Zootaxa 5360 (3): 385–408
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5360.3.3
http://zoobank.org/urn:lsid:zoobank.org:pub:7171B65B-295D-4119-BB9A-BD07D5955294

Re-evaluation of the taxonomic status of four nominal, western Pacific species of tongue soles (Pleuronectoidei: Cynoglossidae: *Cynoglossus*), with redescription of *C. joyneri* Günther, 1878

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Abstract

Striking similarities in morphological characters and significant overlap in meristic features have resulted in different hypotheses regarding the taxonomic status of several nominal species of northwestern Pacific tongue soles of the genus *Cynoglossus*, including *C. joyneri* Günther, 1878, *C. lighti* Norman, 1925, *C. tenuis* (Oshima, 1927), and *C. tshusanensis* Chabanaud, 1951. Previous hypotheses have proposed that each taxon is a valid species; or that *C. lighti* and *C. tshusanensis* are junior subjective synonyms of *C. joyneri*; or that *C. tenuis* is a junior subjective synonym of either *C. joyneri* or *C. lighti*. Although several previous investigations concluded that *C. lighti* is a synonym of *C. joyneri*, names of both nominal species still appear in contemporary literature indicating that taxonomic status of these nominal species remains unresolved. To clarify the taxonomic status of these four nominal species, detailed study of morphological characters of 138 specimens collected from 22 localities in Japan and China, and re-examination of type specimens of three of these nominal species was conducted. The molecular barcodes of mitochondrial DNA from six representative specimens featuring morphological variation purportedly useful for distinguishing *C. lighti* from *C. joyneri* were also analyzed and then compared with sequences reported for *C. joyneri* in the literature. Lectotypes of *C. joyneri* and *C. lighti* differed in only two morphological characters (body depth and position of posterior tip of rostral hook relative to anterior margin of lower eye). However, when these two characters were examined in 138 recently collected non-type specimens, no differences were found among these nominal species. Our results do not support recognizing these as separate species. Results from genetic analyses also support recognizing only a single species among the material examined. Furthermore, overall similarities in morphological features between the holotype of *C. tshusanensis* and specimens of *C. joyneri* support recognizing *C. tshusanensis* as a junior subjective synonym of *C. joyneri*. Likewise, values for morphological features of *C. joyneri* examined in the present study also encompass the range of values reported in the original description of *C. tenuis*. This finding supports conclusions of previous studies that this nominal species is also a junior synonym of *C. joyneri*. Based on morphological and genetic evidence, we conclude that only a single species, *C. joyneri*, should be recognized among the four nominal species included in this study. *Cynoglossus joyneri* is re-described based on data from 492 specimens collected throughout nearly the entire range of the species.

Key words: *Cynoglossus lighti*, *Cynoglossus tenuis*, *Cynoglossus tshusanensis*, morphological variation, molecular analyses, *16S*, *COI*, *12S*, integrative taxonomy, intraspecific variation

摘要

由于舌鳎属部分鱼类的形态特征极度相似，可数特征更是大幅重叠，导致研究人员对部分种类的分类地位持有不同观点，特别是本研究中的短吻红舌鳎 *C. joyneri* Günther, 1878, 长吻红舌鳎 *C. lighti* Norman, 1925, 纤细舌鳎 *C. tenuis* (Oshima, 1927)和舟山舌鳎*C. tshusanensis* Chabanaud, 1951。前人研究中存在上述四个名义种均被认为是有效种、长吻红舌鳎和舟山舌鳎是短吻红舌鳎的次同物异名，以及纤细舌鳎是短吻红舌鳎或长吻红舌鳎的次同物异名等不同描述。虽然一些研究已表明长吻红舌鳎是短吻红舌鳎的次同物异名，但目前仍然有研究认为这

Accepted by B. Frable: 28 Jul. 2023; published: 27 Oct. 2023

两种均为有效种。 为解决这四个名义种的分类问题，我们对采集自中国和日本的22个区域的138尾具有短吻红舌鳎、长吻红舌鳎名义种形态特征的样品，以及短吻红舌鳎、长吻红舌鳎和舟山舌鳎三种类的模式标本（纤细舌鳎的模式标本在首次描述后不久便遗失）进行了详细的形态学研究。同时分析了分别具有前人识别长吻红舌鳎和短吻红舌鳎典型形态特征的6尾代表样品的线粒体分子条形码，并和已报道的短吻红舌鳎相关数据进行了比较。通过比较短吻红舌鳎和长吻红舌鳎选模标本的形态特征，发现两个种类仅在体高与体长比和吻端相对于下眼前缘的位置这两个特征上有区别。然而，当比较采自不同区域的138尾样品时，发现这两个特征均为连续的数值，不存在种间差异。这些形态特征结果表明这两个形态特征均不能用于区分它们。遗传距离的结果也同样支持了短吻红舌鳎和长吻红舌鳎为同一物种。根据舟山舌鳎模式标本和短吻红舌鳎在形态特征上的相似性，我们认为舟山舌鳎是短吻红舌鳎的次同物异名。本研究的短吻红舌鳎形态特征值也包含了纤细舌鳎模式标本原始描述的特征值，该结果支持纤细舌鳎也是短吻红舌鳎的次同物异名。因此，根据形态特征和遗传距离的分析，我们认为短吻红舌鳎、长吻红舌鳎、舟山舌鳎和纤细舌鳎这四个名义种中，只有短吻红舌鳎是有效种类，其余三个种类均为短吻红舌鳎的次同物异名。同时，据本研究基于492 尾样品的的研究结果，我们对短吻红舌鳎进行了详细的再描述。

关键词：长吻红舌鳎, 纤细舌鳎, 舟山舌鳎, 形态变异, 分子分析, *16S*, *COI*, *12S*, 整合分类, 种内变异

Introduction

Tongue soles of the genus *Cynoglossus* Hamilton, 1822 are small- to medium-size flatfishes (adults usually 100–400 mm SL) classified in the pleuronectiform family Cynoglossidae (Regan 1910; Menon 1977; Chapleau 1988). Due to a number of factors, including morphological similarities among many species of *Cynoglossus*, incomplete or inadequate original descriptions, and in some cases, lost or damaged type specimens, it is often difficult to accurately identify these species. Uncertainty in identifications has resulted in different hypotheses regarding the taxonomic status of some nominal species sharing similar morphologies.

One example of this taxonomic uncertainty is found among four nominal species of tongue soles described from coastal waters of the northwestern Pacific Ocean, including *C. joyneri* Günther, 1878, collected at a fish market in Tokyo, Japan; *C. lighti* Norman, 1925, from Amoy (now Xiamen), China; *C. tenuis* (Oshima, 1927), collected at the Tainan fish market in southwestern Taiwan; and *C. tshusanensis* Chabanaud, 1951, collected in the Tshusan Archipelago (now known as the Zhoushan Islands). These nominal species feature similar morphologies, including body size, three lateral lines on the ocular side, no lateral line on the blind side, 10 caudal-fin rays, ctenoid scales on both sides of the body, usually 80 or fewer scales in the middle lateral line (MLL) and uniform brownish to reddish-brown coloration on the ocular side of the body (Günther 1878; Norman 1925; Oshima 1927; Chabanaud 1951; Ochiai 1963; Menon 1977; Li & Wang 1995; Yamada 2000, 2002). Further complicating taxonomic study of these nominal species is that the anterior snout and mouth of the lectotype of *C. joyneri* are deformed, a fact largely unknown or ignored in most studies, and the holotype of *C. tenuis* has been lost (Ho & Shao 2011; Fricke *et al*. 2022), which precludes examining features of this specimen other than those reported in the original description.

Some studies (Fowler 1934; Chabanaud 1951; Kamohara 1953; Ochiai 1963; Chen & Weng 1965; Li & Wang 1995; Cheng 1997; Yamada 2000, 2002; Froese & Pauly 2023) considered *C. lighti* as a valid species, while other works (Matsubara 1955; Menon 1977; Lindberg & Fedorov 1993; Fricke *et al*. 2017; Zhou *et al*. 2017; Wang *et al*. 2018; Fricke *et al*. 2022) concluded that *C. lighti* is a synonym of *C. joyneri*. Chabanaud (1951), in his paper examining the taxonomy of *C. joyneri*, *C. lighti* and *C. tshusanensis,* stated that these three nominal species have many overlapping features and that when additional specimens were available, it likely would be found that only a single species is represented by these three nominal species.

Most previous morphological and molecular studies concluding that *C. joyneri* and *C. lighti* are conspecific, except those of Chabanaud (1951) and Menon (1977), did not examine types of these nominal species, nor did they compare diagnostically important features provided in the original descriptions and subsequent works on these two nominal species. As such, questions arise as to how these specimens were identified, and whether or not specimens included in these studies actually represented both nominal species. Consequently, reliability of conclusions of these earlier studies is difficult to assess. Although several previous investigations concluded that *C. lighti* is a synonym of *C. joyneri* (Matsubara 1955; Menon 1977; Wang *et al*. 2018), *C. lighti* still appears in contemporary literature (Koshiishi *et al*. 2001; Yamaguchi & Kume 2004; Yagi *et al*. 2009; Kume *et al*. 2012; Ping & Liu 2014; Kume *et al*. 2015; Song *et al*. 2015; Wang *et al*. 2018; Sun *et al*. 2021) indicating that taxonomic status of these nominal species remains unresolved.

Following their original descriptions, studies dealing with *C. tenuis* and *C. tshusanensis* have been relatively few. Menon (1977) compared values reported in the original descriptions of *C. tenuis* with those of the lectotype of *C. joyneri* and found no differences between these two nominal species. He also compared several morphological characters between type specimens of *C. tshusanensis* and *C. joyneri* and confirmed that any variation observed between these two nominal species was only that indicative of intraspecific differences. Based on these results, Menon (1977) concluded that both *C. tenuis* and *C. tshusanensis* are junior synonyms of *C. joyneri*. Other researchers also considered *C. tenuis* to be a junior subjective synonym of either *C. joyneri* (Matsubara 1955; Lindberg & Fedorov 1993; Ho & Shao 2011; Kottelat 2013) or *C. lighti* (Wu 1932; Kamohara 1953; Zhang & Wang 1963; Ochiai 1963; Cheng 1997), and some also considered *C. tshusanensis* as a junior synonym only of *C. joyneri* (Lindberg & Fedorov 1993; Desoutter *et al*. 2001; Kottelat 2013; Fricke *et al*. 2017), without providing further comment or evidence to support their conclusions.

It should be noted that many of these studies were limited because conclusions were formed without benefit of having examined type specimens, or the authors did not consult previously published information regarding important diagnostic characters of the types of these nominal species. Furthermore, investigators only examined limited characters from a small number of specimens collected from a limited geographic area. In principle, ensuring the accuracy of species identifications and assigning correct nomenclature requires examining morphological features of type specimens and/or comparing data from the specimens in question with those provided in the original descriptions of the nominal species.

In the present study, we aim to clarify the taxonomic status of *C. joyneri* and *C. lighti* by comparing morphological characters of the lectotypes of both nominal species and also by examining a relatively large number of non-type specimens (N= 138) collected from 22 locations, including type localities of both nominal species. We also compare genetic distances among six representative specimens subsampled from the above 138 specimens. Additionally, we analyzed morphological characters of type specimens of the nominal species, *C. tenuis* and *C. tshusanensis*, to re-evaluate their taxonomic status. The large amount of data available from the specimens examined in this study, together with information garnered from previously published sources considered reliable, provide the necessary information to redescribe *C. joyneri*.

Materials and methods

Specimen information

A total of 141 specimens was examined, including lectotypes of *C. joyneri* (BMNH 1878.4.15.94; Natural History Museum, London, U.K.; Fig. 1A) and *C. lighti* (BMNH 1924.12.15.87; Fig. 1B), the holotype of *C. tshusanensis* (BMNH 1892.12.12.32), and 138 non-type specimens (Fig. 2) with features similar to those of *C. joyneri* or *C. lighti*. Whereabouts of the holotype of *C. tenuis* is unknown and it is presumed lost (Ho & Shao 2011). Information on morphological characters of this type specimen were obtained from the original description of this nominal species. Of 28 characters examined and compared between types of the other species, 20 were directly counted or measured by T. Munroe (unpubl. data).

Non-type specimens (N= 138) were examined from the following institutions: USNM—Smithsonian Institution National Museum of Natural History, Department of Vertebrate Zoology, Division of Fishes, Washington D.C., U.S.A.; ASIZB—Academia Sinica, Institute of Zoology, Beijing, China; SCF—South China Sea Institute of Oceanology, Guangzhou, China. Of these, 16 are museum voucher specimens previously identified as *C. joyneri* (see Material Examined) including three collected from Japanese waters (Fig. 2): Niphon (NJ), Shizuoka (SJ), and Kochi (KJ), and 13 from localities in Chinese waters. Another 122 non-type specimens, now cataloged in the Fish Collection of the Marine Biodiversity Collection of the South China Sea, Chinese Academy of Sciences (SCSMBC), were collected fresh at 19 localities in coastal waters of China (Fig. 2). Abbreviations for collection locations along the Chinese coast are: QH—Qinhuangdao; YT—Yantai; QD—Qingdao; RZ—Rizhao; LY—Lianyungang; LS—Lvsi; SH—Shanghai; ZS—Zhoushan; WL—Wenling; WZ—Wenzhou; FZ—Fuzhou; MW—Mawei; XM—Xiamen; DS—Dongshandao; SW—Shanwei; SZ—Shenzhen; ZH—Zhuhai; JM—Jiangmen; and BM—Baimajing. These fishes were selected from landings of artisanal fishing activities conducted by vessels using bottom trawls. Information associated with these specimens includes catalogue number, location, date and number of specimens.

No specific information is available on depth of capture, substrata, or longitude and latitude associated with these landings. These specimens were selected because they feature three ocular-side lateral lines, 10 caudal-fin rays, ctenoid scales on both sides of the body, two nostrils on each side of the head, less than 80 scales in the midlateral line, less than 13 scale rows between dorso- and midlateral lines and all had uniform reddish-brown, ocular-side coloration.

FIGURE 1. Photographs of ocular sides of lectotypes of two nominal species of *Cynoglossus*. A) *Cynoglossus joyneri* (BMNH 1878.4.15.94, 232.6 mm SL); and B) *Cynoglossus lighti* (BMNH 1924.12.15.87, 172.0 mm SL). Photos by K. Webb (Natural History Museum, London).

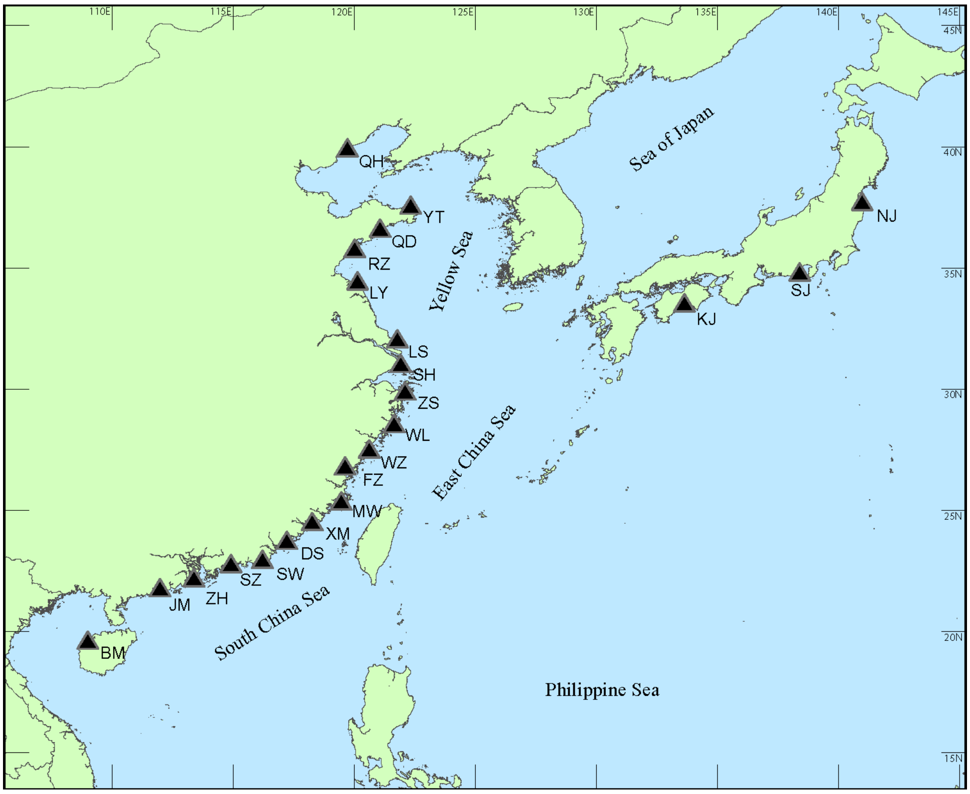

FIGURE 2. Twenty-two sampling locations for 138 specimens of tongue soles examined in this study. Abbreviations for locations are: NJ: Niphon; SJ: Shizuoka; KJ: Kochi; QH: Qinhuangdao; YT: Yantai; QD: Qingdao; RZ: Rizhao; LY: Lianyungang; LS: Lvsi; SH: Shanghai; ZS: Zhoushan; WL: Wenling; WZ: Wenzhou; FZ: Fuzhou; MW: Mawei; XM: Xiamen; DS: Dongshandao; SW: Shanwei; SZ: Shenzhen; ZH: Zhuhai; JM: Jiangmen; BM: Baimajing.

TABLE 1. Selected meristic data and qualitative characters from previous works that recorded only one species (either *Cynoglossus joyneri* or *C. lighti*) or treated *C. lighti* as a junior synonym of *C. joyneri*. Abbreviations defined in text.

Cynoglossus joyneri											
Author	**N**	**SL (mm)**	**CFR**	**DFR**	**AFR**	**TV**	**MLL**	**DMLL**	**PHE[1]**	**Mouth-Eye[2]**	**Color[3]**
Günther (1878)	2	248	-	106–107	79	-	**85**	13	-	-	UB
Jordan & Starks (1907)	-	≤225	-	106–112	83–86	-	70–75	12	H–II	-	B
Wu & Wang (1933)	1	240	-	110	84	-	75	13	-	-	-
Chyung (1954)	-	<300	-	106–112	83–86	-	70–75	13	-	-	RB
Tanaka (1955)	-	≤333	-	106–112	83–86	-	75	-	-	-	RB
Shen (1984)	1	212	-	107	85	-	78	-	-	-	-
Lu & Wu (1986)	1	138	**8**	116	87	-	76	11	-	-	GB
Liu & Qin (1987)	15	78–202	8–11	108–116	85–90	-	69–80	10–13	H–I	M–III	GB
Kim & Choi (1994)	82	129–240	8–10	111–117	87–90	51–53	**78–86**	11–13	-	M–III	RB

Cynoglossus lighti											
Author	**N**	**SL (mm)**	**CFR**	**DFR**	**AFR**	**TV**	**MLL**	**DMLL**	**PHE[1]**	**Mouth-Eye[2]**	**Color[3]**
Norman (1925)	4	120–180	-	115	88	-	75–78	11	H–II	M–III	B

Cynoglossus lighti treated as junior synonym of *C. joyneri*											
Author	**N**	**SL (mm)**	**CFR**	**DFR**	**AFR**	**TV**	**MLL**	**DMLL**	**PHE[1]**	**Mouth-Eye[2]**	**Color[3]**
Zheng (1962)	10	135–185	8–11	107–115	82–88	51	70–76	11–13	H–I	M–III	B
Zhang & Wang (1963)	2	145,151	**8–9**	107–108	87–88	-	71–78	11–13	H–I	-	B
Menon (1977)	9	74–232	10	105–112	81–85	50–53	66–72	11–12	H–I	M–I/II	B
Miao (1984)	14	85–308	10–11	110–117	83–89	-	69–79	9–12	H–I	M–III	B
Lindberg & Federov (1993)	10	152–199	10	114–117	88–90	53–54	-	-	-	-	-

[1]Position of posterior end of rostral hook relative to lower eye: H–I= not reaching lower eye; H–II= reaching anterior margin of lower eye; H–III= extending slightly beyond anterior margin of lower eye. [2]Mouth angle relative to posterior margin of lower eye: M–I= not reaching posterior margin; M–II= reaching posterior margin; M–III= extending slightly beyond posterior margin of lower eye. [3]Ocular-side coloration: UB= uneven brown; B= brown; RB= reddish brown; GB= grayish brown. Numbers in bold differ notably from values reported in other literature for the same character.

All distinguishing characters used in previous studies (Tables 1–5) to diagnose the four nominal species were included among the 30 morphological characters (eight meristic, 16 morphometric, and six descriptive features) examined in this study. Methods for counting and measuring morphometric features follow those used in Wang *et al*. (2016).

TABLE 2. Selected morphometric data of previous works that recorded only one species (either *Cynoglossus joyneri* or *C. lighti*) or treated *C. lighti* as a junior synonym of *C. joyneri*. Abbreviations defined in text. Numbers in bold differ notably from values reported in other literature for the same character.

Author	N	SL (mm)	BD/SL	HL/SL	SNL/HL	IOW/HL	LED/HL	DSM/HL	HL/HW
C. joyneri									
Günther (1878)	2	248	28.6	18.2	37.5	-	-	<50.0	-
Jordan & Starks (1907)	-	≤225	26.3–27.8	20.8–21.4	-	6.3–6.7	6.3–6.7	-	-
Wu & Wang (1933)	1	240	24.4	23.3	-	-	-	-	>1.0
Chyung (1954)	-	<300	26.3–27.8	-	-	-	6.7	-	-
Tanaka (1955)	-	≤333	25	-	-	-	-	-	-
Shen (1984)	1	212	-	-	-	-	-	<50.0	-
Lu & Wu (1986)	1	138	26.3	18.9	**27.8**	7.7	12.3	-	<1.0
Liu & Qin (1987)	15	78–202	20.8–27.0	20.4–24.4	38.5–45.5	5.0–6.0	6.9–9.4	-	≥1.0
Kim & Choi (1994)	82	129–240	21.8–26.1	19.5–21.6	43.0–50.0	2.8–4.5	5.9–8.3	-	-
C. lighti									
Norman (1925)	4	120–180	20.0–22.7	20.0–20.8	40	<7.7	7.7–10.0	50	-
C. lighti* treated as junior synonym of *C. joyneri									
Zheng (1962)	10	135–185	22.4–25.4	20.2–23.1	40.0–47.6	5.1–6.5	7.2–9.3	-	1.0–1.1
Zhang & Wang (1963)	2	145,151	23.3–25.0	20.4–21.3	40.0	6.3–6.7	-	-	≥1.0
Menon (1977)	9	74–232	**20.3–43.6**	**18.9–40.0**	32.7–42.0	4.8–8.0	7.1–10.1	47.6–60.3	-
Miao (1984)	14	85–308	21.3–27.0	20.4–23.3	40.0–47.6	-	6.0–10.0	-	1.0–1.1
Lindberg & Federov (1993)	10	152–199	-	-	-	-	-	-	-

Meristic features included numbers of caudal-fin rays (CFR), pelvic-fin rays (PFR), dorsal-fin rays (DFR), anal-fin rays (AFR), abdominal vertebrae (AV), total vertebrae (TV), midlateral-line scales (MLL), and scale rows between dorsolateral line and midlateral line (DMLL). Counts of vertebrae were made from radiographs; fin-rays were counted from radiographs or from specimens; scales were counted directly from the specimens. Previous studies have used different methods for counting MLL scales. The first method, and the method adopted in this study, is to count MLL scales beginning at the point where the middle lateral line is at the vertical through the indentation in the posterior margin of the opercle. This count continues posteriorly and ends with the scale at the base of the caudal fin (Wang *et al*. 2016). The second method of counting MLL scales begins with counting the first scale at the crossover point of the supraorbital commissure and the middle lateral line and ends at the same point as that described in the first method (Yokogawa *et al*. 2008). A third method is where the MLL count begins at the same point as that described in the second method and ends at the scale equal with the vertical at the ends of the dorsal and ventral lateral lines (Kim & Choi 1994).

Sixteen morphometric features included data from 15 measurements presented as percent of SL or HL, an estimate of the ratio of HW to HL (HW/HL), and one feature (PHE) evaluating the position of the posterior tip of the rostral hook relative to the anterior margin of the lower eye. The following morphometric features were measured: 1. Snout length (SNL); 2. Diameter of lower eye (LED); 3. Interorbital width (IOW); 4. Postorbital Head Length (POL); 5. Length of ocular-side upper jaw (UJL); 6. Mouth angle relative to posterior margin of lower eye, with M–I not reaching posterior margin of eye, M–II reaching posterior margin of lower eye, and, M–III extending slightly beyond posterior margin of lower eye. 7. Snout tip to angle of mouth (DSM); 8. Angle of mouth to opercular margin (AMO); 9. Body depth (BD); 10. Head length (HL); 11. Head width (HW); 12. Upper head-lobe width (UHW); 13. Lower head-lobe width (LHW); 14. Preanal length (PAL); 15. Caudal-fin length (CFL); and 16. Standard Length

TABLE 3. Selected meristic data and qualitative characters from previous works treating *C. joyneri* (CJ) and *C. lighti* (CL) as valid species. Abbreviations defined in text, except CHN= China and JPN= Japan.

Author	Species	N	SL (mm)	Location	DFR	AFR	CFR	DMML	MLL	TV	PL	PHE[1]	Mouth-Eye[2]	Color[3]
Wu (1932)	CJ	3	≤210	QD, CHN	106–113	85–87	10	12–13	70–77	-	-	H–II	M–II	GB
	CL	7	≤200	XM, CHN	109–113	82–86	9–10	11	69–78	-	-	H–III	M–III	B
Chabanaud (1951)	CJ	2	223–228	SJ, JPN	105–109	85–86	10	13	**82–85**	-	-	H–I	M–II	RB
	CL	4	107–171	WZ & XM, CHN	112–113	85–87	10	12	**90–92**	-	-	H–II/III	M–II/III	DB
Zheng (1955)	CJ	5	136–195	CHN	110–116	85–89	10	11–12	70–78	-	-	H–I/II	M–III	B
	CL	10	128–176	CHN	110–117	82–87	10	10–11	68–77	-	-	H–I	M–III	B
Ochiai (1963)	CJ	103	94–245	JPN	99–112	80–89	9–10	11–12	62–76	50–54	-	H–III	M–III	B/YB
	CL	34	109–204	JPN	103–114	82–89	9–10	12	63–76	52–54	Yes	H–III	M–III	B/YB
Li & Wang (1995)	CJ	10	130–202	CHN	106–117	83–90	10	12–13	65–76	54	-	H–III	M–III	RB
	CL	14	66.7–234	CHN	107–114	83–89	8–10	10–11	70–76	54	Yes	H–III	M–II/III	RB
Cheng (1997)	CJ	5	130–195	CHN	110–116	85–89	10	11–12	70–78	-	-	H–I/II	M–III	GB
	CL	5	130–185	CHN	111–117	80–85	10	10–11	70–75	-	Yes	H–I	M–III	B
Yamada (2002)	CJ	-	-	JPN; CHN	107–116	85–90	10	-	71–78	-	Yes	-	-	-
Yamada & Yashida (2013)	CL	-	-	JPN; CHN	103–114	82–89	9–10	-	63–76	-	-	-	-	-

[1]Position of posterior end of rostral hook relative to lower eye: H–I= not reaching eye; H–II= reaching anterior margin eye; H–III= extending slightly beyond anterior margin of lower eye. [2]Mouth angle relative to posterior margin of lower eye: M–I= not reaching posterior margin; M–II= reaching posterior margin; M–III= extending slightly beyond posterior margin. [3]Ocular-side coloration: UB= uneven brown; B= brown; YB= yellowish brown; RB= reddish brown; GB= grayish brown. Values in bold differ notably from values reported in other literature for the same character.

TABLE 4. Selected morphometric data (as % of SL or HL) of previous works treating *Cynoglossus joyneri* (CJ) and *C. lighti* (CL) as valid species. Abbreviations defined in text, except PFL= pelvic-fin length, DFL= dorsal-fin length and AFL= anal-fin length.

Author	Species	N	SL (mm)	BD/ SL	HL/ SL	HW/ SL	HL/ HW	SNL/ HL	LED/ HL	IOW/ HL	POL/ HL	PFL/ HL	CFL/ HL	Snout Shape
Wu (1932)	CJ	3	≤210	25.6–26.3	20.4–21.3	-	<1	38.5	6.9–8.3	6.9–8.3	-	-	-	-
	CL	7	≤200	22.2–23.3	20.8–21.3	-	>1	37.0–41.7	8.0–9.5	<8.0	-	-	-	-
Chabanaud (1951)	CJ	2	223–228	28.0–30.0	19.0–20.6	-	-	-	5.0	3.0–4.0	53–54	-	35–40	-
	CL	4	107–171	23.0–25.0	20.0–23.0	-	-	-	7.0–8.0	2.0	47–48	-	37–40	–
Zheng (1955)	CJ	5	136–195	24.5–26.1	20.2–22.1	19.7–21.4	1	40.3–45.9	7.8–9.3	5.2–6.0	-	21.5–26.7	33.4–40	-
	CL	10	128–176	20.2–24.0	20.7–22.7	15.9–19.6	>1	38.9–45.9	7.5–9.4	4.9–6.1	-	21.3–26.8	35.6–40	-
Ochiai (1963)	CJ	103	94–245	23.8–29.4	20.4–25.0	-	-	32.3–41.7	5.3–11.2	-	-	-	-	Slightly Round
	CL	34	109–204	22.2–26.3	20.0–23.3	-	-	35.7–43.5	6.9–11.8	-	-	-	-	Slightly Pointed
Li & Wang (1995)	CJ	10	130–202	22.7–27.8	20.4–23.8	-	≤1	38.5–43.5	7.0–10.2	2.6–4.9	-	18.9–23.3	34.5–43.5	-
	CL	14	66.7–234.0	22.2–26.3	20.4–24.4	-	>1	41.7–45.5	6.6–10.1	1.8–4.6	-	18.5–26.3	33.3–45.5	-
Cheng (1997)	CJ	5	130–195	25.0–26.3	20.4–22.2	-	≤1	41.7–47.6	7.9–9.3	<7.9	-	-	-	-
	CL	5	130–185	20.0–23.8	20.8–22.2	-	>1	37.0–43.5	7.7–9.3	<7.7	-	-	-	-
Yamada (2002) Yamada & Yashida (2013)	CJ	-	-	25.6–29.4	22.7	-	-	-	-	-	-	-	-	Slightly Round
	CL	-	-	25.0–26.3	21.7	-	-	-	-	-	-	-	-	Slightly Pointed

(SL). All measurements were made on the ocular side using digital calipers and were recorded to the nearest 0.1 millimeter. Values of morphometric features reported in previous works were also converted to percentage values in the present study for comparative purposes.

In previous studies, when describing position of the posterior tip of the rostral hook relative to the anterior margin of the eye, different authors (Jordan & Starks 1907; Norman 1925; Wu 1932; Chabanaud 1951; Ochiai 1963; Li & Wang 1995) have used different terminologies, or used different reference points, including the upper eye, the eye, or the lower eye, to describe the posterior extent of this feature. In this study, we standardized description of this feature as the position of the posterior tip of the rostral hook relative to the vertical at the anterior margin of the lower (non-migrated) eye (PHE) and defined this feature as either not reaching (H–I), reaching (H–II), or extending slightly beyond the vertical at the anterior margin of the lower eye (H–III). These different positions were then quantified corresponding to > 0, = 0, and < 0, respectively, and are illustrated in Figure 3.

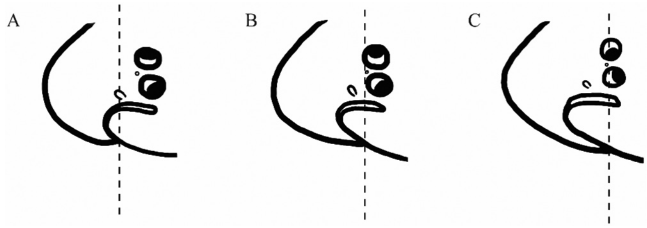

FIGURE 3. Hand-drawn sketches illustrating different positions of posterior tip of rostral hook relative to anterior margin of lower eye (PHE). A) Tip not reaching anterior margin of eye (PHE > 0); B) Tip reaching vertical at anterior margin of eye (PHE = 0); C) Tip reaching vertical slightly beyond anterior margin of eye (PHE < 0).

Six descriptive (qualitative) characters compared among specimens including shape of the anterior snout (slightly pointed or rounded), presence/absence of the preorbital lateral line (PL), body color, fin color, color of outer and inner surfaces of the opercles, and color of the peritoneum were directly observed from the specimens.

Non-type specimens (N = 138) were sorted into three groups (Table 5) based on two characters that differed most obviously between lectotypes of *C. joyneri* and *C. lighti*, BD (measured as percent of SL) and PHE, for further analysis.

Molecular methods

Two representative specimens from each of the three groups identified above were selected for amplification of *COI* and *12S* fragments. These specimens were selected because they represent individuals featuring slightly pointed versus rounded snouts and either have a preorbital line present or absent. Two of four specimens from the first and third groups possessed a slightly rounded anterior snout and a preorbital lateral line (SCF 201511586 and SCF 201604570), while two other specimens (SCF 201510602 and SCF 201507583) from the first and third groups possessed a slightly pointed anterior snout and no preorbital lateral line, respectively. Of the two specimens selected from the second group, one (SCF 201510616) possessed a slightly pointed anterior snout and a preorbital lateral line, while the other (SCF 201510575) had a slightly rounded anterior snout and no preorbital lateral line.

Approximately 30 mg of muscle tissue were taken from each individual, and DNA was extracted using the SQ Tissue DNA Kit (OMEGA) following the manufacturer's protocol, and then stored in a -20° C freezer. Based on the mitochondrial gene fragment sequences of *C. semilaevis* Günther, 1873, amplification primers (*COI* 550 bp; *12S* 900 bp) were designed (Kong *et al.* 2009). The forward and reverse primers of *COI* are 5′-CTAAGCCATCCTACCTGTG-3′ and 5′-TCAACTCCTCCCTTTCTCG-3′, respectively. Those of *12S* are 5′-ATTAAAGCATAACHCTGAAGATGTTAAGAT-3′ and 5′-AGATAGAAACTGACCTGGAT-3′, respectively. PCR was performed in a 20 μl reaction volume containing 1 μl of 0.2–0.5 g/l DNA template, 1 μl each of 10 μM primer, 0.2 μl of 5 U/μl LA Taq (Takara, Dalian, China), 2 μl of 10 × LA Taq Buffer II (Mg2+ Plus), 3.2 μl of 2.5 Mm dNTP Mixture, and 12.6 μl of sterile distilled water. The PCR cycling protocol included an initial denaturation at 95°C for 3 min, followed by 35 cycles of denaturation at 95°C for 30 s, annealing at 48°C for 40 s, and elongation at 68°C for 1–2 min, with a final extension at 72°C for 10 min. The PCR products were detected in 1.0% agarose gels, and then were used directly as templates for cycle sequencing reactions with an ABI 3730 DNA sequencer (Applied Biosystems, USA). The obtained sequences have been submitted to GenBank under accession numbers No. MK838469 to No. MK838480. Other sequences of *C. joyneri* (*COI*: KF979127; *12S rRNA*: LC049621), *Paraplagusia bilineata* (*COI*, *12S rRNA*: NC_023227), and *P. blochii* (*COI*, *12S rRNA*: NC_023228) were downloaded from GenBank (https://www.ncbi.nlm.nih.gov/). Other northwestern Pacific species of *Cynoglossus* featuring three ocular-side lateral lines and for which sequence data were available were included in the analysis of sequence data. Sequences were aligned using MAFFT v.7 (Katoh & Standley 2013) and then concatenated into a single alignment within Geneious 11.1.5 (Kearse *et al*. 2012). The alignment was partitioned and analyzed using IQ-TREE v.2.2.0 (Chernomor *et al*. 2016; Minh *et al*. 2020), which designated two partitions for the dataset: the first including the first, second, and third codon position for *COI* (SYM+G4) and the second for *12s rRNA* (HKY+F+G4). Ten independent tree searches were conducted with *P. blochii* serving as the root.

Results

Comparisons of morphological characters between lectotypes of *C. joyneri* and *C. lighti*

A total of 28 morphological features, some of which are evident in Figures 1 and 4, were compared between lectotypes of *C. joyneri* and *C. lighti* (Table 5), including eight meristic, 17 morphometric, and three descriptive characters. Shape of the anterior snout, which was available only for the lectotype of *C. lighti*, was also examined. The anterior snout and mouth of the lectotype of *C. joyneri* are deformed (Figs. 1A, 4A). Therefore, shape of the snout and the associated PHE value could not be accurately quantified for the lectotype of *C. joyneri*. Although the rostral hook of this specimen does not reach the vertical at the anterior margin of the lower eye, this feature is obviously damaged and the character PHE could not be quantitatively compared between this specimen and that of the lectotype of *C. lighti*. Thus, this character could only be compared between the lectotypes using a verbal (qualitative) description. Additionally, because of long-term preservation effects, four descriptive color characters could not be observed very well on the lectotypes. These four characters also were not analyzed in comparisons of these specimens. To evaluate the taxonomic status of *C. lighti*, we compared 26 meristic, morphometric, and descriptive characters examined in previous studies of cynoglossid tonguefishes with corresponding features of tongue soles identified in this study as *C. joyneri* (Tables 1–6).

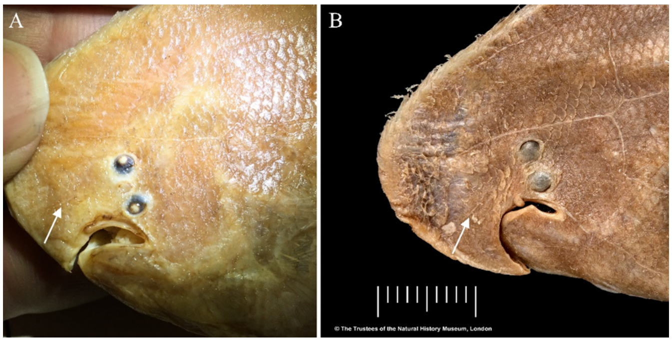

FIGURE 4. Close-up photographs of heads of lectotypes of: A) *Cynoglossus joyneri*; and B) *Cynoglossus lighti*. Preorbital lateral lines indicated by arrows. Photos by J. Maclaine and K. Webb (Natural History Museum, London).

Data appearing in parentheses in this section are for features of *C. joyneri* (listed first) compared with those of *C. lighti*. Among 28 morphological features examined, only values for BD (27.5% of SL vs. 23.1% of SL), SNL (34.7% of HL vs. 40.1% of HL), DSM (41.0% of HL vs. 51.6% of HL), AMO (60.2% of SL vs. 27.5% of HL) and PHE (not reaching vs. reaching anterior margin of lower eye) were obviously different between the two lectotypes. The smaller values noted for measurements of SNL/HL and DSM/HL in the lectotype of *C. joyneri* compared with corresponding values for the lectotype of *C. lighti* likely reflect the damaged condition of the snout region of the lectotype of *C. joyneri* rather than any differences in these features between these nominal species. Fifteen other characters, including DFR (110 vs. 109), MLL scales (80 vs. 73), DMLL scales (13 vs. 12), HW/HL (1.1 vs. 1.0), and LED (6.0% of HL vs. 7.3% of HL), were similar for the two lectotypes. Seven other features were identical or nearly identical between lectotypes. Also, both lectotypes possess a preorbital lateral line (Table 5; Figs. 1 & 4).

We then compared these results with those (Table 5) of the three groups of specimens sorted by features of their BD and PHE. The first group featured BD measurements ranging between 27.5–27.9% of SL, and PHE values ranging from 1.2–3.2 mm. Measurements of both features, including those of three specimens collected from Japanese (type locality of *C. joyneri*) and Chinese waters (Table 5, Fig. 5A), are consistent with corresponding features observed in the lectotype of *C. joyneri*. Comparisons of 23 other characters of this first group of specimens with those of the lectotype of *C. joyneri* showed that 22 of 23 characters of this first group were the same as or similar to those observed for the lectotype of *C. joyneri*. For example, these specimens featured a preorbital line, a feature also present on the lectotype of *C. joyneri*. The meristic and morphometric characters with minimum similarity between this first group and those of the lectotype of *C. joyneri* were DFR (106–109 vs. 110) and DSM/HL (43.0–57.7% vs. 41.0%), respectively. Only the character AMO/HL (42.5–48.0% vs. 60.2%) was significantly different between the lectotype and members of the first group (Table 5).

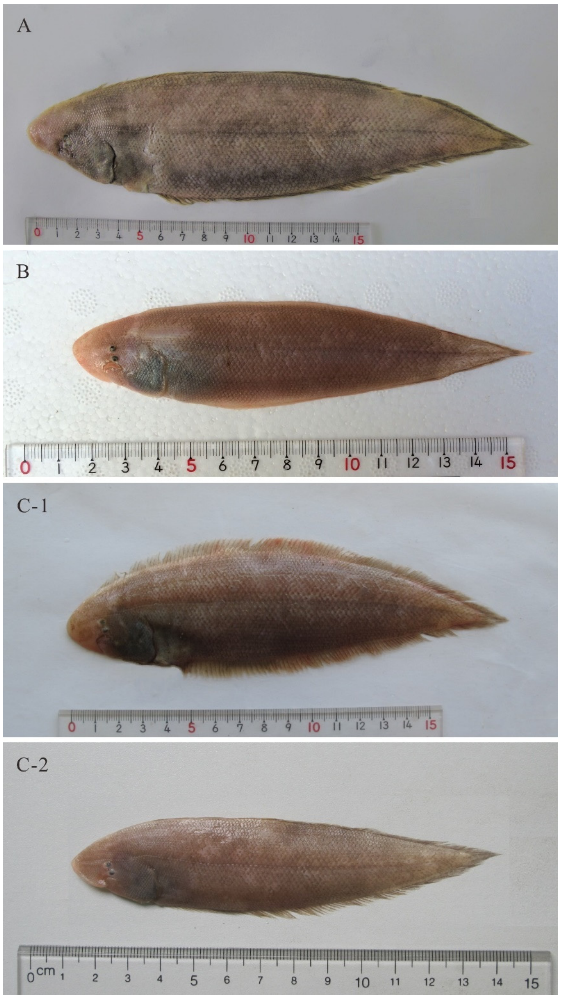

FIGURE 5. Photographs of specimens representing the three groups of tongue soles identified in this study. A) First group featuring wider body and shorter rostral hook. B) Second group featuring narrower body and longer rostral hook. C) Third group: C-1) featuring wider body and longer rostral hook; C-2) featuring narrower body and shorter rostral hook. Photos: A and C-1 by H.-R. Luo; B and C-2 by X.-Y. Kong.

The second group included 26 specimens collected from Chinese waters (type locality of *C. lighti*) that featured body depths ranging from 20.5–23.0% of SL and PHE values of -1.8–0.0 mm. The body depth values are similar to that of the lectotype of *C. lighti* (Table 5, Fig. 5B). Of 24 characters compared between members of the second group and the lectotype of *C. lighti*, ranges for 22 characters of the second group were the same as or included those of the lectotype (Table 5). Differences were found in two descriptive characters: shape of the anterior snout (slightly pointed or slightly rounded vs. pointed in lectotype) and presence or absence of a preorbital line in the second group (vs. presence in the lectotype). Values for two morphometric characters, IOW/HL (3.8–6.9% vs. 2.8%) and HW/HL (1.0–1.2 vs. 1.0), were most similar between members of the second group and the lectotype of *C. lighti*. None of the 24 characters examined were significantly different between those observed in the second group and those of the lectotype (Table 5).

The third group included 109 individuals collected from Japanese and Chinese waters. These specimens featured diagnostic characters different from those of the lectotypes of both *C. joyneri* and *C. lighti* (Table 5; Fig. 5C–1, 5C–2). For this third group of specimens, 30 morphological characters were compared between them and those of the first and second groups (Table 5). Results of comparisons for BD/SL and PHE among the three groups showed that values of BD/SL were continuous and overlapping among members of the three groups (27.5–27.9% in group one, 20.5–23.0% in group two, and 20.9–26.8% in group three). Likewise, values of PHE (1.2–3.2 mm in group one, (-1.8)– 0.0 mm in group two, and (-1.8)–2.9 mm in group three) were also continuous and overlapping among members of these three groups (Table 5). For 28 of the morphological characters examined, 21 characters in the third group were the same as or included within ranges measured in the other two groups (Table 5). These overlapping features comprised seven meristic and 14 morphological characters, including four pigmentation features. Ranges of values for seven other characters in the third group were large and overlapped those in the first and second groups. Examples of features with large overlaps are evident in the percentages of SNL/HL (41.6–48.2%, 39.1–49.8% and 34.3–47.8% for groups one to three, respectively) and UHL/SL (13.4–14.3%, 10.0–20.2% and 10.4–15.4%, for groups one to three, respectively).

To further understand the amount of inclusion and the large overlap in meristic features between specimens of the three groups, frequency distributions of DFR, AFR, TV, MLL, and DMLL, especially, were examined (Table 6). These results revealed that for each of these characters, the ranges in frequency distributions for the three groups overlapped extensively, and modal values of meristic features for each group were the same or very similar (Tables 5–6).

Therefore, measurements for all morphological characters compared among the three groups of tongue soles representing specimens collected over a broad distribution, and also including the lectotypes of *C. joyneri* and *C. lighti*, were the same as, or nearly identical, or overlapped extensively. Exceptional values were those of AMO (42.5–48.0% vs. 60.2%) when compared between the first group (three specimens) and the lectotype of *C. joyneri*. However, the range of AMO values in the third group encompassed that of both the first group and the lectotype of *C. joyneri* (Table 5), which indicates the range of variation in AMO is fairly large compared with the range in values observed for other features. None of the morphological characters for specimens examined in this study, including those of the lectotypes of *C. joyneri* and *C. lighti,* have values that would reflect interspecific differences among any of the specimens.

All tree searches of *COI* (504 bp) and *12S* (895 bp) fragments resulted in a single optimal topology with slightly different branch lengths. The most optimal tree had an ln L = -4701.099. In this tree, all samples identified as *C. joyneri* were recovered in a clade with minimal terminal branch lengths (Fig. 6). This clade of *C. joyneri* was recovered sister to a clade of *C. ochiaii*, *C. nanhaiensis*, and *C. nigropinnatus*. Based on these results, all representative specimens featuring either slightly pointed or slightly rounded snouts, and with a preorbital line either present or absent, are the same species. None of the genetic variation observed in these sequences is indicative of interspecific differences (Fig. 6).

Analyses of both morphological features and molecular markers support the conclusion that specimens partitioned into three groups in this study, as well as, the lectotypes of *C. joyneri* and *C. lighti*, are conspecific. These results offer the opportunity to re-describe *C. joyneri* based on a large series of specimens.

Redescription of *Cynoglossus joyneri* Günther, 1878

Figs. 1, 4–5; Tables 5–6

Cynoglossus joyneri Günther 1878:486; Otaki 1896:421; Jordan & Starks 1907:241; Wu 1932:154; Fowler 1934:216; Chabanaud 1951:269; Chyung 1954:487; Zheng 1955:301; Zheng 1962:1011; Ochiai 1963:88; Zhang & Wang 1963:542; Cheng & Weng 1965:100; Menon 1977:46; Miao 1984:559; Shen 1984:140; Lu & Wu 1986:337; Shen *et al*. 1993:579; Kim & Choi 1994:805; Li & Wang 1995:361; Cheng 1997:463; Munroe 2000:646; Yamada 2000:1391; Ho & Shao 2011:62; Shen 2011:765; Kottelat 2013:466; Yamada & Yagishita 2013:1696; Fricke *et al*. 2017:84; Zhou *et al*. 2017:847.

Cynoglossus (*Areliscus*) *lighti* Norman 1925:270; Wu 1932:155; Chabanaud 1951:270; Kamohara 1953:9; Zheng 1955:300;

Ochiai 1963:90; Cheng & Weng 1965:101; Liu & Qin 1987:441; Li & Wang 1995:363; Cheng 1997:464; Yamada 2000:1391; Yamada & Yagishita 2013:1696.

Areliscus tenuis Oshima 1927:201.

Trulla lighti. Fowler 1934:216.

Cynoglossus tshusanensis Chabanaud 1951:270.

Areliscus joyneri. Chyung 1954:487; Matsubara 1955:1286; Tanaka 1955:125.

Lectotype (Figs. 1, 4): BMNH 1878.4.15.94; Tokyo, Japan.

Diagnosis: *Cynoglossus joyneri* is a medium-sized tongue sole (≤ 333 mm SL) distinguished from congeners by the following combination of characters: caudal-fin rays 10; dorsal-fin rays 98–117; anal-fin rays 79–92; total vertebrae 49–54 (abdominal vertebrae 9; caudal vertebrae 40–45); middle lateral-line scales 62–80; scale rows between dorsolateral and midlateral lines 9–13; eyes small, diameter 4.1–11.5% of HL; head length (18.6–24.7% of SL) equal to or slightly longer than head width (17.6–24.9% of SL); two nostrils on each side of snout; three complete ocular-side lateral lines, no lateral line on blind side; ctenoid scales on both sides of body; ocular side of body and fins uniformly reddish-brown.

Description: Data for meristic and morphometric features are presented in Tables 5–6. Dorsal-fin rays 98–117; anal-fin rays 79–92; pelvic-fin rays 4; caudal-fin rays 10; total vertebrae 49–54 (abdominal vertebrae 9, caudal vertebrae 40–45); middle lateral-line scales 62–80; scale rows between dorsolateral and midlateral lines 9–13.

Body moderately elongate, strongly compressed laterally; body depth (BD) 20.5–27.9% of SL, maximum body depth located at point between verticals through anus and body midpoint. Head relatively long (HL= 18.6–24.7% of SL) and wide (HW= 17.6–24.9% of SL). Head width, slightly subequal to slightly larger than, head length (HW/HL= 0.9–1.2). Snout slightly rounded or bluntly pointed, snout length (SNL) 34.3–49.8% of HL; snout shorter than postorbital head length (POL= 43.5–65.3% of HL). Posterior tip of rostral hook not reaching, reaching, or extending slightly beyond, vertical through anterior margin of lower eye (PHE). Eyes subequal, anterior margin of upper eye slightly in advance of anterior margin of lower eye; eyes not contiguous, separated by narrow, nearly flat, interorbital space (IOW= 2.2–7.4% of HL), with 1–2 rows of minute ctenoid scales at its narrowest point. Mouth sub-terminal; length of upper jaw (UJL) 15.1–27.5% of HL; distance between angle of mouth to opercular margin (AMO) variable (39.1–60.2% of HL); ocular-side mouth cleft nearly straight, blind-side mouth cleft more semi-circular. Angle of mouth located about at vertical through middle of head, extending posteriorly below or slightly beyond posterior margin of lower eye, sometimes lower jaw extending beyond posterior margin of lower eye by distance almost equal to one eye diameter. Lips on both sides smooth without fringed papillae. Teeth absent on ocular-side jaws; blind-side jaws with narrow band of small, villiform teeth. Upper head lobe (UHW= 10.0–20.2% of SL) wider than width of lower head lobe (LHW= 6.9–11.7% of SL). Preanal length (PAL) 20.2–28.0% of SL. Posterior margin of opercle with distinct indentation at, or near, its midpoint. Gill membranes united ventrally; free from isthmus. Gill arches without gillrakers.

Dorsal-, anal-, pelvic-, and caudal-fin rays soft, unbranched. Dorsal-fin origin near tip of snout. Anal-fin origin just posterior to vent. Unpaired (blind side) pelvic fin with membranous connection to first (anteriormost) anal-fin ray. Caudal fin pointed, its length (CFL) 20.5–27.9% of HL. Three lateral lines on ocular side; middle lateral line nearly straight along its length and ending at base of caudal fin or extending onto caudal-fin base by not more than 2 scales; dorsal and ventral lateral lines extending posteriorly along dorsal and ventral contours of body and usually ending at base of posteriormost 4–10 fin-rays of dorsal and anal fins, sometimes extending almost to distal ends of dorsal- and anal-fin rays. Dorsal and middle lateral lines connected by supraorbital commissure. Preorbital line on anterior snout present or absent. Cephalodorsal line well developed along anterior margin of snout and ending at posterior tip of rostral hook, connected to supraorbital line and preorbital line. Preopercular and mandibulo-opercular lines separated from each other; mandibulo-opercular line ending at or near posterior margin of opercle. No lateral line on blind side. Scales ctenoid on both sides of body, including those on lateral lines, except cycloid scales present anteriorly on blind side of snout. Genital papilla a short tube connected to first anal-fin ray.

Pigmentation: Background coloration of ocular side variable, either unevenly or uniformly brown, yellowish brown, reddish brown, or grayish brown. Fins uniformly pigmented with same color as, or with slightly lighter or darker color than, that on body. Oral cavity without conspicuous pigmentation. Outer surfaces of opercle on both sides of head with corresponding coloration as that on each side of body, respectively. Inner surfaces of both opercles dusky or dark brown. Skin behind gills on either side more or less darkly pigmented. Isthmus white. Peritoneum on both sides of body darkly pigmented, usually a dark brown. Blind side of body white.

Distribution: *Cynoglossus joyneri* is widely distributed in coastal marine waters of the northwestern Pacific Ocean, including the southern Sea of Japan, the Yellow and Bohai seas, East China Sea and South China Sea (Günther 1878; Norman 1925; Wu 1932; Chabanaud 1951; Kamohara 1953; Ochiai 1963; Cheng & Weng 1965; Ochiai 1984; Kim & Choi 1994; Kim *et al*. 2005; Li & Wang 1995; Munroe 2000; Choi *et al*. 2002; Shen 2011; Yamada & Yagishita 2013; Munroe 2021).

In Japanese waters, *C. joyneri* occurs in coastal waters of the southern Sea of Japan and in Pacific coastal waters from Honshu to Kyushu. It is a common species reported from many localities, including Wakasa Bay, Suruga Bay, Osaka Bay, Seto Inland Sea, and off Kochi (Günther 1878; Kamohara 1953; Ochiai 1963, 1984; Minami & Tanaka 1992; Baeck *et al*. 2011; Yamada 2000, 2002; Yamada & Yagishita 2013).

Off South Korea, this species has been reported from various locations in the southern Sea of Japan, the Yellow Sea, and in the East China Sea off southern Korea (Lee 1989; Kim & Choi 1994; Hwang *et al*. 1998; Choi *et al*. 2002; Baeck & Huh 2004; Lee *et al*. 2010; Kwak *et al*. 2012; Yoon *et al*. 2013).

In Chinese waters (Fig. 2), this species is known from a variety of locations (Norman 1925; Wu 1932; Chabanaud 1951; Li & Wang 1995; Munroe 2021), including the Bohai Sea (Zheng 1962; Shuozeng 1995a,b), coastal waters of the Yellow Sea (Zheng 1955; Gu *et al*. 2009), the East China Sea, and the South China Sea (Zheng 1962; Zhang & Wang 1963; Munroe 2000; Yamamoto *et al*. 2009), including the Yangtze River estuary (Ruijing *et al*. 2010, Jiang *et al*. 2014; Song *et al*. 2015). It also occurs at Hong Kong (Ni & Kwok 1999, and literature cited therein) and Hainan Island (Lu & Wu 1986; this study).

Cynoglossus joyneri is also known from Taiwan (Oshima 1927; Wu 1932; Chen & Weng 1965; Shen 1984; Shen *et al*. 1993; Shao *et al*. 2008; Shen 2011; Shao 2023). Reports of this species from off the south coast of Viet Nam (Nguyen & Nguyen 2006) and Cambodia (based on museum specimens accessed through the FishNet2 portal) require further verification.

Cynoglossus joyneri lives on the continental shelf at an approximate depth range of 8–58 m (Shuozeng 1995b; Jiang *et al*. 2014; citations in Munroe 2021).

Remarks. Taxonomic status of *C. lighti* in previous works and comparison with the features of *C. joyneri.* Previous studies (Norman 1925; Wu 1932; Fowler 1934; Chabanaud 1951; Kamohara 1953; Zheng 1955; Ochiai 1963; Cheng & Weng 1965; Li & Wang 1995; Cheng 1997; Yamada 2000; Yamada & Yagishita 2013) considered *C. lighti* to be distinct from *C. joyneri*. An assortment of nine morphological characters (Tables 1–4), including MLL, DMLL, BD/SL, HL/SL, HL/HW, PHE, size of lower eye relative to snout, snout shape (pointed or rounded), and presence/absence of a preorbital lateral line, were variously regarded in these studies as diagnostic for distinguishing *C. lighti* from *C. joyneri*. Our comparisons (Table 5) revealed that values for 20/25 features examined, including eight of nine characters purported to be diagnostic for these two species in previous studies, varied only slightly and this amount of variation is indicative of intraspecific differences.

Features differing significantly between those in our study versus those in previously published works (Table 5 compared with Tables 1–4) are the MLL counts recorded by Chabanaud (1951), and values of five other characters (MLL, CFR, BD/SL, HL/SL, and SNL/HL) reported in different studies (Günther 1878; Fowler 1934; Chabanaud 1951; Zhang & Wang 1963; Menon 1977; Kim & Choi 1994). Possible explanations for variation between our results and those reported in historical literature arise from differences in how MLL scales were counted, especially with respect to beginning and end points for this count. Among previous records of MLL values for *C. joyneri*, 82–85 scales were reported for the two syntypes in Chabanaud's (1951) work, whereas 85 scales (2 syntypes) and 78–86 scales (82 non-type specimens) were noted in the works of Günther (1878) and Kim & Choi (1994), respectively. In this study, and in most previous studies (which included a total of more than 321 specimens), MLL counts of 62–80 scales are reported for *C. joyneri* (Table 5). Using the third method of counting MLL scales, we counted 80 MLL scales based on a photograph of the lectotype of *C. joyneri*. This count was similar to or included in the values reported for *C. joyneri* in the works of Chabanaud (1951), Günther (1878), and Kim & Choi (1994). Thus, the variation in reported counts of MLL for *C. joyneri* between our study and these others likely results from different counting methods for this feature, rather than from any actual differences.

Chabanaud (1951) recorded counts of 90–92 MLL scales for the lectotype and paralectotypes of *C. lighti* (Table 3), which is distinctively different from the MLL counts (73, 84, and 79) we estimated using the three different methods for counting MLL scales described above. Chabanaud's counts also differed significantly from the MLL values (75–78) reported for *C. lighti* in the original description (Norman 1925; see Table 1). Given such disparity in the MLL counts between that of Chabanaud's study (1951) and those reported in other studies, it is uncertain how Chabanaud counted MLL scales. Possibly, the counts he reported were in error.

TABLE 5. Selected morphological data for *C. joyneri* (including three groups of specimens defined in this study), *C. tenuis* and *C. tshusanensis* compared between this study and two previous works. Abbreviations defined in text. Characters 1–6 are percent of SL; characters 8–15 are percent of Head Length.

	Oshima (1927)	**Chabanaud (1951)**			**This Study**						
Character	***tenuis* HT**	***tshusanensis* (N=3)**	***joyneri* (N=2)**	***lighti* (N=4)**	***tshusanensis* HT**	***joyneri*[1] (N=498)**	***joyneri* LT**	***lighti* LT**	**First group (N=3)**	**Second group (N=26)**	**Third group (N=109)**
CFR	-	8–10	10	10	10	10	10	10	10	10	10
PFR	4	4	4	4	4	4	4	4	4	4	4
DFR	109	109–113	105–109	112–113	106	98–117	110	109	106–109	101–112	98–115
AFR	82	87–89	85–86	85–87	86	79–92	88	88	80–89	81–89	79–92
AV	-	-	-	-	9	9	9	9	9	9	9
TV	-	-	-	-	54	49–54	51	51	51	51–53	49–54
MLL	-	82–85	82–85	90–92	77	62–80	80	73	68–80	67–80	65–79
DMLL	12	11–12	13	12	11	9–13	13	12	10–12	10–12	10–13
Scales	CT–CT[2]	CT–CT	CT–CT	CT–CT	CT–CT	CT–CT	CT–CT	CT–CT	CT–CT	CT–CT	CT–CT
SL (mm)	170	75–88	223–228	107–171	86.3	51.7–333	232.6	172.0	154.9–212.9	67.7–195.4	51.7–267.4
HL (mm)	34	17–21	19–20	20–23	20.1	13.5–53.9	44.9	35.7	35.8–46.1	13.5–42.1	13.7–53.9
PHE (mm)	-	-	-	-	-	-	-	-	1.2–3.2	(–1.8)–0.0	(–1.8)–2.9
1. BD	22	21–23	28–30	23–25	23.1	20.5–27.9	27.5	23.1	27.5–27.9	20.5–23.0	20.9–26.8
2. HL	20	21–23	19–20	20–23	23.3	18.6–24.7	19.3	20.8	21.7–23.4	19.9–23.8	18.6–24.7
3. HW	-	-	-	-	20.6	17.6–24.9	22.1	21.5	20.8–23.6	18.9–21.8	17.6–24.9

...Continued on the next page

TABLE 5. (Continued)

	Oshima (1927)	Chabanaud (1951)			This Study						
Character	***tenuis* HT**	***tshusanensis* (N=3)**	***joyneri* (N=2)**	***lighti* (N=4)**	***tshusanensis* HT**	***joyneri*[1] (N=498)**	***joyneri* LT**	***lighti* LT**	**First group (N=3)**	**Second group (N=26)**	**Third group (N=109)**
4. UHL	-	-	-	-	11.9	10.0–20.2	12.2	11.9	13.4–14.3	10.0–20.2	10.4–15.4
5. LHL	-	-	-	-	11.0	6.9–11.7	10.7	7.3	9.0–10.8	8.1–10.2	6.9–11.7
6. PAL	-	-	-	-	25.0	20.2–28.0	20.5	21.5	23.1–25.6	21.2–26.5	20.2–28.0
7. HW/HL	-	-	-	-	0.9	0.9–1.2	1.1	1.0	1.0–1.1	1.0–1.2	0.9–1.2
8. SNL	37.6	-	-	-	43.3	34.3–49.8	34.7	40.1	41.6–48.2	39.1–49.8	34.3–47.8
9. LED	9.9	8–9	5	7–8	8.5	4.1–11.5	6.0	7.3	6.4–6.5	4.8–8.9	4.1–11.5
10. IOW	6.3	Appr. 0	3–4	≤2	2.8	2.2–7.4	3.6	2.8	3.9–5.9	3.8–6.9	2.2–7.4
11. POL	-	47–49	53–54	44–48	49.2	43.5–65.3	56.1	48.1	49.7–52.0	44.4–61.5	43.5–65.3
12. UJL	-	-	-	-	19.9	15.1–27.5	19.8	18.8	17.8–22.9	15.8–27.5	15.1–25.2
13. DSM	-	-	-	-	-	41.0–61.1	41.0	51.6	43.0–57.7	51.6–61.1	42.8–60.1
14. AMO	-	-	-	-	-	39.1–60.2	60.2	48.5	42.5–48.0	40.7–50.9	39.1–60.0
15. CFL	-	38–42	35–40	37–40	25.0	20.5–27.9	36.3	23.1	27.5–27.9	20.5–23.0	20.9–26.8
PL	?	?	?	?	?	Present/ Absent	Present	Present	Present	Present/ Absent	Present/ Absent

[1]Morphological characters of *C. joyneri* based on data of 498+ specimens combined from this study and previous works. [2]CT–CT represents ctenoid scales on ocular and blind sides of body (excluding cycloid scales anteriorly on blind side of snout). HT= Holotype; LT= Lectotype.

TABLE 6. Frequency distributions of five meristic features for three groups of specimens collected in Chinese waters featuring similar counts to those of *C. joyneri*.

Dorsal-Fin Rays

Group	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	N
First	–	–	–	–	–	–	–	–	1	1	–	1	–	–	–	–	–	–	3
Second	–	–	–	1	–	2	1	3	2	2	6	2	4	2	1	–	–	–	26
Third	1	1	2	3	5	9	8	6	6	6	11	15	13	4	7	5	5	1	108

Anal-Fin rays

Group	79	80	81	82	83	84	85	86	87	88	89	90	91	92	N
First	–	1	–	1	–	–	–	0	–	–	1	–	–	–	3
Second	–	–	1	–	2	3	2	6	4	3	5	–	–	–	26
Third	5	6	1	7	14	13	17	5	12	5	10	7	5	1	108

Scales in Middle Lateral-Line (MLL)

Group	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	N
First	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	1	3
Second	–	–	2	–	4	1	3	1	3	3	–	4	1	1	2	1	26
Third	2	2	–	3	6	8	11	14	8	8	14	12	4	9	7	–	108

Scales Between Dorsal and MidLateral Lines (DMLL)						Total Vertebrae							
Group	10	11	12	13	N	Group	49	50	51	52	53	54	N
First	1	1	1	–	3	First	–	–	1	–	–	–	1
Second	5	16	5	–	26	Second	–	–	1	–	1	–	2
Third	13	46	42	7	108	Third	1	1	2	3	2	1	10

Counts for CFR of *C. joyneri* have also varied in previous studies (Tables 1, 3), ranging from 8 to 11 fin rays (Liu & Qin 1987; Li & Wang 1995). In these different studies, CFR counts have varied from 9–10 fin rays (based on 144 specimens), 8–10 (96 specimens), 10 (63 specimens), 8–11 (25 specimens), 10–11 (14 specimens), 8–9 (2 specimens) and 8 (1 specimen), respectively (Tables 1, 3, 5). We counted 10 CFR for the lectotypes of both *C. joyneri* and *C. lighti*, and also for 133/138 non-type specimens examined in this study. Considering the symmetrical arrangement of caudal-fin rays in members of the Cynoglossidae and the relative conservative nature of this count, as well as the fact that 10 and 9–10 CFR were counted in our study and most previous studies, respectively, we consider 10 CFR to be the typical count for this feature in *C. joyneri*.

Values for some morphometric features have also varied between studies. For example, HL measurements expressed as a percentage of SL for *C. joyneri* were 18.6–24.7% based on data combined from more than 473 specimens included in our study and previous works where identifications were deemed reliable (Tables 4–5). These values differ from those (HL= 18.9–40.0% of SL) recorded by Menon (1977) based on nine specimens, including the holotype of *C. tshusanensis* (see Table 2). Likewise, the range of values for BD/SL (20.5–27.9%) in the present study is much lower compared with that (20.3–43.6%) reported in Menon (1977). We can offer no explanation for such differences in head length and body depth measurements between those in our study and most previous literature compared with the values for these features listed in Menon (1977). Menon did not provide data for individual fish examined in his study, so it is impossible to identify the particular specimen(s) responsible for these higher values. Therefore, we consider the HL/SL and BD/SL measurements of 40.0% and 43.6% reported in Menon (1977) as extreme outliers or possibly as erroneous altogether.

Lastly, values of SNL/HL ranged from 34.3–49.8% of HL in our work (Table 5). This range of values for *C. joyneri* is larger than that (27.8%) appearing in Lu & Wu (1986) based on a single specimen (Table 2). We are unsure how this feature was measured by Lu & Wu, and thus, we consider their estimate of SNL/HL as an outlier value.

Several previous studies have examined molecular variation in specimens identified as *C. joyneri* and/or *C. lighti*. However, it is difficult to compare our results with those of these other studies (Xu *et al*. 2008; Liu *et al*. 2010; Miao *et al*. 2013; Song *et al*. 2015; Wang *et al*. 2018). For example, Xu *et al*. (2008) and Liu *et al*. (2010) used different markers, such as *16S r*RNA, ITS1 and *Cytb*. Liu *et al*. (2010) reported that *C. joyneri* and *C. lighti* could be possible synonyms but made no statement on the impact of this result regarding the taxonomic status of these nominal species. Song *et al*. (2015) also found only minor differences (0.007) between specimens they identified as *C. joyneri* and *C. lighti*, but made no statement on the impact of this result on taxonomic status. Also, these authors (Song *et al*. 2015) did not submit sequences to GenBank so it is impossible to compare their sequences with those obtained in our study. Other studies, such as that by Wang *et al*. (2018), used the same *COI* marker as that in our study and concluded that they could not separate *C. joyneri* and *C. lighti* using this marker. Again, these authors did not elaborate on the taxonomic impact of this finding. Also, these authors did not provide morphological data for their specimens, so it is uncertain what criteria they used to identify their fish.

Values for all eight morphological characters purportedly diagnostic for distinguishing *C. lighti* from *C. joyneri* in previous studies demonstrated no interspecific differences between these nominal species when a large series of specimens were examined. Additionally, data from several molecular studies, including our study, and using a variety of different markers, also demonstrate that only a single species is represented among the material examined in these studies. Thus, the overall morphological and genetic similarities between both nominal species strongly support the hypothesis that these specimens are conspecific, and that *C. lighti* should be regarded as a junior subjective synonym of *C. joyneri*.

Taxonomic status of *C. tenuis* and *C. tshusanensis*. As mentioned above, previous works have regarded *C. tenuis* as a junior subjective synonym of either *C. joyneri* or *C. lighti*, and *C. tshusanensis* has been considered a junior subjective synonym of *C. joyneri*. After checking the works wherein *C. tenuis* was regarded as a junior synonym of *C. lighti*, we found that all also treated *C. lighti* and *C. joyneri* as valid species (Wu 1932; Kamohara 1953; Zheng 1955; Ochiai 1963; Cheng & Weng 1965; Cheng 1997). According to our conclusion that *C. lighti* and *C. joyneri* are conspecific, only comparisons between *C. joyneri* and *C. tenuis* were explored further in our study.

Because the holotype of *C. tenuis* has been lost, we relied on meristic, morphometric, and descriptive information about morphological features of *C. tenuis* reported in the original description to compare with those of *C. joyneri*. Twelve features of *C. tenuis* from the original description (Table 5) were compared with those of *C. joyneri*, including two characters, BD/SL and type of scales on both sides of the body. Both characters were regarded by Oshima (1927) as being diagnostic for distinguishing these two nominal species. All 12 characters of *C. tenuis* were the same as or included in the ranges of characters observed in *C. joyneri* (Table 5). These results support the opinion previously proposed by Kamohara (1953), Ochiai (1963), Menon (1977) and others (Lindberg & Fedorov 1993; Ho & Shao 2011; Kottelat 2013) that *C. tenuis* (Oshima) is a junior synonym of *C. joyneri*.

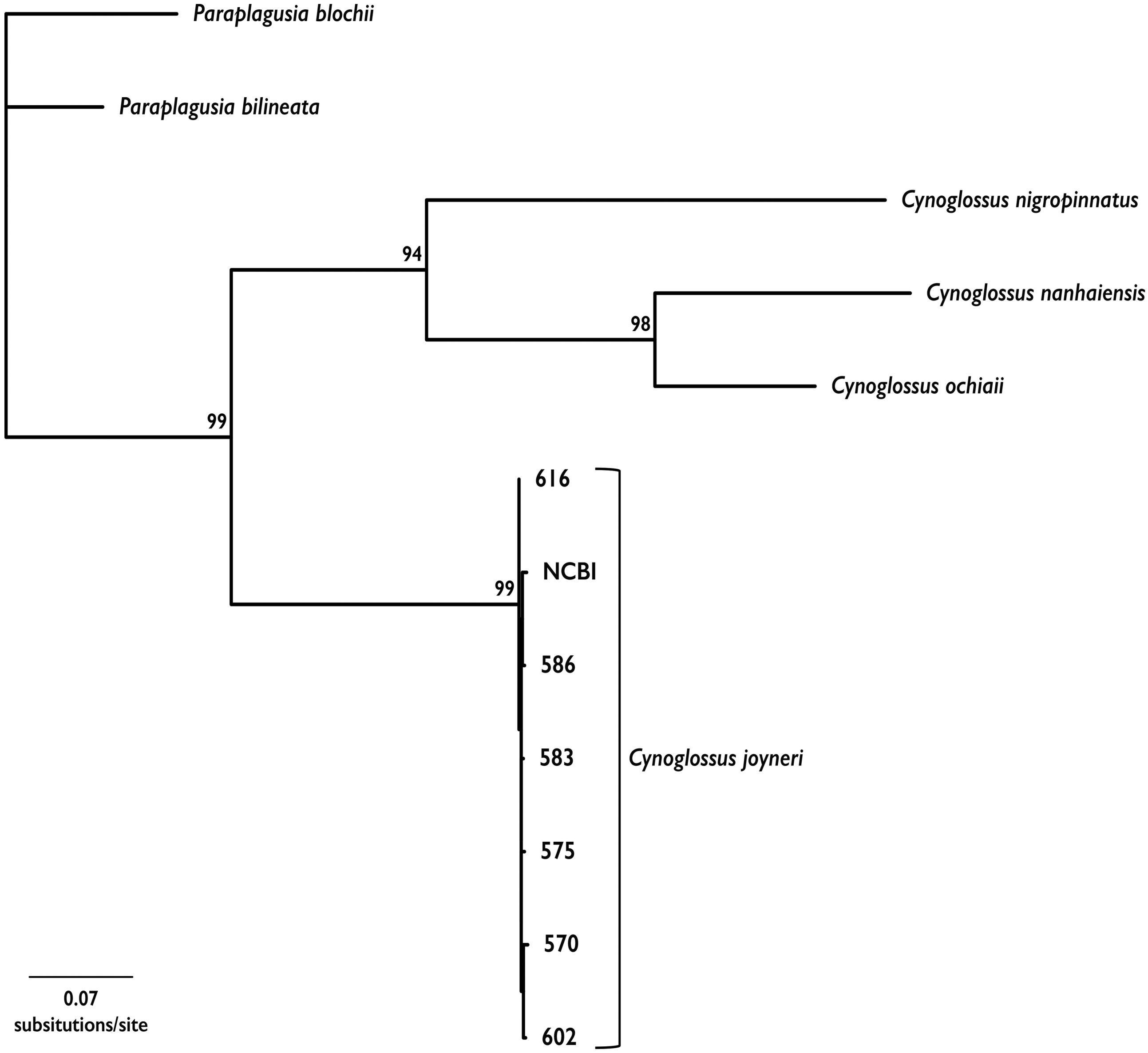

FIGURE 6. Maximum-likelihood (ML) phylogeny of selected species of *Cynoglossus* from the northwestern Pacific Ocean based on 12S rRNA and *COI* gene fragments. Taxon listed as "NCBI" indicates 12S (LC049621) and *COI* (KF979127) gene fragments downloaded from GenBank. Numbers above nodes indicate bootstrap values in percentage (based on 100 replicates). Values below 70% not shown.

For *C. tshusanensis*, Chabanaud (1951) examined 12 morphological features (Table 5) and pointed out that, although similar in many features, this species could be distinguished from *C. joyneri* and *C. lighti* by differences in three meristic characters (AFR, DMLL, and MLL) and six morphometric features (HL/SL, SNL/HL, LED/HL, IOW/HL, POL/HL and BD/SL). We examined the holotype of *C. tshusanensis* and compared 22 of its morphological features with those of *C. joyneri* and *C. lighti* (Table 5). All of these morphological characters overlapped completely or were very similar between *C. tshusanensis* and *C. joyneri* (Table 5), except for the count of MLL. We obtained an MLL count for the holotype of *C. tshusanensis* of 77 scales, which is lower than that (82–85 and 90–92) reported by Chabanaud (1951) in his study of the type specimens of *C. joyneri* and *C. lighti*, respectively (Table 5), but within the range of MLL counts (62–80) we observed for specimens of *C. joyneri*. We regard these differences in MLL counts to be the result of different methods for counting these scales between our study and that employed by Chabanaud (1951). We conclude that these differences do not reflect interspecific differences between nominal species, instead, based on the overall similarity between these nominal species, our results support the view expressed in previous works (Menon 1977; Lindberg & Fedorov 1993; Desoutter *et al*. 2001; Kottelat 2013; Fricke *et al*. 2017) that *C. tshusanensis* is a junior synonym of *C. joyneri*.

Conclusions

After re-examining types of *C. joyneri*, *C. lighti* and *C. tshusanensis*, after analyzing characters from the original description of *C. tenuis*, and after integrating data obtained from more than 496 non-type specimens including our study specimens (Tables 5–6) and those previously reported as *C. joyneri* or *C. lighti* (Tables 1–5), we find that only a single species, *C. joyneri*, is represented among this extensive collection of specimens. This conclusion is supported not only by morphological data but also by molecular sequence data (Fig. 6). Therefore, we conclude that *C. lighti*, *C. tshusanensis* and *C. tenuis* should be regarded as junior subjective synonyms of *C. joyneri*.

Material examined

Cynoglossus joyneri

Japan. Lectotype BMNH 1878.4.15.94, Tokyo; USNM 006122, Niphon; USNM 151796, Shizuoka; USNM 059763, Kochi.

China. Qinhuangdao: Apr 2010, SCSMBC 30578–9 (2), SCSMBC 30645 (1); USNM 085887 (3). Qingdao: Nov 2008: SCSMBC 30580–1 (2); Jul 2015, SCSMBC 30582–97 (16), SCF 201507583 (1). Rizhao: Nov 2009, SCSMBC 30598–600 (3); ASIZB 38175 (1). Lianyungang: May 2010, SCF 201005286 (1); May 2011, SCF 201105002 (1). Lvsi: Oct 2015, SCSMBC 30601–17 (17), SCF 201510602 (1); Apr 2016, SCSMBC 30618–21 (4). Shanghai: Apr 2016, SCSMBC 30622–3 (2); SCSMBC 30628–36 (9); Oct 2015, SCSMBC 30624–7 (4). Zhoushan: Oct 2015, SCSMBC 30637 (1); Apr 2016, SCSMBC 30638–43 (6). Wenling: Oct 2010, SCSMBC 30644 (1); Oct 2015, SCSMBC 30646 (1), SCF 201510575 (1). Wenzhou: Oct 2015, SCSMBC 30647 (1); Apr 2016, SCSMBC 30648–50 (3). Fuzhou: Oct 2015, SCSMBC 30651–5 (5), SCF 201510566 (1), SCF 201510616 (1); USNM 087051 (2). Mawei: Oct 2015, SCSMBC 30656–60 (5). Xiamen: Oct 2015, SCSMBC 30661 (1), SCF 201604570 (1); ASIZB 172026–7 (2). Dongshandao: Oct 2015, SCSMBC 30662–3 (2). Shanwei: Aug 2012, SCF 201208287 (1); Nov 2015, SCF 201511586 (1). Shenzhen: Nov 2015, SCSMBC 30664–6 (3); ASIZB 180063. Zhuhai: Aug 2009, SCSMBC 30667–8 (2); Nov 2009, SCSMBC 30669–73 (5); Nov 2015, SCSMBC 30674 (1). Jiangmen: Mar 2013, SCSMBC 30675–80 (6); no month 2014, SCSMBC 30681 (1); Jun 2016, SCSMBC 30682–5 (4), SCF 201606686–7 (2). Baimajing: Sep 2005, SCSMBC 30686–7 (2). Yantai: ASIZB 38178–80 (3), ASIZB 172030 (1).

C. lighti. China, Lectotype BMNH 1924.12.15.87; Amoy (now Xiamen).

C. tshusanensis. China, Holotype BMNH 1892.12.12.32; Tshusan Archipelago (now known as the Zhoushan Islands), about 30°N, 122°E.

Acknowledgements

We thank S.J. Raredon and J. Clayton (National Museum of Natural History, Smithsonian Institution) and L. Willis (National Systematics Laboratory, NMFS/NOAA, Smithsonian Institution) for their help with specimens and for taking X-ray digital photographs. We appreciate the efforts of J. Maclaine and K. Webb (Vertebrates Division, Natural History Museum, London) in providing photographs of the lectotypes of *C. joyneri* and *C. lighti*, and for assistance in checking morphological characters of these specimens. A. Reft (National Systematics Laboratory) assisted with figure preparation. D. Cole (Smithsonian Institution) drew the map figure. The authors are grateful to E.-Q. Ye and L. Meng (Institute of Zoology of Chinese Academy of Sciences, ASIZB) for providing assistance in managing loans of specimens, and for assisting with taking measurements. We thank M. Girard (National Museum of Natural History, Smithsonian Institution) for providing invaluable advice regarding the analysis of molecular data presented in this study. Comments and suggestions provided by reviewers of an earlier draft improved the manuscript. This study was supported by the National Nature Science Foundation of China (grant numbers 31872570 and 31071890) and the Science and Technology Planning Project of Guangdong Province (2020B1212060058).

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