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Taxonomic clarifications on the floating frogs (Anura: Dicroglossidae: *Occidozyga* sensu lato) in southeastern China

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Abstract

The recognition for the floating frogs' genus *Occidozyga* is in controversy for decades, and the species diversity of these frogs has recently been considered to be underestimated. In southeastern China, two floating frog species are currently recorded, namely *Occidozyga lima* and *Occidozyga martensii*. However, their current taxonomic statuses are unresolved after a series of recent taxonomic revisions. In this work, we perform morphological examinations and phylogenetic analyses on these two recorded floating frogs from southeastern China, to clarify their current taxonomic placements. The population previously recorded as *Occidozyga lima* should be re-assigned to the nomenclature *Occidozyga obscura* comb. nov., and the population previously recorded as *Occidozyga martensii* should be an undescribed species which is erected as *Occidozyga lingnanica* sp. nov. in this work.

Keywords

Diversity, Generic recognition, *Occidozyga lingnanica* sp. nov., *Occidozyga obscura* comb. nov., *Phrynoglossus*

Introduction

The floating frog subfamily Occidozyginae Fei, Ye & Huang, 1990 was originally established as a subfamily under the family Ranidae Batsch, 1796 (Fei et al. 1990), and was subsequently transferred to the family Dicroglossidae Anderson, 1871 (Frost et al. 2006). Currently, Occidozyginae is comprised of 19 recognized species distributed in northeastern India, Bangladesh, southern China, and mainland and islands of Southeast Asia (Frost 2022). These frogs usually inhabit wetlands such as paddy fields, natural or artificial ponds, ditches, and

even small temporary puddles, thus most of the species are also known as " floating frogs" or "puddle frogs". Due to their morphological similarities, the taxonomy of these frogs was in prolonged controversy, especially for the membership of its type genus *Occidozyga* Kuhl & Van Hasselt, 1822 (Stoliczka 1872; Boulenger 1882; Smith 1931; Dubois 1981, 1987; Inger 1996; Frost et al. 2006; Fei et al. 2010; Pyron & Wiens 2011; Dubois et al. 2021; Flury et al. 2021; Köhler et al. 2021; Trageser et al. 2021; Frost 2022; summarized in Table 1 in this study).

As the earliest introduced genus and also the type genus of Occidozyginae, *Occidozyga* was erected with its type species *Rana lima* (Kuhl & Van Hasselt 1822; Stejneger 1925). Subsequently, several genera were respectively proposed for some other floating frogs, such as *Houlema* Gray, 1831 (type species *H. obscura*), *Phrynoglossus* Peters, 1867 (type species *P. martensii*), *Microdiscopus* Peters, 1877 (type species *M. sumatranus*), *Oreobatrachus* Boulenger, 1896 (type species *Oreobatrachus baluensis*), *Osteosternum* Wu, 1929 (type species *Osteosternum amoyense* Wu, 1929), and *Frethia* Dubois, Ohler & Pyron, 2021 (type species *Oxyglossus laevis*). Nonetheless, the validations for all of these generic nomenclatures are in controversy (Table 1; Frost 2022). A recent work based on morphology, bioacoustics, molecules, and behaviors, has suggested *Occidozyga* is monotypic with *O. lima* and resurrected *Phrynoglossus* as a full genus for all other congeners (Köhler et al. 2021). Published on the same day, Dubois et al. (2021) resurrected genera *Phrynoglossus* and *Oreobatrachus*, and further proposed a new genus *Frethia*. Nevertheless, due to the inadequate sampling in these studies for settling the phylogeny for all of the floating frogs species, Frost (2022) considered to retain the sole genus *Occidozyga* sensu lato tentatively.

Despite the continuous controversy on the generic recognitions, taxonomic studies on species level of *Occidozyga* floating frogs are relatively stagnant, until recent years. Chan (2013) suggested the cryptic diversity within *O. lima* based on phylogeny but did not carry out corresponding taxonomic revision. *O. martensii* is revealed to be a species complex, and two populations from Myanmar and Bangladesh have been described as new species respectively (Köhler et al. 2021; Trageser et al. 2021). Matsui et al. (2021) described a new species *O. berbeza* which is suggested phylogenetically close to *O. martensii* and *O. lima*, while this species is confused with another congener *O. rhacoda* (Frost 2022). Several phylogenetic analyses also discovered a number of candidate species of floating frogs from Southeast Asia recently (Zug et al. 2018; Chan et al. 2020; Flury et al. 2021), but related taxonomic descriptions were not presented either.

In southeastern China where includes the subdivisions of Guangdong, Hong Kong, Macao, Fujian, and Hainan, two *Occidozyga* floating frog species are currently recorded, i.e. *O. lima* and *O. martensii* (Fei et al. 2009, 2012). Nevertheless, these records were majorly based on early morphological identifications. Their current taxonomic statuses are unresolved after the dramatic taxonomic changes mentioned above, especially for their phylogenetic relationships as samples from this region

Table 1. Different generic affiliations for the congeners of *Occidozyga* sensu lato in several important revisions, and the subclade assignment in this study. NA: species was not involved in the relative revision.

Species original nomen	Authorship	Frost et al. 2006	Köhler et al. 2021	Dubois et al. 2021	Subclade in this study	References for morphological characters
Rana lima	Gravenhorst, 1829	*Occidozyga*	*Occidozyga*	*Occidozyga*	I: *Occidozyga* sensu stricto	Gravenhorst 1829; Iskandar 1998; Iskandar et al. 2011; Köhler et al. 2021; Trageser et al. 2021
Houlema obscura	Gray, 1831	NA	NA	NA	I: *Occidozyga* sensu stricto	Gray 1831; Müller 1878; Stejneger 1925; Wu 1929; Pope 1931; Smith 1931; Liu & Hu 1961; Fei et al. 1990, 2009, 2010, 2012; this study
Rana rhacoda	Inger, Boeadi & Taufik, 1996	NA	NA	NA	II	Inger et al. 1996; Flury et al. 2021
Occidozyga berbeza	Matsui, Nishikawa, Eto, Hamidy, Hossman & Fukuyama, 2021	NA	NA	NA	II	Matsui et al. 2021; Trageser et al. 2021
Occidozyga shiwandashanensis	Chen, Peng, Liu, Huang, Liao & Mo, 2022	NA	NA	NA	III	This study
Oreobatrachus baluensis	Boulenger, 1896	*Occidozyga*	*Phrynoglossus*	*Oreobatrachus*	IV: *Oreobatrachus*	Boulenger 1896; Smith 1931; Inger 1966; Iskandar et al. 2011; Trageser et al. 2021
Micrixalus diminutiva	Taylor, 1922	*Occidozyga*	*Phrynoglossus*	*Frethia*	IV: *Oreobatrachus*	Taylor 1922; Inger 1954; Iskandar et al. 2011; Trageser et al. 2021
Microdiscopus sumatranus	Peters, 1877	*Occidozyga*	*Phrynoglossus*	*Phrynoglossus*	V: *Microdiscopus*	Peters 1877; Iskandar 1998; Iskandar et al. 2011; Eto & Matsui 2012 Matsui et al. 2021; Köhler et al. 2021; Trageser et al. 2021
Oxyglossus laevis	Günther, 1858	*Occidozyga*	*Phrynoglossus*	*Frethia*	VI: *Frethia*	Günther 1858; Inger 1954; Iskandar 1998; Iskandar et al. 2011; Trageser et al. 2021

Species original nomen	Authorship	Frost et al. 2006	Köhler et al. 2021	Dubois et al. 2021	Subclade in this study	References for morphological characters
Micrixalus magnapustulosus	Taylor & Elbel, 1958	*Occidozyga*	*Phrynoglossus*	*Phrynoglossus*	VIII: *Phrynoglossus*	Taylor & Elbel 1958; Iskandar et al. 2011; Köhler et al. 2021; Trageser et al. 2021
Phrynoglossus myanhessei	Köhler, Vargas, Than & Thammachoti, 2021	NA	*Phrynoglossus*	NA	VIII: *Phrynoglossus*	Köhler et al. 2021; Trageser et al. 2021
Phrynoglossus swanbornorum	Trageser, Al-Razi, Maria, Nobel, Asaduzzaman & Rahman, 2021	NA	NA	NA	VIII: *Phrynoglossus*	Trageser et al. 2021
Occidozyga lingnanica	Lyu & Wang sp. nov.	NA	NA	NA	VIII: *Phrynoglossus*	This study
Phrynoglossus martensii	Peters, 1867	*Occidozyga*	*Phrynoglossus*	*Phrynoglossus*	VIII: *Phrynoglossus*	Peters 1867; Taylor 1962; Inger 1966; Iskandar et al. 2011; Poyarkov 2020; Köhler et al. 2021; Trageser et al. 2021
Ooeidozyga celebensis	Smith, 1927	*Occidozyga*	*Phrynoglossus*	*Frethia*	NA	Smith 1927, 1931; Iskandar et al. 2011; Trageser et al. 2021
Oxydozyga floresiana	Mertens, 1927	*Occidozyga*	*Phrynoglossus*	*Frethia*	NA	Mertens 1927; Smith 1931; Iskandar et al. 2011; Trageser et al. 2021
Ooeidozyga semipalmata	Smith, 1927	*Occidozyga*	*Phrynoglossus*	*Frethia*	NA	Smith 1927, 1931; Inger 1954; Iskandar et al. 2011; Trageser et al. 2021
Occidozyga tompotika	Iskandar, Arifin & Rachmanasah, 2011	NA	*Phrynoglossus*	*Frethia*	NA	Iskandar et al. 2011; Trageser et al. 2021

were seldom included in such recent publications (Zug et al. 2018; Chan et al. 2020; Flury et al. 2021; Köhler et al. 2021; Trageser et al. 2021). In this work, we perform morphological examinations and phylogenetic analyses on these two recorded floating frogs from southeastern China, to clarify their current taxonomic placements.

Material and methods

Phylogenetic sampling and analyses

Thirty-two newly collected samples of *Occidozyga* floating frogs were used in this study, encompassing 9 samples previously recorded as *O. lima*, and 23 samples previously recorded as *O. martensii*. Additional three samples of species of Dicroglossinae are used as outgroups (Table 2). All samples were attained after euthanasia of specimens, and then preserved in 95% ethanol and stored at –40 °C. Genomic DNA was extracted from muscle tissue, using a DNA extraction kit from Tiangen Biotech (Beijing) Co., Ltd. Segments of mitochondrial genes for 16S ribosomal RNA (16S) and cytochrome C oxidase subunit I (CO1) were amplified using the primers and conditions employed by Lyu et al. (2019). PCR products were purified with spin columns and then sequenced with both forward and reverse primers using BigDye Terminator Cycle Sequencing Kit following the guidelines, on an ABI Prism 3730 automated DNA sequencer by Wuhan Tianyi Huiyuan Bioscience & Technology Inc.

For phylogenetic analyses, 108 additional sequences of floating frogs species were obtained from GenBank and incorporated into our dataset (Table 2). DNA sequences were aligned by the Clustal W algorithm with default parameters (Thompson et al. 1997). The final alignment includes 1,069 base pairs (bp) of 16S and 666 bp of CO1. PartitionFinder2 was used to test the best partitioning scheme and jModelTest v2.1.2 was used to test the best fitting nucleotide substitution models, resulting in the partition by gene and for CO1 further partitioned by codon position, and the best fit models for all partitions as GTR+I+G. Sequenced data were analyzed using Bayesian inference (BI) in MrBayes 3.2.4 (Ronquist et al. 2012), and maximum likelihood (ML) in RaxmlGUI 1.3 (Silvestro & Michalak 2012). Two independent runs were conducted in a BI analysis, each of which was performed for 100,000,000 generations and sampled every 1000 generations with the first 25% samples discarded as burn-in, resulting in a potential scale reduction factor (PSRF) of < 0.005. Convergence of the Markov Chain Monte Carlo simulations was assessed using Tracer v1.5 (Rambaut & Drummond 2009), verifying that all ESS values exceeded 200. In the ML analysis, the bootstrap consensus tree inferred from 1000 replicates was used to represent the evolutionary history of the taxa analyzed. Genetic distances based on 16S gene among samples were calculated in MEGA 6 using the uncorrected *p*-distance model.

Table 2. Localities, vouchers, and GenBank accession numbers for all samples used in this study.

ID	Species	Voucher	Locality	16s	CO1
1	*Occidozyga lima*	Alive individual	Indonesia: Java	AB530619	/
2	*O.* cf. *lima*	JBS 5405	Myanmar: Mandalay: Na Htoe Gyi	MG935923	MG935629
3	*O.* cf. *lima*	USNM 520376	Myanmar: Sagaing: Chatthin	MG935924	MG935630
4	*O.* cf. *lima*	SMF 103817	Myanmar: Naypyidaw: near Yamethin	MW217494	/
5	*O.* cf. *lima*	CAS 213254	Myanmar: Yangon: Hlaw Ga Park	DQ283224	/
6	*O.* cf. *lima*	SMF 103815	Myanmar: Yangon: near Taw Hlan village	MW217492	/
7	*O.* cf. *lima*	USNM 586924	Myanmar: Tanintharyi: Yeybu village	MG935925	MG935631
8	*O.* cf. *lima*	MNHN 0086Y	Thailand: Prachuap Khiri Khan: Huay Yang NP	KR827958	/
9	*O.* cf. *lima*	SMF GK7721	Thailand: Rayong: near Rayong	MW217498	/
10	*O.* cf. *lima*	MNHN 2003.0327	Cambodia: Pouthisat: Pneum Kravanh	KR827959	KR087831
11	*O.* cf. *lima*	MNHN T2814	Laos: Louangphrabang: Luang Prabang	KR827960	KR087832
12	*O. obscura* comb. nov.	SYS a008397	China: Guangdong: Mt Danxia	ON615073	ON615613
13	*O. obscura* comb. nov.	SYS a008118	China: Guangdong: Yingde	ON615066	ON615606
14	*O. obscura* comb. nov.	SYS a008119	China: Guangdong: Yingde	ON615067	ON615607
15	*O. obscura* comb. nov.	SYS a008120	China: Guangdong: Yingde	ON615068	ON615608
16	*O. obscura* comb. nov.	SYS a008121	China: Guangdong: Yingde	ON615069	ON615609
17	*O. obscura* comb. nov.	SYS a008122	China: Guangdong: Yingde	ON615070	ON615610
18	*O. obscura* comb. nov.	SYS a008123	China: Guangdong: Yingde	ON615071	ON615611
19	*O. obscura* comb. nov.	SYS a008124	China: Guangdong: Yingde	ON615072	ON615612
20	*O. obscura* comb. nov.	SYS a008195	China: Guangxi: Guiping	ON615074	ON615614
21	*O. lingnanica* sp. nov.	SYS a005585	China: Guangdong: Shenzhen	ON615075	ON615615
22	*O. lingnanica* sp. nov.	SYS a005586	China: Guangdong: Shenzhen	ON615076	ON615616
23	*O. lingnanica* sp. nov.	SYS a005587	China: Guangdong: Shenzhen	ON615077	ON615617
24	*O. lingnanica* sp. nov.	SYS a005588	China: Guangdong: Shenzhen	ON615078	ON615618
25	*O. lingnanica* sp. nov.	SYS a005589	China: Guangdong: Shenzhen	ON615079	ON615619
26	*O. lingnanica* sp. nov.	SYS a005590	China: Guangdong: Shenzhen	ON615080	ON615620
27	*O. lingnanica* sp. nov.	SYS a004650	China: Guangdong: Xinyi	ON615081	ON615621
28	*O. lingnanica* sp. nov.	SYS a007657	China: Guangdong: Xinyi	ON615082	ON615622
29	*O. lingnanica* sp. nov.	SYS a007658	China: Guangdong: Xinyi	ON615083	ON615623
30	*O. lingnanica* sp. nov.	SYS a005540	China: Guangdong: Zhanjiang	ON615084	ON615624
31	*O. lingnanica* sp. nov.	SYS a005541	China: Guangdong: Zhanjiang	ON615085	ON615625
32	*O. lingnanica* sp. nov.	SYS a007645	China: Guangdong: Zhuhai	ON615086	ON615626
33	*O. lingnanica* sp. nov.	SYS a007646	China: Guangdong: Zhuhai	ON615087	ON615627
34	*O. lingnanica* sp. nov.	SYS a005441	China: Hainan: Changjiang	ON615096	ON615636
35	*O. lingnanica* sp. nov.	SYS a005442	China: Hainan: Changjiang	ON615097	ON615637
36	*O. lingnanica* sp. nov.	SYS a005267	China: Hainan: Mt Diaoluo	ON615095	ON615635
37	*O. martensii* sensu stricto	Not given	Malaysia: Kuala Lumpur	AB488903	/
38	*O. martensii* sensu stricto	USNM 586941	Myanmar: Tanintharyi, Yeybu village	MG935929	MG935635
39	*O. martensii* sensu stricto	USNM 586942	Myanmar: Tanintharyi, Yeybu village	MG935941	MG935647
40	*O. martensii* sensu stricto	CUMZ PT2634	Thailand: Bangkok: Bangkok	MW217475	/
41	*O. martensii* sensu stricto	KUHE 19790	Thailand: Chachoengso	KP318725	/
42	*O. martensii* sensu stricto	SMF GK7349	Thailand: Chonburi: Ya Teng Homestay	MW217491	/
43	*O. martensii* sensu stricto	MNHN P324	Thailand: Phangnga: Sa Nang Manora	KR827986	KR087857
44	*O. martensii* sensu stricto	Alive idividual	Thailand: Ranong	AB530610	/
45	*O. martensii* sensu stricto	FMNH 266020	Thailand: Sa Kaeo	MW007312	/
46	*O. martensii* sensu stricto	CUMZ PT2754	Thailand: Songkhla: Wang Pha	MW217483	/
47	*O. martensii* sensu stricto	CUMZ PT2755	Thailand: Songkhla: Wang Pha	MW217482	/
48	*O. martensii* sensu stricto	FMNH 268335	Thailand: Surat Thani	MW007314	/
49	*O. martensii* sensu stricto	FMNH 268805	Thailand: Krabi	MW007315	/
50	*O. martensii* sensu stricto	SMF GK7713	Thailand: Trat: Ko Kut Resort	MW217505	/
51	*O. martensii* sensu stricto	SMF GK7695	Thailand: Trat: Trat	MW217504	/
52	*O. martensii* L1	SYS a002967	China: Yunnan: Jinghong	ON615088	ON615628
53	*O. martensii* L1	SYS a003935	China: Yunnan: Jinghong	ON615089	ON615629
54	*O. martensii* L1	SYS a003029	China: Yunnan: Mengla	ON615090	ON615630
55	*O. martensii* L1	SYS a008259	China: Yunnan: Mengla	ON615091	ON615631

ID	Species	Voucher	Locality	16s	CO1
56	*O. martensii* L1	SYS a008260	China: Yunnan: Mengla	ON615092	ON615632
57	*O. martensii* L1	SYS a007810	China: Yunnan: Menglian	ON615093	ON615633
58	*O. martensii* L1	SYS a007811	China: Yunnan: Menglian	ON615094	ON615634
59	*O. martensii* L1	SCUM H020	China	DQ458254	/
60	*O. martensii* L1	MNHN 2004.0357	Laos: Phongsali: Buon Tai	KR827983	KR087854
61	*O. martensii* L1	CUMZ PT0167	Thailand: Chaiyaphume: Ban Na Si Nuan	MW217484	/
62	*O. martensii* L1	CUMZ PT1543	Thailand: Chiang Mai: Huai Hong Khrai	MW217477	/
63	*O. martensii* L1	CUMZ PT1544	Thailand: Chiang Mai: Huai Hong Khrai	MW217476	/
64	*O. martensii* L1	MNHN 0119Y	Thailand: Phetchabun: Thung Salaeng Luang	KR827985	KR087856
65	*O. martensii* L1	MNHN 0026Y	Thailand: Uttaradit: Nam Pad district	KR827984	KR087855
66	*O. martensii* L2	JBS 19932	Myanmar: Yangon: Mingalardon	MG935921	MG935627
67	*O. martensii* L2	USNM 587386	Myanmar: Yangon: Mingalardon	MG935914	MG935620
68	*O. martensii* L2	USNM 587389	Myanmar: Yangon: Mingalardon	MG935919	MG935625
69	*O. swanbornorum*	JnUZool-A0719	Bangladesh: Chattogram	MN705433	/
70	*O. swanbornorum*	JnUZool-A0819	Bangladesh: Chattogram	MN705434	/
71	*O. swanbornorum*	JnUZool-A0919	Bangladesh: Chattogram	MN705435	/
72	*O. swanbornorum*	JnUZool-A1019	Bangladesh: Chattogram	MN705436	/
73	*O. swanbornorum*	JnUZool-A1117	Bangladesh: Chattogram	MN705437	/
74	*O. magnapustulosus*	MNHN 712D	Laos: Vientiane: Viangchan	KR827981	KR087852
75	*O. magnapustulosus*	FMNH 255134	Laos: Champasak: Mounlapamok	MW007295	/
76	*O. magnapustulosus*	NKMA 2196-15	Thailand: Kalasin	MW007297	/
77	*O. magnapustulosus*	SMF GK7855	Thailand: Nakhon Phanom: Ban Kan Luang	MW217490	/
78	*O. magnapustulosus*	SMF GK7396	Thailand: Roi Et: near Ban Sa At Na Di	MW217487	/
79	*O. magnapustulosus*	SMF GK7532	Thailand: Sakon Nakhon: Ban Phaeng Yai	MW217486	/
80	*O. magnapustulosus*	SMF GK7533	Thailand: Sakon Nakhon: Ban Phaeng Yai	MW217485	/
81	*O. magnapustulosus*	FMNH 261789	Cambodia: Koh Kong	MW007298	/
82	*O. myanhessei*	USNM 587105	Myanmar: Bago: Dawei	MG935916	MG935622
83	*O. myanhessei*	USNM 587107	Myanmar: Bago: Dawei	MG935920	MG935626
84	*O. myanhessei*	SMF 103800	Myanmar: Magwe: near Taungdwingyi	MW217503	/
85	*O. myanhessei*	SMF 103840	Myanmar: Yangon: East Yangon University	MW217499	/
86	*O. myanhessei*	SMF 103841	Myanmar: Yangon: East Yangon University	MW217500	/
87	*O. myanhessei*	USNM 587402	Myanmar: Yangon: Mingalardon	MG935917	MG935623
88	*O. shiwandashanensis*	NNU 202103284	China: Guangxi: Mt Shiwandashan	MZ747455	/
89	*O. shiwandashanensis*	NNU 202103285	China: Guangxi: Mt Shiwandashan	MZ747456	/
90	*O. shiwandashanensis*	NNU 202103320	China: Guangxi: Mt Shiwandashan	MZ747457	/
91	*O. shiwandashanensis*	NNU 202103321	China: Guangxi: Mt Shiwandashan	MZ747458	/
92	*O. berbeza*	KUHE 17327	Malaysia: Sarawak: Matang	LC593607	/
93	*O. berbeza*	KUHE 17327	Malaysia: Sarawak: Matang	LC593609	/
94	*O. berbeza*	KUHE 17327	Malaysia: Sarawak: Matang	LC593610	/
95	*O. rhacoda* complex	NMBE 1064176	Malaysia: Sarawak: Kubah NP	MW007293	/
96	*O. rhacoda* complex	NMBE 1065363	Malaysia: Sarawak: Gunung Penrissen	MW007173	/
97	*O. rhacoda* complex	NMBE 1061694	Malaysia: Sarawak: Gunung Murud	MW007275	/
98	*O. rhacoda* complex	NMBE 1066057	Malaysia: Sarawak: Payeh Maga	MW007281	/
99	*O. rhacoda* complex	NMBE 1069835	Malaysia: Sarawak: Usun Apau	MW007274	/
100	*O. rhacoda* complex	NMBE 1074010	Malaysia: Sarawak: Batang Ai	MW007290	/
101	*O. laevis* complex	NMBE 1072307	Malaysia: Sabah: Danum Valley Conservation Area	MW007227	/
102	*O. laevis* complex	FMNH 234895	Malaysia: Sabah: Sipitang	MW007219	/
103	*O. laevis* complex	NMBE1072456	Malaysia: Sabah: Tawau Hills NP	MW007254	/
104	*O. laevis* complex	NMBE 1056418	Malaysia: Sarawak: Gunung Mulu NP	MW007217	/
105	*O. laevis* complex	KU 310493	Philippinen: Eastern Samar: Taft	MW007237	/
106	*O. laevis* complex	FMNH 259486	Philippinen: Kalinga: Balbalasang	MW007236	/
107	*O. laevis* complex	KU 306652	Philippinen: Negros Oriental: Valencia	MW007235	/
108	*O. laevis* complex	PNM 7446	Philippinen: Quezon: Lao	AY313684	/
109	*O. laevis* complex	KU 302276	Philippinen: Romblon: Magdiwang	MW007234	/
110	*O. laevis* complex	EMD 424	Philippines: Agusan Del Norte	MT820178	/
111	*O. laevis* complex	PNM ACD2011	Philippines: Isabela	MT820166	/
112	*O. laevis* complex	KU 302322	Philippines: Oriental Mindoro	MT820171	/

ID	Species	Voucher	Locality	16s	CO1
113	*O. laevis* complex	KU 308966	Philippines: Palawan: Irawan	MW007231	/
114	*O. laevis* complex	PNM ACD5414	Philippines: South Cotobato	MT820170	/
115	*O. laevis* complex	KU 306301	Philippines: Western Samar	MT820173	/
116	*O. laevis* complex	KU 314471	Philippines: Zamboanga: Pasonanca	MT820168	/
117	*Occidozyga* sp.	USNM 586929	Myanmar: Tanintharyi: Yeybu village	MG935915	MG935621
118	*Occidozyga* sp.	USNM 586928	Myanmar: Tanintharyi: Yeybu village	MG935922	MG935628
119	*O. sumatrana* complex	MZB Amph 16392	Indonesia: Java	LC593611	/
120	*O. sumatrana* complex	MZB RMB2134	Indonesia: Java	MT820186	/
121	*O. sumatrana* complex	Not given	Indonesia: Sumatra: Bukit Barisan Selatan NP	MW007270	/
122	*O. sumatrana* complex	Not given	Indonesia: Sumatra: Hutan Harapan	MW007273	/
123	*O. sumatrana* complex	Not given	Indonesia: Sumatra: Hutan Harapan	MW007269	/
124	*O. sumatrana* complex	FRIM 1136	Malaysia: Pahang: Bukit Rengit	MT820183	/
125	*O. sumatrana* complex	FMNH 267890	Malaysia: Sarawak: Bintulu	MW007260	/
126	*O. sumatrana* complex	FMNH 269753	Malaysia: Sarawak: Binyo-Penyilam	MW007268	/
127	*O. sumatrana* complex	FRIM 1132	Malaysia: Selangor: Kepong	MT820181	/
128	*O. baluensis* complex	NMBE 1072541	Malaysia: Sabah: Danum Valley Conservation Area	MW007193	/
129	*O. baluensis* complex	FMNH 235605	Malaysia: Sabah: Kota Marudu	MW007178	/
130	*O. baluensis* complex	FMNH 242747	Malaysia: Sabah: Sipitang	DQ283143	/
131	*O. baluensis* complex	FMNH273695	Malaysia: Sarawak: Bintulu	MW007215	/
132	*O. baluensis* complex	NMBE 1064771	Malaysia: Sarawak: Gunung Mulu NP	MW007177	/
133	*O. baluensis* complex	NMBE 1073926	Malaysia: Sarawak: Payeh Maga	MW007211	/
134	*O. baluensis* complex	Not given	Malaysia: Sarawak: Pelagus NP	MW007175	/
135	*O. baluensis* complex	Not given	Malaysia: Sarawak: Pelagus NP	MW007216	/
136	*O. diminutiva*	KU 321225	Philippines: Mindanao: Zamboanga: Pasonanca	MT820199	/
137	*O. diminutiva*	KU 321226	Philippines: Mindanao: Zamboanga: Pasonanca	MT820200	/
138	*O. diminutiva*	KU 321227	Philippines: Mindanao: Zamboanga: Pasonanca	MT820201	/
139	*Ingerana tenasserimensis*	USNM 587302	Myanmar: Mon: Kyaikhtiyo Wildlife Sanctuary	MG935840	MG935546
140	*Ingerana tenasserimensis*	USNM 586921	Myanmar: Tanintharyi: Yeybu village	MG935837	MG935543
141	*Hoplobatrachus rugulosus*	SYS a006157	China: Guangdong: Mt Danxia	ON615100	ON615640
142	*Nanorana parkeri*	SYS a006617	China: Tibet: Jiacha	ON615099	ON615639
143	*Quasipaa shini*	SYS a006594	China: Guangxi: Mt Dayao	ON615098	ON615638

Specimens and morphological examination

Thirty-one newly collected samples of *Occidozyga* floating frogs were used in this study, encompassing 10 specimens previously recorded as *O. lima*, and 21 samples previously recorded as *O. martensii*. Detailed collection data for these specimens are given in the Taxonomic accounts. Abbreviations for museums are **SYS** (the Museum of Biology, Sun Yat-sen University, Guangzhou, China), **CIB** (Herpetological Museum, Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu, China), and **BMNH** (British Museum Natural History, now Natural History Museum, London, UK).

External measurements were made on the examined specimens, using digital calipers (Neiko 01407A Stainless Steel 6-Inch Digital Caliper) to the nearest 0.1 mm, including snout–vent length (SVL) from the tip of snout to posterior margin of the vent, head length (HDL) from the tip of snout to the articulation of the jaw, head width (HDW) at the commissure of the jaws, snout length (SNT) from the tip of snout to the anterior corner of the eye, internasal distance (IND), the shortest interorbital distance between the upper eyelids (IOD), eye diameter (ED) from the anterior corner of the eye to posterior corner of the eye, hand length (HND) from the proximal border of the outer palmar tubercle to the tip of digit III, radioulna length (RAD) from the flexed elbow to the proximal border of the outer palmar tubercle, foot length (FTL) from the distal end of the shank to the tip of digit IV, and tibial length (TIB) from the outer surface of the flexed knee to the heel.

Results

The BI and ML analyses resulted in identical topologies (Fig. 1). The *p*-distances based on the 16S gene among all samples used in this study are presented in Supplementary Table S1.

As illustrated in the phylogenetics, all samples of genus *Occidozyga* sensu lato gather together in a clade with Bayesian posterior probabilities (BPP) = 1.00 and ML bootstrap supports (BS) = 100, forming the sister taxon to the other genus *Ingerana* Dubois, 1987 within the subfamily. The clade of *Occidozyga* sensu lato can be further divided into eight subclades, however, the phylogenetic relationships among these eight subclades remain unresolved due to the weak supports.

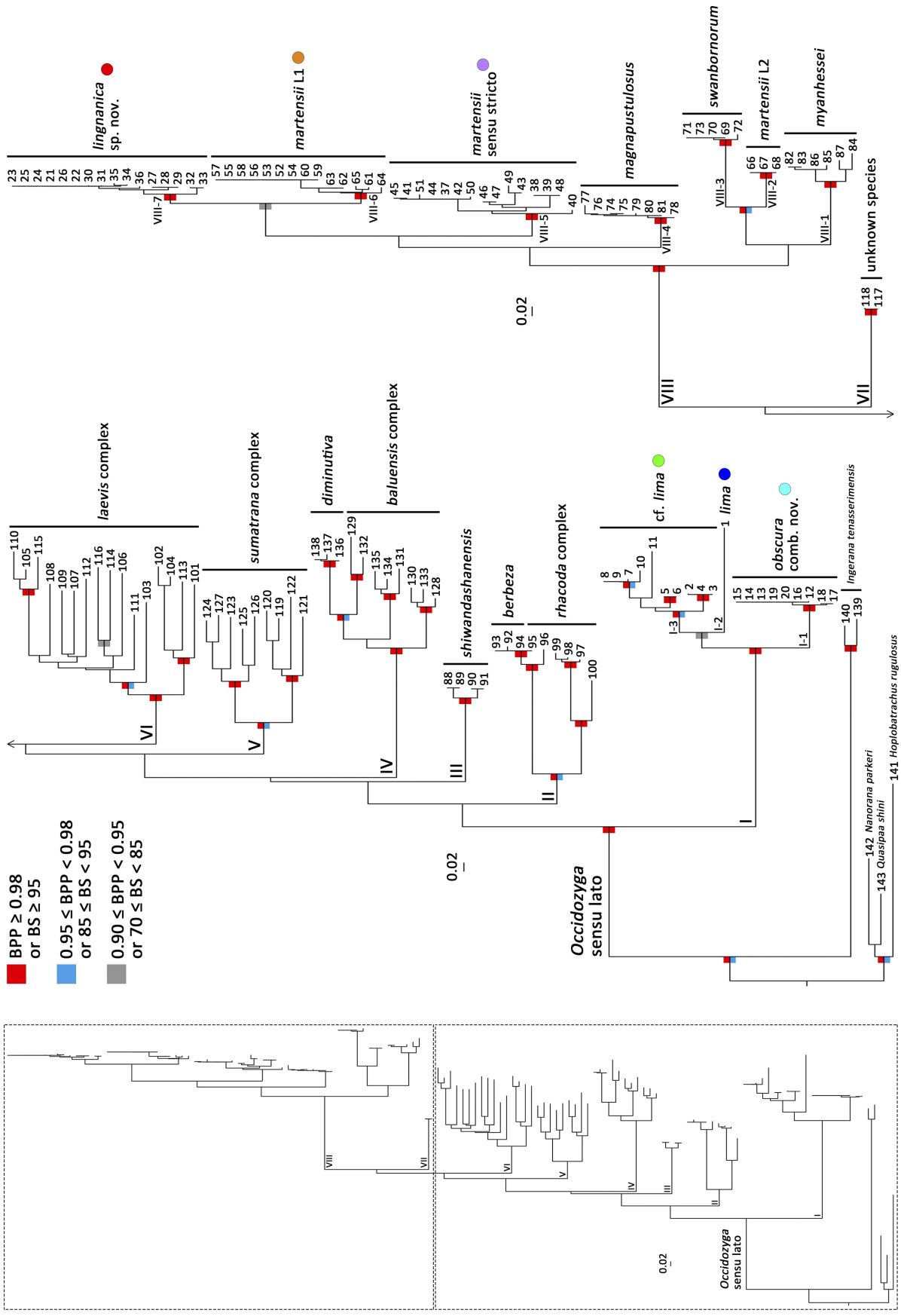

Figure 1. Phylogenetic trees of the genus *Occidozyga* sensu lato based on mitochondrial genes 16S and CO1. Bayesian posterior probabilities (BPP) and bootstrap supports (BS) are labeled above and below the nodes respectively. Numbers at the terminal of the lineages correspond to the IDs in Table 1.

All samples previously recorded as *O. lima* formed the subclade I, which represents the concept of "*Occidozyga* sensu stricto" (BPP=1.00, BS=100). This subclade was composed of three lineages. The single sample from the type locality of *O. lima* in Java, Indonesia (ID 1 in Figs. 1, 2) formed an independent lineage I-2. The samples from Indochina Peninsula (ID 2–11) formed a complicated lineage I-3 (BPP=1.00, BS=86) with distinct inner diver-

gences (*p*-distance 0.0–4.4% in 16S), which was provisionally designated as *O.* cf. *lima* here. The samples from southeastern China (ID 12–20) formed the remaining lineage I-1 (BPP=1.00, BS=100) without divergence (*p*-distance 0), which was the basal lineage of the subclade I and distinctly separated from the other two lineages. The relationships among these lineages remain unresolved due to the weak supports.

All samples previously recorded as *O. martensii* were seated in the subclade VIII (BPP=1.00, BS=100) which represents the concept of "*Phrynoglossus*". This subclade was composed of seven lineages. Three lineages VIII-1, VIII-3, and VIII-4 were corresponding to three recognized species *O. myanhessei* comb. nov. (BPP=1.00, BS=98), *O. swanbornorum* comb. nov. (BPP=1.00, BS=100), and *O. magnapustulosa* (Taylor & Elbel, 1958) (BPP=1.00, BS=99), respectively. Samples in the remaining four lineages were all previously recorded as *O. martensii* (actually *O. myanhessei* comb. nov. and *O. swanbornorum* comb. nov. were also recorded as *O. martensii* for decades and just recognized recently), however, they were paraphyletic. The sample from the type locality of *O. martensii* in Bangkok, Thailand (ID 40 in Figs. 1, 2) was clustered with the samples from southern and peninsular Thailand, peninsular Myanmar, and peninsular Malaysia (ID 37–51), which represented the lineage VIII-5 of the *O. martensii* sensu stricto (BPP=1.00, BS=99). Samples from Yangon, Myanmar (ID 66–68) formed an independent lineage VIII-2 (BPP=1.00, BS=100), and were provisionally designated as *O. martensii* L2 here. The lineage VIII-6 (BPP=1.00, BS=87) contained samples from Yunnan, southwestern China (ID 52–59) and northern Indochina Peninsula (ID 60–65), which was provisionally designated as *O. martensii* L1. Samples from southeastern China (ID 21–36) formed the last lineage VIII-7 (BPP=1.00, BS=100). The relationships among these lineages remain unresolved either, due to the weak supports.

The inner relationships for the other subclades of *Occidozyga* sensu lato were also complicated. Subclade II (BPP=1.00, BS=90) included samples of *O. berbeza* (ID 92–94) and *O. rhacoda* (ID 95–100), while the samples identified as *O. rhacoda* were paraphyletic and separated into three distinct lineages. Furthermore, a sample of *O. rhacoda* (ID 95) was indeed conspecific with samples of *O. berbeza*. The most recently described species *O. shiwandashanensis* (ID 88–91) formed a monotypic subclade III (BPP=1.00, BS=100). Subclade IV (BPP=1.00, BS=100) included samples of *O. baluensis* (ID 128–135) and *O. diminutiva* (ID 136–138), while the samples identified as *O. baluensis* were paraphyletic and separated into three distinct lineages too, indicating that this species should be a species complex. Samples identified as *O. sumatrana* (ID 119–127) and *O. laevis* (ID 101–116) formed the subclade V (BPP=0.99, BS=89) and subclade VI (BPP=1.00, BS=100) respectively, however, distinct deep divergences were presented in these two subclades. The remaining subclade VII (BPP=1.00, BS=100) was consist of two unknown samples from peninsular Myanmar.

Discussion

Generic recognition for *Occidozyga* sensu lato

In this work, it is the first time to integrate the molecular data of floating frogs published in recent years (e.g. Chan et al. 2020; Flury et al. 2021; Köhler et al. 2021; Matsui et al. 2021) to reconstruct the phylogeny of *Occidozyga* sensu lato. As indicated by the phylogenetic result, the genus *Occidozyga* sensu lato can be divided into eight subclades, while the relationships among these eight subclades were not clearly revealed. It seems that these subclades are partly corresponding to the different generic nomenclatures proposed in the taxonomic history, i.e., subclade I for "*Occidozyga* sensu stricto" (type species *R. lima*), subclade IV for "*Oreobatrachus*" (type species *Oreobatrachus baluensis*), subclade V for "*Microdiscopus*" (type species *M. sumatranus*), subclade VI for "*Frethia*" (type species *Oxyglossus laevis*), and subclade VIII for "*Phrynoglossus*" (type species *P. martensii*). However, because of the inadequate species sampling (four congeners *O. celebensis*, *O. floresiana*, *O. semipalmata*, and *O. tompotika* were not included) and the inadequate genetic segments employed (most of the samples lack comparable nuDNA segments which are unable to perform the phylogeny of nuDNA), we consider to cautiously retaining all these species within a sole genus *Occidozyga* sensu lato. Thus, two new combinations of nomenclatures appeared due to this suggestion, namely *O. myanhessei* comb. nov. and *O. swanbornorum* comb. nov. as they were originally described under the generic name *Phrynoglossus* (Köhler et al. 2021; Trageser et al. 2021).

Particularly, since there are distinct morphological differences among some of these subclades (especially between the "*Phrynoglossus*" and "*Occidozyga* sensu stricto" subclades), we speculate that *Occidozyga* sensu lato would be partitioned into multiple genera after comprehensive phylogenetic analyses and detailed morphological re-examination in the future.

Species diversity of floating frogs

The species diversity of floating frogs is dramatically underestimated as indicated in our analysis. Deep divergences are presented among the samples currently identified as *O. rhacoda*, and similar situations are also revealed in those of *O. baluensis*, *O. sumatrana*, and *O. laevis*. Therefore, these four species are all tentatively designated as species complex in this work, and further clarifications with morphological study are required. Particularly, the relationship between *O. rhacoda* and *O. berbeza* are still unclear, and the data from the topotype of *O. rhacoda* are required to settle this puzzle.

Within subclade I ("*Occidozyga* sensu stricto" subclade), similar to the result by Chan (2013), *O. lima* is revealed to include three lineages for the populations from

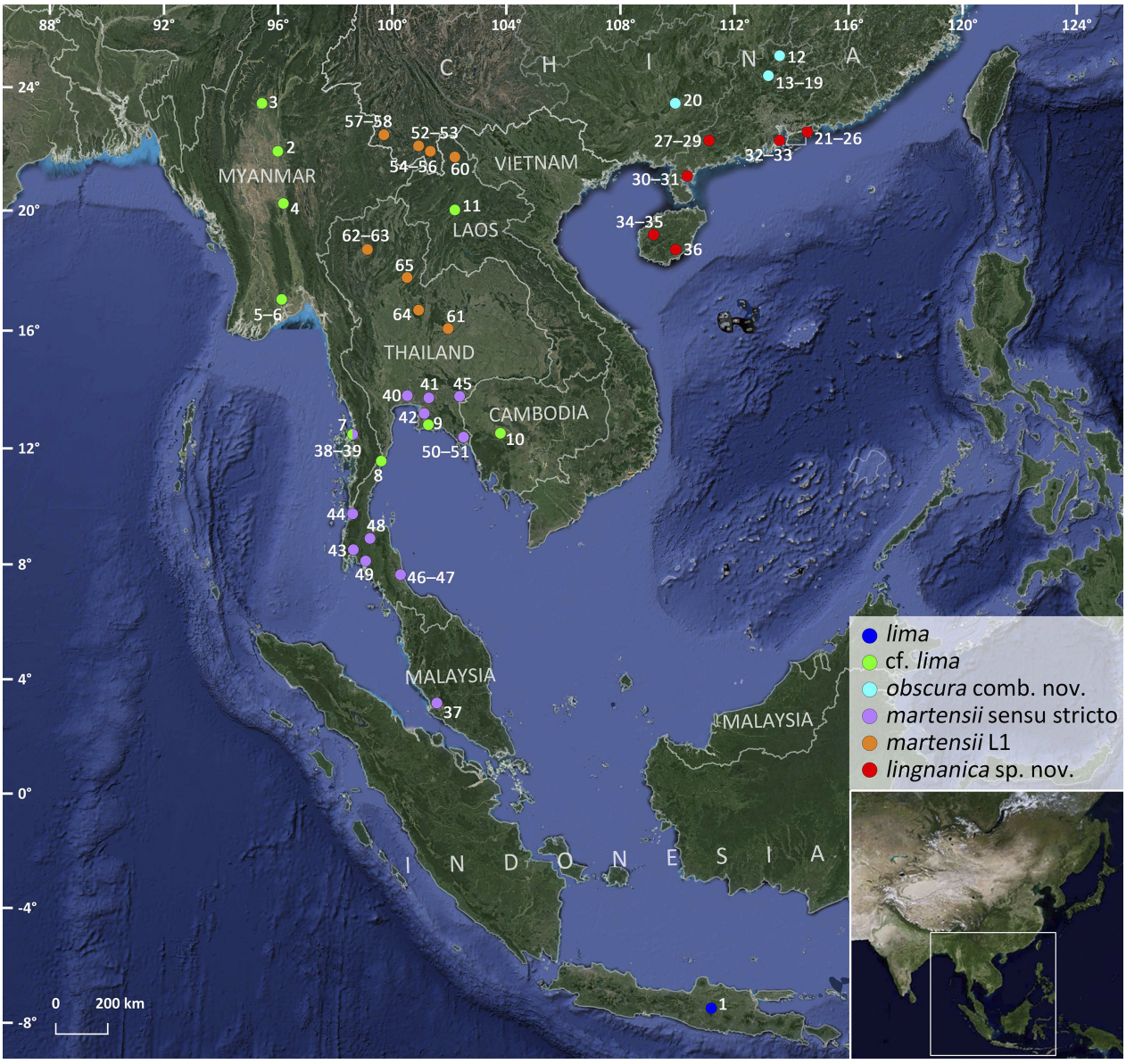

Figure 2. Map showing the floating frogs *Occidozyga obscura* comb. nov., *Occidozyga lingnanica* sp. nov., and their closest congeners. Numbers correspond to the IDs in Table 1.

type locality Java, Indonesia (ID 1), Indochina Peninsula (ID 2–11), and southeastern China (ID 12–20). The relationships among these three lineages are unresolved due to the weak support values. Morphological examination on the specimens from lineage I-1 substantiates their differences from the populations in Indonesia and Indochina (see below in Taxonomic accounts). Therefore, we resurrect the former nomenclature *Houlema obscura* to accommodate the lineage of the southeastern China population as *Occidozyga obscura* comb. nov., with providing a re-description for this species based on the newly collected fresh specimens. The lineage I-3 for the Indochina Peninsula population is tentatively designated as *O.* cf. *lima* due to the unstable supported values (BS=86) and complicated inner relationship, calling for detailed morphological examinations on the related specimens.

Within subclade VIII ("*Phrynoglossus*" subclade), the samples previously recorded as *O. martensii* are paraphyletic into four different lineages, among which the relationships are also unresolved, due to the weak support values. The lineage VIII-5 of *O. martensii* sensu stricto involves populations throughout southern and peninsular Thailand, peninsular Myanmar, and peninsular Malaysia (ID 37–51). The lineage VIII-7 for the population from Guangdong and Hainan, southeastern China (ID 21–36) is considered to be an undescribed species of the genus *Occidozyga*, based on the phylogenetic results and the morphological differences (see below in Taxonomic accounts). Because of the unstable supported values (BS=87) and inadequate specimens, the taxonomic status for the lineage VIII-6 of *O. martensii* L1 is not defined in this work. This lineage might be close to the nomen *Oxyglossus laevis* var. *vittata* Andersson, 1942 and further study is in preparation. The lineage VIII-2 of *O. martensii* L2 seems to represent another cryptic species, calling for detailed morphological examinations on the related specimens.

Taxonomic accounts

Occidozyga obscura (Gray, 1831) comb. nov.

Houlema obscura Gray 1831
Oxyglossa lima var. *chinens* Müller 1878
Oxydozyga lima — Stejneger 1925
Osteosternum amoyense Wu 1929
Ooeidozyga lima — Pope 1931; Smith 1931; Liu & Hu 1961
Occidozyga lima — Dubois 1981; Fei et al. 1990, 2009, 2010, 2012; Zhao & Adler 1993; Li et al. 2011; Mo et al. 2014.

Type materials. Holotype. BMNH 1932.5.1.2, adult female, collected from China (discussion for the exact locality see Remarks below).

Specimens examined. Seven adult males and three adult females. Males CIB 44475–44476, from Guangzhou, Guangdong Province, China; male SYS a000534, from Mt Danxia (25.0347 N, 113.7407 E), Renhua County, Guangdong; males SYS a008120–8121, 8123, 8125, and females SYS a008122, 8124, from Shimentai Nature Reserve (24.3818 N, 113.3927 E), Yingde City, Guangdong; female SYS a000488, from Mt Luoyang, Lingshan County, Guangxi Zhuang Autonomous Region, China.

Etymology. The specific name *obscura* means 'obscure' in Latin.

Common name. "Chinese floating frog" in English / "中国浮蛙 (zhōng guó fú wā)" in Chinese.

Diagnosis. (1) Body stocky, size small, SVL 24.2–27.5 mm in adult males (n=7) and 31.5–32.2 mm in adult females (n=3); (2) snout short triangular shaped; (3) nostrils located dorsally; (4) eye orientation vertically; (5) loreal region oblique, not concave or convex; (6) interorbital space narrower than internarial distance; (7) tongue narrow and slender, unnotched, pointed distally, lingual papilla absent; (8) vomerine ridge and vomerine teeth absent; (9) supratympanic fold distinct, raised, and granulated, curved on the temporal region; (10) tympanum hidden, edge invisible; (11) fingers with rudimentary webs, toes with full webs; (12) heels not meeting, tibio-tarsal articulation reaching between the posterior and anterior of the eye.

Comparisons. *Occidozyga obscura* comb. nov. was previously synonymized with *O. lima*. These two species are most similar to each other. However, *Occidozyga obscura* comb. nov. can be distinguished by the combination of the following characteristics: loreal region oblique, not concave or convex (vs. slightly concave in *O. lima*), interorbital space narrower than internarial distance (vs. subequal), supratympanic fold distinct, raised, and granulated (vs. indistinct), inner metatarsal tubercle large and raised (vs. weakly projecting), and tibio-tarsal articulation reaching between the posterior and anterior of the eye (vs. reaching tip of nostril).

Occidozyga obscura comb. nov. furthers differs from *O. berbeza* by the supratympanic fold curved on the temporal region (vs. straight), fingers with rudimentary webs (vs. unwebbed), and outer metatarsal tubercle present (vs. absent). *O. obscura* comb. nov. distinctly differs from *O. rhacoda* by the dorsolateral fold absent (vs. present), and fingers with rudimentary webs (vs. unwebbed).

Occidozyga obscura comb. nov. can be easily distinguished from the remaining 13 congeners *O. baluensis*, *O. celebensis*, *O. diminutiva*, *O. floresiana*, *O. laevis*, *O. magnapustulosa*, *O. martensii*, *O. myanhessei* comb. nov., *O. semipalmata*, *O. sumatrana*, *O. shiwandashanensis*, *O. swanbornorum* comb. nov., and *O. tompotika*, by the tongue narrow and slender (vs. wide and swollen in all of these 13 species).

Re-description. Based on the examined specimens (n=10). All specimens were similar in morphology. The measurements are given in Table 3.

Body stocky, small-sized, SVL 24.2–27.5 mm (n=7) in males and 31.5–32.2 mm (n=3) in females. Head flat above, almost as wide as long (HDW/HDL 0.97–1.09, n=10); pineal ocellus absent; snout short triangular shaped, distinctly protruding beyond lower jaw, tip of snout rounded in dorsal view and profile; canthus rostralis absent, loreal region oblique, not concave or convex; nostril rounded, located dorsally, distinctly raised, closer to the tip of snout than to the eye; eye orientation vertically, pupil diamond shaped; interorbital space narrower than internarial distance; tympanum hidden, edge invisible; vomerine ridge and teeth absent; tongue narrow and slender, unnotched, pointed distally, lingual papilla absent.

Forelimbs short, lower arm 13–18% (n=10) of SVL and hand 26–32% (n=10) of SVL; fingers distinctly thin and long, relative finger lengths I<II<IV<III; tips of fingers pointed, not dilated, and without disks; distinct lateral fringes on inner and outer sides of each finger, fingers with rudimentary webs, more distinct between fingers I and II; subarticular tubercles present at the bases of each finger, prominent and rounded; supernumerary tubercles absent; inner and outer palmar tubercles prominent and rounded.

Hind limbs robust, tibia 41–47% (n=8) of SVL and foot 66–80% (n=8) of SVL; heels not meeting when hind limbs flexed at right angles to the axis of the body; tibio-tarsal articulation reaching between the posterior and anterior of the eye when hind limb is stretched along the side of the body; toes distinctly long and thin, relative lengths I<II<III<V<IV; tips of toes pointed, dilated into pear-shaped disks; toes with full webs, metatarsal web present, distinct lateral fringes on lateral edges of toes I and V; subarticular tubercles rounded, prominent; inner metatarsal tubercle large and long-elliptic, slightly raised, length twice the width; outer metatarsal tubercle relatively smaller than the inner metatarsal tubercle, distinctly raised and pointed, length slightly larger than width; inner tarsal fold relatively flat, in contact with the inner metatarsal tubercle; tarsal tubercle large and distinctly raised, close to the tibio-tarsal articulation.

Table 3. Measurements (in mm) of the examined specimens of *Occidozyga obscura* comb. nov.

Specimen	CIB 44475	CIB 44476	SYS a000534	SYS a008120	SYS a008121	SYS a008123	SYS a008125	SYS a008122	SYS a008124	SYS a000488
Sex	Male	Male	Male	Male	Male	Male	Male	Female	Female	Female
SVL	24.2	24.7	27.5	24.3	26.2	27.0	24.8	32.2	32.0	31.5
HDL	9.1	9.4	8.9	8.8	9.4	9.4	8.8	10.4	10.4	10.1
HDW	8.8	9.6	9.7	8.6	9.4	9.3	8.6	11.0	11.4	10.0
SNT	2.7	3.1	3.3	2.8	3.3	3.1	3.2	4.2	4.0	3.7
IND	1.5	1.3	1.6	1.4	1.4	1.5	1.2	1.6	1.5	1.6
IOD	1.5	1.2	1.5	1.3	1.4	1.4	1.1	1.5	1.4	1.4
ED	3.2	2.8	2.7	2.7	2.8	2.9	2.6	3.1	3.0	3.2
HND	7.7	7.5	7.8	7.1	7.3	7.4	6.6	8.2	8.8	8.5
RAD	4.0	4.5	3.6	4.1	4.4	4.0	3.9	4.9	5.1	4.9
FTL	19.3	18.4	18.4	18.0	18.8	18.8	17.5	21.3	21.5	21.6
TIB	11.3	11.4	11.2	11.1	11.7	11.5	10.9	13.4	13.6	12.8

Dorsal surface relatively rough, transverse wrinkles and dense tubercles on the dorsum, head, flanks, and limbs; small granules on the dorsal rears of hands and tarsi; not bearing spinules on the dorsal skin; supratympanic fold distinct, raised and granulated, extending from the posterior corner of the eye, curved on the temporal region, to the previous shoulder; dorsolateral fold absent. Ventral surface with large flattened tubercles, denser on the throat and thighs; dense granules on the ventral feet and tarsi.

Coloration. In life (Fig. 3), dorsal surfaces vary from olive brown to dark brown; dorsum and flanks interspersed with irregular black speckles; mid-dorsal stripe grass-green with distinct border; lateral line system grayish brown to yellowish brown. Pupil bordered with yellow, iris beige to brown. Supratympanic fold olive-brown to dark brown. Skin of throat, chest, and belly uniform creamy white; gular with a pair of distinct or indistinct longitudinal dark stripes; skin of limbs dark gray, tubercles on ventral thighs and tibias creamy white.

In preservative (Fig. 4A, B), dorsum light gray; black speckles on dorsal surface light brown; mid-dorsal stripe fainted and the border indistinct; ventral skin grayish white; tubercles on ventral surface more distinct.

Male secondary sexual characteristics. Male with a single subgular vocal sac; in breeding season, a single, light grey nuptial pad on the dorsal surface of finger I, nuptial spinules invisible. Males (SVL 24.2–27.5 mm) distinctly smaller than females (SVL 31.5–32.2 mm) (Fig. 4A, B).

Ecology. This frog inhabits natural or artificial ponds and paddy fields in plain areas. They quickly dive underwater after being disturbed during the daytime, while become relatively insensitive at night. Males call in the water surface or waterside grass from dusk to dawn, more active during the rain. The breeding season is from April to August (this study; Fei et al. 2009).

Distribution. *Occidozyga obscura* comb. nov. can be recognized from several localities of Guangdong and Guangxi, southeastern China (Figs. 1, 2), based on the analyzed vouchers in this work. The previous records of *O. lima* from Guangdong, Guangxi, Hong Kong, Macao, and Fujian, southeastern China are reassigned to *O. obscura* currently (see Remarks below). The records of *O. lima* from Yunnan require further clarifications with molecular and morphological vouchers (which might be close to the lineage of *O.* cf. *lima* based on the biogeographical similarity).

Conservation status. This species was previously reported as common and widespread species in southeastern China under the nomen *O. lima*, but its population quantity is found rapidly declining due to the influence of human activities such as pesticide abuse and urban construction. The populations in Hong Kong, Macao, Shenzhen, Guangzhou, and Xiamen might disappear, as no more reports and vouchers in nearly 20 years (this study; Chan 2013). We recommend *Occidozyga obscura* comb. nov. to be listed as Endangered (EN) [IUCN Red List criteria A2cd].

Remarks. The type specimen of *Occidozyga obscura* comb. nov. was collected by John Reeves (1774–1856) but the exact type locality was not given in the original description (Gray 1831). Zhao & Adler (1993) speculated that the type specimens may be from somewhere in southeastern China, especially Macao or Canton (= Guangzhou) in Pearl River Delta, where John Reeves lived and worked in.

Moreover, there were two historic species currently regarded as synonymies of *O. lima*, namely *Oxyglossa lima* var. *chinens* and *Osteosternum amoyense* (Stejneger 1925; Smith 1931; Pope 1931). The type locality for *Oxyglossa lima* var. *chinens* is Lilong, Canton (= Lilang, Shenzhen, Guangdong), and for *Osteosternum amoyense* is Amoy (= Xiamen, Fujian). During our field surveys, we are unable to observe any frogs that resembled these two historic species from Shenzhen or Xiamen, possibly

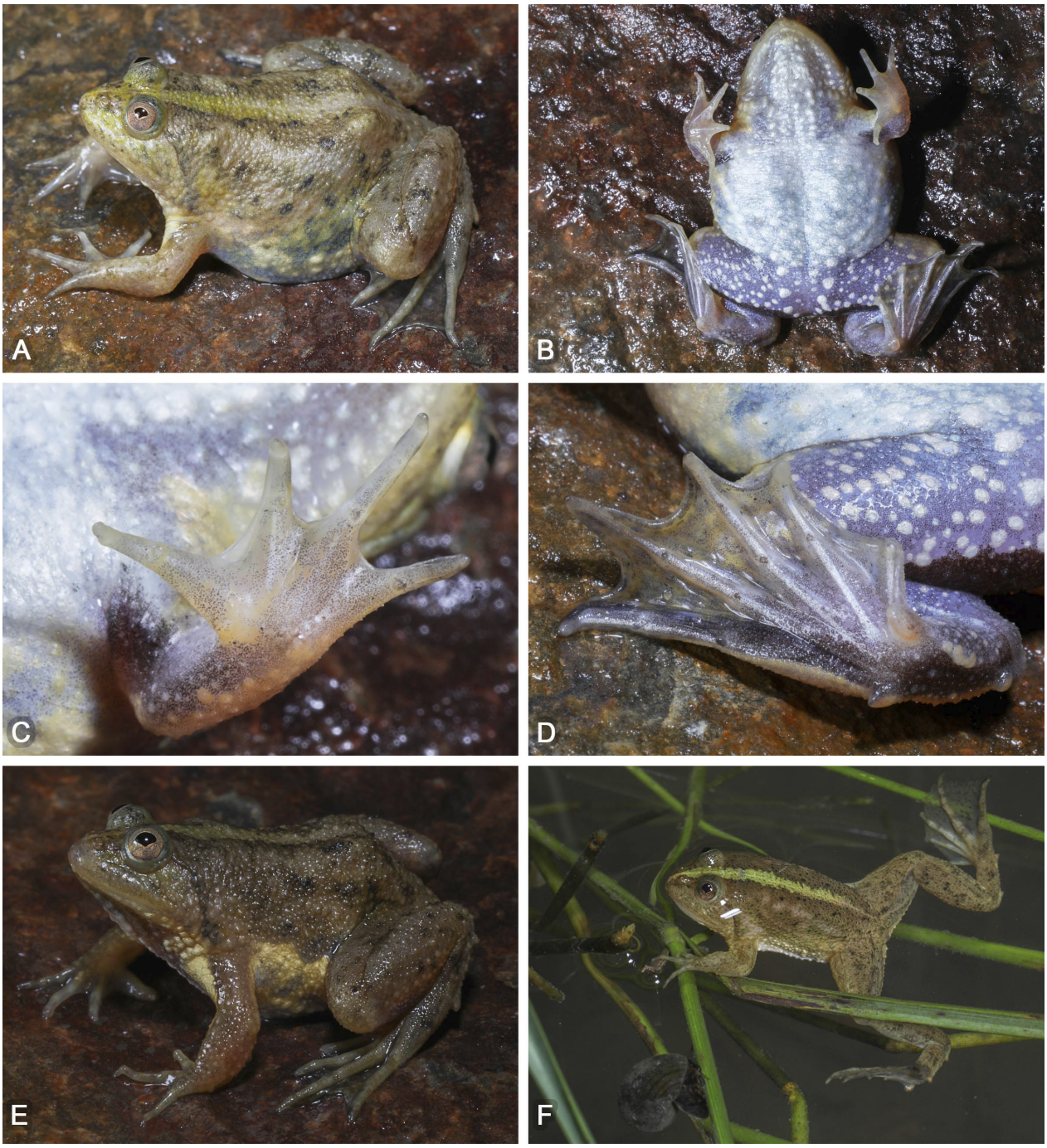

Figure 3. Morphological features of *Occidozyga obscura* comb. nov. in life. **A**–**D** dorsolateral view, ventral view, left hand, and right foot of SYS a008122 **E** dorsolateral view of SYS a008123 **F** dorsolateral view of an uncaptured individual in situ from Shimentai Nature Reserve.

due to the dramatic urbanization of these two cities. Nevertheless, according to their original descriptions and distributions, we propose to transfer these two taxa to be the synonymy of *Occidozyga obscura* comb. nov.

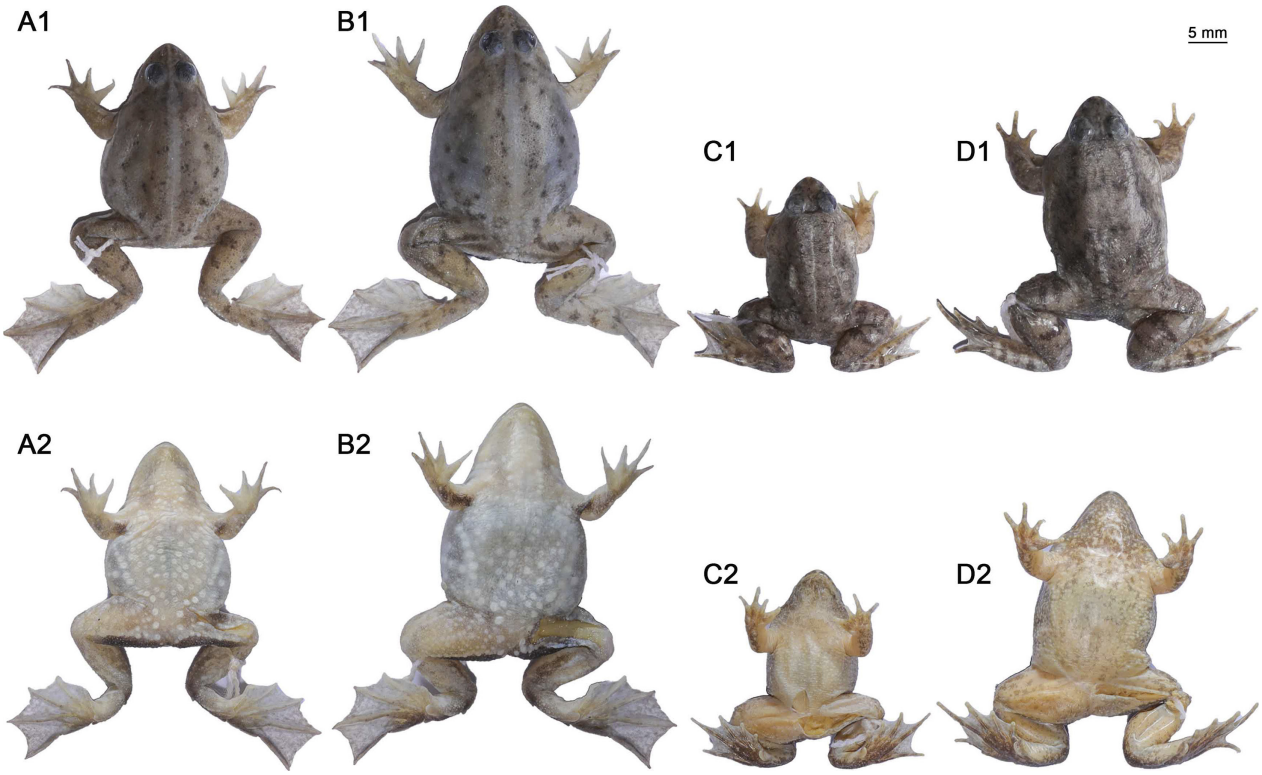

Figure 4. Morphological features of *Occidozyga obscura* comb. nov. and *Occidozyga lingnanica* sp. nov. in preservative. *Occidozyga obscura* comb. nov.: **A** adult male SYS a008121 **B** adult female SYS a008122; *Occidozyga lingnanica* sp. nov.: **C** adult male paratype SYS a007373 **D** adult female paratype SYS a007375. **1** dorsal view **2** ventral view.

Occidozyga lingnanica Lyu & Wang sp. nov.

https://zoobank.org/064C120B-3811-42D8-9550-0231528-D723C

Ooeidozyga laevis martensi — Pope 1931; Liu & Hu 1961
Occidozyga martensii — Fei et al. 1990; Zhao & Adler 1993; Li et al. 2011
Phrynoglossus martensii — Fei et al. 2009, 2010, 2012

Type materials. Holotype. SYS a008846, adult male, collected on 18 July 2021 by Zhi-Tong Lyu from Mt Wugongling (22.5914 N, 114.4927 E), Shenzhen City, Guangdong. **Paratypes.** Seven adult males and three adult females. Male SYS a008847 CIB 118529, collected at the same time as the holotype; males SYS a005589–90, collected on 15 November 2016 by Zhi-Tong Lyu and Jian Wang from Mt Wugongling; males SYS a007372–7373, and females SYS a07374–7375, collected on 5 September 2018 by Jian Wang and Hong-Hui Chen from Qi'ao Island (22.4140 N, 113.6446 E), Zhuhai City, Guangdong Province, China; female SYS a004650, collected on 14 April 2016 by Jian Wang from Mt Yunkai (22.2786 N, 111.1886 E), Xinyi City, Guangdong; males SYS a007657–7658, collected on 8 April 2019 by Jian Wang from Mt Yunkai.

Other examined specimens. Five adult males and five adult females. Male SYS a005543 and female SYS a005542, from Mt Jiaoyiling (21.1592 N, 110.3093 E), Zhanjiang City, Guangdong; female SYS a005267, from Mt. Diaoluo (18.6408 N, 109.9317 E), Lingshui Li Autonomous County, Hainan; males SYS a005436–5437, 5440–5441 and females SYS a005438–5439, 5442, from Mt Bawangling (19.0944 N, 109.0491 E), Changjiang Li Autonomous County, Hainan.

Etymology. The specific name *lingnanica* refers to the lingnan region, a geographic area covering Guangdong, Guangxi, and Hainan in southeastern China, where this new frog species occurs in. This specific name is also dedicated to the former Lingnan University (1888–1952) that was incorporated into Sun Yat-sen University after 1953.

Common name. "Lingnan floating frog" in English / "岭南浮蛙 (lǐng nán fú wā)" in Chinese.

Diagnosis. (1) Body stocky, size small, SVL 19.9–22.1 mm in males (n=8) and 26.8–28.8 mm in females (n=3); (2) snout short triangular shaped; (3) nostrils located laterally; (4) eye orientation laterally; (5) canthus rostralis visible, rounded; (6) loreal region vertical, not concave/convex; (7) tongue wide and swollen, unnotched, rounded distally, lingual papilla absent; (8) vomerine ridge and vomerine teeth absent; (9) supratympanic fold distinct and raised, slightly curved on the temporal region; (10) tympanum hidden, edge invisible; (11) relative finger lengths II=I<IV<III, relative toe lengths I<II<V<III<IV; (12) fingers without webs, toes with two third webs; (13) heels not meeting, tibio-tarsal articulation reaching at the

Table 4. Measurements (in mm) of the examined specimens of *Occidozyga lingnanica* sp. nov.

Specimen	SYS a007372	SYS a007373	SYS a008846	SYS a008847	SYS a005589	SYS a005590	SYS a007657	SYS a007658	SYS a007374	SYS a007375	SYS a004650
Sex	Male	Male	Male	Male	Male	Male	Male	Male	Female	Female	Female
SVL	22.1	21.6	21.4	21.5	19.9	20.2	21.8	21.7	26.8	28.5	28.8
HDL	7.8	7.1	7.5	7.5	6.6	6.6	7.1	7.8	9.0	9.5	9.0
HDW	7.4	6.7	7.2	7.2	6.5	6.5	6.6	7.5	8.9	9.3	9.0
SNT	2.9	2.7	2.5	2.6	2.3	2.3	2.9	2.9	3.0	3.5	3.3
IND	1.9	1.8	1.6	1.6	1.5	1.6	1.7	1.8	2.1	2.2	2.3
IOD	1.5	1.4	1.1	1.2	1.0	1.1	1.3	1.3	1.7	1.8	1.9
ED	2.6	2.5	2.5	2.5	2.3	2.3	2.5	2.7	3.3	3.4	3.0
HND	5.4	5.3	5.3	5.3	4.7	4.6	5.5	5.4	5.6	6.8	6.1
RAD	3.7	3.5	3.2	3.4	3.5	3.7	3.4	3.3	4.2	4.4	4.8
FTL	14.1	14.4	13.4	14.2	12.9	13.8	14.7	14.1	17.9	19.2	19.5
TIB	9.8	9.7	9.4	9.8	8.6	9.2	9.5	9.5	11.7	11.4	11.8

posterior margin of supratympanic fold; (14) tarsal fold absent.

Comparisons. *Occidozyga lingnanica* sp. nov. has been long-term misidentified as *O. martensii*, however, it differs from the latter by a combination of the following morphological characters: tympanum hidden, edge invisible (vs. tympanum edge raised), relative finger lengths II=I<IV (vs. II=IV<I), relative toe lengths V<III (vs. III<V), tarsal fold absent (vs. present), tibio-tarsal articulation reaching the posterior margin of supratympanic fold (vs. reaching the region of eye).

Occidozyga lingnanica sp. nov. can be distinguished from the remaining three known congeners in Clade VIII (Fig. 1) by the canthus rostralis rounded (vs. absent in *O. magnapustulosa*), loreal region oblique, not concave or convex (vs. slight convex in *O. magnapustulosa* and *O. swanbornorum* comb. nov.), relative finger lengths II=I<IV (vs. II<IV<I in *O. myanhessei* comb. nov., IV<II<I in *O. swanbornorum* comb. nov.), tarsal fold absent (vs. present in *O. magnapustulosa* and *O. myanhessei* comb. nov.).

For the remaining 13 congeners, *Occidozyga lingnanica* sp. nov. distinctly differs from *O. lima*, *O. obscura* comb. nov., and *O. berbeza* by the tongue wide and swollen (vs. narrow and slender); from *O. rhacoda* by the dorsolateral fold absent (vs. present); from *O. shiwandashanensis* by the tarsal fold absent (vs. present); from *O. celebensis*, *O. laevis*, and *O. sumatrana* by the eye orientation laterally (vs. vertically); from *O. baluensis*, *O. floresiana*, and *O. semipalmata* by the canthus rostralis rounded (vs. absent); from *O. diminutiva* and *O. tompotika* by the supratympanic fold curved (vs. straight).

Description of holotype. SYS a008846, adult male (Fig. 5). Body stocky, small-sized, SVL 21.4 mm. Head longer than wide (HDW/HDL 0.97), plat above; pineal ocellus distinct; snout short triangular shaped, distinctly protruding beyond lower jaw, tip of snout rounded in dorsal view and profile; canthus rostralis rounded, loreal region oblique, not concave or convex; nostril rounded, laterally, not raised, at the middle between tip of snout and eye; eye orientation laterally, pupil diamond shaped; interorbital space distinctly narrower than internarial distance; tympanum hidden, edge invisible; vomerine ridge and teeth absent; tongue wide and swollen, unnotched, rounded distally, lingual papilla absent.

Forelimbs short, lower arm 15% of SVL and hand 25% of SVL; fingers relatively thin and long, relative finger lengths II=I<IV<III; tips of fingers rounded, not dilated and without disks; fingers without webs and fringes; subarticular tubercles present at the bases of each finger, prominent and rounded; supernumerary tubercles absent; inner and outer palmar tubercles prominent and rounded.

Hind limbs robust, tibia 44% of SVL and foot 63% of SVL; heels not meeting when hind limbs flexed at right angles to the axis of the body; tibio-tarsal articulation reaching at the posterior margin of supratympanic fold when hind limb is stretched along the side of the body; toes distinctly long and thin, relative lengths I < II < V < III < IV; tips of toes rounded, dilated into rounded disks; toes with two third webs, metatarsal web present, distinct lateral fringes on lateral edges of toes I and V; subarticular tubercles rounded, prominent; inner metatarsal tubercle large and long-elliptic, distinctly raised, length triple the width; outer metatarsal tubercle absent; tarsal fold absent.

Dorsal surface relatively rough, large tubercles scattering on skin of dorsum, flanks, and dorsal limbs, not bearing spinules on the dorsal skin; a faint fold across head between orbits; supratympanic fold distinct, raised, extending from the posterior corner of the eye, slightly curved on the temporal region, to the previous shoulder; dorsolateral fold absent. Ventral surface with large flattened tubercles; a fold across breast; dense granules on the ventral tarsi.

Coloration of holotype. In life (Fig. 5), dorsal surface grayish brown with irregular black speckles; dorsal limbs with dark brown transverse bars; mid-dorsal stripe yellowish brown but indistinct; a narrow transverse bar between orbits; supratympanic fold dark brown. Pupil bordered with yellow; iris brown with irregular dark or light speckles. Skin of throat dark with white mottling; skin of chest and belly uniform creamy white; ventral surface of

Figure 5. Morphological features of the adult male holotype SYS a008846 of *Occidozyga lingnanica* sp. nov. in life. **A** dorsolateral view **B** ventral view **C** left hand **D** right foot **E** dorsal view of right hand showing the nuptial pad **F** calling in situ showing the subgular vocal sac.

limbs grayish pink with dark speckles. Nuptial pad light yellow, slightly transparent.

In preservative, dorsum light gray; black speckles on dorsum and transverse bars on limbs light brown; mid-dorsal stripe grayish white and more distinct; nuptial pad light gray, slightly transparent; ventral surface grayish white; mottling on throat gray white.

Variation. The measurements of the type series are given in Table 4. All individuals were similar in morphology. Dorsal coloration varies in life, from light brown, yellowish brown, to dark brown (Figs. 5, 6); mid-dorsal stripe varies among individuals, distinct (Figs. 4C, 6C), indistinct (Fig. 5), or absent (Figs. 4D, 6A, B, D–F); an irregular orange marking on the occipital region in some individuals (Fig. 6F).

Male secondary sexual characteristics. Male with a single subgular vocal sac; in breeding season, a single, light yellow, swollen, and granular nuptial pad on the dorsal surface of finger I, nuptial spinules invisible. Males (SVL 19.9–22.1 mm) distinctly smaller than females (SVL 26.8–28.8 mm) (Fig. 4C, D).

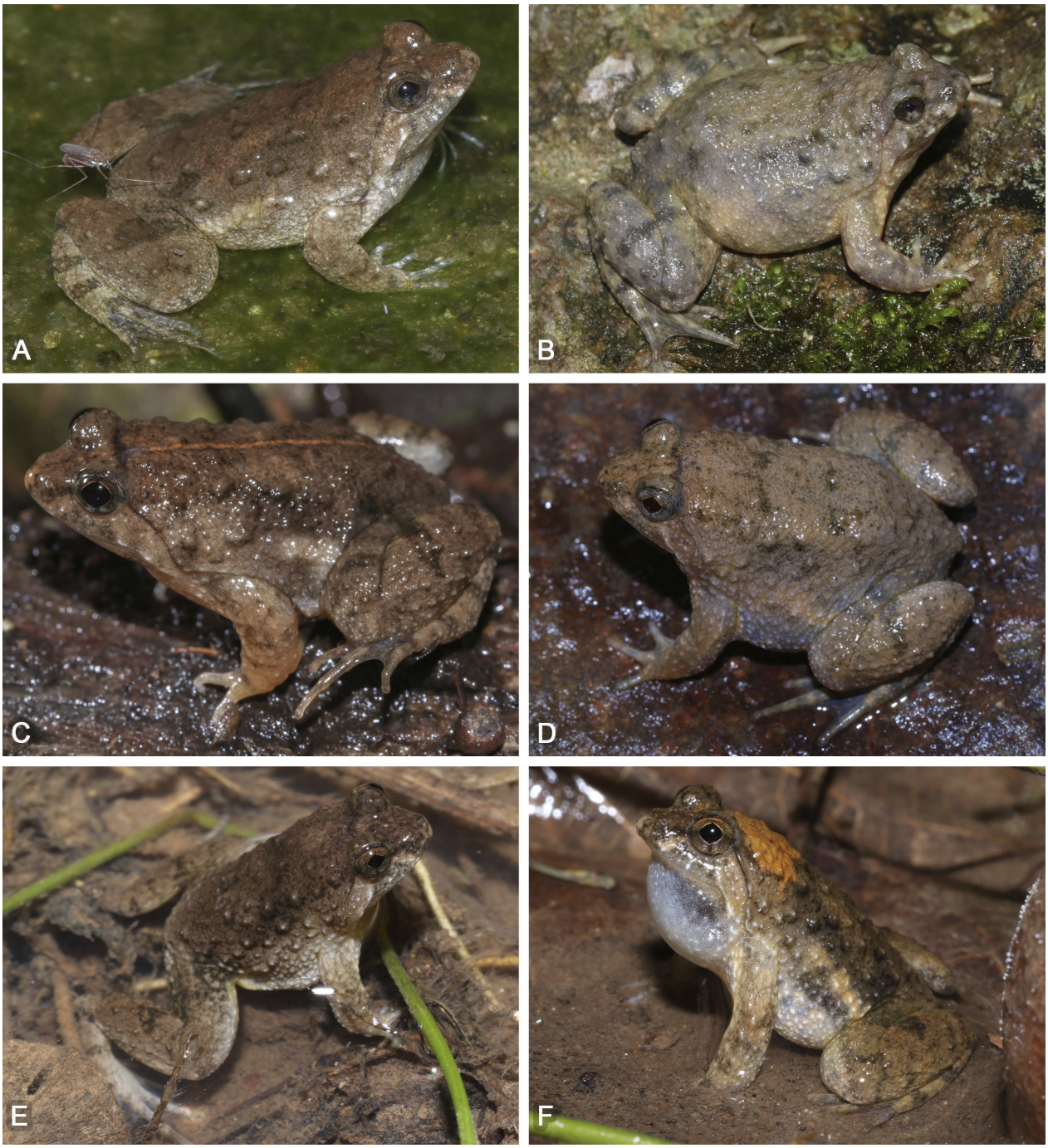

Figure 6. Color variation of *Occidozyga lingnanica* sp. nov. in life. **A** adult male paratype SYS a008847 **B** adult female paratype SYS a004650 **C** adult male paratype SYS a007373 **D** adult female paratype SYS a007375 **E** adult male SYS a005437 **F** adult male SYS a005440.

Ecology. This frog inhabits natural or artificial ponds and paddy fields in hilly regions. Males call in the water surface or waterside grass from dusk to dawn. The breeding season is from May to August (this study; Fei et al. 2009). In southeastern China, *Occidozyga lingnanica* sp. nov. shares a similar environment to that of *Occidozyga obscura* comb. nov., but prefers to hilly regions compared with the latter in plain areas.

Distribution. *Occidozyga lingnanica* sp. nov. can be recognized from multiple localities in Guangdong and Hainan of southeastern China based on the phylogenetic result in this work (Figs. 1, 2). The records of *O. martensi* from Yunnan, southwestern China require further clarifications with morphological examinations (see Discussion).

Conservation status. *Occidozyga lingnanica* sp. nov. was previously reported as common and widespread species in southeastern China under the nomen *O. martensii*. Nevertheless, during our repeated surveys throughout southeastern China, the population quantity of this species is found rapidly declining due to the influence of human activities such as pesticide abuse and urban construction. We recommend *Occidozyga lingnanica* sp. nov.

to be listed as Vulnerable (VU) [IUCN Red List criteria B1b(ii)(iii)].

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Supplementary material 1

Table S1

Authors: Lyu Z-T, Wang J, Zeng Z-C, Luo L, Zhang Y-W, Guo C-P, Ren J-L, Qi S, Mo Y-M, Wang Y-Y (2022)
Data type: .xlsx
Explanation note: Pairwise distances based on the 16S gene among all Occidozyga samples used in this study.

Link: https://doi.org/10.3897/vz.72.e80019.suppl1