new species group is needed for this species but did not provide relevant taxonomic analysis or morphological diagnosis. Conversely, Wu et al. (2020) suggested to retain A. chayuensis inside the A. monticola group as the most basal lineage using anchored hybrid enrichment data.

Morphologically, although *A. chayuensis* has true dorsolateral folds and smooth skin, but it lacks lateral side of head dark, with a light-colored upper lip-stripe extending to the shoulder (for *A. chayuensis*, lateral head process the same color as dorsal side and lacking light-colored upper lip-stripe; from Che et al., 2020; Sun et al., 2013; this study), which is a diagnostic character of the *A. monticola* group. Phylogenetically, *A. chayuensis* was consistently recovered as a distinct monophyletic clade, thus the distinctiveness of *A. chayuensis* should be recognized (Figure 2). Therefore, we support Zeng et al. (2020) and suggest that *A. chayuensis* be removed from the *A. monticola* group to form an independent *A. chayuensis* species group.

The Vietnamese species *A. spinapectoralis* Inger, Orlov & Darevsky, 1999 is phylogenetically recognized as sister to the *A. hainanensis*, *A. daiyunensis* and *A. ricketti* groups clade but cannot be placed into any recognized species group (Wu et al., 2020). Morphologically, *A. spinapectoralis* can be distinguished from the *A. hainanensis*, *A. daiyunensis* and *A. ricketti* groups, as well as other known species groups, based on the following characters: disc of first finger distinctly larger than disc of second finger, nuptial pad in males containing whitish conical spines, and chest of males with oval area of similar spines. Therefore, we suggest the establishment of a new species group, i.e., *A. spinapectoralis* group, to contain this single species.

Revised memberships and diagnoses for *Amolops* species groups: Wu et al. (2020) proposed a new species group, i.e., *A. viridimaculatus* group, which contained *A.*

viridimaculatus, A. medogensis, and four undescribed species (three were described in Che et al., 2020). Before the new group was proposed, A. viridimaculatus and A. medogensis were placed in the A. mantzorum group and A. marmoratus group, respectively (Fei et al., 2009b; Lyu et al., 2019b). Furthermore, three new species (A. beibengensis Jiang, Li, Zou, Yan & Che, 2020, A. gyirongensis Jiang, Wang, Wang, Pan & Che, 2020, and A. wangyufani Jiang, 2020) clustered with species in the A. viridimaculatus group were described in Che et al. (2020). However, diagnostic revisions of the A. mantzorum, A. marmoratus, and A. viridimaculatus groups are needed. Together with re-assigning A. gerbillus and the establishment of the A. chayuensis and A. spinapectoralis groups, we present an overall revision of all species groups as follows:

I. Diagnosis and content of revised A. monticola group

Diagnosis: (1) true dorsolateral folds present (not formed by incomplete series of glands); (2) skin smooth; (3) lateral side of head dark, with light-colored upper lip stripe extending to shoulder

Content (21 species): A. aniqiaoensis, A. akhaorum, A. archotaphus, A. bellulus, A. chakrataensis, A. chaochin sp. nov., A. chunganensis, A. compotrix, A. cucae, A. daorum, A. deng, A. kohimaensis, A. iriodes, A. mengdingensis, A. mengyangensis, A. monticola, A. nyingchiensis, A. putaoensis, A. tuanjieensis, A. vitreus, and A. wenshanensis.

Remarks: Placements are supported by both molecular and morphological data (Che et al., 2020; Gan et al., 2020a, 2020b; Liu et al., 2000; Ray, 1992; Zeng et al., 2020; this study), except for *A. kohimaensis* (Biju et al., 2010) and *A. monticola* (Anderson, 1871; Boulenger, 1920), which are supported by morphological data only.

II. Diagnosis and content of newly proposed A. chayuensis group

Diagnosis: (1) true dorsolateral folds present (not formed by incomplete series of glands); (2) skin smooth; (3) lateral side of head same color as dorsal side, light-colored upper lip stripe extending to shoulder absent.

Content (one species): A. chayuensis.

Remarks: Placement is supported by both molecular and morphological data (Che et al., 2020; Sun et al., 2013; Zeng et al., 2020; this study).

III. Diagnosis and content of revised A. mantzorum group

Diagnosis: (1) moderate or small body size, usually SVL<65 mm in males; (2) true dorsolateral folds absent, but well-developed glands present in incomplete series along dorsolateral junction of body on each side in several species; (3) vomerine teeth present, except for *A. loloensis* and *A. ottorum*; (4) circummarginal groove on disc of finger I absent; (5) tarsal fold and tarsal glands absent; (6) vocal sac present or absent in males; (7) nuptial pad present on first finger in males

Content (10 species): *A. granulosus* (Liu & Hu, 1961), *A. mantzorum*, *A. jinjiangensis* Su, Yang & Li, 1986, *A. lifanensis* (Liu, 1945), *A. loloensis* (Liu, 1950), *A. minutus* Orlov & Ho, 2007, *A. ottorum* Pham, Sung, Pham, Le, Ziegler & Nguyen, 2019, *A. shuichengicus* Lyu & Wang, 2019, *A. tuberodepressus* Liu & Yang, 2000, and *A. xinduqiao* Fei, Ye, Wang & Jiang, 2017.

Remarks: Placements are supported by both molecular and morphological data (Lyu et al., 2019b; Pham et al., 2019; Wu et al., 2020; Zeng et al., 2020), except for *A. minutus* (Orlov & Ho, 2007), which is supported by morphological data only.

IV. Diagnosis and content of revised A. marmoratus group

Diagnosis: (1) true dorsolateral folds absent, but well-developed glands present in incomplete series along dorsolateral junction of body on each side in individuals of several species; (2) vomerine teeth present; (3) circummarginal groove on disc of finger I present; (4) tarsal fold and tarsal glands absent; (5) vocal sac present in males; (6) nuptial pad present on first finger in males.

Content (10 species): A. afghanus (Günther, 1858), A. assamensis Sengupta, Hussain, Choudhury, Gogoi, Ahmed & Choudhury, 2008, A. gerbillus, A. indoburmanensis Dever, Fuiten, Konu & Wilkinson, 2012, A. jaunsari Ray, 1992, A. mahabharatensis, A. marmoratus, A. nepalicus, A. panhai Matsui & Nabhitabhata, 2006, and A. yarlungzangbo Jiang, Wang, Li, Qi, Li & Che, 2020.

Remarks: Placements are supported by both molecular and morphological data (Che et al., 2020; Khatiwada et al., 2020; Wang et al., 2020; Wu et al., 2020), except for *A. assamensis* (Sengupta et al., 2008), which is supported by morphological data only. Furthermore, *A. jaunsari* is suggested to be closely related to *A. afghanus* (Dutta, 1997).

V. Diagnosis and content of revised *A. viridimaculatus* group Diagnosis: (1) large body size, usually SVL>70 mm in males, except for *A. gyirongensis* and *A. wangyufani*; (2) dorsolateral folds absent; (3) vomerine teeth distinct; (4) circummarginal groove on disc of finger I present or absent; (5) tarsal fold and tarsal glands absent; (6) vocal sac absent in males; (7) nuptial pad present on first finger in males.

Content (13 species): A. beibengensis (as Amolops sp. 2 in Wu et al., 2020), A. caelumnoctis Rao & Wilkinson, 2007, A formosus (Günther, 1875), A. gyirongensis (as Amolops sp. 4 in Wu et al., 2020), A. himalayanus (Boulenger, 1888), A. kaulbacki (Smith, 1940), A. longimanus (Andersson, 1938), A. medogensis Li & Rao, 2005, A. nidorbellus Biju, Mahony & Kamei, 2010, A. pallasitatus Qi, Zhou, Lyu, Lu & Li, 2019, A. splendissimus Orlov & Ho, 2007, A. viridimaculatus (Jiang, 1983), and A. wangyufani (as Amolops sp. 3 in Wu et al., 2020).

Remarks: Placements are supported by both molecular and morphological data (Che et al., 2020; Qi et al., 2019; Wu et al., 2020; Zeng et al. 2020), except for *A. caelumnoctis* (Rao & Wilkinson, 2007), *A. formosus* (Günther, 1875; Boulenger, 1920), *A. himalayanus* (Boulenger, 1888; Nidup et al., 2016), *A. kaulbacki* (Smith, 1940), *A. longimanus* (Andersson, 1938; Dubois, 1986), *A. nidorbellus* (Biju et al., 2010), and *A. splendissimus* (Orlov & Ho, 2007), which are supported by morphological data only.

VI. Diagnosis and content of newly proposed A. spinapectoralis group

Diagnosis: (1) dorsolateral folds absent; (2) vomerine teeth present; (3) circummarginal groove on disc of finger I present; (4) disc of first finger distinctly larger than that of second finger; (5) vocal sac present in males; (6) nuptial pad with whitish conical spines present on first finger in males; (7) chest with oval area of similar spines in males.

Content (one species): A. spinapectoralis.

Remarks: Placement is supported by both molecular and morphological data (Inger et al., 1999; Wu et al., 2020).

VII. Diagnosis and content of A. larutensis group

Diagnosis: (1) dorsolateral folds absent; (2) tympanum distinct; (3) vomerine teeth present; (4) circummarginal groove on disc of finger I present; (5) tarsal fold or tarsal glands present; (6) vocal sac present in males; (7) nuptial pad present on first finger in males.

Content (four species): *A. australis* Chan, Abraham, Grismer & Grismer, 2018, *A. cremnobatus* Inger & Kottelat, 1998, *A. gerutu* Chan, Abraham, Grismer & Grismer, 2018, and *A. larutensis* (Boulenger, 1899).

Remarks: Placements are supported by both molecular and morphological data (Inger & Kottelat, 1998; Chan et al., 2018; Wu et al., 2020).

VIII. Diagnosis and content of A. ricketti group

Diagnosis: (1) dorsolateral folds absent; (2) vomerine teeth present or absent; (3) circummarginal groove on disc of finger I present; (4) disc of first finger distinctly smaller than that of second finger; (5) tarsal fold and tarsal glands absent; (6) vocal sac present or absent in males; (7) nuptial pad with conical or papillate spines present on first finger in males.

Content (six species): *A. albispinus* Sung, Wang & Wang, 2016, *A. ricketti* (Boulenger, 1899), *A. sinensis* Lyu, Wang & Wang, 2019, *A. wuyiensis*, *A. yatseni* Lyu, Wang & Wang, 2019, and *A. yunkaiensis* Lyu, Wang, Liu, Zeng & Wang, 2018

Remarks: Placements are supported by both molecular and morphological data (Lyu et al., 2019a; Wu et al., 2020; Zeng et al., 2020).

IX. Diagnosis and content of A. daiyunensis group

Diagnosis: (1) dorsolateral folds absent; (2) tympanum distinct or hidden; (3) vomerine teeth absent; (4) circummarginal groove on disc of finger I present; (5) tarsal glands present; (6) vocal sac present in males; (7) nuptial pad present on first finger in males.

Content (two species): A. daiyunensis (Liu & Hu, 1975) and A. hongkongensis (Pope & Romer, 1951).

Remarks: Placements are supported by both molecular and morphological data (Fei et al., 2009b; Wu et al., 2020; Zeng et al., 2020).

X. Diagnosis and content of A. hainanensis group

Diagnosis: (1) dorsolateral folds absent; (2) tympanum distinct; (3) vomerine teeth absent; (4) circummarginal groove on disc of finger I present; (5) tarsal fold or tarsal glands present; (6) vocal sac present or absent in males; (7) nuptial pad absent in males.

Content (two species): *A. hainanensis* (Boulenger, 1900) and *A. torrentis* (Smith, 1923).

Remarks: Placements are supported by both molecular and morphological data (Fei et al., 2009b; Wu et al., 2020; Zeng et al., 2020).

Key to Amolops species group

1a) True dorsolateral folds present	2
1b) True dorsolateral folds absent	
2a) Light-colored upper lip stripe extending to shoulder	
A monticula group	_

2b) Light-colored upper lip stripe absent
3a) Males without nuptial pad on first finger
3b) Males with nuptial pad on first finger
7b) Tarsal fold or tarsal glands present
Key to Chinese species of Amolops monticola group 1a) Vocal sacs absent in males
2b) Circummarginal groove present on tip of finger I
A. mengdingensis 5b) Indistinct transverse bands on dorsal surfaces of limbs, without white spinules on posterior part of dorsolateral folds
7b) Snout-vent length in males less than 50 mm
8b) Tympanum diameter larger than half of eye diameter9 9a) White tubercles present on dorsal side of posterior body, distinct tubercles on dorsal thigh, white spinose tubercles on dorsal tibia, and white tubercles on temporal region, toe webbing not reaching disk but reaching disk by dermal fringe on inner side of toe II

NOMENCLATURAL 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 nomenclatural 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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SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Permission for field surveys in Chengdu was granted by the Chengdu Municipal Park City Construction and Management Bureau (No. CDGYCS2019-SW08).

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

K.J., J.L.R., and Z.T.L. prepared the manuscript with input from all other authors. J.W.W. and J.T.L. revised the manuscript. J.L.R. and Z.T.L. collected the specimens in the field. K.J. and K.L. collected morphological data. D.W. and Z.W. collected genetic data. J.L.R. analyzed the data. All authors read and approved the final version of the manuscript.

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