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A new species of genus *Zenion* Jordan & Evermann, 1896 (Zeiformes: Zeniontidae), with comments on its congeners *sensu lato*

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Abstract

Zenion Jordan & Evermann, 1896 is currently an understudied genus. A cosmopolitan species with multiple records as "*Zenion japonicum*" is reidentified as a new species, named *Zenion retrojaponicum* n. sp., based on both morphological and molecular evidence. This new species can be morphologically distinguished from other species in terms of the lower margin of the orbit below the lower end of the pectoral-fin base, ventral-fin origin posterior to dorsal-fin origin, a thinner caudal peduncle, branchiostegal rays completely hidden in the inner side of or above the preopercular, and pored lateral-line scales less than 50. Molecularly, its mitochondrial marker, cytochrome C Oxidase subunit I gene sequence, exhibits a minimum interspecific Kimura-Two-Parameter genetic distance of 9.88% with its sister group. The real *Zenion japonicum* Kamohara, 1934, described by Kamohara (1934), is herein referred to as a junior synonym of *Zenion hololepis* (Goode & Bean, 1896). In addtion, all species that belong to or belonged to *Zenion* Jordan & Evermann, 1896 are discussed. Among them, for a rarely mentioned species, which was originally described as *Cyttula macropus* Weber, 1913 and has been reduced to junior synonym of *Zenion hololepis* (Goode & Bean, 1896), a new subfamily, Cyttulinae, is established with its redetermination to be under the original genus *Cyttula* Weber, 1913, based on both its morphological characters, including, two functional lateral lines, long ventral-fin soft rays, mouth almost vertical, profile of spinous dorsal-fin a positively skewed parabola, absent spiny ridges and absent locking mechanism, and molecular character of a minimum interspecific Kimura-Two-Parameter genetic distance of 7.56 % in multigene phylogeny among all the members under Parazenidae McAllister, 1968, and its monophyly does not disturb any other subfamilies and families, with available genetic information.

Keywords: Dory, Undescribed, New Subfamily, Redescription, Marine Fish, China

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Introduction

Goode & Bean (1896) described a new species, *Cyttus hololepis* Goode & Bean, 1896, under *Cyttus* Günther, 1860. Shortly after, Jordan & Evermann (1896) established a new genus, *Zenion* Jordan & Evermann, 1896, and moved *Cyttus hololepis* Goode & Bean, 1896 under it. Weber (1913) described a new genus and species, *Cyttula macropus* Weber, 1913, and stated the difference between *Cyttula* Weber, 1913 and *Zenion* Jordan & Evermann, 1896, which is the lack of spiny ridges at dorsal-fin and anal-fin base. *Cyttus leptolepis* Gilchrist & von Bonde, 1924 was a species published under *Cyttus* Günther, 1860, but also possesses several characters corresponding to those of *Zenion* Jordan & Evermann, 1896, as described in its original description (Gilchrist & von Bonde, 1924). One year later, Barnard (1925) shifted *Cyttus leptolepis* Gilchrist & von Bonde, 1924 to be under *Zenion* Jordan & Evermann, 1896. Afterwards, Kamohara (1934) described a new species, *Zenion japonicum* Kamohara, 1934. After a long time, *Zenion longipinnis* Kotthaus, 1970 was published as a new species. Heemstra (1980) suggested that *Cyttula* Weber, 1913 was congeneric with *Zenion* Jordan & Evermann, 1896. Later, Shimizu (1983) transferred the only species under *Cyttula* Weber, 1913 to *Zenion* Jordan & Evermann, 1896, placing *Cyttula* Weber, 1913 in synonymy with *Zenion* Jordan & Evermann, 1896, but without any significant revision. Afterwards, Meng *et al.* (1995) reduced *Zenion japonicus* Kamohara, 1934 to a junior synonym of *Zenion hololepis* (Goode & Bean, 1896), and Heemstra (1999) confirmed this reduction and also reduced *Cyttula macropus* Weber, 1913 to a junior synonym of *Zenion hololepis* (Goode & Bean, 1896). Recently, Heemstra (2016) regarded *Zenion longipinnis* Kotthaus, 1970 as a junior synonym of *Zenion hololepis* (Goode & Bean, 1896). Very recently, Lin *et al.* (2025) described a new species, *Zenion boops* Lin *et al.*, 2025, which is herein determined under *Cyttula* Weber, 1913. In this paper, a new species, *Zenion retrojaponicum* n. sp., is described.

Only Shimizu (1983) briefly mentioned and reviewed all the species under *Zenion*, including those that are now considered invalid. Shimizu (1983) distinguished species through minute differences in their fin formula. Therefore, this review does not provide sufficient information.

The genus *Zenion* Jordan & Evermann, 1896 is placed under the family named according to *Zenion* Jordan & Evermann, 1896, Zeniontidae Myers 1960. As mentioned above, this genus contains seven described species, namely *Cyttus hololepis* Goode & Bean, 1896, *Cyttula macropus* Weber, 1913, *Cyttus leptolepis* Gilchrist & von Bonde, 1924, *Zenion japonicum* Kamohara, 1934, *Zenion longipinnis* Kotthaus, 1970, *Zenion boops* Lin *et al.*, 2025 and *Zenion retrojaponicum* n. sp.. Among them, five species, *Zenion hololepis* (Goode & Bean, 1896), *Cyttula macropus* (Weber, 1913), *Zenion leptolepis* (Gilchrist & von Bonde, 1924), *Zenion boops* Lin *et al.*, 2025, and *Zenion retrojaponicum* n. sp. are considered valid, among which, *Cyttula macropus* (Weber, 1913), is determined back to its original genus *Cyttula* Weber, 1913, with a new subfamily, Cyttulinae, established for it, under family Parazenidae McAllister, 1968, as well as for *Zenion boops* Lin *et al.*, 2025, to be *Cyttula boops* (Lin *et al.*, 2025).

Materials and Methods

All new specimens were trawled from the South China Sea, retained in Marine Biological Museum, Chinese Academy of Science. Terminology, including abbreviations and counting and measuring methods, followed that described by Arratia *et al.* (2013), Heemstra *et al.* (2022a), Heemstra *et al.* (2022b), Tyler *et al.* (2003), Wu & Zhong (2021), and Xie (2010). For instance, “vertical” = “latitudinal”, “horizontal” = “longitudinal”; fin formula: D: dorsal fin, P: pectoral fin, V: ventral fin, A: anal fin, C: caudal fin, capital Roman numerals: spines, lowercase Roman numerals: simple soft rays or spiny soft rays, Arabic numerals: non-simple soft rays, when elements separated, “+” connecting them.

For the specimens, their mouths were tightly closed, neither squashed into the head nor loosely protruding or open. Similarly, because the bones, as well as the bony joints, are very fragile, the intactness of the osteologic distinguishing characters of the specimens was carefully confirmed. Often, if the mouth would not close tightly, or the isthmus excessively ridged, or a ventral fin was not flexible, certain osteological characters, especially the head length and the position of the branchiostegal rays, could not be measured accurately due to twisting and thus were not included in this study.

Because the eyes are fragile and often drop from the orbit in this genus, it was better to use “preorbital length” than “snout length”. Preorbital length is the distance between the latitudinal level of the anterior-most point of the orbit and the latitudinal level of the anterior-most point of the head, excluding the lower lip but including the upper lip. Microcharacters, including serrations, were observed it under a microscope. Internal characters, including the anal-fin spine covered by skin, were observed under X-ray. In certain species or specimens of a species, the second anal-fin spine is hidden under the skin and not exposed (Tyler *et al.* 2003). Thus, the author separately stated the total anal-fin spines, hidden anal-fin spines and exposed anal-fin spines. The anal-fin base included the base of the anal-fin spine, simplying the midpoint of the anal-fin base is the midpoint between the first anal-fin spine base and the last anal-fin soft-ray base. A morphological phylogenetic tree was constructed on IQ-TREE 2 (Minh *et al.*, 2020).

The sequences were obtained via Sanger dideoxy sequencing. Multigene phylogenetic analyses were constructed with seven markers: Cytochrome c Oxidase subunit I gene (COI), Mitochondrial small subunit ribosomal Ribonucleic Acid gene (12SrRNA), Mitochondrial large subunit ribosomal Ribonucleic Acid gene (16SrRNA), SRC Homology 3 domain and Phagocytic Oxidase domain-containing protein 3-like protein gene (Sh3px3), Pleomorphic Adenoma zinc finger protein-like zinc finger 2 gene (PLAGL2), Glycine Transferase gene (Glyt), and Myosin Heavy chain gene 6 (MYH6). The primers used to amplify the markers are listed in Table 1. All the primary genetic information in this study has been uploaded to GenBank, and the other gene sequences were downloaded from GenBank (Table 2.). Gene pairwise alignment was performed using Geneious (Kearse *et al.*, 2012); multiple sequence alignment was performed twice, first using Geneious, followed by using Multiple Sequence Comparison by Log-Expectation (MUSCLE) (Edgar, 2004) of European Molecular Biology Laboratory’s European Bioinformatics (EMBL-EBI) as a proofreader; the substitution model were chosen in Molecular Evolutionary Genetics Analysis (MEGA) (Kumar *et al.*, 2016), and molecular phylogenetic trees were constructed in Phylosuite (Zhang *et al.*, 2020) and optimised in MEGA and Geneious, and the coalescence was performed in Phylosuite. The Kimura-Two-Parameter (K2P) genetic distances between samples were calculated in MEGA. The standard for confirming interspecific COI divergence followed that described by Hebert *et al.* (2003), which is a K2P genetic distance between two individuals of greater than 0.03 or 3%. Whether two species belong to two genera was determined by whether the K2P genetic distance between these two species was considerably greater than the greatest interspecific K2P genetic distance of the polytypic genera under the same family, and whether the monophyly of this genus would not be disturbed if this species were moved under another genus (Grande *et al.*, 2025). Whether two genera belong to two subfamilies was determined by whether the K2P genetic distance between the species under these two genera was considerably greater than the greatest interspecific K2P genetic distance of polytypic subfamilies under the same family, and whether the monophyly of this subfamily and family would not be disturbed if this species were moved under another subfamily (Grande *et al.*, 2018; Tongboonkua *et al.*, 2025).

TABLE 1. Primers used in PCR (upper: forward, lower: reverse).

Marker	Primer pair	Annealing temperature	Reference
COI	FishF1: 5'-TCAACCAACCACAAAGACATTGGCAC-3' FishR1: 5'-TAGACTTCTGGGTGGCCAAAGAATCA-3'	54℃	Ward *et al.* (2005)
12SrRNA	MiFish-U-F: 5'-GTCGGTAAAACTCGTGCCAGC-3' MiFish-U-R: 5'-CATAGTGGGGTATCTAATCCCAGTTTG-3'	56.6℃ 56.5℃	Miya *et al.* (2015)
16SrRNA	Fish16SrRNAF/D: 5'-GACCCTATGGAGCTTTAGAC-3' 16SrRNA2R: 5'-CGCTGTTATCCCTADRGTAACT-3'	54℃	Berry *et al.* (2017) Deagle *et al.* (2007)
Sh3px3	SH3PX3_F461: 5'-GTATGGTSGGCAGGAACYTGAA-3' SH3PX3_R1303: 5'-CAAACAKCTCYCCGATGTTCTC-3'	55℃	Li *et al.* (2007)
PLAGL2	plagl2_F9: 5'-CCACACACTCYCCACAGAA-3' plagl2_R930: 5'-TTCTCAAGCAGGTATGAGGTAGA-3'	55℃	Li *et al.* (2007)
GlyT	Glyt_F559: 5'-GGACTGTCMAAGATGACCACMT-3' Glyt_R1562: 5'-CCCAAGAGGTTCTTGTTRAAGAT-3'	55℃	Li *et al.* (2007)
MYH6	myh6_F459: 5'-CATMTTYTCCATCTCAGATAATGC-3' myh6_R1325: 5'-ATTCTCACCACCATCCAGTTGAA-3'	53℃	Li *et al.* (2007)

TABLE 2. Sequences used in the molecular analysis of this study. *Low quality (overall %HQ=76.7 %–94.1 %). Other sequences from this study are of comparatively high quality (overall %HQ=96.3 %–99.6 %).

Accession number	Voucher	Marker	Organism (follow GenBank)	Locality	Source
PX945068	MBM288291	COI	*Cyttula macropus*	South China Sea	This study
*PZ012201	MBM288291	12SrRNA	*Cyttula macropus*	South China Sea	This study
*PZ006375	MBM288291	16SrRNA	*Cyttula macropus*	South China Sea	This study
*PZ017027	MBM288291	Sh3px3	*Cyttula macropus*	South China Sea	This study
*PZ017022	MBM288291	PLAGL2	*Cyttula macropus*	South China Sea	This study
PZ017012	MBM288291	GlyT	*Cyttula macropus*	South China Sea	This study
*PZ017017	MBM288291	MYH6	*Cyttula macropus*	South China Sea	This study
PX945069	MBM288292	COI	*Cyttula macropus*	South China Sea	This study
*PZ012202	MBM288292	12SrRNA	*Cyttula macropus*	South China Sea	This study
*PZ006376	MBM288292	16SrRNA	*Cyttula macropus*	South China Sea	This study
*PZ017028	MBM288292	Sh3px3	*Cyttula macropus*	South China Sea	This study
*PZ017023	MBM288292	PLAGL2	*Cyttula macropus*	South China Sea	This study
PZ017013	MBM288292	GlyT	*Cyttula macropus*	South China Sea	This study
*PZ017018	MBM288292	MYH6	*Cyttula macropus*	South China Sea	This study
PX251996	MBM288311	COI	*Zenion retroaponicum*	South China Sea	This study
PZ012203	MBM288311	12SrRNA	*Zenion retroaponicum*	South China Sea	This study
PZ006377	MBM288311	16SrRNA	*Zenion retroaponicum*	South China Sea	This study
PZ017029	MBM288311	Sh3px3	*Zenion retroaponicum*	South China Sea	This study
PZ017024	MBM288311	PLAGL2	*Zenion retroaponicum*	South China Sea	This study
PZ017014	MBM288311	GlyT	*Zenion retroaponicum*	South China Sea	This study
PZ017019	MBM288311	MYH6	*Zenion retroaponicum*	South China Sea	This study
PX251997	MBM288312	COI	*Zenion retroaponicum*	South China Sea	This study
PZ012204	MBM288312	12SrRNA	*Zenion retroaponicum*	South China Sea	This study
PZ006378	MBM288312	16SrRNA	*Zenion retroaponicum*	South China Sea	This study
PZ017030	MBM288312	Sh3px3	*Zenion retroaponicum*	South China Sea	This study
PZ017025	MBM288312	PLAGL2	*Zenion retroaponicum*	South China Sea	This study
PZ017015	MBM288312	GlyT	*Zenion retroaponicum*	South China Sea	This study
PZ017020	MBM288312	MYH6	*Zenion retroaponicum*	South China Sea	This study
PX251998	MBM288313	COI	*Zenion retroaponicum*	South China Sea	This study
PZ012205	MBM288313	12SrRNA	*Zenion retroaponicum*	South China Sea	This study
PZ006379	MBM288313	16SrRNA	*Zenion retroaponicum*	South China Sea	This study
PZ017031	MBM288313	Sh3px3	*Zenion retroaponicum*	South China Sea	This study
PZ017026	MBM288313	PLAGL2	*Zenion retroaponicum*	South China Sea	This study
PZ017016	MBM288313	GlyT	*Zenion retroaponicum*	South China Sea	This study
PZ017021	MBM288313	MYH6	*Zenion retroaponicum*	South China Sea	This study
PQ524198.1	ASIZP0082291	COI	*Zenion* sp. bo	Dongsha Island	GenBank
PQ524199.1	ASIZP0082292	COI	*Zenion* sp. bo	Dongsha Island	GenBank

PQ524200.1	ASIZP0082293	COI	*Zenion* sp. bo	Dongsha Island	GenBank
PV704604.1	USNM:FISH:471022	COI	*Zenion* sp.	North Atlantic	GenBank
KY873727.1	ASIZP 0910704	COI	*Zenion* sp.	East China Sea	GenBank
JF718831.1	MLFPI98	COI	*Zenion hololepis*	Portugal	GenBank
JF718832.1	MLFPI96	COI	*Zenion hololepis*	Portugal	GenBank
JF718833.1	MLFPI1	COI	*Zenion hololepis*	Portugal	GenBank
JF718834.1	MLFPI94	COI	*Zenion hololepis*	Portugal	GenBank
JF718835.1	MLFPI93	COI	*Zenion hololepis*	Portugal	GenBank
MF041591.1	RIE 0212	COI	*Zenion hololepis*	Gulf of Mexico	GenBank
MG856787.1	DPND 4128	COI	*Zenion hololepis*	Gulf of Mexico	GenBank
KY873667.1	USNM:407025	12SrRNA	*Zenion hololepis*	Panama	GenBank
KY873713.1	USNM:407025	16SrRNA	*Zenion hololepis*	Panama	GenBank
KY873981.1	USNM:407025	Sh3px3	*Zenion hololepis*	Panama	GenBank
KY873932.1	SAIAB:82155	PLAGL2	*Zenion hololepis*	Mozambique	GenBank
KY873787.1	USNM:407025	GlyT	*Zenion hololepis*	Panama	GenBank
KY873878,1	USNM:407025	MYH6	*Zenion hololepis*	Panama	GenBank
KY873733.1	HM07-437; SAIAB:82155	COI	*Zenion hololepis*	Mozambique	GenBank
MN915266.1	NMNZP.052317	COI	*Zenion leptolepis*	New Zealand	GenBank
PQ524204.1	ASIZP0082290	COI	*Zenion japonicum*	Dongsha Island	GenBank
JN312452.1	BW-A10800	COI	*Zenion japonicum*	Australia	GenBank
KY873735.1	CSIRO:GT H 7136-19; GT H 5810	COI	*Zenion japonicum*	Western Australia	GenBank
KY873736.1	CSIRO:GT H 7136-19; GT H 5811	COI	*Zenion japonicum*	Western Australia	GenBank
KY873724.1	LUC 2; LUC CA2	COI	*Capromimus abbreviatus*	New Zealand	GenBank
KY873641.1	LUC 2; LUC CA2	12SrRNA	*Capromimus abbreviates*	New Zealand	GenBank
KY873684.1	LUC 2; LUC CA2	16SrRNA	*Capromimus abbreviates*	New Zealand	GenBank
KY873954.1	LUC 2; LUC CA2	Sh3px3	*Capromimus abbreviates*	New Zealand	GenBank
KY873905.1	LUC 2; LUC CA2	PLAGL2	*Capromimus abbreviates*	New Zealand	GenBank
KY873757.1	LUC 2; LUC CA2	GlyT	*Capromimus abbreviates*	New Zealand	GenBank
KY873851.1	LUC 2; LUC CA2	MYH6	*Capromimus abbreviatus*	New Zealand	GenBank
JQ681446.1	FNSIC045-11	COI	*Cyttopsis cypho*	South China Sea	GenBank
PV852182.1	KTS_02607	COI	*Cyttopsis rosea*	Taiwan	GenBank
KY873645.1	NMV<AUS>:A 25169.5	12SrRNA	*Cyttopsis rosea*	Tasman Sea	GenBank
JX121801.1	KU 8315; USNM 388259	16SrRNA	*Cyttopsis rosea*	North Carolina	GenBank
KY873959.1	NMV<AUS>:A 25169.5	Sh3px3	*Cyttopsis rosea*	Tasman Sea	GenBank
KY873910.1	NMV<AUS>:A 25169.5	PLAGL2	*Cyttopsis rosea*	Tasman Sea	GenBank
KY873761.1	KU 8315; USNM 388259	GlyT	*Cyttopsis rosea*	North Carolina	GenBank
KY873855.1	KU 8315; USNM 388259	MYH6	*Cyttopsis rosea*	North Carolina	GenBank
GU804929.1	ADC09_138.2A#1	COI	*Parazen pacificus*	Tugela Banks	GenBank
KY873660.1	HM07-471; SAIAB:82404	12SrRNA	*Parazen pacificus*	Mozambique	GenBank
KY873705.1	HM07-471; SAIAB:82404	16SrRNA	*Parazen pacificus*	Mozambique	GenBank
KY873975.1	USNM:407006	Sh3px3	*Parazen pacificus*	North Atlantic	GenBank
KY873926.1	USNM:407006	PLAGL2	*Parazen pacificus*	North Atlantic	GenBank
KY873778.1	HM07-471; SAIAB:82404	GlyT	*Parazen pacificus*	Mozambique	GenBank
KY873871.1	USNM:407006	MYH6	*Parazen pacificus*	North Atlantic	GenBank
EF609340.1	BIOUG<CAN>:BW-2001	COI	*Cyttus australis*	Victoria	GenBank
KY873646.1	AMS:I 34165.022	12SrRNA	*Cyttus australis*	Australia	GenBank
KY873690.1	AMS:I 34165.022	16SrRNA	*Cyttus australis*	Australia	GenBank
KY873960.1	AMS:I 34165.022	Sh3px3	*Cyttus australis*	Australia	GenBank
KY873911.1	AMS:I 34165.022	PLAGL2	*Cyttus australis*	Australia	GenBank
KY873763.1	AMS:I 34165.022	GlyT	*Cyttus australis*	Australia	GenBank
KY873856.1	AMS:I 34165.022	MYH6	*Cyttus australis*	Australia	GenBank
KY873730.1	NMV<AUS>:A 25180.1	COI	*Cyttus traversi*	Australia	GenBank
KY873649.1	NMV<AUS>:A 25180.1	12SrRNA	*Cyttus traversi*	Australia	GenBank
KY873693.1	NMV<AUS>:A 25180.1	16SrRNA	*Cyttus traversi*	Australia	GenBank
KY873963.1	NMV<AUS>:A 25180.1	Sh3px3	*Cyttus traversi*	Australia	GenBank
KY873914.1	NMV<AUS>:A 25180.1	PLAGL2	*Cyttus traversi*	Australia	GenBank
KY873766.1	NMV<AUS>:A 25180.1	GlyT	*Cyttus traversi*	Australia	GenBank

KY873859.1	NMV<AUS>:A 25180.1	MYH6	*Cyttus traversi*	Australia	GenBank
KC501893.1	TR1936EK	COI	*Zeus faber*	Turkey	GenBank
KY873676.1	AMS:I 37682-001; SAIAB:I 99	12SrRNA	*Zeus faber*	Namibia	GenBank
KY873722.1	AMS:I 37682-001; SAIAB:I 99	16SrRNA	*Zeus faber*	Namibia	GenBank
KY873989.1	AMS:I 37682-001; SAIAB:I 99	Sh3px3	*Zeus faber*	Namibia	GenBank
KY873940.1	AMS:I 37682-001; SAIAB:I 99	PLAGL2	*Zeus faber*	Namibia	GenBank
KY873795.1	AMS:I 37682-001; SAIAB:I 99	GlyT	*Zeus faber*	Namibia	GenBank
KY873886.1	AMS:I 37682-001; SAIAB:I 99	MYH6	*Zeus faber*	Namibia	GenBank
KC016043.1	05-880	COI	*Zenopsis conchifer*	USA	GenBank
KY873670.1	KUI 26983; KU:IT:1074	12SrRNA	*Zenopsis conchifer*	mid Atlantic bight	GenBank
KY873716.1	KUI 26983; KU:IT:1074	16SrRNA	*Zenopsis conchifer*	mid Atlantic bight	GenBank
KY873985.1	KUI 26983; KU:IT:1074	Sh3px3	*Zenopsis conchifer*	mid Atlantic bight	GenBank
KY873936.1	KUI 26983; KU:IT:1074	PLAGL2	*Zenopsis conchifer*	mid Atlantic bight	GenBank
KY873791.1	KUI 26983; KU:IT:1074	GlyT	*Zenopsis conchifer*	mid Atlantic bight	GenBank
KY873882.1	KUI 26983; KU:IT:1074	MYH6	*Zenopsis conchifer*	mid Atlantic bight	GenBank
GU804904.1	ADC09_140.2#2.2	COI	*Xenolepidichthys dalgleishi*	Tugela Deep	GenBank
KY873665.1	KU:IT:8348; MCZ:167668	12SrRNA	*Xenolepidichthys dalgleishi*	New Jersey	GenBank
KY873711.1	KU:IT:8348; MCZ:167668	16SrRNA	*Xenolepidichthys dalgleishi*	New Jersey	GenBank
KY873979.1	KU:IT:8348; MCZ:167668	Sh3px3	*Xenolepidichthys dalgleishi*	New Jersey	GenBank
KY873931.1	KU:IT:8348; MCZ:167668	PLAGL2	*Xenolepidichthys dalgleishi*	New Jersey	GenBank
KY873785.1	KU:IT:8348; MCZ:167668	GlyT	*Xenolepidichthys dalgleishi*	New Jersey	GenBank
KY873876.1	KU:IT:8348; MCZ:167668	MYH6	*Xenolepidichthys dalgleishi*	New Jersey	GenBank
KY873731.1	NMV<AUS>:A 25107.2	COI	*Grammicolepis brachiusculus*	Tasman Sea	GenBank
KY873651.1	NMV<AUS>:A 25107.2	12SrRNA	*Grammicolepis brachiusculus*	Tasman Sea	GenBank
KY873695.1	NMV<AUS>:A 25107.2	16SrRNA	*Grammicolepis brachiusculus*	Tasman Sea	GenBank
KY873965.1	NMV<AUS>:A 25107.2	Sh3px3	*Grammicolepis brachiusculus*	Tasman Sea	GenBank
KY873916.1	NMV<AUS>:A 25107.2	PLAGL2	*Grammicolepis brachiusculus*	Tasman Sea	GenBank
KY873768.1	NMV<AUS>:A 25107.2	GlyT	*Grammicolepis brachiusculus*	Tasman Sea	GenBank
KY873861.1	NMV<AUS>:A 25107.2	MYH6	*Grammicolepis brachiusculus*	Tasman Sea	GenBank
DQ108085.1	BIOUG<CAN>:BW-A336	COI	*Pseudocyttus maculatus*	Maatsuyker Hill	GenBank
KY873663.1	CSIRO:H3972-01	12SrRNA	*Pseudocyttus maculatus*	Tasmania	GenBank
KY873709.1	CSIRO:266 H Psemac 3972-01	16SrRNA	*Pseudocyttus maculatus*	Tasmania	GenBank
KY873977.1	CSIRO:266 H Psemac 3972-01	Sh3px3	*Pseudocyttus maculatus*	Tasmania	GenBank
KY873928.1	CSIRO:266 H Psemac 3972-01	PLAGL2	*Pseudocyttus maculatus*	Tasmania	GenBank
KY873782.1	CSIRO:266 H Psemac 3972-01	GlyT	*Pseudocyttus maculatus*	Tasmania	GenBank
KY873873.1	CSIRO:266 H Psemac 3972-01	MYH6	*Pseudocyttus maculatus*	Tasmania	GenBank
DQ108067.1	BIOUG<CAN>:BW-A359	COI	*Allocyttus verrucosus*	Pedra Branca	GenBank
KY873638.1	SAIAB:87336	12SrRNA	*Allocyttus verrucosus*	Namibia	GenBank
KY873681.1	SAIAB:87336	16SrRNA	*Allocyttus verrucosus*	Namibia	GenBank
KY873952.1	SAIAB:87336	Sh3px3	*Allocyttus verrucosus*	Namibia	GenBank
KY873902.1	SAIAB:87336	PLAGL2	*Allocyttus verrucosus*	Namibia	GenBank
KY873754.1	SAIAB:87336	GlyT	*Allocyttus verrucosus*	Namibia	GenBank
KY873848.1	SAIAB:87336	MYH6	*Allocyttus verrucosus*	Namibia	GenBank
KC015385.1	06-103	COI	*Gadus morhua*	Georges Bank	GenBank
KY873635.1	KU:IT:3776	12SrRNA	*Gadus morhua*	Tromso Fjord	GenBank
JX121817.1	KU 2937; MCZ 155780	16SrRNA	*Gadus morhua*	mid Atlantic bight	GenBank
EU002070.1	KU:IT:3776	Sh3px3	*Gadus morhua*	Tromso Fjord	GenBank
KY873893.1	KU:IT:3776	PLAGL2	*Gadus morhua*	Tromso Fjord	GenBank
KY873746.1	KU:IT:3776	GlyT	*Gadus morhua*	Tromso Fjord	GenBank
EU001906.1	KU:IT:3776	MYH6	*Gadus morhua*	Tromso Fjord	GenBank

The data from the references were carefully evaluated to determine whether these were obtained from the same methods used in this study and remained unchanged. All the measured numeric data were approximated to the nearest 1 decimal in millimetres (mm), and all the ratios were approximated to the nearest 2 decimals in percents (%); all the numeric genetic data were approximated to the nearest 2 decimals in percents (%). The longitudes and latitudes in the locality were approximated to the nearest 2 decimal places, and depths were approximated to the nearest tens-place integer.

All the nomenclatures obeyed Ride *et al.* (2007).

Results

Zenion retrojaponicum n. sp.

Zenion japonicum (non Kamohara, 1934): Cheng & Tian, 1981: 243, 244 (figure 9); Shimizu, 1983, 287; Wang & Xu, 1988: 210, 211 (figure 167); Masuda *et al.*,1992a: 118; Masuda *et al.*,1992b: plate 103 (D); Martins *et al.*, 2012: 2; Nakabo & Kai, 2013: 599; Sun & Chen, 2013: 347 (figure 607); Sun *et al.*, 2013: 126 (upper figure); Ikeda & Nakabo, 2015: 83 (plate 82), 336; Fricke *et al.*, 2019: 88, figure. 32; Ho *et al.*, 2021: 500, 515 (plate 5); Wu & Zhong, 2021: 462 (figure 1410).
Zenion japonicus (non Kamohara, 1934) = *Zenion hololepis* (non Goode & Bean, 1896): Meng *et al.*, 1995: 504.
Zenion hololepis (non Goode & Bean, 1896): Meng *et al.*, 1995: 503 (figure 674).
Zenion sp.: Kailola & Gloerfelt-Tarp, 1984: 106 (Figure *Zenion* sp.), 107.
? *Zenion japonicum* (non Kamohara, 1934): Paxton & Hanley, 1989: 387; Yamada *et al.*, 2007: xxii (plate 18, 2), 377; Yamada *et al.*, 2009: 34 (173), 263 (173); Sáez & Lamilla 2017: 98 (figure 7).
? *Zenion hololepis* (non Goode & Bean, 1896): Paulin *et al.*, 1989: 159 (fig. 92.1); Chen *et al.*, 2016: 106.

Holotype: MBM288314, *Zenion retrojaponicum*, Holotype, 51.8 mm SL, trawl, 180 m, (12°42' N, 115°17' E), South China Sea, HW, 02/05/2025, ethanol.

Type locality: 180 m depth, (12°42' N, 115°17' E), South China Sea.

Paratypes: MBM288311, *Zenion retrojaponicum*, Paratype, 60.0 mm SL, trawl, 180 m, (12°42' N, 115°17' E), South China Sea, HW, 02/05/2025, ethanol, GenBank: PX251996 PZ012203 PZ006377 PZ017029 PZ017024 PZ017014 PZ017019; MBM288312, *Zenion retrojaponicum*, Paratype, 51.6 mm SL, trawl, 180 m, (12°42' N, 115°17' E), South China Sea, HW, 02/05/2025, ethanol, GenBank: PX251997 PZ012204 PZ006378 PZ017030 PZ017025 PZ017015 PZ017020; MBM288313, *Zenion retrojaponicum*, Paratype, 50.9 mm SL, trawl, 180 m, (12°43' N, 115°15' E), South China Sea, HW, 02/05/2025, ethanol, GenBank: PX251998 PZ012205 PZ006379 PZ017031 PZ017026 PZ017016 PZ017021; MBM288315, *Zenion retrojaponicum*, Paratype, 50.1 mm SL, trawl, 180 m, (12°42' N, 115°17' E), South China Sea, HW, 02/05/2025, ethanol; MBM288316, *Zenion retrojaponicum*, Paratype, 52.0 mm SL, trawl, 180 m, (12°42' N, 115°17' E), South China Sea, HW, 02/05/2025, ethanol; MBM288317, *Zenion retrojaponicum*, Paratype, 54.5 mm SL, trawl, 180 m, (12°42' N, 115°17' E), South China Sea, HW, 02/05/2025, ethanol; MBM288318, *Zenion retrojaponicum*, Paratype, 49.9 mm SL, trawl, 180 m, (12°43' N, 115°15' E), South China Sea, HW, 02/05/2025, ethanol; MBM288319, *Zenion retrojaponicum*, Paratype, 55.1 mm SL, trawl, 180 m, (12°42' N, 115°17' E), South China Sea, HW, 02/05/2025, ethanol; MBM288320, *Zenion retrojaponicum*, Paratype, 51.8 mm SL, trawl, 180 m, (12°42' N, 115°17' E), South China Sea, HW, 02/05/2025, ethanol; MBM288321, *Zenion retrojaponicum*, Paratype, 50.9 mm SL, trawl, 180 m, (12°43' N, 115°15' E), South China Sea, HW, 02/05/2025, ethanol; MBM288322, *Zenion retrojaponicum*, Paratype, 52.3 mm SL, trawl, 180 m, (12°42' N, 115°17' E), South China Sea, HW, 02/05/2025, ethanol; MBM288323, *Zenion retrojaponicum*, Paratype, 52.2 mm SL, trawl, 180 m, (12°42' N, 115°17' E), South China Sea, HW, 02/05/2025, ethanol; MBM288324, *Zenion retrojaponicum*, Paratype, 46.8 mm SL, trawl, 180 m, (12°42' N, 115°17' E), South China Sea, HW, 02/05/2025, ethanol; MBM288325, *Zenion retrojaponicum*, Paratype, 54.2 mm SL, trawl, 180 m, (12°42' N, 115°17' E), South China Sea, HW, 02/05/2025, ethanol; MBM288326, *Zenion retrojaponicum*, Paratype, 45.0 mm SL, trawl, 180 m, (12°42' N, 115°17' E), South China Sea, HW, 02/05/2025, ethanol; MBM288327, *Zenion retrojaponicum*, Paratype, 52.7 mm SL, trawl, 180 m, (12°42' N, 115°17' E), South China Sea, HW, 02/05/2025, ethanol; MBM288328, *Zenion retrojaponicum*, Paratype, 56.8 mm SL, trawl, 180 m, (12°42' N, 115°17' E), South China Sea, HW, 02/05/2025, ethanol; MBM288329, *Zenion retrojaponicum*, Paratype, 55.6 mm SL, trawl, 180 m, (12°42' N, 115°14' E), South China Sea, HW, 02/05/2025, ethanol; MBM288330, *Zenion retrojaponicum*, Paratype, 51.3 mm SL, trawl, 180 m, (12°40' N, 115°13' E), South China Sea, HW, 02/05/2025, ethanol; MBM288331, *Zenion retrojaponicum*, Paratype, 50.4 mm SL, trawl, 180 m, (12°40' N, 115°13' E), South China Sea, HW, 02/05/2025, ethanol.

Diagnosis. One functional lateral line; firm pterygiophore-derived bony ridges present at dorsal-fin and anal-fin bases; ventral-fin spine strong, nearly same as second dorsal-fin spine, maximum diameter of unbranched part of first ventral-fin soft ray less than 2/3 of maximum diameter of ventral-fin spine; first dorsal-fin spine attached to second dorsal-fin spine, with locking mechanism; profile of spinous dorsal-fin an acute angle; the length of first dorsal-fin spine less than 1/4 of the length of second dorsal-fin spine; ventral-fin origin slightly posterior to dorsal-fin origin; ventral fin with locking mechanism; when depressed, ventral-fin tip far anterior to the midpoint of anal-fin base; anal-fin-base length less than body height; second anal-fin spine, covered by skin, distinctly shorter than first anal-fin spine; branchiostegal rays completely hidden in the inner side of or above the preopercular; number of pored lateral-line scales approximately 45.
D: VI-VII + 27-29; P: 17; V: I 6; A: I + I + 26-27; C: iii + 1 11 1 + ii.

Description. Head large, compressed, without any spines, except the prolonged lower rear preopercular; the rest of the preopercular a boomerang. Eye lateral, large; upper margin of orbit serrated, on the upper margin of the head; approximately 8 infraorbitals, 5 developed with serrate and vertical supporting flanges, exclusive of lachrymal and dermosphenotic; lachrymal and dermosphenotic deep; dermosphenotic separated from sphenotic. Parietal present, small, almost at the same longitudinal level of upper margin of eye. Exoccipital facets closed together. Lower process of hyomandibular absent. Basisphenoid present as a long, oblique shaft connecting parasphenoid and prootic in the front of posterior myodome. Basihyal present. Mouth, albeit rather vertical than horizontal, inferior, slightly leaning forwards from corner of mouth to tip. Upper-jaw bone depressed at its extremity, where premaxillary connects the two sides of maxillary, which is the place for mandibular tip, depression stuffed by the succulent lip; a pouch on the upper margin of the head between eyes is the place for the ascending premaxillary, premaxillary ascending process reaches about the latitudinal level of 1/3 into orbit, premaxillary alveolar process ventrally intended and form a pair of blunt lobes; postmaxillary process present as a thin triangle. Mandibular lower margin double concave; two moderate cartilages, each attached anteriorly to the dentary and lying sequentially one behind the other, of about the same size; serrations on dentary lower border present as multiple serrations behind the symphysis. Maxillary and mandibular with tiny teeth in irregular rows; vomerine dentition two longitudinal oval patches, each on one side of the longitudinal midline of the anterior part of the ventral side of vomerine, slightly scattered; fifth-ceratobranchial teeth dentition oval; ectopterygoid dentition oval; premaxillary, fourth-upper-pharyngeal, and palatine without teeth. Palatine bulged, coarse, orientated distinctly obliquely to the body axis and has a single, pivotal, articulation with the lateral ethmoid, resulting in a little mobility; levator arcus palatine does not connect to the infrapostorbital mandibular adductor A2, both reduced. Tongue short, tip free. Metapterygoid present but reduced. Symplectic ventral flange present but indistinct. Gill cavity large, 3+1/2 gills, approximately 7 gill rakers on each. Gill opening wide, extending from the longitudinal level of the upper half of the eye to corner of mouth; gill membrane of two sides connected under corner of mouth; gill-slit opening between the fourth and the fifth ceratobranchials absent. Branchiostegal rays 7, completely hidden in the inner side of or above the preopercular, along the ventral edges of both the ceratohyal and epihyal; percopsoid projection on fourth branchiostegal ray absent. Prominent notches present on lower margin of ceratohyal; beryciform foramen present as an open, deep groove along the lateral surface of the ceratohyal. Ceratohyal-epihyal articulation through cartilage. Depth of the anterior end of epihyal almost equal to the depth of the adjacent part of the ceratohyal. Urohyal large, far longer than the ceratohyal. First-epibranchial uncinate process absent. Second-pharyngobranchial suspensory shaft long, length approximately equal to 2/3 of length of first-pharyngobranchial shaft; third-pharyngobranchial suspensory shaft moderately moderately long, length far longer than width of second-pharyngobranchial tooth patch, far less than second-pharyngobranchial shaft. Upper surface of posterior part of first-basibranchial is level with those of basihyal and second basibranchial posteriorly. Interarcual cartilage absent. Cephalic bones without honeycomb sculpturing. Body short oval, rather compressed than depressed, slightly to moderately elongated, deepest at dorsal-fin origin. Nape ascended. Abdomen flat. Anus at the anterior half of the individual. Tail tapered until caudal peduncle, which is biconcave on its upper and lower profile. Total vertebrae 27; 11 precaudal; 16 caudal, among which 5 caudal-peduncle. Dorsal extension of neural spine of first vertebra plastered to the skull proximally, while with a long dorsal portion free from the skull beyond the curvature of the supraoccipital and the exoccipitals distally. All precaudal neural spines but the first two orientated posterodorsally; almost all haemal spines of the precaudal vertebrae, especially posteriorly, with a prominent process in midline below bridge under haemal canal; ossified ribs present on all precaudal vertebrae except first one; ossified epineurals present on all developed precaudal ribs. Neural and haemal spines of first two caudal-peduncle vertebrae specialised into wide plates with anterior and posterior margins ridged. Hyperstosis absent in any bony components.

Scales weak-ctenoid, very large and deciduous due to reduced pockets hidden under the scales, evenly loosely covering trunk, including nape and isthmus, and tail, including caudal-fin base and a short distance of proximal caudal-fin rays; no scales on head. Lateral line 1, the lower unfunctional remnant, excluded. Minimum scales rows between spinous dorsal fin and lateral line approximately 10. Pored lateral-line scale approximately 45; lateral line ridged, as the pored lateral-line scales are larger weak scutes with pore, overlapping respectively one scale above and below lateral line, and thus looser. Lateral line begins at the top point of the opercular, then slightly descended until the end of the base of spinous dorsal fin, then rapidly descended until the longitudinal midline of body, at about the midpoint of anal-fin base, then turns straight until reaching caudal-fin base through the longitudinal midline of caudal peduncle. Dorsal-fin base and anal-fin base scaleless. Buclers absent.

Pectoral fin rounded, 17 soft rays; soft rays slightly flattened and branched at tip, two branches on one soft ray attached to each other and thus inseparable. Girdle simple; pectoral-fin radial, lateral flange on the lowermost, absent, 1 postcleithrum, without flange; supracleithral serration present, supracleithrum ventral end simple; cleithrum posteriorly with a cleithral process, as a prong above the articulation with the postcleithrum; extrascapular present as a long tubular bone; scapular foramen bounded by scapula. First dorsal fin consists of 6 or 7 spines; locking mechanism present among the spines, spines can open to less than 90°; when first dorsal fin fully erected, only if both the first and the third spines are pushed backwards concurrently, first dorsal fin can be depressed; first spine shortest, length approximately same as the last spine, less than 1/4 of the length of second dorsal-fin spine; second spine the longest, the following fin-membrane margin descended; profile of first dorsal fin an acute angle; anterior-most margin of second dorsal-fin spine serrated. Membrane between first and second dorsal fin present. Second dorsal fin consists of 27 to 29 soft rays; margin curved, ascended then descended; except for the first soft ray, other soft rays branched; soft rays slightly flattened and branched at tip, two branches on one soft ray attached to each other and thus inseparable; last two soft rays distinctly thinner. Pterygiophore-derived bony ridges present at dorsal-fin base; dorsal-fin base scaleless. Interneural gaps 2, which is the sixth and seventh interneural space, in a group; 3 dorsal-fin pterygiophores anterior to fourth neural spine. First dorsal-fin pterygiophore inserted in first interneural space, contact with first vertebra. A supraneural, with thin cartilage at distal end inserted between first neural spine and skull. Ventral fin originates approximately at the same latitudinal level of but slightly posterior to dorsal-fin origin, first element a spine, which is the longest element in ventral fin with locking mechanism, can open approximately 90°, followed by 6 segmented branched soft rays, without serration or anterolateral process; spine strong, maximum diameter of unbranched part of first ventral-fin soft ray less than 2/3 of maximum diameter of ventral-fin spine; the length of ventral-fin soft rays gradually decreased; when depressed, ventral-fin tip far anterior to the midpoint of anal-fin base, ratio of the length of ventral-fin spine in the length of the longest ventral-fin soft ray less than 1.5. Pelvis fragile, two sides of pelvis connected weakly; medial processes of basipterygia broadly overlap at the level of the pelvic fin; posterior process of pelvis behind pelvic-fin base moderate in length, in a shape of flattened shaft; pelvis easily twisted with the soft abdominal cavity being compressed and thus changes ventral-fin origin. Anal fin originates with two spines immediately after anus, under the anterior section of second dorsal fin, approximately at the midpoint of dorsal-fin base; first anal-fin spine exposed; second anal-fin spine often covered by skin; locking mechanism present between anal-fin spines, first anal-fin spine unfused with its pterygiophore; anal-fin spines followed, after a short gap, by 26 to 27 soft rays considerably longer than the spines; no evidence that membrane present between spinous and soft anal fin; margin of the soft anal fin curved, ascended then descended; soft rays slightly flattened and branched at tip, two branches on one soft ray attached to each other and thus inseparable; last two soft rays are distinctly thinner; anal-fin-base length less than body height; pterygiophore-derived bony ridges present at anal-fin base; anal-fin base scaleless. Pterygiophores in second caudal interhaemal space 2; pterygiophores before third caudal haemal spine approximately 6. Pterygiophores of soft dorsal-fin and soft anal-fin almost symmetrical. Caudal fin, albeit middle rays shorter than outer rays, convex, consists of soft rays only; uppermost 3 accessory soft rays short, free, simple and spinous, followed by 1 free segmented unbranched soft ray that is comparatively shorter than other branched soft rays, followed by 11 segmented branched soft rays, followed by free 1 segmented unbranched soft rays that is relatively shorter than other branched soft rays, followed by the 2 lowermost short free simple spinous accessory soft rays; all the branched caudal-fin soft rays with branches more than two, branched obviously. Antepenultimate vertebra is the first vertebra with a modified spine to support the caudal fin, which is the neural spine; hypurapophysis present; 2 epurals, separated anteriorly, connected posteriorly; articulation of proximal end of parhypural to urostylar centrum slightly removed from and not embracing the centrum; hypurals 1–2 fused together, hypurals 3–4 fused together, both free from the centrum, as well as hypural 5; any extra caudal ossicle absent between haemal spine of penultimate and antepenultimate centrum; interradiales located across and between caudal-fin soft rays, insertions of interradiales present between principal caudal rays only. All fin membranes fragile.

Measurements in Table 3.

TABLE 3. Morphometric data of *Zenion retrojaponicum* n. sp. and its available congeners.

	Zenion retrojapnicum n. sp.		*Zenion hololepis*	? *Zenion hololepis*	"*Zenion japonicum*"
	Holotype (n=1)	Type specimens (n=21)	Martins *et al.*, 2012 (n=5)	Rufus *et al.*, 2021 (n=1)	Lin *et al.*, 2025 (n=20)
Total length (mm)	64.9	55.3–72.3	79–134	67.9	61.5–74.6
Standard length (mm)	51.8	45.0–60.0	60–110	53.0	46.7–61.9
%(Standard length)					
Total length	125.29	113.45–131.63	-	128.1	-
Body height	46.53	40.33–48.10	37.6–43.2	41.8	32.9–34.6
Body width	19.50	13.33–22.22	-	-	-
Head length	42.47	34.52–43.27	35.7–41.8	43.8	35.8–37.2
Trunk length	19.50	17.61–24.67	-	-	-
Tail length	63.32	61.10–71.73	-	-	-
Pre-dorsal-fin length	41.31	36.34–43.16	40.3–45.2	41.5	40.5–42.7
Pre-anal-fin length	61.78	56.67–69.54	-	-	-
Pre-anus length (Body length)	57.72	53.33–65.85	-	-	-
Mouth length	17.37	16.09–19.56	-	-	-

Preorbital length	6.56	5.32-8.96	-	-	-
Minimum interorbital length	13.13	11.70–16.45	-	-	-
Maximum orbital diameter	22.39	19.08–22.44	-	-	-
Gill-opening length	35.71	31.75–41.65	-	-	-
Dorsal-fin base length	53.67	47.89–57.88	53.2–56.1	54.4	49.1–51.6
Anal-fin base length	28.96	28.78-35.47	33.3–35.9	35.8	30.9–32.4
Pectoral-fin length	10.04	8.99–14.44	-	-	-
Ventral-fin length	23.36	19.83–28.63	-	-	-
Caudal-fin length	25.29	20.77–30.06	23.4–28.9	23.7	14.4–16.3
Caudal-peduncle length	9.65	8.05–12.02	-	-	-
Caudal-peduncle height	6.18	4.83–7.31	-	-	-
Length of first dorsal-fin spine	4.63	3.47–6.09	-	-	-
Length of second dorsal-fin spine	22.20	19.12–25.78	-	-	-
Length of third dorsal-fin spine	17.18	13.58–20.36	-	-	-
%(Body height)			-	-	-
Head length	91.29	79.41–100.89	-	-	-
Maximum orbital diameter	48.13	45.97–52.48	-	-	-
Anal-fin base length	62.24	51.06–92.98	-	-	-
Caudal-peduncle height	13.28	11.98–17.86	-	-	-
Length of first dorsal-fin spine	9.96	8.44–12.81	-	-	-
Length of second dorsal-fin spine	47.72	42.92–57.14	-	-	-
Length of third dorsal-fin spine	36.92	30.47–44.81	-	-	-
%(Maximum orbital diameter)			-	-	-
Head length	207.76	190.55–222.02	-	-	-
Preorbital length	29.31	27.18–42.24	-	-	-
Length of first dorsal-fin spine	20.69	16.67–26.80	-	-	-
Length of second dorsal-fin spine	9.91	89.29–118.27	-	-	-
Length of third dorsal-fin spine	76.72	63.39–91.07	-	-	-
				-	
%(Length of second dorsal-fin spine)			-	-	-
Trunk length	87.82	78.04-113.15	-	-	-
Length of first dorsal-fin spine	20.87	16.26–24.41	-	-	-
Length of third dorsal-fin spine	77.39	68.57–90.35	-	-	-

Fresh colouration. Head greyish and shiny, anterior part slightly pinkish. Scales transparent, but when they densely distributed on the body, seem greyish, due to diffuse reflection. Under the scales, body pinkish and shiny, more pinkish and less shiny on the dorsal side of the body. Spinous dorsal fin translucent near base, distal three-fourths to two-thirds black; soft dorsal fin transparent. Anal fin transparent. Ventral fin translucent with distal parts pinkish. Caudal fin with proximal part transparent, distal parts brownish red. (Figure 1. C).

Ethanol-preserved colouration. Entirely brownish, except for the white-translucent fins and distinct white lenses.

Size. Approximately a maximum of 12-centimetre total length, 10-centimetre standard length (specimen unpreserved).

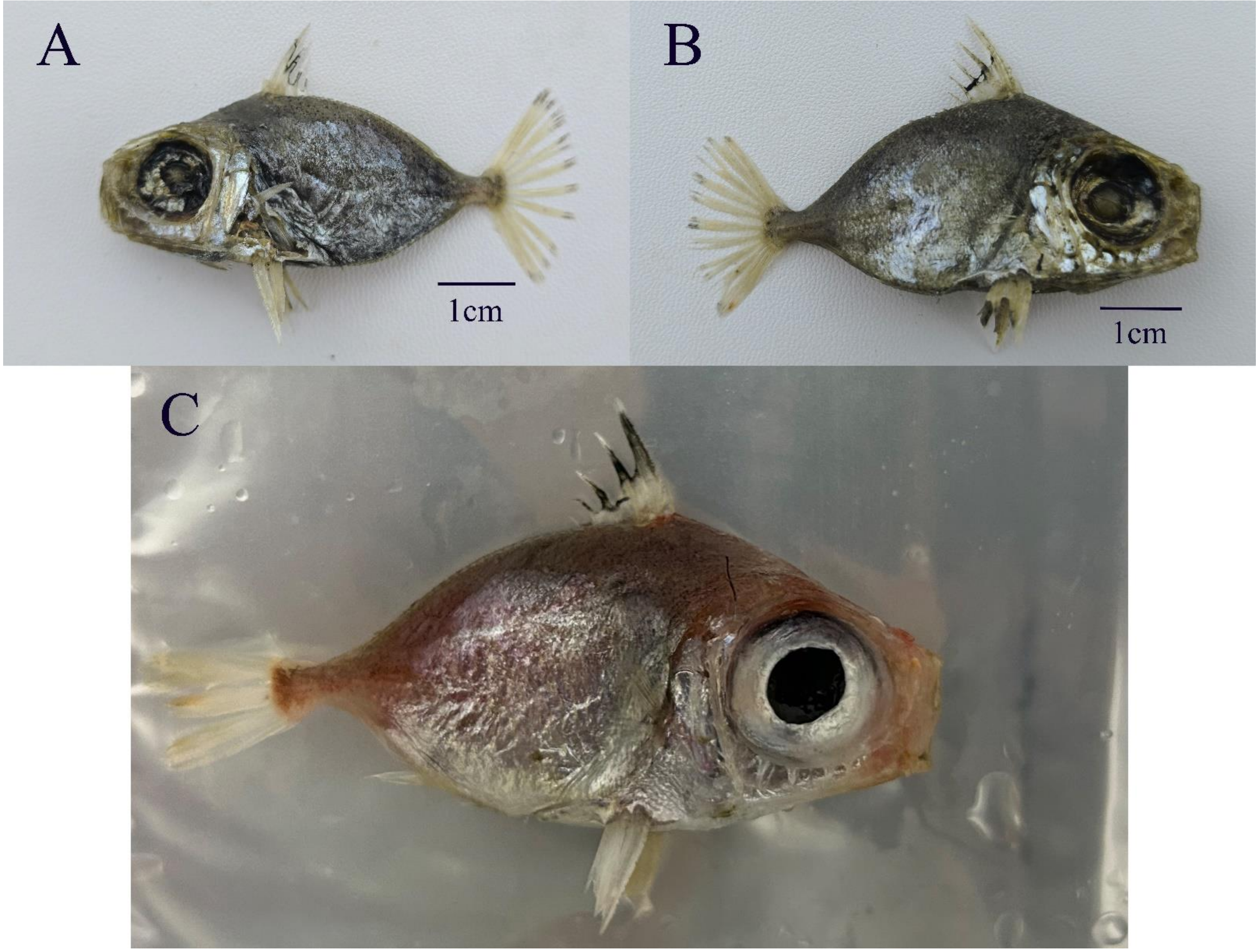

Figure 1. *Zenion retrojaponicum* n. sp.. A: scalebar: 1 cm, left side, MBM288331, Nontype, 50.4 mm SL; B: scalebar: 1 cm, right side, MBM288314, Holotype, 51.8 mm SL; C: right side of a fresh body not retained.

Etymology. This name is derived from *japonicum*, and "*retro*-" is a Latin prefix meaning "previous". Thus, the specific epithet, *retrojaponicum*, represents this species that had been regarded as *Zenion japonicum* Kamohara, 1934. This specific epithet does not indicate the type locality of the new species. The Greek suffix "*-um*" makes the specific epithet an adjective adjunct to the neuter generic name.

Distribution. South China Sea (This study, Figure 4.), 150 m to 400 m depth; Japan (Nakabo & Kai, 2013); New Ireland, Papua New Guinea (Fricke *et al.*, 2019); Australia (Kailola & Gloerfelt-Tarp, 1984); questionably in Chile (Sáez & Lamilla, 2017).

Genetic analysis. With *Gadus morhua* Linnaeus, 1758 as outgroup, within the sequenced specimens of *Zenion*, including the available sequences online, except for *Zenion boops* (= *Cyttula boops*), the sister group of the new species is *Zenion hololepis* (Figure 5.), The new species shares the highest identity with *Zenion hololepis*, with the minimum interspecific K2P genetic distance to *Zenion hololepis* among the species under *Zenion*, approximately 9.88%. It has the maximum interspecific K2P genetic distance with an undescribed species, *Zenion* sp. ‘‘*Cyttomimus affinis*’’, from Grande *et al.* (2018), among the species under *Zenion*, of approximately 12.81%. The intraspecific K2P genetic distances of COI between the new species range from 0.00% to 0.32% (Figure 5.).

Remarks. Meng *et al.* (1995) regarded *Zenion japonicus*, the misspelled nomenclature of *Zenion japonicum*, as a junior synonym of *Zenion hololepis*, which was correct. However, it might be for the wrong reasons, as both *Zenion japonicus* and *Zenion hololepis* from Meng *et al.* (1995) seem to be *Zenion retrojaponicum* n. sp.. Kailola & Gloerfelt-Tarp (1984) reported *Zenion* sp., a specimen with the same characters as the specimens that would be treated as *Zenion japonicum* by many researchers (Nakabo & Kai, 2013;

Sun *et al.*, 2013; Fricke *et al.*, 2019) are considered to be *Zenion retrojaponicum* n. sp.. Sáez & Lamilla (2017) reported that *Zenion japonicum* has the first dorsal-fin spine longer than the second one; this is probably erroneous, as the very short first dorsal-fin spine might be ignored or broken, and the first dorsal-fin spine of zeiform species, if not filamentous, is never the longest. Other provided characters are similar to those of *Zenion retrojaponicum* n. sp., but the provided characters are too few. Thus, the status of the *Zenion japonicum* reported by Sáez & Lamilla (2017) remains uncertain, possibly *Zenion retrojaponicum* n. sp..

Although this species has been misidentified as *Zenion japonicum* (Cheng & Tian, 1981; Shimizu, 1983; Wang & Xu, 1988; Masuda *et al.*, 1992a; Masuda *et al.*, 1992b; Martins *et al.*, 2012; Nakabo & Kai, 2013; Sun & Chen, 2013; Sun *et al.*, 2013; Ikeda & Nakabo, 2015; Fricke *et al.*, 2019; Ho *et al.*, 2021; Wu & Zhong, 2021), this species is not identical with the original description of *Zenion japonicum* Kamohara, 1934 (This study: subheading "Comments": subheading "*Zenion japonicum* Kamohara, 1934 (= *Zenion hololepis* (Goode & Bean, 1896))").

Cyttulinae new subfamily

Zeidae (non Rafinesque, 1815): Weber, 1913: 409.
Macrurocyttidae (non Myers, 1960): Heemstra, 1999: 2258.
Zeniontidae (non Myers, 1960): Heemstra, 1980: 2.

Description. A subfamily whose type genus is *Cyttula*, information under the following subheading, "*Cyttula macropus* Weber, 1913", as well as "*Cyttula boops* (Lin *et al.*, 2025)".
Etymology. According to its type genus, *Cyttula*.

Cyttula Weber, 1913

Cyttula Weber, 1913: 411, plate II. (fig. 3, fig. 3a).
Zenion (non Jordan & Evermann, 1896): Shimizu, 1983: 287.
Zen (non Fowler, 1934): Cheng & Zheng, 1987a, 257.

Description. A genus whose type species is *Cyttula macropus* Weber, 1913, information under the following subheading, "*Cyttula macropus* Weber, 1913", as well as "*Cyttula boops* (Lin *et al.*, 2025)".

Cyttula macropus Weber, 1913

Cyttula macropus Weber, 1913: 411, plate II. (Fig. 3, Fig. 3a).
Cyttula macropus: Weber & de Beaufort, 1929: 221 (fig. 62); Kotthaus, 1970: 65; Karrer, 1990: 629.
Zenion macrops: Shimizu, 1983, 287.
Zenion hololepis (non Goode & Bean, 1896): Yang *et al.*, 1980: 108 (figure 34); Yang *et al.*, 1996: 168 (figure 118); Sun & Chen, 2013: 347 (figure 608); Wu & Zhong, 2021: 462 (figure 1411).
Zenion japonicum (non Kamohara, 1934): Sun *et al.*, 2013: 126 (lower figure).
Zen cypha (non Fowler, 1934): Cheng & Zheng, 1987a, 257; Cheng & Zheng, 1987b, 1004 (figure 1279).
Zenion sp.2: Koeda *et al.*, 2022: 78, 85 (figure 1).
? *Zenion japonicum* (non Kamohara, 1934): Konishi: 501 (unlabelled figure).

New specimens: MBM288291, *Cyttula macropus*, Nontype, 82.4 mm SL, trawl, 400 m, (12°41' N, 115°19' E), South China Sea, HW, 03/05/2025, ethanol, GenBank: PX945068 PZ012201 PZ006375 PZ017027 PZ017022 PZ017012 PZ017017; MBM288292, *Cyttula macropus*, Nontype, 89.3 mm SL, trawl, 400 m, (12°41' N, 115°19' E), South China Sea, HW, 03/05/2025, ethanol, GenBank: PX945069 PZ012202 PZ006376 PZ017028 PZ017023 PZ017013 PZ017018; MBM288293, *Cyttula macropus*, Nontype, 84.1 mm SL, trawl, 400 m, (12°41' N, 115°19' E), South China Sea, HW, 03/05/2025, ethanol, GenBank: ; MBM288294, *Cyttula macropus*, Nontype, 86.7 mm SL, trawl, 400 m, (12°44' N, 115°15' E), South China Sea, HW, 03/05/2025, ethanol, GenBank: ; MBM288295, *Cyttula macropus*, Nontype, 79.5 mm SL, trawl, 400 m, (12°41' N, 115°19' E), South China Sea, HW, 03/05/2025, ethanol, GenBank: ; MBM288296, *Cyttula macropus*, Nontype, 77.7 mm SL, trawl, 400 m, (12°41' N, 115°19' E), South China Sea, HW, 03/05/2025, ethanol, GenBank: ; MBM288297, *Cyttula macropus*, Nontype, 72.9 mm SL, trawl, 400 m, (12°41' N, 115°19' E), South China Sea, HW, 03/05/2025, ethanol, GenBank: ; MBM288298, *Cyttula macropus*, Nontype, 67.5 mm SL, trawl, 400 m, (12°41' N, 115°19' E), South China Sea, HW, 03/05/2025, ethanol, GenBank: ; MBM288299, *Cyttula macropus*, Nontype, 88.4 mm SL, trawl, 400 m, (12°44' N, 115°15' E), South China Sea, HW, 03/05/2025, ethanol, GenBank: ; MBM288300, *Cyttula macropus*, Nontype, 63.0 mm SL, trawl, 400 m, (12°41' N, 115°19' E), South China Sea, HW, 03/05/2025, ethanol; MBM288301, *Cyttula macropus*, Nontype, 86.6 mm SL, trawl, 400 m, (12°44' N, 115°15' E), South China Sea, HW, 03/05/2025, ethanol; MBM288302, *Cyttula macropus*, Nontype, 91.2 mm SL, trawl, 400 m, (12°44' N, 115°15' E), South China Sea, HW, 03/05/2025, ethanol; MBM288303, *Cyttula macropus*, Nontype, 63.9 mm SL, trawl, 400 m, (12°44' N, 115°15' E), South China Sea, HW, 03/05/2025, ethanol; MBM288304, *Cyttula macropus*, Nontype, 94.5 mm SL, trawl, 400 m, (12°41' N, 115°19' E), South China Sea, HW, 03/05/2025, ethanol; MBM288305, *Cyttula macropus*, Nontype, 91.6 mm SL, trawl, 400 m, (12°41' N, 115°19' E), South China Sea, HW, 03/05/2025, ethanol; MBM288306, *Cyttula macropus*, Nontype, 78.0 mm SL, trawl, 400 m, (12°41' N, 115°19' E), South China Sea, HW, 03/05/2025, ethanol; MBM288307, *Cyttula macropus*, Nontype, 77.6 mm SL, trawl, 400 m, (12°41' N, 115°19' E), South China Sea, HW, 03/05/2025, ethanol; MBM288308, *Cyttula macropus*, Nontype, 75.5 mm SL, trawl, 400 m, (12°39' N, 115°16' E), South China Sea, HW, 03/05/2025, ethanol; MBM288309, *Cyttula macropus*, Nontype, 82.6 mm SL, trawl, 400 m, (12°39' N, 115°16' E), South China Sea, HW, 03/05/2025, ethanol; MBM288310, *Cyttula macropus*, Nontype, 81.8 mm SL, trawl, 400 m, (12°39' N, 115°16' E), South China Sea, HW, 03/05/2025, ethanol.

Type specimens: *Cyttula macropus* Weber, 1913, lectotype (syntype), ZMA 102.357; *Cyttula macropus* Weber, 1913, paralectotypes (syntypes), ZMA 102.358.

Diagnosis. Head compressed, without any spines. Eye lateral, large, maximum orbital diameter greater than 1/2 of body height. Mouth, albeit rather vertical than horizontal, inferior, slightly leaning forwards from corner of mouth to tip; upper jaw depressed at its extremity; a pouch on the upper margin of the head between eyes is the place for the ascending premaxillary. Body rather compressed than depressed, slightly elongated, deepest at dorsal-fin origin. Nape ascended. Anus at the anterior half of the individual. Tail tapered until caudal peduncle, which is biconcave on its upper and lower profile. Scales ctenoid, evenly loosely covering trunk, but comparatively firm and small, including nape and isthmus, and tail, including caudal-fin base and a short distance of proximal caudal-fin rays; no scales on head. Lateral lines 2; upper pored lateral-line scale distinctly larger than others, upper lateral line distinct, lower lateral line indistinct; pored scales on upper lateral line approximately 47; scales on lower lateral line approximately 90. Pectoral fin consists of soft rays only. First dorsal fin originates behind the opercular, consists of spines only; first spine length greater than 1/3 of the second spine, free from the second spine, second spine the longest; profile of first dorsal fin a positively skewed parabola; second dorsal fin consists of soft rays only. Ventral-fin origin far anterior to dorsal-fin origin, first element a spine, followed by segmented and branched soft rays; ventral fin without locking mechanism; ventral fin long, when depressed, tip reaches the midpoint of anal-fin base; pelvis strong, two sides of pelvis connected firmly. Anal fin originates with two spines that both protrude out of the skin, followed by soft rays. Caudal fin double concave, consists of soft rays only, with uppermost and lowermost several soft accessory rays free, simple and spinous. Branchiostegal rays 7, incompletely hidden in the inner side of or above the preopercular, lower ones completely or partially exceed the lower margin of preopercular
D: VI-VII + 27; P:17-18; V: I 6; A: II + 25-26; C: iii + 1 11 1 + ii.

Description. Head large, compressed, without any spines, except the prolonged lower rear preopercular, rest of the preopercular a boomerang. Eye lateral, large, maximum orbital diameter greater than 1/2 of body height; upper margin of orbit serrated, on the upper margin of the head; approximately 8 infraorbitals, 4 developed with serrate and vertical supporting flanges, exclusive of lachrymal and dermosphenotic; lachrymal and dermosphenotic deep; dermosphenotic separated from sphenotic. Parietal present, small, almost at the same longitudinal level of upper margin of eye. Exoccipital facets closed together. Lower process of hyomandibular absent. Basisphenoid present as a long, oblique shaft connecting parasphenoid and prootic in the front of posterior myodome. Basihyal present. Mouth, albeit rather vertical than horizontal, inferior, slightly leaning forwards from corner of mouth to tip; upper-jaw bone depressed at its extremity, where premaxillary connects the two sides of maxillary, which is the place for mandibular tip, depression stuffed by the succulent lip; a pouch on the upper margin of the head between eyes is the place for the ascending premaxillary, premaxillary ascending process reaches about the latitudinal level of 1/3 into orbit, premaxillary alveolar process prolonged and simple, with a flat posterior margin; postmaxillary process present as a broad triangle. Mandibular lower margin double concave; two moderate cartilages, each attached anteriorly to the dentary and lying sequentially one behind the other, the first shorter than the second; serrations on dentary lower border present as a single barb near the symphysis. Maxillary and mandibular with tiny teeth in irregular rows; vomerine dentition a curved line occupying the anterior margin of vomerine; fifth-ceratobranchial teeth dentition oval; ectopterygoid dentition oval; premaxillary, fourth-upper-pharyngeal, and palatine without teeth. Palatine bulged, coarse, orientated distinctly obliquely to the body axis and has a single, pivotal, articulation with the lateral ethmoid, resulting in a little mobility; levator arcus palatine does not connect to the infrapostorbital mandibular adductor A2, both reduced. Tongue short, tip free. Metapterygoid present but reduced. Symplectic ventral flange present but indistinct. Gill cavity large, 3+1/2 gills, approximately 8 gill rakers on each. Gill openings wide, extend from the longitudinal level of the upper half of the eye to corner of mouth; gill membranes of two sides connected under corner of mouth. Branchiostegal rays 7, incompletely hidden in the inner side of or above the preopercular, lower ones completely or partially exceed the lower margin of preopercular, along the ventral edges of both the ceratohyal and epihyal; percopsoid projection on fourth branchiostegal ray absent. Prominent notches present on lower margin of ceratohyal; beryciform foramen present as an enclosed opening. Ceratohyal-epihyal articulation through cartilage. Depth of the anterior end of epihyal less deep than the depth of the adjacent part of the ceratohyal. Urohyal large, far longer than the ceratohyal. First-epibranchial uncinate process absent. Second-pharyngobranchial suspensory shaft long, length approximately equal to 2/3 of length of first-pharyngobranchial shaft; third-pharyngobranchial suspensory shaft moderately moderately long, length far longer than width of second-pharyngobranchial tooth patch, far less than second-pharyngobranchial shaft. Upper surface of posterior part of first-basibranchial is level with those of basihyal and second basibranchial posteriorly. Interarcual cartilage absent. Cephalic bones without honeycomb sculpturing.

Body oval, rather compressed than depressed, slightly to moderately elongated, deepest at dorsal-fin origin. Nape ascended. Abdomen flat. Anus at the anterior half of the individual. Tail tapered until caudal peduncle, which is biconcave on its upper and lower profile. Total vertebrae 27; 11 precaudal; 16 caudal, among which 3 caudal-peduncle. Dorsal extension of neural spine of first vertebra plastered to the skull proximally, while with a long dorsal portion free from the skull beyond the curvature of the supraoccipital and the exoccipitals distally. All precaudal neural spines orientated posterodorsally, but certain middle ones distinctly bent anterodorsally; almost all haemal spines of the precaudal vertebrae, especially posteriorly, with a prominent process in midline below bridge under haemal canal; ossified ribs present on all precaudal vertebrae except first two; ossified epineurals present on middle precaudal ribs only. Neural and haemal spines of first two caudal-peduncle vertebrae specialised into thin plates only ridged medially. Hyperstosis absent in any bony components.

Scales ctenoid, evenly loosely covering trunk due to reduced pockets hidden under the scales, but comparatively firm and small, including nape and isthmus, and tail, including caudal-fin base and a short distance of proximal caudal-fin rays; no scales on head. Lateral lines 2. Minimum scales rows between spinous dorsal fin and lateral line approximately 16 or 17. Upper lateral line developed, with distinctly enlarged pored scales approximately 47 and pores on skin. Lower lateral line vestigial but still functional, with indistinctly enlarged scales approximately 90, pores on which scales absent, but present on the skin, uncountable. Upper lateral line begins at the top point of the opercular, then slightly descended until reaching caudal-fin base through the upper half of caudal peduncle. Lower lateral line originates approximately 4 scales below the origin of the upper lateral line, then slightly descended until the same latitudinal level of the midpoint of dorsal-fin base, where it begins to slightly rise until very close to the upper lateral line and descended until reaching caudal-fin base through the lower half of caudal peduncle. Two lateral lines do not intercept or reach each other. Dorsal-fin base and anal-fin base scaleless. Bucklers absent.

Pectoral fin rounded, consists of 17 or 18 soft rays; soft rays slightly flattened and branched at tip, two branches on one soft ray attached to each other and thus inseparable. Girdle simple; pectoral-fin radial, lateral flange on the lowermost, present as a weak ridge, 2 postcleithrums, without flange; supracleithral serration present, supracleithrum ventral end simple; cleithrum posteriorly without a cleithral process; extrascapular present as a long bone, distal parts less ossified; scapular foramen bounded by scapula. First dorsal fin originates behind the opercular, consists of 6 or 7 spines; locking mechanism absent among the spines; first spine comparatively long, approximately as long as the fourth spine, greater than 1/3 of the length of the second dorsal-fin spine; second spine the longest, anterior-most margin of second dorsal-fin spine smooth, while its ambilateral anterior margin serrated. Membrane between first and second dorsal fin present. Second dorsal fin consists of 27 soft rays; margin curved, ascended then descended; except for the first soft ray, other soft rays branched; soft rays slightly flattened and branched at tip, two branches on one soft ray attached to each other and thus inseparable. Dorsal-fin base without bony ridge, scaleless. Interneural gaps 2, which is the seventh and ninth interneural space, separated; 3 dorsal-fin pterygiophores anterior to fourth neural spine. First dorsal-fin pterygiophore inserted in first interneural space, contact with first vertebra. A supraneural, without cartilage at distal end inserted between first neural spine and skull. Ventral-fin origin far anterior to dorsal-fin origin; first element a spine, without locking mechanism, can open to approximately 180°, followed by 6 segmented branched soft rays without serration, with anterolateral processes of the medial surfaces present as broad flanges from the ray bases; anterior-most margin of ventral-fin spine smooth, while the ambilateral anterior margin of them serrated; spine strong, maximum diameter of unbranched part of first ventral-fin soft ray less than 2/3 of maximum diameter of ventral-fin spine; second to sixth soft rays very long and fragile, when depressed, tip reaches the middle point of anal-fin base, ratio of the length of ventral-fin spine in the length of the longest ventral-fin soft ray greater than 1.5; all ventral-fin soft rays longer than ventral-fin spine. Pelvis fragile, two sides of pelvis connected firmly; medial processes of basipterygia broadly overlap at the level of the pelvic fin; posterior process of pelvis behind pelvic-fin base moderate in length, in a shape of broad plate. Anal fin originates with two short spines immediately after anus, about under the last spine of first dorsal fin; second anal-fin spine protrudes out of skin, slightly shorter than the first one; locking mechanism absent between anal-fin spines, first anal-fin spine unfused with its pterygiophore; anal-fin spines followed, after a short gap, by 25 to 26 soft rays considerably longer than the spines, about under the origin of second dorsal fin; no evidence that membrane present between spinous and soft anal fin; margin of the soft anal fin curved, ascended then descended; soft rays slightly flattened and branched at tip, two branches on one soft ray attached to each other and thus inseparable; anal-fin-base length less than body height; anal-fin base without bony ridges, scaleless. Pterygiophores in second caudal interhaemal space 2; pterygiophores before third caudal haemal spine approximately 6. Pterygiophores of soft dorsal-fin and soft anal-fin almost symmetrical. Caudal fin double concave, middle rays of approximate the same length as the outer rays, consists of soft rays only; uppermost 3 accessory soft rays short, free, simple and spinous, followed by 1 free segmented unbranched soft ray which is comparatively shorter than other branched soft rays, followed by 11 segmented branched soft rays, followed by free 1 segmented unbranched soft rays which is comparatively shorter than other branched soft rays, followed by the 2 lowermost short free simple spinous accessory soft rays; all the branched caudal-fin soft rays with branches more than two, branched obviously. Antepenultimate vertebra is the first vertebra with a modified spine to support the caudal fin, which is the neural spine; hypurapophysis absent; one broad epural, its high broadness might represent that it is fused by two, but no borders observed within it, also no other evidence present; articulation of proximal end of parhypural to urostylar centrum laterally expanded as a specialized weak peg; hypural 1–4 fused together, hypurals 1–2 firmly fused to last centrum and connected with haemal spine of penultimate centrum, and hypurals 3–4 fused to last centrum, hypural 5 rather free; any extra caudal ossicle absent between haemal spine of penultimate and antepenultimate centrum; interradiales located across and between caudal-fin soft rays, insertions of interradiales present between principal caudal rays only. All fin membranes fragile.

Measurements in Table 4.

TABLE 4. Morphometric data of *Cyttula*.

	Cyttula macropus	*Cyttula boops*
	Nontypes (n=21)	Lin *et al.*, 2025 (n=30)
Total length (mm)	77.1–117.3	90.3–132.1
Standard length (mm)	63.0–94.5	79.3–109.2
%(Standard length)		
Total length	118.81–132.47	-
Body height	39.53–51.09	40.2–48.6
Body width	17.93–25.77	-
Head length	39.89–43.26	44.2–49.1
Trunk length	6.90–14.71	-
Tail length	62.74–77.32	-
Pre-dorsal-fin length	44.91–54.60	48.6–53.1
Pre-anal-fin length	52.08–72.22	56.5–61.1
Pre-anus length (Body length)	50.49–69.05	-
Mouth length	15.11–23.06	-
Preorbital length	6.77–11.54	-
Minimum interorbital length	7.94–12.89	-
Maximum orbital diameter	21.93–28.09	-
Gill-opening length	34.07–46.36	-
Dorsal-fin base length	41.37–54.81	43.4–49.1
Anal-fin base length	27.85–36.61	25.2–31.9
Pectoral-fin length	6.86–12.68	-
Ventral-fin length	37.57–51.54 (n=6)	-
Caudal-fin length	13.77–28.22	10.1–11.5
Caudal-peduncle length	7.60–12.06	-
Caudal-peduncle height	7.46–10.60	-
Length of first dorsal-fin spine	6.11–11.20	-
Length of second dorsal-fin spine	15.58–22.38	-
Length of third dorsal-fin spine	11.76–17.35	-
%(Body height)		
Head length	68.01–105.65	-
Maximum orbital diameter	50.50–65.52	-
Anal-fin base length	54.54–96.27	-
Caudal-peduncle height	15.85–24.84	-
Length of first dorsal-fin spine	14.29–27.35	-

Length of second dorsal-fin spine	36.39–48.18	-
Length of third dorsal-fin spine	18.89–37.88	-
%(Maximum orbital diameter)		
Head length	159.01–192.25	-
Preorbital length	25.94–47.39	-
Length of first dorsal-fin spine	26.24–40.40	-
Length of second dorsal-fin spine	66.35–94.70	-
Length of third dorsal-fin spine	48.61–67.57	-
%(Length of second dorsal-fin spine)		
Trunk length	33.33–83.23	-
Length of first dorsal-fin spine	35.10–57.23	-
Length of third dorsal-fin spine	68.21–95.33	-

Fresh colouration. Head red; skin red. Ventral fin completely red in proximal one-third; distal two-thirds with black fin-membranes between fin rays and red fin-membranes covering fin-rays. Proximal half of spinous dorsal fin translucent, distal half with grey fin-membranes covering spines and black fin-membranes between spines. Proximal half of soft dorsal-fin with black fin-membranes covering soft rays and grey fin-membranes between soft rays; distal half with white fin-membranes covering soft rays and white-translucent fin-membranes between soft rays. Spinous anal fin transparent; soft anal fin entirely red to pink. Caudal fin completely transparent, base black. (Figure 2. E)

Ethanol-preserved colouration. Entirely brownish, except for the white-translucent fins and distinct white lenses. (Figure 2. F)

Size. Approximately a maximum of 16-centimetre total length, 13-centimetre standard length (specimen unpreserved).

Distribution. South China Sea (This study, Figure 4.), depth from 400 m to 700 m; Flores Sea (Weber, 1913), Australia (Weber, 1929); Pointe-Noire, 0 m to 600 m (Marteau, 1967).

Phylogenetic analysis. Within the sequenced specimens of *Cyttula macropus*, for which no genetic information is available online, the intraspecific K2P genetic distance of COI between every two of them are 0.00 %~0.16 % (Figure 5.). Single-gene COI phylogeny shows the union of *Cyttula macropus* and *Zenion boops* is the basal group of *Zenion*.

In morphological phylogenetic analysis (Appendix; Table 5; Figure 6), with *Capromimus abbreviates* (Hector, 1875), *Cyttomimus stelgis* Gilbert, 1905, *Zenion hololepis* (Goode & Bean, 1896), and *Zenion retrojaponicum* n. sp. as representatives of Zeniontidae Myers, 1960, *Cyttopsis rosea* (Lowe, 1843), *Stethopristes eos* Gilbert, 1905, and *Parazen pacificus* Kamohara, 1935 as other representatives of Parazenidae McAllister, 1968, *Cyttus australis* (Richardson, 1843), *Cyttus traversi* Hutton, 1872, and *Cyttus novaezealandiae* (Arthur, 1885) as representatives of Cyttidae Günther, 1860, *Oreosoma atlanticum* Cuvier, 1829, *Neocyttus rhomboidalis* Gilchrist, 1906, *Pseudocyttus maculatus* Gilchrist, 1906, *Allocyttus verrucosus* (Gilchrist, 1906), and *Allocyttus niger* James, Inada & Nakamura, 1988, as representatives of Oreosomatidae Bleeker, 1859, *Xenolepidichthys dalgleishi* Gilchrist, 1922 and *Grammicolepis brachiusculus* Poey, 1873 as representatives of Grammicolepididae Poey, 1873, and *Zeus faber* Linnaeus, 1758, *Zenopsis nebulosa* (Temminck & Schlegel, 1845), and *Zenopsis conchifer* (Lowe, 1852) as representatives of Zeidae Rafinesque, 1815, *Macrurocyttus acanthopodus* Fowler, 1934 as a representative of monotypic Macrurocyttidae Myers, 1960, *Cyttula macropus* Weber, 1913, representing Cyttulinae, is the sister group of Cyttopsinae Greenwood *et al.*, 1966, with a shortest distance among available species under Zeiformes approximately 26.18%, with *Cyttopsis rosea* (Lowe, 1843). However, the results show that Parazeninae is the basal group of Zeiformes, which might be erroneous due to the incomprehensiveness of the morphological matrix, a situation that is acceptable (Tyler *et al.*, 2003). Zeniontidae Myers, 1960 is monophyletic here.

In the multigene analysis (Table 2.; Figure 7.), with *Capromimus abbreviates* (Hector, 1875), *Zenion hololepis* (Goode & Bean, 1896), and *Zenion retrojaponicum* n. sp. as representatives of Zeniontidae Myers, 1960, *Cyttopsis rosea* (Lowe, 1843) and *Parazen pacificus* Kamohara, 1935 as other representatives of Parazenidae McAllister, 1968, *Cyttus australis* (Richardson, 1843) and *Cyttus traversi* Hutton, 1872 as representatives of Cyttidae Günther, 1860, *Pseudocyttus maculatus* Gilchrist, 1906 and *Allocyttus verrucosus* (Gilchrist, 1906) as representatives of Oreosomatidae Bleeker, 1859, *Xenolepidichthys dalgleishi* Gilchrist, 1922 and *Grammicolepis brachiusculus* Poey, 1873 as representatives of Grammicolepididae Poey, 1873, and *Zeus faber* Linnaeus, 1758 and

Zenopsis conchifer (Lowe, 1852) as representatives of Zeidae Rafinesque, 1815 (Figure 7.), but without Macrurocyttidae Myers, 1960 because of its lack of genetic information, *Cyttula macropus* Weber, 1913, representing Cyttulinae, is the sister group of Cyttopsinae Greenwood *et al.*, 1966, and the minimum interspecific K2P genetic distance in multigene phylogeny among all the members under Parazenidae McAllister, 1968 is 7.56 %, with Cyttopsinae Greenwood *et al.*, 1966, while maximum is 8.34 %, with Parazeninae McAllister, 1968. Family Parazenidae McAllister, 1968, whose multigene monophyly failed to be constructed (Grande *et al.*, 2018), is herein determined to be monophyletic by adding a new subfamily, Cyttulinae, resulting in 3 subfamilies under Parazenidae McAllister, 1968: Cyttulinae new subfamily, Cyttopsinae Greenwood *et al.*, 1966, and Parazeninae McAllister, 1968. The morphological phylogeny also supports that Cyttulinae new subfamily is the sister group of Cyttopsinae Greenwood *et al.*, 1966. The molecular monophyly of Zeniontidae Myers, 1960 remains unsolved, which is acceptable in phylogenetic analysis of other taxa (Grande *et al.*, 2018; Figure 7.).

Figure 2. Left sides of *Cyttula macropus* Weber, 1913. A: Syntype, ZMA 102.357, with original label (photo by Esther Dondorp and Melvin Veenendaal); B: Syntype, ZMA 102.357, closer view (photo by Esther Dondorp and Melvin Veenendaal); C: Syntype, ZMA 102.358 (including several bodies) (photo by Esther Dondorp and Melvin Veenendaal); D: One dissected body of the bodies of Syntype, ZMA 102.358 (photo by Esther Dondorp and Melvin Veenendaal); E: a fresh body not retained; F: scalebar: 1 cm, MBM288295, Nontype, 79.5 mm SL.

The position of Parazeninae McAllister, 1968 was unclear, as the morphological evidence (Figure 6.: basal group of Zeiformes Greenwood *et al.*, 1966) and molecular evidence (Figure 7.: sister group of the rest of Parazenidae McAllister, 1968 with low support of 42 %) resulting in its different positions. However, the morphological phylogeny is often less efficient due to its indirectness. Thus, it should be treated as an additional reference only. No evidence supports placing Cyttulinae within Zeniontidae, as Parazenidae and Zeniontidae do not conflict with each other in both morphological and molecular analyses, and the most striking common character, a vertical mouth, is more likely a symplesiomorphy.

Remarks. There were two labels for five comparatively intact specimens and some remains of the syntypes of this species (Nijssen *et al.*, 1993), among which, “ZMA 102.357” represents one syntype, and “ZMA 102.358” represents four syntypes. Weber designated one “lectotype”: “ZMA 102.357” (labelled as “Holotype”) and four “paralectotypes”: “ZMA 102.358”, which were not published (Karrer, 1990). Thus, the “lectotype” and “paralectotypes” are, at least up to now, still syntypes.

Many researchers reported zeiform specimens with very long ventral-fin spines. Firstly, they were recorded as *Zenion hololepis* (Yang *et al.*, 1980), with an original drawing that has been afterwards used and cited by many researchers as follows. This drawing was then regarded as *Zen cypha* by Cheng & Zheng (1987a) and Cheng & Zheng (1987b). After a long time, this drawing was revised to be *Zenion hololepis* (Yang *et al.*, 1996; Wu & Zhong, 2021) or also *Zenion japonicum* (Sun *et al.*, 2013). However, in this study, although the author has not examined these specimens, because of the specimens were not collected with vouchers, the author considers this drawing as *Cyttula macropus*, as the long ventral-fin spine is probably the long ventral-fin soft ray adhering to the ventral-fin spine; otherwise, long ventral-fin spines seem not present in any species under Zeiformes (Stark, 1898; Regan, 1910; Tyler *et al.*, 2003).

Allometry is still very significant in adults (This study). More details about the allometry will be published in a more comprehensive revision.

Certain sequences from *Cyttula macropus* are of lower quality (Table 1) compared to *Zenion retrojaponicum* n. sp., whereas the same primers were used to amplify the sequences of both species. This may indicate that their primer-binding sites are more divergent than expected. Upstream primers are prepared, and more accurate results, including the phylogenetic analysis, including the primer-binding sites, will be published in further study.

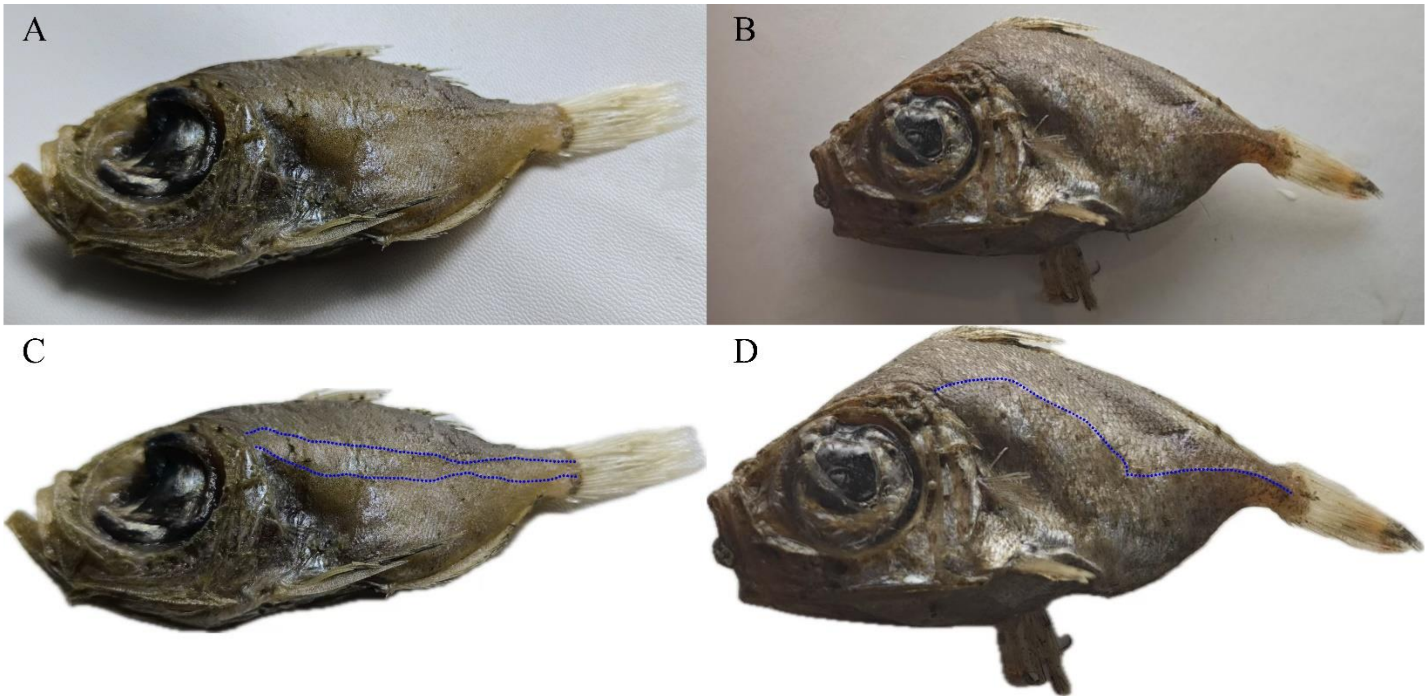

Figure 3. Left lateral lines of specimens, photographs taken at certain angles to sharpen the lateral lines. A: *Cyttula macropus* Weber, 1913, MBM288308, Nontype, original photograph; B: *Zenion retrojaponicum* n. sp., MBM288314, Holotype, original photograph; C: *Cyttula macropus* Weber, 1913, MBM288308, Nontype, lateral lines traced by blue dotted lines; D: *Zenion retrojaponicum* n. sp., MBM288314, Holotype, lateral line traced by blue dotted line.

Zenion Jordan & Evermann, 1896

Zenion Jordan & Evermann, 1896: 418 (2104).
Cyttus (non Günther, 1860): Goode & Bean, 1896: 225, plate LXV (233, 233a, 233b).

Diagnoses. Head compressed, without any spines, except the prolonged lower rear preopercular; the rest of the preopercular a boomerang. Eye, lateral, large. Mouth, albeit rather vertical than horizontal, inferior, slightly leaning forwards from corner of mouth to tip; a pouch on the upper margin of the head between eyes is the place for the ascending premaxillary. Body rather compressed than depressed, slightly to moderately elongated. Anus approximately located in the middle part of the individual. Tail tapered until caudal peduncle, which is biconcave on its upper and lower profile. Scales ctenoid, large, evenly loosely covering trunk, including nape and isthmus, and tail, including caudal-fin base and a short distance of proximal caudal-fin rays; no scales on head. Pored lateral-line scale slightly or distinctly larger than others, lateral line comparatively distinct; pored lateral line one. Pectoral fin consists of soft rays only. First dorsal fin consists of spines only, can open to less than 90° because of its locking mechanism, first spine small, attached to the second spine, second spine the longest; second dorsal fin consists of soft rays only. Ventral-fin origin approximately at the same latitudinal level of dorsal-fin origin, first element a spine with locking mechanism, followed by branched soft rays; tip does not reach midpoint of anal fin; ratio of the length of ventral-fin spine in the length of the longest ventral-fin soft ray greater than 1.5; pelvis fragile, two sides of pelvis connected weakly. Anal fin originates with two spines, the second one often covered by skin, followed by soft rays. Caudal fin convex, slightly well-separated, double concave, consists of soft rays only, with uppermost and lowermost several soft rays simple and spinous. (This study; Tyler *et al.*, 2003)

Ecology. The ecology of this genus remains rarely known. This genus is widespread, ranging from tropical to subtropical seas and has been recorded from all the oceans except the Arctic. Among these species, *Zenion hololepis* (Goode & Bean, 1896) is recorded from the Pacific, Indian, and Atlantic Oceans (Goode & Bean, 1896; Heemstra, 1999; Heemstra *et al.*, 2022b; Martins *et al.*, 2012), whereas *Zenion leptolepis* (Gilchrist & von Bonde, 1924) and *Zenion retrojaponicum* n. sp. are recorded from the Pacific and Indian Oceans only. This genus is typically distributed in deep seas, ranging from approximate 1000 m (Fricke *et al.*, 2019) to 100 m depth, near the bottom with slopes (Maurin, 1968; Maurin & Quéro, 1982), and the slopes are often gentle (This study). The population of this genus is comparatively rare, but always gregarious in great numbers, possibly interspecifically gregarious (This study). *Zenion* possibly has a greater global and regional gamma diversity than expected.

Remarks. Species under *Zenion* show allometry in which multiple proportions vary significantly with size during the adult stage. According to the primary statistics from all the specimens the author obtained and can access, the ratio of orbital diameter in either standard length or body height both show positive allometries with standard length in *Zenion hololepis* (Ditty, 2005; Fahay, 2007; Martins *et al.*, 2012; Heemstra *et al.*, 2022b; Myers, 1960; Rufus *et al.*, 2021; Tyler *et al.*, 2003; Unpublished materials from the author); the ratio of orbital diameter in standard length first shows a slightly negative allometry then shows an evidently positive allometry in standard length, and the ratio of orbital diameter in body height first shows a slight positive allometry then shows an evident negative allometry in standard length in *Zenion retrojaponicum* n. sp. (This study; Unpublished materials from the author); *Zenion leptolepis* lacks information. The ratio of body height in standard length shows a negative allometry in standard length in *Zenion hololepis* (Ditty, 2005; Fahay, 2007; Martins *et al.*, 2012; Heemstra *et al.*, 2022b; Myers, 1960; Rufus *et al.*, 2021; Tyler *et al.*, 2003; Unpublished materials from the author); the ratio of body height in standard length first shows a slight negative allometry, then shows an evident positive allometry in standard length in *Zenion retrojaponicum* n. sp. (This study; Unpublished materials from the author); *Zenion leptolepis* lacks information. For example, when the adults of *Zenion retrojaponicum* n. sp. become more mature, the ratio of orbital diameter in body height changes from greater than 2 to less than 2 (This study; Unpublished materials from the author); in *Zenion hololepis*, this ratio changes from less than 2 to greater than 2 (Ditty, 2005; Fahay, 2007; Martins *et al.*, 2012; Heemstra *et al.*, 2022b; Myers, 1960; Rufus *et al.*, 2021; Tyler *et al.*, 2003; Unpublished materials from the author). More detailed information on the allometry of *Zenion* is prepared and will be published in a comprehensive review of this genus.

In all the species, the subadults have greater ratios of head height in head length and of orbital diameter in standard length than the adults of the corresponding species; subadults have transparent fins, a silver body whose dorsal side is darker, unlike the adults. Those mentioned above increased the difficulties in identifying the species morphologically. Otoliths of *Zenion* also vary extraordinarily with their standard length (This study; Chen *et al.*, 2016; Conversani *et al.*, 2017). Distinguishing species through otoliths is still not a mature method.

All species under *Zenion* have 2 anal-fin spines, both diminutive (Tyler *et al.*, 2003). The second anal-fin spine is extremely diminutive (Tyler *et al.*, 2003). Tyler *et al.* (2003) emphasised this character, but it has only been accepted by a few researchers, including Fahay (2007) and partly by Ditty (2005). Johnson & Patterson (1993) reported that *Zenion* possesses first soft ray of ventral fin not segmented, while there is no evidence that Johnson & Patterson (1993) examined other species than *Zenion hololepis*. However, *Zenion retrojaponicum* n. sp., as observed in this study, possesses the first soft ray of ventral fin indistinctly segmented

(This study). Caudal fin is convex or slightly well-separated double concave (This study). Any reports that the caudal fin is concave (Kamohara, 1934) might be due to the caudal fin not fully expanded. All the former reports of the pored lateral-line scales of *Zenion* need review.

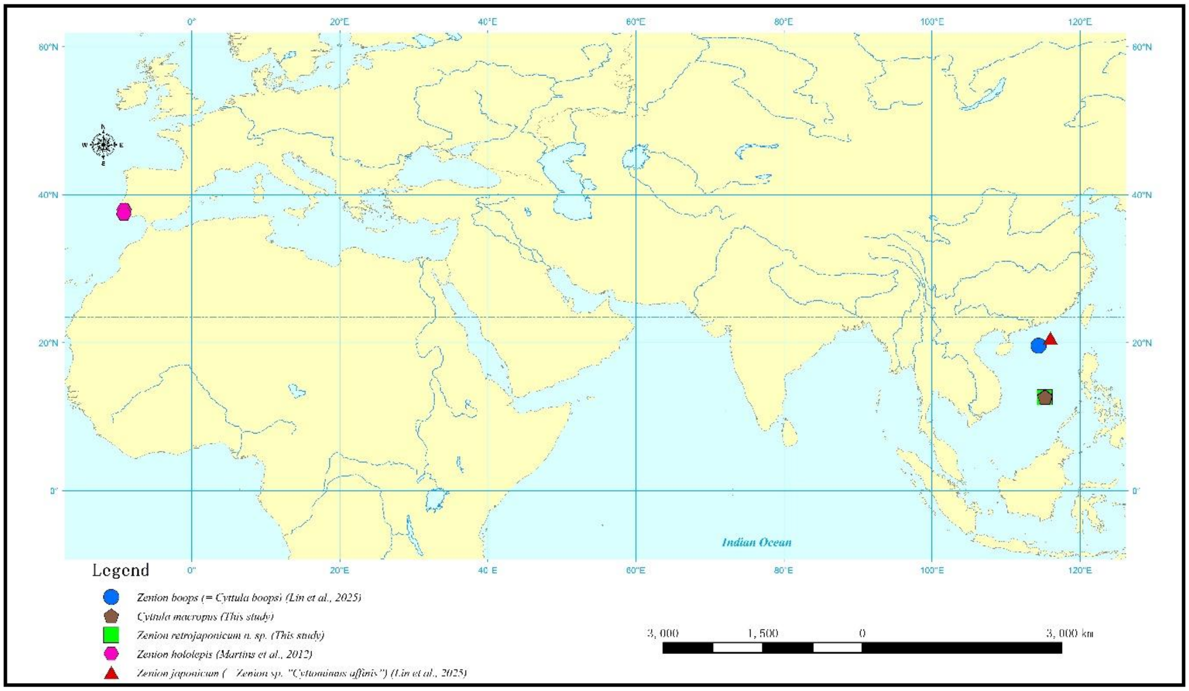

Figure 4. Documented records of vertical-mouthed dory species with both genetic and geographic information available. Blue circle: *Zenion boops* (= *Cyttula boops*), (Lin *et al.*, 2025: (18°49'00'' N–20°45'00'' N, 112°46'00'' E–116°15'00'' E)); Brown pentagon: *Cyttula macropus*, (This study: (12°41' N, 115°19' E), (12°44' N, 115°15' E), (12°39' N, 115°16' E)); Green square: *Zenion retrojaponicum*, (This study: (12°42' N, 115°17' E), (12°43' N, 115°15' E), (12°42' N, 115°14' E), (12°40' N, 115°13' E)); Pink hexagon: *Zenion hololepis*, (Martins *et al.*, 2012: (38°0.2' N, 09°7.2' W), (37°57.4' N, 09°08.6' W), (37°21.40' N, 09°10.2' W), (37°24.9' N, 09°09.6' W)); Red triangle: *Zenion japonicum* (= *Zenion* sp. ‘‘*Cyttomimus affinis*’’), (Lin *et al.*, 2025: (18°49'00'' N–20°45'00'' N, 112°46'00'' E–116°15'00'' E)). Scalebar: 3000km + 3000 km.

Comments

Cyttula boops (Lin *et al.*, 2025)

Zenion boops Lin *et al.*, 2025: 2.
? *Zenion* sp.: Ng *et al.*, 2024: 202 (figure 30. H), 203 (figure 32. C), 230.

Lin *et al.* (2025) described a new species, *Zenion boops* and doubted whether it is *Cyttula macropus*. Lin *et al.* (2025) did not state the difference between *Cyttula macropus* and *Zenion boops*. One difference might be that Weber (1913) described *Cyttula macropus* as possessing 2 anal-fin spines, whereas Lin *et al.* (2025) described *Zenion boops* as possessing only 1 anal-fin spine. However, according to the figure 5 (a) and figure 5 (b) of Lin *et al.* (2025), there are clearly two anal-fin spines. The number of anal-fin spines needs further clarification.

Allometry is very significant in adults (This study). The ratio of standard length in head length of *Cyttula macropus* in this study (39.89–43.26) completely mismatched with Lin *et al.* 2025 (44.2–49.1), possibly due to allometry, or also affected by the mouth not being tightly closed in Lin *et al.* (2025).

Especially, the higher taxon that *Zenion boops* belongs to needs further research, as *Zenion boops* are morphologically very close to *Cyttula macropus* under Cyttulinae. Albeit the non-monophyly of *Cyttula macropus*, the non-monophyly of *Zenion boops*, the monophyly of the union of *Cyttula macropus* and *Zenion boops*, and very the short K2P genetic distance between *Cyttula macropus* and *Zenion boops* (0.00 %~0.32 %) (Figure 5.), the author still has not robust evidence to reduce *Zenion boops* to a junior synonym of *Cyttula macropus*, as more markers should be phylogenetically analysed to verify its status. Despite these, it is clear that *Zenion boops* should be a species under *Cyttula*, because of the very short COI phylogenetic distance between *Cyttula macropus* and *Cyttula boops* (Figure 5.). The COI phylogeny show it is the basal group of *Zenion* (This study; Lin *et al.*, 2025). Hence, when *Zenion boops* is rearranged under Cyttulinae, this molecular evidence also agrees that the monophyly of COI of the genus *Zenion* is not disturbed.

Zenion hololepis **(Goode & Bean, 1896)**

Cyttus hololepis Goode & Bean, 1896: 225, plate LXV (233, 233a, 233b).
Cyttus hololepis: Gilchrist & von Bonde, 1924: 17 (35).
Zenion hololepis: Jordan & Evermann, 1896: 418 (2104); Jordan & Evermann, 1898: 1661 (2077); Barnard, 1925: 379; Kamohara, 1934: 598; Longley & Hildebrand, 1941: 51; Smith, 1949: 145 (272); Poll, 1954: 23 (fig. 6) Blache *et al.*, 1970: 271 (figure 730); Kotthaus, 1970: 65; Shimizu, 1983, 287; Rosen, 1984: 18 (fig. 18); Heemstra, 1986: 441 (141. 1); Scott & Scott, 1988: 331 (unlabelled figure); Cervigón, 1991: 258, 259 (fig 192); McEachran & Fechhelm, 1998: 1029; Heemstra, 1999: 2258; Heemstra, 2002: 1205, 1206; Bernardes, *et al.*, 2005: 189; Ditty, 2005: 1112 (table Zeiformes 2. (Continued).); Fahay, 2007: 906; Martins *et al.*, 2012: 1, 2 (figure 2., table 1.); Iwamoto & McCosker, 2014: 286, 321 (figure 85); Lins Oliveira, 2015: 130; Heemstra, 2016: 2215; Conversani *et al.*, 2017: 407, 430 (plate 10); Sáez & Lamilla 2017: 98 (figure 6.); Reiner, 2019: 146; Heemstra, 2022b: 422, plate 75 (*Zenion hololepis*, dwarf dory, 12 cm TL (Mozambique). O Alvheim © IMR);
Zenion japonicum Kamohara, 1934: 597, unlabelled figure.
Zenion japonicum: Kamohara, 1936a: 25 (5.), 26 (fig. 4); Kamohara, 1936b: 44; Kamohara, 1961: 5, pl. III fig 1.; Lindberg, & Legeza, 1965: 320; Ida, 1982: 216 (142); Shimizu, 1983, 287; Kamohara, 1985: 40 (193), plate 39 (193) (similar figure modified from Kamohara, 1961); Machida, 1985: 448 (228); Ditty, 2005: 1112 (table Zeiformes 2. (Continued).); Shen & Wu, 2011: 301; Nakabo & Kai, 2013: 599 Chen & Zhang, 2015: 700; Zhang *et al.*, 2016: 443, 444 (figure 314 (From Hiroshi Senou)); Ng *et al.*, 2024: 196, figure 30, figure 32.
Zenion longipinnis Kotthaus, 1970: 63, 64 (unlabelled form); 69 (Abb. 210., Abb. 213.), 70 (Abb. 211., Abb. 212.).
Zenion sp.: Shimizu, 1983, 287 (NSMT-P 40248); Rober *et al.*, 2015: 1040 (146.2, fig. 146.2).
? *Zenion hololepis* (non Goode & Bean, 1896): Maurin & Quéro, 1982: 49, 51 (fig. 37); Roa-Varón *et al.*, 2003: 10 (figure 4.); Rufus *et al.*, 2021: 109, fig. 2.
? *Zenion leptolepis* (non Gilchrist & von Bonde, 1924): Heemstra, 2022b: plate 75 (*Zenion leptolepis*, elongate dory, 7 cm SL (N Mozambique). ©F Uiblein, IMR).

Type specimens: *Cyttus hololepis* Goode & Bean, 1896, syntype, CAS-SU 9549.

In the original description of *Zenion hololepis* (Goode & Bean, 1896) (as *Cyttus hololepis*), it was misdescribed as possessing dorsal fin and anal fin originating at the same latitudinal level, possessing a preanal spine and no anal-fin spine. About dorsal fin and anal fin originating at the same latitudinal level, the slight dislocation might be ignored, and ventral fin should originate slightly anterior to dorsal fin; about the preanal spine, it is an anal-fin spine.

The reports that *Zenion hololepis* has not anal-fin spines (Okada & Matsubara, 1938; Smith, 1949; Kotthaus, 1970; Heemsta, 1999; Xie, 2010; Li, 2013) are presumably erroneous, as the whole Order has anal-fin spines and there is no evidence that the anal-fin spines can be secondarily lost (Stark, 1898; Regan, 1910; Tyler *et al.*, 2003), while the anal-fin spine of *Zenion* is fragile and too diminutive to be observed easily.

Although *Zenion hololepis* is the first species and a worldwide-distributed species under *Zenion*, this species is more mysterious because many other valid species were previously included under *Zenion hololepis*, resulting in its description containing characters of multiple other species. More information is required to solve many specimens misidentified as *Zenion hololepis*.
Lin *et al.*, 2025 stated that this species is restricted to Atlantic, because the genetic record of *Zenion hololepis* is restricted to Atlantic, which needs more evidence to prove that the records of Heemstra (1999) and Heemstra *et al.* (2022b) were erroneous.

Zenion japonicum **Kamohara, 1934 (=** ***Zenion hololepis*** **(Goode & Bean, 1896))**

Zenion japonicum Kamohara, 1934: 597, unlabelled figure.
Zenion japonicum: Kamohara, 1936a: 25 (5), 26 (fig. 4); Kamohara, 1936b: 44; Kamohara, 1961: 5, pl. III fig 1.; Ida, 1982: 216 (142); Shimizu, 1983, 287; Kamohara, 1985: 40 (193), PLATE 39 (193) (similar figure modified from Kamohara, 1961); Machida, 1985: 448 (228); Ditty, 2005: 1112 (table Zeiformes 2. (Continued).); Shen & Wu, 2011: 301; Nakabo & Kai, 2013: 599 Chen & Zhang, 2015: 700; Zhang *et al.*, 2016: 443, 444 (figure 314 (From Hiroshi Senou)); Ng *et al.*, 2024: 196, Figure 30, Figure 32; Lin *et al.*, 2025: 4.

Zenion japonicum was described based on three specimens, with only a "Type" specimen designated, but no holotype is designated (Kamohara, 1934). There is a remaining enigma in the original description of *Zenion japonicum* Kamohara, 1934, which is about the preanal spine and the anal-fin spine. Preanal spine usually means "the spine anterior to anal fin and posterior to anus". This species is described as possessing an anal-fin spine, which is the first element of its anal fin; it is also described as possessing a "preanal spine" (Kamohara, 1934). In the unlabelled figure in the original description of *Zenion japonicum* Kamohara, 1934, there is an unannotated dashed line, while it should point at the anus, and after this dashed line is a spine, just followed by segmented anal-fin elements that must not be spines, as spines must be unsegmented. If this spine is a preanal spine, the anal-fin spine is absent in the figure; if this spine is an anal-fin spine, the preanal spine is lacking in the figure. In this study, the preanal spine is provisionally treated as a misidentification of anal-fin spine.

Unfortunately, the "Type" of this species was destroyed in a war fire in 1945, and the designation of the neotype (Kamohara, 1961) with only with a short description of the locality and the neotype is not acceptable. Despite of that, in the designation of the "neotype", "preanal spine" was not mentioned, and anal fin was still described as possessing one spine. The figure of the "neotype" was simply a drawing from the original description (Kamohara, 1934), with only some details added (Kamohara, 1961).

Holotype absent, "Type" destroyed, "neotype" not acceptable, the only way to judge whether this ambiguous species is valid is referring to the original description. Kamohara (1934) concluded that *Zenion japonicum* differs from *Zenion hololepis* as follows: distal tip of maxillary depressed (vs. obtuse); caudal fin slightly concave (vs. slightly rounded); preanal spine present (vs. absent). However, what is depressed is not the maxillary but the upper jaw. Whether the upper-jaw tip is depressed is related to whether the lip is still fresh and thus succulent, as the depression is on the bone and is stuffed by soft tissue of the upper lip. If the upper lip is still fresh and succulent, the depression shown on the lip is comparatively broad and shallow, and fresh specimens of both species has their upper lip with a slight concavity, while the specimens dehydrated in air or ethanol of both species also have the concavity more deep and evident, because the lip is dried and the depression on the bone is more apparent. Caudal fin of both species is rounded or slightly well-separated double concave. Preanal spine were mentioned to be present in both species, but actually, preanal spine are probably absent in both species. The drawing in the original description of *Zenion japonicum* also does not show any differences from *Zenion hololepis*. Thus, there are no discriminative differences between these two species, the author agreeing with Meng *et al.* (1995), Heemstra (1999), Randall & Lim (2000) and Heemstra (2016) to treat *Zenion japonicum* Kamohara, 1934 as a junior synonym of *Zenion hololepis* (Goode & Bean, 1896).

Besides, according to the original description (Kamohara, 1934) of *Zenion japonicum*, it can be distinguished from *Zenion leptolepis* by pored lateral-line scale about 75 (vs. greater than 85) (Gilchrist & von Bonde, 1924), from *Cyttula macropus* by pterygiophore-derived bony ridges absent from dorsal-fin and anal-fin bases (vs. absent) (Weber, 1913), from *Zenion retrojaponicum* n. sp. by pored lateral-line scale about 75 (vs. approximately 45) (This study; Kamohara, 1934).

***Zenion longipinnis* Kotthaus, 1970 (= *Zenion hololepis* (Goode & Bean, 1896))**

Zenion longipinnis Kotthaus, 1970: 63, 64 (unlabelled form); 69 (Abb. 210., Abb. 213.), 70 (Abb. 211., Abb. 212.).
Zenion longipinnis: Shimizu, 1983, 287; Ditty, 2005: 1112 (table Zeiformes 2. (Continued).).

In the original description, Kotthaus (1970) stated a few differences between *Zenion longipinnis* and other known species. According to that, *Zenion longipinnis* differs *Zenion hololepis* in: ventral-fin spines separated from ventral-fin soft rays (vs. connected to); second dorsal-fin spine serrated strongly (vs. not strongly); lateral line descended under the midpoint of soft dorsal-fin base (vs. under spinous dorsal fin); scales on isthmus extend to the anterior-most point (vs. do not); transverse scales between isthmus and pectoral-fin base from 14 to 15 (vs. 25); lateral-line scales 95 (vs. 66-67). However, the membrane between ventral-fin spine and ventral-fin soft rays is very fragile and easy to break; whether the serration is strong is ambiguous; lateral-line trend is variable among individuals, especially sizes, with allometry; scales are loose and deciduous. Having examined the specimens of *Zenion longipinnis*, Heemstra (2016) indicated that the lateral-line scales of *Zenion longipinnis* and *Zenion hololepis* are the same. In this study, the author also endorses that, as the lateral lines in specimens that are not fresh are hard for the author to observe, and the lateral-line scales easily drop, and thus, the scales under the lateral-line scale, which are smaller and denser, might be erroneously counted as pored lateral-line scale, resulting in more pored lateral-line scales counted than real.

In addition, according to the original description (Kotthaus, 1970) of *Zenion longipinnis*, it can be distinguished from *Zenion leptolepis* by anal-fin base shorter than body height (vs. longer) (Gilchrist & von Bonde, 1924), from *Cyttula macropus* by pterygiophore-derived bony ridges absent from dorsal-fin and anal-fin bases (vs. absent) (Weber, 1913), and the holotype of *Zenion longipinnis* can be distinguished from *Zenion retrojaponicum* n. sp. by lower branchiostegal rays completely exceed the lower margin of preopercular (vs. hidden in the inner side or above) (This study; Kotthaus, 1970). However, the position of the branchiostegal rays is only informative under a non-twisted condition. Whether it is twisted is hard to identify.

Zenion leptolepis **(Gilchrist & von Bonde, 1924)**

Cyttus leptolepis Gilchrist & von Bonde, 1924: 17 (36).
Zenion leptolepis: Barnard, 1925: 379; Kamohara, 1934: 598; Smith, 1949: 145 (273); Kotthaus, 1970: 65; Shimizu, 1983, 287; Heemstra, 1986: 441 (141. 2); Meng *et al.*, 1995: 504; Adam *et al.*, 1998: 11; Ditty, 2005: 1112 (table Zeiformes 2. (Continued).); Heemstra, 2022b: 423.
Zenion longipinnis (non Kotthaus, 1970): Fricke *et al.*, 2015: 6 (fig. 13).
? *Zenion leptolepis* (non Gilchrist & von Bonde, 1924): Paul, 2000: 75.
? *Zenion* sp.: Quero, 1978: fig. 4, 57.

The specimens shown in the plates of Heemstra *et al.* (2022b) are suspected to be *Zenion hololepis*, although the description of *Zenion leptolepis* (Heemstra *et al.*, 2022a) is correct, which is that *Zenion hololepis* has a short anal-fin-base length, less than body height, while *Zenion leptolepis* has a long anal-fin base, greater than body height. However, in the case that the photograph of the specimen which is shown in the plate was taken from a view evidently inclined forwards instead of perpendicular to the left side of the fish, which could shorten the body height, this fish still seems to have an anal-fin base just slightly greater than the body height that is shortened in the inclined photographing. Thus, in reality, its anal-fin-base length might not be greater than body height. It is still *Zenion hololepis*.

Fricke *et al.* (2015) reported *Zenion longipinnis* from New Caledonia. While the figure shows a very slender body with an anal-fin base longer than body height. Hence, it must not be *Zenion longipinnis* or its senior synonym *Zenion hololepis*, but should be *Zenion leptolepis* or a cryptic species similar to *Zenion leptolepis*.

Zenion **sp. A from McMillan *et al.*, 2011**

Zenion sp. A: McMillan *et al.*, 2011: 24 (286), 189; McMillan *et al.*, 2024: 173.
? *Zenion* sp.1: Koeda *et al.*, 2022: 78, 85 (figure 1).
? *Zenion japonicum*: Paxton & Hanley, 1989: 387.

McMillan *et al.* (2011) firstly reported an indeterminate species as *Zenion* sp. A, with few characters provided and no characters for distinguishing it from other species provided. However, it still seems a new species given the following characters from the blurred figures provided. The ventral-fin spine seems broken, with the cross-sectional area very small, maximum diameter of ventral-fin spine less than 2/3 of maximum diameter of unbranched part of first ventral-fin soft ray. Anal-fin base length less than body depth.

Koeda *et al.* (2022) reported an indeterminate species as *Zenion* sp. 1, but no characters for distinguishing were provided. This species was similar to *Zenion leptolepis* and that *Zenion leptolepis* needs a taxonomic review was mentioned, but also how this species is similar to *Zenion leptolepis* was also not mentioned. However, according to "figure 1." from Koeda *et al.* (2022), what can be roughly seen was that the anal-fin-base length less than body height, and *Zenion* sp. 1 can also be distinguished from all the species under *Zenion* according to its weak ventral-fin spine obviously weaker than the second dorsal-fin spine, maximum diameter of unbranched part of first ventral-fin soft ray less than 2/3 of maximum diameter of ventral-fin spine. This species highly resembles *Zenion* sp. A from McMillan *et al.* (2011).

Whether those are an undescribed species or a malformed specimen of another described species still pending, more information is needed from either examining this specimen or collecting new specimens to determine its validity. In this study, the author provisionally treats them as an indeterminate independent species.

Paxton & Hanley (1989) conjectured that *Zenion japonicum* is a junior synonym of *Zenion leptolepis*, as critical characters of both species could be found on one specimen that they collected. However, no morphometric or molecular information was provided. Paxton & Hanley (1989) also reported an unidentified species, also without any characters. *Zenion* sp. A from McMillan *et al.* (2011), *Zenion* sp.1 from Koeda *et al.* (2022) and Paxton & Hanley's specimens were both reported in Oceanian seas and were related to *Zenion leptolepis*. Whether these specimens were all *Zenion leptolepis* or separate species would be important in redescribing the understudied species, or more likely, a complex of, *Zenion leptolepis*.

Zenion **sp. ''*Cyttomimus affinis*'' from Grande *et al.*, 2018**

Zenion sp. ''*Cyttomimus affinis*'': Grande *et al.*, 2018, 24 (table 1. Continued.)
Zenion japonicum (non Kamohara, 1934): Lin *et al.*, 2025: 4.
? *Zenion hololepis* (non Goode & Bean, 1896): Lin & Chang, 2012: 22, (Zeniontidae ②), 80 (Zeniontidae, lower-right corner), 245

(plate 20), 313 (plate 88).

No morphological characters are provided when firstly mentioned (Grande *et al.*, 2018), while the molecular evidence shows that it is a sister group of *Zenion leptolepis*, and the K2P genetic distance between them is approximately 5.34% (Figure 5.).

Lin *et al.* (2025) reported some specimens identified as *Zenion japonicum*, which shows a very short distance, 0.65 %, with *Zenion* sp. ‘‘*Cyttomimus affinis*’’ from Grande *et al.*, 2018 (Figure 5.). Morphological evidence also supports that “*Zenion japonicum*” from Lin *et al.* (2025) are not the same species as *Zenion japonicum* Kamohara, 1934 (= *Zenion hololepis* (Goode & Bean, 1896)) described by Kamohara (1934), by “*Zenion japonicum*” from Lin *et al.* (2025) possessing the anal-fin-base length greater than body height (vs. less than), and anal-fin rays 24 (vs. more than 27). Lin *et al.* (2025) also indicated that it is a sister group of *Zenion leptolepis* molecularly, which is also known for possessing the anal-fin-base length greater than body height. However, “*Zenion japonicum*” from Lin *et al.* (2025) can also be distinguished from *Zenion leptolepis* from its ventral-fin origin slightly anterior to dorsal-fin origin (vs. posterior), and anal-fin rays 24 (vs. more than 28) (Gilchrist & von Bonde, 1924; Heemstra, 2022b).

Thus, *Zenion* sp. ‘‘*Cyttomimus affinis*’’ from Grande *et al.*, 2018 and “*Zenion japonicum*” from Lin *et al.* (2025) might be the same species, as well as a new species undescribed.

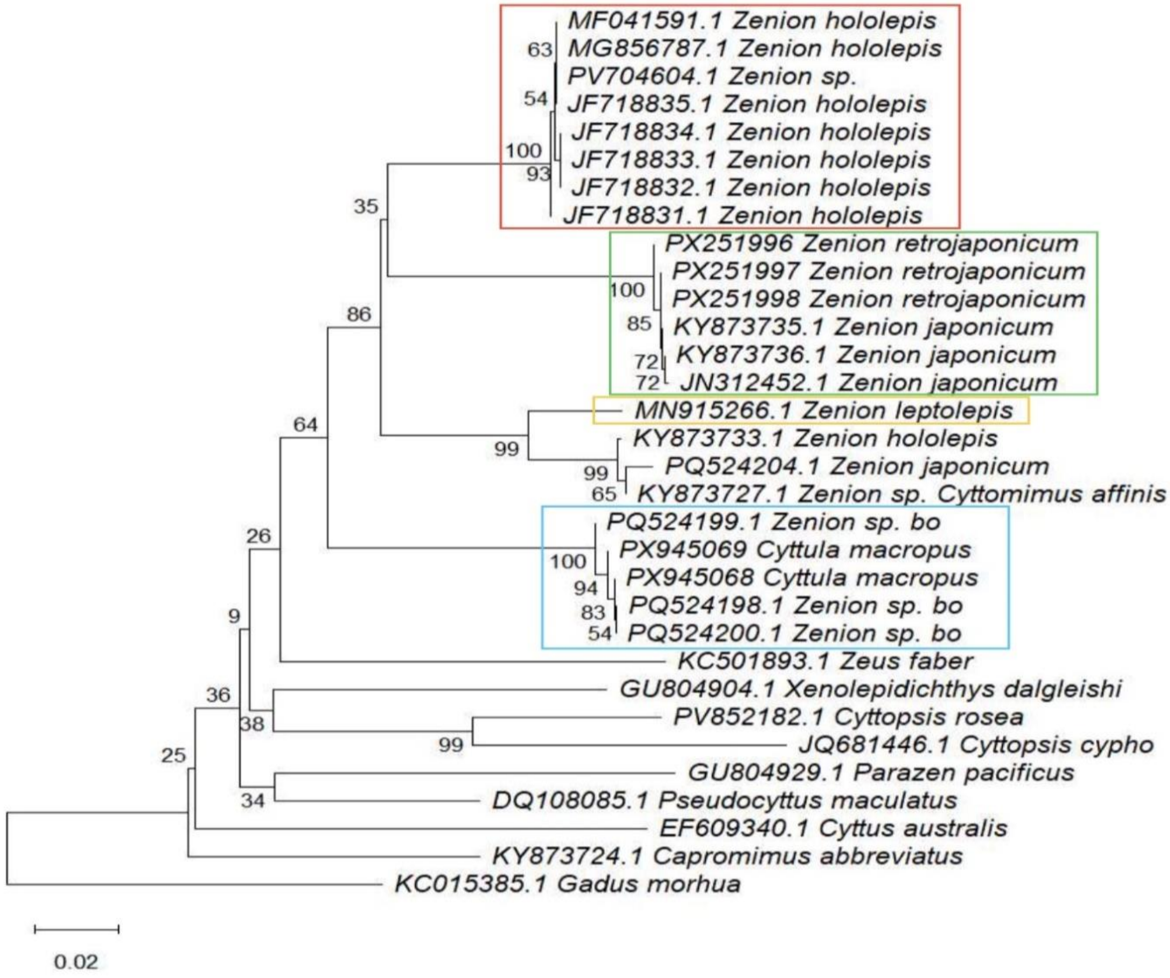

Figure 5. Molecular neighbour-joining phylogenetic tree of some zeiform species of COI, under K2P distance model, G+I substitution model for codon positions 1–3. Node labels for confidence of the topology within 10000 bootstrap values; scalebar: branch lengths 0.02=2%. KC014385.1 *Gadus morhua* as outgroup. Frames indicate the focused species in this study. Red frame: *Zenion hololepis*; Green frame: *Zenion retrojaponicum* n. sp.; Yellow frame: *Zenion leptolepis*; Blue frame: *Cyttula*.

Key to the families of Zeiformes, as well as subfamilies of Parazenidae (modified from Heemstra *et al.* (2022b); Hoshino *et al.* (2022); Myers (1960); Regan (1910); Tyler *et al.* (2003)) *,**

*Except for *Cyttula boops* (Lin *et al.*, 2025), due to a lack of information.
**This key is not constructed along with the phylogeny.

1 Large buckler scales present along dorsal-fin base and anal-fin base ……………………………………… Zeidae Rafinesque, 1815
- No large buckler scales present along bases of dorsal and anal fins ……………………………………………………………… 2
2 Scutes along ventral surface of isthmus in a zipper-like arrangement; bucklers absent along ventral surface ………………………………………………………………………………………………… Cyttidae Günther, 1860
- Scutes absent along ventral surface of isthmus; bucklers present or absent along ventral surface ………………………………… 3
3 Lateral scales vertically elongated, with most length in depth greater than 3 ……………………… Grammicolepididae Poey, 1873
- Lateral scales, if present, rounded, with most length in depth considerably less than 2 …………………………………………… 4
4 Thick scales firmly enclosed by pocket ………………………………………………………………… Oreosomatidae Bleeker, 1859
- Scales, if present, thin, with vestigial pocket underneath them ……………………………………………………………………… 5
5 Pterygiophore-derived bony ridges present along dorsal-fin base and anal-fin base ……………………… Zeniontidae Myers, 1960
- Pterygiophore-derived bony ridges absent along dorsal-fin base and anal-fin base ……………………………………………… 6
6 Scales never observed, may present but highly deciduous or absent; procurrent caudal-fin rays absent ……………………………………………………………………………………………… Macrurocyttidae Myers, 1960
- Scales present; procurrent caudal-fin rays present ………………………………………………… 7 (Parazenidae McAllister, 1968)
7 Mouth rather vertical than horizontal …………………………………………………………………… Cyttulinae new subfamily
- Mouth rather horizontal than vertical ……………………………………………………………………………………………… 8
8 Ratio of the length of first ventral-fin element in the length of the longest ventral-fin soft ray greater than 1.5; ventral-fin origin under pectoral-fin origin ……………………………………………………………………… Cyttopsinae Greenwood *et al.*, 1966
- Ratio of the length of first ventral-fin element in the length of the longest ventral-fin soft ray less than 1.5; ventral-fin origin far posterior to pectoral-fin origin ………………………………………………………………………… Parazeninae McAllister, 1968

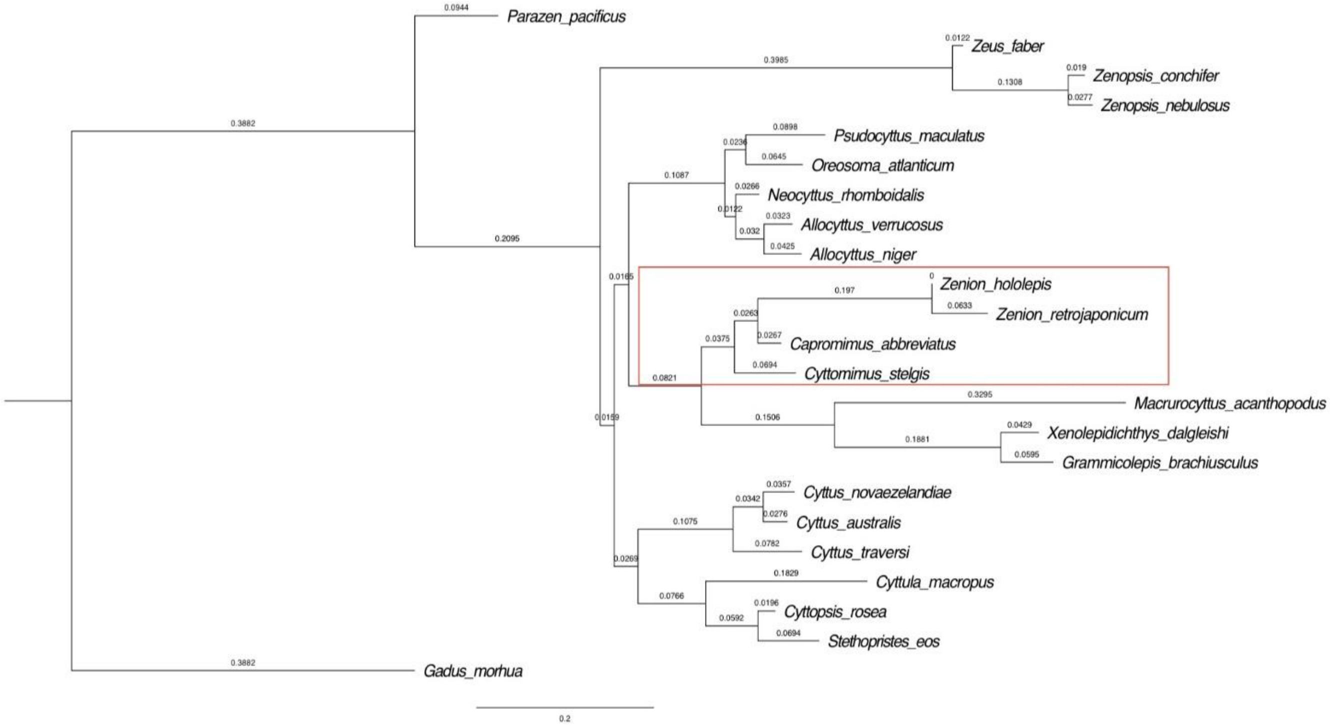

Figure 6. Morphological maximum-parsimony phylogenetic tree proposed based on Appendix and Table 5, with 10000 bootstrap values. *Gadus morhua* as outgroup. Scale bar: branch lengths: 0.2=20%. Branch labels: branch length. Red frame: Zeniontidae.

Key to the adults of vertical-mouthed zeiform species (modified from Lin *et al.* (2025)) *,**

*Except for *Cyttula boops* (Lin *et al.*, 2025), due to a lack of information.
**This key is not constructed along with the phylogeny.

1 Pored lateral lines 2; pterygiophore-derived bony ridges absent from dorsal-fin and anal-fin bases; maximum orbital diameter greater than 1/2 of body height; ventral-fin spine strong, nearly same as second dorsal-fin spine, maximum diameter of unbranched part of first ventral-fin soft ray less than 2/3 of maximum diameter of ventral-fin spine; first dorsal-fin spine flexible, without locking mechanism with second dorsal-fin spine; profile of first dorsal-fin a positively skewed parabola; the length of the first dorsal-fin spine greater than 1/3 of the length of second dorsal-fin spine; ventral fin can open to approximately 180°; when depressed, ventral-fin tip reaches the midpoint of anal-fin base; anal-fin-base length less than body height; ventral-fin origin evidently anterior to dorsal-fin origin; second anal-fin spine protrudes out of skin, slightly shorter than first anal-fin spine; branchiostegal rays incompletely hidden in the inner side of or above the preopercular, lower ones completely or partially exceed the lower margin of preopercular …………………………………………………………………………… (Cyttulinae) *Cyttula macropus* (Weber, 1913)

- Pored lateral line 1; pterygiophore-derived bony ridges present at dorsal-fin and anal-fin bases; maximum orbital diameter greater or less than 1/2 of body height; ventral-fin spine weak or strong; first dorsal-fin spine attached to second dorsal-fin spine, with locking mechanism with second dorsal-fin spine; profile of first dorsal-fin an acute angle; the length of the first dorsal-fin spine subequal to or less than 1/4 of the length of second dorsal-fin spine; ventral fin can open to approximately 90°; when depressed, ventral-fin tip far anterior to the midpoint of anal-fin base; anal-fin-base length greater than or less than body height; ventral-fin origin slightly anterior to or slightly posterior to dorsal-fin origin; second anal-fin spine covered by skin, distinctly shorter than first anal-fin spine; branchiostegal rays completely or incompletely hidden in the inner side of or above the preopercular ………………………………………………………………………………… 2 (*Zenion* Jordan & Evermann, 1896)

2 Maximum orbital diameter greater than 1/2 of body height; ventral-fin spine strong, same as or slightly weaker than second dorsal-fin spine, maximum diameter of unbranched part of first ventral-fin soft ray less than 2/3 of maximum diameter of ventral-fin spine; anal-fin-base length greater than body height ……………………………………………………………………………………… 3

- Maximum orbital diameter greater or less than 1/2 of body height; ventral-fin spine weak or strong; anal-fin-base length less than body height; ventral-fin origin slightly anterior to or slightly posterior to dorsal-fin origin …………………………………………… 4

3 Ventral-fin origin slightly posterior to dorsal-fin origin; anal-fin rays more than 28; pored lateral-line scales more than 85 ……………………………………………………………………………………… *Zenion leptolepis* (Gilchrist & von Bonde, 1924)

- Ventral-fin origin slightly anterior to dorsal-fin origin; anal-fin rays 24; pored lateral-line scales more or less than 85 ………………………………………………………………………… *Zenion* sp. ‘‘*Cyttomimus affinis*’’ from Grande *et al.*, 2018

4 Maximum orbital diameter greater than 1/2 of body height; ventral-fin spine weak, obviously weaker than second dorsal-fin spine, 2/3 of maximum diameter of ventral-fin spine less than maximum diameter of unbranched part of first ventral-fin soft ray; branchiostegal rays incompletely hidden in the inner side of or above the preopercular, lower ones completely or partially exceed the lower margin of preopercular; pored lateral-line scales more or less than 85 ……………… *Zenion* sp. A from McMillan *et al.*, 2011

- Maximum orbital diameter greater or less than 1/2 of body height; ventral-fin spine strong, nearly same as second dorsal-fin spine, maximum diameter of unbranched part of first ventral-fin soft ray less than 2/3 of maximum diameter of ventral-fin spine; branchiostegal rays incompletely hidden in the inner side of or above the preopercular, lower ones completely or partially exceed the lower margin of preopercular; lateral-line scales less than 85 ……………………………………………………………………… 5

5 Ventral-fin origin slightly anterior to dorsal-fin origin; branchiostegal rays incompletely hidden in the inner side of or above the preopercular, lower ones completely or partially exceed the lower margin of preopercular; lower margin of orbit above the lower end of pectoral-fin base; lateral-line scales more than 63 …………………………………………… *Zenion hololepis* (Goode & Bean, 1896)

- Ventral-fin origin slightly posterior to dorsal-fin origin; branchiostegal rays completely hidden in the inner side of or above the preopercular; lower margin of orbit below the lower end of pectoral-fin base; lateral-line scales less than 50 ……………………………………………………………………………………………………… *Zenion retrojaponicum* n. sp.

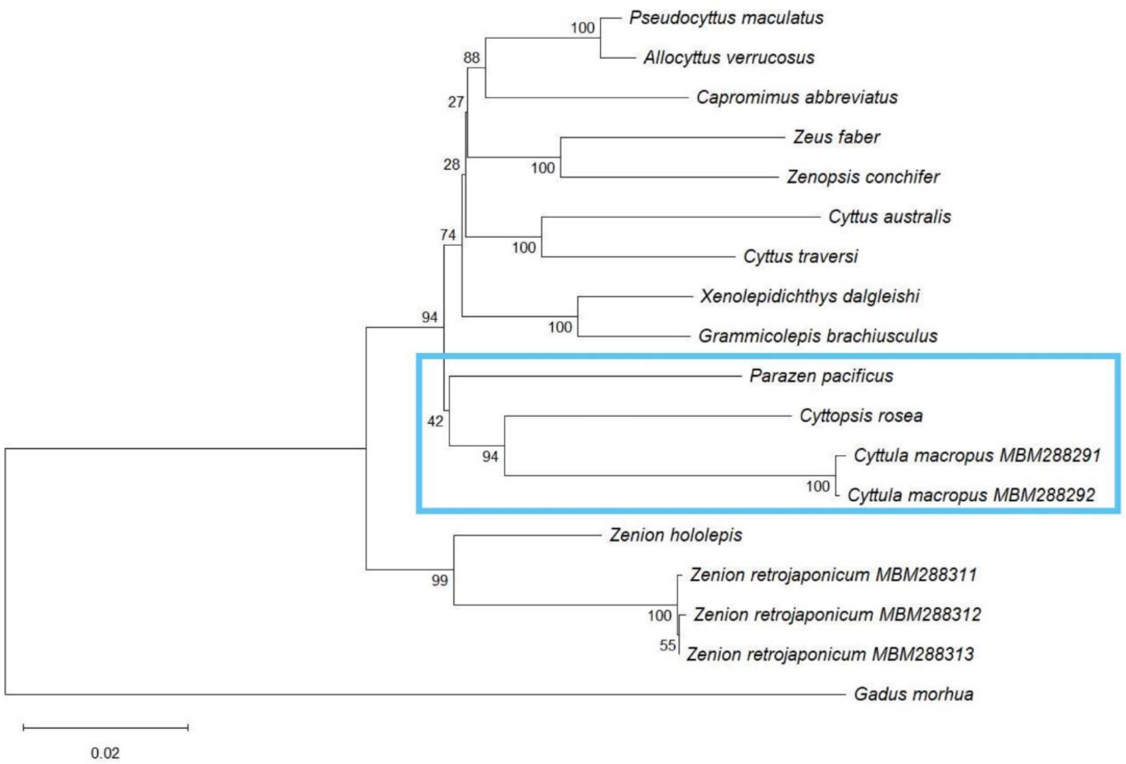

Figure 7. Multigene coalecent neighbour-joining phylogenetic trees of some zeiform species, under K2P model, with HKY+G+I substitution model for 12SrRNA, 16SrRNA, G+I substitution model for COI codon positions 1–3, GlyT codon positions 1–3, MYH6 codon positions 1–2, PLAGL2 codon positions 2–3, Sh3px3 codon positions 2–3, PLAGL2 codon positions 2–3, Sh3px3 codon positions 2–3, HKY substitution model for MYH6 codon position 3, G substitution model for PLAGL2 codon position 1, Sh3px3 codon position 1. Node labels for confidence of the topology within 100000 bootstrap values; scalebar: branch lengths 0.02=2%. *Gadus morhua* as outgroup. Blue frame: Parazenidae (*Parazen pacificus* as a representative of Parazeninae, *Cyttopsis rosea* as a representative of Cyttopsinae, *Cyttula macropus* as a representative of Cyttulinae).

Appendix

List of characters used in the morphological matrix, modified from: This study; Arratia *et al.* (2013); Bañón *et al.* (2025); Endo (2002); Goode & Bean (1896); Grande *et al.* (2018); Greenwood *et al.* (1966); Heemstra *et al.* (2022b); Hoshino *et al.* (2022); Johnson & Patterson (1993); Koeda *et al.* (2024); Konishi (2014); Kotthaus (1970); Li (2013); Lindberg (1974); Meng *et al.* (1995); Myers (1960); Nelson *et al.* (2016); Regan (1910); Rosen (1973); Rosen (1984); Tyler *et al.* (2003); Tyler & Santini (2005); Wu & Zhong (2021); Xie (2010); Yang *et al.* (1980).

i. Presence of parietal (0: present; 1: absent).
ii. Presence of basisphenoid (0: present as a moderate to long, oblique shaft connecting the parasphenoid and the prootic in front of the posterior myodome; 1: present as a short shaft at the front of the roof of the posterior myodome; 2: absent).
iii. Presence of honeycomb bone sculpturing on skull, opercles, and lachrymal-infraorbitals (0: absent; 1: present).
iv. Presence of supraocular serrations on frontal (0: present; 1: absent; 2: present at smaller sizes, lost when larger).
v. Lachrymal size (0: large, deep, height about one to four times in the length; 1: moderate, height about five to seven times in the length; 2: slender, height more than seven times in length).
vi. Infraorbital number (well-developed elements exclusive of the lachrymal, dermosphenotic, and of variable rudiments) (0: 0; 1: 3–4; 2: 5–6; 3: 7–8; 4: 9–10; 5: 11–12; 6: high variable, 5–8; 7: high variable, 7–10).
vii. Shape of most Infraorbitals (0: relatively slender and tubular; 1: deep, with large pores and bridges or open lacunae between the upper and lower edges; 2: deep, with serrate vertical supporting flanges; 3: absent).

viii. Character of dermosphenotic (0: a distinctly separate ossification from the sphenotic, sometimes relatively free from the skull; 1: fused or highly consolidated with the sphenotic; 2: non-observable).
ix. Mouth size (0: large, alveolar process of the premaxilla equal to or longer than the lateral ethmoid depth; 1: small, alveolar process no greater and usually considerably less than the lateral ethmoid depth).
x. Presence of postmaxillary process (0: present; 1: absent).
xi. Shape of premaxilla alveolar process (0: simple; 1: ventrally indented to form a pair of blunt lobes; 2: deeply bifurcated ventrally).
xii. Length premaxilla ascending process (0: reaching to a level in front of the orbit or to about the front of the orbit and the lateral ethmoid, no more than the level of 1/5 into the orbit; 1: reaching distinctly behind the lateral ethmoid to about the level of 1/3 into the orbit; 2: reaching to about the level of 1/2 into the orbit; 3: reaching to the level of the rear of the orbit).
xiii. Presence of ectopterygoid teeth (0: present; 1: absent).
xiv. Chatacters of palatine articulation with the cranium (0: the main axis of the palatine is relatively parallel, or only moderately oblique, to the body axis and has a fixed, dual articulation with the lateral ethmoid and the ethmo-vomerine region; 1: the palatine is usually orientated distinctly obliquely to the body axis and has a single, pivotal, articulation with the lateral ethmoid, resulting in considerable mobility).
xv. Metapterygoid characters (0: relatively large, length approximately 3/4 or more of the length of the quadrate, and articulating with it; 1: reduced, length approximately equal to or less of the length of the quadrate, and not articulating with it; 2: absent).
xvi. Presence of symplectic ventral flange (0: absent; 1: present).
xvii. Presence of dentary cartilages on lateral surface of dentary (0: absent or unconsolidated; 1: two moderate cartilages, each attached anteriorly to the dentary and lying sequentially one behind the other, the first shorter than the second; 2: two moderate cartilages, each attached anteriorly to the dentary and lying sequentially one behind the other, of about the same size or the first only slightly shorter than the second).
xviii. Presence of dentary serrations on the lower border (0: absent; 1: present, a single barb near the symphysis; 2: present, multiple serrations behind the symphysis; 3: present, both a single barb near the symphysis and multiple serrations behind the symphysis).
xix. Presences of gill-slit opening between the fourth and the fifth ceratobranchials (0: present; 1: absent).
xx. Gill number (0: four complete gills (one complete gill of two hemibranchs on each complete gill arch), or eight hemibranchs; 1: three and a half gills, or seven hemibranchs, with no hemibranch on the rear of the fourth ceratobranchial).
xxi. Presence of first-epibranchial uncinate process (0: absent; 1: present).
xxii. Presence of interarcual cartilage (0: absent; 1: present).
xxiii. Presence of second-pharyngobranchial suspensory shaft (0: absent or short, length approximately equal to width of second-pharyngobranchial tooth patch; 1: moderately long, length far longer than width of second-pharyngobranchial tooth patch, far less than 2/3 of the length of first-pharyngobranchial shaft; 2: long, length approximately equal to 2/3 of the length of first-pharyngobranchial shaft; 3: 2: very long, length approximately equal to the length of first-pharyngobranchial shaft).
xxiv. Presence of third-pharyngobranchial suspensory shaft (0: absent or short, length approximately equal to width of second-pharyngobranchial tooth patch; 1: moderately long, length far longer than width of second-pharyngobranchial tooth patch, far less than second-pharyngobranchial shaft; 2: long, almost as long as the shaft of the second pharyngobranchial).
xxv. Position of first basibranchial (0: the upper surface is level with those of the basihyal and the second basibran-chial, at least posteriorly; 1: the upper surface is entirely below the level of the dorsal surface of the basihyal and the second basibranchial).
xxvi. Presence of fourth-upper-pharyngeal toothplate (0: present; 1: absent).
xxvii. Presence of teeth on fifth ceratobranchial (0: present; 1: absent).
xxviii. Presence of beryciform foramen (0: present as a completely enclosed opening; 1: a deep groove along the lateral surface of the ceratohyal, often onto the dorsal hypohyal; 2: a deep concavity on the dorsal surface of the ceratohyal; 3: no lateral groove and no deep dorsal concavity, no deeper than ventral concavity; 4: present as a completely enclosed opening and a deep groove along the lateral surface of the ceratohyal, often onto the dorsal hypohyal).
xxix. Placement of branchiostegal rays in heads of the rear group (0: over the surface or along the ventral edges of both the ceratohyal and epihyal; 1: clustered along the ossified posterior border of the ceratohyal).
xxx. Presence of notches on the lower border of ceratohyal (0: prominent notches for the heads of some of the branchiostegal rays in the anterior group; 1: no prominent notches).
xxxi. Characters of ceratohyal-epihyal articulation (0: exclusively through cartilage; 1: through cartilage, but with bony interdigitated articulations in some specimens, especially with increasing specimen size; 2: bony inter-digitated articulations in all specimens at all sizes).
xxxii. Depth of the anterior end of the epihyal (0: equal, or almost equal, to the depth of the adjacent part of the ceratohyal; 1: distinctly less deep than the adjacent part of the ceratohyal).
xxxiii. Urohyal, size (0: small to moderate, no longer than the ceratohyal; 1: large, longer than the ceratohyal; 2: absent or fused).
xxxiv. First vertebra in the caudal peduncle with a modified neural or haemal spine (0: penultimate centrum; 1: antepenultimate

centrum).

xxxv. Position of the dorsal extension of the neural spine of the first vertebra, when the neural arch and spine are plastered to the skull (0: the neural spine extending only slightly, or not at all, dorsally above its attachment to the skull; 1: the neural spine with a long dorsal portion free from the skull beyond the curvature of the supraoccipital and the exoccipitals).

xxxvi. Neural-spine orientation (0: the neural spines of all, or all but the first few, of the precaudal vertebrae are orientated posterodorsally; 1: several of the neural spines of the posterior abdominal and/or anterior caudal vertebrae are orientated anterodorsally, or at least vertically, or general posterodorsally but extinctly bent anterodorsally).

xxxvii. Characters of the abdominal haemal spines (0: many of the haemal spines of the precaudal vertebrae, especially posteriorly, with a prominent process in the midline below the bridge under the haemal canal; 1: the haemal arches with a transverse bony bridge below the haemal canal, but without a median spine below the bridge, although short vertical projections may occur below the bridge on each side).

xxxviii. Presence of ossified ribs (0: present on most of the precaudal vertebrae behind the fourth; 1: present only on the last few precaudal vertebrae; 2: present only on a few of the middle precaudal vertebrae; 3: absent; 4: present on all of the precaudal vertebrae except the first; 5: present on all of the precaudal vertebrae except the first two).

xxxix. Presence of ossified epineurals (0: present on most of the precaudal vertebrae or their ribs; 1: present only on a few of the anterior precaudal vertebrae; 2: present only on a few of the middle precaudal vertebrae; 3: no ossified epineurals).

xl. Presence of hypurapophysis (0: present; 1: absent).

xli. Epural number (0: one; 1: two).

xlii. Characters of the parhypural articulation of the proximal end to the urostylar centrum (0: laterally expanded as a specialized peg, with the pegs on each side of the parhypural fitting into sockets on each side of the centrum; 1: slightly removed from and not embracing the centrum).

xliii. Degree of hypural fusion (0: hypurals 1–2 are fused together and to the centrum, and hypurals 3–4 only are fused together and free from the centrum, or hypurals 1–4 only are fused together and to the centrum; 1: hypurals 1–2 are fused together and to the centrum, and hypurals 3–4 only are fused together and free from centrum; 2: hypurals 1–4 only are fused together and to the centrum; 3: hypurals 1–2 are fused together, and hypurals 3–4 only are fused together, and they are separate from each other, and both plates are free from the centrum; 4: hypurals 1–2 are fused together and free from the centrum, and hypurals 3–5 are fused together; 5: all hypurals are fused together and to the centrum; 6: all the hypurals are fused to the centrum, or hypural 5 is observably free).

xliv. Presence of extra caudal ossicle between haemal spine of the penultimate and antepenultimate centrum (0: absent; 1: present, in at least some specimens).

xlv. Prescence of locking mechanism between elements in first dorsal fin (0: absent; 1: present between the first and second dorsal-fin spines; 2: present between the second and third dorsal-fin spines; 3: present between the first, second, and third or further dorsal-fin spines).

xlvi. Maximum mumber of groups of interneural gaps, where two or more contiguous interneural spaces, before the end of dorsal fin, are vacant (0: 1; 1: 2; 2: 3; 3: 4; 4: 2, but one groups is consists of 3 gaps; 5: 3, but one group is consists of 3 gaps; 6: not applicable, when interneural gaps are not grouped or absent).

xlvii. Number of dorsal-fin pterygiophores anterior to the neural spine of the fourth precaudal vertebra (0: none; 1: two; 2: three; 3: four).

xlviii. Placement of the first pterygiophore of the first dorsal fin (0: behind the first interneural space; 1: inserted in the first interneural space).

xlix. Position of dorsal-fin pterygiophore (0: middle to rear, not in contact with the skull and the neural arch and spine of the first vertebra; 1: front, or fills the space, in contact with the skull and first vertebra between the two sides of the neural arch and spine of the first vertebra).

l. Symmetricity of the pterygiophores of the soft dorsal-fin and the pterygiophores of the soft anal-fin (0: asymmetrical; 1: symmetrical).

li. Presence of supraneurals, number (0: none; 1: present, without cartilage at the distal end; 2: present, with cartilage at the distal end).

lii. Presence of locking mechanism of anal-fin spines (0: absent, when two or more spines are present; 1: present between the first and second spines; 2: not applicable, when number of anal-fin spines less than 2).

liii. Characters of the articulation of the first anal-fin spine with its pterygiophore (0: unfused; 1: fused in some populations or at larger specimen sizes; 2: fused in all specimens; 3: not applicable, when number of anal-fin spines absent).

liv. Length of the second anal-fin spine (0: moderate to long, more than one-half the length of the first spine; 1: short, less than one-half the length of the first spine; 2: not applicable, second anal spine absent).

lv. Number of the anal-fin pterygiophores in the second caudal interhaemal space (0: 1; 1:2; 2: 3; 3: non-observable).

lvi. Number of anal-fin pterygiophores anterior to the haemal spine of the third caudal vertebra (0: 2; 1: 4; 2: 5; 3: 6; 4: 7; 5: 9 or more).

lvii. Branchiness of dorsal-fin, anal-fin, and pectoral-fin soft rays (0: branched; 1: unbranched).
lviii. Lateral flange on the lowermost pectoral-fin radial (0: absent; 1: present).
lix. Number of separate bony elements of postcleithrum (0: 2; 1: 1).
lx. Presence of single-postcleithrum flange (0: flange absent on the single postcleithrum; 1: a flange present along the posterior border of the single postcleithrum, and the flange may be laterally flared; 2: not applicable, when two postcleithra present).
lxi. Presence of supracleithral serrations (0: none; 1: present).
lxii. Shape of the ventral end of supracleithrum (0: simple; 1: deeply bifurcate).
lxiii. Profile of the posterior edge of cleithrum (0: without a posterodorsal prong above the articulation with the postcleithrum; 1: cleithral process present as a prong above the articulation with the postcleithrum).
lxiv. Characters of extrascapulars (0: one long bone, sometimes forming an open tube, more or less closely held to the skull and integrated in line with the crest between the posttemporal and the parietal; 1: two tubular bones, not closely held to the skull, except at larger specimen sizes; 2: non-observable).
lxv. Position of ventral fin (0: approximately midway between the anus and the pectoral-fin base; 1: slightly behind the pectoral-fin base; 2: under or anterior to the pectoral-fin base).
lxvi. Presence of ventral-fin spines (0: present; 1: absent).
lxvii. Presence of anterolateral processes of the medial surfaces of the ventral-fin soft rays (0: absent; 1: present as prongs from the medial surfaces of the ray bases; 2: present as broad flanges from the ray bases).
lxviii. Presence of serrations of ventral-fin soft rays (0: absent; 1: present on crests on the anterior or upper and/or the lower posterior surfaces of several rays; 2: present on broad flanges from the medial (lower) surface of several rays).
lxix. Characters of the articulation of basipterygia (0: the medial processes of the basipterygia broadly overlap at the level of the ventral fin; 1: in contact in the midline of the middle region, but with little or no overlap; 2: not in close contact in the middle region, although often in contact at the anterior ends; 3: tightly adherent or partially fused along a broad area of midline contact).
lxx. Presence of posterior process of pelvis, behind ventral-fin base (0: short to moderate in length, and in shape a moderate to broad plate or flattened shaft, usually slightly to distinctly obliquely orientated, with or without flanges and retrorse projections; 1: long and rod-like, moderately separated from its oppo-site member along the midline).
lxxi. General presence of scales on most of the body (0: moderate to small, spiny ‘ctenoid’ (spinoid) scales; 1: moderate to small, cycloid scales; 2: scales greatly elongate vertically; 3: scales absent).
lxxii. Presence of buckler-like, greatly enlarged scales (0: absent; 1: present only from the isthmus to the anus; 2: present midabdominally and from the rear end of the spinous dorsal fin to the end of the soft dorsal-fin base; 3: present midabdominally and from below the spinous dorsal-fin base (usually from the front to middle region) to the end of the soft dorsal-fin base).
lxxiii. Presence of scute-like, slightly enlarged scales (0: absent; 1: present from the isthmus to the ventral-fin base, and sometimes more posteriorly; 2: present as lateral-line scales).
lxxiv. Presence of scales along the bases of the dorsal-fin and anal-fin soft rays (0: present along the bases of the fin rays, usually as a low sheath of scales that lack spiny processes; 1: absent from the bases of the rays, and the scales nearby without spiny projections and not extending beyond the lateral expansions of the distal ends of the dorsal- and anal-fin pterygiophores; 2: absent along the bases of the rays, but spiny processes present on the scales alongside the lateral expansions of the distal ends of the dorsal- and anal-fin pterygiophores; 3: absent).
lxxv. Presence of hyperostosis (0: absent; 1: present in the supraoccipital and the first dorsal-fin pterygiophore of some specimens; 2: present in the preventral scale bucklers).
lxxvi. Total number of vertebrae (0: 26 or fewer; 1: 27–28; 2: 29–30; 3: 31–32; 4: 33–34; 5: 35–36; 6: 37–38; 7: 39–40; 8: 41–42; 9: 43 or more).
lxxvii. Precaudal-vertebrae number (0: nine or fewer; 1: 10; 2: 11; 3: 12; 4: 13; 5: 14; 6: 15; 7: more than 15).
lxxviii. Caudal-peduncle-vertebrae number (0: 3; 1: 4; 2: 5; 3: 6; 4: 7; 5: 8; 6: 9; 7: 10; 8: 11 or more).
lxxix. Number of principal caudal-fin rays (0: 16 or more; 1: 15; 2: 14; 3: 13; 4: 12; 5: 11).
lxxx. Number of procurrent caudal-fin rays of dorsal and ventral sides (0: 0; 1: 1; 2: 2; 3: 3; 4: 4; 5: dorsal 2, ventral 3; 6: dorsal 3, ventral 2; 7: dorsal 8, ventral 7; 8: 3–4; 9: 9 or more).
lxxxi. Number of dorsal-fin spines (0: 4 or fewer; 1: 5; 2: 6; 3: 7; 4: 8; 5: 9; 6: variable, between 6–7; 7: variable, between 8–11; 8: 0).
lxxxii. Total interneural gaps, posterior to the first dorsal-fin pterygiophore, anterior to the last dorsal-fin pterygiophore (0: 0; 1: 1; 2: 2; 3: 3; 4: 4; 5: 5; 6: 7; 7: 8; 8: 9).
lxxxiii. Number of anal-fin spines (0: 0; 1: 1; 2: 2; 3: 3; 4: 4; 5: variable, 3–4).
lxxxiv. Number of pectoral-fin soft rays (0: 16 or fewer; 1: 17 or above).
lxxxv. Total number of ventral-fin elements (0: 9; 1: 8; 2: 7; 3: 6; 4: 5; 5: 4; 6: 3; 7: 1).
lxxxvi. Spatial relationship of levator arcus palatine to the infrapostorbital mandibular adductor A2 (0: medial or does not connect

to the infrapostorbital mandibular adductor A2; 1: lateral to the dorsal border of infrapostorbital mandibular adductor A2).

lxxxvii. Distance between exoccipital facets (0: close together; 1: widely separated).
lxxxviii. Presence of basihyal (0: present; 1: absent).
lxxxix. Presence of percopsoid projections (0: absent; 1: present).
xc. Character of capular foramen (0: bounded by scapula; 1: not bounded solely by scapula).
xci. Presence of lower process of hyomandibula (0: absent; 1: present).
xcii. Location of interradialis (0: across and between rays; 1: between fin rays only).
xciii. Insertion site of interradialis (0: principal caudal rays only; 1: principal caudal rays plus procurrent and/or anal-fin/dorsal-fin rays).
xciv. Number of functional lateral lines (0: one; 1: two).
xcv. Lateral-line interception (0: unobservable; 1: two lateral lines (including the unfunctional one) completely separated; 2: two lateral lines (including the unfunctional one) fused together somewhere).
xcvi. Gradient of upper jaw (0: rather horizontal than vertical; 1: rather vertical than horizontal).
xcvii. Presence of pterygiophore-derived spiny ridges at dorsal-fin base (0: present; 1: absent).
xcviii. Presence of pterygiophore-derived spiny ridges at anal-fin base (0: present; 1: absent).
xcix. Vomerine-dentition shape (0: absent; 1: laterally extended patch occupying the anterior section of the vomerine, curved or not; 2: two longitudinal oval patches, each on one side of the longitudinal midline of the anterior part of the ventral side of the vomerine).
c. First-dorsal-fin profile (0: triangular; 1: a positively skewed parabola).
ci. Presence of ventral-fin spine (0: present; 1: absent).
cii. Ratio of the length of first ventral-fin element in the length of the longest ventral-fin soft ray (0: less than 1.5; 1: greater than 1.5).
ciii. Presence of serration along anterior margin of second element of first dorsal fin (0: present; 1: absent).
civ. Presence of serration along ambilateral anterior margin of second element of first dorsal fin (0: absent; 1: present)
cv. Presence of serration along first element of ventral fin (0: present; 1: absent).
cvi. Presence of serration along ambilateral anterior margin of first element of ventral fin (0: present; 1: absent).
cvii. Presence of locking mechanism in ventral fin (0: absent; 1: present).
cviii. Condition of second anal-fin spine (0: tip exposed; 1: tip covered by skin; 2: absent).
cix. Condition of the neural and haemal spines of the first two caudal-peduncle vertebrae (0: wide plates with the anterior and posterior margins ridged; 1: thin plates with only one margin ridged, or only medially ridged).

TABLE 5. Local morphology matrix of adults, modified from: modified from: This study; Arratia *et al.* (2013); Bañón *et al.* (2025); Endo (2002); Goode & Bean (1896); Grande *et al.* (2018); Greenwood *et al.* (1966); Heemstra *et al.* (2022b); Hoshino *et al.* (2022); Johnson & Patterson (1993); Koeda *et al.* (2024); Konishi (2014); Kotthaus (1970); Li (2013); Lindberg (1974); Meng *et al.* (1995); Myers (1960); Nelson *et al.* (2016); Regan (1910); Rosen (1973); Rosen (1984); Tyler *et al.* (2003); Tyler & Santini (2005); Wu & Zhong (2021); Xie (2010); Yang *et al.* (1980). Based on Appendix.

Characters	i	ii	iii	iv	v	vi	vii	viii	ix	x	xi	xii	xiii	xiv	xv	xvi	xvii	xviii	xix	xx	xxi	xxii	xxiii	xxiv	xxv	xxvi	xxvii	xxviii
Cyttula macropus	0	0	0	0	0	1	2	0	0	0	0	1	1	1	1	0	1	1	1	1	0	0	2	1	0	1	0	0
Cyttus novaezelandiae	0	0	0	0	0	7	0	0	0	0	0	2	1	1	1	0	1	3	1	1	0	0	0	0	1	1	0	0
Cyttus australis	0	0	0	0	0	6	0	0	0	0	0	2	1	1	1	0	1	2	1	1	0	0	0	0	1	1	0	0
Cyttus traversi	0	0	0	0	0	3	0	0	0	0	0	2	1	1	1	0	1	2	1	1	0	0	0	0	1	1	0	0
Psudocyttus maculatus	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	0	1	1	0	0	1	1	0	1	0	0
Oreosoma atlanticum	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	2	1	1	0	0	0	0	0	1	0	0
Neocyttus rhomboidalis	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	2	1	1	0	0	1	1	0	1	0	0
Allocyttus verrucosus	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	2	1	1	0	0	1	1	0	1	0	4

Allocyttus niger	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	2	1	1	0	0	2	2	0	1	0	4
Parazen pacificus	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	2	0	1	1	0	0	2	2	0	1	0	1
Cyttopsis rosea	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	1	0	0	1	1	0	1	0	0
Stethopristes eos	0	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	0	1	1	0	0	2	1	0	1	0	0
Zenion hololepis	0	0	0	0	0	2	2	0	0	0	1	1	1	1	1	1	2	2	1	1	0	0	2	1	0	1	0	4
Zenion retrojaponicum	0	0	0	0	0	2	2	0	0	0	1	1	1	1	1	1	2	2	1	1	0	0	2	1	0	1	0	4
Capromimus abbreviatus	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	0	1	2	1	1	0	0	2	1	0	1	0	2
Cyttomimus stelgis	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	1	2	1	1	0	0	2	1	0	1	0	2
Macrurocyttus acanthopodus	1	2	0	0	1	0	3	2	0	0	0	0	1	1	2	0	1	3	1	1	0	0	0	0	0	1	1	1
Xenolepidichthys dalgleishi	0	1	0	0	1	1	0	0	1	1	0	0	1	1	1	1	0	0	1	1	0	0	0	0	1	1	1	0
Grammicolepis brachiusculus	0	1	0	0	1	2	0	0	1	1	0	0	1	1	1	1	0	2	1	1	0	0	0	0	1	1	1	0
Zeus faber	0	2	0	1	1	6	0	1	0	0	2	0	1	1	1	0	1	1	1	1	0	0	2	1	0	1	0	0
Zenopsis conchifer	0	2	0	2	2	4	0	1	0	0	2	0	1	1	1	0	1	0	1	1	0	0	2	1	0	1	0	0
Zenopsis nebulosus	0	2	0	2	2	5	0	1	0	0	2	0	1	1	1	0	1	0	1	1	0	0	2	1	0	1	0	0
Gadus morhua	0	2	0	0	1	1	0	0	0	0	0	0	1	0	0	0	2	0	0	0	1	1	3	2	0	0	0	3

Characters	xxix	xxx	xxxi	xxxii	xxxiii	xxxiv	xxxv	xxxvi	xxxvii	xxxviii	xxxix	xl	xli	xlii	xliii	xliv	xlv	xlvi	xlvii	xlviii	xlix	l	li	lii	liii	liv	lv
Cyttula macropus	0	0	0	1	1	1	1	1	0	5	2	1	0	0	2	0	0	6	2	1	1	1	1	0	0	0	1
Cyttus novaezelandiae	0	0	0	1	0	1	0	1	0	3	1	1	1	1	2	0	0	6	2	1	1	1	1	0	1	0	1
Cyttus australis	0	0	1	1	0	1	0	1	0	3	1	1	1	1	2	0	0	6	2	1	1	1	1	0	0	0	1
Cyttus traversi	0	0	0	1	0	1	0	1	0	3	1	0	1	1	2	0	0	1	2	1	1	1	1	0	2	0	3
Psudocyttus maculatus	0	0	0	1	0	1	0	1	1	1	0	1	1	1	2	0	0	1	1	1	1	1	2	1	0	0	1
Oreosoma atlanticum	0	0	0	1	0	1	0	1	1	1	1	1	1	1	1	0	3	5	1	1	1	1	2	1	0	0	1
Neocyttus rhomboidalis	0	0	1	1	0	1	0	1	1	1	0	1	1	1	1	0	3	1	1	1	1	1	1	1	0	0	1
Allocyttus verrucosus	0	0	1	1	0	1	0	1	1	1	0	1	1	1	1	0	3	4	1	1	1	1	1	1	0	0	1
Allocyttus niger	0	0	1	1	0	1	0	1	1	1	0	1	1	1	0	0	3	2	1	1	1	1	1	1	0	0	1
Parazen pacificus	0	0	0	1	0	0	0	0	0	1	0	0	1	1	1	0	1	6	2	1	0	1	0	2	0	2	2
Cyttopsis rosea	0	0	0	1	0	1	0	1	0	1	2	1	1	1	2	0	0	1	2	1	1	1	1	0	0	0	1
Stethopristes eos	0	0	0	0	0	1	0	1	0	1	3	1	0	1	2	0	0	1	2	1	1	1	1	0	0	0	1
Zenion hololepis	0	0	0	0	1	1	1	0	0	1	0	1	1	1	2	0	3	1	2	1	1	1	1	1	0	1	1
Zenion retrojaponicum	0	0	0	0	1	1	1	0	0	4	0	0	1	1	3	0	3	1	2	1	1	1	2	1	0	1	1

Capromimus abbreviatus	0	0	0	0	0	1	0	1	0	2	0	1	0	1	2	0	2	1	2	1	1	1	1	1	0	1	2
Cyttomimus stelgis	0	0	0	0	0	1	0	1	0	3	0	0	0	1	2	0	2	6	2	1	1	1	1	1	0	0	1
Macrurocyttus acanthopodus	0	1	0	0	2	0	1	1	1	3	3	1	0	1	5	0	2	2	2	1	1	1	1	2	3	2	1
Xenolepidichthys dalgleishi	0	1	0	1	0	1	1	1	0	1	0	0	1	0	2	0	2	1	1	1	1	1	2	1	0	1	1
Grammicolepis brachiusculus	0	1	0	1	0	1	1	1	1	5	0	0	1	0	2	0	2	1	1	1	1	1	2	0	0	0	1
Zeus faber	0	0	1	1	0	1	0	1	0	0	1	1	0	1	6	1	3	5	3	1	1	1	0	1	0	0	1
Zenopsis conchifer	0	0	2	1	0	0	0	1	0	0	0	1	0	1	2	1	3	2	3	1	1	1	0	1	0	0	1
Zenopsis nebulosus	0	0	2	1	0	0	0	1	0	0	1	1	0	1	2	1	3	2	2	1	1	1	0	1	0	0	1
Gadus morhua	1	1	2	0	0	0	0	0	1	0	3	1	1	1	4	1	0	6	0	0	0	0	0	2	3	2	0

Characters	lvi	lvii	lviii	lix	lx	lxi	lxii	lxiii	lxiv	lxv	lxvi	lxvii	lxviii	lxix	lxx	lxxi	lxxii	lxxiii	lxxiv	lxxv	lxxvi	lxxvii	lxxviii	lxxix	lxxx	lxxxi	lxxxii
Cyttula macropus	3	0	1	0	2	1	0	0	0	2	0	2	0	0	0	0	0	0	1	0	1	2	0	3	6	6	2
Cyttus novaezelandiae	4	1	1	1	1	0	0	0	0	2	0	1	0	1	0	1	0	1	0	0	3	2	2	3	2	4	1
Cyttus australis	4	1	1	1	1	1	0	0	0	2	0	1	0	1	0	0	0	1	0	1	3	2	2	3	2	4	1
Cyttus traversi	2	1	1	1	1	1	0	0	0	2	0	1	0	1	0	0	0	1	0	0	8	2	4	3	5	5	2
Psudocyttus maculatus	0	1	0	1	1	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	8	4	3	3	5	1	6
Oreosoma atlanticum	3	1	0	1	1	1	0	0	0	2	0	0	0	1	0	0	0	0	0	0	6	4	4	3	2	3	7
Neocyttus rhomboidalis	4	1	0	1	1	1	0	0	0	2	0	0	0	1	0	0	0	0	0	0	7	5	4	3	5	3	8
Allocyttus verrucosus	2	1	0	1	1	1	0	0	0	2	0	0	0	1	0	0	0	0	0	0	6	4	3	3	2	2	7
Allocyttus niger	2	1	0	1	1	1	0	0	0	2	0	0	0	1	0	0	0	0	0	0	7	5	4	3	2	3	7
Parazen pacificus	3	1	0	0	2	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	4	3	4	3	7	4	1
Cyttopsis rosea	1	0	1	0	2	0	0	0	0	2	0	2	0	2	0	1	1	0	1	0	3	2	3	3	8	3	3
Stethopristes eos	1	0	1	0	2	0	0	0	0	2	1	2	0	2	0	1	1	0	1	0	3	2	3	3	4	2	3
Zenion hololepis	3	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	2	0	1	2	2	3	6	2	2
Zenion retrojaponicum	3	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	2	2	0	1	2	2	3	6	6	2
Capromimus abbreviatus	4	1	0	1	0	1	0	0	0	2	0	2	2	0	0	0	0	0	2	0	3	2	4	3	8	3	2
Cyttomimus stelgis	4	1	0	1	1	1	0	0	0	2	0	2	0	0	0	0	0	0	2	0	2	2	2	3	3	4	1
Macrurocyttus acanthopodus	2	1	0	1	0	0	0	0	2	2	0	0	0	0	0	3	0	0	3	0	5	4	1	3	0	3	5
Xenolepidichthys dalgleishi	2	1	0	1	0	0	0	0	0	2	0	0	1	2	0	2	0	0	2	0	6	1	5	1	1	2	4
Grammicolepis brachiusculus	3	1	0	1	0	0	0	0	0	2	0	0	1	2	0	2	0	0	2	0	9	2	7	1	1	3	4
Zeus faber	3	1	0	1	0	0	1	1	1	2	0	1	0	2	1	1	2	0	1	0	3	5	1	3	1	7	5

Zenopsis conchifer	3	1	0	1	0	0	1	1	1	2	1	1	0	2	1	3	3	0	1	2	5	5	1	3	1	7	5
Zenopsis nebulosus	4	1	0	1	0	0	1	1	1	2	1	1	0	2	1	3	3	0	1	0	5	6	1	3	1	7	5
Gadus morhua	5	0	0	1	1	0	0	1	0	2	1	0	0	2	0	1	0	0	0	0	9	7	8	0	9	8	1

Characters	lxxxiii	lxxxiv	lxxxv	lxxxvi	lxxxvii	lxxxviii	lxxxix	xc	xci	xcii	xciii	xciv	xcv	xcvi	xcvii	xcviii	xcix	c	ci	cii	ciii	civ	cv	cvi	cvii	cviii	cix
Cyttula macropus	2	1	2	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1
Cyttus novaezelandiae	2	0	2	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	1	0	1	0	0	0	1
Cyttus australis	1	0	2	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	1	0	1	0	0	0	1
Cyttus traversi	2	1	2	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	1	0	0	0	1
Psudocyttus maculatus	2	1	3	0	0	0	0	0	0	0	0	0	2	0	1	1	0	0	0	0	1	0	1	0	1	0	1
Oreosoma atlanticum	3	1	2	0	0	0	0	0	0	0	0	0	2	0	1	1	0	1	0	0	1	0	1	0	1	0	1
Neocyttus rhomboidalis	5	1	2	0	0	0	0	0	0	0	0	0	2	0	1	1	1	0	0	0	1	0	1	0	1	0	1
Allocyttus verrucosus	2	1	2	0	0	0	0	0	0	0	0	0	2	1	1	1	1	0	0	0	1	0	1	0	1	0	1
Allocyttus niger	3	1	2	0	0	0	0	0	0	0	0	0	2	1	1	1	1	0	0	0	1	0	1	0	1	0	1
Parazen pacificus	1	0	2	0	0	0	0	0	0	0	1	1	2	0	1	1	1	1	1	0	1	0	1	0	0	0	1
Cyttopsis rosea	2	0	0	0	0	0	0	0	0	0	0	0	2	0	1	1	1	1	0	1	1	0	0	0	0	0	1
Stethopristes eos	2	0	0	0	0	0	0	0	0	0	0	0	2	0	1	1	1	1	1	1	1	0	1	0	0	0	1
Zenion hololepis	2	0	2	0	0	0	0	0	0	0	0	0	2	1	0	0	2	0	0	0	0	0	0	0	1	1	0
Zenion retrojaponicum	2	1	2	0	0	0	0	0	0	0	0	0	2	1	0	0	2	0	0	0	0	0	0	0	1	1	0
Capromimus abbreviatus	2	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0	0	1	0	1
Cyttomimus stelgis	2	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0	0	1	0	1
Macrurocyttus acanthopodus	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1
Xenolepidichthys dalgleishi	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Grammicolepis brachiusculus	2	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Zeus faber	4	0	1	0	0	0	0	0	0	0	0	0	2	0	1	1	2	1	0	0	1	0	1	0	0	0	1
Zenopsis conchifer	3	0	3	0	0	0	0	0	0	0	0	0	2	1	1	1	2	1	1	0	1	0	1	0	0	0	1
Zenopsis nebulosus	3	0	3	0	0	0	0	0	0	0	0	0	2	1	1	1	2	1	1	0	1	0	1	0	0	0	1
Gadus morhua	0	1	3	1	1	1	1	1	1	1	1	0	2	0	1	1	1	1	1	1	1	0	1	0	0	2	1

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