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PENSOFT

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Taxonomic resolution of the hillstream suck-loach *Beaufortia pingi* species group (Cypriniformes, Gastromyzontidae) and two new species from Southwest China–*Beaufortia granulopinna* and *Beaufortia viridis*

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Abstract

Two new species, *Beaufortia granulopinna* and *Beaufortia viridis*, are described from the upper Pearl River system in southwest China. Both species share the characteristics of the *Beaufortia pingi* species group, including prominent vertical stripes on the lateral body and pinnate-type lower lips, distinguishing them from other *Beaufortia* species. *Beaufortia granulopinna* is differentiated from other species in the group by possessing a unique set of characteristics: the presence of well-developed prominent tubercles on the first 6–9 pectoral fin rays in adults; and a significant proportion (54.76%) of individuals experiencing blurriness or absence of vertical stripes in the mid-section of the lateral body upon reaching adulthood. The minimum interspecific genetic distance within the genus based on mitochondrial *cyt*b gene sequences is 10.80%. *Beaufortia viridis* is distinguished from other species in the group by consistently exhibiting vertical stripes of uniform length, width, and spacing across all stages of growth; the absence of tubercles on the branched rays of pectoral fins; and a body coloration of dark cyan to green. The minimum interspecific genetic distance within the genus based on mitochondrial *cyt*b gene sequences is 4.60%. Molecular phylogenetic results confirm that the *Beaufortia pingi* species group forms a monophyletic clade, which is congruent with morphological classification findings. This study also addresses and resolves the taxonomic ambiguity surrounding *Beaufortia pingi* and *Beaufortia zebroida*, providing a redescription of these taxa.

Key Words

Beaufortia pingi, *Beaufortia zebroida*, *Beaufortia*, morphology, molecular phylogeny, redescription

Introduction

The genus *Beaufortia*, belonging to the order Cypriniformes and family Gastromyzontidae, is distributed in the upper and middle reaches of the Yangtze River system, the Pearl River system, Hainan Island, and from Yunnan in China to the northern part of the Red River system in Vietnam (Kottelat 2012). This genus comprises small, benthic fish species that inhabit mountain streams. To adapt to fast-flowing environments, these rheophilic fish have undergone significant morphological specializations, including a compressed body, a flattened ventral surface, and greatly expanded paired fins forming a suction cup-like structure. These adaptations enable them to adhere to the rocky substrate, resisting the currents while feeding on algae and invertebrates.

In 1932, Hora established the genus *Beaufortia* for *Gastromyzon* species distributed in China, based on the absence of a continuous, elongated skin flap between the bases of the pectoral and ventral fins. Other characteristics of this genus as defined by Hora include small gill openings restricted to above the pectoral fins, the posterior edges of the ventral fins fused into a fin disk, a mouth slit smaller than 1/3 of the head width, and pectoral fins extending beyond the origin of the ventral fins (Hora 1932). These diagnostic features have been widely accepted over time, and several species have subsequently been discovered and classified within this genus.

At the onset of this study, the Catalog of Fishes had recorded 13 valid species within the genus, 12 of which were distributed in China (Frice et al. 2024). Among these, *Beaufortia yunnanensis* (Li, Lu & Mao, 1998) is particularly controversial. It was initially classified under the genus *Paraprotomyzon*, and its type specimen has been lost; it was later reassigned to the genus *Beaufortia* by Kottelat (Li et al. 1998; Kottelat 2012). *B. buas* (Mai, 1978) was deemed questionable due to unclear locality data, low identification clarity in hand-drawn illustrations, and rudimentary morphological information (Kottelat 2012). Historically, six other species have been included in the genus *Beaufortia* based on Vietnamese literature. Among these, *B. fasciolata* Nguyen, 2005; *B. multiocellata* Nguyen, 2005; and *B. triocellata* Nguyen, 2005 are now considered junior synonyms of *B. zebroida* (Fang, 1930) (Kottelat 2012). *Gastromyzon daon* Mai, 1978; *Gastromyzon elongata* Mai, 1978; and *Gastromyzon loos* Mai, 1978, which were described in the same publication as *Beaufortia buas*, also suffer from unclear locality data, low identification clarity in hand-drawn illustrations, and rudimentary morphological information and are currently regarded as species inquirenda and assigned to the genus *Pseudogastromyzon* (Kottelat 2012). Kottelat (2013) included them as species inquirenda within the genus *Beaufortia*. According to Chen et al. (2023), species of the genus *Pseudogastromyzon* are restricted to southeastern mainland China and do not extend to Vietnam. Therefore, the validity and taxonomic status of these species remain contentious.

Following extensive sampling of specimens from the genus *Beaufortia* and through morphological and phylogenetic analyses, we identified two new species: *Beaufortia granulopinna* Chen & Tang, 2024, sp. nov. and *Beaufortia viridis* Chen & Tang, 2024, sp. nov. Additionally, we addressed the taxonomic issues surrounding *Beaufortia pingi* and *Beaufortia zebroida*, providing redescriptions of these two species.

Materials and methods

Sample collection

Handheld dip nets were utilized as the primary tool for sample collection. According to documented literature, the distribution range of the *B. pingi* species group includes Lingyun County, Tian'e County, Tianlin County, and Longzhou County in Guangxi Province, and Guangnan County in Yunnan Province, where specimen collection was conducted (Fang 1930; Chen 1990; Chen and Tang 2000). Due to various natural and anthropogenic factors leading to habitat alterations, no specimens were collected in Tian'e County and Longzhou County. Extensive exploration of other potential distribution areas was conducted, leading to the discovery and collection of specimens in the Youjiang District of Baise City, Debao County, Xilin County, Napo County, and Wuming District of Nanning City in Guangxi Province, and Wenshan Zhuang and Miao Autonomous Prefecture in Yunnan Province. Additional collections of *B. szechuanensis* (Fang, 1930), *B. liui* Chang, 1944, *B. niulanensis* Chen, Huang & Yang, 2009, *B. polylepis* Chen, 1982, *B. kweichowensis* (Fang, 1931), and *B. leveretti* (Nichols & Pope, 1927) specimens were conducted from the middle and upper reaches of the Yangtze River in Sichuan Province, the Jinsha River basin and Nanpan River basin in Yunnan Province, the Li River basin in Guangxi Province, and the Duliu River basin in Guizhou Province, as well as from Hainan Province for comparative purposes. Following euthanasia, specimens were preserved in a 95% ethanol or 0.3% formalin solution, with 3–5 individuals randomly selected from each batch for mitochondrial cytb gene sequencing. Despite repeated attempts, no specimens of *B. yunnanensis*, *B. huangguoshuensis* Zheng & Zhang, 1987, *B. intermedia* Tang & Wang, 1997, and *B. cyclica* Chen, 1980 were obtained, and morphological data were cited from their original descriptions based on examination of their holotypes or paratypes. All fish collections followed the Law of the People's Republic of China on the Protection of Wildlife, and we strictly adhered to all applicable international, national, and institutional guidelines for the care and use of animals.

For other questionable species with unobtainable specimens and disputed taxonomic status, their original morphological descriptions were referenced.

Morphometric data measurement

Countable characteristics were examined using a stereoscopic microscope. The last branched anal-fin and dorsal-fin rays located on the last complex pterygiophore were counted as a single ray (Fig. 1). A considerable percentage of the population belonged to a phenotype characterized by attenuated and unbranched terminal fin rays in the paired fins. This specific anatomical feature was quantitatively assessed as equivalent to 0.5 of a standard branched fin ray. Following the photographic documentation of specimens in dorsal, lateral, and ventral views, measurements were conducted using TPSDIG2 software (Rohlf 2016), as depicted in Fig. 1. Statistical analyses of the measurable characteristics were conducted using SPSS v.26.0 (IBM Corp. 2020) to assess the significance of differences.

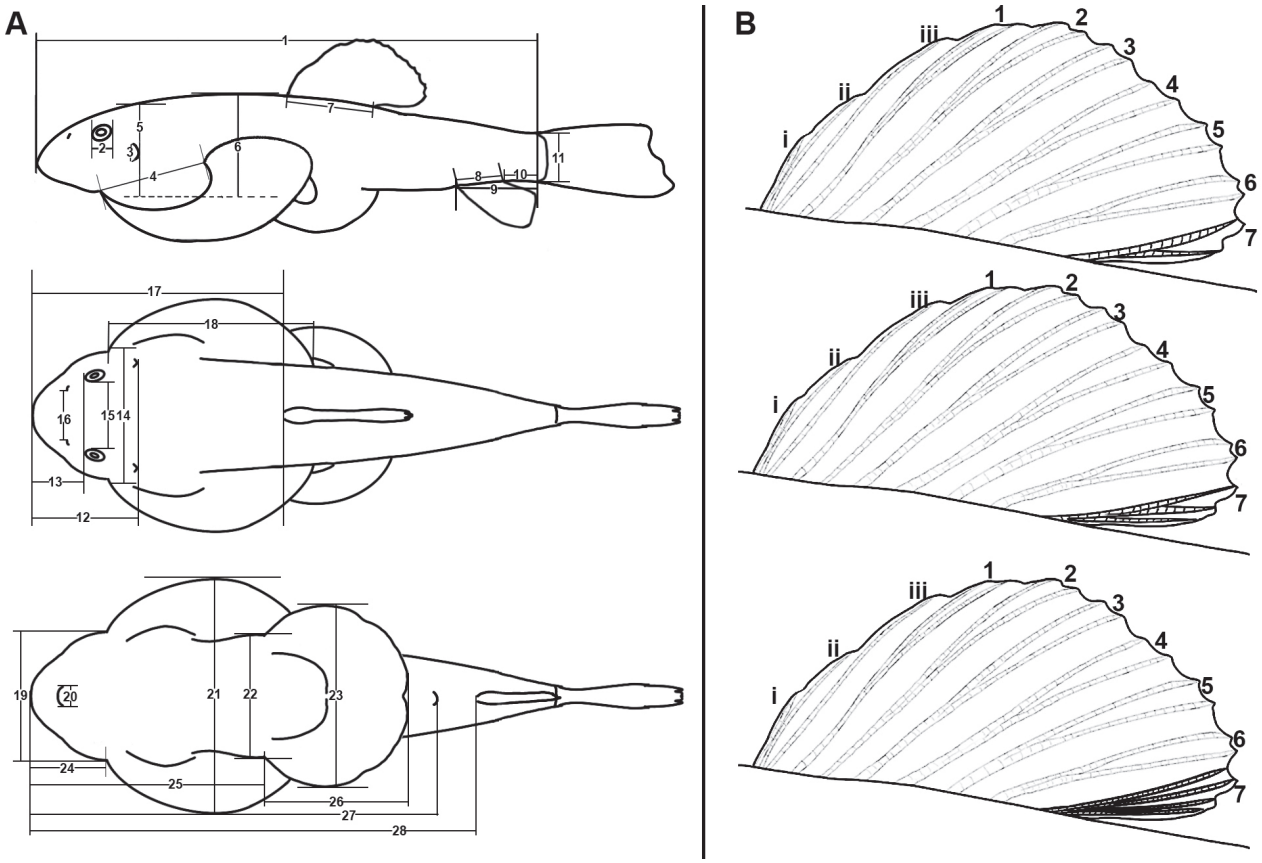

Figure 1. A. Morphometric measurement methodology for species within the genus *Beaufortia*: 1 - Standard length (SL); 2 - Eye diameter (ED); 3 - Gill slit length (GSL); 4 - Pectoral fin base length (PBL); 5 - Head length (HL); 6 - Body depth (BD); 7 - Dorsal fin base length (DBL); 8 - Anal fin base length (ABL); 9 - Post-anal fin length (PoAL); 10 - Caudal peduncle length (CL); 11 - Caudal peduncle depth (CD); 12 - Head length (HL); 13 - Snout Length (SnL); 14 – Head width (HW); 15 - Interorbital distance (IOD); 16 - Distance between nostrils (ND); 17 - Pre-dorsal Length (PrDL); 18 - Pectoral fin disc length (PL); 19 - Head width at pectoral fin origin (HWPO); 20 - Mouth slit width (MW); 21 - Pectoral fin disc width (PW); 22 - Body width (BW); 23 - Pelvic fin disc width (PvW); 24 – Pre-pectoral length (PrPL); 25 – Pre-pelvic length (PrPvL); 26 - Pelvic fin disc length (PvL); 27 - Pre-anal pore length (PrApL); 28 - Pre-anal fin length (PrAL); **B.** The last branched anal-fin and dorsal-fin rays located on the last complex pterygiophore were counted as a single ray.

Mitochondrial *cyt*b gene sequencing

DNA was extracted from the right pectoral fin rays using a kit produced by Sangon Biotech (Shanghai) Co., Ltd., following the protocol provided. Primers GAC TTG AAG AAC CAC CGT TGT TAT T 5'–3' and TCT TCG GAT TAC AAG ACC GAT GCT TT 5'–3' were employed to amplify the *cyt*b gene. The PCR mixture consisted of 1μL DNA template, 1μL of each primer (10 μM), 12.5μL Taq Mix (Sangon Biotech), and 9.5μL deionized water, totaling a reaction volume of 25μL. The PCR conditions included an initial denaturation at 95 °C for 3 minutes, followed by 35 cycles of 94 °C for 30 seconds, 55 °C for 45 seconds, and 72 °C for 60 seconds, with a final extension at 72 °C for 5 minutes and a hold at 4 °C. Amplified products were sequenced by Sangon Biotech, and the sequences were verified for accuracy before submission to the National Center for Biotechnology Information (NCBI). The collection sites for the molecular materials are listed in Table 1.

Phylogenetic analysis and genetic distance estimation

A total of 35 mitochondrial *cyt*b gene haplotypes were identified. The *cyt*b sequence of *Plesiomyzon baotingensis* (KF732713), retrieved from NCBI, was utilized as the outgroup, with a haplotype of *B. szechuanensis* (NC027291) included as additional material. Phylogenetic analyses were conducted using PHYLOSUITE (Zhang et al. 2020) with sequence alignment performed by MAFFT (Katoh and Standley 2013) set to automatic strategy and normal alignment mode. ModelFinder (Kalyaanamoorthy et al. 2017) was used to determine the best-fit models for both Maximum Likelihood (ML) and Bayesian Inference (BI) methods. The ML phylogenetic tree was constructed using IQ-TREE (Nguyen et al. 2015), with the best-fit model according to BIC being MGK+G4, and the outgroup set to *Plesiomyzon baotingensis*, with default parameters for other settings. The BI phylogenetic tree was constructed using MRBAYES 3.2.6 (Ronquist

Table 1. Collection localities and accession numbers of molecular samples.

Species	Specimen voucher	Sampling localities	River system	GenBank accession
Beaufortia granulopinna sp. nov.	SHOU20240103028	Tianlin County, Guangxi	Pearl River (upper reaches)	PP482589
	SHOU20240102801	Tianlin County, Guangxi		PP482590
	SHOU20240103650	Tianlin County, Guangxi		PP482592
	SHOU20240103652	Tianlin County, Guangxi		PP482593
	SHOU20240115013	Guangnan County, Yunnan		PP482591
Beaufortia viridis sp. nov.	SHOU20240103615	Nanning City, Guangxi		PP482580
	SHOU20240126801	Lingyun County, Guangxi		PP482581
	SHOU20240112104	Guangnan County, Yunnan		PP482578
	SHOU20240111616	Guangnan County, Yunnan		PP482579
	SHOU20240112103	Guangnan County, Yunnan		PP482582
Beaufortia pingi	SHOU20240102207	Lingyun County, Guangxi		PP482563
	SHOU20240102216	Lingyun County, Guangxi		PP482564
	SHOU20240102217	Lingyun County, Guangxi		PP482565
	SHOU20240102206	Lingyun County, Guangxi		PP482566
	SHOU20240102602	Lingyun County, Guangxi		PP482567
	SHOU20240126802	Baise City, Guangxi		PP482561
	SHOU20240102212	Baise City, Guangxi		PP482568
	SHOU20240103210	Debao County, Guangxi		PP482562
Beaufortia zebroida	SHOU20240111304	Guangnan County, Yunnan	Red River (lower reaches, North bank)	PP482585
	SHOU20240111302	Guangnan County, Yunnan		PP482588
	SHOU20240111313	Malipo County, Yunnan		PP482586
	SHOU20240111312	Funing County, Yunnan		PP482587
Beaufortia kweichowensis	SHOU20231212604	Congjiang County, Guangxi	Pearl River (upper reaches)	PP482574
	SHOU20231212645	Lingchuan County, Guangxi		PP482576
	SHOU20231212620	Huizhou City, Guangdong	Pearl River (lower reaches)	PP482575
Beaufortia leveretti	SHOU20231212641	Baisha County, Hainan	Nandu River	PP482577
Beaufortia szechuanensis	SHOU20231220642	Neijiang City, Sichuan	Yangtze River (upper reaches)	PP482569
Beaufortia niulanensis	SHOU20240120617	Qujing District, Yunnan		PP482583
	SHOU20240120616	Qujing District, Yunnan		PP482584
Beaufortia polylepis	SHOU20231220644	Kaiyuan City, Yunnan	Pearl River (upper reaches)	PP482570
	SHOU20231220619	Shizong County, Yunnan		PP482571
	SHOU20231220630	Luoping County, Yunnan		PP482572
	SHOU20231220636	Luoping County, Yunnan		PP482594
Beaufortia cf. *szechuanensis*	SHOU20231220611	Qijiang District, Chongqing	Yangtze River (upper reaches)	PP482573

et al. 2012), with the model set to HKY+F+G4 and the outgroup as *Plesiomyzon baotingensis*, maintaining default parameters for other settings. The resulting tree files were visualized and embellished using FIGTREE v1.4.4 (Rambaut 2018).

Genetic distances were calculated using MEGA11 (Tamura et al. 2021) with the Kimura 2-parameter model (rates among sites: G4), computing distances among all samples, average interspecific genetic distances, and average intraspecific genetic distances.

Results

Taxonomic account

Beaufortia granulopinna Chen & Tang, sp. nov.

https://zoobank.org/8A80A35D-C2A8-4B55-80D1-2BFDBA68B374

Figs 2–4

Gastromyzon pingi Fang, 1930: 35–36, No. 955, paratype, former Lingyun County, near the border of Yunnan.

Beaufortia pingi: Chen and Zhang (2006): 376–377, Tianlin County, Guangxi (fig. X98).

Type material. ***Holotype.*** SHOU20240103001, 72.48 mm total length (TL), 57.17 mm standard length (SL), adult (Fig. 2). Collected by Jing-Chen Chen and Qian-Yu Liang on 24 December 2023, from Lizhou River, a stream tributary of Bo′ai River of Pearl River basin, at Tianlin County, Guangxi Province, China (24°20.34'N, 106°21.624'E; c. 470m a.s.l.) (Fig. 5).

Paratypes. 21 specimens from the same locality as holotype, SHOU20240103002-022, 21.41–54.00 mm SL, were collected by Qian-Yu Liang and Jing-Chen Chen on 24 December 2023; 12 specimens from Guangnan County, Wenshan Zhuang, and Miao Autonomous Prefecture, Yunnan Province, China, SHOU20240115001-012, 31.86–44.07 mm SL, were collected by Xinrui Pu and Jing-Chen Chen on 08 January 2024.

Additional materials. Seven specimens from the type locality, SHOU20240103023-29, were collected by Qian-Yu Liang from December 2022 to April 2023; one specimen from Guangnan County, Wenshan Zhuang, and Miao Autonomous Prefecture, Yunnan Province, China, SHOU20240115013 was collected by Lin Yang and Lao Xing in December 2022.

Diagnosis. *B. granulopinna* sp. nov. shares typical characteristics with members of the *B. pingi* species group,

Figure 2. Lateral (top), dorsal (middle), and ventral (bottom) views of *Beaufortia granulopinna* sp. nov., holotype, adult, SHOU20240103001, 57.17 mm SL; from Lizhou River, a stream tributary of Bo′ai River of the Pearl River basin, at Tianlin County, Guangxi Province, China.

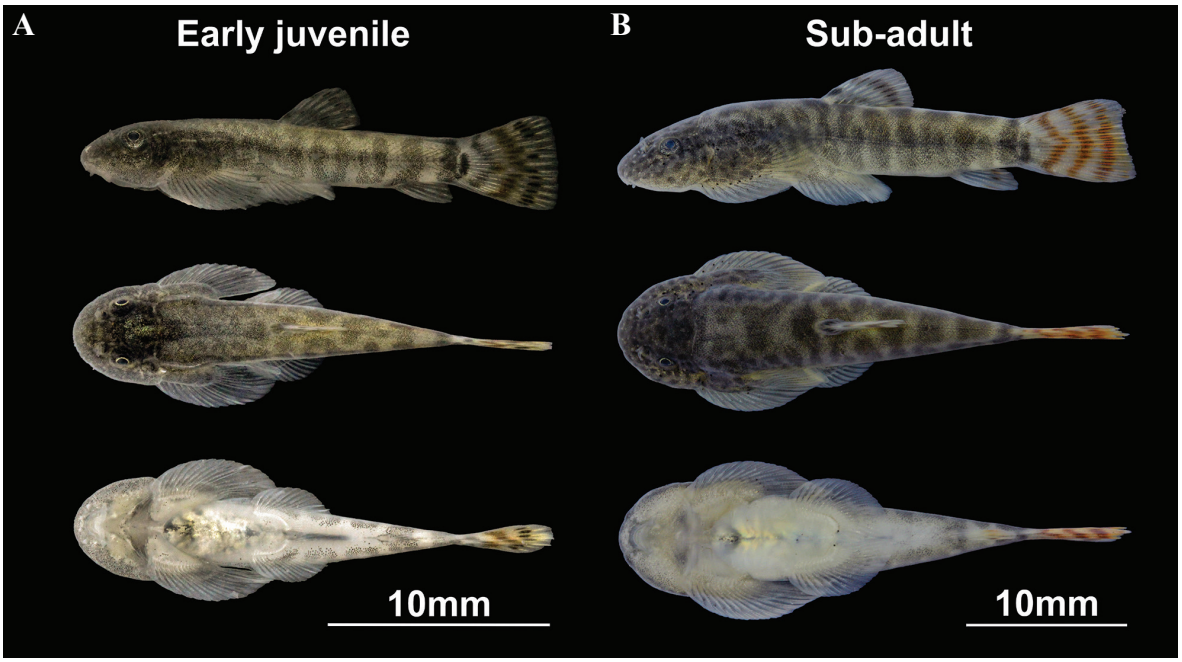

Figure 3. Lateral (top), dorsal (middle), and ventral (bottom) views of *Beaufortia granulopinna* sp. nov. during early juvenile and sub-adult stages. **A.** Early juvenile stage, SHOU20240103658, from type locality, 16.09 mm SL, pelvic fins completely separated; **B.** Sub-adult stage, SHOU20240103005, paratype, 24.21 mm SL.

with distinct vertical stripes on the flank, and a pinnate-type lower lip (vs. lacking prominent vertical stripes and having a dicot-type lower lip in other congeneric species apart from this group) (see Figs 6D, 7, Table 2). *B. granulopinna* can be clearly distinguished from *B. pingi*, *B. zebroida*, and *B. viridis* sp. nov. by the presence of well-developed tubercles on the anterior 6–9 pectoral fin rays (vs. absent or inconspicuous tubercles on pectoral fin rays). Moreover, *B. granulopinna* can be distinguished from *B. pingi* by generally fewer branched fin rays in the paired fins, with 18.5–22 (mean 20.11±0.77) in pectoral fins (vs. 21–24 (mean 22.19±0.78)) and 15–18 (mean 16.51±0.86) in pelvic fins (vs. 17–21 (mean 18.64±0.97)). It can be further differentiated from *B. viridis* sp. nov. and *B. zebroida* by a certain proportion (54.76%) of individuals exhibiting blurred or vanished vertical stripes in the mid-section of the lateral body in adulthood (vs. stable presence of vertical stripes at all growth stages).

Description. Dorsal iii-6–7(6.98±0.15), anal ii-4, pectoral i-18.5-22(20.11±0.77), pelvic i-15-18(16.51±0.86). Lateral-line canal pores and scales: 63–73 (68.76±2.5) (see Table 2).

Morphometric measurements for the specimens examined are given in Table 3. See Fig. 2 for lateral, dorsal, and ventral views of the body.

Head-thorax cylindrical, dorsal slightly humped medially, flattened ventrally, body compressed from pelvic fins to caudal peduncle. Head broad, blunt, length slightly less than width, more than depth, nuptial tubercles well-developed on lower half of head in mature individuals, snout rounded, length about half of head length. Mouth inferior, narrow, width about one-fifth head width, horseshoe-shaped, angle about 96° from midpoint to ends. Upper lip smooth, without distinct papillae; lower lip pinnate-type, slightly concave medially with multi-lobed sides; jaw edges slightly protrude. Shallow groove between upper lip and snout, extending to mouth corners. Lateral grooves shallow or indistinct. Two pairs of rostral barbels present, with outer pair slightly longer, space between rostral barbels with leaf-like folds, edges of which rounded and poor developed. One pair of maxillary barbels, length about equal to outer rostral barbels. Nostrils with tubular nasal flaps, distance between nostrils equals one-third head width. Eyes supralateral, medium-sized, eye diameter about one-quarter head length, interorbital space flat, width about half head width. Gill opening small, about equal to eye diameter, originated about vertically above the second branched pectoral fin ray, limited to dorsal side of head. Scales small, diameter smaller than pupil, dorsal surface of head, base of paired fins, and ventral area before pelvic fin bases nude. Lateral line complete, at midlateral.

Dorsal fin base about equal to pre-pectoral length, starting around midpoint from snout to caudal fin base, adpressed extending to about midway between dorsal fin origin and caudal fin base. Anal fin base length about half of that of dorsal fin base, adpressed extending slightly beyond caudal fin base. Paired fins extending outwards, forming disc-like structure with body. Pectoral fin base slightly longer than head length, starting at the posterior one-third point of head, pectoral fin length about twice head length, tips of which reaching pelvic fin base midpoint, pectoral disc width about 1.5 times head width at pectoral origin. Anterior 6–9 pectoral fin rays

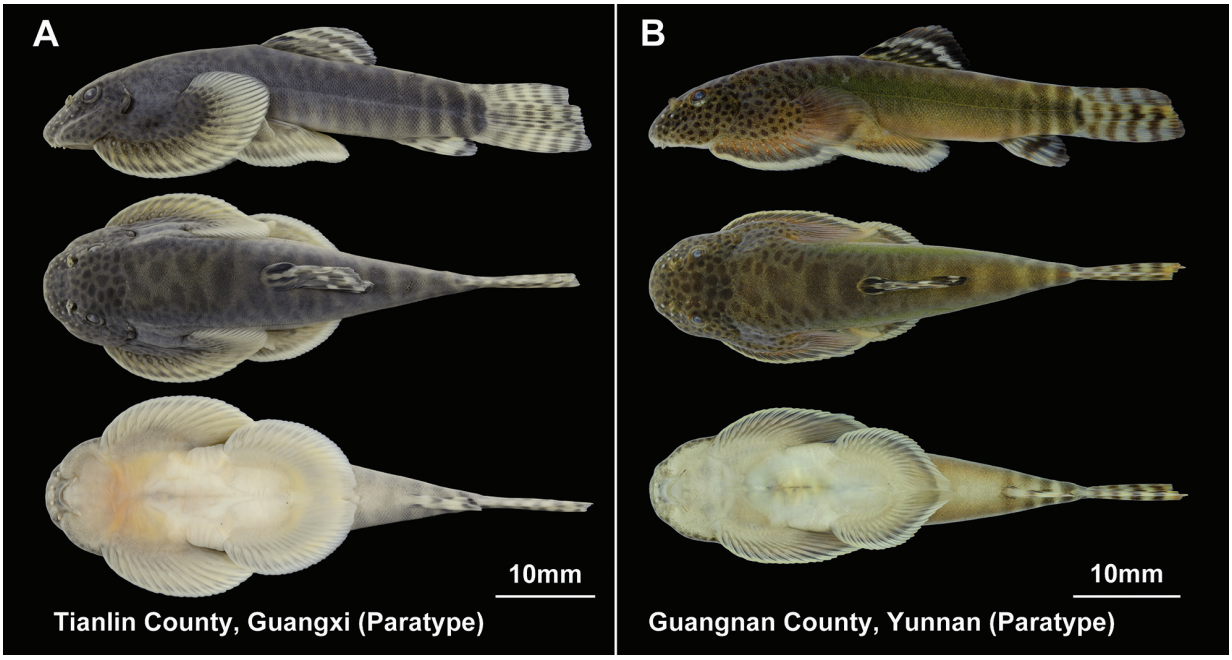

Figure 4. Lateral (top), dorsal (middle), and ventral (bottom) views of one common phenotypic variation of *Beaufortia granulopinna* sp. nov. and other regional phenotypes. **A.** Phenotype with persistent vertical stripe on lateral body, paratype, SHOU20240103003, 40.77 mm SL, from Tianlin County, Guangxi; **B.** Regional phenotype from Qingshui River, Guangnan County, Yunnan Province, paratype, SHOU20240115001, 39.01 mm SL.

Table 2. Key diagnostic features and countable characteristics of species within the genus *Beaufortia*.

Species	Vertical stripes on flank	Type of lower lip	Pectoral branch rays		Pelvic branch rays		Dorsal branch rays		Anal branch rays		Lateral-line canal-pores and scales		N
			Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	
***B. granulopinna* Chen & Tang 2024, sp. nov.**	present	pinnate	18.5–22	20.11 ± 0.77	15–18	16.51 ± 0.86	6–7	6.98 ± 0.15	4	4	63–73	68.76 ± 2.5	42
***B. viridis* Chen & Tang 2024, sp. nov.**	present	pinnate	19–23	21.09 ± 1.03	14.5–19	17.11 ± 1.02	7	7	4	4	65–83	73.51 ± 4.26	36
***B. pingi* (Fang, 1930)**	present	pinnate	21–24	22.19 ± 0.78	17–21	18.64 ± 0.97	7–8	7.08 ± 0.27	3–4	3.98 ± 0.14	68–92	75.28 ± 4.01	50
***B. zebroida* (Fang, 1930)**	present	pinnate	20–23	21.5 ± 0.73	16–19	17.53 ± 0.86	7	7	3–4	3.94 ± 0.24	70–84	75.12 ± 3.55	17
? *B. fasciolata* Nguyen, 2005	present	pinnate	21	21	16	16	7	7	5	5	87–88	–	2
? *B. triocellata* Nguyen, 2005	present	pinnate	21–22	–	16–17	–	7	7	5	5	86–96	–	3
? *B. multiocellata* Nguyen, 2005	present	pinnate	21–22	–	15–16	–	7	7	5	5	91–102	–	7
B. szechuanensis (Fang, 1930)	absent	Dicot	25–26.5	25.9 ± 0.55	18.5–20.5	19.6 ± 0.82	7	7	5	5	82–95	89.4 ± 5.32	5
B. liui Chang, 1944	absent	Dicot	21	21	17	17	7	7	5	5	92	92	1
B. huangguoshuensis Zheng & Zhang, 1987	absent	Dicot	27	27	19	17	6	6	5	5	84	84	1
B. polylepis Chen, 1982	absent	Dicot	26–27	26.5 ± 0.71	19–21	20 ± 1.41	6–7	6.5 ± 0.71	5	5	80–84	82 ± 2.83	2
B. intermedia Tang & Wang, 1997	absent	Dicot	25–28	–	24	–	7–8	–	5	5	81–86	–	9
B. niulanensis Chen, Huang & Yang, 2009	absent	Dicot	25.5–27.5	26.17 ± 1.15	20	20	7	7	5	5	78–90	84.33 ± 6.03	3
? *B. yunnanensis* (Li, Lu & Mao, 1998)	absent	Dicot	26	26	20	20	8	8	5	5	87	87	1
B. leveretti (Nichols & Pope, 1927)	absent	Dicot	23–25	24.4 ± 0.89	19.5–23.5	21.5 ± 1.77	8	8	4–5	4.4 ± 0.55	59–63	60.6 ± 1.82	5
B. kweichowensis (Fang, 1931)	absent	Dicot	24–25.5	24.9 ± 0.55	21.5–24.5	23 ± 1.22	8	8	4–5	4.4 ± 0.55	60–64	62.4 ± 1.52	5
B. cyclica Chen, 1980	absent	Dicot	30	30	20	20	7	7	5	5	72	72	1
? *B. buas* (Mai, 1978)	absent	–	24	24	19	19	8	8	5	5	55–65	–	–
? *B. daon* (Mai, 1978)	absent	–	25	25	19	19	9	9	5	5	75–85	–	–
? *B. elongata* (Mai, 1978)	absent	–	27	27	20	20	8	8	5	5	65	65	–
? *B. loos* (Mai, 1978)	absent	–	25	25	21	21	8	8	5	5	–	–	–

Species belonging to the *Beaufortia pingi* species group are highlighted in bold; a question mark "?" indicates substantial taxonomic controversy surrounding the species, and "-" stands for no corresponding data.

Figure 5. Collection site of the holotype (SHOU20240103001) of *Beaufortia granulopinna* sp. nov., from Lizhou River, a stream tributary of Bo′ai River of the Pearl River basin, Tianlin County, Guangxi Province, China. Photographed by Qian-Yu Liang on 24 December 2023.

Table 3. Morphometric results for species within the *Beaufortia pingi* group.

Characters	*B. granulopinna* sp. nov. (N=42)			*B. viridis* sp. nov. (N=36)			*B. pingi* (N=50)		*B. zebroida* (N=17)	
	Holotype	All materials		Holotype	All materials		Range	Mean ± SD	Range	Mean ± SD
		Range	Mean ± SD		Range	Mean ± SD				
Standard length (mm)	57.17	21.41–57.17	36.34±8.30	38.03	18.82–59.85	41.64±11.37	27.64–58.12	47.53±6.94	33.24–49.96	41.25±5.18
Vertical stripe blurring propotion	54.76% (N=23)			0			94.00% (N=47)		0	
Ratio of standard length to										
Body depth	3.97	3.97–6.27	**5.10±0.43***	5.36	4.25–6.11	5.31±0.54	3.91–6.48	**5.09±0.71***	4.90–5.98	5.47±0.33
Body width	3.93	3.92–5.34	4.61±0.35	4.54	3.79–5.46	4.43±0.41	3.65–4.88	**4.20±0.36***	3.93–5.19	4.62±0.37
Head length	4.94	4.19–5.05	4.63±0.21	4.40	3.91–4.98	4.45±0.24	4.42–5.32	**4.9±0.18***	4.28–5.06	4.61±0.19
Caudal peduncle length	17.17	10.42–21.40	14.38±2.61	13.11	9.72–17.16	12.53±1.78	10.85–17.99	13.77±1.57	9.62–16.94	12.37±1.85
Caudal peduncle depth	7.67	7.32–9.89	**8.36±0.52***	9.51	7.89–11.53	9.87±1.01	8.52–11.93	10.21±1.00	8.84–10.9	10.01±0.48
Predorsal length	2.03	1.88–2.11	1.97±0.06	1.99	1.81–2.14	1.98±0.07	1.95–2.21	2.04±0.06	1.90–2.47	2.01±0.13
Prepelvic length	2.40	2.14–2.40	2.29±0.06	2.34	2.07–2.52	2.28±0.08	2.19–2.49	2.36±0.08	2.15–2.38	2.28±0.06
Prepectoral length	7.36	5.70–7.73	6.72±0.51	6.83	5.54–7.51	6.71±0.41	6.60–8.24*	**7.42±0.39***	5.94–7.52	6.84±0.42
Pectoral base length	4.46	4.00–5.46	4.67±0.37	4.48	3.89–5.37	4.55±0.29	4.06–5.24	4.59±0.29	4.32–5.3	4.80±0.28
Pectoral length	2.56	2.44–3.56	2.63±0.19	2.47	2.37–2.84	2.55±0.12	2.43–2.84	2.63±0.09	1.94–2.73	2.50±0.18
Pectoral width	2.30	2.21–2.97	2.55±0.18	2.59	2.18–2.80	2.44±0.15	2.13–3.11	2.43±0.21	2.34–2.85	2.59±0.18
Pelvic length	3.27	3.03–3.88	3.46±0.20	3.30	2.97–4.04	3.33±0.23	2.94–3.67	3.26±0.18	3.29–3.65	3.44±0.11
Ratio of caudal peduncle length to										
Caudal peduncle depth	0.45	0.37–0.80	0.60±0.11	0.73	0.53–1.17	0.81±0.16	0.57–0.99	0.75±0.12	0.61–1.13	0.82±0.12
Ratio of head length to										
Head depth	1.05	1.01–1.66	1.27±0.12	1.54	1.19–1.72	1.41±0.13	1.05–1.58	1.26±0.13	1.13–1.72	1.35±0.15
Head width	0.71	0.71–0.91	0.82±0.05	0.87	0.70–0.97	0.84±0.06	0.65–0.88	0.77±0.06	0.78–1.07	0.88±0.06
Snout length	2.08	1.97–2.77	2.31±0.18	2.24	1.89–2.59	2.24±0.19	1.76–3.24	2.09±0.22	2.15–2.49	2.30±0.10
Eye diameter	5.15	3.37–5.23	4.30±0.50	4.41	3.51–6.95	4.59±0.76	3.86–5.58	4.53±0.41	3.62–5.35	4.36±0.47
Interorbital width	1.38	1.35–2.38	1.73±0.26	1.60	1.48–1.99	1.68±0.14	1.18–2.30	1.51±0.24	1.47–2.32	1.78±0.28
Prepectoral length	1.49	1.26–1.65	1.45±0.10	1.55	1.38–1.75	1.51±0.08	1.39–1.68	1.51±0.07	1.30–1.62	1.49±0.09
Ratio of head width to										
Mouth width	4.59	4.27–6.40	5.19±0.46	4.99	4.32–6.60	5.44±0.63	4.69–6.72	**5.79±0.50***	4.37–5.73	5.02±0.36
Internostril width	3.97	2.80–4.37	3.56±0.38	3.12	3.09–4.07	3.51±0.27	2.69–4.53	3.31±0.35	2.76–3.79	3.32±0.31
Ratio of postanal length to										
Caudal peduncle depth	1.21	1.06–1.49	**1.29±0.11***	1.67	1.17–2.08	1.61±0.22	1.29–1.86	1.55±0.15	1.38–1.86	1.66±0.15
Ratio of prepelvic length to										
Length of pelvic origin to anal origin	1.01	0.97–1.21	1.07±0.06	1.08	0.95–1.33	1.11±0.10	0.90–1.27	**1.00±0.07***	1.02–1.29	1.11±0.07

"*" denotes that, in a one-way ANOVA test, post-hoc comparisons reveal that the trait in question significantly differs from those of other species (without "*") ($p < 0.05$).

with nuptial tubercles in adults. Pelvic fin shorter than pectoral, well-developed fleshy flap at dorsal base, last 1–3 branched rays partially connected by fin membrane forming pelvic disc, connected part about two-thirds ray length, remaining parts separated, forming notch in middle rear edge, exposing anus. Pelvic disc width about equal to length. Anus at or near posterior edge of pelvic disc, distance to which less than to anal fin origin. Caudal fin length about equal to pelvic fin, slanted end, lower lobe slightly longer.

Coloration in preservation. Preserved specimens from sub-adult to adult stage, body dark brown to grey, white ventrally. Head with black spots or vermiculations dorsally, 2–5 larger black blotches along mid-dorsal body anterior to dorsal fin. Sides with 4–15 thick dark vertical stripes, stripes posterior to dorsal fin origin wider than intervals. In smaller individuals, stripes clear and distinguishable, in larger individuals, stripes anterior to caudal peduncle sometimes blur or disappear. Paired fin with white margin, black arc, or dotted-arc line inside white ring. Dorsal fin with alternating black, white stripes, anal fin hyaline with black stripes.

Coloration in live. In life, dorsal body dark brown to green. Mature individuals with metallic, green longitudinal band along lateral line, area below lateral line behind pelvic fins and base of paired fins sometimes light orange, more pronounced in Qing Shui River basin populations, Yunnan. Dorsal fin black pattern wider than white.

Juvenile morphology. Pelvic fins completely separated, dorsal body side gray-brown, few wider vertical dark stripes on flank, 2–3 vertical black stripes on caudal fin, other fins hyaline or with inconspicuous black lines (see Fig. 3).

Sexual dimorphism. In fully mature individuals, males slightly larger than females, with well-developed nuptial tubercles (see Fig. 8E, F).

Geographic variation. Qing Shui River basin populations, Yunnan, more pronounced orange color below lateral line behind pelvic fins, dorsal side of paired-fins base after sexual maturity compared to type locality Tianlin County populations (see Fig. 4B).

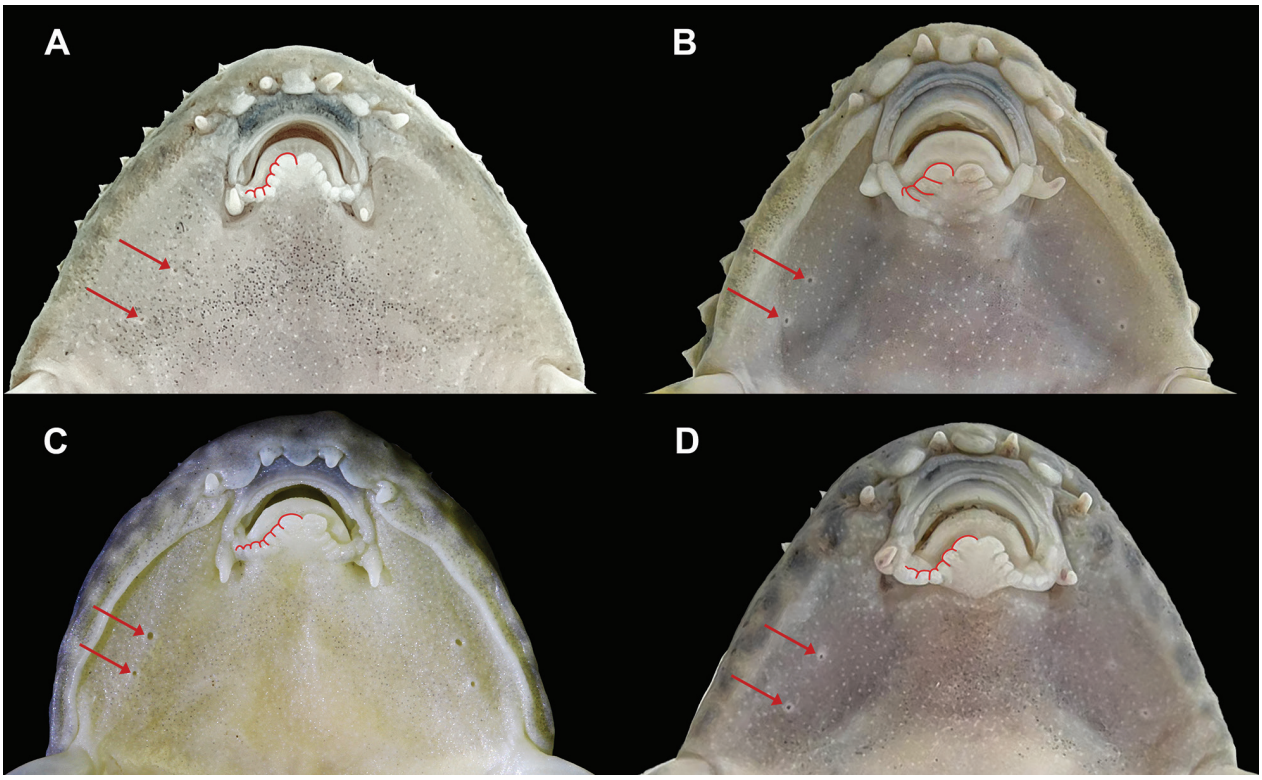

Figure 6. Pinnate-type lower lip of the *Beaufortia pingi* species group, elongated, with the lower lip on both sides being multilobed, typically comprising more than three lobes, with deep divisions; the extremities of the lower lip extend to the corners of the mouth, with several wart-like protrusions present on the extended parts. The red line outlines the left side of the lower lip contour; the red arrow indicates the position of the ventral head sensory canal-pores located anterior to the origin of the pectoral fins. **A.** *B. pingi*, from the type locality; **B.** *B. zebroida*, from Napo County, Guangxi Province; **C.** *B. viridis*, from the type locality; **D.** *B. granulopinna*, from the type locality.

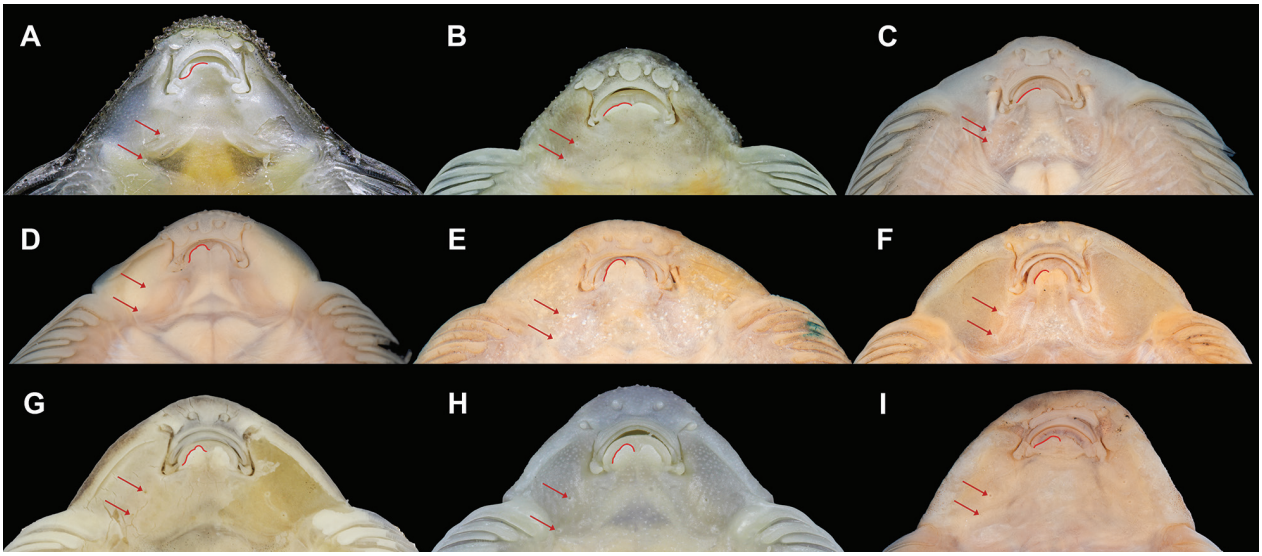

Figure 7. Dicot-type lower lip of species outside the *Beaufortia pingi* group, shorter, with the sides of the lower lip being smooth or featuring 1–2 shallow notches; the ends of the lower lip do not extend to the corners of the mouth, or the extension is poor-developed and lacks protrusions. The red line outlines the left side of the lower lip contour; the red arrow indicates the position of the ventral head sensory canal-pores, with the second pair of canal-pores located posterior to the origin of the pectoral fins in all species except *B. liui*. **A.** *B. leveretti*, from the type locality; **B.** *B. kweichowensis*, from Congjiang County, Guizhou Province, downstream near the type locality; **C.** *B. cyclica*, holotype; **D.** *B. intermedia*, paratype; **E.** *B. polylepis*, syntype; **F.** *B. huangguoshuensis*, syntype; **G.** *B. szechuanensis*, from Neijiang City, Sichuan Province; **H.** *B. niulanensis*, from the type locality; **I.** *B. liui*, syntype. (C-F and I were photographed by Yi-Yang Xu, Institute of Hydrobiology, Chinese Academy of Sciences.)

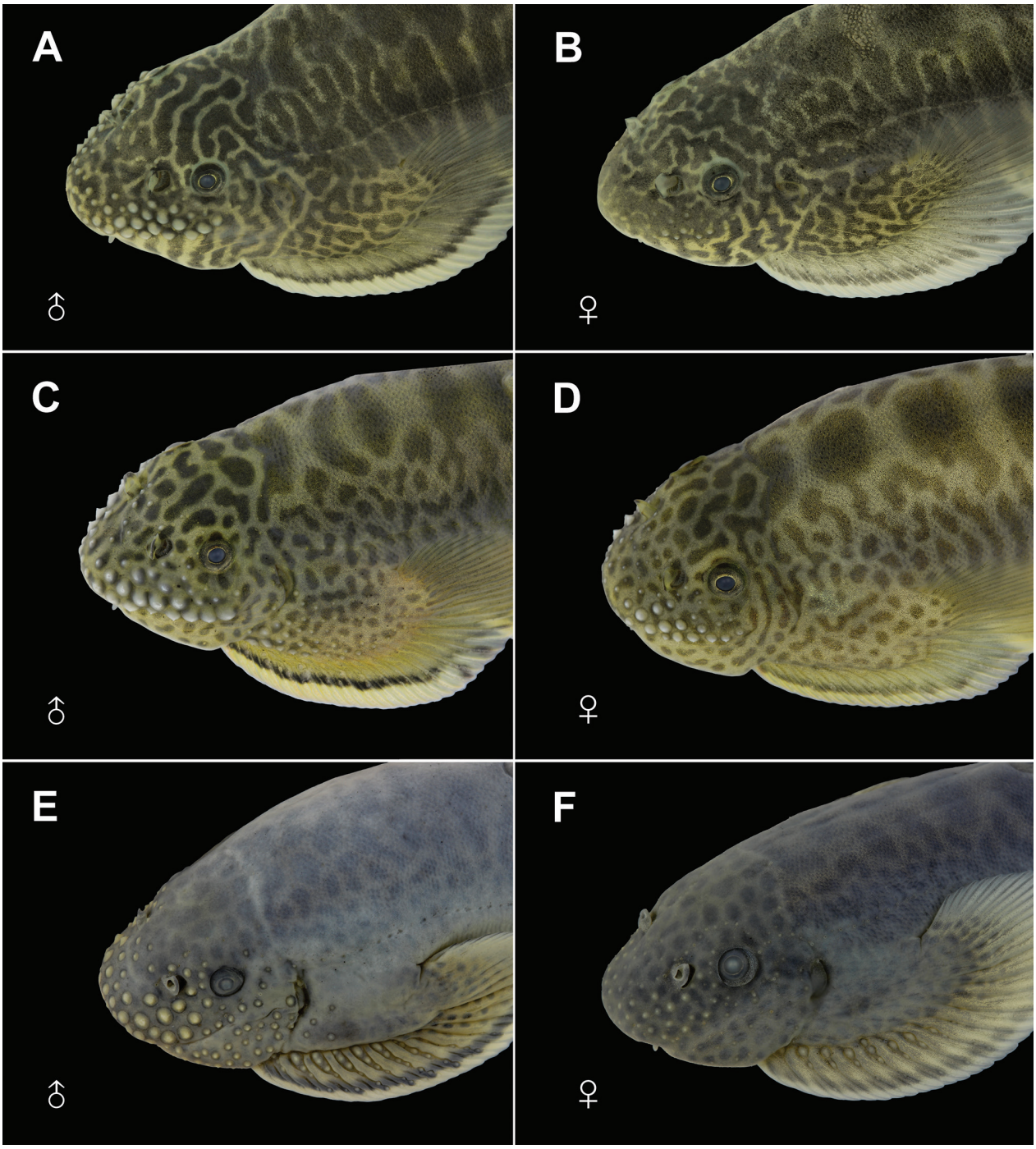

Figure 8. Sexual dimorphism within the *Beaufortia pingi* species group, with males exhibiting well-developed and numerous nuptial tubercles on the head compared to females. **A, B.** *B. viridis* sp. nov.; **C, D.** *B. pingi*; and **E, F.** *B. granulopinna* sp. nov.

Individual variation. Among the 42 specimens examined, one (SHOU20240103017) with six branched rays in dorsal fin.

Ethology. Inhabits shallow streams with rapid currents and smooth pebble substrates that adhere to crevices between stones. Feeds on algae and small invertebrates and consumes mucus from fresh fish carcasses. Exhibits strong territorial behavior and aggression; adults may head-butt and extend dorsal fins to drive away rivals.

Distribution. Found exclusively in the small tributaries of the Bo′ai River basin, ranging from the northwestern part of Guangxi to the eastern part of Yunnan in China, as well as in the small tributaries of the Qingshui River section and its downstream Nanpan River basin, upper reaches of the Pearl River system (see Fig. 9).

Etymology. The specific epithet *granulopinna* combines Latin "*granulo-*," meaning grainy, and "*-pinna*," meaning fin, referring to the well-developed tubercles on pectoral fins; the term is in the nominative masculine singular. We propose the Chinese common specific name "珠鳍爬岩鳅".

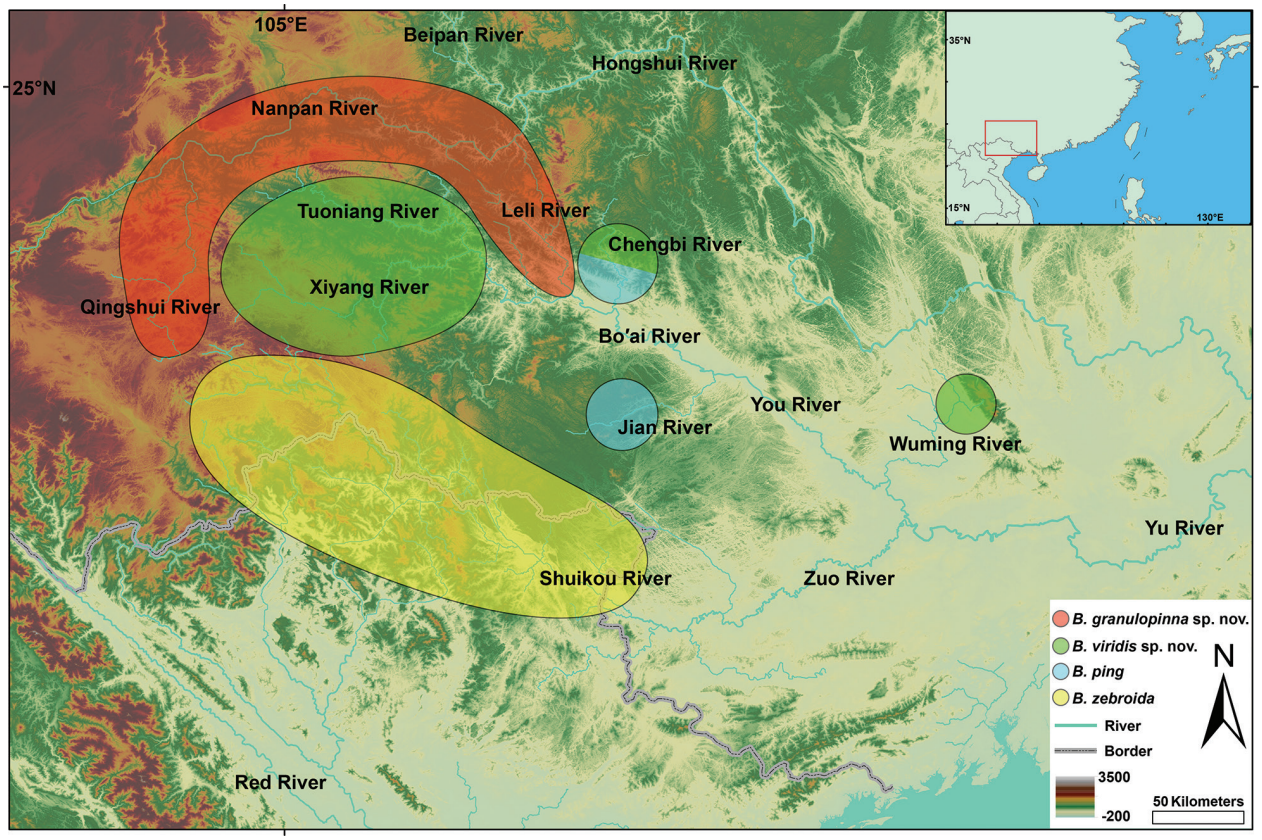

Figure 9. Distribution map of species within the *Beaufortia pingi* species group. Light red: *B. granulopinna* sp. nov.; light green: *B. viridis* sp. nov.; light blue: *B. pingi*; light yellow: *B. zebroida*. Rivers are labeled with their names in Chinese: Qingshui River (清水江), Nanpan River (南盘江), Beipan River (北盘江), Hongshui River (红水河), Tuoniang (驮娘江), Xiyang River (西洋江), Leli River (乐里河), Chengbi River (澄碧河), Bo'ai River (剥隘河), Jian River (鉴河), You River (右江), Wuming River (武鸣河), Yu River (郁江), Shuikou River (水口河, known as Sông Bằng in Vietnamese), and Red River (红河).

Beaufortia viridis Chen & Tang, sp. nov.

https://zoobank.org/268BD22A-C14B-4662-BFFC-A8C3369DACC7

Figs 10–12

Beaufortia pingi: Yue (1981): 170–172, Lingyun County, Guangxi, admixed within *B. pingi*. Zheng (1989): 257–258, Lingyun County, Guangxi, admixed within *B. pingi*.

Beaufortia pingi: Chen (1990): 85–87, Xiyang River, Guangnan County, Yunnan.

Beaufortia zebroidus: Chen and Tang (2000): 504–505, Tian'e County, Guangxi. Chen (2013): 292, Xiyang River, Yunnan.

Type material. ***Holotype.*** SHOU20240103101, 48.42 mm total length (TL), 38.03 mm standard length (SL), adult (Fig. 10). Collected by Jing-Chen Chen and Qian-Yu Liang on 27 December 2023, from Wuming River, a stream tributary to the You River of the Pearl River basin, at Wuming District, Nanning City, Guangxi Province, China (24°20.34'N, 106°21.624'E; c. 160 m a.s.l.) (Fig. 13).

Paratypes. 15 specimens from the same locality as holotype, SHOU20240103102-116, 18.82–46.64 mm SL, were collected by Qian-Yu Liang and Jing-Chen Chen on 27 December 2023; eight specimens from Lingyun County, Baise City, Guangxi Province, China, SHOU20240126101-108, 50–59.85mm SL, were collected by Qian-Yu Liang and Jing-Chen Chen on 24 January 2024; five specimens from Guangnan County, Wenshan Zhuang, and Miao Autonomous Prefecture, Yunnan Province, China, SHOU20240109101-105, 36.23–54.20mm SL, were collected by Lao Xing on 28 December 2023.

Additional materials. Seven specimens from Guangnan County, Wenshan Zhuang, and Miao Autonomous Prefecture, Yunnan Province, China, SHOU20240112101-107, 39.97–48.64mm SL, were collected by Lin Yang and Lao Xing from December 2022 to February 2023.

Diagnosis. *B. viridis* sp. nov. shares the typical characteristics with members of the *B. pingi* species group, with distinct vertical stripes on lateral body and a pinnate-type lower lip (vs. lacking prominent vertical stripes and having a dicot-type lower lip in other congeneric species apart from this group) (see Figs 6C, 7, Table 2). *B. viridis* sp. nov. can be clearly distinguished from *B. granulopinna*, *B. pingi*, and *B. zebroida* by consistent vertical stripes with uniform length, width, and inter-spacing at all growth stages (stripes on mid-section lateral body occasionally shorten in individuals from the Xiayang and Tuoniang Rivers in Yunnan) (vs. a certain proportion (54.76%) of adults exhibit blurred or vanished vertical stripes on mid-section lateral body in *B. granulopinna*;

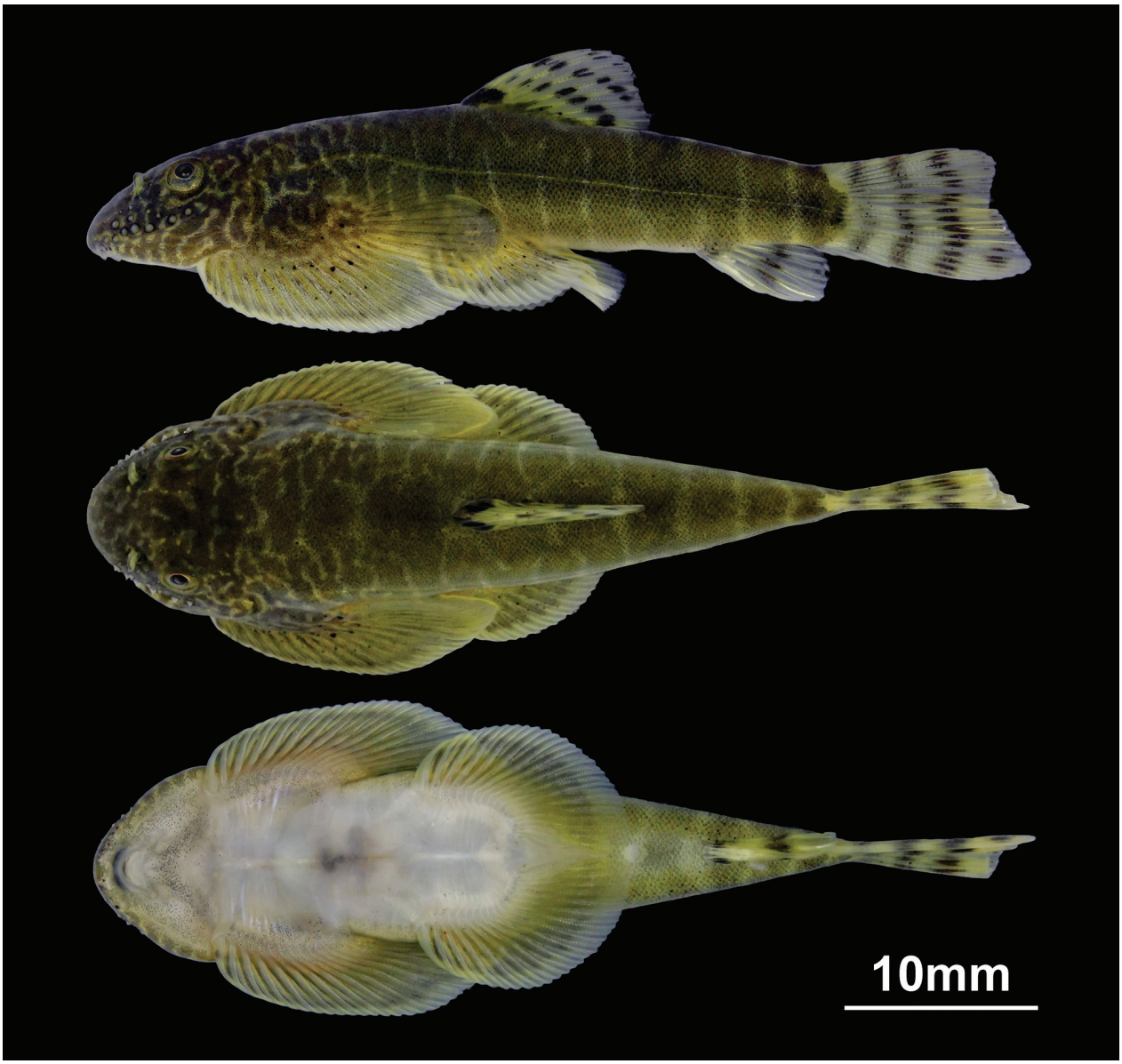

Figure 10. Lateral (top), dorsal (middle), and ventral (bottom) views of *Beaufortia viridis* sp. nov., holotype, adult, SHOU20240103101, 38.03mm SL; from Wuming River, a stream tributary to the You River of the Pearl River basin, at Wuming District, Nanning City, Guangxi Province, China.

stripe length and width uneven, with a high proportion (94.00%) of adults showing blurred or vanished mid-section vertical stripes in *B.pingi*; stripe length and width uneven, typically narrower than inter-spacing, sometimes reduced to dots in *B. zebroida*). *B. viridis* sp. nov. can be further distinguished from *B. granulopinna* sp. nov. by the lack of prominent tubercles on the branched rays of the pectoral fins (vs. well-developed tubercles on anterior 6–9 rays of the pectoral fins present). Moreover, *B. viridis* sp. nov. differs from *B. zebroida* by body dark cyan to green in dorsal profile (vs. brown yellow to golden).

Description. Dorsal iii-7, anal ii-4, pectoral i-19–23 (21.08±1.02), pelvic i-14.5–19 (17.11±1.01). Lateral-line canal pores and scales: 65–83 (73.47±4.21) (see Table 2).

Morphometric measurements for the specimens examined are given in Table 3. See Fig. 10 for lateral, dorsal, and ventral views of the body.

Head-thorax cylindrical, dorsal slightly humped medially, flattened ventrally, body compressed from pelvic fins to caudal peduncle. Head broad, blunt, length slightly less than width, more than depth, nuptial tubercles well-developed on lower half of head in mature individuals, snout rounded, length about half of head length. Mouth inferior, narrow, width about one-fifth head width, horseshoe-shaped, angle about 94° from midpoint to ends. Upper lip smooth, without distinct papillae; lower lip pinnate-type, slightly concave medially with multilobed sides; jaw edges slightly protrude. Shallow groove between upper lip and snout, extending to mouth corners. Lateral grooves shallow or indistinct. Two pairs of rostral barbels present, with outer pair slightly longer, space between rostral barbels with leaf-like folds, edges of which rounded and poor developed. One pair of maxillary barbels, length about equal to outer rostral barbels. Nostrils with tubu-

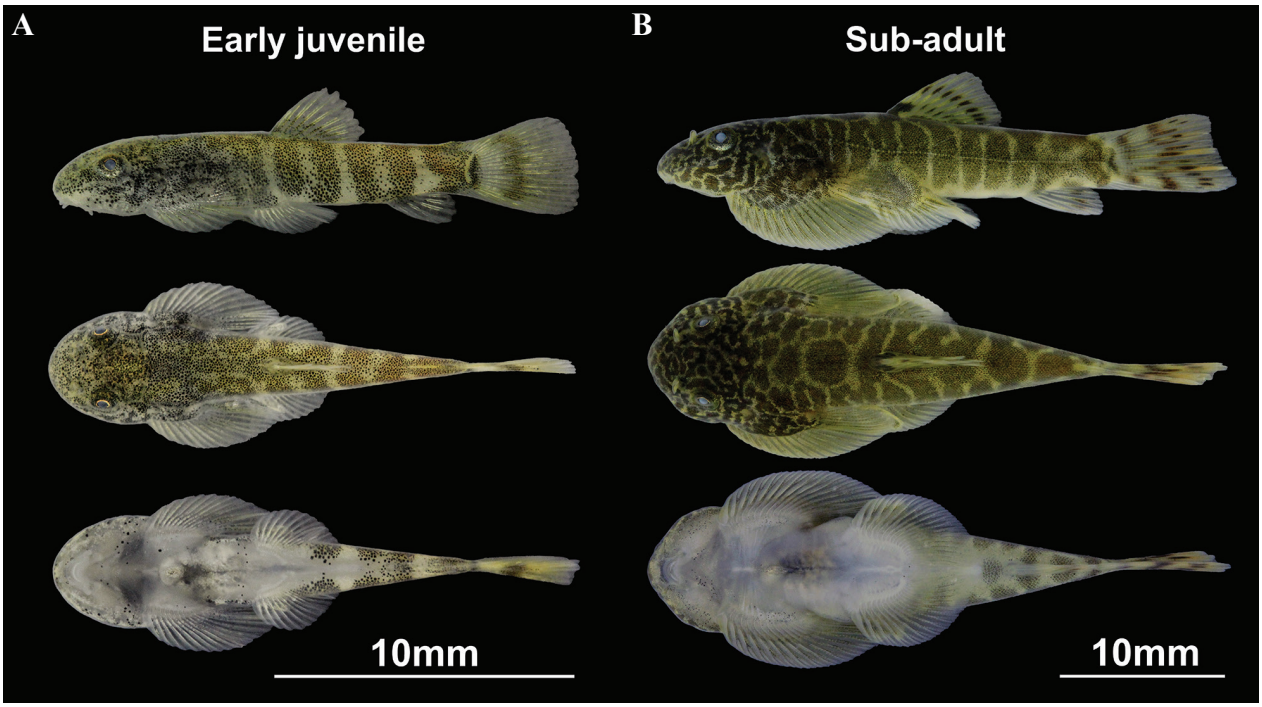

Figure 11. Lateral (top), dorsal (middle), and ventral (bottom) views of *Beaufortia viridis* sp. nov. during early juvenile and sub-adult stages. **A.** Early juvenile stage, SHOU20240103623, from type locality, 12.64 mm SL, pelvic fins completely separated; **B.** Sub-adult stage, SHOU20240103102, paratype, 25.81 mm SL.

lar nasal flaps, distance between nostrils equals one-third head width. Eyes supralateral, medium-sized, eye diameter about one-quarter head length, interorbital space flat, width about half head width. Gill opening small, about equal to eye diameter, originated about vertically above the second to third branched pectoral fin ray, limited to dorsal side of head. Scales small, diameter smaller than pupil, dorsal surface of head, base of paired fins, and ventral area before pelvic fin bases nude. Lateral line complete, at midlateral.

Dorsal fin base about equal to pre-pectoral length, starting around midpoint from snout to caudal fin base, adpressed extending to about midway between dorsal fin origin and caudal fin base. Anal fin base length about half of that of dorsal fin base, adpressed extending to slightly beyond caudal fin base. Paired fins extending outwards, forming disc-like structure with body. Pectoral fin base slightly longer than head length, starting at the posterior one-third point of head, pectoral fin length about twice to head length, tip of which reaching pelvic fin base midpoint, pectoral disc width about 1.5 times head width at pectoral origin, tubercles on rays absent. Pelvic fin shorter than pectoral, with well-developed fleshy flap at dorsal base, last 1–3 branched rays partially connected by fin membrane forming pelvic disc, connected part about two-thirds ray length, remaining parts separated, forming notch in middle rear edge, exposing anus. Pelvic disc width about equal to length. Anus at or near posterior edge of pelvic disc, distance to which less than to anal fin origin. Caudal fin length about equal to pelvic fin, slanted end, lower lobe slightly longer.

Coloration in preservation. Preserved specimen from sub-adult to adult stage, body dark green to grey, white ventrally. Head with black spots or vermiculation dorsally, 2–5 larger black blotches along mid-dorsal body anterior to dorsal fin. Sides with 9–15 thick dark vertical stripes, with uniform length, width, and inter-spacing, easily recognizable at all ages. Paired fin with pale-white or hyaline margin, inner edges with continuous or dotted black arc. Dorsal fin hyaline with black stripes, one black spot present on the root before the second branched ray.

Coloration in live. In life, sides of body dark cyan to green. After maturity, black stripes and spots on body turn metallic green, inter-spacing and hyaline fin membranes pale yellow.

Juvenile morphology. Pelvic fins completely separated, body dark green in dorsal profile, few wider vertical dark stripes on sides, 2–3 vertical black stripes on caudal fin, other fins hyaline or with inconspicuous black lines (see Fig. 11).

Sexual dimorphism. In fully mature individuals, males generally slightly larger than females, with well-developed tubercles (see Fig. 8A, B).

Geographic variation. From east to west, vertical stripes generally tend to become thinner. Specimens from type locality, inter-spacings narrower than dark stripes, sometimes appearing fissure-like (see Fig. 10). In contrast, Lingyun County populations typically exhibit broader and taller bodies, shorter and thicker caudal peduncles, longer snouts, and wider inter-spacings (see Fig. 12A, Table 4). In populations from the Xiyang River and Tuoniang River, vertical stripes vary greatly, sometimes becoming finer, inter-spacings wider than stripes, few individuals with shorter stripes before caudal peduncle (see Fig. 12B).

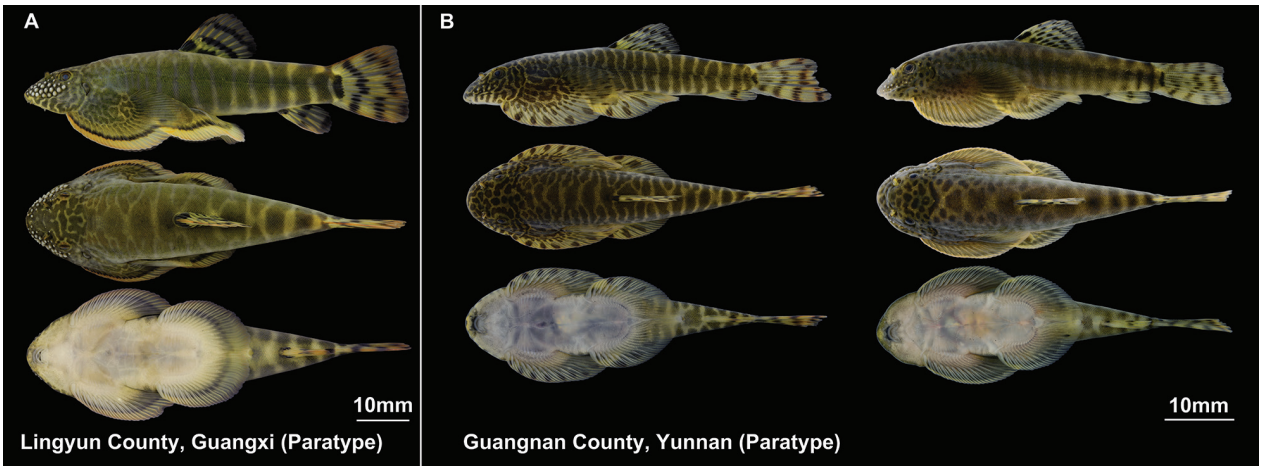

Figure 12. Lateral (top), dorsal (middle), and ventral (bottom) views of different regional phenotypes of *Beaufortia viridis* sp. nov. **A.** Regional phenotype from Lingyun County, Guangxi, SHOU20240126104, paratype, 58.71 mm SL; **B.** Regional phenotype from Tuoniang River, Guangnan County, Yunnan, SHOU20240109105, paratype, 40.15 mm SL (left); SHOU20240109103, paratype, 39.36 mm SL (right).

Table 4. Morphological variations among populations of *Beaufortia viridis* sp. nov. and *Beaufortia pingi* from different distribution areas.

***B. viridis* sp. nov.**	**Wuming County (N=16)**		**Linyun County (N=8)**		**Tuoniang River and Xiyang River (N=12)**	
Characters	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD
Pectoral branched rays	19–21	20.25±0.68	21–22	21.37±0.44	21–23	22±0.74
Pelvic branched rays	14.5–17	16.5±0.71	17–19	17.62±0.74	16–19	17.58±1.10
Ratio of prepelvic length to						
Head width	1.53–1.88	1.65±0.08	1.40–1.65	**1.53±0.08***	1.54–1.85	1.67±0.12
Pectoral width	1.01–1.30	1.11±0.07	0.94–1.03	**0.99±0.03***	0.96–1.19	1.08±0.07
Body width	1.79–2.63	2.04±0.22	1.62–1.82	**1.73±0.07***	1.79–2.29	1.97±0.15
Body depth	2.19–2.77	2.50±0.17	1.76–2.20	**1.98±0.15***	2.09–2.65	2.34±0.21
Head depth	2.53–3.27	2.89±0.22	2.30–2.67	**2.48±0.12***	2.40–3.14	2.79±0.25
Caudal peduncle depth	4.07–5.16	4.54±0.29	3.26–4.11	**3.59±0.28***	3.90–5.05	4.55±0.37
Pelvic width	1.31–2.02	1.43±0.17	1.15–1.30	**1.25±0.05***	1.21–1.74	1.44±0.17
Ratio of head length to						
Snout length	2.23–2.59	**2.40±0.11***	1.89–2.12	**2.01±0.08***	1.98–2.43	**2.19±0.12***
Ratio of postanal length to						
Caudal peduncle depth	1.48–2.08	1.10±0.16	1.17–1.39	**1.28±0.08***	1.37–1.94	1.70±0.15
Ratio of prepelvic length to						
Length of pelvic origin to anal origin	1.06–1.33	**1.19±0.74***	0.95–1.17	1.02±0.71	0.96–1.17	1.08±0.58
B. pingi	Linyun County & Youjiang County (N=38)		Debao County (N=12)			
Characters	Range	Mean ± SD	Range	Mean ± SD		
Pelvic branched rays	17.5–21	18.95±0.89	17–18.5	17.67±0.39		
Ratio of pectoral width to						
Body depth	1.67–2.50	2.02±0.21	1.92–2.49	**2.32±0.19****		
Ratio of postanal length to						
Caudal peduncle depth	1.29–1.77	1.50±0.13	1.58–1.86	**1.69±0.09****		
Ratio of prepelvic length to						
Length of pelvic origin to anal origin	0.90–1.27	**0.98±0.66****	0.97–1.14	1.07±0.52		

"*" indicates that, in a one-way ANOVA test, post-hoc comparisons show significant differences in the trait in question from populations in other regions ($p < 0.05$).
"**" indicates that, in an independent sample T-test, the trait in question significantly differs from populations in other regions ($p < 0.01$).

Individual variation. Two specimens, SHOU20240109101 and SHOU20240112102, from Tuoniang River, Guangnan County, Yunnan, vertical stripes notably shortened. One specimen, SHOU20240109701, from Chengbi River, Lingyun County, Guangxi, possesses completely separated pelvic fins.

Ethology. Inhabits shallow streams with rapid currents and smooth pebble substrates that adhere to crevices between stones. Feeds on algae and small invertebrates and consumes mucus from fresh fish carcasses. Exhibits territorial behavior.

Distribution. Found exclusively in small tributaries from the Tuoniang River, Xiyang River, Leli River, and Wuming River to the You River basin, the upper reaches of the Pearl River system, central Guangxi, and eastern Yunnan, China (see Fig. 9).

Etymology. Species epithet "*viridis*," from Latin, meaning "green," describes bright green coloration over dorsal body after sexual maturity, in nominative masculine. We propose the Chinese common specific name "绿斑爬岩鳅."

Figure 13. Collection site of the holotype (SHOU20240103101) of *Beaufortia viridis* sp. nov., from Wuming River, a stream tributary to the You River of the Pearl River basin, Wuming District, Nanning City, Guangxi Province, China. Photographed by Jing-Chen Chen on 27 December 2023.

Beaufortia pingi (Fang 1930)

Fig. 14

Gastromyzon pingi Fang, 1930: 31–34 (original description: former Lingyun County, near the border of Yunnan and Guangxi; Damaoping Village, Lingyun County, Guangxi). Nichols (1943): 231.

Beaufortia pingi: Hora (1932): 319.

Gastromyzon pingi: Nichols (1943): 231.

Beaufortia pingi: Chen (1980): 113–114 (Xi River, Guangxi).

Comparative materials. 23 specimens from type locality, SHOU20240102201-217, SHOU20240126201-206, 27.64–56.89 mm SL, were collected by Qian-Yu Liang and Jing-Chen Chen from December 2022 to January 2024; 15 specimens from Youjiang District, Baise City, Guangxi Province, China, SHOU20240110201-204, SHOU20240127201-211, 43.53–56.28 mm SL, were collected by Qian-Yu Liang and Jing-Chen Chen from December 2021 to January 2024; 12 specimens from Debao County, Baise City, Guangxi Province, China, SHOU20240112201-202, SHOU20240103201-210, 44.53–58.12 mm SL, were collected by Qian-Yu Liang from April 2023 to January 2024.

Diagnosis. *B. pingi* shares the typical characteristics with members of the *B. pingi* species group, with distinct vertical stripes on the flank and a pinnate-type lower lip (vs. lacking prominent vertical stripes and having a dicot-type lower lip in other congeneric species apart from this group) (see Figs 6A, 7, Table 2). *B. pingi* can be clearly distinguished from *B. granulopinna* sp. nov. by absent or inconspicuous tubercles on pectoral fin rays (vs. well-developed tubercles present on anterior 6–9 rays of pectoral fins); paired fins with more branched rays, with 21–24 (mean 22.19±0.78) in pectoral fins and 17–21 (mean 18.64±0.97) in pelvic fins (vs. 18.5–22 (mean 20.11±0.77) and 15–18 (mean 16.51±0.86)). *B. pingi* can be clearly distinguished from *B. viridis* sp. nov. by vertical stripes uneven in length and width and a significant proportion (94.00%) of adults displaying blurred or vanished stripes on the mid-section flank (vs. the stable presence of uniform vertical stripes in length, width, and inter-spacing at all growth stages). *B. pingi* differs from *B. zebroida* by having a larger proportion of adults with blurred or vanished mid-section vertical stripes (vs. stable presence of vertical stripes) and body dark brown to green in dorsal profile (vs. brown yellow to golden).

Redescription. Dorsal iii-7–8 (7.08±0.27), anal ii-3–4 (3.98±0.14); pectoral i-21–24 (22.19±0.78); pelvic i-17–21 (18.64±0.97). Lateral-line canal pores and scales: 68–92 (75.28±4.01).

Morphometric measurements for the specimens examined are given in Table 3. See Fig. 14 for lateral, dorsal, and ventral views of the body.

Body closely resembles *B. viridis* sp. nov. in general shape and structure but significantly different in stripes pattern and coloration. Tubercles on rays absent or poor developed, only faintly visible in large males.

Coloration in preservation. Preserved specimens from sub-adult to adult stage, body dark brown to grey, white ventrally. Head with black spots or vermiculation dorsally, 2–5 larger black blotches along mid-dorsal body anterior to dorsal fin. Sides of body with 4–15 vertical dark stripes, length and width of stripes uneven. In smaller individuals, stripes clear and distinguishable, in larger individuals, a significant proportion possesses a blur region before caudal peduncle, extending to dorsal fin origin at maximum, caudal peduncle with 2–5 distinct vertical stripes. Paired fin margins hyaline or pale white, inner edges with continuous or dotted black arc. Dorsal fin hyaline, with black stripes, one black spot on the root before the first branched ray.

Coloration in live. In life, dorsal body dark brown to green. Mature individuals with metallic green longitudinal band along lateral line, area below lateral line behind

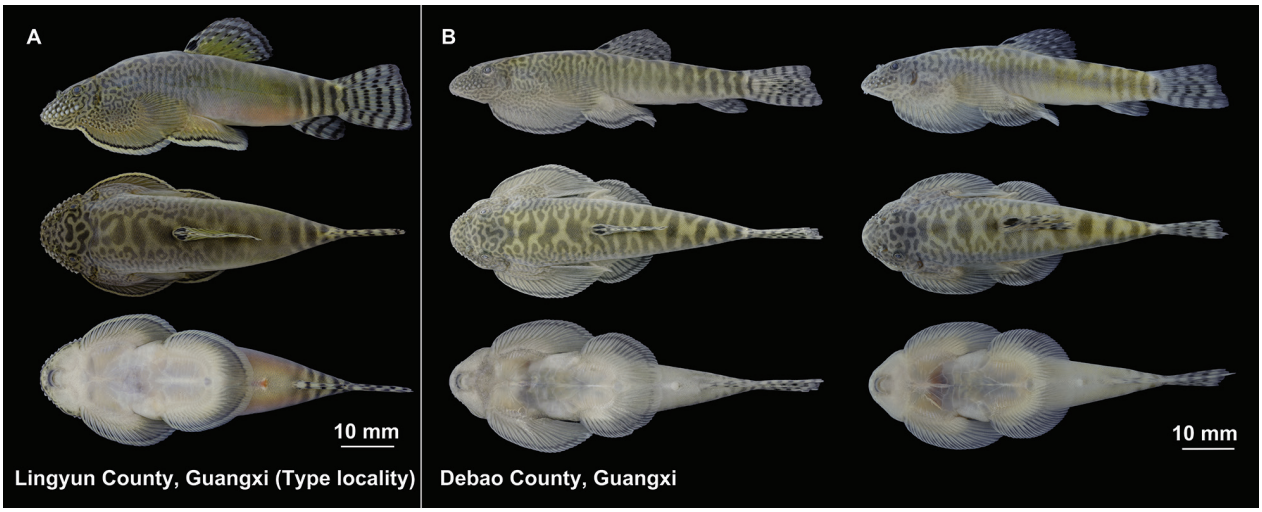

Figure 14. Lateral (top), dorsal (middle), and ventral (bottom) views of different regional phenotypes of *Beaufortia pingi*. **A.** Regional phenotype from Lingyun County, Guangxi, SHOU20240126202, from type locality, 56.89mm SL. **B.** Regional phenotype from Debao County, Guangxi, SHOU20240103203, 58.12 mm SL (left), with clearer vertical stripes; SHOU20240103204, 53.18 mm SL (right), with blurred vertical stripes.

pelvic fins and base of paired fins sometimes light orange, fin membranes pale green.

Sexual dimorphism. In fully mature individuals, males slightly larger than females, with well-developed nuptial tubercles (see Fig. 8C, D).

Geographic variation. Compared to type locality, Lingyun County, Guangxi, population in Debao County, Guangxi with more compressed body, and more elongated tail (see Fig. 14B, Table 4).

Individual variation. Among 50 specimens, four (SHOU20240102213, SHOU20240102215, SHOU20240126205, and SHOU20240127211) with eight dorsal fin-branched rays; one (SHOU20240127204) with three anal fin-branched rays.

Ethology. Inhabits shallow streams with rapid currents and smooth pebble substrates that adhere to crevices between stones. Feeds on algae and small invertebrates and consumes mucus from fresh fish carcasses. Exhibits territorial behavior and aggression; adults may head-butt and extend dorsal fins to drive away rivals.

Distribution. Found exclusively in the small tributaries of the Chengbi River and Jian River to the You River basin, upper reaches of the Pearl River system, Western Guangxi, China (see Fig. 9).

Beaufortia zebroida (Fang 1930)

Fig. 15

Gastromyzon pingi zebroidus Fang, 1930: 35 (original description: Donggui River, Longzhou County, Guangxi).
Beaufortia zebroidus: Hora (1932): 319.
Gastromyzon pingi zebroidus: Nichols (1943): 231.
Beaufortia pingi: Nguyen and Nguyen (2005): 282–283
Beaufortia fasciolata Nguyen & Nguyen, 2005: 588–590.
Beaufortia multiocellata Nguyen & Nguyen, 2005: 590–592.
Beaufortia triocellata Nguyen & Nguyen, 2005: 592–594.
Beaufortia zebroida: Kottelat (2012): 59–60.

Comparative materials. MMNHN1544, one specimen, holotype, not found yet, refers to the original description. SHOU20240111301-317, 33.24–49.96 mm SL, 17 specimens from Guangnan County, Xichou County, Malipo County, Funing County, Yunnan, and Napo County, Guangxi, SHOU20240111301-317, 33.24–49.96 mm SL, were collected by Lao Xing and Lin Yang from December 2021 to January 2024.

Diagnosis. *B. zebroida* shares the typical characteristics with members of the *B. pingi* species group, with distinct vertical stripes on lateral body and a pinnate-type lower lip (vs. lacking prominent vertical stripes and having a dicot-type lower lip in other congeneric species apart from this group) (see Figs 6B, 7, Table 2). *B. zebroida* can be clearly distinguished from *B. granulopinna* sp. nov. by the absence of prominent tubercles on the pectoral fin rays (vs. well-developed tubercles present on anterior 6–9 rays of pectoral fins); vertical stripes slender, narrower than inter-spacing, present consistently at all growth stages (vs. vertical stripes typically wider than inter-spacing, with a certain proportion (54.76%) of adults exhibiting blurred or vanished mid-section stripes). *B. zebroida* can be clearly distinguished from *B. viridis* sp. nov. by the vertical stripes present uneven in width and length, typically narrower than inter-spacing, sometimes reduced to dots (vs. stripes of consistent length, width, and inter-spacing); body brown yellow to golden in dorsal profile (vs. dark cyan to green). *B. zebroida* can be clearly distinguished from *B. pingi* by the stable presence of vertical stripes at all growth stages (vs. a large proportion (94.00%) of adults with blurred or vanished vertical stripes at mid-section of lateral body) and body brown yellow to golden in dorsal profile (vs. dark brown to green).

Redescription. Dorsal iii-7; anal ii-3–4 (3.98±0.14); pectoral i-20–23 (21.5±0.73); pelvic i-16–19 (17.53±0.86). Lateral-line canal pores and scales: 70–84 (75.12±3.55).

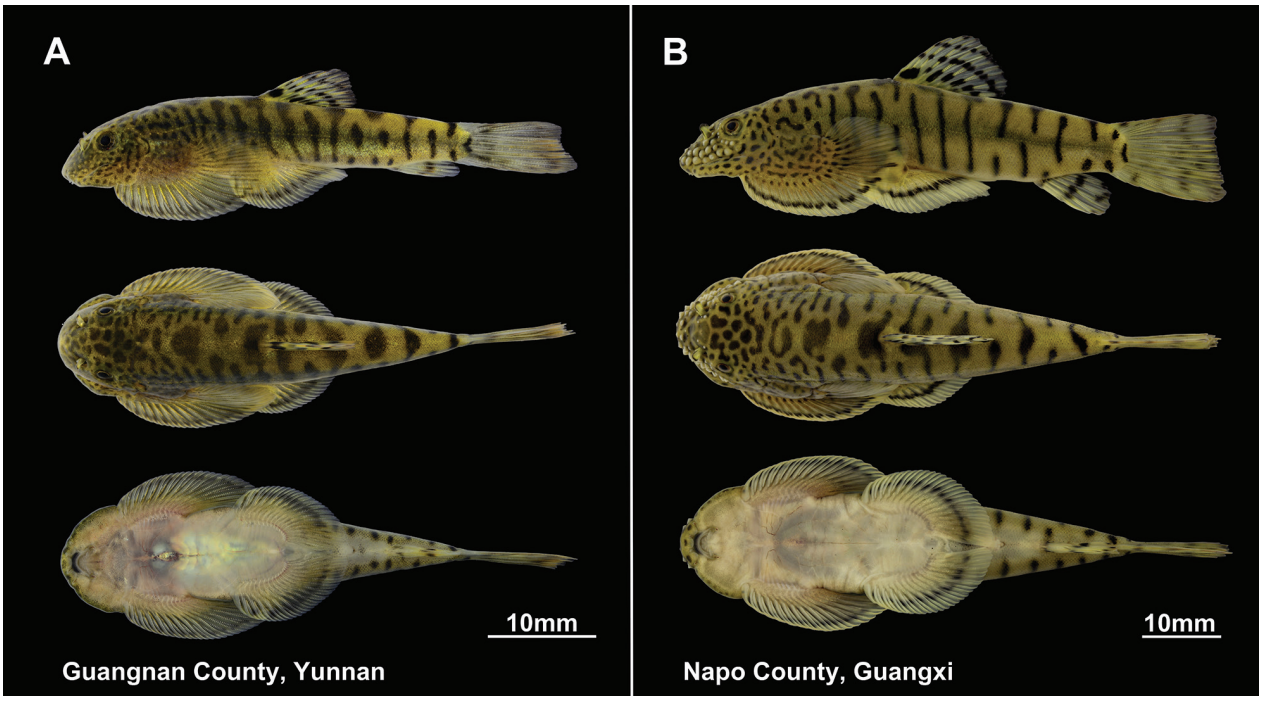

Figure 15. Lateral (top), dorsal (middle), and ventral (bottom) views of different regional phenotypes of *Beaufortia zebroida*. **A.** Regional phenotype from a stream tributary to the Red River, Guangnan County, Yunnan, SHOU20240111308, 36.64 mm SL; **B.** Regional phenotype from Napo County, Guangxi, SHOU20240316602, 56.12 mm SL, originating from upstream within the same basin as the type locality.

Morphometric measurements for the specimens examined are given in Table 3. See Fig. 15 for lateral, dorsal, and ventral views of the body.

Body closely resembles *B. viridis* sp. nov. in general shape and structure, but significantly different in stripes pattern and coloration.

Coloration in preservation. Preserved specimens from sub-adult to adult stage, body brown yellow to grey, white ventrally. Head with black spots or vermiculation dorsally, 2–5 larger black blotches along mid-dorsal body anterior to dorsal fin. Sides with 8–15 vertical dark stripes, varying greatly in length, which sometimes appearing as dots, stripe width narrower than inter-spacing, present at all growth stages. Paired fin margins hyaline or pale white, inner edges with continuous or dotted black arc. Dorsal fin hyaline, with black stripes, one black spot on the root before the second branched ray.

Coloration in live. In life, body brown yellow to golden in dorsal profile. Mature individuals with a more vivid golden coloration, and fin membranes pale yellow.

Individual variation. Among 17 specimens, one (SHOU20240111307) had three branched anal fin rays.

Ethology. Inhabits shallow streams with rapid currents and smooth pebble substrates that adhere to crevices between stones. Feeds on algae and small invertebrates and consumes mucus from fresh fish carcasses. Exhibits territorial behavior.

Distribution. Exclusively in small tributaries on the north bank of the mid-lower Red River system and the upper Shuikou River to Zuo River basin (upper Pearl River system), from Maguan County, Wenshan Zhuang, and Miao Autonomous Prefecture, Yunnan, to Longzhou County, Guangxi, near the China-Vietnam border, extending into northeastern Vietnam (see Fig. 9).

Genetic distances and phylogenetic analysis

A total of 35 mitochondrial *cyt*b gene haplotypes were obtained. The computed genetic distances revealed that *B. granulopinna* sp. nov. shared the smallest average genetic distance with *B. zebroida* at 10.80% (with the maximum interspecific genetic distance reaching 11.37%). Intraspecific genetic distances ranged from 0.26% to 5.12%, with an average of 3.63%, surpassing the average intraspecific genetic distances of all other species within the same genus. *B. viridis* sp. nov. exhibited a minimum average interspecific genetic distance with *B. pingi* of 4.60% (with a maximum interspecific genetic distance of 5.2%), significantly exceeding the current minimum intrageneric interspecific distance. Intraspecific genetic distances ranged from 0.09% to 2.80%, with an average of 1.47%, exceeding the average intraspecific genetic distances of all other congeneric species except for *B. granulopinna* sp. nov. *B. zebroida* had a minimum average genetic distance with *B. pingi* of 5.62% (with the maximum interspecific genetic distance at 5.88%), considerably above the current minimum intrageneric interspecific distance. The genetic distances between the aforementioned species and those within the *B. pingi* species group were smaller, indicating

their affiliation with the *B. pingi* species group, aligning with morphological classification results.

Notably, the genetic distance between *B. niulanensis* and *B. szechuanensis* was only 0.53%, whereas the *B.* cf. *szechuanensis* collected from Qijiang, Chongqing (a tributary on the southern bank of the upper Yangtze River) morphologically conformed to *B. szechuanensis* but exhibited a genetic distance of 2.30% from *B. szechuanensis*, exceeding the genetic distance between *B. polylepis* and *B. szechuanensis* (2.20%) (see Table 5).

Phylogenetic trees generated using maximum likelihood and Bayesian inference methods exhibited identical topological structures, with all nodes demonstrating high support values. All species within the *B. pingi* species group coalesced to form a single clade, with each species within this clade establishing distinct lineages. Among these, *B. pingi* and *B. viridis* sp. nov. were identified as sister taxa positioned at the derived end of the phylogenetic tree, followed by *B. zebroida* as a sister group to the aforementioned species. *B. granulopinna* sp. nov. was situated at the most basal position within the *B. pingi* species group clade, with a relatively longer branch length indicating an early divergence.

The remaining species formed another clade, distinctly divergent from the *B. pingi* species group, which aligns with the classification results based on morphological characteristics. Within this clade, two significantly divergent lineages were identified. One lineage was composed of all haplotypes of *B. kweichowensis* and *B. leveretti*. The other lineages included *B. szechuanensis*, *B. polylepis*, *B. niulanensis*, and *B.* cf. *szechuanensis*. (see Fig. 16).

Table 5. Inter-specific mean mitochondrial *cyt*b genetic distances, maximum genetic distances among species, and intra-specific genetic distances within the genus *Beaufortia* in Kimura 2-parameter genetic distance analysis.

	Species (haplotype count)	Between species mean distance (below diagonal) and maximum distance (above diagonal)) (%)										Within species distance (%)	
		1	2	3	4	5	6	7	8	9	10	Range	Mean
1	***B. viridis* sp. nov.** (5)		5.20	7.52	11.45	15.71	15.74	17.40	17.67	17.54	17..83	0.09–2.80	1.47
2	*B. pingi* (8)	4.60		5.88	11.46	15.70	16.33	17.37	17.77	17.26	17.93	0.09–0.89	0.50
3	*B. zebroida* (4)	7.07	5.62		11.37	16.29	15.56	16.27	16.66	16.04	16.31	0.09–0.53	0.28
4	***B. granulopinna* sp. nov.** (5)	10.86	11.15	10.80		16.43	16.97	17.78	17.51	17.18	17.67	0.26–5.12	3.63
5	*B. kweichowensis* (3)	15.31	15.53	15.68	16.13		3.86	14.22	14.00	14.24	14.02	0.09–2.06	1.37
6	*B. leveretti* (1)	15.51	16.19	15.50	16.25	3.44		13.64	13.65	13.89	13.80	–	–
7	*B. niulanensis* (2)	15.77	16.92	16.05	17.04	13.80	13.58		0.71	2.34	2.25	0.09	0.09
8	*B. szechuanensis* (2)	16.16	17.25	16.31	17.39	13.71	13.53	0.53		2.43	2.53	0.44	0.44
9	*B. polylepis* (4)	16.28	16.84	15.84	16.94	13.91	13.77	2.11	2.20		3.09	0.18–0.35	0.23
10	*B.* cf. *szechuanensis* (1)	16.44	17.54	16.16	17.37	13.82	13.80	2.20	2.30	2.90		–	–

"-" stands for no corresponding data.

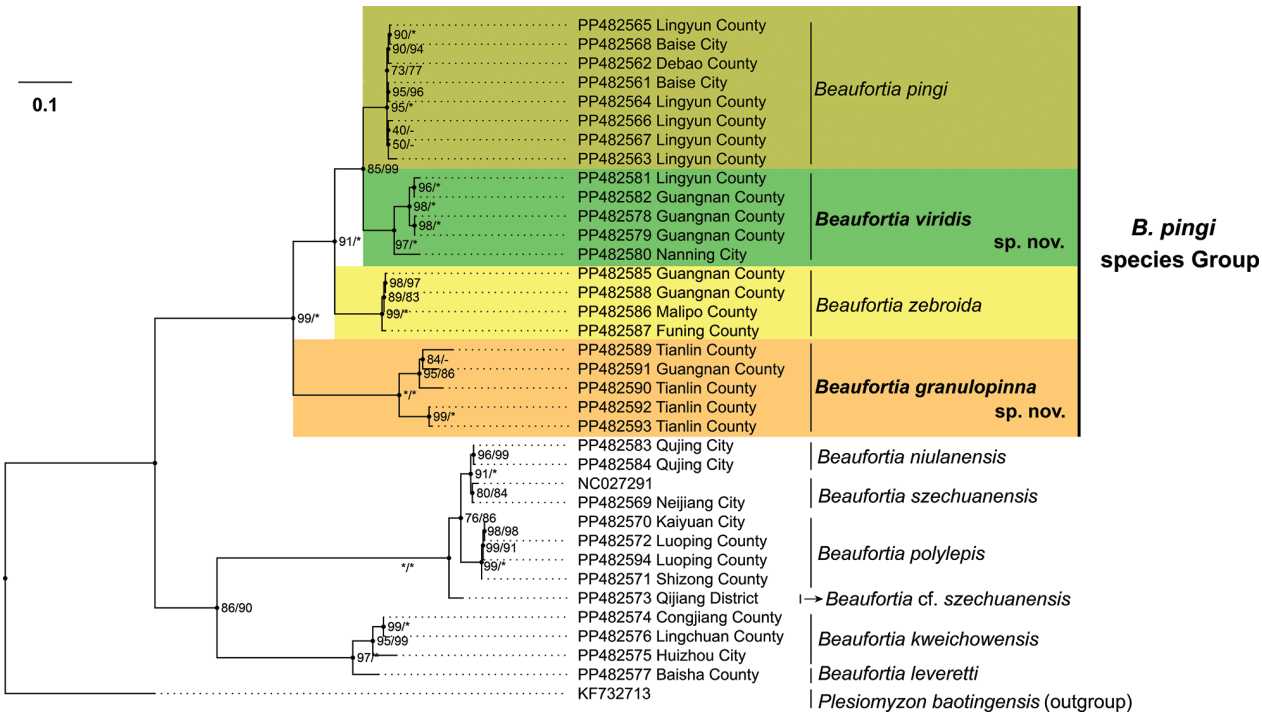

Figure 16. Phylogenetic tree of *Beaufortia* species based on haplotypes of mitochondrial *cyt*b genes, with the tree topology inferred through maximum likelihood (ML) and Bayesian inference (BI) methods. Support values for each branch are indicated at the nodes (ML/BI), with "*" denoting bootstrap values of 100% or posterior probabilities of 1, and "-" indicating insufficient genetic variation to display posterior probabilities.

Morphological characteristics of the *Beaufortia pingi* species group

The preceding phylogenetic results have confirmed that the *Beaufortia pingi* species group constitutes a monophyletic clade and exhibits significant genetic divergence from other *Beaufortia* species. Morphologically, this group is distinctly differentiated from other species. The lower lip of the species group can be represented by a pinnate-type appearance, being overall slender with a central indentation and multiple lobed sides. There is variation among individuals in the number of lobes and the depth of the clefts, with most specimens possessing no fewer than three lobes and the depth of clefts exceeding that found in species outside this group. The extremities of the lower lip extend to the corners of the mouth, with several wart-like protrusions present on the extended parts (Fig. 6). In contrast, species outside this group possess a dicot-type lower lip, which is broad and short with a central indentation, and sides that are not lobed but occasionally have 0–2 shallow notches. The ends of the lower lip do not extend to the corners of the mouth, or the extension is poorly developed and lacks protrusions (Fig. 7). Additionally, the *Beaufortia pingi* species group is characterized by distinct vertical stripes along the body sides, a feature absent in other *Beaufortia* species.

Morphometric variability within the *Beaufortia pingi* species group

B. pingi has more branched rays in its paired fins, with an average of 22.19±0.78 in pectoral fins and 18.64±0.97 in pelvic fins. In contrast, *B. granulopinna* sp. nov. exhibits fewer branched rays in its paired fins, averaging 20.11±0.77 in pectoral fins and 16.51±0.86 in pelvic fins.

Differences in morphometric proportions were observed among the four species within the *Beaufortia pingi* group. *B. granulopinna* sp. nov. and *B. pingi* have comparatively taller bodies, as reflected in lower mean SL/BD ratios (5.10±0.43 and 5.09±0.71, respectively) compared to those observed in *B. viridis* sp. nov. and *B. zebroida* (5.31±0.54 and 5.47±0.33, respectively). *B. pingi* is distinguished by a broader body, as evidenced by smaller mean ratios of SL/BW and SL/PW (4.2±0.36 and 7.42±0.39, respectively), a shorter head, indicated by a larger mean SL/HL (4.9±0.18), and a narrower mouth, denoted by a larger mean HW/MW (5.79±0.5). Compared to the other three species, *B. granulopinna* sp. nov. features a shorter and thicker caudal peduncle, as shown by the smaller mean SL/CD and PoAL/CD (8.36±0.52 and 1.29±0.11, respectively).

Variability in morphometric characteristics is observed within populations of *B. viridis* sp. nov. from different regions. Specimens from Lingyun County possess a more robust anterior body segment, with wider and taller heads and trunks (PrPvL/HW=1.53±0.08, PrPvL/PW=0.99±0.03, PrPvL/BW=1.73±0.07, PrPvL/BD=1.98±0.15, PrPvL/HD=2.48±0.12, PrPvL/PW=1.25±0.05), and a thicker caudal peduncle (PrPvL/CD=3.59±0.28). The population from the type locality, Wuming District, Nanning City, exhibits fewer branched rays in the paired fins (pectoral fins 20.25±0.68, pelvic fins 16.5±0.71).

Compared to the type locality, the population from Debao County is characterized by a broader and flatter body (PW/BD=2.32±0.19) and a thinner caudal part (PoAL/CD=1.69±0.09) (see Table 4).

It is noteworthy that, despite the statistically significant and visually discernible differences in measurable characteristics, the presence of overlap among different species precludes recommending these characteristics as reliable bases for species identification.

Discussion

Taxonomic clarification and redescription of *Beaufortia pingi*

In 1930, Fang described *Gastromyzon pingi* with the type locality specified as Lingyun County in 1928. He mentioned two collection sites, one near the boundary of Yunnan Province (type locality) and the other in Damaoping Village. At that time, the jurisdiction of Lingyun County was more extensive, bordering Yunnan and encompassing the current eastern area of Tianlin County. The county's watershed includes the Xiyang River, Bo′ai River, Jia River (currently Leli River), and Chengbi River. This broad and somewhat vague collection range coincides with the primary distribution area of the *Beaufortia pingi* species group. Given the relatively short geographical distances between distribution areas of different species within this region, it is highly probable that the type specimens could actually belong to different species. The paratype specimen NO. 955 exhibits a notably lower count of pectoral fin rays, a distinguishing characteristic of *B. granulopinna* sp. nov. from *B. pingi*. Excluding the lateral line scale count, the morphological features of the remaining specimens align with those of *B. pingi* specimens collected from the Chengbi River basin within the current boundaries of Lingyun County. The scales of the *B. pingi* species group are exceptionally fine, often less than 0.5 mm in diameter, suggesting that the original counts might have been inaccurately high due to the limitations of observation equipment.

Apart from the Chengbi River basin, *B. pingi* was also collected from the Jian River basin in Debao County. Compared to the holotype, these specimens have slightly fewer ventral fin rays and a somewhat broader and flatter body, but they share the main differential features of the species. The genetic distance of the mitochondrial *cyt*b gene is less than 1%, indicating minor genetic variation, and phylogenetically, these specimens cluster within the same lineage as *B. pingi*.

In summary, the species within the *Beaufortia pingi group* are geographically proximate and morphologically similar. The type locality of *B. pingi* is relatively indistinct, and the age of the specimens complicates identification. The inclusion of other species among the paratypes, the original vague description, and some inaccuracies in detail present challenges. Considering these issues, we have conducted a redescription of *B. pingi* based on extensive specimen collection, morphological comparisons, and molecular phylogenetic analysis.

Taxonomic clarification and redescription of *Beaufortia zebroida*

Gastromyzon pingi zebroidus was also described in the same article, in which Fang (1930) described *Gastromyzon pingi* with a single-type specimen collected from the Dongui River along the China-Vietnam border in Longzhou County, Guangxi Province. Since its publication, no further records of this species have been found in that basin. Despite multiple surveys in Longzhou County, the species was not rediscovered, and the local rivers, mostly altered by human activities and facing severe bioinvasions, significantly reduced the habitats suitable for gastromyzonids.

The limited information from a single specimen, coupled with the low distinctiveness of the illustrations and the relatively vague morphological description of *Gastromyzon pingi zebroidus*, has led to significant controversy over the identity of this species and multiple changes in its taxonomic status.

In the original description, Fang (1930) distinguished this subspecies by the anal pore's proximity to the posterior edge of the ventral fins and the presence of stripes along the entire flank (vs. the anal position being further from the posterior edge of the ventral disc and stripes being pronounced at the caudal peduncle in *Gastromyzon pingi*). Later, Hora (1932) elevated its taxonomic status to species level as *Beaufortia zebroidus* without providing justification. Nichols (1943) followed Fang's (1930) perspective, considering it a subspecies of *Gastromyzon pingi*.

Chen (1980), upon examination of two specimens from the Xijiang River (location unspecified), with total lengths of 29 mm and 52 mm, respectively, observed that both specimens exhibited pronounced or faint vertical stripes and noted the anal pore situated at a considerable distance from the ventral fins. Consequently, Chen tentatively synonymized *Beaufortia zebroidus* with *Beaufortia pingi*, pending further collection of specimens for a definitive conclusion. According to our observations, the vertical stripes on juvenile stages of *B. pingi* typically do not disappear, and the specimen measuring 29 mm in length is likely in a late juvenile stage. Therefore, the species in question is inferred to be *B. pingi*.

Yue (1981), upon examination of nine specimens from Lingyun County, Guangxi, identified them as *B. pingi* and noted the presence of 2–4 transverse vertical stripes on the caudal peduncle. The presence and clarity of stripes anterior to the caudal peduncle varied among individuals, with some exhibiting up to 10 distinct stripes. The anal pore was observed to be closer to the anal fins than to the posterior edge of the ventral fins, with distance varying across the specimens. Notably, one specimen, No.74664, possessed an anal pore precisely at the posterior edge of the ventral fins. Based on these findings, Yue proposed that *B. zebroidus* could be a synonym of *B. pingi* or not a valid subspecies. Zheng (1989) examined 15 specimens from Lingyun County, Guangxi, and Xingyi County, Guizhou, and identified them as *B. pingi*. Zheng observed the terminal rays of the ventral fins connecting medially on both sides, with a notch at the end (presumably a typographical error for "a pair of notches"), the posterior edges located near the anal pore or slightly distant, and 11–13 transverse bands across the dorsal midline accompanied by approximately 20 vertical stripes. The presence of unclear stripes, visible only at the caudal peduncle in some individuals, led Zheng to consider *B. zebroidus* a junior synonym of *B. pingi*. Both researchers examined the specimens from the type locality, and given that Lingyun County is habitat to both *B. pingi* and *B. viridis* sp. nov., the possibility of these specimens comprising two distinct species cannot be excluded.

Subsequently, Chen (1990) examined 21 specimens from the Xiyang River in Guangnan County, Yunnan, identifying them as *B. pingi*. The observations revealed that the tips of the pelvic fin rays were proximal to the anal pore in all specimens, with numerous dark and light stripes along the dorsal midline and flanks. Chen thus regarded *B. zebroidus* as a junior synonym of *B. pingi*. Our research indicates that the species distributed in the Xiyang River is *B. viridis* sp. nov., and given the consistent presence of vertical stripes in all specimens, the referenced species is likely *B. viridis* sp. nov.

Later, Chen and Tang (2000) measured three specimens from Tian'e, Guangxi, noting that the posterior edges of the pelvic fins were proximal to the anal pore. The dorsal and lateral sides exhibited approximately 20 black vertical stripes, with the pre-pelvic length significantly exceeding the distance from the pelvic fin origin to the anal fin origin. The branched ray count in the paired fins (pectoral 19, pelvic 15–16) was slightly lower than that observed in the specimens from the type locality of *B. pingi* (pectoral 21–23, pelvic 18–20), leading them to recognize *B. zebroidus* as a valid species. We noted that the branched ray counts in the paired fins of the specimens collected from Tian'e County fell within the variation range of the specimens from the type locality of *B. viridis* sp. nov., with the pre-pelvic length generally greater than the length from the pelvic origin to the anal origin (mean PrPvL/POAO=1.19±0.74), distinct from the specimens from the type locality of *B. pingi* (PrPvL/POAO=0.98±0.66). Hence, the specimens collected from Tian'e County are identified as *B. viridis* sp. nov.

Chen and Zhang (2006), after examining six specimens from Tianlin County and Lingyun County and referencing Chen and Tang (2000), encountered individuals exhibiting characteristics of both *B. pingi* and *B. zebroidus* (presence or absence of vertical stripes, count of branched rays in paired fins, PrPvL/POAO ratio), thereby considering *B. zebroidus* a synonym of *B. pingi*. Tianlin County serves as the type locality for *B. granulopinna* sp. nov. Our statistical analysis indicates that a certain proportion of vertical stripes disappear in the adult stages of both *B. granulopinna* sp. nov. and *B. pingi* (54.76% and 94.00%, respectively). The branched ray counts in the paired fins of *B. granulopinna* sp. nov. are also marginally less than those of *B. pingi*, and the PrPvL/POAO ratios for both species fluctuate around 100% (as shown in Table 3). Moreover, we observed that the photographs provided by the authors (original fig. X 98), which depicted *B. granulopinna* sp. nov., showed the first few rays of the pectoral fins exhibiting well-developed tubercles. Therefore, the batch of specimens actually represents a mix of *B. pingi* and *B. granulopinna* sp. nov. from their type localities.

Finally, Kottelat (2012) recognized *B. zebroidus* as a valid species, changing the suffix to -a, and synonymized *B. fasciolata*, *B. multiocellata*, and *B. triocellata*, collected from the China-Vietnam border, with *B. zebroida*.

After investigating all possible distribution areas and combining morphological analysis with mitochondrial *cyt*b gene phylogenetic analysis, we conclude the following:

The type locality of *B. zebroida* is the border river between China and Vietnam. Among all the literature records, the ones closest to the type locality are the collection sites of *B. fasciolata*, *B. multiocellata*, and *B. triocellata*. Although the type specimens of these three species are lost, their original descriptions and unclear illustrations still confirm that they belong to the same species as our specimens collected from the southeastern Yunnan Province to the western Guangxi border area with Vietnam. Fang (1930) mentioned the specimen color as pale fleshy, which aligns with the body color of the aforementioned populations but not with *B. pingi* and *B. viridis* sp. nov. Thus, we consider *B. zebroida* a species distributed from Maguan County in Yunnan Province to Longzhou County in Guangxi Province along the China-Vietnam border, as well as in northeastern Vietnam. The region contains small tributaries flowing to both the Red River and the Zuo River (Pearl River system), closely spaced due to the karst landscape, facilitating stream capture and exchange. The type locality, Longzhou County, represents the eastern boundary of the species' distribution, but due to habitat destruction and bioinvasions, no further records of this species have been found there. Besides this area, the species has been discovered in Maguan County, Guangnan County, Xichou County, Malipo County, Funing County, and Napo County (stream tributary to the upper reaches of the Shuikou River, same basin as the type locality) within China and northeastern Vietnam. Following the clarification of its taxonomic status, we have provided a redescription of *B. zebroida*.

Key to the *Beaufortia pingi* species group

1 Vertical black stripe on flank absent; lower lip dicot-type, sides not lobed or with 1–2 small notches...other *Beaufortia* species
– Flank with multiple vertical dark stripes; lower lip pinnate-type, sides multilobed 2
2 Adult pectoral fins with 6–9 rays bearing well-developed granular nuptial tubercles ..... *B. granulopinna*
– Nuptial tubercles on adult pectoral fin rays absent or indistinct 3
3 Vertical stripes in a large proportion (94.00%) of adults show blurred or vanished before caudal peduncle ..... *B. pingi*
– Vertical stripes consistently present at all developmental stages, not blurring or vanishing 4
4 Vertical stripes uniform in width and length, often wider than spacing; dorsal body dark cyan to green..... *B.viridis*
– Stripes uneven in width and length, often narrower than spacing, sometimes reduced to dots; body brown yellow to golden dorsally..... *B.zebroida*

Survival status and conservation recommendations for the *Beaufortia pingi* species group

The research on the Beaufortia *pingi* group is mostly in its initial stages; however, their situation is far from optimistic. These species have become popular ornamental fish in China. Aquarium trade operators reap substantial profits through the capture and sale of these fish from the wild, yet among them are those who act with disregard for sustainability; their harvesting practices are often destructive. Given their rheophilic nature, projects that obstruct rivers can easily lead to regional extinction. Their low pollution tolerance and sensitivity to changes in water quality also contribute to the significant reductions in population that many species are suffering. In the type locality of *B. viridis* sp. nov., Wuming District, Nanning City, most small tributaries have been modified into step-like reservoirs for water storage, and those near agricultural irrigation areas are polluted, rendering these areas unsuitable for their survival. Interestingly, a stable population was discovered inside a commercial eco-camping site. To satisfy consumers' pursuit of "pristine nature," contractors have left some river sections poor developed, providing a refuge for this species. We suggest that future efforts should focus on increasing attention to these species, conducting

fundamental research, and further exploring their scientific and economic potential. Simultaneously, it is crucial to enhance habitat conservation awareness, scientifically plan, and develop sustainably, ensuring harmonious coexistence between humans and nature.

Comparative materials

Beaufortia szechuanensis: SHOU20231220601, one specimen, 59.18 mm SL, from Wanzhou District, Chongqing, upper Yangtze River basin. SHOU20231220602, one specimen, 42.94 mm SL, from Qijiang District, Chongqing, upper Yangtze River basin. SHOU20231220640-642, three specimens, 46.17–54.93 mm SL, from Neijiang City, Sichuan, upper Yangtze River basin. Collected by Jing-Chen Chen and Hao-Tian Lei.

Beaufortia liui: SHOU20240225701, one specimen, 36.64 mm SL, from Huidong County, Sichuan, upper Yangtze River basin. Collected by Can Liu. IHASW83VI0424-425, two specimens, from Huidong County, Sichuan, upper Yangtze River basin, inspection only. IHW 2247, 2446, two specimens, syntype, inspection only.

Beaufortia niulanensis: SHOU20231220614-615, SHOU20231220617, three specimens, 41.38–43.66 mm SL, from type locality, Qujing City, Yunnan, upper Yangtze River basin. Yangtze River basin. Collected by Xin-Rui Pu, Lao Xing, and Lingzi.

Beaufortia polylepis: SHOU20231220643-644, two specimens, 40.06–41.02 mm SL, from downstream near the type locality, Kaiyuan City, Yunnan, upper Nanpan River (Pearl River system). Collected by Lin Yang. IHW 774330, one specimen, syntype, inspection only.

Beaufortia huangguoshuensis: IHASW83IV0049, one specimen, syntype, and fin rays were counted; the other data refers to Chen and Tang (2000).

Beaufortia intermedia: IHW 87IV516, one specimen, paratype, inspection only. Measurement data refers to Tang et al. (1997).

Beaufortia leveretti: SHOU20231212626-627, two specimens, 44.65–52.42 mm, from Fangchenggang City, Guangxi, collated by Qian-Yu Liang. SHOU20231212628-630, three specimens, 59.94–64.71 mm, from type locality, Baisha County, Hainan, collector unknown.

Beaufortia kweichowensis: SHOU20231212601-602, two specimens, 53.77–55.24 mm, from Congjiang County, Guizhou, Duliu River (Pearl River system). SHOU20231212614-616, three specimens, 44.38–47.77 mm, from Pingle County, Guangxi, Li River (Pearl River system). Collected by Jing-Chen Chen.

Beaufortia cyclica: IHASW75IV1417, one specimen, holotype, inspection only. Measurement data refers to the original description.

Beaufortia yunnanensis, *Beaufortia fasciolata*, *Beaufortia triocellata*, *Beaufortia multiocellata*, *Beaufortia buas*, *Beaufortia daon*, *Beaufortia elongata*, and *Beaufortia loos*: Referenced original descriptions (Li et al. 1998; Kottelat 2001; Nguyen and Nguyen 2005).

Contributions

Jing-Chen Chen conducted sample collection, specimen identification and measurement, photography, map drafting, molecular genetic analysis, and manuscript composition. Jia-Jia Li was responsible for specimen measurement, illustration of measurement methodologies, and molecular genetic experimentation. Wen-Qiao Tang provided guidance on research concepts as well as review and revision of the manuscript. Xin-Rui Pu participated in sample collection and specimen identification. Hao-Tian Lei carried out specimen collection and grammatical checks.

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