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Taxonomic determination of *Hypselotriton* populations distributed in eastern Guangdong, China (Caudata, Salamandridae), with description of a new species and a new subgenus

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Abstract

In this work, the *Hypselotriton* populations distributed in eastern Guangdong, China are studied in detail to clarify their taxonomic status. Based on morphological comparison and phylogenetic analysis, *H. glaucus* **syn. nov.** is synonymised with *H. orphicus*. *Hypselotriton* (*Cynotriton*) *oolong* **sp. nov.** from Mt Fenghuang in Chaozhou which used to be misidentified as *H. orphicus*, is revealed to be an independent lineage of subgenus *Cynotriton* and can be distinguished from all known congeners in morphology. By contrast, *H. orphicus* did not cluster within *Cynotriton*, but gathered with *H. jiaoren* **comb. nov.** to form a distinct unnamed clade within the genus. We therefore re-delimitate the intrageneric classification of the genus and a new subgenus *Hakkatriton* **subgen. nov.** is erected, corresponding to this unnamed clade. The Chinese Fire-bellied Newt genus *Hypselotriton* currently contains three subgenera and about ten known species. Identified keys to the subgenera and related congeners of genus *Hypselotriton* are further provided.

Key Words

Chaozhou, *Cynops*, *Hakkatriton* subgen. nov., *Hypselotriton* (*Cynotriton*) *oolong* sp. nov., Jiexi

Introduction

The Fire-bellied Newts contain about 18 species distributed in China and Japan in East Asia (Raffaëlli 2022; Lyu et al. 2023a). In traditional configuration, these species were provisionally placed in a single genus *Cynops* Tschudi, 1838, in spite of several controversies (Zhao and Hu 1984; Zhao et al. 1988; Lyu et al. 2023a). However, recent phylogenetic studies suggested the Chinese and Japanese congeners are paraphyletic from each other (Rancilhac et al. 2021; Yuan et al. 2022). In the phylogenetic analysis, the Fire-bellied Newt species distributed in Japanese Archipelago are revealed to be the basal lineage of the Modern Asian Newts. Compared with the insular species, the Fire-bellied Newt species occurring in mainland China are phylogenetically closer to other newt genera from mainland China and Indochina, i.e. *Pachytriton* Boulenger, 1878, *Paramesotriton* Chang, 1935 and *Laotriton* Dubois & Raffaëlli, 2009 (Rancilhac et al. 2021; Yuan et al. 2022). Thus, Raffaëlli (2022) partitioned these species into two independent genera, *Cynops* for the Japanese Fire-bellied Newts and *Hypselotriton* Wolterstorff, 1934 for the Chinese Fire-bellied Newts and which was followed in this work. Particularly, a recent work has described two new species of Chinese Fire-bellied Newts (Lyu et al. 2023a), but did not adopt the latest taxonomic proposal by Raffaëlli (2022) in a timely manner, resulting in two new nomenclature combinations in this work, *H. jiaoren* (Lyu, Qi & Wang, 2023), comb. nov. and *H. maguae* (Lyu, Qi & Wang, 2023), comb. nov.

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Within the genus *Hypselotriton*, Dubois and Raffaëlli (2011) classified the congeners into two subgenera, based on morphological and geographical characteristics, *Hypselotriton* and *Cynotriton* Dubois & Raffaëlli, 2011, corresponding to the former *Cynops wolterstorffi* and *Cynops orientalis* groups, respectively (Zhao et al. 1988; Raffaëlli 2022). Nonetheless, phylogenetic analysis has suggested three distinct and divergent clades within the genus, indicating that the intrageneric classification of this genus requires re-delimitation (Lyu et al. 2023a).

The species diversity of Fire-bellied Newts was considered underestimated. Tominaga et al. (2013, 2015) have revealed multiple distinct lineages within *Cynops pyrrhogaster* (Boie, 1826). Compared with the traditional recognition of two known species for Japanese Fire-bellied Newts, Raffaëlli (2022) documented four nominated species and four unnamed species within the insular genus *Cynops*. Meanwhile, four new species of *Hypselotriton* have been described from Southeast Chinese Hilly Area since 2010, dramatically raising the diversity of this mainland genus (Wu et al. 2010; Yuan et al. 2013; Lyu et al. 2023a). However, the taxonomic status for several *Hypselotriton* species remains unresolved. Lyu et al. (2023a) have discussed the taxonomic confusion on the congeners from Yunnan-Guizhou Plateau in southwestern China that still require further studies. During our fieldwork and study on the *Hypselotriton* populations from Guangdong in southeastern China, we have found that the recognition on *H. orphicus* (Risch, 1983) is also with confusion, especially for its delimitation from another congener in eastern Guangdong, *H. glaucus* (Yuan, Jiang, Ding, Zhang & Che, 2013).

Hypselotriton orphicus was nominated by Risch (1983), based on specimens collected and primarily described by Gressitt (1941) from "Dayang (Tai-Yong), Shantou Region [now belonging to Jiexi County, Jieyang City], 23°35'N, 115°51'E [= 23.58°N, 115.85°E], altitude 640 m" (Fig. 1, sites 2–3). *Hypselotriton glaucus* was described, based on specimens collected from "Meiguang Village (23.67°N, 115.80°E; elevation 742 m), in Mt Lianhua, Wuhua County, Meizhou" (Fig. 1, site 9) (Yuan et al. 2013), where it is in close proximity to the type locality of *H. orphicus*. When proposing *H. glaucus*, the data from Jiexi County were not mentioned. Instead, two separate populations collected from Mt Fenghuang of Guangdong and Mt Daiyun of Fujian were recorded as *H. orphicus* and used for comparison (Yuan et al. 2013). Morphologically, the diagnostic characters of *H. glaucus* almost match the description of *H. orphicus* in Risch (1983), except for the irregular greyish-blue patches on the dorsum of *H. glaucus*. Such colour pattern was not described by Gressitt (1941) based on living or freshly-preserved specimens and would fade after preservation. Particularly, Risch (1983) has mentioned that the type series of *H. orphicus* are morphologically different from the population from central Fujian. Thus, the employment of specimens from Mt Daiyun, central Fujian (as well as those from Mt Fenghuang, eastern Guangdong) as *H. orphicus* might be problematic, which further adds to the confusion on the proposal of *H. glaucus*.

In this work, we perform morphological comparisons and molecular analyses on the topotypical population of *Hypselotriton orphicus* and *H. glaucus*, as well as on the *Hypselotriton* population from Mt Fenghuang (Fig. 1, site 1). The results suggest that *H. glaucus* is conspecific with *H. orphicus*, while the population from Mt Fenghuang represents an unnamed lineage of genus *Hypselotriton* that is described hereby. The taxonomic status for the population from central Fujian is also discussed. Furthermore, we re-delimitate the intrageneric classification of the genus, as well as proposing a new subgenus for the clade comprised of *H. orphicus* and *H. jiaoren* comb. nov.

Materials and methods

Specimens and morphological analyses

A series of museum specimens of the genus *Hypselotriton* from eastern Guangdong were examined. Detailed information for these specimens is presented in related species accounts below. Abbreviations for museums and institutes include: **GEP** (Guangdong Polytechnic of Environmental Protection Engineering, Foshan, China), **CIB** (Herpetological Museum, Chengdu Institute of Biology, the Chinese Academy of Sciences, Chengdu, China), **SYS** (The Museum of Biology, Sun Yat-sen University, Guangzhou, China), **MVZ** (Museum of Vertebrate Zoology, University of California, Berkeley, USA), **MNHN** (Museum national d'Histoire naturelle, Paris, France), **AMNH** (American Museum of Natural History, New York, USA) and **CAS** (California Academy of Sciences, San Francisco, USA).

External measurements were made for the unnamed specimens with digital calipers (Neiko 01407A Stainless Steel 6-Inch Digital Caliper) to the nearest 0.1 mm. These measurements are as follows: total length (**TOL**) from tip of snout to tip of tail; snout–vent length (**SVL**) from tip of snout to posterior edge of vent; tail length (**TAL**) from posterior edge of vent to tip of tail; maximum tail depth (**TAD**); head length (**HL**) from tip of snout to the posterior edge of the parotoid gland; maximum head width (**HW**); snout length (**SL**) from tip of snout to the anterior corner of eye; eye diameter (**ED**) from the anterior corner to the posterior corner of the eye; interorbital distance (**IOD**) between the anterior corner of each eye; eye–nostril length (**EN**) from the anterior corner of the eye to the nostril; internasal distance (**IND**) between the external nares; axilla–groin length (**AG**) between the axilla and the groin along the body; fore-limb length (**FLL**) from elbow to tip of finger III; and hind-limb length (**HLL**) from knee to tip of toe III.

The morphological comparisons for known *Hypselotriton* congeners were attained from literature of the original and subsequently supplemental descriptions (David 1873; Boulenger 1905; Gressitt 1941; Liu et al. 1962; Kou and Xing 1983; Risch 1983; Yang 1983; Fei and Ye 1983, 2016; Fei et al. 2006; Wu et al. 2010; Yuan et al. 2013; Raffaëlli 2022; Lyu et al. 2023a).

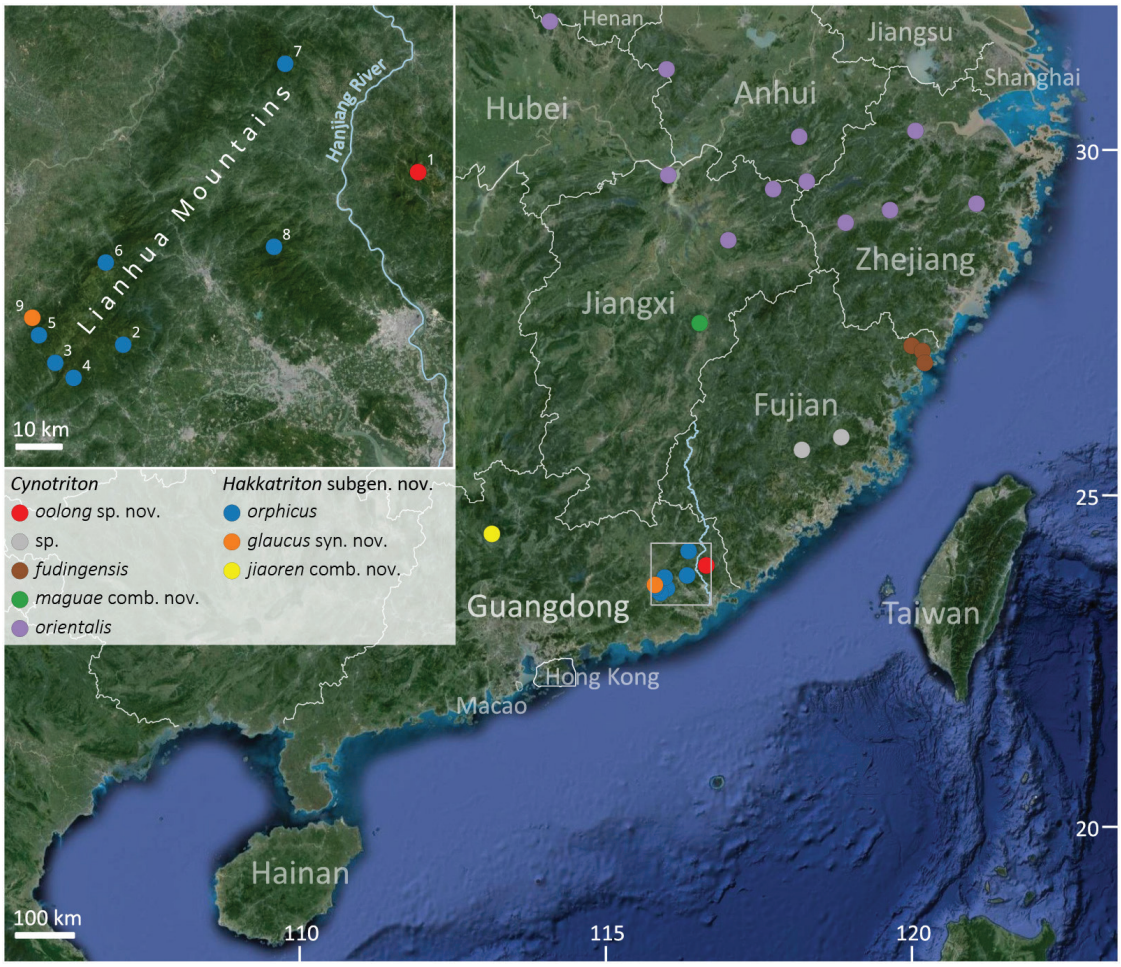

Figure 1. Map showing the localities for congeners of genus *Hypselotriton* from Southeast Chinese Hilly Area. Inset map on top left zooms in eastern Guangdong Province, showing the localities for *H.* (*Cynotriton*) *oolong* sp. nov. and *H.* (*Hakkatriton*) *orphicus*: **1.** Mt Fenghuang, Chao'an District, Chaozhou City (type locality of *H. oolong* sp. nov.); **2.** Dayang Township, Jiexi County, Jieyang City (purported type locality of *H. orphicus*; see Remarks in the species account for locality delimitation); **3.** Liangtian Township, Jiexi County (type locality of *H. orphicus* according to the original coordinate); **4.** Mt Dabei, Jiexi County; **5.** Mt Liwangzhang, Jiexi County; **6.** Mt Hongtuzhang, Fengshun County, Meizhou City; **7.** Mt Tongguzhang, Fengshun County; **8.** Mt Shijiadong, Fengshun County; **9.** Meiguang Village, Mt Lianhua, Wuhua County, Meizhou City (type locality of *H. glaucus* syn. nov.). The map is derived from Tianditu (www.tianditu.gov.cn).

Phylogenetic analyses

In total, 76 samples were used for phylogenetic analyses, encompassing 11 newly-sequenced individuals (three of the *Hypselotriton* population from Mt Fenghuang, four of *H. orphicus* from Jiexi County and two from Fengshun County in Guangdong and two of *H. yunnanensis* from Honghe County in Yunnan) and others obtained from GenBank.

Genomic DNA was extracted, using a DNA extraction kit from Tiangen Biotech (Beijing) Co., Ltd. Two mitochondrion genes, namely NADH dehydrogenase subunit 2 (*ND2*) and Cytochrome b (*cytb*) were amplified for phylogenetic analyses. Primers for *ND2* were L4437 (5'-AAGCTTTCGGGCCCATACC-3') and 5081R (5'-GTCGTAGGGTCAAAGCCTGC-3') and, for *cytb*, these were 14052F (5'-CCTGGGCTCTAACCAAGACC-3') and 15293R (5'-TCGGCTTACAAGACCGATGT-3'). PCR amplifications were processed with the cycling conditions of: initial denaturing step at 95 °C for 4 min, 35 cycles of denaturing at 95 °C for 40 s, annealing at 53 °C for 34 s and extension at 72 °C for 60 s and a final extension step at 72 °C for 10 min. PCR products were purified with spin columns and then sequenced with both forward and reverse primers using BigDye Terminator Cycle Sequencing Kit from Applied Biosystems, on an ABI Prism 3730 automated DNA sequencer by Guangzhou Jierui Biotechnology Co., Ltd. All sequences were deposited in GenBank (Table 1).

For phylogenetic analyses, DNA sequences were aligned by the Clustal W algorithm with default parameters (Thompson et al. 1997). PartitionFinder2 was used to test the best partitioning scheme and jModelTest v.2.1.2 was used to test the best fitting nucleotide substitution model. Bayesian Inference (BI) in MrBayes 3.2.4 (Ronquist et al. 2012) and Maximum Likelihood (ML) in RAxML GUI (Silvestro and Michalak 2012) were used to conduct phylogenetic analyses. For the ML analysis, an optimal tree was obtained and branch supports were evaluated with 1000 rapid bootstrapping replicates.

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

ID	Genus / Species	Voucher	Locality	ND2	Cytb
1	*Hypselotriton oolong* sp. nov.	CIB 121429	China: Guangdong: Chaozhou: Mt Fenghuang	PP987004	PP987015
2	*Hypselotriton oolong* sp. nov.	CIB 121430	China: Guangdong: Chaozhou: Mt Fenghuang	PP987005	PP987016
3	*Hypselotriton oolong* sp. nov.	SYS a009274	China: Guangdong: Chaozhou: Mt Fenghuang	PP987003	PP987014
4	*Hypselotriton oolong* sp. nov.	KIZ 09816	China: Guangdong: Chaozhou: Mt Fenghuang	ON793719	ON793672
5	*Hypselotriton oolong* sp. nov.	KIZ 09819	China: Guangdong: Chaozhou: Mt Fenghuang	ON793720	ON793673
6	*Hypselotriton oolong* sp. nov.	KIZ 09820	China: Guangdong: Chaozhou: Mt Fenghuang	ON793721	ON793674
7	*Hypselotriton oolong* sp. nov.	KIZ 09821	China: Guangdong: Chaozhou: Mt Fenghuang	ON793722	ON793675
8	*Hypselotriton* sp.	KIZ 09839	China: Fujian: Dehua: Mt Daiyun	ON793723	ON793676
9	*Hypselotriton* sp.	KIZ 09843	China: Fujian: Dehua: Mt Daiyun	ON793725	ON793678
10	*Hypselotriton* sp.	KIZ 09905	China: Fujian: Yongtai	ON793728	ON793681
11	*Hypselotriton* sp.	KIZ 09908	China: Fujian: Yongtai	ON793730	ON793683
12	*Hypselotriton orphicus*	GEP a008	China: Guangdong: Jiexi: Mt Dabei	PP986999	PP987010
13	*Hypselotriton orphicus*	GEP a009	China: Guangdong: Jiexi: Mt Dabei	PP987000	PP987011
14	*Hypselotriton orphicus*	GEP a010	China: Guangdong: Jiexi: Mt Dabei	PP987001	PP987012
15	*Hypselotriton orphicus*	GEP a011	China: Guangdong: Jiexi: Mt Dabei	PP987002	PP987013
16	*Hypselotriton orphicus*	GEP a314	China: Guangdong: Fengshun: Mt Shijiadong	PP987008	PP987019
17	*Hypselotriton orphicus*	GEP a315	China: Guangdong: Fengshun: Mt Shijiadong	PP987009	PP987020
18	*Hypselotriton glaucus* syn. nov.	KIZ 09793	China: Guangdong: Wuhua: Mianyang	ON793715	ON793668
19	*Hypselotriton glaucus* syn. nov.	KIZ 09799	China: Guangdong: Wuhua: Mianyang	ON793716	ON793669
20	*Hypselotriton cyanurus*	KIZ 02330	China: Guizhou: Shuicheng	/	ON793711
21	*Hypselotriton cyanurus*	KIZ 02331	China: Guizhou: Shuicheng	ON793754	ON793712
22	*Hypselotriton cyanurus*	KIZ 02332	China: Guizhou: Shuicheng	ON793755	ON793713
23	*Hypselotriton fudingensis*	KIZ 012918	China: Fujian: Zherong	ON793745	ON793698
24	*Hypselotriton fudingensis*	KIZ 012214	China: Fujian: Ningde: Qingyu	ON793743	ON793696
25	*Hypselotriton fudingensis*	KIZ 012217	China: Fujian: Ningde: Qingyu	ON793744	ON793697
26	*Hypselotriton jiaoren* comb. nov.	SYS a008787	China: Guangdong: Yingde	OQ116680	/
27	*Hypselotriton jiaoren* comb. nov.	SYS a008788	China: Guangdong: Yingde	OQ116681	/
28	*Hypselotriton jiaoren* comb. nov.	SYS a008789	China: Guangdong: Yingde	OQ116682	/
29	*Hypselotriton maguae* comb. nov.	CIB 118535	China: Jiangxi: Nancheng: Mt Magu	OQ116685	/
30	*Hypselotriton maguae* comb. nov.	SYS a007032	China: Jiangxi: Nancheng: Mt Magu	OQ116686	/
31	*Hypselotriton orientalis*	KIZ 06358	China: Zhejiang: Jinhua	ON793718	ON793671
32	*Hypselotriton orientalis*	CIB 97919	China: Zhejiang: Quzhou	GU301790	/
33	*Hypselotriton orientalis*	KIZ 012940	China: Zhejiang: Tiantai	ON793731	ON793684
34	*Hypselotriton orientalis*	MVZ 230345	China: Zhejiang: Hanzhou	EU880311	EU880311
35	*Hypselotriton orientalis*	CIB 97867	China: Jiangxi: Wannian	GU301788	/
36	*Hypselotriton orientalis*	KIZ 013017	China: Henan: Xinyang: Mt Jigong	ON793734	ON793687
37	*Hypselotriton orientalis*	YPX25002	China: Jiangxi: Wuyuan	ON793740	ON793694
38	*Hypselotriton orientalis*	KIZ 020536	China: Jiangxi: Jiujiang	ON793738	ON793692
39	*Hypselotriton orientalis*	KIZ 021962	China: Anhui: Xiuning	ON793737	ON793691
40	*Hypselotriton orientalis*	KIZ 021844	China: Anhui: Huoshan	ON793742	ON793695
41	*Hypselotriton yunnanensis*	CIB 121432	China: Yunnan: Honghe	PP987006	PP987017
42	*Hypselotriton yunnanensis*	CIB 121433	China: Yunnan: Honghe	PP987007	PP987018
43	*Hypselotriton yunnanensis*	SYS a007780	China: Yunnan: Shiping	OQ116687	/
44	*Hypselotriton yunnanensis*	KIZ 01445	China: Yunnan: Ning'er	ON793756	ON793714
45	*Hypselotriton yunnanensis*	KIZ 021922	China: Yunnan: Chuxiong: Zijing	ON793749	ON793706
46	*Hypselotriton yunnanensis*	KIZ 022157	China: Yunnan: Kunming: Huahongdong	ON793751	ON793708
47	*Hypselotriton yunnanensis*	KIZ 022161	China: Yunnan: Kunming: Gulu	ON793753	ON793710
48	*Cynops pyrrhogaster*	KIZ 09755	Japan	/	ON793699
49	*Cynops pyrrhogaster*	KIZ 09757	Japan	/	ON793701
50	*Cynops pyrrhogaster*	MVZ 263718	Japan	EU880313	EU880313
51	*Laotriton laoensis*	FMNH 255452	Laos	EU880328	EU880328
52	*Pachytriton airobranchiatus*	SWUF YZY0301	China: Guangdong: Huizhou: Mt Lianhua	MG732934	MG732932
53	*Pachytriton archospotus*	CIB 95950	China: Jiangxi: Ganzhou: Mt Qiyun	GQ303629	GQ303666
54	*Pachytriton brevipes*	KIZ 08926	China: Fujian: Nanping: Mt Wuyi	ON793903	ON793838
55	*Pachytriton feii*	KIZ 04228	China: Anhui: Huangshan: Mt Huangshan	ON793879	ON793813
56	*Pachytriton granulosus*	KIZ 012977	China: Zhejiang: Taizhou: Tiantai	ON793920	ON793856
57	*Pachytriton inexpectatus*	KIZ 05203	China: Guangxi: Laibin: Mt Dayao	ON793885	ON793819
58	*Pachytriton moi*	KIZ 07767	China: Guangxi: Guilin: Mt Mao'er	ON793895	ON793830
59	*Pachytriton wuguanfui*	KIZ 08756	China: Guangxi: Hezhou	ON793901	ON793836
60	*Pachytriton xanthospilos*	KIZ 06750	China: Hunan: Chenzhou: Mt Mangshan	ON793907	ON793842
61	*Paramesotriton aurantius*	KIZ 012879	China: Fujian: Ningde: Zherong	ON794099	ON794033
62	*Paramesotriton caudopunctatus*	KIZ 03903	China: Guizhou: Qiandongnan: Mt Leigong	ON794069	ON794003
63	*Paramesotriton chinensis*	KIZ 013010	China: Zhejiang: Ningbo: Baixi	ON794108	ON794042

ID	Genus / Species	Voucher	Locality	ND2	Cytb
64	*Paramesotriton deloustali*	MVZ 223629	Vietnam: Tam Dao: Yinh Yen	FJ744600	GQ303669
65	*Paramesotriton fuzhongensis*	KIZ 08568	China: Guangxi: Hezhou: Chaodong	ON794073	ON794007
66	*Paramesotriton guangxiensis*	KIZ 09285	China: Guangxi: Chongzuo: Ningming	ON794071	ON794005
67	*Paramesotriton hongkongensis*	KIZ 01577	China: Hong Kong: Tai Mo Shan	ON794111	ON794045
68	*Paramesotriton labiatus*	KIZ 08769	China: Guangxi: Laibin: Mt Dayao	ON794077	ON794011
69	*Paramesotriton longliensis*	KIZ 03343	China: Guizhou: Qiannan: Longli	ON794064	ON793998
70	*Paramesotriton maolanensis*	GZNU 2006030004	China: Guizhou: Qiannan: Libo	JF438993	JX480887
71	*Paramesotriton qixilingensis*	KIZ 022289	China: Jiangxi: Ji'an: Mt Qixiling	ON794120	ON794055
72	*Paramesotriton wulingensis*	KIZ 03102	China: Chongqing: Youyang	ON794123	ON794058
73	*Paramesotriton yunwuensis*	KIZ 09676	China: Guangdong: Yunfu: Luoding	ON794086	ON794020
74	*Paramesotriton zhijinensis*	KIZ YPX6178	China: Guizhou: Bijie: Zhijing	ON794067	ON794001
75	*Calotriton asper*	Vieites 01	NA	EU880307	EU880307
76	*Euproctus platycephalus*	DBW-MVZ 01	NA	EU880317	EU880317

For the BI analysis, two independent runs with four Markov Chain Monte Carlo simulations were performed for ten million iterations and sampled every 1000 iterations. The first 25% of the samples were discarded as burn-in after the standard deviation of split frequencies of the two runs was less than a value of 0.01. The remaining trees were used to create a consensus tree.

Results

The BI and ML analyses resulted in identical topologies (Fig. 2). Most major nodes were well supported with the Bayesian posterior probabilities (BPP) > 0.95 and the ML bootstrap supports (BS) > 70. All samples of *Hypselotriton* formed a monophyletic group, as the sister taxon to the monophyletic group including *Paramesotriton*, *Pachytriton* and *Laotriton*, but paraphyletic with *Cynops*. This is corresponding to previous studies (Rancilhac et al. 2021; Yuan et al. 2022), supporting the resurrection of *Hypselotriton* as a distinct genus.

Within *Hypselotriton*, three distinct and divergent clades were revealed, as those recovered in Lyu et al. (2023a). Morphological comparisons further sustained the differences amongst these clades (present below), which are treated as representing three subgenera. The clade involving *H. orientalis* has been proposed as subgenus *Cynotriton* and the clade involving *H. cyanurus* is considered to represent the nominotypical subgenus *Hypselotriton* (Dubois and Raffaëlli 2011; Raffaëlli 2022). A new subgenus is nominated in this work to accommodate species within the remaining unnamed clade.

As shown in the tree, the *Hypselotriton* populations distributed in eastern Guangdong have been separated into two distinct and distant lineages. Topotypical samples of *H. orphicus* from Jiexi were clustered with samples of type series of *H. glaucus* in a lineage and almost without genetic divergences, indicating these samples should be conspecific. Morphological examination further confirmed such insight (present below). This lineage was the sister taxon to *H. jiaoren* comb. nov. from northern Guangdong and collectively constituted the new subgenus as mentioned above.

Samples of *Hypselotriton* population from Mt Fenghuang, which was employed as *H. orphicus* (Yuan et al. 2013, 2022; Lyu et al. 2023a), formed an independent lineage within the subgenus *Cynotriton*, representing the southernmost lineage of this subgenus (Fig. 1). Specimens of this lineage showed distinct differences in morphology that can be distinguished from *H. orphicus*, as well as all known congeners of *Hypselotriton*. Thus, this lineage represents an unnamed species that is described in this work. Moreover, the samples of *Hypselotriton* population from central Fujian, which was also employed as *H. orphicus* (Yuan et al. 2013, 2022; Lyu et al. 2023a), formed a distinct lineage as the sister taxon to the Mt Fenghuang lineage, with small genetic divergence. The taxonomic status of this lineage is further remarked below.

Systematics

Genus *Hypselotriton* Wolterstorff, 1934

Type species. *Molge wolterstorffi* Boulenger, 1905, by original designation.

Common name. Chinese Fire-bellied Newts (in English) / diān yuán shǔ (滇螈属 in Chinese).

Distribution. Endemic in mainland China.

Remark. In spite of the paraphyletic relationships and distinct geographical isolation, species of the mainland genus *Hypselotriton* are very similar to those of insular genus *Cynops* in morphology, resulting in the prolonged categorising of these Fire-bellied Newts in a single genus. *Hypselotriton* can be distinguished from *Cynops* by the inconspicuous parotoid gland (vs. well developed) and smooth or slightly granular skin (vs. distinctly granular).

Key to subgenus within *Hypselotriton*

1 Distinct orange-red spot behind the eye present; blue lateral stripe on tail in breeding males present ..... *Hypselotriton*
– Distinct orange-red spot behind the eye absent; blue lateral stripe on tail in breeding males absent 2

2 Mid-dorsal vertebral ridge continuous; irregular greyish-blue patches on dorsum and lateral tail in breeding males and females present ..... *Hakkatriton* subgen. nov.
– Mid-dorsal vertebral ridge interrupted; irregular greyish-blue patches on dorsum and lateral tail in breeding males and females absent..... *Cynotriton*

Subgenus *Hypselotriton* Wolterstorff, 1934

Type species. *Molge wolterstorffi* Boulenger, 1905, by original designation.

Diagnosis. (1) small to large size; (2) gular fold present; (3) mid-dorsal vertebral ridge continuous; (4) metacarpal and metatarsal tubercles on external side of hands and feet present; (5) postocular orange spot present; (6) blue lateral stripe on tail in breeding males present.

Content and remarks. This subgenus includes all known Fire-bellied Newts populations distributed in the Yunnan-Guizhou Plateau in southwestern China. Currently, four nomenclatures have been provisionally documented, i.e. *H.* (*Hy.*) *chenggongensis* (Kou & Xing, 1983), *H.* (*Hy.*) *cyanurus* (Liu, Hu & Yang, 1962), *H.* (*Hy.*) *wolterstorffi* (Boulenger, 1905) and *H.* (*Hy.*) *yunnanensis* (Yang, 1979) (Lyu et al. 2023a). However, the exact taxonomic status for these populations/species is still unresolved (Raffaëlli 2022; Lyu et al. 2023a). Thus, it is improper to present a key to these nomenclatures before a comprehensive study to precisely delimitate their taxonomic placements.

Subgenus *Hakkatriton* subgen. nov.

https://zoobank.org/504DCCDF-32D2-4894-AFBA-5766752AD418

Type species. *Cynops orphicus* Risch, 1983, by present designation.

Etymology. The nomen of *Hakkatriton* subgen. nov. is derived from Hakka, referring to its distribution in northern and eastern Guangdong where is the settlement of Hakka people and generic nomen *Triton* Laurenti, 1768.

Diagnosis. (1) small size; (2) gular fold absent; (3) mid-dorsal vertebral ridge continuous; (4) metacarpal and metatarsal tubercles on external side of hands and feet absent; (5) postocular orange spot absent; (6) blue lateral stripe on tail in breeding males absent; (7) irregular greyish-blue patches on dorsum and lateral tail in breeding males and females present.

Content. Two species distributed in isolated regions in northern and eastern Guangdong in southern China, respectively (Fig. 1).

Key to species of the subgenus *Hakkatriton* subgen. nov.

1 Ventral forearms and shanks uniformly dark brown; tail uniformly coloured ..... *H.* (*Ha.*) *jiaoren*
– Ventral forearms and shanks with bright orange patches; tail with irregular black spots ..... *H.* (*Ha.*) *orphicus*

Hypselotriton (*Hakkatriton*) *orphicus* (Risch, 1983)

Pachytriton brevipes (Sauvage, 1876) – Pope and Boring (1940); Gressitt (1941)
Cynops shataukokensis Freytag & Eberhardt, 1977 – Freytag (1979)
Cynops orphicus Risch, 1983 – Risch (1983); Fei et al. (2006, 2012); Fei and Ye (2016)
Hypselotriton (*Pingia*) *orphicus* – Dubois and Raffaëlli (2009)
Hypselotriton (*Cynotriton*) *orphicus* – Dubois and Raffaëlli (2011)
Cynops glaucus Yuan, Jiang, Ding, Zhang & Che, 2013 syn. nov. – Yuan et al. (2013, 2022); Fei and Ye (2016); Lyu et al. (2023a)
Hypselotriton (*Cynotriton*) *glaucus* – Raffaëlli (2022)

Type. ***Holotype.*** China • ♂; Guangdong Province, Shantou Region [now belonging to Jieyang City, Jiexi County], Tai-Yong [Dayang Township]; 23°35'N, 115°51'E [=23.58°N, 115.85°E; located in Liangtian Township, see remarks below], 640 m elev.; 4 Aug. 1936; JL Gressitt leg.; MVZ 22474.

Paratypes. China • 97 adult specimens; same data as for holotype; MVZ 22416–73, 22475–506 [90 specimens], MNHN 1980.4096–4098 [3 specimens, formerly MVZ 24134–36], AMNH 46174, CAS 78704, 2 unnumbered specimens in the Department of Biology, Yenching University [probably lost according to Risch (1983)].

Examined specimens. China • 4♂♂; Guangdong Province, Jieyang City, Jiexi County, Mt Dabei; 23.55°N, 115.89°E, ca. 490 m elev.; GEP a008, 010–011, CIB 121434 • 2♀♀; same data as for preceding; GEP a009, CIB 121435 • 2♂♂; Guangdong Province, Meizhou City, Fengshun County, Mt Hongtuzhang; 23.78°N, 115.96°E, ca. 1200 m elev.; GEP a263–264 • 3♂♂; Guangdong Province, Meizhou City, Fengshun County, Mt Shijiadong; 23.81°N, 116.33°E, ca. 1140 m elev.; GEP a314–316 • 3♀♀; same data as for preceding; GEP a317–319.

Referred specimens. Seven specimens labelled as "*Cynops glaucus*" in Lyu et al. (2023a). China • 2♀♀; Guangdong Province, Jieyang City, Jiexi County, Mt Dabei; SYS a000729, 8511 • 1♂; Guangdong Province, Jieyang City, Jiexi County, Mt. Liwangzhang; 23.64°N, 115.81°E, ca. 990 m elev.; SYS a008602 • 1♀; same data as for preceding; SYS a008601 • 2♀♀; Guangdong Province, Meizhou City, Fengshun County, Mt. Tongguzhang; 24.18°N, 116.35°E, ca. 1500 m elev.; SYS a000730, 4743 • 1♀; same data as for preceding; SYS a000731.

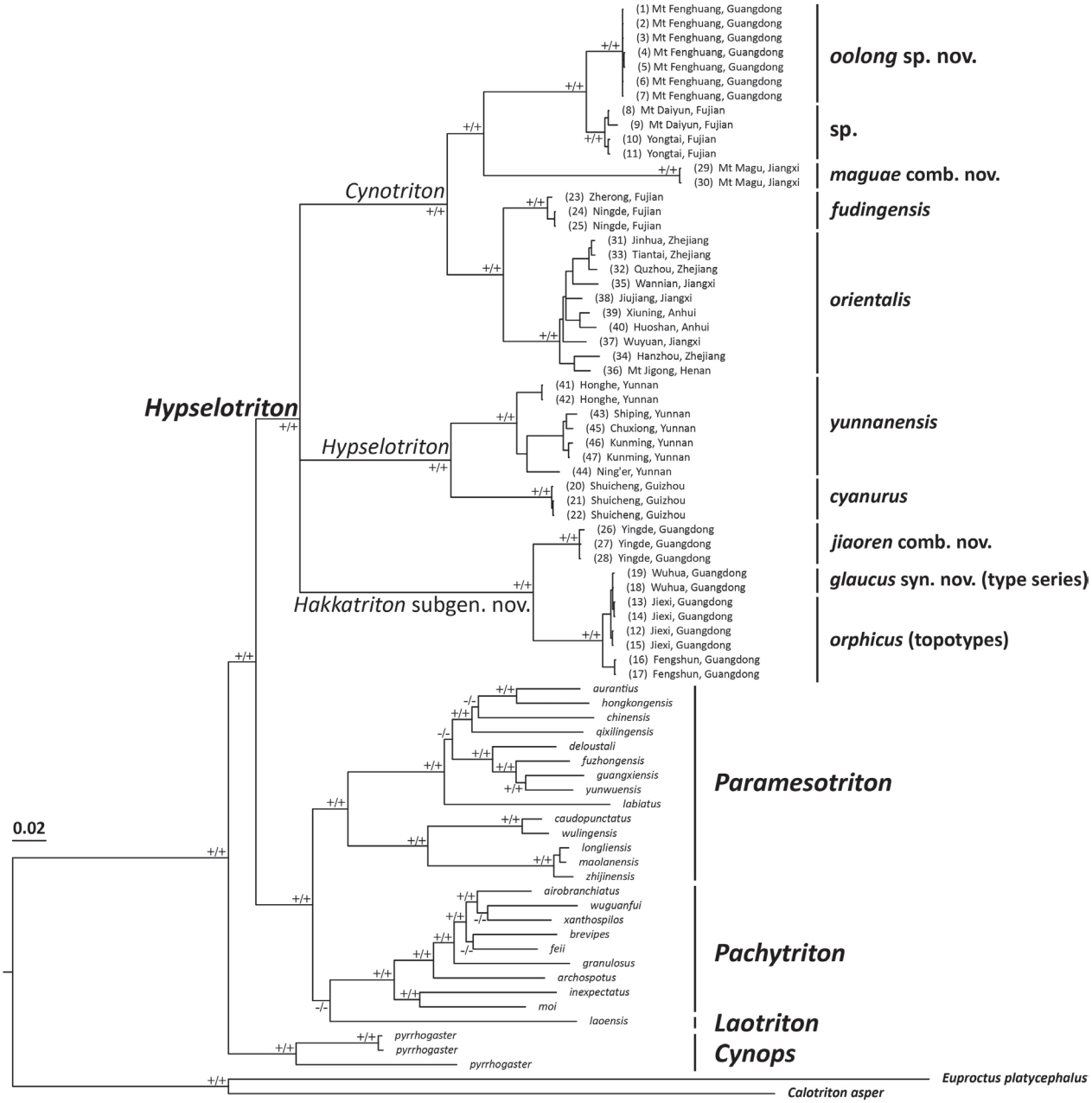

Figure 2. Bayesian Inference and Maximum-Likelihood phylogenies, based on mitochondrial *ND2* and *cytb* genes. Bayesian posterior probabilities (BPP) > 0.95 and the bootstrap supports (BS) > 70 are labelled with "+" and otherwise labelled with "-".

Etymology. The specific name *orphicus* is derived from the Greek legendary musician and poet Orpheus, in memory of several people who passed away in 1982 (Risch 1983).

Common name. Dayang Fire-bellied Newt (in English) / cháo shàn róng yuán (潮汕蝾螈 in Chinese).

Revised diagnosis. (1) small body size, TOL 68.5–77.0 mm in adult males, 85.1–99.7 mm in adult females; (2) parotoid gland inconspicuous; (3) postocular orange spot absent; (4) surface smooth, finely granulated, gular fold absent; (5) continuous vertebral ridge weak and inconspicuous; (6) fingers and toes overlapping when fore-limb and hind-limb adpressed towards each other along body; (7) ground colour dark brown to olive brown, with irregular greyish-blue patches on dorsum and lateral tail in breeding males and females; (8) lateral tail with black spots; (9) ground colour of venter dark brown with irregular bright orange patches, bright orange blotches on chin, ventral limbs and cloaca; (10) ventral tail with a bright orange stripe.

Description of new specimens. Body slender and small-sized, TOL 68.5–77.0 mm in adult males, 85.1–99.7 mm in adult females, with detailed measurements listed in Table 2. Head oval in dorsal view; snout truncate, projecting slightly beyond mandible; nostril small, but conspicuous; labial fold developed on posterior part of upper jaw; tongue elongate, enlarged anteriorly, with free lateral margin; vomerine tooth patch "^"-shaped; eye small, not extending beyond lateral margins of head; an inconspicuous longitudinal ridge found posterior to each eye; parotoid gland inconspicuous, gill remnants absent; gular fold absent.

Table 2. Measurements (in mm) of *Hypselotriton* (*Hakkatriton*) *orphicus* and *H.* (*Cynotriton*) *oolong* sp. nov.

Voucher	Sex	TOL	SVL	TAL	TAD	HL	HW	SL	ED	IOD	EN	IND	AG	FLL	HLL
Hypselotriton (*Hakkatriton*) *orphicus*															
GEP a008	M	73.5	41.9	29.1	6.1	13.1	8.8	4.5	2.6	4.1	2.8	2.9	20.6	10.6	12.1
GEP a010	M	73.5	43.3	32.3	5.0	12.5	8.8	4.2	2.5	4.1	2.7	2.9	20.8	8.8	9.4
GEP a011	M	77.0	44.2	32.8	6.5	12.8	9.7	4.2	2.7	4.7	2.8	3.2	19.5	10.6	11.5
GEP a263	M	75.6	44.3	31.3	4.8	10.0	8.6	4.3	2.8	4.4	3.0	3.1	18.8	8.7	10.3
GEP a264	M	75.9	43.0	32.9	4.9	12.6	8.7	4.4	2.6	4.5	3.1	3.2	18.8	9.2	10.6
GEP a314	M	72.1	42.3	29.8	6.6	12.5	10.0	4.4	2.6	5.1	3.0	3.1	18.9	10.4	11.2
GEP a315	M	70.7	40.8	29.9	6.4	11.8	9.4	3.9	2.8	4.4	2.6	2.9	18.0	9.6	9.8
GEP a316	M	74.5	42.2	32.3	6.2	12.2	9.3	4.3	2.9	4.9	2.7	2.9	18.2	8.8	10.2
CIB 121434	M	68.5	41.3	27.2	5.7	11.9	8.7	4.2	2.7	4.2	2.8	3.0	18.4	9.2	9.8
SYS a000730	M	70.7	43.4	27.3	6.8	12.2	9.2	4.7	2.4	5.6	2.9	3.2	18.6	8.6	8.8
SYS a004743	M	79.8	49.9	29.9	6.8	12.2	10.4	4.7	2.5	6.1	3.0	3.6	19.8	10.4	10.6
SYS a008602	M	73.5	43.5	30.0	6.4	12.5	10.0	4.8	2.5	5.7	2.9	3.3	19.4	9.1	10.1
GEP a009	F	85.1	48.7	36.4	6.6	14.1	9.9	4.5	2.8	5.2	3.4	3.2	22.2	10.0	11.0
GEP a317	F	86.1	48.1	38.1	6.1	13.6	10.8	4.6	2.8	5.2	3.6	3.7	24.0	10.1	10.3
GEP a318	F	91.2	50.3	40.9	7.4	14.6	10.8	4.9	2.9	5.4	3.5	3.2	23.9	10.5	10.7
GEP a319	F	91.0	50.6	40.4	6.3	14.2	10.7	4.6	2.9	5.0	3.6	3.3	25.4	9.7	10.6
CIB 121435	F	88.9	48.6	40.3	5.7	13.5	10.3	4.7	2.8	4.9	2.8	3.0	22.3	11.0	11.4
SYS a000729	F	87.5	50.2	37.3	5.9	13.7	10.1	4.5	2.5	6.0	2.8	3.4	23.6	10.3	10.6
SYS a000731	F	88.6	49.6	39.0	6.9	14.1	11.4	4.9	2.5	6.5	3.0	3.6	21.4	10.2	11.2
SYS a008511	F	90.2	50.6	39.6	5.7	13.7	10.5	4.8	2.6	5.8	3.0	3.6	23.5	10.6	11.0
SYS a008601	F	99.7	55.6	44.1	7.5	14.8	11.6	5.8	2.7	6.6	3.8	3.9	25.3	11.7	11.9
Hypselotriton (*Cynotriton*) *oolong* sp. nov.															
CIB 121430	M	70.7	45.2	25.5	6.1	12.5	9.1	4.1	2.9	4.5	2.8	2.5	22.7	9.5	10.4
CIB 121429	M	69.9	43.0	26.9	5.2	12.4	8.6	4.1	2.8	4.5	3.3	2.5	21.0	9.2	9.6
SYS a009274	M	70.0	43.5	26.5	5.0	11.6	8.4	4.1	2.6	4.5	2.9	2.6	20.0	9.2	9.6

Surface smooth, finely granular; a few inconspicuous longitudinal wrinkles present on chin; continuous vertebral ridge weak and inconspicuous; cloacal opening oval, slightly protruding.

Limbs slender, fingers and toes overlapping when forelimb and hind-limb adpressed towards each other along body; four fingers and five toes, slender and elongated, lack webbing; relative length of fingers I < IV < II < III; relative length of toes I < V < II < IV < III. Tail laterally compressed, tapering posteriorly; caudal fin distinct; tail tip bluntly pointed.

Colouration of new specimens. In life, ground colour dark brown to olive brown, with irregular greyish-blue patches on dorsum and lateral tail; lateral tail with black spots; a single bright orange dot on insertion of upper forearm; tips of digits light yellow to bright orange; ground colour of venter dark brown with irregular bright orange patches, bright orange blotches on chin, ventral limbs and cloaca; ventral tail with a bright orange stripe (Fig. 3).

In preservation, ground colour dark brown, irregular greyish-blue patches on dorsum and lateral tail faded and almost invisible; black spots on lateral tail and bright orange dot on insertion of upper forearm faded; bright orange blotches on ventral trunk and tail, bright orange blotches on chin, ventral limbs and cloaca slightly faded, dark patches more distinct.

Variations. For measurements, see Table 2. Larger body size in females; cloaca wider and more swollen in males than in females; tail proportionally shorter and wider in males than in females; variable greyish-blue patches on dorsum and lateral tail in both breeding males and females.

Distribution and natural history. This species is known from multiple localities at elevations of 490–1500 m in the Lianhua Mountains and on the west of the Hanjiang River in eastern Guangdong (Fig. 1).

Adults are observed in wetlands, seasonal ponds, cultivated valleys and small lakes surrounded by forests from March to September. The breeding season is spring to summer. When breeding, a large number of individuals gather in the lentic water area. Males chase the females and show their courtship willingness by wagging their tails. Females lay eggs with jelly coating on tips of the leaves of aquatic plants. Eggs develop into larvae after about half a month and larvae develop into adults after about six to eight months. The newts feed on a variety of food sources, mainly small molluscs and arthropods in their habitat. Risch (1983) surmises that the newt might inhabit water all year round; however, adults leave the water from late September to early March to live on land until the next spring rains arrive.

Remarks. The type specimens of this species were reported to be collected from Tai-yong (Gressitt 1937, 1941; Fig. 1, site 2). When describing them as a new species, Risch (1983) provided the type locality from traditional transliteration "Tai-yong" to current Pinyin as "Dayang". Risch (1983) further provided the coordinates for this locality as "23°35'N, 115°51'E [= 23.58°N, 115.85°E]"; however, this coordinate is located in Liangtian Township

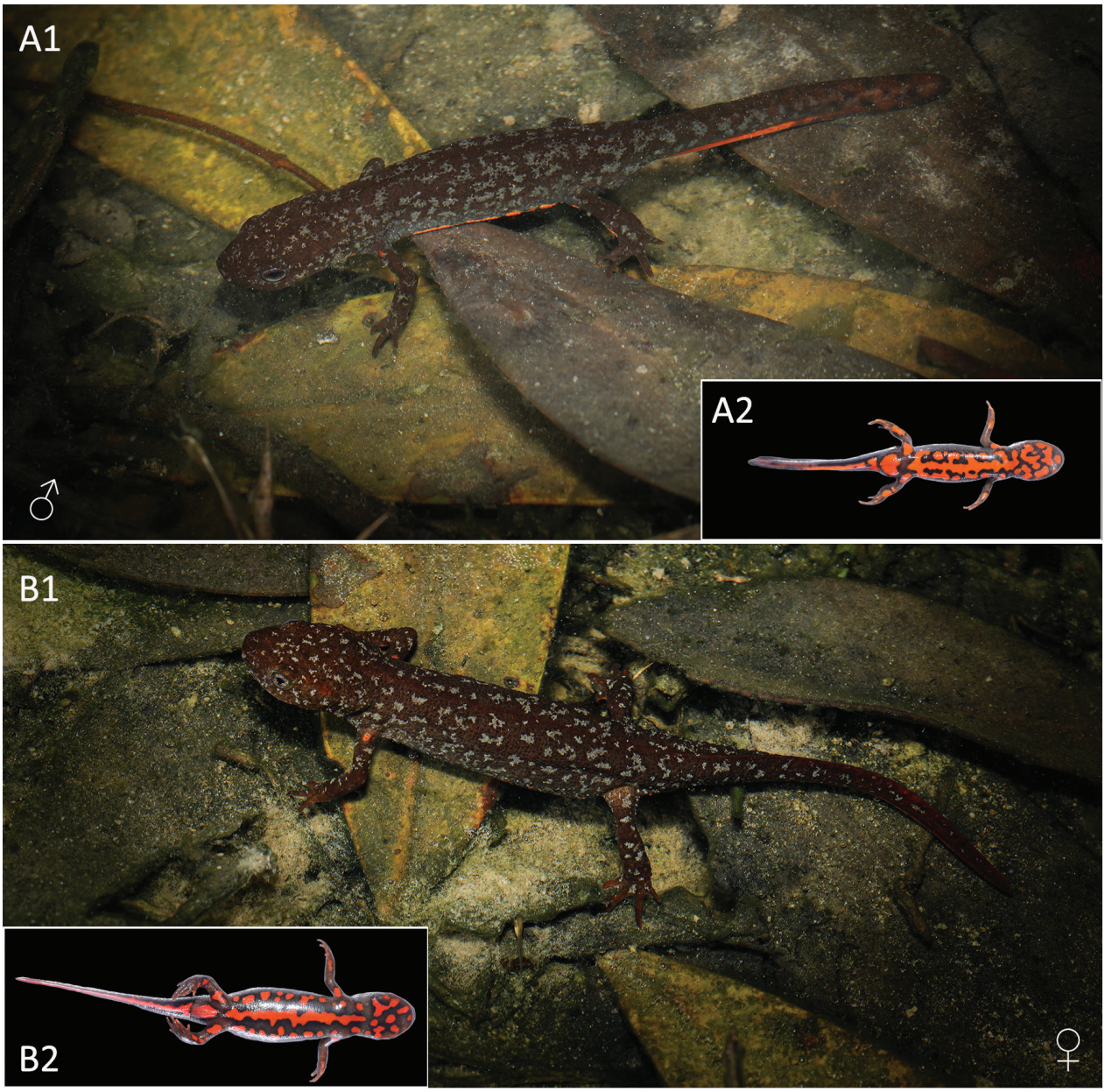

Figure 3. *Hypselotriton* (*Hakkatriton*) *orphicus* in life. **A.** CIB 121434, adult male; **B.** CIB 121435, adult female; **1.** Dorsal view in situ; **2.** Ventral view.

(Fig. 1, site 3) which is ca. 15 km from Dayang Township. During the surveys across the region in Jiexi and Fengshun counties encompassing these two localities, we failed to observed *Hypselotriton* populations from the vicinity of both sites 2 and 3, possibly due to the development of urbanisation. Nonetheless, morphological characters of the specimens from neighbouring Mt Dabei, Mt Liwangzhang, Mt Hongtuzhang, Mt Tongguzhang and Mt Shijiadong (Fig. 1, sites 4–8) all match the original description of *H. orphicus*.

According to the original descriptions of *Hypselotriton glaucus* syn. nov. and *H.* (*Ha.*) *orphicus*, the only difference between them is the irregular greyish-blue patches on dorsum. Such colour pattern just occurs in the breeding living individuals and will fade after preservation according to our examinations. Thus, based on the morphological and phylogenetic results, we synonymised *H. glaucus* syn. nov. with *H.* (*Ha.*) *orphicus*.

Subgenus *Cynotriton* Dubois & Raffaëlli, 2011

Type species. *Triton* (*Cynops*) *orientalis* David, 1875, by original designation.

Diagnosis. (1) small size; (2) gular fold present or absent; (3) mid-dorsal vertebral ridge interrupted; (4) metacarpal and metatarsal tubercles on external side of hands and feet absent; (5) postocular orange spot absent; (6) blue lateral stripe on tail in breeding males absent; (7) irregular greyish-blue patches on dorsum and lateral tail in breeding males and females absent.

Content. Four recognised species distributed in eastern China (Fig. 1).

Key to species of the subgenus *Cynotriton*

1	Gular fold absent	*H.* (*C.*) *maguae*
–	Gular fold present	2
2	Mid-dorsal vertebral ridge weak; dorsal skin smooth	*H.* (*C.*) *orientalis*
–	Mid-dorsal vertebral ridge bulged; dorsal skin relatively granular	3
3	Ventral surface almost entirely bright orange	*H.* (*C.*) *fudingensis*
–	Ground colour of venter dark brown with irregular bright orange patches	*H.* (*C.*) *oolong* sp. nov.

Hypselotriton (*Cynotriton*) *oolong* sp. nov.

https://zoobank.org/7E9557A2-9C78-4227-B7C1-07ED6930D045

Cynops orphicus Risch, 1983 – Fei et al. (2006, 2012); Yuan et al. (2013, 2022); Sparreboom (2014); Fei and Ye (2016); Lyu et al. (2023a)
Hypselotriton (*Cynotriton*) *orphicus* – Raffaëlli (2022)

Type. ***Holotype.*** China • ♂; Guangdong Province, Chaozhou City, Chao'an District, Mt Fenghuang, Peak Wudongding, Tianchi Lake; 23.96°N, 116.64°E, ca. 1320 m elev.; 21 Sep. 2019; Tian-Li Wei leg.; CIB 121430 [field number GEP a192] (Fig. 4).

Paratypes. China • 2♂♂; same data as for holotype; CIB 121429 [field number GEP a191], SYS a009274 [field number GEP a190].

Etymology. The specific name *oolong* is used as a noun in apposition, derived from oolong tea. The type locality of this species, Mt Fenghuang, is famous for the cultivation and production of the Phoenix Oolong Tea. Yet, the developments of tea cultivation have affected and threatened the habitats of this species. We name this new species after the most famous local economic output in the hope that it would bring attention on the green and sustainable development as well as the harmonious co-existence between humanity and nature. This species name is also in memory of the Japanese manga artist Akira Toriyama (1955–2024). His most famous work, *Dragon Ball*, was originally inspired by Chinese culture and one of the characters is named as Oolong who makes the first shown wish with the Dragon Balls.

Common name. Oolong Fire-bellied Newt (in English) / wū lóng róng yuán (乌龙蝾螈 in Chinese).

Diagnosis. (1) small body size, TOL 69.9–70.7 mm in adult males; (2) parotoid gland inconspicuous; (3) postocular orange spot absent; (4) surface rough and granulated, gular fold present; (5) interrupted vertebral ridge conspicuous and bulged; (6) fingers and toes overlapping when fore-limb and hind-limb adpressed towards each other along body; (7) ground colour dark brown to olive brown with black spots; (8) lateral tail with black spots; (9) ground colour of venter dark brown with irregular bright orange patches, bright orange blotches on chin, base of ventral limbs and anterior half of cloaca; (10) ventral tail with a bright orange stripe.

Description of the holotype. Body slender and small-sized, TOL 70.7 mm. Head oval in dorsal view; snout truncate, projecting slightly beyond mandible; nostril small, but conspicuous; labial fold well developed on posterior part of upper jaw; tongue elongate, enlarged anteriorly, with free lateral margin; vomerine tooth patch "^"-shaped; eye small, not extending beyond lateral margins of head; a conspicuous longitudinal ridge found posterior to each eye; parotoid gland inconspicuous, gill remnants absent; gular fold present.

Surface rough, dense tapered granules and tiny spines on dorsum, flanks, limbs and tail; dense granules and inconspicuous wrinkles on venter; interrupted vertebral ridge conspicuous and bulged; cloacal opening oval, slightly protruding.

Limbs slender, fingers and toes overlapping when fore-limb and hind-limb adpressed towards each other along body; four fingers and five toes, slender and elongated, lack webbing; relative length of fingers I < IV < II < III; relative length of toes I < V < II < IV < III. Tail laterally compressed, tapers posteriorly; caudal fin distinct; tail tip bluntly pointed.

Colouration of the holotype. In life, ground colour dark brown with black spots; vertebral ridge and upper margin of tail yellowish-brown; lateral tail with black spots; tips of digits light yellow; irregular bright orange stripe bordering dark patches on ventral trunk, bright orange blotches on chin, base of ventral limbs and anterior half of cloaca; ventral tail with a bright orange stripe.

In preservation, ground colour faded, greyish, black spots absent; vertebral ridge, upper margin of tail and digits dark grey; black spots on lateral tail indistinct; bright orange stripe on ventral trunk and tail, bright orange blotches on chin, ventral limbs and anterior half of cloaca slightly faded, dark patches more distinct.

Variations. Measurements of the type series are given in Table 2. All male specimens are similar in body proportions; however, the number, shape and position of ventral orange blotches vary amongst individuals.

Distribution and natural history. This species is known only from Tianchi Lake and surrounding streams of Mt Fenghuang at elevations of ca. 1300 m. This locality is situated on the east of the Hanjiang River in eastern Guangdong, while the populations of *H.* (*Ha.*) *orphicus* were all discovered from the west of the Hanjiang River (Fig. 1).

The adult individuals inhabit puddles and slow streams that are surrounded by bushes and weeds. Fei et al. (2006) reported that 26 adults were observed from Mt Fenghuang during a survey in July 2002. However, only nine adults were observed in September 2019. The type locality is being threatened by the developments of tourism and tea planting, which might cause negative effects on this species.

Remarks. The *Hypselotriton* populations from central Fujian were originally reported as *Cynops orientalis* (Hu

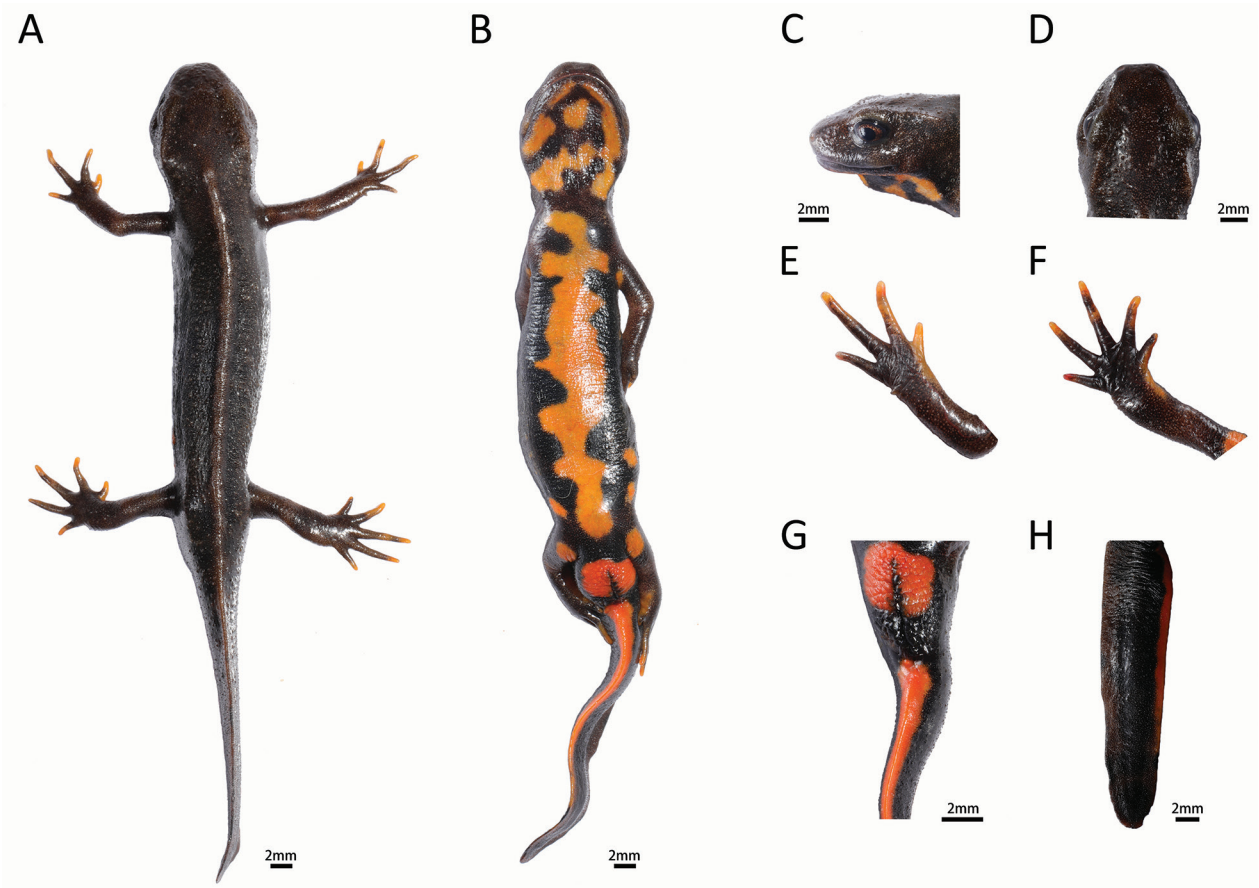

Figure 4. The holotype CIB 121430 of *Hypselotriton* (*Cynotriton*) *oolong* sp. nov. in life. **A.** Dorsal view; **B.** Ventral view; **C.** Lateral view of head; **D.** Dorsal view of head; **E.** Ventral view of hand; **F.** Ventral view of foot; **G.** Cloaca slit; **H.** Lateral view of tail.

et al. 1978; Risch 1983). Fei et al. (2006) re-identified the specimens from Mt Daiyun as *C. orphicus*, based on the ventral colouration that is similar to the paratypes of *C. orphicus* preserved in MNHN. However, our morphological examinations found that such colouration could not be a distinguished character between the two species, which led to the misidentification. The phylogenetic analysis revealed close relationships between the central Fujian populations and the new species, however, with distinct genetic divergences. Their distribution areas are also distantly isolated (Fig. 1). As there is a lack of detailed morphological data of the Fujian populations for accurate identification, we prudently label them as *Hypselotriton* sp. in this work provisionally.

Discussion

For the intrageneric classification in zoology, subgenus and species group are usually employed.

Several recent works have referred to the usage of these ranks in particular groups (e.g. Lyu et al. (2021, 2023b)). Subgenus is more official as it is regulated by the International Code of Zoological Nomenclature (the Code; available on https://www.iczn.org/the-code/the-codeonline/) in which a series of articles is formulated. For example, one of the requirements for the availability of a new subgenus is to provide a description or definition to differentiate the taxon (Article 13.1.1 of the Code). The species group is relatively flexible without clear rules, which was usually simply proposed for distinct phylogenetic clades and morphological definition is not mandatory (e.g. *Boulenophrys omeimontis* group in Lyu et al. (2023b)). In some cases, especially in the large genus containing numerous congeners, the subgenus and species group can be used simultaneously, while subgenus is always at the higher rank than species group indicating the subgenus possesses more distinct differences and divergences than the species group. Regardless, there are no strict standards on when to adopt subgenus or species group for classification and it usually depends on custom or subject tendencies. In the taxonomy of newt groups, subgenus is more welcome and widely used than species group. In a recent case for the intrageneric division of another newt genus *Tylototriton* Anderson, 1871, Lyu et al. (2021) suggested to partition the genus into three species groups while Raffaëlli (2022) replaced them with three subgenera that were previously nominated. Another newt genus *Echinotriton* Nussbaum & Brodie, 1982 has recently been partitioned into two subgenera(Dufresnes and Hernandez 2022).

The intrageneric classification of genus *Hypselotriton* is suggested for re-delimitation, as the result of a recent phylogenetic analysis (Lyu et al. 2023a). In this work, we

further perform the morphological comparison amongst the three distinct lineages of the genus, which sustains the phylogenetic insights. Since two clades have been previously nominated, we provided a new subgenus for the third clade as *Hakkatriton* subgen. nov. (Fig. 2). Geographically, the subgenus *Hypselotriton* is endemic in Yunnan-Guizhou Plateau in southwestern China that is distinctly isolated from the other two subgenera. *Cynotriton* is primarily distributed in eastern China. The basal lineage of *Cynotriton* including *H.* (*C.*) *orientalis* and *H.* (*C.*) *fudingensis* occurs in the relatively northern area, while the southern members *H.* (*C.*) *oolong* sp. nov. and *Hypselotriton* sp. from Fujian are revealed to be relatively terminal in phylogeny, suggesting the subgenus immigrated and separated from north to south. *Hakkatriton* subgen. nov. is primarily distributed in southern China. *Hypselotriton* (*Ha.*) *orphicus* and *H.* (*C.*) *oolong* sp. nov. both occur in neighbouring areas of eastern Guangdong and Hanjiang River might act as an isolation barrier between them (Fig. 1).

During the reviewing stage, an anonymous reviewer has raised an important issue which requires the skeletal data for the subgeneric comparisons. We appreciate this comment very much, even though we have different considerations. Indeed, we would like to include the skeletal data when we initially proposed the new subgenus. Nonetheless, when we reviewed the literature, the published skeletal data is very inadequate for comprehensive comparison. Based on the limited skeletal data, Fei et al. (2006) and Fei and Ye (2016) compared *Hypselotriton* (*Cynotriton*) *orientalis* (as *Cynops orientalis orientalis* and *Cynops orientalis qianshan* Fei, Ye & Jiang, 2012), *H.* (*Hy.*) *cyanurus* (as *Cynops cyanurus cyanurus*), *H.* (*Hy.*) *yunnanensis* (as *Cynops cyanurus chuxiongensis* Fei & Ye, 1983), *H.* (*Hy.*) *wolterstorffi* and *Cynops ensicauda* (Hallowell, 1861). Their results showed that *H.* (*Hy.*) *wolterstorffi* possesses relatively different skeletal characters while those amongst other species are very similar. Thus, we consider that, in this newt group, the skeletal characters are not suitable to be used for subgeneric diagnosis, as it might vary within a subgenus such as *H.* (*Hy.*) *wolterstorffi* vs. *H.* (*Hy.*) *yunnanensis*, while it may be with little differences amongst subgenera or genera, such as *H.* (*Hy.*) *cyanurus* vs. *H.* (*C.*) *orientalis* vs. *Cynops ensicauda*. Besides, when Dubois and Raffaëlli (2011) erected the subgenus *Cynotriton*, the skeletal data were also excluded. The recognition of this subgenus has been steadily supported by both genetic relationship and external morphology. Furthermore, as the developments of new biotechnology, more and more higher ranks of amphibian groups are erected without skeletal data, but are supported by multiple series of molecular and external morphological evidences, such as the anuran genera *Ghatixalus* Biju, Roelants & Bossuyt, 2008, *Sumaterana* Arifin, Smart, Hertwig, Smith, Iskandar & 2018, *Jingophrys* Lyu & Wang, 2023 and the newt genus *Laotriton* Dubois & Raffaëlli, 2009 and subgenera *Hightonia* Vieites, Nieto-Román, Wake & Wake, 2011 and *Sinotriton* Hernandez & Dufresnes, 2022. The recognition of these ranks is not seriously affected despite the absence of skeletal data.

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