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On the identity of *Culter oxycephalus* (Teleostei, Cypriniforms, Xenocyprididae), with notes on the validity of eight cultrin fish species from East Asia

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1 On the identity of *Culter oxycephalus* (Teleostei, Cypriniforms,

2 Xenocyprididae), with notes on the validity of eight cultrin

3 fish species from East Asia

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9 Abstract

10 The identification problems of cultrin fish species from East Asia are discussed. Culter oxycephalus Bleeker, 1871 is found to be a senior synonym of Culter 11 oxycephaloides Kreyenberg & Pappenheim, 1908 and is redescribed. Culter 12 abramoides Dybowski, 1872 is a senior synonym of Erythroculter dabryi shinkainensis 13 Yi & Zhu, 1959. Examination of three specimens identified as Erythroculter 14 15 recurviceps and Culter oxycephalus by John Treadwell Nichols was found to be in error. Based on the data obtained during the field survey and coupled with known literature 16 and the latest taxonomic development of relevant taxa, there are five and six cultrin 17 fishes in Lake Dongting and Lake Xingkai, respectively, namely the Bream-shaped 18 Culter Chanodichthys abramoides, Dabry's Culter Chanodichthys dabryi, Topmouth 19 Culter Chanodichthys erthropterus, Mongolian Culter Chanodichthys mongolicus, 20 Sharphead Culter Chanodichthys oxycephalus, Predatory Culter Culter alburnus and 21 Culter compressocorpus. This study clarifies the interrelationships between 22 23 Chanodichthys oxycephalus and Chanodichthys oxycephaloides, and taxonomically explains the absence of records of the Sharphead Culter for more than half a century. 24 We also report six cultrin fishes distributing in the Heilong-Jiang basin of China: 25 Chanodichthys abramoides, Ch. dabryi, Ch. erythropterus, Ch. mongolicus, Culter 26 alburnus and C. compressocorpus. 27

28 Key words

29 Taxonomy; Morphological character; Species and distribution; Culter; Chanodichthys

30 Introduction

Cultrin fishes of the genus Chanodichthys and Culter belong to the family 31 32 Xenocyprididae (Cypriniformes) (Fricke et al. 2024), and constitute an important part 33 of this endemic carp family of East Asia (Chen et al., 2022a). Both genera are widely distributed in Russia, Korea Peninsula, Vietnam, and throughout China, except the 34 Tibetan Plateau (Xiong et al., 2019). Most species of this group are common fishes in 35 rivers and lakes and have an important economic value (Peng et al., 2009; Wang et al., 36 2017). The vast majority of the cultrin fishes of the Xenocyprididae belongs to East 37 Asian taxa with a relatively short evolutionary history (about 12 Myr), and the 38 phylogenetic relationships among them are still unclear (Chen et al., 1998). 39

Previous studies on cultrin fishes are numerous, but mainly focused on the 40 taxonomy of the genera Chanodichthys and Culter, e.g., Bleeker (1871b); Berg (1934); 41 Smith (1938); Myer (1940); Yi and Zhu (1959); Bănărescu (1967a); Li (1992); Luo 42 (1994); Luo and Yue (1996); as well as studies on basic biology and population 43 dynamics, e.g., Chen (1959); Yang et al. (2009); Duan et al. (2015); Hu et al. (2015); 44 Wang et al. (2016); Wang et al. (2017); Lin et al. (2021). Phylogenetic studies of the 45 traditional subfamily Cultrinae suggest that the current classification system of this 46 subfamily may be inaccurate (Wang, 2007; Tang et al., 2013; Chen et al., 2022a). 47

Previous studies on the genera Chanodichthys Bleeker, 1860 and Culter 48 49 Basilewsky, 1855, such as Huang et al. (2005); Feng et al. (2008); Feng et al. (2009); Peng et al. (2009), have mainly focused on a few species, such as Dabry's Culter 50 (Chanodichthys dabryi), Mongolian Culter (Chanodichthys mongolicus), Topmouth 51 Culter (Chanodichthys erthropterus), and Predatory Culter (Culter alburnus). Other 52 cultrin fish species have received less attention, and the related studies basically 53 remained at the population level (Liu and Yang, 2014; Xu et al., 2014; Zhang et al., 54 2014; Yang et al., 2016; Xiang et al., 2021), examples are studies on Hainan Culter, 55

Shinkai Dabry's Culter and Sharphead Culter. Especially for the Sharphead Culter 56 (Chanodichthys oxycephalus), relevant records are scarce after Bleeker's (1871a) 57 original description. The available records can be divided into two parts, one consists 58 of generalized summaries of historical literature, such as Sauvage and Dabry de 59 Thiersant (1874); Nichols (1943); Wu (1964); Zhang and Zhao (2016); and the other 60 part consists of ecological surveys that lack a taxonomic scrutiny, such as Zhang (2007); 61 Tang et al. (2011); Tang et al. (2015); Yang et al. (2022). During this period there have 62 been published some taxonomic studies involving the Sharphead Culter with different 63 conclusions, such as Bogutskaya and Naseka (2004); Zhang et al. (2008); Kottelat 64 (2013) and Wang et al. (2019). 65

Recent studies on cultrin fishes, e.g., Kottelat (2013) and Chen *et al.* (2022b)
suggest that the genus *Culter* Bleeker, 1860, consists of two species, *Culter alburnus*Basilewsky, 1855 and *Culter compressocorpus* Yi & Zhu, 1959 (authors also seen as
Yih & Chu) (Fricke *et al.* 2024). All other species formerly included in the genus *Culter*should be placed in the genus *Chanodichthys* Basilewsky, 1855.

71 To investigate the problem of the validity of several cultrin fish species, we collected fishes in various waters of the Yangtze River (= Chang-Jiang in Chinese) basin. 72 We collected 103 specimens provisionally identified as Chanodichthys oxycephalus and 73 / or *Chanodichthys oxycephaloides*. We also reviewed the curated specimens (71 ind.) 74 from other basins (Heilong-Jiang, Lake Xingkai) to clarify the relationship between 75 Chanodichthys oxycephalus and Ch. oxycephaloides, and we tried to give a 76 taxonomically rational explanation for the lack of official records of the Sharphead 77 Culter for more than 60 years. This study once again revealed and emphasized the 78 79 importance of reviewing type specimens and consulting the literature with the original descriptions. 80

81 Material and methods

82 Specimen sampling and preservation

83 Specimens utilised for this study were sampled in accordance with the Chinese

Laboratory Animal Welfare and Ethics animal welfare laws (GB / T 35892–2018). After being anaesthetised, all captured individuals were fixed by immersion in ethanol or formalin. Specimens were collected using gill nets, trap nets and electrofishing. Caught specimens of cultrin fishes were stored in 10% formalin for morphological examination. The voucher specimens are deposited in the collection of the Museum of Aquatic Organisms at the Institute of Hydrobiology (IHB), Chinese Academy of Sciences (CAS).

91 Morphological analysis

Measurements were taken point to point (schematic picture see Fig. 1) with a digital 92 caliper connected directly to a data-recording computer and data recorded to the nearest 93 0.1 mm. Measurements were taken on the left side of specimens whenever possible, 94 95 following methods used by Kottelat (2001) and Song et al. (2018). The head length and measurements of other parts of the body are given as percentages of standard length 96 (SL). Measurements of parts of the head are given as proportions of the head length 97 (HL) (Tables 1, 2). The counts of vertebrae were taken from radiographs of Micro-CT 98 99 or X-rays. The specimens examined in this study are deposited in the collections of: AMNH American Museum of Natural History, New York; IBTS Taxonomy Research 100 Group, Research Centres in Biology Field, University of Bucharest, Tr. Savulescu, 101 Bucharest, Romania; IHB Institute of Hydrobiology, Wuhan, China; MCZ Museum of 102 Comparative Zoology, Harvard University, Cambridge, Massachusetts; MHNL 103 Muséum d'histoire naturelle de Lyon, Lyon; MNHN Muséum National d'Histoire 104 Naturelle, Paris; ZIN Zoological Institute of the Russian Academy of Sciences, St. 105 Petersburg; ZMB Museum für Naturkunde - Leibniz Institute for Evolution and 106 107 Biodiversity Science, Berlin; ZMFMIB Zoologial Museum, Fan Memorial Institute of 108 Biology, Tsinghua University, Beijing, China (now in ASIZB).

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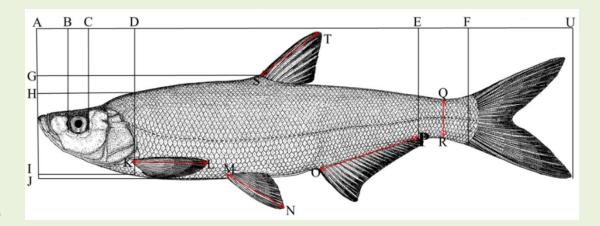




Fig. 1 Schematic picture of a cultrin fish (Illustrated by Zhi-Xian Sun). A-F: Standard
length (SL: mm); A-U: Total length; A-B: Snout length; B-C: Eye diameter; A-D: Head
length; H-I: Head depth; G-J: Body depth; E-F: Caudal peduncle length; Q-R: Caudal
peduncle depth; K-L: Pectoral length; M-N: Pelvic length; O-P: Anal length; S-T:
Dorsal length.

Table 1. Morphometry of *Chanodichthys oxycephalus*. Measurements are in percentage
of standard length, except for standard length (SL). SD: standard deviation; r: Pearson's
correlation coefficient; p: significance; linear regression parameters calculated from
measurements.

Measurements	N	Min	Max	Mean	SD	slope	intercept	r	5
Measurements	IN	IVIIII	IVIAX	Mean	3D	(b)	(a)	(SL)	р
SI (mm)	3	66.	236.	136.8	52.				
SL (mm)	0	71	74	4 8 43					
Snout length	3	4.6	17.5	10.38	3.8	13.36	-1.75	0.99	<0.
	0	7	5	10.38	9	15.50	-1.75		01
	3	4.4	10.8	7 22	1.9	26.91	-60.39	0.99	<0.
Eye diameter	0	1	8	7.33	2	20.91			01
Head langth	3	17.	59.6	26 12	13.	2.01	-5.62	0.99	<0.
Head length	0	00	9	36.43	33	3.91	-3.02	0.99	01
Eve donth	3	1.3	0.45	196	2.2	22.21	29.51	0.07	<0.
Eye depth	0	8	9.45	4.86	9	22.31	28.51	0.97	01

Eye-Head depth	3	7.1	24.0	13.26	4.8	10.60	-3.66	0.99	<0.
Eye-nead depui	0	1	2	15.20	8	10.00	-3.00	0.99	01
Haad danth	3	9.8	32.6	18.66	7.0	7.40	-1.30	1.00	<0.
Head depth	0	2	5	18.00	5	7.40	-1.50	1.00	01
Dody donth	3	15.	69.9	35.65	16.	3.24	21.45	0.99	<0.
Body depth	0	19	4	55.05	04	5.24	21.43	0.99	01
Caudal peduncle	3	8.9	26.6	15.86	5.2	9.49	-13.63	0.95	<0.
length	0	6	6	13.00	3	9.49	-13.03	0.95	01
Caudal peduncle	3	6.0	25.8	12.45	6.0	8.39	32.43	0.07	<0.
depth	0	3	4	12.43	8	0.39	52.45	0.97	01
Destoral langth	3	11.	47.7	23.02	10.	4.82	25.04	0.96	<0.
Pectoral length	0	47	4	25.02	50	4.02	25.94	0.90	01
Pectoral height	3	2.9	12.6	6.74	3.0	16.07	28.54	0.95	<0.
	0	9	4		9				01
Pectoral-Body	3	12.	57.1	28.92	12.	4.00	21.19	0.98	<0.
depth	0	98	3	20.92	88	4.00	21.19	0.98	01
Pelvic length	3	8.8	42.4	20.59	9.6	5.33	27.19	0.98	<0.
r ervic length	0	2	6	20.39	4	5.55	27.19	0.98	01
Anal length	3	8.6	29.4	16.88	6.7	7.72	6.66	0.99	<0.
Allar length	0	8	4	10.00	3	1.12	0.00	0.99	01
Dorsal length	3	13.	41.0	28.21	8.8	5.57	-20.17	0.94	<0.
Dorsar length	0	87	9	20.21	7	5.57	-20.17	0.94	01
Mouth depth	3	3.5	11.2	5.48	2.2	18.35	36.40	0.80	<0.
Would deput	0	7	6	5.40	8	10.33	36.40	0.80	01
Mouth width	3	4.0	15.0	8.59	3.3	15.67	2.24	0.99	<0.
	0	5	7	0.37	2	15.07	2.34	0.99	01
Head width	3	6.4	24.2	13.27	5.3	9.69	8.27	0.99	<0.
	0	9	3	13.27	6	7.07		0.99	01

De der midth	3	5.4	28.1	6 13.24	.6 7.76	34.19	0.98	<0.
Body width	0	9	9	13.24	1	54.19	0.98	01

121 Table 2. Morphometric measurements for four cultrin fishes: Chanodichthys

122	abramoides,	C. dabr	<i>yi</i> , <i>C</i> .	erthrop	<i>pterus</i> and	С. то	ngolicus.
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	C		(2.	C	· ·	С.		
Character	abramoides (n = 21)		dał	oryi	erthro	erthropterus		mongolicus	
			(n =	(n = 23)		(n = 14)		(n = 13)	
	Range	Mean ±SD	Range	Mean ±SD	Range	Mean ±SD	Range	Mean ±SD	
	149.81	±3D 208.6	73.7-	±3D 140.4	114.2	±3D 148.1	111.37	±5D 156.5	
SL (mm)	149.01	3 ± 30.0	193.4	$5\pm34.$	2-	± 32.0	111.37	150.5 9±42.	
SL (IIIII)	- 270.94	<u>3</u> <u>1</u> 30. 87	8	97-34.	226.5	<u>+</u> 32.0	- 282.26	9 <u>+</u> 42. 81	
Morphometr	270.74	07	0)1	220.3	1	202.20	01	
ic data									
% of SL									
	0.26-	$0.28\pm$	0.21-	$0.24 \pm$	0.19-	0.21±	0.22-	0.23±	
Body depth	0.31	0.02	0.28	0.02	0.24	0.01	0.26	0.01	
	0.08-	0.09±	0.09-	0.1±0	0.07-	$0.08\pm$	0.08-	0.1±0.	
Body width	0.1	0	0.12	.01	0.09	0.01	0.11	01	
Caudal	0.11	0.10	0.00	0.10	0.10	0.1.4		0.10	
peduncle	0.11-	0.12±	0.08-	0.12±	0.12-	0.14±	0.12-	0.13±	
length	0.14	0.01	0.14	0.02	0.17	0.01	0.16	0.01	
Caudal	0.09	0.1+0	0.09	0.00	0.09	0.08	0.09	0.00	
peduncle	0.08-	0.1±0	0.08-	$0.09\pm$	0.08-	$0.08\pm$	0.08-	$0.09\pm$	
depth	0.11	.01	0.11	0.01	0.09	0	0.1	0.01	
Pectoral	0.18-	0.2±0	0.18-	$0.19\pm$	0.17-	$0.19\pm$	0.13-	0.16±	
length	0.22	.01	0.21	0.01	0.22	0.02	0.19	0.02	
Pectoral	0.76-	$0.84\pm$	0.81-	$0.88\pm$	0.77-	$0.87\pm$	0.77-	$0.84\pm$	
position	0.91	0.05	0.95	0.04	0.95	0.05	0.91	0.04	
Pelvic length	0.16-	$0.17\pm$	0.16-	$0.17\pm$	0.14-	$0.16\pm$	0.12-	$0.14\pm$	
i civic length	0.2	0.01	0.19	0.01	0.18	0.01	0.18	0.01	
Anal length	0.22-	$0.25\pm$	0.1-	$0.12\pm$	0.07-	$0.12 \pm$	0.08-	0.1±0.	
7 mai lengui	0.27	0.02	0.14	0.01	0.15	0.02	0.12	01	
Dorsal length	0.18-	$0.21\pm$	0.14-	0.2 ± 0	0.15-	$0.18\pm$	0.17-	0.19±	
Dorbar lengui	0.23	0.02	0.24	.02	0.21	0.02	0.23	0.02	
Head length	0.25-	$0.27\pm$	0.24-	$0.26 \pm$	0.23-	$0.24 \pm$	0.24-	$0.26 \pm$	
-	0.3	0.01	0.27	0.01	0.26	0.01	0.27	0.01	
% of HL									
Head depth	0.67-	0.8±0	0.53-	$0.58 \pm$	0.52-	$0.58 \pm$	0.51-	$0.55 \pm$	
	0.84	.05	0.64	0.03	0.65	0.03	0.6	0.03	

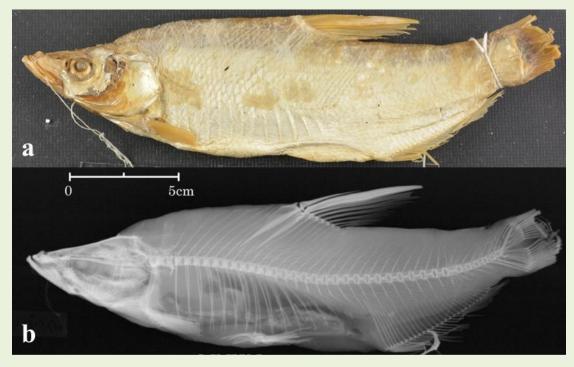
Head width	0.34-	$0.38\pm$	0.35-	0.39±	0.34-	$0.37\pm$	0.37-	0.41±
Head widdli	0.42	0.02	0.45	0.02	0.42	0.03	0.47	0.03
Snout length	0.26-	0.3±0	0.23-	$0.28\pm$	0.27-	0.3±0	0.26-	0.3±0.
Shout length	0.33	.02	0.32	0.02	0.33	.02	0.33	02
Euo diamotor	0.16-	$0.19\pm$	0.18-	$0.22\pm$	0.19-	$0.23\pm$	0.15-	0.2±0.
Eye diameter	0.36	0.05	0.27	0.03	0.3	0.03	0.25	02
Eva position	0.36-	$0.55\pm$	0.16-	$0.33\pm$	0.31-	$0.39\pm$	0.3-	$0.36\pm$
Eye position	1.96	0.41	0.43	0.05	0.45	0.04	0.42	0.04
Mouth donth	0.3-	$0.35\pm$	0.26-	$0.32\pm$	0.26-	$0.33\pm$	0.28-	$0.33\pm$
Mouth depth	0.55	0.06	0.4	0.04	0.53	0.07	0.41	0.03
Marsth width	0.64-	$0.73\pm$	0.52-	$0.61\pm$	0.56-	$0.62\pm$	0.56-	0.61±
Mouth width	0.88	0.07	0.75	0.05	0.69	0.04	0.66	0.03
Aspect ratio								
Body aspect	0.29-	$0.32\pm$	0.35-	$0.39\pm$	0.33-	$0.38\pm$	0.35-	$0.41\pm$
ratio	0.34	0.02	0.44	0.03	0.42	0.03	0.47	0.04
Caudal	1.00	1.26	0.00	1.05	1.40	1 (0)	1 10	1 45
peduncle	1.06-	1.26±	0.89-	1.25±	1.46-	1.69±	1.12-	1.45±
aspect ratio	1.53	0.14	1.59	0.19	1.97	0.16	1.93	0.21
Head aspect	0.41-	$0.47\pm$	0.58-	$0.67\pm$	0.59-	$0.64\pm$	0.68-	$0.74\pm$
ratio	0.55	0.03	0.74	0.04	0.71	0.04	0.79	0.04
Meristic								
counts								
Lateral-line	(1 (0	68±0.	64-70	67±0.	80-92	85±0.	(0.77	70±0.
scales	64-69	5	04-70	7	80-92	6	69-77	7
Scale rows		12.0		12.0		10+0		15.0
above lateral	12-13	12±0. 5	13-14	13±0. 5	18-20	19±0. 4	13-16	15±0.
line		5		5		4		5
Scale rows								
below lateral	8-9	8±0.5	6-7	6±0.5	7-8	7±0.4	6-7	6±0.5
line								
Circumpedun	20.22	22±0.	20.22	21±0.	24.26	25±0.	22.24	22±0.
cular scales	20-23	5	20-22	5	24-26	4	22-24	5

124 Photographic examination of relevant specimens

Some of specimens utilised by Yi and Zhu (1959), by Bănărescu (1972) and by Luo (1994) in the published taxonomic revisions of the genus *Culter* Basilewsky, 1855, were collected from Lake Dongting, Lake Xingkai and some other waters. These specimens were not extensively examined by Chinese workers when they revised the species of this genus. Because we could not access all those specimens, we inspected photographs of some critical species, including the holotypes of *Culter abramoides*Dybowski, 1872, *C. dabryi* Bleeker, 1871, *C. oxycephalus* Bleeker, 1871, *C. oxycephaloides* Kreyenberg & Pappenheim, 1908 and *Erythroculter dabryi shinkainensis* Yi & Zhu, 1959. We further examined some topotypical specimens.

134 *Culter oxycephalus* Bleeker, 1871

Culter oxycephalus was described by Bleeker in 1871 on the basis of a single 135 specimen (SL 290 mm) collected in January 1868 from Yang-tse-kiang (i.e., Yangtze 136 River) by Dabry de Thiersant, a French consular official in China (Luo, 2005; MNHN, 137 2022). According to Israeli (1989), the consulate where Dabry de Thiersant served 138 during that period was located in Hankau (Hankou), so it is hypothesized that the type 139 140 locality of Culter oxycephalus would be in the Hankou District, Wuhan City, middle Chang-Jiang River mainstream. In this study, we examined the type specimen of the 141 Sharphead Culter (MNHN 0000-5050) by photographs, the lateral-line scales and 142 circumpeduncular scales could not be counted, probably due to the poor preservation 143 quality of the specimen (Fig. 2a). 144



145

Fig. 2 Lateral view (a) and X-ray (b) of *Culter oxycephalus* Bleeker, 1871 (MNHN 0000-5050), holotype.

Comparing with the type specimen of C. oxycephaloides (ZMB 16686, Fig. 5), it 148 was found that except for the lateral-line scales and circumpeduncular scales, all other 149 characters (such as the number of anal fin rays and vertebrae) were in agreement with 150 that of C. oxycephalus. Therefore, it seems likely that C. oxycephalus Bleeker, 1871 is 151 a senior synonym of Culter oxycephaloides Kreyenberg & Pappenheim, 1908. 152 Comparing the original descriptions, Kreyenberg and Pappenheim (1908) concluded 153 that the lateral-line scales of C. oxycephalus differed significantly from those of C. 154 oxycephaloides, and that the differences in other characteristics such as body length / 155 body height or caudal peduncle length / caudal peduncle height were not significant. 156 The large difference in the number of lateral-line scales prompted this study to revisit 157 the original descriptions of these two fishes. The low number of lateral-line scales (65) 158 in Bleeker's (1871a) description and figure (see Fig. 3) has led to two hypotheses: (1) 159 the research environment at that time was not concerned with the feature of scales. Wu 160 (1964) already argued that there were inconsistencies in Bleeker's account. (2) the 161 original descriptions were not sufficiently accurate. Yi et al. (2011) stated that Bleeker's 162 163 (1871a) original description looked for evidence from the erroneous scales in Basilewsky's (1855) supplementary illustration. The errors in the accompanying 164 drawings can be seen in several details in the plates, e.g., (a) some fishes with distinct 165 lateral-line scales do not even reflect the lateral line, as in Tab II, Acanthorhodeus 166 macropterus [= Acheilognathus macropterus (Bleeker, 1871)] or are not clearly defined, 167 as in Tab IV, Sarcochilichthys sinensis Bleeker, 1871; (b) the number of lateral lines is 168 clearly wrong in some fishes, e.g., Hemibarbus dissimilis (= Paracanthobrama 169 guichenoti Bleeker, 1864) in Tab VI, where the number of lateral line is not obvious 170 and incorrect. Furthermore, the scales of cultrin fishes are inherently prone to shedding, 171 which, together with the abnormal condition of a teratological specimen, may result in 172 a low lateral-line scale count. 173



- 174
- 175

Fig. 3 A copy of Bleeker's (1871) illustration of the holotype of *Culter oxycephalus*

Berg (1949) incorrectly treated Culter abramoides Dybowski, 1872 (type ZMB 177 7933) from Lake Khanka (i.e., Lake Xingkai / Chanka), Ussuri River, southeastern 178 Russia, as a senior synonym of Erythroculter oxycephalus (Bleeker 1871). According 179 to Berg's (1949) description, he did not review the holotype of Culter oxycephalus 180 Bleeker, 1871 (nor were the dates correct). Yi and Zhu (1959) assigned the Sharphead 181 182 Culter to the genus *Culter*, based on the description of the ventral keel by Berg (1909). However, the holotype was not examined, and specimens were assumed that harvested 183 from Lake Xingkai of Ussuri River basin based on the erroneous number of lateral-line 184 scales (65). Culter abramoides Dybowski, 1872 was hence synonymized as Sharphead 185 Culter and the outline drawing was provided (Fig. 4a), then the distribution of 186 Sharphead Culter was confirmed in Lake Xingkai and Chang-Jiang. In the book 187 "Chinese fishes of Cyprinidae", the fish was supplemented with scales and fins (Fig. 188 4b) (Wu, 1964). Li (1992) agreed with Berg (1909) that the names and type species of 189 the genera Culter and Erythroculter Berg, 1909, as used by Yi and Wu (1964), were 190 191 inaccurately recognized, but that statement did not attract more ichthyologists' attention. Luo (1994) considered Chanodichthys Bleeker, 1860 to be a junior synonym of Culter 192 Basilewsky, 1855 and merged both genera. He also followed Smith's (1938) view to 193 include the species of Erythoculter in the genus Cultrichthys Smith, 1938; "Fauna 194 Sinica" agreed with this view, while retaining Wu's (1964) figure (Fig. 4c) (Chen et al., 195 1998). Subsequently, most Chinese scholars have used this figure without validation, 196 11

and the name has appeared in various local ichthyological records, e.g., Ren (1981); 197 Zhang (1995); Guo et al. (2021). Bogutskaya and Naseka (1997) considered both Culter 198 oxycephalus Bleeker, 1871 and Culter abramoides Dybowski, 1872 to be senior 199 synonyms of *Chanodichthys dabryi* (Bleeker, 1871), and a similar point was made by 200 Bănărescu (1967a) and Dyldin et al. (2023). Recent studies, e.g., Kottelat (2013) and 201 Chen et al. (2022b) suggest that the genus Cultrichthys should be restored to Culter and 202 only two species are recognized, Culter alburnus Basilewsky, 1855 and Culter 203 204 compressocorpus Yi and Zhu, 1959. All other species formerly aligned with the genus *Culter* now belong to the genus *Chanodichthys*, including the fish of our concern: 205 Chanodichthys oxycephalus. 206



Fig. 4 A copy of Yi and Zhu' (1959) (a), Yi and Wu' (1964) (b) and Chen *et al.*'s (1998)
(c) illustrations of *Chanodichthys oxycephalus* (formerly *Culter o.*)

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In this study, we examined the holotype (ZMB 7933) of Culter abramoides (Fig. 211 6), which has a number of lateral-line scales of 65-66, protruding mandible, 212 significantly longer lower jaw than the upper jaw, dorsal fin sclerotized spine that is 213 approximately equal to head length, and pectoral fin that ends close to or beyond the 214 base of the ventral fin. Except for the characteristics such as the number of lateral-line 215 scales, all the other characteristics of Culter abramoides are not consistent with the 216 217 current concept of Chanodichthys oxycephalus. Therefore, this study concludes that the two are not the same species. Three voucher specimens of Sharphead Culter from 218 "Fauna Sinica", taken from Lake Liangzi, Hubei Province and Lake Xiaoxingkai, 219 Heilongjiang Province, were also examined, and showed characteristics diagnostic for 220 Chanodichthys dabryi (Bleeker, 1871) and Chanodichthys abramoides (Dybowski, 221 222 1872), respectively.

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Comparison of the holotype characters of Culter abramoides Dybowski, 1872

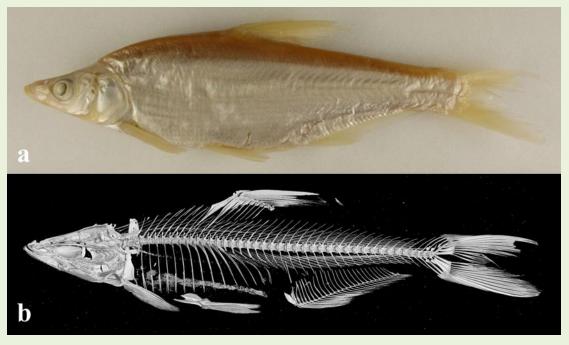
(ZMB 7933, see Fig. 6) and Culter dabrvi Bleeker, 1871 (MNHN 0000-5078, see Fig. 224 7) showed that they were different and should be treated as different species. At the 225 same time, the holotype of Erythroculter dabryi shinkainensis Yi and Zhu, 1959 (IHB 226 58-1558, see Fig. 8) was examined, and it was found that shared the following 227 characteristics with *Chanodichthys abramoides*: (1) snout length / head length; (2) 228 relative position of the dorsal and ventral fins; and (3) number of anal fin rays and 229 vertebrae. Therefore, the present study considers Erythroculter dabryi shinkainensis Yi 230 231 and Zhu, 1959 a synonym of Chanodichthys abramoides (Dybowski, 1872). Recent studies such as Bogutskaya and Naseka (2004); Bogutskaya et al. (2008) and Kottelat 232 (2013) also support the view of the present study. Erythroculter dabryi shinkainensis 233 was described as a subspecies of Chanodichthys dabryi (Bleeker, 1871) (then in 234 Erythroculter, Yi and Zhu, 1959), but the degree of dorsal elevation of the posterior part 235 of the head varies with development, and although the snout length / interorbital 236 distance and body coloration of the two are almost the same, there are some slight 237 differences, such as the anterior end of the upper jaw protruding (vs. no protrusion), the 238 239 interorbital distance is slightly smaller than the snout length (vs. slightly larger than that), the ventral fins reaching to the beginning of the anal fins (vs. almost reaching to 240 the anus), and the body coloration silvery (vs. dorsal grey-black, abdominal silvery-241 white), so there are many differences in the geometrical morphological analyses (Zhang 242 et al., 2008). Based on these characteristics, Shinkai Dabry's Culter is considered a 243 synonym of the Bream-shaped Culter Chanodichthys abramoides, which is clearly 244 different from Dabry's Culter. Therefore, according to the principle of nomenclatural 245 priority, Chanodichthys abramoides (Dybowski, 1872) is the senior synonym of 246 247 Erythroculter dabryi shinkainensis Yi & Zhu, 1959, and Chanodichthys dabryi (Bleeker, 1871) is a different valid species. 248

249 Culter oxycephaloides Kreyenberg & Pappenheim, 1908

Kreyenberg and Pappenheim (1908) collected one cultrin fish with a relatively
pointed head (SL 172 mm) during surveys in Tungtingsee (i.e., Lake Dongting) and

considered a new undescribed species. Without examining the holotype of the
Sharphead Culter, and only by comparing with its original description, it was concluded
that there were morphological differences such as more lateral-line scales (85 vs. 65),
more slender body shape (vs. relatively stubby), and more elongated caudal peduncle

256 (vs. relatively stubby) (Fig. 5).



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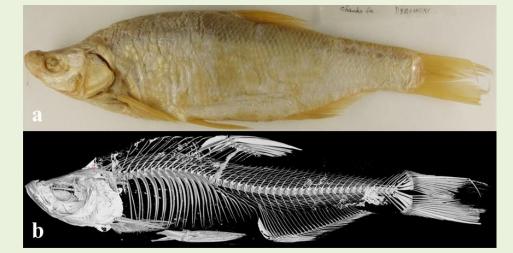
Fig. 5 Lateral view (a) and X-ray (b) of *Culter oxycephaloides* Kreyenberg &
Pappenheim, 1908 (ZMB 16686), holotype.

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As previously analysed, the original description of the lateral-line scales of *Culter oxycephalus* in Bleeker (1871a) may have been problematic. Yi and Zhu (1959) also provided a sketch of *Culter oxycephaloides* without reviewing the holotype, followed by Yi and Wu (1964); Chen *et al.* (1998) expanded on it. *Culter oxycephalus* is redescribed hereinafter, and *Culter oxycephaloides* is recognized as a junior synonym of *Chanodichthys oxycephalus*.

267 *Culter abramoides* Dybowski, 1872

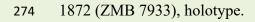
Culter abramoides was described by Dybowski in 1872 on the basis of a single
specimen (ZMB 7933, TL 310 mm) collected in 1869 from Ussuri River, Lake Xingkai.
Bogutskaya and Naseka (1996) merged *Culter abramoides* Dybowski, 1872 into



271 Chanodichthys dabryi (Bleeker, 1871). But, as we noted above, both species are valid.

272

Fig. 6 Lateral view (a) and X-rayed photograph (b) in Culter abramoides Dybowski,



275 *Culter dabryi* Bleeker, 1871

Culter dabryi was also described by Bleeker in 1871 based on a single specimen
(MNHN 0000-5078, SL 270 mm) collected in 1868 by Dabry de Thiersant, from Yangtse-kiang. In accordance with recent taxonomic advances, *Culter dabryi* was formally
renamed as *Chanodichthys dabryi* (Bleeker, 1871).



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Fig. 7 Lateral view (a) and X-ray (b) of Culter dabryi Bleeker, 1871 (MNHN 0000-

282 5078), holotype.

283 Erythroculter dabryi shinkainensis Yi and Zhu, 1959

Yi and Zhu (1959) collected 11 and 21 fish from Lake Daxingkai in 1957 and 1958, 284 respectively, i.e., Erythroculter dabryi shinkainensis (Fig. 8), and the traits of lateral-285 line scales, gill rakers, and anal fin rays were similar to those of Culter dabryi. The 286 difference in body size is remarkable, with extremely bulbous dorsum behind the head 287 and very high body. Body height equals or exceeds head length. The pectoral fins end 288 beyond the base of the ventral fins, and the ventral fins end at the beginning of the anal 289 fins. The caudal peduncle is long. The swim bladder chambers are especially enlarged. 290 As already shown above, Erythroculter dabryi shinkainensis should be treated as a 291 292 junior synonym of Chanodichthys abramoides (Dybowski, 1872).



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Fig. 8 Erythroculter dabryi shinkainensis Syntype IHB 58-1558

295 Culter hypselonotus Bleeker, 1871

Culter hypselonotus was also described by Bleeker in 1871 on the basis of a single 296 specimen (SL 210 mm) collected from Yang-tse-kiang in 1868 by Dabry de Thiersant. 297 The holotype of *Culter hypselonotus* could not be found (personal communication with 298 MNHN and MHNL). However, based on Bleeker's original description and figure (see 299 300 Fig. 9), the main identifying characters are diagnostic for *Chanodichthys dabryi*, and the present study concludes that the holotype of *Culter hypselonotus* is a specimen of 301 Chanodichthys dabryi (Bleeker 1871). This view is in agreement with Bogutskaya et 302 al. (1996) and Kottelat (2001). 303



Fig. 9 A copy of Bleeker's (1871) illustration for *Culter hypselonotus*

306 Culter pekinensis Basilewsky, 1855

In 1849, the 13th mission from Tsarist Russia came to China. Among them were 307 308 some enthusiastic museum specimen collectors, such as Stephano Basilewsky, the mission's physician, who collected fish specimens around Beijing. Culter pekinensis 309 was described by Basilewsky in 1855 based on a single specimen taken from streams 310 draining to the Gulf of Tschili (today Bohai Bay) from Pekin (i.e., Beijing). The North 311 Canal is the only one of the five major water systems in Beijing that originates in 312 Beijing, so the type locality of this species should be the North Canal. According to 313 Basilewsky's (1855) original description of Culter pekinensis, its abdomen (the part in 314 front of the ventral fins) protrudes (abdomen non-compressed, see Fig. 11b), which, 315 together with other identifying characters, is believed in this study to diagnose the genus 316 Chanodichthys. Kottelat (2006, 2013) considered that it may be a synonym of 317 Chanodichthys mongolicus (Basilewsky 1855). Important characteristics are the 318 anterior dorsal fin elevation (anterius elevato = raised in front) and the silvery-gray 319 320 body / fins (Pinnae albeseentes = whitish fins) in the original text (Basilewsky, 1855). Furthermore, only C. dabryi, a common economic fish in Beijing (Wang, 1984; Zhang 321 and Zhao, 2013), was not mentioned. Therefore, this species may be a synonym of 322 Culter dabryi. The name pekinensis has, evidently priority over dabryi. Yet the 323 identification of the first named is not sure (and the locality could be in error), while 324

the second is based on a still existing holotype, therefore the name in usage must be retained. The holotype was searched for at the curatorial site, the Russian Academy of Sciences, and may have been lost (pers. comm.), so its validity is open to question and its taxonomic status is provisionally retained here, a synonym of *Chanodichthys mongolicus* (Basilewsky, 1855).

330 Culter exiquus Basilewsky, 1855

Culter exiguus was originally described by Basilewsky in 1855 on the basis of 331 specimens taken from near Beijing. Bleeker (1871a, b; 1873) considered Culter exiquus 332 (he spelled C. exiguus) together with C. pekinensis to be valid species of the genus 333 Pseudoculter Bleeker, 1860. Based on the original descriptions of two species of the 334 genus (Culter pekinensis and Culter exiquus), they have a non-compressed protruding 335 336 abdomen (see Fig. 11b). In combination with other identifying characters, the present study suggests that both names should be in *Chanodichthys*. This is in agreement with 337 Kottelat's (2013) and Zhang and Zhao's (2016) conclusions. Exiquus means small and 338 the specimen may be a juvenile of some cultrin fish. Given the close resemblance to C. 339 pekinensis (as already noted by Bleeker), the name could be a synonym of 340 Chanodichthys mongolicus (Basilewsky, 1855). The holotype was also searched at the 341 curatorial site, the Russian Academy of Sciences, but it could not be found (pers. 342 comm.), so its validity remains in dispute, and, for the time being, its taxonomic status 343 344 has to be considered as a Nomen Dubium.

345 *Culter kashinensis* Shaw, 1930

Culter kashinensis was originally described by Tsen-Hwang Shaw (i.e., Zhenhuang Shou) in 1930 on the basis of a single specimen taken from Jiaxing City, Zhejiang Province (Shaw, 1930). The species was recorded by Nichols (1943) without comparison. Berg (1949) believed that this species was closely related to *Culter alburnus*. According to its original description and accompanying drawing (see Fig. 10), *Culter kashinensis* has angular abdominal ribs extending forward to the base of the

pectoral fins (see Fig. 11a), mouth terminal, large eye diameter (head length / eye 352 diameter 4.7), small interorbital distance (head length / interorbital distance 3.8), 353 pectoral fins terminating close to the base of the ventral fins, 21 branched anal fin rays, 354 and according to the original author "with some features close to Erythroculter 355 mongolicus or Culter recurviceps". This is in agreement with Yi and Zhu (1959). It is 356 hypothesized that may be a hybrid of Chanodichthys mongolicus, Chanodichthys 357 recurviceps or Culter alburnus in the present study, and similar circumstances occur in 358 Leptocephalus mongolicus Basilewsky, 1855 (Bănărescu, 1967a; 1972). The fish has 359 not been reported since 1930. The holotype ZMFMIB 5120 was attempted to locate at 360 the curatorial site, now ASIZB, but the type was not found (pers. comm.), so its validity 361 is open to question and its taxonomic status is provisionally retained here. 362

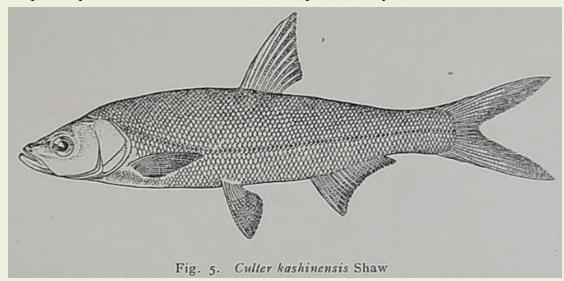


Fig. 10 A copy of Shaw' (1930) illustration of the holotype of *C. kashinensis*.

365 **Results**

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Redescription of *Chanodichthys oxycephalus* (Bleeker, 1871)

Holotype: *Culter oxycephalus* Bleeker 1871:74, Pl. 5 [Memoire sur les Cyprinoïdes de
Chine], China, Chang-Jiang. Appeared first as name only in Bleeker 1870:252,
[Mededeeling omtrent eenige nieuwe vischsoorten van China]. Also appeared in
Bleeker 1871:87 [Sur les espèces du genre *Culter* Basil.].

371 Synonym: Culter oxycephaloides Kreyenberg & Pappenheim 1908:104 [Ein Beitrag

zur Kenntnis der Fische der Jangtze und seiner Zuflüsse] Tungtingsee, southeast central
China. Also appeared as new in Kreyenberg 1910:19 [Ein Beitrag zur Kenntniss der

- 374 Fische der Yangtze und seiner Zuflüsse].
- 375 *Culter oxycephaloides* Kreyenberg & Pappenheim, 1908 Sitz. Ges. Nat. Freunde Berl
- 376 (4): 104 (Lake Dongting); Yunlin Luo, 1994, Acta Hydrobiologica Sinica 18 (1); 47.
- 377 Erythroculter oxycephaloides: Nichols, 1928, Bull. Am. Mus. Nat. Hist. 58: 30 (Lake
- 378 Dongting); Bolu Yi, Zhirong Zhu, 1959, Acta Hydrobiologica Sinica (2): 87 (Lake
- Liangzi, Hubei); Bolu Yi, Qingjiang Wu, 1964, Fauna of Cyprinidae China: 103 (Lake
- 380 Liangzi, Yunxian, Mudong, Hechuan, Hunan).
- 381 *Culter (Erythroculter) oxycephaloides*: Kimura, 1934, J. Shanghai Sci. Inst. (3) 1: 107
 382 (Chongqing).
- 383 Specimens examined
- MNHN 0000-5050, 1 holotype, 290mm SL, China: Chang-Jiang (photograph examination); ZMB 16686, 172mm SL, China: Lake Dongting (photograph examination).
- 387 IHB 201807055611–5614, 8 specimens, 65.9–122.4 mm SL; China: Hunan Province:
- Menggu Village, Xiangyin County (28°48'4.88"N, 112°53'28.42"E); collected by X.
- 389 Chen, C. An, Z. Wang, W. Shao, 5 July 2018. IHB 201805055611–5614, 3 specimens,
- 390 65.9–122.4 mm SL; China: Hunan Province: Chenglingji, Yueyang City, Lake
- 391 Dongting (29°26'9.73"N, 113°08'43.87"E); collected by X. Chen, T. Nguyen Dinh, L.
- 392 Zhang, 10 May 2018. IHB 201807165611–5614, 4 specimens, 65.9–122.4 mm SL;
- 393 China: Hunan Province: Hongqihu, Yueyang City, Lake Dongting (29°13'56.86"N,
- ³⁹⁴ 112°57'11.99"E); collected by X. Chen, L. Cao, L. Qiu, 16 June 2018.
- 395 Diagnosis
- 396 *Chanodichthys oxycephalus* is distinct from all other congeneric species, except *C*.
- 397 *dabryi* and *C. abramoides*, in having sub-superior and oblique mouth and unbranched
- anal fin rays 26-29. It differs from these two species in having a red lower lobe of caudal
- fin, a long and pointed head, and pored scales 73-85.
- 400 **Description**
- 401
- Morphometric data for type specimens given in Table 1. General body appearance

of holotype shown in Fig. 2a. Body elongate, laterally compressed, dorsal bulge behind 402 head, arcuate, abdomen with ventral ribs from ventral fin to anus (Fig. 11b), caudal 403 peduncle high. Head small, pointed, laterally compressed, head length less than body 404 height. Snout pointed, snout longer than eye diameter. Mouth sub-superior, slit, 405 mandible slightly longer than maxilla, end of maxilla reaching below nostrils. Eyes 406 large, situated on anterior half of head. The interocular space is wide and slightly 407 convex, and the interorbital distance is larger than eye diameter. The nostrils are located 408 409 near the anterior margin of the eye, with the lower margins above the upper margin of the eye. Gill aperture broad, extending forward approximately below posterior margin 410 of eye; gill cover membrane united to isthmus; isthmus narrow. Scales medium to large. 411 Lateral line straight, approximately centered on the side of the body, slightly curved 412 anteriorly, straight posteriorly, reaching to the base of the caudal fin. 413

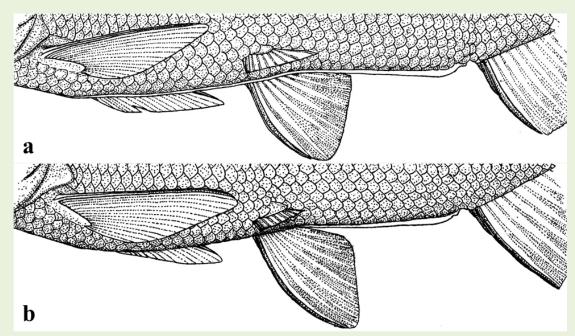


Fig. 11 Figure of the keel of a cultrin fish species: entire keel (a); half keel (b).(Illustrated by Zhi-Xian Sun).

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Dorsal fin located posteriorly above base of ventral fin, outer margin oblique, terminal unbranched fin smooth and stiffly spined, length of spines shorter than head length. Anal fin located posteriorly below base of dorsal fin, outer margin concave, distance from beginning to base of ventral fin much smaller than to base of caudal fin. 422 Pectoral fins are short, pointed, and do not reach the beginning of the ventral fin. Ventral
423 fin located anteriorly and inferiorly to dorsal fin, shorter than pectoral fin. The caudal
424 fin is deeply forked and the upper and lower lobes are pointed at ends.

First gill arch lateral gill rakers 19-22. Gill rakers medium-long, densely arranged. Hypopharyngeal bones narrow, hooked, forearms longer than hindarms, without conspicuous antennal projections. Pharyngeal teeth subconical, pointed and slightly hooked at the end. Swim bladder 3-chambered, middle chamber largest, posterior chamber finely pointed. Intestine short, curved anteriorly and posteriorly, length of intestine shorter than body length. Peritoneum grayish white.

Lateral line complete and almost straight, extending along mid-lateral of body, with 73 (7) or 75 (7) pored scales; scale rows above and below lateral lines 5 and 3; circumpeduncular scales 21 (7) or 22 (7) and pre-dorsal mid-line scales 13 (14). Body covered with moderately-sized scales. Vertebral counts 4+41 (see **Fig. 2b**).

435 Colouration

In freshly-collected specimens, head and dorsum of body grey black, underside and abdomen silver white; back and lateral head peppered with dark spots. Back darker and belly lighter. Fins silver white, with orange-red anal and lower lobe of the caudal fin.

In formalin-stored specimens, ground colour slightly faded; body dorsally greyish
and ventrally greyish-white and the back of the head becoming yellowish-brown.
Dorsal, pectoral, and pelvic fins light greyish, anal fin and lower lobe of the caudal fin
orange-red with black distal margin.

No sexual dimorphism was observed in the specimens examined.

444 Sexual dimorphism

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Geographical distribution and habitat

C. oxycephalus is confined to the Chang-Jiang basin in Sichuan, Hubei, Hunan,
Jiangxi, Anhui and Jiangsu provinces, southern China. Specimens examined in this
study were collected from the Lake Dongting in Yueyang and Yuanjiang City. *C. oxycephalus* usually occurs in turbid rapid-flowing water with mixed substrate
including boulders, gravel and pebbles. Coexisting fishes include *Chanodichthys*

452 erythropterus, Chanodichthys dabryi, Chanodichthys mongolicus, Tachysurus eupogon,
453 Siniperca scherzeri, Coilia brachygnathus and Channa asiatica.

In the past, ichthyologists identified the species based on a single specimen or even mutilated or teratological specimens, and the original descriptions were sketchy, often establishing new species with minor trait differences. Since the type specimens (including topotypes) cannot always be reexamined, and the original records are often plausible, or the lack of diagrams, the problem of confusion cannot always be resolved.

459 A review of specimens of species such as C. oxycephalus and C. oxycephaloides in this study revealed that Sharphead Culter described in "Fauna Sinica" is actually 460 'neither fish nor fowl' and is a combination of features spliced from several species 461 (including C. oxycephaloides, C. abramoides and C. dabryi). This is the reason why 462 there is no official record of Sharphead Culter since 1959. Topmouth Culter, Mongolian 463 Culter and Predatory Culter can be the dominant and economically important fishes in 464 many waters (Yi and Wu, 1964), and all these fishes belong to the mid-lower Chang-465 Jiang fluvio-lacustrine ecosystem. The true Sharphead Culter is only found in Chang-466 467 Jiang Basin and its subsidiary water bodies.

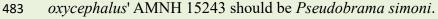
468 Discussion

469 Culter from Lake Dongting

Richardson (1846) described *Leuciscus recurviceps* Richardson, 1846 (= *Chanodichthys recurviceps* (Richardson 1846) based solely on an illustration from
Canton (i.e., Guangzhou) by Reeves (Whitehead, 1970) (Fig. 12). This species was the
first described cultrin fish and is now known to occur in the Pearl River and on Hainan
Island (Chen *et al.*, 1998; Yang *et al.*, 2016; Xiang *et al.*, 2021)

Nichols (1928, 1943) recorded a batch of cultrin fishes taken by Clifford Pope in
1921 from the Huping of Lake Dongting (today Yueyang City, Hunan Province) and
identified these as *Erythroculter dabryi*, *E. erythropterus*, *E. mongolicus*, *E. oxycephalus*, *E. recurviceps*, *E. oxycephaloides*. By examining the specimens stored in
AMNH and MCZ (Fig. 13), this study found errors in some of the identifications: '*E*.

recurviceps' MCZ 32640, AMNH 10842, 10850 should be Chanodichthys 480 erythropterus; 'E. recurviceps' AMNH 12166 should be Chanodichthys mongolicus; 'E. 481 oxycephaloides' AMNH 10871, 10875 should be Chanodichthys oxycephalus; 'E. 482



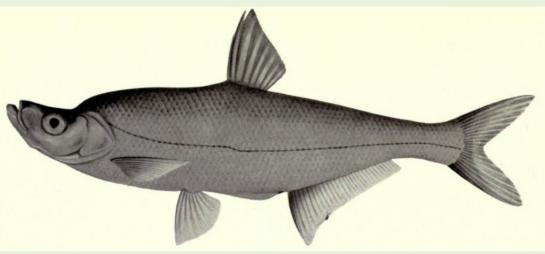
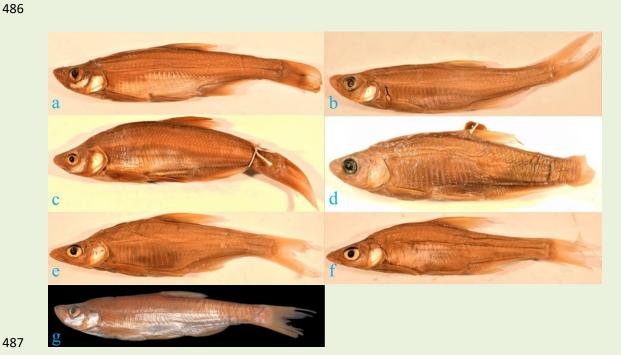


Fig. 12 A copy of Richardson's (1846) illustration of *Culter recurviceps*.



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Fig. 13 Cultrin fish specimens from Lake Dongting collected by Clifford Pope (a: 488 'Erythroculter recurviceps' AMNH 10842; b: 'E. recurviceps' AMNH 10850; c: 'E. 489 recurviceps' AMNH 12166; d: 'E. oxycephalus' AMNH 15243; e: E. oxycephaloides 490 AMNH 10871; f: E. oxycephaloides AMNH 10875; g: 'E. recurviceps' MCZ 32640). 491 492

Chen et al. (2022b) concluded that six species of cultrin fishes should be present 493 in Lake Dongting based on field sampling and historical records from 2012-2019, while 494 Cultrichthys erythropterus (sensu Chen et al. 1998) was the misidentification of Culter 495 alburnus. As explained above, Culter, as here delimited, includes two species: C. 496 alburnus and C. compressocorpus. All other species currently placed in Culter by 497 Chinese authors should be referred to the genus Chanodichthys. According to the 498 present study, five species should be present in Lake Dongting: Chanodichthys dabryi 499 500 (Bleeker, 1871), Ch. erythropterus (Basilewsky, 1855), Ch. mongolicus (Basilewsky, 1855), Ch. oxycephalus (Bleeker, 1871) and Culter alburnus (Basilewsky, 1855). In 501 addition to Lake Dongting, Culter oxycephalus also occurs in Lake Honghu, middle 502 reach of Chang-Jiang (unpublished data) and the lower Chang-Jiang mainstream at the 503 Nanjing City section (Wang, 2022). Based on the present study, it is suggested that 504 previous records of specimens from the upper Chang-Jiang and Heilong-Jiang could be 505 a misidentification of Chanodichthys dabryi, a view also supported by Bănărescu 506 (1967a, b). Thus, the distribution area of Chanodichthys oxycephalus is restricted to the 507 508 mid-lower Chang-Jiang mainstream and its subsidiary water bodies.

509 Culter from Lake Xingkai

Previous studies on Lake Xingkai are more numerous and mainly carried out by 510 Chinese and Russian researchers, such as Berg (1909); Yi and Zhu (1959); Wu (1964); 511 Naseka and Bogutskaya (2004); Bohlen et al. (2006) and Svirsky and Barabanshchikov 512 (2010). Dybowski (1872) described four new species of Culter in Lake Xingkai as 513 Culter abramoides Dybowski, 1872 (= Chanodichthys abramoides), C. sieboldii [= 514 *Chanodichthys erythropterus*], *C. rutilus* [= *Chanodichthys mongolicus*], *C. lucidus* [= 515 516 Hemiculter lucidus (Dybowski, 1872)]. Yi and Zhu (1959) described Erythroculter dabryi shinkainensis and Culter compressocorpus, based on a batch of specimens from 517 Lake Xingkai, while a batch of cultrin fishes from the first Songhua-Jiang in the middle 518 Heilong-Jiang was described as Erythroculter ilishaeformis sungarinensis Yi & Zhu, 519 1959, which was later resolved by Luo (1994) as a synonym of Chanodichthys 520

erythropterus. Bogutskaya and Naseka (1997) concluded that four species of cultrin 521 fishes should be present in Lake Xingkai based on field sampling, namely 522 Chanodichthys dabryi (Bleeker, 1871), Ch. erythropterus (Basilewsky, 1855), Ch. 523 mongolicus (Basilewsky, 1855) and Culter alburnus (Basilewsky, 1855). Bogutskaya 524 et al. (2008) considered two more species from Lake Xingkai, namely also 525 Chanodichthys abramoides (Dybowski, 1872) and Chanodichthys oxycephalus 526 (Bleeker, 1871). Turanov et al. (2019) explored the phylogenetic relationships of these 527 fishes from Lake Xingkai with the help of DNA. They used Ch. erythropterus, Ch. 528 mongolicus, Ch. oxycephalus and Culter alburnus. Based on the specimens' and 529 photographic examinations' result during this study, it is suggested that six cultrin fish 530 species could be present in Lake Xingkai, namely Chanodichthy abramoides, Ch. 531 dabryi, Ch. erythropterus, Ch. mongolicus, Culter alburnus and C. compressocorpus. 532

Zhao (2022) recorded 7 cultrin fish species from the Heilong-Jiang basin in China. 533 Based on the results of our study, Shinkai Dabry's Culter (Erythroculter dabryi 534 shinkainensis) in the Handbook may represent Chanodichthys abramoides, based on 535 536 the longer pectoral fin reaching the base of the pelvic fin, sub-superior mouth, 64-68 pored scales. The Sharphead Culter Chanodichthys oxycephalus is not distributed in 537 Heilong-Jiang Basin, Zhao's (2022) displayed species may represent Chanodichthys 538 dabryi based on the larger eye diameter, lesser lateral scales, grey caudal and the distal 539 margin of the anal fin. Thus, there are six cultrin fishes distributing in the Heilong-Jiang 540 basin of China, i.e., Chanodichthys abramoides, Ch. dabryi, Ch. erythropterus, Ch. 541 mongolicus, Culter alburnus and C. compressocorpus. 542

543 Reviews on differences between morphological and molecular analysis

Zhang *et al.* (2008) showed that *Culter* spp. can be divided by morphological
methods into four separate species groups: (1) *C. alburnus + C. recurviceps*; (2) *C. dabryi dabryi + C. oxycephalus + C. dabryi shinkainensis*; (3) *C. oxycephaloides*; (4) *C. mongolicus mongolicus + C. mongolicus elongatus + C. mongolicus qionghaiensis*.
We have reexamined the specimens of '*Culter oxycephalus*' used by Zhang *et al.* (2008)

housed in the Museum of Aquatic Biology (IHB-CAS) and all of them were found to
be *Chanodichthys dabryi* based on significantly different characteristics.

The phylogenies from Wang *et al.* (2019) using Cytb and COI as molecular markers indicated that '*Culter oxycephalus*' and '*Culter oxycephaloides*' have a very small genetic distance and therefore always clustered together and cannot be effectively separated.

555 Kreyenberg & Pappenheim's uncritical original description of *Culter* 556 *oxycephaloides* and the incorrect morphological description and drawing in "Fauna 557 Sinica" since 1998, are hypothesized to have contributed to the longstanding confusion 558 about the relationship between *Ch. oxycephalus* and *Ch. oxycephaloides* in the studies 559 of Zhang *et al.* (2008) and Wang *et al.* (2019).

560 Taxonomic implication of type specimens and original literature

561 Kreyenberg and Pappenheim (1908) failed to review types and consult the original 562 literature, leading to the creation of '*Culter oxycephaloides*', and to more than a century 563 of misunderstanding. Similarly, due to the scientific conditions at that time, Yi and Zhu 564 (1959) could not compare the holotypes of *Culter oxycephalus* with those of *Culter* 565 *oxycephaloides*, and incorrectly recognized *Culter abramoides* as a synonym of *Culter* 566 *oxycephalus* by the number of lateral-line scales.

Therefore, in order to avoid the recurrence of such confusion, ichthyologists 567 should identify fish species based on complete specimens, with original descriptions 568 documented in as much detail as possible, and with as much knowledge as possible of 569 the fish's life-history cycle (including habitat, habits, coloration, etc.). Ichthyologists 570 need to understand that fish exhibit different traits at different growth periods and in 571 572 different sexes to avoid misidentifying species based on minor trait differences. At the same time, the exchange of literature and specimens should be strengthened so that the 573 same fishes will not be categorized into different groups, or different species will not 574 be treated as a single species. The number of species with synonyms will be suppressed, 575 as well as the phenomenon of mistakenly categorizing different species into one species. 576

- 577 Even if problems are found later, they can be rechecked by obtaining name-bearing type
- 578 specimens, voucher specimens, original records, accompanying drawings, or topotypes.

579 Comparative material

- 580 Abramis pekinensis ZIN 5637 (3), Syntypes, Rivers leading to Tschili Bay, China.
- 581 *Culter abramoides* **ZMB** 7933 (1), Syntype, Ussuri River and Lake Khanka, 582 southeastern Russia.
- 583 *Culter alburnus* **ZIN** 5585 (1), Lectotype, Rivers draining to the Gulf of Tschili, China.
- 584 Culter aokii FMNH 59110 (1), Lectotype, Lake Candidius (Jitsugetsutan), Taiwan,
- 585 China.
- 586 *Culter brevicauda* **BMNH** 1865.10.29.29 (1). Lectotype; **BMNH** 1865.10.29.30-31 (2),
- 587 1865.10.29.32 (1). Paralectotypes: Taiwan, China.
- 588 *Culter compressocorpus* **IHB** 58-1572~1575 (6); Dongbei-0520~0523, Syntypes, Lake
- 589 Xiaoxingkai & Lake Jingpo, China.
- 590 *Culter dabryi* MNHN 5078 (1), Holotype, Chang-Jiang, China.
- 591 *Culter lucidus* **ZMB** 7935 (2), Lectotype, Lake Khanka, southeastern Russia.
- 592 Culter mongolicus ZIN 2950-51 (2). Lectotype and paralectotype: Mongolia and
- 593 Manchura, northern China.
- 594 *Culter recurvirostris* **MNHN** 1884-0078 (1), Holotype, Near Hanoi, northern Vietnam.
- *Culter rutilus* ZMB 7934 (1), Syntype, Ussuri River and Lake Khanka, southeastern
 Russia.
- 597 Culter sieboldii ZMB 7932 (1), Syntype, Middle Amur River, Ussuri River, Sungari
- 598 River, and Lake Khanka, China.
- 599 *Erythroculter dabryi shinkainensis* **IHB** 58-1548~1567 (21), Syntypes, Lake 600 Daxingkai, Heilong-Jiang, China.
- 601 Erythroculter hypselonotus daovantieni IBTS 625 (1), Holotype, Boi River, northern
- 602 Vietnam.
- 603 Erythroculter ilishaeformis MNHN 0000-5055 (1), Syntype, Chang-Jiang, China.

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