

Review of the genus *Brachytarsophrys* (Anura: Megophryidae), with revalidation of *Brachytarsophrys platyparietus* and description of a new species from China

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ABSTRACT

The genus-level recognition of monophyletic short-legged toads (*Brachytarsophrys*) has been recently implicated in the taxonomic debate of *Megophrys sensu lato*. In the present study, *Brachytarsophrys* is reasonably regarded as a distinct genus based on significant morphological differentiations and recent molecular analyses. Furthermore, a comprehensive review of this genus is performed, with two species groups proposed based on morphological differences and phylogenetic relationships. Particularly, *Brachytarsophrys platyparietus* is removed as a synonym of *Brachytarsophrys carinense* and considered a valid species due to significant genetic divergence and distinct morphological differences. In addition, a new species, *Brachytarsophrys orientalis* **sp. nov.**, is described based on a series of specimens collected from southeastern China. This work takes the

member species of the genus *Brachytarsophrys* to seven, suggesting that the diversity of *Brachytarsophrys* is underestimated. In addition, the genus levels of other monophyletic groups within the subfamily Megophryinae are discussed.

Keywords: Genus level; Megophryinae; Morphology; Phylogeny; Revision

INTRODUCTION

Systematics of the subfamily Megophryinae have been debated for decades (Dubois, 1987; Dubois & Ohler, 1998; Fei et al., 2009; Fei & Ye, 2016; Frost et al., 2006; Jiang et al., 2003; Li & Wang, 2008; Rao & Yang, 1997; Zheng et al., 2004). Based on multilocus nuclear-gene and matrilineal

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mtDNA genealogy, three recent studies revealed highly similar phylogenetic relationships within Megophryinae, resolving the following monophyletic groups: i.e., *A tympanophrys*, *Brachytarsophrys*, *Megophrys*, *Ophryophryne*, *Panophrys*, *Pelobatrachus*, and *Xenophrys* (Chen et al., 2017; Liu et al., 2018; Mahony et al., 2017). However, disagreements remain regarding taxonomic proposals at the genus level among these monophyletic groups. Chen et al. (2017) considered the subfamily Megophryinae to be valid and composed of five genera: i.e., *A tympanophrys* Tian & Hu, 1983, *Brachytarsophrys* Tian & Hu, 1983, *Megophrys* Kuhl & Van Hasselt, 1822, *Ophryophryne* Boulenger, 1903, and *Xenophrys* Günther, 1864. Mahony et al. (2017) treated the entire Megophryinae subfamily as a single genus *Megophrys* and regarded the seven molecularly resolved clades in their phylogenetic tree as seven subgenera: i.e., *A tympanophrys*, *Brachytarsophrys*, *Megophrys*, *Ophryophryne*, *Panophrys* Rao & Yang, 1997, *Pelobatrachus* Beddard, 1908, and *Xenophrys*. Although the phylogenetic results of the above two studies are highly similar, the taxonomic proposals represent different views, and the focus of the taxonomic debate returns to the previous problem of morphological cognizance at the genus level.

The short-legged toad genus *Brachytarsophrys* within Megophryinae was established by Tian & Hu (1983), with *Leptobranchium carinense* Boulenger, 1889 as the type species. Based on a combination of morphological characteristics, *Brachytarsophrys* differs significantly from other groups within Megophryinae and has been regarded as a valid genus for a long time (Delorme et al., 2006; Fei et al., 2009; Fei & Ye, 2016; Frost et al., 2006; Pyron & Wiens, 2011; Xie & Wang, 2000; Zhao & Adler, 1993). Recent phylogenetic results have also confirmed *Brachytarsophrys* as a monophyletic lineage against other Megophryinae groups (Chen et al., 2017; Deuti et al., 2017; Liu et al., 2018; Mahony et al., 2017; Orlov et al., 2015; Poyarkov et al., 2017; Zhang et al., 2017). Therefore, we regard *Brachytarsophrys* as a distinct genus in this study.

Currently, the genus *Brachytarsophrys* is widely distributed in southern China, Myanmar, Vietnam, Laos, and northern Thailand, and contains five recognized species: i.e., *Brachytarsophrys carinense* (Boulenger, 1889), *Brachytarsophrys feae* (Boulenger, 1886), *Brachytarsophrys intermedia* (Smith, 1921), *Brachytarsophrys chuannanensis* Fei, Ye & Huang, 2001, and *Brachytarsophrys popei* Zhao, Yang, Chen, Chen & Wang, 2014. Rao & Yang (1997) also described *Brachytarsophrys platyparietus* as a species from northern Yunnan and considered that the previous records of *B. carinense* from southern and southwestern China should be *B. platyparietus*, with *B. carinense* being endemic to Myanmar and Thailand. However, after examining a series of specimens from China and a single specimen (MNHN 1893.0527) from Yado, Myanmar, Fei et al. (2009) temporarily treated *B. platyparietus* as a synonym of *B. carinense*, though also suggested that the validity of *B. platyparietus* requires further research and evidence.

In the present work, a series of *Brachytarsophrys* specimens and samples were collected from multiple localities (Figure 1A), covering potential unnamed populations and all recognized species. The phylogenetic relationships among *Brachytarsophrys* congeners were reconstructed and detailed morphological comparisons were performed, leading to a comprehensive review of this genus. Both the morphological comparisons and molecular results confirm that *B. platyparietus* should be re-considered as a valid species (see below for supplementary description). In addition, populations of *Brachytarsophrys* from Jiangxi and Fujian in southeastern China are revealed as a new species, named *Brachytarsophrys orientalis* sp. nov., based on morphological and molecular differences, thus demonstrating that *Brachytarsophrys* diversity is underestimated.

MATERIALS AND METHODS

Morphological characters

Measurements followed the protocols described by Fei et al. (2009) with digital calipers to the nearest 0.1 mm. These measurements were as follows: SVL: Snout–vent length (from tip of snout to vent); HDL: Head length (from tip of snout to posterior of articulation of jaw); HDW: Head width (maximum distance between both sides of articulation of jaw); SKL: Skull length (from tip of snout to posterior margin of occipital); SNT: Snout length (from tip of snout to anterior corner of eye); IOD: Interorbital distance (minimum distance between upper eyelids); IND: Internasal distance (distance between nares); ED: Eye diameter (eyeball diameter parallel to axis of body); HND: Hand length (from distal end of radioulnar to tip of finger III); RAD: Radioulnar length (from flexed elbow to proximal margin of outer palmar tubercle); TIB: Tibia length (from outer surface of flexed knee to heel); FTL: Foot length (from distal end of tibia to tip of toe IV); BL: Body length (from tip of snout to origin of tail in tadpole); TL: Tail length (from origin to tip of tail in tadpole). To show body size variation among adult males, we plotted the boxplot of SVL in R-3.6.2 (R Core Team, 2019).

The toe webbing formula followed the protocol described by Savage (1975). To describe toe webbing of *Brachytarsophrys* species accurately, the location of the web on the phalange articulation was designated as follows: - (distal part of phalange articulation); none (middle part of phalange articulation); + (proximal part of phalange articulation); ++ (lower part of phalange articulation) (Figure 2).

Sex was determined by observation of secondary sexual characters, i.e., presence of internal vocal sac openings and nuptial spines in males. Tadpole stage was identified following Gosner (1960).

Comparative morphological data of all recognized *Brachytarsophrys* species were obtained from the literature (Boulenger, 1889, 1890, 1908; Fei & Ye, 2001; Fei et al., 2009; Smith, 1921; Taylor, 1962; Zhao et al., 2014) and from examined specimens of *B. feae*, *B. chuannanensis*, and *B. popei*.

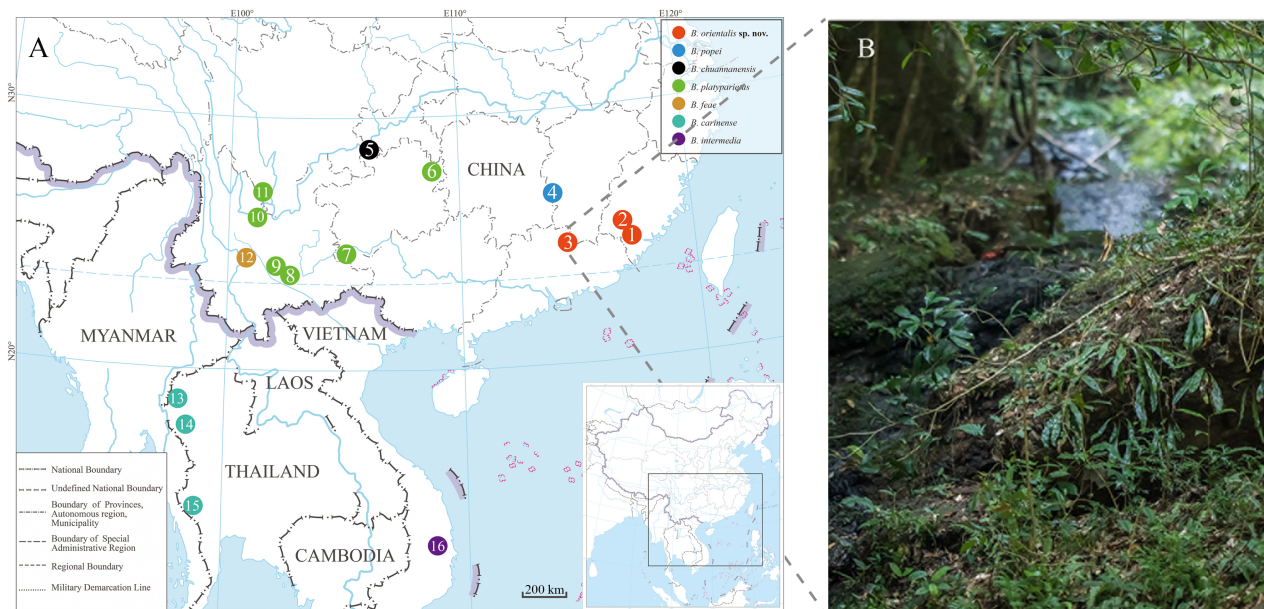


Figure 1 Collection localities of samples used in this study and habitat of *Brachytarsophrys orientalis* sp. nov.

A: Localities of *Brachytarsophrys orientalis* sp. nov.: 1: Huboliao Nature Reserve, Fujian; 2: Shanghang County, Fujian; 3: Jiulianshan Nature Reserve, Jiangxi. Localities of *B. popei*; 4: Taoyuandong Nature Reserve, Hunan. Localities of *B. chuannanensis*; 5: Hejiang County, Sichuan. Localities of *B. platyparietus*; 6: Mt. Fanjing, Guizhou; 7: Mt. Jinzhong, Guangxi; 8: Shiping County, Yunnan; 9: Mt. Mopan, Yunnan; 10: Dayao County, Yunnan; 11: Yanbian County, Yunnan. Localities of *B. feae*; 12: Jingdong County, Yunnan. Localities of *B. carinense*; 13: Mae Surin NP., Mae Hong Son, Thailand; 14: Omkoi, Chiang Mai, Thailand; 15: Thong Pha Phum, Kanchanaburi, Thailand. Localities of *B. intermedia*; 16: Krong Pa, Gia Lai, Vietnam. B: Habitat of *Brachytarsophrys orientalis* sp. nov. in Jiulianshan Nature Reserve, Jiangxi Province.

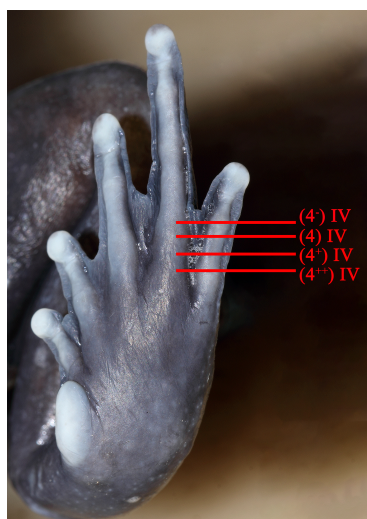


Figure 2 Location of web on phalange articulation

(4-) IV: Distal part of articulation between fourth phalange and metatarsal; (4) IV: Middle part of articulation between fourth phalange and metatarsal; (4+) IV: Proximal part of articulation between fourth phalange and metatarsal; (4++) IV: Lower part of articulation between fourth phalange and metatarsal.

All specimens were fixed in 10% buffered formalin, then transferred to 75% ethanol for preservation, and deposited in

The Museum of Biology, Sun Yat-Sen University (SYS) and Chengdu Institute of Biology (CIB), Chinese Academy of Sciences (CAS), China. Other collection abbreviations for specimens or samples include the Kunming Institute of Zoology (KIZ), CAS, China; Muséum National d'Histoire Naturelle (MNHN), France; and Royal Ontario Museum (ROM), Canada.

Molecular sampling

For molecular analyses, a total of 28 *Brachytarsophrys* samples were used, including 11 samples from the five recognized species (*B. carinense*, *B. feae*, *B. intermedia*, *B. chuannanensis*, and *B. popei*), one topotype sample of *B. platyparietus*, and 16 samples of unidentified species. Additionally, one sequence of *B. carinense* and out-group sequences of *A tympanophrys shapingensis* (Liu, 1950) and *Xenophrys mangshanensis* (Fei & Ye, 1990) were obtained from GenBank and incorporated into our dataset (Figure 1A and Table 1). All muscle samples were taken from euthanized specimens and then preserved in 95% ethanol before fixation.

Extraction, polymerase chain reaction (PCR), and sequencing

DNA was extracted from muscle tissue using an extraction kit from Tiangen Biotech (Beijing) Co., Ltd. (China). Partial cytochrome c oxidase I (COI) and cytochrome b (cyt b) genes were amplified using the primers listed in Table 2. PCR amplifications were performed in a 20 µl reaction volume with

Table 1 Localities, voucher information, and GenBank accession Nos. of all samples used in this study

ID	Species	Localities (*: Type locality)	Specimen No.	COI	cyt b
1	<i>Brachytarsophrys orientalis</i> sp. nov.	*China: Jiulianshan Nature Reserve, Longnan County, Jiangxi	SYS a004225	MT162625	MT162650
2	<i>Brachytarsophrys orientalis</i> sp. nov.	*China: Jiulianshan Nature Reserve, Longnan County, Jiangxi	SYS a004226	MT162626	MT162651
3	<i>Brachytarsophrys orientalis</i> sp. nov.	*China: Jiulianshan Nature Reserve, Longnan County, Jiangxi	SYS a004227	MT162627	MT162652
4	<i>Brachytarsophrys orientalis</i> sp. nov.	*China: Jiulianshan Nature Reserve, Longnan County, Jiangxi	SYS a004228	MT162628	MT162653
5	<i>Brachytarsophrys orientalis</i> sp. nov.	*China: Jiulianshan Nature Reserve, Longnan County, Jiangxi	SYS a004486	MT162629	MT162654
6	<i>Brachytarsophrys orientalis</i> sp. nov.	*China: Jiulianshan Nature Reserve, Longnan County, Jiangxi	SYS a005451	MT162632	MT162655
7	<i>Brachytarsophrys orientalis</i> sp. nov.	China: Gutian Township, Shanghang County, Fujian	SYS a003249	MT162623	MT162648
8	<i>Brachytarsophrys orientalis</i> sp. nov.	China: Huboliao Nature Reserve, Nanjing County, Fujian	SYS a003340	MT162624	MT162649
9	<i>Brachytarsophrys carinense</i>	Thailand: Doi Chiang Dao, Chiang Mai	K3001	KR087626	–
10	<i>Brachytarsophrys carinense</i>	Thailand: Omkoi, Chiang Mai	KIZ024170	MT162640	MT162663
11	<i>Brachytarsophrys carinense</i>	Thailand: Mae Surin NP., Mae Hong Son	KIZ024429	MT162641	MT162664
12	<i>Brachytarsophrys carinense</i>	Thailand: Thong Pha Phum, Kanchanaburi	KIZ024640	MT162642	MT162665
13	<i>Brachytarsophrys chuannanensis</i>	*China: Zihuai Township, Hejiang County, Sichuan	SYS a004926	MT162630	–
14	<i>Brachytarsophrys chuannanensis</i>	*China: Zihuai Township, Hejiang County, Sichuan	SYS a004927	MT162631	–
15	<i>Brachytarsophrys feae</i>	China: Jingdong County, Yunnan	SYS a003912	MH406362	MH407192
16	<i>Brachytarsophrys feae</i>	China: Jingdong County, Yunnan	SYS a003913	MH406363	MH407193
17	<i>Brachytarsophrys intermedia</i>	Vietnam: Krong Pa, Gia Lai	ROM 23794	MT162643	MT162666
18	<i>Brachytarsophrys platyparietus</i>	*China: Duodihe, Dayao county, Yunnan	SYS a005919	MT162633	MT162656
19	<i>Brachytarsophrys platyparietus</i>	China: Mt. Jinzhong, Longlin County, Guangxi	SYS a002236	MT162622	MT162647
20	<i>Brachytarsophrys platyparietus</i>	China: Mt. Fanjing, Tongren City, Guizhou	YPX43968	MT162644	MT162667
21	<i>Brachytarsophrys platyparietus</i>	China: Mt. Mopan, Xiping County, Yunnan	SYS a007774	MT162634	MT162657
22	<i>Brachytarsophrys platyparietus</i>	China: Mt. Mopan, Xiping County, Yunnan	SYS a007775	MT162635	MT162658
23	<i>Brachytarsophrys platyparietus</i>	China: Mt. Mopan, Xiping County, Yunnan	SYS a007776	MT162636	MT162659
24	<i>Brachytarsophrys platyparietus</i>	China: Mt. Mopan, Xiping County, Yunnan	SYS a007777	MT162637	MT162660
25	<i>Brachytarsophrys platyparietus</i>	China: Yilong Township, Shiping County, Yunnan	SYS a007790	MT162638	MT162661
26	<i>Brachytarsophrys platyparietus</i>	China: Yumen Township, Yanbian County, Sichuan	SYS a007853	MT162639	MT162662
27	<i>Brachytarsophrys popei</i>	*China: Taoyuandong Nature Reserve, Yanling County, Hunan	SYS a001864	MH406361	MH407191
28	<i>Brachytarsophrys popei</i>	*China: Taoyuandong Nature Reserve, Yanling County, Hunan	SYS a001865	MT162620	MT162645
29	<i>Brachytarsophrys popei</i>	*China: Taoyuandong Nature Reserve, Yanling County, Hunan	SYS a001866	MT162621	MT162646
30	<i>Atympanophrys shapingensis</i>	China: Mt. Wawu, Hongya County, Sichuan	SYS a005310	MH406352	MH407182
31	<i>Atympanophrys shapingensis</i>	China: Zhaojue County, Sichuan	SYS a005339	MH406359	MH407189
32	<i>Xenophrys mangshanensis</i>	China: Mt. Dayao, Jinxiu County, Guangxi	SYS a004870	MH406323	MH407153
33	<i>Xenophrys mangshanensis</i>	China: Mt. Dayao, Jinxiu County, Guangxi	SYS a004871	MH406324	MH407154

–: Not available.

Table 2 Primer pairs used in this study

Gene	Forward primer	Reverse primer	References
COI	Chmf4 (5'-TYTCWACWAAYCAYAAAGAYATCGG-3')	Chmr4 (5'-ACYTCRGGRTGRCCRAARAATCA-3')	Che et al., 2012
COI	Dglco (5'-GGTCAACAAATCATAAAGAYATYGG-3')	Dghco (5'-TAAACTTCAGGGTGACCAAAARAAYCA-3')	Meyer et al., 2005
cyt b	PFGlu14140L(5'-GAAAACCACTGTTGTHHYTCAACTA-3')	PFThr15310 (5'-CGGYTTACAAGACCGRTGCTTT-3')	Zhang et al., 2013

the following cycling conditions: initial denaturing step at 95 °C for 4 min; 35 cycles of denaturing at 95 °C for 40 s, annealing at 50 °C for 40 s, and extension at 72 °C for 1 min; and final extension step at 72 °C for 10 min. PCR products were purified with spin columns. The purified products were sequenced with both forward and reverse primers using the BigDye Terminator Cycle Sequencing Kit according to the guidelines of the manufacturer on an ABI Prism 3730 automated DNA sequencer from Shanghai Majorbio Biopharm

Technology Co., Ltd. (China). All sequences were deposited in GenBank (Table 1).

Phylogenetic analyses

Sequences were aligned using ClustalX 2.0 (Thompson et al., 1997) with default parameters in MEGA 6 (Tamura et al., 2013). The two gene segments (627 base pairs (bp) for *COI* and 1 050 bp for *cyt b*) were concatenated seriatim into a 1 677 bp sequence and further divided into two partitions based

upon each gene. The two partitions were tested respectively in jModelTest 2.1.2 (Darriba et al., 2012) based on Akaike information criteria, resulting in the both best-fitting nucleotide substitution models of GTR+G+I. Phylogenetic trees were constructed using maximum likelihood (ML) implemented in RaxmlGUI 1.3 (Silvestro & Michalak, 2012) and Bayesian inference (BI) in MrBayes 3.2.4 (Ronquist et al., 2012). For ML analysis, the majority rule consensus tree was calculated with 1 000 bootstrap replicates. For BI analysis, two independent runs with four Markov Chain Monte Carlo simulations were performed for 10 million iterations, with sampling every 1 000 generations and the first 25% of samples discarded as burn-in. Convergence of the Markov Chain Monte Carlo simulations was assessed by checking the average standard deviation of split frequencies between two runs using Tracer v.1.4 (<http://tree.bio.ed.ac.uk/software/tracer/>). We also calculated

uncorrected pairwise genetic distances (*P*-distance) in MEGA 6.

RESULTS

The ML and BI analyses, which resulted in essentially identical topologies, were integrated, as shown in Figure 3. All major nodes were sufficiently supported with Bayesian posterior probabilities (BPP) >0.95 and maximum likelihood bootstrap supports (BS) >90. The mean *P*-distances among all *Brachytarsophrys* species are given in Table 3.

All *Brachytarsophrys* samples were clustered into two major, deeply divergent, and strongly supported monophyletic groups (BPP=1.00, BS=100), designated in this study as Group I and Group II, respectively. Group I was composed of species from the Indochina Peninsula, namely, *B. carinense* and *B. intermedia*. All samples from China formed Group II, which could be divided into two clades with strong node

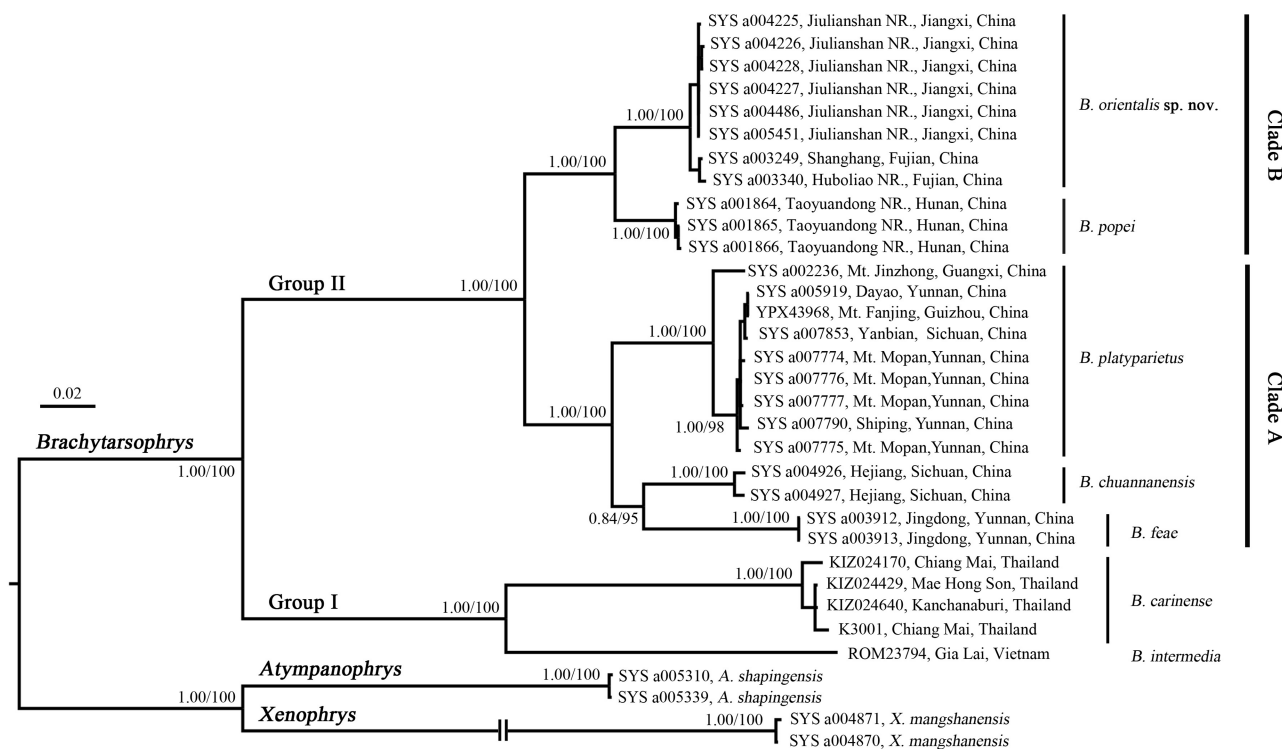


Figure 3 Bayesian inference and maximum-likelihood phylogenies

Numbers before slashes are Bayesian posterior probabilities, and numbers after slashes are maximum-likelihood bootstrap supports.

Table 3 Uncorrected *P*-distances (mean, in %) among species of the genus *Brachytarsophrys* based on partial mitochondrial *COI* gene

ID	Species	1–8	9–12	13–14	15–16	17	18–26	27–29
1–8	<i>Brachytarsophrys orientalis</i> sp. nov.	0.3						
9–12	<i>B. carinense</i>	15.8	0.6					
13–14	<i>B. chuannanensis</i>	8.5	14.7	0.5				
15–16	<i>B. feae</i>	9.4	15.3	6.3	0.0			
17	<i>B. intermedia</i>	15.7	12.1	16.3	15.2	–		
18–26	<i>B. platyparietus</i>	8.4	14.6	5.8	6.8	15.9	0.5	
27–29	<i>B. popei</i>	4.3	15.8	8.7	10.4	15.7	7.7	0.1

support (BPP=1.00, BS=100), representing populations from southwestern and southeastern China and designated as clade A and clade B, respectively.

In clade A, the topotype sample of "*B. platyparietus*" from Dayao County clustered with eight samples from multiple localities in southwestern China to form a monophyletic lineage with strong node support (BPP=1.00, BS=100) and small divergence (mean *P*-distance 0.5%), representing the "*B. platyparietus*" lineage. This lineage was the sister taxon to (*B. chuannanensis*+*B. feae*) with strong node support (BPP=1.00, BS=100), but was distant from *B. carinense* in phylogeny. In clade B, *Brachytarsophrys* samples from Jiangxi and Fujian were grouped into a monophyletic lineage with strong node support (BPP=1.00, BS=100) and small divergence (mean *P*-distance 0.3%). This was the sister taxon to *B. popei* with moderate genetic difference (mean *P*-distance 4.3%) and represented a separately evolving undescribed lineage.

The measurements and body proportions of *Brachytarsophrys* species are shown in Table 4, and the boxplot of adult male SVL is shown in Figure 4 (*B. carinense* data were insufficient and excluded). The morphological comparisons within *Brachytarsophrys* are shown in Table 5.

Adult male body size varies significantly among *Brachytarsophrys* congeners. The specimens from southeastern China are significantly smaller than that from southwestern China and Indochina. *Brachytarsophrys popei* possesses the smallest body size (SVL 70.7–83.5 mm), although the undescribed *Brachytarsophrys* species partly overlaps (SVL 76.8–82.7 mm). The undescribed specimens also present a combination of morphological characteristics not observed in other known congeners, including small body size (SVL 76.8–82.7 mm in seven adult males), moderate webbing, and absence of transversal stripes on chest in tadpoles. Therefore, based on the morphological and molecular differences, these specimens are proposed as a new species, *Brachytarsophrys orientalis* **sp. nov.**, in this study.

Furthermore, the specimens of "*B. platyparietus*" differ from all known congeners by numerous small, conical, horny tubercles on pectoral region, lateral belly to lower flank of body, ventral surface, and rear of limbs, and by absence of dermal ridge or glandular fold on dorsum. Rao & Yang (1997) found that the previously reported populations of *B. carinense* in China lacked paired elongate granular folds on dorsum, and besides their geographical distribution range was separated by another valid species (*B. feae*). Therefore, they suggested that the Chinese populations of *B. carinense* should be a distinct species (*B. platyparietus*), with *B. carinense* only being distributed in Myanmar and Thailand (Boulenger, 1889; Taylor, 1962). Our study supports this suggestion. Thus, the "*B. platyparietus*" lineage should be recognized as a distinct valid species within the genus (supplementary description on this species is given below). Currently, the species *B. platyparietus* is recognized from eastern and northern Yunnan, southern Sichuan, western Guangxi, and northeastern

Guizhou.

DISCUSSION

In morphology, *Brachytarsophrys* differs significantly from other groups within Megophryinae by a combination of morphological characters (see Systematics below). Phylogenetically, *Brachytarsophrys* is a monophyletic group (Chen et al., 2017; Deuti et al., 2017; Mahony et al., 2017; Poyarkov et al., 2017; Zhang et al., 2017) and differentiated from other groups within Megophryinae with a series of geological and ecological changes ca. 38.94 million years ago (Liu et al., 2018). Ecologically, *Brachytarsophrys* species usually hide in deep crevices between rocks or boulders in streams during the breeding season (Fei & Ye, 2001; Fei et al., 2009; Smith, 1921; Taylor, 1962; Zhao et al., 2014), which is different from other species of Megophryinae (Wang et al., 2019; Yang et al., 2018). Therefore, *Brachytarsophrys* exhibits significant differences from other groups of Megophryinae in every aspect and should be considered a distinct genus.

For the two Megophryinae taxonomic proposals suggested by Chen et al. (2017) and Mahony et al. (2017), Chen's suggestion is inapposite because the genus *Xenophrys* (including *Panophrys*) is not monophyletic and the genus *Ophryophryne* is inserted between *Xenophrys* and *Panophrys*. The treatment by Mahony et al. (2017) is also controversial as it underrated the significant differences among several groups of Megophryinae, for instance, the species of *Brachytarsophrys*. Regarding the recognition of genus *Brachytarsophrys* and the principle of monophyly, these taxonomic conflicts may be resolved by elevation of the seven subgenera proposed by Mahony et al. (2017) to genus level, which fulfills the following three criteria to be descriptively useful: reasonably compact, monophyletic, and ecologically, morphologically, or biogeographically distinct (Gill et al., 2005).

The revalidation of *B. platyparietus* and the discovery of *Brachytarsophrys orientalis* **sp. nov.** take the members of the genus to seven species. Based on the morphological differences and phylogenetic relationships, we propose two species groups within *Brachytarsophrys*: i.e., (1) *Brachytarsophrys carinense* group (Group I in Figure 3), characterized by presence of dermal ridge or glandular fold on dorsum and large body size, including two species, *B. carinense* and *B. intermedia*; (2) *Brachytarsophrys feae* group (Group II in Figure 3), characterized by absence of dermal ridge or glandular fold on dorsum and large or small body size, including five species, *B. chuannanensis*, *B. feae*, *Brachytarsophrys orientalis* **sp. nov.**, *B. platyparietus*, and *B. popei*.

Key to species of genus *Brachytarsophrys*

For identification, the seven species of *Brachytarsophrys* can be distinguished as follows:

- 1a) Presence of dermal ridge or glandular fold on dorsum.....2 (*B. carinense* group)

Table 4 Measurements (in mm; minimum–maximum, mean±SD) and body proportions of examined specimens of *Brachytarsophrys*

	<i>Brachytarsophrys orientalis</i> sp. nov.		<i>B. popei</i>		<i>B. platyparietus</i>		<i>B. chuannanensis</i>	<i>B. feae</i>	<i>B. intermedia</i>	
	M (n=7)	F (n=1)	M (n=13)	F (n=1)	M (n=6)	F (n=3)	M (n=12)	M (n=5)	M (n=7)	F (n=1)
SVL	76.8–82.7 (79.9±2.6)	88.6	70.7–83.5 (76.9±3.5)	86.2	88.5–113.0 (101.8±9.6)	118.5–131.0 (124.8±6.3)	91.4–109.4 (105.3 in CIB 98A0045)	78.5–94.9 (86.9±7.4)	86.0–103.0 (95.6±6.1)	92.0
HDL	32.8–35.0 (33.6±0.7)	40.8	29.8–34.2 (32.2±1.3)	36.0	37.1–47.0 (42.0±3.9)	46.5–52.5 (49.1±3.1)	44.8 in CIB 98A0045	31.5–35.9 (33.8±1.6)	–	–
SKL	20.1–21.5 (20.9±0.5)	24.6	17.7–20.6 (19.6±1.0)	21.2	23.9 in SYS a005919	30.6 in SYS a002236	–	21.0–23.3 (22.1±0.9)	23.0–28.0 (25.3±1.5)	27.0
HDW	39.1–42.3 (40.8±1.4)	48.8	36.0–40.8 (39.1±1.6)	42.5	43.1–57.0 (50.8±5.2)	55.7–61.0 (58.9±2.8)	54.1 in CIB 98A0045	37.7–44.4 (41.3±2.4)	44.0–51.0 (47.3±2.3)	50.0
SNT	9.0–10.6 (9.8±0.6)	12.2	8.5–10.3 (9.6±0.5)	10.6	9.9 in SYS a005919	13.5 in SYS a002236	–	9.2–10.5 (9.7±0.5)	11.0–13.0 (12.0±0.6)	12.0
IND	7.6–9.0 (8.4±0.5)	9.5	7.0–8.7 (7.8±0.4)	8.2	8.2 in SYS a005919	10.3 in SYS a002236	–	7.3–8.7 (8.3±0.6)	–	–
IOD	8.9–13.6 (12.0±1.7)	14.6	11.1–14.0 (12.0±1.2)	13.9	10.6 in SYS a005919	14.0 in SYS a002236	–	8.8–13.9 (11.0±2.0)	12.0–13.0 (12.4±0.5)	13.0
ED	8.5–10.7 (9.8±0.9)	10.4	7.8–10.6 (9.3±1.0)	9.8	8.7 in SYS a005919	9.9 in SYS a002236	–	7.6–11.3 (9.1±1.4)	–	–
HND	20.0–22.5 (21.3±0.8)	22.6	18.6–21.6 (19.8±1.0)	20.5	26.7 in SYS a005919	32.1 in SYS a002236	–	21.3–24.0 (22.7±1.0)	23.0–27.0 (24.4±1.3)	25.0
RAD	14.7–19.7 (17.5±1.7)	17.4	15.6–17.9 (16.9±0.8)	17.3	17.6 in SYS a005919	23.2 in SYS a002236	–	17.0–19.1 (17.8±0.9)	–	–
TIB	31.1–33.5 (32.1±1.0)	33.1	28.0–33.5 (30.8±1.6)	31.4	34.3 in SYS a005919	43.8 in SYS a002236	42.7 in CIB 98A0045	31.3–36.6 (33.6±1.9)	32.0–39.0 (35.9±2.1)	36.0
FTL	46.9–50.5 (48.4±1.1)	51.0	42.0–49.7 (46.1±2.3)	49.5	57.4 in SYS a005919	70.6 in SYS a002236	–	47.1–50.9 (48.9±1.4)	–	–
HDL/SVL	0.41–0.43 (0.42±0.01)	0.46	0.40–0.43 (0.42±0.01)	0.42	0.39–0.45 (0.41±0.02)	0.39–0.40 (0.39±0.01)	0.43 in CIB 98A0045	0.37–0.42 (0.39±0.02)	–	–
HDW/SVL	0.49–0.53 (0.51±0.01)	0.55	0.47–0.53 (0.51±0.02)	0.49	0.46–0.54 (0.50±0.03)	0.47–0.48 (0.47±0.01)	0.51 in CIB 98A0045	0.45–0.53 (0.48±0.03)	0.47–0.51 (0.50±0.02)	0.54
HDW/SKL	1.89–2.02 (1.95±0.05)	1.98	1.89–2.24 (2.00±0.09)	2.00	1.80 in SYS a005919	1.96 in SYS a002236	–	1.73–1.96 (1.87±0.10)	1.82–1.92 (1.87±0.04)	1.85
HDW/HDL	1.17–1.26 (1.22±0.04)	1.20	1.18–1.26 (1.21±0.03)	1.18	1.16–1.24 (1.21±0.03)	1.16–1.24 (1.20±0.04)	1.21 in CIB 98A0045	1.20–1.25 (1.22±0.02)	–	–
SNT/HDL	0.27–0.31 (0.29±0.01)	0.30	0.28–0.31 (0.30±0.01)	0.29	0.27 in SYS a005919	0.28 in SYS a002236	–	0.27–0.31 (0.29±0.02)	–	–
SNT/SVL	0.12–0.13 (0.12±0.01)	0.14	0.12–0.13 (0.13±0.00)	0.12	0.10 in SYS a005919	0.11 in SYS a002236	–	0.10–0.12 (0.11±0.01)	0.12–0.13 (0.13±0.00)	0.13
IND/IOD	0.60–0.92 (0.71±0.11)	0.65	0.60–0.71 (0.65±0.03)	0.59	0.77 in SYS a005919	0.74 in SYS a002236	–	0.61–0.94 (0.77±0.15)	–	–
IND/HDW	0.19–0.23 (0.21±0.02)	0.19	0.18–0.21 (0.20±0.01)	0.19	0.19 in SYS a005919	0.17 in SYS a002236	–	0.18–0.22 (0.20±0.01)	–	–
IOD/HDW	0.22–0.32 (0.29±0.04)	0.30	0.29–0.35 (0.31±0.02)	0.33	0.25 in SYS a005919	0.23 in SYS a002236	–	0.23–0.31 (0.26±0.03)	–	–
ED/HDL	0.26–0.32 (0.29±0.02)	0.25	0.25–0.33 (0.29±0.02)	0.27	0.23 in SYS a005919	0.20 in SYS a002236	–	0.24–0.31 (0.27±0.03)	–	–
ED/SVL	0.11–0.14 (0.12±0.01)	0.12	0.11–0.14 (0.12±0.01)	0.11	0.09 in SYS a005919	0.08 in SYS a002236	–	0.09–0.12 (0.10±0.02)	–	–
HND/SVL	0.25–0.28 (0.27±0.01)	0.26	0.24–0.28 (0.26±0.01)	0.24	0.28 in SYS a005919	0.26 in SYS a002236	–	0.25–0.29 (0.26±0.02)	0.23–0.27 (0.26±0.01)	0.27
RAD/SVL	0.19–0.24 (0.22±0.02)	0.20	0.20–0.24 (0.22±0.01)	0.20	0.19 in SYS a005919	0.19 in SYS a002236	–	0.19–0.23 (0.21±0.02)	–	–
TIB/SVL	0.39–0.42 (0.40±0.01)	0.37	0.38–0.43 (0.40±0.01)	0.36	0.36 in SYS a005919	0.35 in SYS a002236	0.41 in CIB 98A0045	0.36–0.42 (0.39±0.02)	0.35–0.41 (0.37±0.02)	0.39
FTL/SVL	0.58–0.65 (0.61±0.03)	0.58	0.57–0.63 (0.60±0.02)	0.57	0.61 in SYS a005919	0.57 in SYS a002236	–	0.53–0.61 (0.57±0.03)	–	–
References	This study		Zhao et al., 2014		Rao & Yang, 1997; this study		Fei & Ye, 2001; this study	This study	Smith, 1921	

F: Female; M: Male. –: Not available.

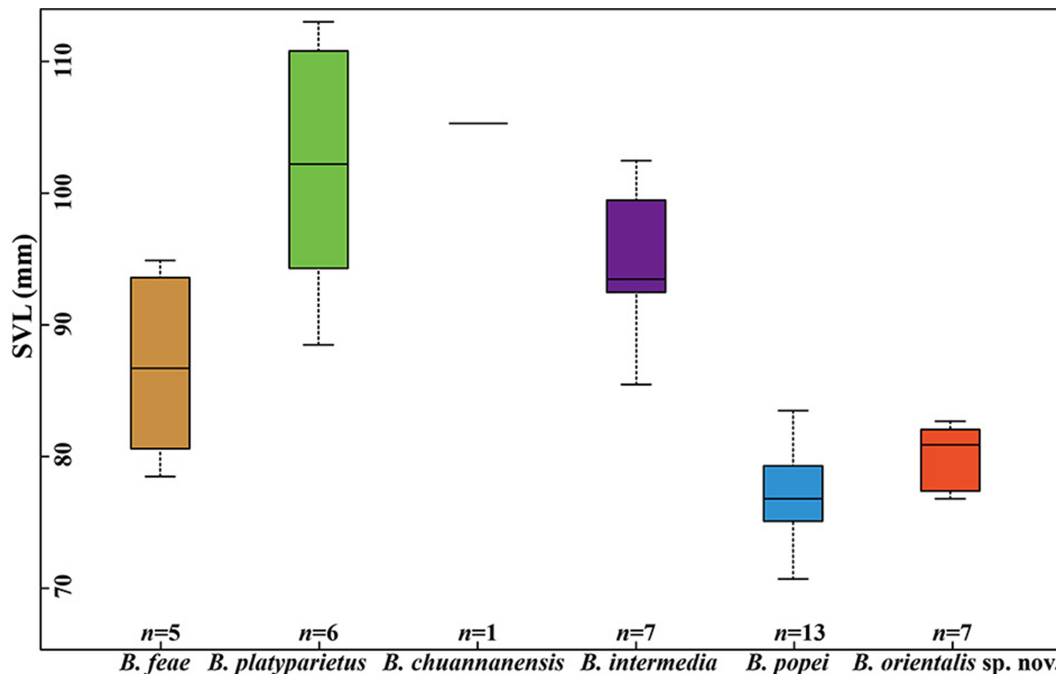


Figure 4 Boxplot of SVL showing body size variation among adult *Brachytarsophrys* males (data deficiency of *B. chuannanensis* and *B. carinense*)

Horizontal lines within each box represent median, and boxes encompass 75th and 25th percentile.

- 1b) Absence of dermal ridge or glandular fold on dorsum.....3 (*B. feae* group)
- 2a) Large body size, SVL 124.0–168.0 mm in females, 91.6–123.0 mm in males, tibiotarsal articulation reaching to axilla in females, to commissure of jaw in males....
..... *B. carinense*
- 2b) Moderate body size, SVL 92.0 mm in females, 86.0–103.0 mm in males, tibiotarsal articulation nearly reaching commissure of jaw.....*B. intermedia*
- 3a) Pectoral region, lateral belly to lower flank of body, ventral surface, and rear of limbs with dense small, conical, horny tubercles.....*B. platyparietus*
- 3b) Pectoral region, lateral belly to lower flank of body, ventral surface, and rear of limbs without horny tubercles.....4
- 4a) Toe webbing rudimentary.....5
- 4b) Toe webbing well developed.....6
- 5a) Inter metatarsal tubercle approximately equal to first toe.....*B. chuannanensis*
- 5b) Inter metatarsal tubercle longer than first toe....
.....*B. feae*
- 6a) Tongue feebly notched, smaller webbing, free web margin of IV toe only reaching base of articulation between fourth phalange and metatarsal, formula (4) IV (4).....
.....*Brachytarsophrys orientalis sp. nov.*
- 6b) Tongue deeply notched, larger webbing, free web margin of IV toe far beyond articulation between fourth phalange and metatarsal, formula (3%) IV (3%).....
..... *B. popei*

SYSTEMATICS

Family Megophryidae Bonaparte, 1850

Subfamily Megophryinae Bonaparte, 1850

Genus *Brachytarsophrys* Tian & Hu, 1983

Type species: *Leptobrachium carinense* Boulenger, 1889

Diagnosis: (1) Large body size, habitus thickset and stout; (2) head enormous, and extremely depressed, head width approximately twice skull length; (3) presence of transverse groove, defining head behind; (4) tympanum hidden; (5) maxillary teeth present; (6) pupil vertical; (7) upper eyelid with several conical tubercles, one elongated, forming conical or flattened horn; (8) hindlimbs short and strongly thickset, heels not meeting, separated by greater distance; (9) toes with webbing and fringes; (10) inhabits deep crevices between rocks or boulders of streams during breeding season.

Suggested common name: Short-Legged Toads (in English) / Duan Tui Chan (短腿蟾 in Chinese).

Distribution: Tropical and subtropical eastern and southeastern mainland Asia, including southern China, Myanmar, Vietnam, Laos, and northern Thailand.

Remarks: The genus *Brachytarsophrys* was established with designating *Leptobrachium carinense* Boulenger, 1889 as the type species (Tian & Hu, 1983). However, from the original literature, the examined specimen of *L. carinense* by Tian & Hu (1983) was collected from Jingdong, Yunnan, China, and should not be identified as *B. carinense* but as *B. feae* (Boulenger, 1886).

Table 5 Diagnostic characters separating the seven *Brachytarsophrys* species from each other

Morphological characters	<i>Brachytarsophrys orientalis</i> sp. nov.	<i>B. popei</i>	<i>B. carinense</i>	<i>B. platyparietus</i>	<i>B. chuannanensis</i>	<i>B. feae</i>	<i>B. intermedia</i>
SVL of males (in mm)	76.8–82.7	70.7–83.5	91.6–123.0	88.5–113.0	91.4–109.4	78.5–94.9	86.0–103.0
SVL of females (in mm)	88.6	86.2	124.0–168.0	118.5–131.0	–	–	92.0
Tongue	Feebly notched behind	Deeply notched behind	Feebly notched behind	Feebly notched behind	Feebly notched behind	Feebly notched behind	Feebly notched behind
Dermal ridge or glandular fold on dorsum	Absent	Absent	Dermal ridge on dorsum	Absent	Absent	Absent	Glandular fold on dorsum
Small, conical, horny tubercles	Absent	Absent	Absent	Present on pectoral region, lateral belly to lower flank of body, ventral surface, and rear of limbs	Absent	Absent	Absent
Stellate bony	Absent	Absent	Stellate bony deposits in skin of parietal region and anterior part of dorsum	Absent	Absent	Stellate bony deposits on each side of parietal region	Absent
Webbing formula of male	I (1½)-(2) II (1½)-(3) III (2½)-(4) IV (4)-(2) V	I (1½)-(2) II (1½)-(3) III (2½)-(3½) IV (3½)-(2) V	–	I (1½)-(2*) II (1½)-(3) III (2½)-(3½) IV (3½)-(2) V	I (1½)-(2**) II (2)-(3**) III (3)-(4) IV (4**)-(2½) V	I (2)-(2**) II (2)-(3) III (2½)-(4) IV (4)-(2½) V	–
Webbing formula of female	I (2)-(2*) II (1½)-(3) III (3)-(4) IV (4*)-(2½) V	I (1½)-(2*) II (1½)-(3) III (2½)-(4) IV (4*)-(2) V	–	I (1½)-(2*) II (1½)-(3) III (2½)-(4) IV (4*)-(2½) V	–	–	–
Lateral fringes on toes of male	One third as broad as distal toe phalanx	One fourth as broad as distal toe phalanx	–	Half as broad as distal toe phalanx	One fifth as broad as distal toe phalanx in CIB 98A0045	One fourth as broad as distal toe phalanx	–
Lateral fringes on toes of female	One sixth as broad as distal toe phalanx	One fifth as broad as distal toe phalanx	–	One fourth as broad as distal toe phalanx	–	–	–
Position of tibiotarsal articulation reaching	Commissure of jaw	Commissure of jaw	Axilla in females, angle of mouth in males	Commissure of jaw	Shoulder or commissure of jaw	Shoulder in females, commissure of jaw in males	Commissure of jaw
Transversal stripe on chest in tadpole	Absent	A transversal stripe on chest	–	–	A transversal stripe on chest	Several transversal stripes on chest	–

–: Not available.

***Brachytarsophrys carinense* group**

***Brachytarsophrys carinense* (Boulenger, 1889)**

Leptobrachium carinense: Boulenger, 1889.

Megophrys carinensis: Bourret, 1942.

Brachytarsophrys carinensis: Tian & Hu, 1983; Rao & Yang, 1997.

Megophrys (Brachytarsophrys) carinensis: Dubois, 1987.

Brachytarsophrys carinense: Delorme et al., 2006.

Megophrys (Brachytarsophrys) carinense: Mahony et al., 2017.

Syntypes: BMNH and NHMW 2291.1-2 (according to Häupl & Tiedemann (1978)) and MSNG 29689 (designated lectotype by Capocaccia (1957)), collected from western slopes of Karens Mountains (800 m a.s.l.), East of Toungoo, Myanmar.

Diagnosis: Based on the original description of Boulenger (1889) and supplementary description of Taylor (1962) and Mahony et al. (2017). (1) Large body size, SVL 124.0–168.0 mm in females, 91.6–123.0 mm in males; (2) head enormous, extremely depressed, head width nearly twice skull length; (3) tongue large, feebly notched behind; (4) canthus rostralis distinct, loreal region to temporal region very oblique; (5) tympanum hidden; (6) maxillary teeth present, vomerine teeth present on two widely-separated vomerine ridges; (7) digits without subarticular tubercles, tibiotarsal articulation reaching axilla in females, commissure of mouth in males; (8) very large, flat, oval inner metatarsal tubercle; (9) toes one third webbed; (10) presence of transverse fold separating head from body; (11) upper eyelid with two to four horn-like conical tubercles; (12) oblique dermal ridge on each side of anterior part of dorsum; (13) stellate bony deposits in skin of parietal region and anterior part of dorsum; (14) single subgular vocal sac in males.

Suggested common name: Broad-Headed Short-Legged Toad (in English) / Kuan Tou Duan Tui Chan (宽头短腿蟾 in Chinese).

Distribution and habitats: Currently, *B. carinense* is recognized from southern Myanmar and adjacent northern Thailand at elevations of 800 m and upwards. This toad hides in crevices between rocks or between the roots of shrubs during the day (Boulenger, 1889; Taylor, 1962).

***Brachytarsophrys intermedia* (Smith, 1921)**

Megalophrys intermedius: Smith, 1921.

Megophrys intermedia: Bourret, 1942.

Brachytarsophrys intermedia: Rao & Yang, 1997.

Megophrys (Brachytarsophrys) intermedia: Mahony et al., 2017.

Syntypes: BMNH (11 specimens—formerly M. Smith) 2067, 2073, 2075–76, 2078, 2085–86, adult males, 2070, adult female, 2083–84, young females, and 2074, without gender data, collected from the Langbian Plateau (1 500 m a.s.l.), Vietnam.

Diagnosis: Based on the original description of Smith (1921). (1) Medium body size, SVL 92.0 mm in one adult female, 86.0–103.0 mm in seven adult males; (2) head enormous and depressed, head width nearly twice skull length; (3) tongue

feebly notched behind; (4) maxillary teeth present, vomerine teeth present on two widely-separated vomerine ridges; (5) snout round, not protruding beyond margin of lower jaw, canthus rostralis distinct; (6) loreal region to temporal region very oblique; (7) tympanum hidden; (8) presence of transverse groove behind head, separating head from body; (9) digits without subarticular tubercles, tibiotarsal articulation reaching to commissure of jaw; (10) large, flat, oval inner metatarsal tubercles; (11) toes one third to one half webbed, web extending as fringe along either side of toes; (12) paired oblique glandular folds on dorsum; (13) upper eyelid with several conical tubercles, one enlarged to form long horn.

Suggested common name: Annam Short-Legged Toad (in English) / Yue Nan Duan Tui Chan (越南短腿蟾 in Chinese).

Distribution and habitats: The species occurs in the central highlands of southern Vietnam and Laos at elevations above 900 m. Most specimens have been discovered in deep crevices between the rocks or boulders of streams. Loud, harsh male croaks can be heard at all times of the day and night (Smith, 1921).

***Brachytarsophrys feae* group**

***Brachytarsophrys chuannanensis* Fei, Ye & Huang, 2001**

(Figure 5)

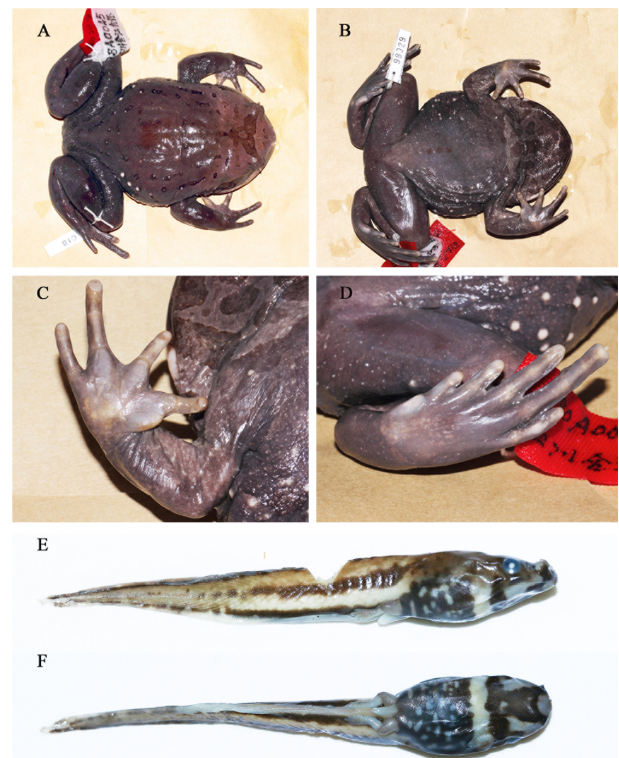


Figure 5 General aspect of *Brachytarsophrys chuannanensis*

A: Dorsolateral view of adult male holotype CIB 98A0045 in preservative; B: Ventral view of holotype CIB 98A0045 in preservative; C, D: Hand and foot of holotype CIB 98A0045 in preservative; E, F: Ventral view of 38th stage tadpole of *B. chuannanensis*.

Brachytarsophrys chuannanensis: Fei & Ye, 2001.

Megophrys (Brachytarsophrys) chuannanensis: Mahony et al., 2017.

Holotype: CIB 98A0045, adult male, collected from Zihuai (E105°49', N28°48'; 850 m a.s.l.), Hejiang County, Sichuan Province, China.

Paratypes: Eleven adult males without specimen number data.

Examined specimens: One specimen. Holotype CIB 98A0045.

Diagnosis: Based on the original description of Fei & Ye (2001) and examined specimen. (1) Large body size, SVL 91.4–109.4 mm in 12 adult males; (2) head enormous and depressed, head width nearly twice skull length; (3) maxillary teeth well developed, vomerine teeth present on two widely-separated vomerine ridges; (4) snout round, slightly protruding beyond margin of lower jaw; (5) tympanum hidden; (6) toes with rudimentary webbing; (7) heels not meeting; (8) tibiotarsal articulation reaching to shoulder or posterior margin of mouth; (9) inner metatarsal tubercle approximately equal to first toe; (10) upper eyelids with several small tubercles, one enlarged, forming horn; (11) presence of transverse groove, defining head behind; (12) male with single subgular vocal sac, dorsal surface of first and second finger bases with black brown nuptial pad; (13) tadpole with a transversal stripe on ventral surface.

Suggested common name: Southern Sichuan Short-Legged Toad (in English) / Chuan Nan Duan Tui Chan (川南短腿蟾 in Chinese).

Distribution and habitats: The species is distributed in Hejiang and Junlian counties, Sichuan Province, southwestern China, at 800 to 1 400 m a.s.l.. Specimens are found in or near montane streams surrounded by lush vegetation. They usually hide in crevices between rocks or dirt burrows in streams during the day. Males emit a series of croaks at about 23:00h. The spawning season is around the middle of May (Fei & Ye, 2001).

***Brachytarsophrys feae* (Boulenger, 1886)** (Figure 6)

Megalophrys feae: Boulenger, 1886.

Leptobrachium feae: Boulenger, 1889.

Megophrys feae: Gee & Boring, 1929.

Brachytarsophrys feae: Rao & Yang, 1997.

Megophrys (Brachytarsophrys) feae: Mahony et al., 2017.

Holotype: MSNG 29763, female (according to Capocaccia (1957)), collected from Khakhyen Hills, East of Bhamò, Myanmar.

Examined specimens: Five specimens. SYS a001770–1771, adult males, collected from Zhenyuan County, Yunnan Province, China; SYS a003912–3914, adult males, collected from Jingdong County, Yunnan Province, China.

Diagnosis: Based on the original description of Boulenger (1886), supplementary description of Fei et al. (2009), and examined specimens. (1) Moderate body size, SVL 78.5–94.9 mm in five adult males; (2) head enormous, extremely depressed, head width approximately twice skull length; (3)



Figure 6 General aspect of *Brachytarsophrys feae*

A: Dorsolateral view of adult male SYS a003914 in life; B: Ventral view of adult male SYS a003914 in life; C, D: Hand and foot of adult male SYS a003914 in life; E: Ventral view of 44th stage tadpole of *B. feae*.

tongue pyriform, feebly notched behind; (4) maxillary teeth present, vomerine teeth present on two vomerine ridges; (5) canthus rostralis indistinct, loreal region concave, temporal region oblique; (6) tympanum hidden; (7) tibiotarsal articulation reaching axilla or commissure of jaw; (8) very large, flat, oval inner metatarsal tubercle, longer than first toe; (9) toes with rudimentary webbing; (10) upper eyelid with several small tubercles, one enlarged, forming horn; (11) absence of dermal ridge on dorsum; (12) stellate bony deposits on each side of parietal region; (13) male with single subgular vocal sac, dorsal surface of first and second finger bases with black brown nuptial pad; (14) tadpole with several transversal stripes on ventral surface.

Suggested common name: Fea's Short-Legged Toad (in English) / Fei Shi Duan Tui Chan (费氏短腿蟾 in Chinese).

Distribution and habitats: This species is currently recognized from northern Myanmar and Yunnan Province in southwestern China at 650 to 2 100 m a.s.l.. Specimens are found in montane streams, under rocks or deep burrows surrounded by moist evergreen broadleaf forests. Male individuals begin to emit a series of croaks in April. The spawning season is from May to June (Fei & Ye, 2009; this study).

***Brachytarsophrys popei* Zhao, Yang, Chen, Chen & Wang, 2014** (Figure 7)

Brachytarsophrys popei: Zhao et al., 2014.

Megophrys (Brachytarsophrys) popei: Mahony et al., 2017.

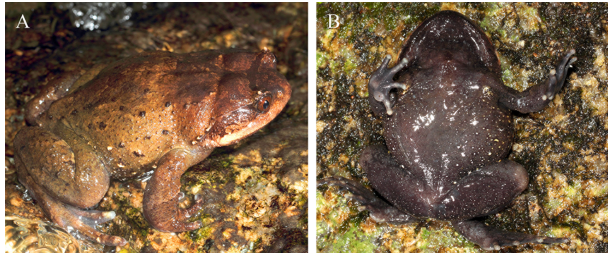


Figure 7 General aspect of *Brachytarsophrys popei*

A: Dorsolateral view of adult male holotype SYS a001867 in life; B: Ventral view of holotype SYS a001867 in life.

Holotype: SYS a001867, adult male, collected from Taoyuangdong Nature Reserve (N26°30'8.79", E114°03'38.27"; 1 045 m a.s.l.), Yanling County, Hunan Province, China.

Paratypes: SYS a001864–1866, adult males, collected from same locality as holotype; SYS a001874, 1876–1878, adult males, SYS a001875, adult female, collected from Mount Jinggang (N26°29'51.85", E114°04'50.68"; 923 m–1 270 m a.s.l.), Jinggangshan City, Jiangxi Province, China; SYS a000583–0585, 0588–0589, adult males, collected from Nanling Nature Reserve (N24°56'14.19", E113°0'13.12"; 1 089 m–1 304 m a.s.l.), Ruyuan County, Guangdong Province, China.

Examined specimens: Nine specimens. Holotype SYS 001867 and paratypes SYS a001864–1866, SYS a001874–1878.

Diagnosis: Based on the original description of Zhao et al. (2014) and examined specimens. (1) Relatively small body size, SVL 86.2 mm in one adult female, 70.7–83.5 mm in 13 adult males; (2) head enormous, and extremely depressed, head width approximately twice skull length; (3) tongue pyriform, deeply notched behind; (4) maxillary teeth present, vomerine teeth present on two vomerine ridges; (5) tympanum hidden; (6) heels not meeting; (7) tibiotarsal articulation reaching to commissure of jaw; (8) toes about one third to two thirds webbed in males; (9) upper eyelid with several tubercles, one enlarged, forming horn; (10) males with single subgular vocal sac, first and second finger bases with dense tiny black nuptial spines; (11) tadpole with a transverse white stripe on chest reaching spiracle.

Suggested common name: Pope's Short-Legged Toad (in English) / Po Pu Duan Tui Chan (珀普短腿蟾 in Chinese).

Distribution and habitats: *Brachytarsophrys popei* populations occur in Taoyuangdong Nature Reserve, Hunan Province, adjacent Mt. Jinggang, Jiangxi Province, and Nanling Reserve, Guangdong Province, southeastern China, at 900 to 1 300 m a.s.l.. The species can be found under rocks in montane streams surrounded by moist subtropical evergreen broadleaf forests. Males emit a series of croaks from July to September (Zhao et al., 2014).

***Brachytarsophrys platyparietus* Rao & Yang, 1997** (Figure 8)

Brachytarsophrys platyparietus: Rao & Yang, 1997.



Figure 8 General aspect of *Brachytarsophrys platyparietus*

A: Dorsolateral view of adult male SYS a005919 in life; B: Ventral view of adult male SYS a005919 in life; C, D: Hand and foot of adult male SYS a005919 in life.

Brachytarsophrys carinensis: Fei et al., 2009.

Brachytarsophrys carinense: Chen et al., 2017.

Holotype: KIZ 90275, adult male, collected from Duodihe, Santai Township, Dayao County, Yunnan Province, China.

Paratypes: KIZ 90274, adult male, and KIZ 90276, adult female, collected from same locality as holotype.

Examined specimens: Thirteen specimens. KIZ 91001, 91002, 90267, 90273, adult males, KIZ 90270, adult female, and SYS a005919, adult male, collected from same locality as holotype; SYS a007774–7777, adult males, collected from Mt. Mopan, Xiping Yi and Dai Autonomous County, Yunnan Province, China; SYS a007790, adult male, collected from Yilong Township, Shiping County, Yunnan Province, China; SYS a007853, adult male, collected from Yumen Township, Yanbian County, Sichuan Province, China; SYS a002236, adult female, collected from Mt. Jinzhong, Longlin Various Nationalities Autonomous County, Guangxi Zhuang Autonomous Region, China.

Revision of diagnosis: *Brachytarsophrys platyparietus* differs from other known congeners by the following combination of morphological characters: (1) relatively large body size, SVL 118.5–131.0 mm in three adult females, SVL 88.5–113.0 mm in six adult males; (2) head enormous, slightly flattened, head width nearly 1.2 times as long as head length, and nearly twice skull length; (3) tibiotarsal articulation reaching to commissure of jaw in males and females; (4) outer metatarsal tubercle absent, inner metatarsal tubercle approximately equal to first toe; (5) slightly larger webbing, from distal metatarsals to basal toes, webbing formula I (1½)-(2⁺) II (1½)-(3) III (2⅔)-(3⅔) IV (3⅔)-(2) V in males; (6) lateral fringes of males more developed than those of females, nearly half as broad as distal toe phalanx in males; (7) horn-shaped tubercle on upper eyelid extremely elongate, forming a long pointed and compressed horn in female; (8) dorsum and flank of body without dermal ridge; (9) numerous small, conical, horny

tubercles scattered on pectoral region, lateral belly to lower flank of body, ventral surface, and rear of limbs.

Comparisons: *Brachytarsophrys platyparietus* has been treated as a synonym of *B. carinense*, but differs significantly from *B. carinense* by a combination of the following characters: dermal ridge on dorsal surface absent (vs. present in *B. carinense*); stellate bony deposits in skin absent (vs. stellate bony deposits in skin of parietal region and anterior part of dorsum in *B. carinense*); large warts on dorsal limbs present, but dermal ridges absent (vs. slight oblique dermal ridges across limbs in *B. carinense*); first finger longer than second (vs. first finger not extending beyond second in *B. carinense*); tibiotarsal articulation reaching commissure of jaw in females (vs. reaching axilla in females of *B. carinense*).

Brachytarsophrys platyparietus differs from all remaining congeners by a combination of the following characters: numerous small, conical, horny tubercles on pectoral region, lateral belly to lower flank of body, ventral surface, and rear of limbs (Figure 9 and Table 5). *Brachytarsophrys platyparietus* differs from *B. feae* by slightly larger webbing, from distal metatarsals to basal toes, webbing formula I (1½)-(2⁺) II (1½)-(3) III (2⅓)-(3⅔) IV (3⅔)-(2⁻) V in males (vs. smaller webbing, from distal metatarsals to basal toes, webbing formula I (2)-(2⁺⁺) II (2)-(3) III (2⅔)-(4) IV (4)-(2⅔) V in males of *B. feae*); lateral fringes on toes wide, nearly half as broad as distal toe phalanx in males (vs. narrow, less than one fourth of distal toe phalanx in males of *B. feae*); stellate bony deposits absent (vs. stellate bony deposits on each side of parietal region in *B. feae*); inner metatarsal tubercle approximately equal to first toe (vs. inner metatarsal tubercle longer than first toe in *B. feae*). *Brachytarsophrys platyparietus* differs from *B. chuannanensis* by foot with slightly larger webbing, from distal metatarsals to basal toes, webbing formula I (1½)-(2⁺) II (1½)-(3) III (2⅓)-(3⅔) IV (3⅔)-(2⁻) V in males (vs. smaller webbing, from distal metatarsals to basal toes, webbing formula I (1½)-(2⁺⁺) II (2)-(3⁺⁺) III (3)-(4) IV (4⁺⁺)-(2½) V in holotype CIB 98A0045 of *B. chuannanensis*); wide lateral fringes on toes,

nearly half as broad as distal toe phalanx in males (vs. narrow, less than one fifth of distal toe phalanx in holotype CIB 98A0045 of *B. chuannanensis*).

Brachytarsophrys platyparietus differs from *B. popei* by a combination of the following characters: large body size, SVL 118.5–131.0 mm in three adult females, SVL 88.5–113.0 mm in six adult males (vs. 86.2 mm in one adult female, 70.7–83.5 mm in 13 adult males in *B. popei*); outer metacarpal tubercles absent (vs. present in *B. popei*); horn-shaped tubercle on upper eyelid extremely elongate, pointed, and compressed in females (vs. relatively short, blunt, and conical in females of *B. popei*). *Brachytarsophrys platyparietus* differs from *B. intermedia* by oblique glandular fold on dorsum absent (vs. present in *B. intermedia*); folds across limbs absent (vs. present in *B. intermedia*).

Description of topotype specimen: SYS a005919, adult male. Body stout, large body size, SVL 94.3 mm; head enormous and flattened, head width nearly 1.2 times as long as head length, and nearly twice skull length (HDW/SKL ratio 1.80); two visible, large rounded bulges on occipital region, forming broad longitudinal concave groove along middle line across occiput, and distinct transverse groove, defining head behind; snout short (SNT/SVL ratio 0.10), rounded in dorsal view, slightly protruding beyond margin of lower jaw; canthus rostralis rounded; loreal region oblique, slightly concave; nostril oval, close to tip of snout; internasal distance significantly smaller than interorbital distance (IND/IOD ratio 0.77); pupil vertical; temporal region oblique; tympanum completely hidden; choanae partly concealed by maxillary shelves; maxillary teeth well developed; vomerine teeth present on two vomerine ridges between choanae; vomerine ridges long, posterior level behind posterior level of choanae, widely separated by large distance approximately two times as long as length of one ridge; tongue pyriform, feebly notched behind.

Forelimbs short and moderately robust; hands short (HND/SVL ratio 0.28); relative finger lengths II<I<IV<III; tips of digits round, slightly dilated; no webbing or lateral fringes on fingers; no subarticular tubercles and no outer metacarpal tubercle, inner metacarpal tubercle significantly enlarged.

Hindlimbs short and robust (TIB/SVL ratio 0.36); tibiotarsal articulation reaching commissure of jaw when hindlimbs stretched alongside body; heels not meeting, separated by 8.0 mm when hindlimbs flexed at right angles to axis of body; relative toe lengths I<II<V<III<IV; tips of toes round, moderately dilated; no subarticular tubercles; no tarsal gland; inter metatarsal tubercle prominent, elongate, approximately equal to first toe, outer metatarsal tubercle absent; slightly larger webbing, from distal metatarsals to basal toes, webbing formula I (1½)-(2⁺) II (1½)-(3) III (2⅓)-(3⅔) IV (3⅔)-(2⁻) V; webbing extending as wide fringe along either side of toes, nearly half as broad as distal toe phalanx.

Dorsal skin of head smooth; upper eyelid with several large conical tubercles, middle one extremely elongate, forming long conical horn; supratympanic fold distinct, from posterior corner of eye to upper arm insertion on each side; dorsum and flank



Figure 9 Numerous small, conical, horny tubercles in *Brachytarsophrys platyparietus*.

A, B: Conical horny tubercles in adult male SYS a005919; C, D: Conical horny tubercles in adult female SYS a002236.

of body slightly rough without dermal ridge, scattered with some large glandular warts and small tubercles; pair of symmetrical conical warts on front of shoulders; dorsal limbs with several large warts and small tubercles, not arranged in row; ventral surface of head, body, and limbs smooth, with several glandular warts arranged on rear of thigh and around vent; numerous small, conical, horny tubercles scattered on pectoral region, lateral belly to lower flank of body, ventral surface, and rear of limbs; pectoral gland and femoral gland invisible.

Measurements (in mm): SVL 94.3, HDL 37.1, SKL 23.9, HDW 43.1, SNT 9.9, IND 8.2, IOD 10.6, ED 8.7, HND 26.7, RAD 17.6, TIB 34.3, FTL 57.4.

Coloration: In life, dorsal surface of head brown with dark blotches and stripes; wide dark brown stripe bordered with yellow between eyes, pair of short oblique discontinuous dark stripes bordered with yellow above shoulder; warts and tubercles light-colored bordered with yellow; eyes surrounded by star-shaped dark brown marking bordered with yellow; temporal region under supratympanic fold with broad dark brown stripe bordered with light yellow; dorsal digits with black cross-bars; chin, throat, pectoral region brown with faint dark blotches, two large longitudinal dark stripes edged with yellow on lateral throat; pupils black; iris brownish red.

In preservative, dorsal and ventral surfaces dark brown, yellow border edge on stripes between eyes, above shoulder, and on lateral throat faded to light yellow, inter metatarsal tubercle faded to grayish-white.

Variation: Measurements are given in Table 4 and variations are as follows: SYS a007776 and SYS a007777, slightly larger webbing, toe webbing formula I (1½)-(2) II (1½)-(3) III (2½)-(3½) IV (3½)-(2) V. SYS a002236, adult female, heels not meeting, separated by 9.5 mm; foot webbing and lateral fringes of toes slightly smaller than those of adult male specimens, toe webbing formula I (1½)-(2⁺) II (1½)-(3) III (2½)-(4⁻) IV (4⁻)-(2½) V; webbing extending as fringe along either side of toes, nearly one fourth as broad as distal toe phalanx; yellowish brown body.

Male secondary sexual characteristics: Male with single subgular vocal sac; dorsal surface of first and second finger bases with indistinct, not elevated nuptial pad, bearing dense tiny black nuptial spines (in preservative).

Suggested common name: Flat-Headed Short-Legged Toad (in English) / Ping Tou Duan Tui Chan (平头短腿蟾 in Chinese).

Distribution and habitats: Currently, *Brachytarsophrys platyparietus* is recognized from Duodihe of Dayao County, Mt. Mopan of Xinping County, Yilong Township of Shiping County, Mt. Jinzhong of Longlin County, Mt. Fanjing of Tongren City, Yumen Township of Yanbian County, indicating its potential distribution areas, which range across central southwestern China at around 2 000 m a.s.l.. These toads inhabit montane streams surrounded by moist subtropical evergreen broadleaf forests. Some adult males have been found near batches of eggs attached to the bottom of a rock, suggesting that adult males may exhibit egg protection

behavior (Figure 10).

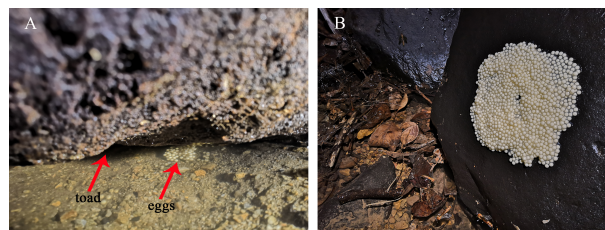


Figure 10 Egg protection behavior in *Brachytarsophrys platyparietus*

A: Under rock, adult male on left protected eggs on right; B: Eggs of *B. platyparietus*.

***Brachytarsophrys orientalis* sp. nov.** Y Li, Lyu, J Wang & YY Wang (Figure 11)

Holotype: SYS a004227, adult male, collected by Jian Wang and Hai-Long He, on 4 August 2015 from Jiulianshan Nature Reserve (N24°34'47", E114°26'9"; 400 m a.s.l.), Longnan County, Jiangxi Province, China.

Paratypes: Five specimens from the same locality as the holotype: SYS a004225/ CIB 110009, SYS a004226 and 4228, adult males, same collection data as holotype; SYS a004486, adult female, collected by Jiang Wang and Hai-Long He on 22 September 2015; SYS a005451, adult male, collected by Zhi-Tong Lyu and Hai-Long He on 21 August 2016.

Other examined specimens: SYS a003249, adult male, collected by Run-Lin Li on 20 August 2014 from Gutian Township (N25°13'11", E116°49'43"; 700 m a.s.l.), Shanghang County, Fujian Province, China; SYS a003340, adult male, collected by Zhi-Tong Lyu and Zu-Yao Liu on 22 August 2014 from Huboliao Natural Reserve (N24°40'28", E117°5'21"; 200 m a.s.l.), Nanjing County, Fujian Province, China; SYS



Figure 11 General aspect of *Brachytarsophrys orientalis* sp. nov.

A: Dorsolateral view of adult male holotype SYS a004227 in life; B: Ventral view of holotype SYS a004227 in life; C, D: Hand and foot of holotype SYS a004227 in life.

a004622, tadpole in stage 36, collected from same locality as holotype by Jian Wang, Zhi-Tong Lyu and Hai-Long He on 01 April 2016.

Diagnosis: *Brachytarsophrys orientalis* sp. nov. is characterized by the following combination of morphological characters: (1) relatively small body size, SVL 88.6 mm in single adult female, SVL 76.8–82.7 mm in seven adult males; (2) head enormous and depressed, head width nearly 1.2 times as long as head length and nearly twice skull length; (3) tongue pyriform, feebly notched behind; (4) heels not meeting; (5) tibiotarsal articulation reaching to commissure of jaw; (6) outer metatarsal tubercle absent, inner metatarsal tubercle approximately equal to first toe; (7) smaller webbing, from distal metatarsals to basal toes, webbing formula I (1½)-(2) II (1½)-(3) III (2½)-(4) IV (4)-(2) V in males; (8) lateral fringes of males more developed than those of females, nearly one third as broad as distal toe phalanx in males; (9) absence of a transversal stripe on chest in tadpole.

Comparisons: Comparative data of *Brachytarsophrys orientalis* sp. nov. with other congeners are listed in Table 5. *Brachytarsophrys orientalis* sp. nov. differs from its sister taxon *B. popei* by the following characters: tongue feebly notched (vs. tongue deeply notched in *B. popei*); smaller webbing, webbing formula I (1½)-(2) II (1½)-(3) III (2½)-(4) IV (4)-(2) V in males, I (2)-(2*) II (1½)-(3) III (3)-(4) IV (4*)-(2½) V in females (vs. slightly larger webbing, webbing formula I (1½)-(2) II (1½)-(3) III (2½)-(3½) IV (3½)-(2) V in males, I (1½)-(2*) II (1½)-(3) III (2½)-(4) IV (4)-(2) V in females of *B. popei*) (Figure 12A–D); transversal stripe on chest in tadpole absent (vs. a transversal stripe reaching spiracle in *B. popei*) (Figure 12E–H).

Brachytarsophrys orientalis sp. nov. differs from the remaining five congeners by the following combination of morphological characters: small body size, SVL 88.6 mm in one adult female, SVL 76.8–82.7 mm in seven adult males (vs. 124.0–168.0 mm in adult females, 91.6–123.0 mm in adult males in *B. carinense*; 118.5–131.0 mm in three adult females, 88.5–113.0 mm in six adult males in *B. platyparietus*; 91.4–109.4 mm in 12 adult males in *B. chuannanensis*; 92.0 mm in one adult female, 86.0–103.0 mm in seven adult males in *B. intermedia*). *Brachytarsophrys orientalis* sp. nov. further differs from *B. platyparietus* by absence of numerous small, conical, horny tubercles on pectoral region, lateral belly to lower flank of body, ventral surface, and rear of limbs (vs. present in *B. platyparietus*). *Brachytarsophrys orientalis* sp. nov. further differs from *B. chuannanensis* and *B. feae* by lateral fringes on toes wide, nearly one third as broad as distal toe phalanx in males (vs. narrow, less than one fourth of distal toe phalanx in males of *B. feae*, less than one fifth in *B. chuannanensis*); transversal stripe on chest in tadpoles absent (vs. transversal stripe reaching spiracle in tadpole in *B. chuannanensis* and *B. feae*). *Brachytarsophrys orientalis* sp. nov. differs from *B. carinense* and *B. intermedia* by lack of dermal ridge on dorsum (vs. oblique dermal ridge on each side of anterior half dorsum in *B. carinense*, oblique glandular fold on dorsum in *B. intermedia*).

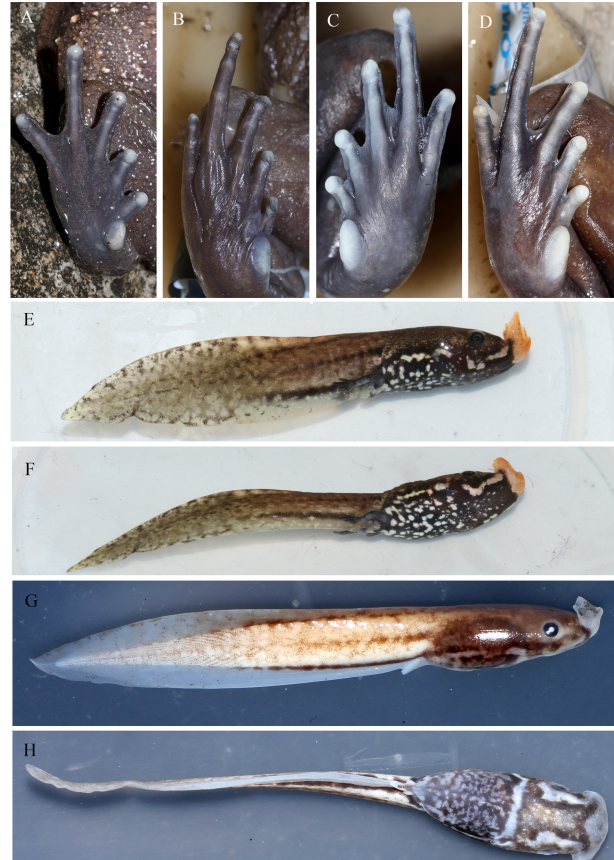


Figure 12 Morphological differences between *Brachytarsophrys orientalis* sp. nov. and *B. popei*

A: Sole of feet in male holotype SYS a004227 of *Brachytarsophrys orientalis* sp. nov.; B: Sole of feet in female paratype SYS a004486 of *Brachytarsophrys orientalis* sp. nov.; C: Sole of feet in male holotype SYS a001867 of *B. popei*; D: Sole of feet in female paratype SYS a001875 of *B. popei*; E, F: Ventral view of 36th stage tadpole of *Brachytarsophrys orientalis* sp. nov.; G, H: Ventral view of 29th stage tadpole of *B. popei*.

Description of holotype: Body stout, moderate body size, SVL 82.7 mm; head enormous and depressed, head width nearly 1.2 times as long as head length, and nearly twice skull length (HDW/SKL ratio 1.98); two visible large rounded bulges on occipital region, forming broad longitudinal concave groove along middle line across occiput, and distinct transverse groove, defining head behind; snout short (SNT/SVL ratio 0.12) and round, slightly protruding beyond margin of lower jaw; canthus rostralis indistinct, not sharp; loreal region oblique, slightly concave; nostril oval, close to tip of snout; internasal distance smaller than interorbital distance (IND/IOD ratio 0.63); pupil vertical; temporal region oblique, slightly concave; tympanum hidden; maxillary teeth well developed; vomerine teeth present on two vomerine ridges between choanae; vomerine ridges long, posterior level behind posterior level of choanae, widely separated by large distance

approximately 1.5 times as long as length of one ridge; tongue pyriform, feebly notched behind.

Forelimbs short and moderately robust; hands short (HND/SVL ratio 0.26); relative finger lengths II<I<IV<III; tips of digits round, slightly dilated; no webbing or lateral fringes on fingers; no subarticular tubercles; inner metacarpal tubercle significantly enlarged, outer metacarpal tubercle slightly enlarged.

Hindlimbs short and robust (TIB/SVL ratio 0.40); tibiotarsal articulation reaching commissure of jaw when hindlimbs stretched alongside body; heels not meeting, separated by 5.6 mm when hindlimbs flexed at right angles to axis of body; relative toe lengths I<II<V<III<IV; tips of toes round, moderately dilated; no subarticular tubercles; no tarsal glands; inter metatarsal tubercle prominent, elongate, approximately equal to first toe, outer metatarsal tubercle absent; smaller webbing, from distal metatarsals to basal toes; webbing formula I (1½)-(2) II (1½)-(3) III (2½)-(4) IV (4)-(2) V; webbing extending as wide fringe along either side of toes, nearly one third as broad as distal toe phalanx.

Dorsal skin of head smooth; upper eyelids with several large conical tubercles, one enlarged, forming horn; supratympanic fold distinct, from posterior corner of eye to upper arm insertion on each side; dorsum and flank of body slightly rough, scattered with some large glandular warts and small tubercles; dorsal limbs with some small tubercles; ventral surface of head, body, and limbs smooth, some tubercles arranged on rear of thigh and around vent; pectoral gland distinct and irregular, femoral gland indistinct.

Measurements (in mm): SVL 82.7, HDL 33.8, SKL 21.3, HDW 42.2, SNT 10.3, IND 8.6, IOD 13.6, ED 10.2, HND 21.6, RAD 19.7, TIB 33.3, FTL 48.6.

Coloration: In life, dorsal surface of head and body brown with dark blotches and stripes; irregular dark brown V-shaped marking between eyes, some small dark blotches on posterior of occiput forming distinct wide streak; dark tubercles on dorsum, cream yellow tubercles on sides of body; upper lip light brown; tympanic region brown; some irregular black blotches on dorsal limbs; dorsal digits with brown blotches and cream white blotches; ventral surface grayish brown with small white granular spots; pectoral gland yellowish; tip of digits, metacarpal tubercles, and inner metatarsal tubercle pale; pupils black; iris brownish.

In preservative, dorsal and ventral surfaces dark brown; upper lip cream; irregular dark brown V-shaped marking becoming indistinct, pectoral gland and tubercles fading to grayish-white.

Description of tadpole: Body slender, oval; tail depth slightly larger than body depth; dorsal fin arising just before origin of tail, tapering gradually to narrow, pointed tip; tail 2.2 times as long as body length, BL 12.3 mm and TL 27.6 mm in 36th stage tadpole (Figure 12E–F). Eyes large, lateral; nostrils dorsolateral; spiracle on left side of body, closer to eye than to end of body; anal tube long, attached to ventral fin; oral disk with lips expanded vertically forming dorsally oriented funnel.

Body brown; two short, longitudinal white stripes on sides of

ventral surface of head; posteriorly absent transversal white stripe on chest; two short longitudinal white stripes along sides of body; belly mottled with dense white speckles between two longitudinal stripes; tail with three short dark longitudinal stripes, one at base of dorsal fin, one at base of ventral fin, one on middle line of tail of tadpole.

Variation: Measurements of type series are given in Table 4. All specimens were similar in morphology and color pattern. The female paratype SYS a004486 differs from males by foot webbing and lateral fringes of toes slightly smaller than those of adult male specimens, toe webbing formula I (2)-(2*) II (1⅔)-(3) III (3)-(4) IV (4*)-(2½) V in female; webbing extending as fringe along either side of toes, nearly one sixth as broad as distal toe phalanx; yellowish brown body. Enlarged tubercles on edge of upper eyelid longer in SYS a004225 and SYS a004226.

Male secondary sexual characteristics: Male with single subgular vocal sac; nuptial pad on dorsal surface of first and second fingers, nuptial spines black (in preservative).

Etymology: The specific name “*orientalis*” refers to the distribution of the new species, which is the easternmost species within the genus *Brachytarsophrys*.

Suggested common name: Oriental Short-Legged Toad (in English) / Dong Fang Duan Tui Chan (东方短腿蟾 in Chinese).

Distribution and habitats: Currently, *Brachytarsophrys orientalis* sp. nov. is only known from the Jiulianshan Nature Reserve in Jiangxi Province and Gutian Township and Huboliao Nature Reserve in Fujian Province, China, at 200 to 700 m a.s.l.. This species is found under rocks in montane streams surrounded by moist subtropical evergreen broadleaf forests (Figure 1B). All male individuals were observed in August and emitted a series of croaks from hidden positions.

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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Brachytarsophrys orientalis LSID:

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SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Permission for field surveys in Jiulianshan National Nature Reserve,

Longnan County, Jiangxi Province was granted by the Jiangxi Jiulianshan National Nature Reserve Administration.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHOR CONTRIBUTIONS

Y.Y.W and D.D.Z conceived and designed the study. Y.L, Z.T.L, J.W, Y.L.L, Z.Y.L, H.H.C, D.Q.R, Z.F.J and C.Y.Z collected materials. Y.L performed the experiments, analyzed the data and prepared the manuscript. D.D.Z, Z.T.L, J.W, and Y.Y.W revised the manuscript. All authors read and approved the final version of the manuscript.

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