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Cryptic diversity of the slipper lobster genus *Scyllarides* (Crustacea: Decapoda: Scyllaridae) in the Pacific

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Abstract

Fourteen extant species of slipper lobsters have been described in the genus *Scyllarides*, with six species known from the Indo-Pacific. Previous DNA barcoding of *Scyllarides* phyllosoma larvae collected from the western and central North Pacific revealed two enigmatic types, labeled as *Scyllarides* sp-B and sp-C, which could not be conclusively identified. In this study, mitochondrial COI and 16S rDNA sequences from museum specimens of *Scyllarides* species were examined, revealing that these two types represent previously undescribed species. The lineages most closely related to the *Scyllarides* sp-B and sp-C phyllosoma larvae were *S. squammosus* and *S. deceptor*, respectively, with substantial differentiation. *Scyllarides squammosus* was thought to be distributed in the Indo-Central Pacific, but no larvae of this species were collected in the central North Pacific where *Scyllarides* sp-B larvae were collected. This suggests that the population referred to as *S. squammosus* in the Hawaiian Islands is *Scyllarides* sp-B. Additionally, substantial genetic differentiation was observed between the western and central to eastern Pacific samples of *S. haanii*. These findings not only reveal previously unknown species within the genus *Scyllarides* but also significant genetic differentiation between populations, highlighting the cryptic diversity and the need for further taxonomic revision.

Key words: slipper lobster; *Scyllarides*; DNA barcoding; cryptic species; genetic differentiation

Introduction

Fourteen extant slipper lobster species are described in the genus *Scyllarides* (Holthuis 1991, 1993; Webber and Booth 2007; Chan 2010) (Table 1). These species, all shallow water dwellers, are economically important due to their large adult sizes, making them a substitute for overfished palinurid lobsters. Unlike the butterfly fan lobsters of the genus *Ibacus* and the flathead lobsters of the genus *Thenus*, most *Scyllarides* species inhabit small caves and crevices of complex substrate in shallow coastal waters and are rarely caught by mechanical fishing such as bottom trawling. However, human activities using scuba diving, gill net, and trap have made their stock status vulnerable.

Six *Scyllarides* species are known to occur in the Indo-Pacific region (Table 1). Among these, *S. squammosus* and *S. haanii* are widely distributed in the Indo-Pacific region (Morin and MacDonald 1984; Holthuis 1991; Webber and Booth 2007; Báez et al. 2022). *Scyllarides astori* and *S. roggeveeni* are restricted to the eastern Pacific, while *S. elisabethae* and *S. tridacnophaga* are found exclusively in the Indian Ocean (Holthuis 1991; Webber and Booth 2007).

DNA barcoding using mitochondrial COI and/or 16S rDNA sequences has been applied to identify the species of *Scyllarides* phyllosoma larvae collected in the Pacific, in which mid- to final stage phyllosoma larvae of *S. squammosus* and *S. haanii* were accurately identified, and their morphological characteristics

Table 1. Slipper lobster species in the genus *Scyllarides* and the COI and 16S rDNA sequences available to date.

species	Distribution[§]	GenBank/DDBJ/EMBL accession No.	
		COI	16S
S. aequinoctialis	W Atlantic Ocean	–	–
S. astori	E Pacific Ocean	–	–
S. brasiliensis	W Atlantic Ocean	JX896692–896755[1], KF827966[2]	KF828186[2]
S. deceptor	SW Atlantic Ocean	MF490045[3]	MF490148[3]
S. delfosi	W Atlantic Ocean	–	–
S. elisabethae	W Indian Ocean	KX275387[4], MK113932[5]*	–
S. haanii	Indo-Pacific Ocean	JN701655[6], JN701656[6], MN817127[7], MW699539[8]	JN701690[6], JN701691[6], LC763119[9], MN817127[7]
S. herklotsii	E Atlantic Ocean	FJ174946[10]	FJ174906[10]
S. latus	NE Atlantic Ocean, Mediterranean Sea	FJ174947[10], JF928170–928194[11], JQ306104–306108[12], JQ623990[13], KC107814[14], KC311420–311424[13], KC789434–789453[13]	DQ377974[15], FJ174907[10], KC107814[14]
S. nodifer	NW Atlantic Ocean	JN701657[6], OR612317[16]	JN701692[6], U96088[17], OR612317[16]
S. obtusus	CS Atlantic Ocean	–	–
S. roggeveeni	SE Pacific Ocean	–	–
S. squammosus	Indo-Pacific Ocean	JN701654[6], KX275388[4], KX275389[4], KX373661–373667[18], MK371348–371352[19], MK783265[20], OP379522[21], OP379523[21], OQ891087–891093[22]	JN701689[6], MK783265[20], OK353659–353666[23], OP379972[21], OP379973[21]
S. tridacnophaga	Indian Ocean	–	–
Scyllarides sp-B	CN Pacific Ocean	OK350746–350748[23]	OK353668–353675[23]
Scyllarides sp-C	NW Pacific Ocean	–	OK353667[23]

[1]Rodríguez-Rey et al. (2014), [2]Bracken-Grissom et al. (2014), [3]Mantelatto et al. (2018), [4]Singh et al. (2017), [5]Govender et al. (2019), [6]Yang et al. (2012), [7]Liu et al. (unpublished), [8]Báez et al. (2022), [9]Konishi et al. (2024), [10]Palero et al. (2009), [11]Froufe et al. (2011), [12]Matzen da Silva et al. (2011), [13]Keskin and Atar (2013), [14]Shen et al. (2013), [15]Cannas et al. (unpublished), [16]Baeza et al. (unpublished), [17]Tam and Kornfield (1998), [18]Palero et al. (2016), [19]Woodings, et al. (2019), [20]Liu et al. (2019), [21]Hidaka et al. (2022), [22]Chow and Yanagimoto (unpublished), [23]Chow et al. (2022). [§]CN: central north, CS: central south, E: eastern, NE: northeast, NW: northwest, SE: southeast, SW: southwest. *not used due to short sequence.

were documented (Palero et al. 2016; Chow et al. 2022; Konishi et al. 2024). Chow et al. (2022) detected two types of *Scyllarides* phyllosoma larvae (designated as *Scyllarides* sp-B and sp-C) collected from the central and western North Pacific, respectively, for which no highly homologous nucleotide sequence was found in the database. The nucleotide sequences of *S. astori*, *S. roggeveeni*, and *S. tridacnophaga* remain undetermined (Table 1), suggesting that *Scyllarides* sp-B and sp-C might be these species. However, morphology of the mid- to final stage *S. astori* phyllosoma larvae (Robertson 1969; Johnson 1968a, 1970, 1971a; Johnson and Knight 1975) is substantially different from that of *Scyllarides* sp-B and sp-C phyllosoma larvae (Chow et al. 2022). Furthermore, based on geographic distance, larvae of *S. astori*, *S. roggeveeni*, and *S. tridacnophaga* are unlikely to occur in the central and western North Pacific. Recently, Hidaka et al. (2022) observed substantial genetic differentiation between the western and central Pacific specimens of *S. haanii*, although the sample size was quite small (two for

each).

Thus, it is highly likely that there are undescribed species and regional populations with significant genetic differentiation within the genus *Scyllarides* in the Pacific. To investigate these possibilities, we have attempted to determine the COI and 16S rDNA sequences of *S. astori*, *S. haanii*, *S. roggeveeni*, *S. squammosus*, and *S. tridacnophaga* from the museum specimens.

Table 2. Slipper lobster specimens of the genus *Scyllarides* provided from [1]Naturalis Biodiversity Center and [2]Kanagawa Prefectural Museum of Natural History for the present study.

species	voucher	Collection		Sample code
		location	date	
Scyllarides astori	[1]RMNH.CRUS.D.21138	Galapagos Isl.	29 Sep., 1964	SA138
S. haanii	[2]KPM-NH0001170	western Pacific	May, 1988	SH070
S. haanii	[2]KPM-NH0140646	Hachijo Isl., Japan	Aug., 1963	SH646
S. haanii	[2]KPM-NH0140746	Wakayama, Japan	Apr., 1962	SH746
S. haanii	[2]KPM-NH0163089*	Miyazaki, Japan	1965	SH089
S. haanii	[2]KPM-NH0163090*	Miyazaki, Japan	1965	SH090
S. haanii	[2]KPM-NH0163270*	Wakayama, Japan	1964	SH270
S. haanii	[2]KPM-NH0200052*	western South Pacific	May, 1989	SH052
S. roggeveeni	[1]RMNH.CRUS.D.21258	Easter Isl.	1965	SR258f, SR258t
S. squammosus	[2]KPM-NH0150297*	Chiba, Japan	Mar., 1963	SS297
S. squammosus	[2]KPM-NH0150309*	Wakayama, Japan	Oct., 1962	SS309
S. squammosus	[2]KPM-NH0163267*	Kanagawa, Japan	Nov., 1965	SS267
S. squammosus	[2]KPM-NH0200084*	–	–	SS084
S. tridacnophaga	[1]RMNH.CRUS.D.23023	Gulf of Aqaba	1965	ST023

*dried specimen.

Materials and Methods

Lobster specimens loaned from the museum and analyzed in this study are presented in Table 2. Preservation solution (ethanol, c.a. 50 ml) was collected from the bottom of the preservation bottle containing the holotype of *S. roggeveeni*. Muscle or cuticle tissues of the paratypes of *S. astori*, *S. haanii*, *S. squammosus*, and *S. tridacnophaga* were dissected from the leg, abdomen, antennule, or tail fan. These samples were sent to Aquos Institute, Japan. A tiny tissue (designated as SR258t) was found in the preservation solution of the holotype *S. roggeveeni* and separated into 1.5 ml Eppendorf tube. Remaining solution was centrifuged at 5,000 rpm for 10 min, supernatant was removed, and the precipitate (designated as SR258f) was used for DNA extraction. DNA extraction from these samples was performed using a DNA extraction kit (Genomic Prep Cell and Tissue DNA Isolation Kit, Amersham Bioscience). DNA of a phyllosoma specimen of *S. haanii* (designated as KY13-5-102) collected in the research cruise for spawning stock of neon squid *Ommastrephes bartramii* in the North Pacific Ocean performed by R/V Kaiyo-Maru, Fisheries Agency of Japan (see Konishi et al. 2024) was also used. Primers used for amplifying partial mitochondrial COI and 16S rDNA regions are presented in Table 3. PCR amplification was

Table 3. Oligo nucleotide primers used for amplifying partial mitochondrial COI and 16S rDNA regions of *Scyllarides* samples.

primer	nucleotide sequence (5'-3')
SCOIF1	AAYCATAAAGACATTGGTAC
SCOIF2	CTYAGTTTAATTATYCGYGC
SCOIF3	CGYATAAAYAATATRAGATT
SCOIR1	CTAATATRGCRTARATTATTCC
SCOIR2	AATGATTCTTTYTTYCCRGA
SCOIR3	GAAATTATYCCRAATGCYGG
SCOIR4	AATCTYATATTRTTTATRCG
SCOIR5	ACTATRAARAAAATTATWAC
16Sar-L*	CGCCTGTTTATCAAAAACAT
S16SF1	AGACCCTRTAAATCTTTATA
S16SF2	RTATTTTGTTGGGGWGACAG
S16SR1	TAATTCAACATCGAGGTCGC
16Sbr-H*	CCGGTCTGAACTCAGATCACGT

*adopted from Palumbi et al. (1991).

performed in 12 μL reaction mixture containing 1 μL of template DNA, 1.2 μL of 10 x reaction buffer, 1.2 μL of dNTP (2.5 mM each), 0.7 μL of each primer (10 M), 0.3 μL of EX Taq HS polymerase (5 units) (Takara Bio, Inc.), and 7.6 μL of distilled water. The reaction mixtures were preheated at 94 ºC for 5 min, followed by 35 amplification cycles (denaturation at 94 ºC for 30 sec, annealing at 50 ºC for 30 sec and extension at 72 ºC for 30 sec or 1 min), with a final extension at 72 ºC for 7 min. We first attempted PCR with primer combinations designed to amplify longer fragments (SCOIF1 × SCOIR1, SCOIF2 × SCOIR2, and SCOIF3 × SCOIR3 for COI; 16Sar-L × 16Sbr-H and 16SF1 × 16SR1 for 16S). When no amplicon was observed in these first round PCR, we subsequently used these PCR products as templates for nested PCR using primer pairs designed to amplify shorter fragments. Amplicons were treated with ExoSAP-IT (Amersham Biosciences) and subjected to direct nucleotide sequencing with the primers used for PCR amplification. When eminent double peaks were observed, the PCR products were cloned and subjected to nucleotide sequencing as previously reported (Chow et al. 2021, 2024).

Accession numbers of COI and 16S rDNA sequences of *Scyllarides* species available in the database to date are presented in Table 1. For species with many sequences registered, five most divergent haplotypes were selected. Nucleotide sequences of mitten lobsters *Parribacus antarcticus* and *P. japonicus* were used as out-group species. Nucleotide sequence alignment by the ClustalW algorithm was performed using GENETYX ver. 12 (GENETYX Co., Tokyo) followed by manual editing. Calculation of Kimura two parameter distance (K2P) between sequences and construction of phylogenetic tree were performed using MEGA 6 (Tamura et al. 2013).

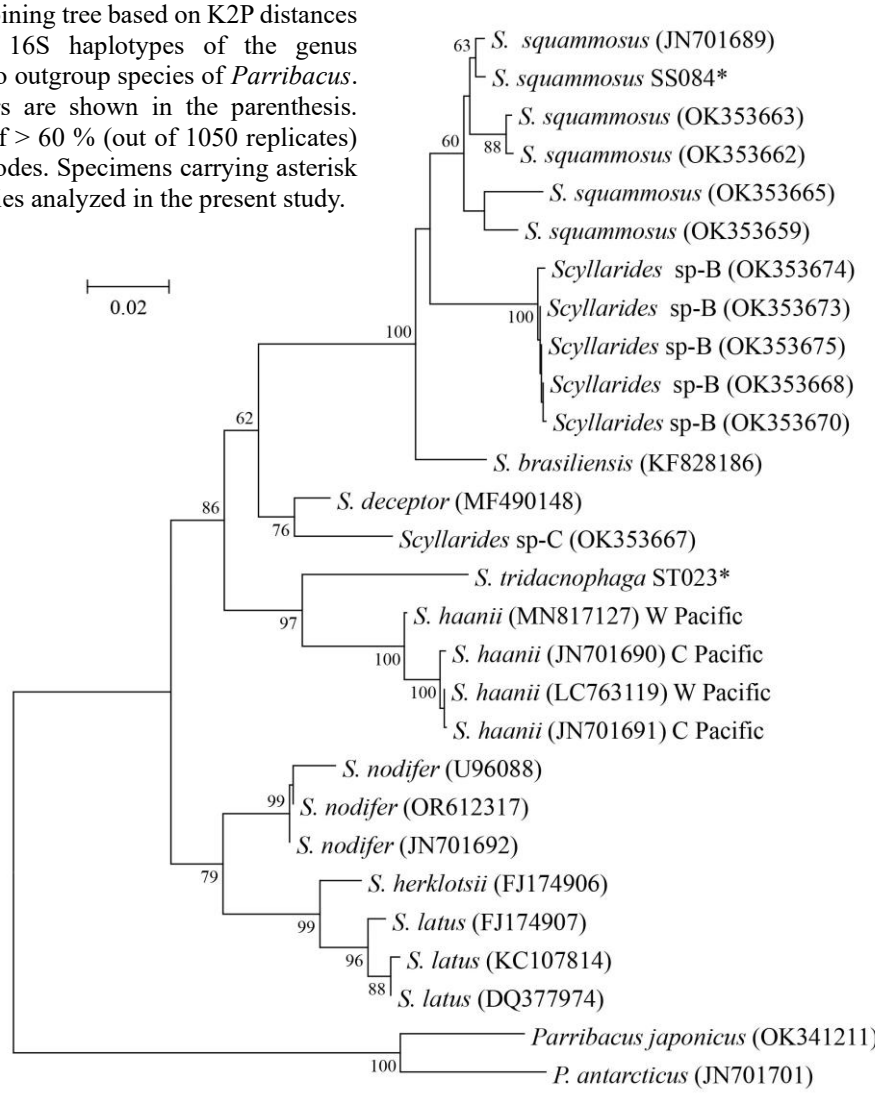
Results

For the museum specimens, amplicons from the first round PCR for COI were obtained in *S. tridacnophaga* (ST023), and one each of *S. haanii* (SH746) and *S. squammosus* (SS084) examined, and those for 16S were obtained in *S. tridacnophaga* (ST023) and one of *S. squammosus* (SS084) examined. All nested PCR attempts failed to obtain amplicons from *S. astori*, *S. roggenveeni*, and the remaining museum specimens of *S. haanii* and *S. squammosus*. Eminent double peaks were observed in the COI sequence electrophenogram of *S. haanii* (SH746), and subsequent nucleotide sequencing for eight clones examined revealed two divergent sequences designated as SH746-C1 and SH746-C2. The nucleotide sequences successfully determined were deposited in International Nucleotide Sequence Database Collection (INSDC) under accession numbers of LC763120, LC824044–LC824048, LC829464.

Phylogenetic trees (Figs. 1 and 2) strongly supported the sibling status of *S. braziliensis*, *S. squammosus*, and *Scyllarides* sp-B (designated as *S. squammosus* group), in which K2P distances between them ranged from 4.06 to 4.47 % in 16S and from 7.66 to 8.49 % in COI (Table 4). *Scyllarides* sp-C and *S. deceptor* were identified as sister lineages in 16S tree (Fig. 1) with K2P of 3.23 % (Table 4).

No apparent differentiation was observed between the western (from Japan, China, and Taiwan) and the central Pacific samples (Hawaiian Island) of *S. haanii* in the 16S tree (Fig. 1), with small K2P distance of 0.54 % between them (Table 4). On the other hand, a striking divergence in *S. haanii* was observed in the COI tree (Fig. 2). One clone sequence (SH746-C1) obtained from SH746 was determined as the legitimate mtDNA sequence and the other (SH746-C2) as a nuclear mitochondrial pseudogene (NUMT). SH746-C2 had three nucleotide insertions from all other samples examined, and five amino acid substitutions were observed between SH746-C1 and SH746-C2. K2P distances between SH746-C2 and the other western Pacific *S. haanii* samples ranged from 15.65 to 16.08 % and those between SH746-C2 and central to eastern Pacific samples ranged from 7.04 to 9.55 %.

Fig. 1. Neighbor-joining tree based on K2P distances between selected 16S haplotypes of the genus *Scyllarides* and two outgroup species of *Parribacus*. Accession numbers are shown in the parenthesis. Bootstrap values of > 60 % (out of 1050 replicates) are shown at the nodes. Specimens carrying asterisk are *Scyllrides* species analyzed in the present study.



Excluding this NUMT sequence, K2P distance between the western and central to eastern Pacific samples ranged from 7.42 to 10.41 with an average of 9.02 ± 1.09 % (Table 4). These K2P distances were comparable to or even greater than those between species of the *S. squammosus* group and between *S. herklotsii* and *S. latus* (Table 4).

Discussion

Except for the 16S nucleotide sequence divergence between the western and central Pacific samples of *S. haanii*, the pairwise divergence estimates between samples used in the present study (Table 4) were all comparable to or even greater than the minimum thresholds between congeneric crustacean species (Lefébure et al. 2006; Costa et al. 2007; Matzen da Silva et al. 2011; Barua et al. 2021), indicating that *Scyllarides* sp-B and *Scyllarides* sp-C are good species. Although the nucleotide sequences of *S. astori* and *S. roggenveeni* have not been determined, larval morphology and adult distribution may indicate that they are not the parental species for *Scyllarides* sp-B and *Scyllarides* sp-C phyllosoma larvae. Robertson (1969) noted that within the genus *Scyllarides* there were two morphological groups of mid- to final stage phyllosoma larvae, one with a small fifth pereiopod with a rudimentary exopod and the other with a well-developed fifth pereiopod with a setose exopod. Subsequently, Konishi et al. (2024) organized these characters and designated the former as Type 2 and the

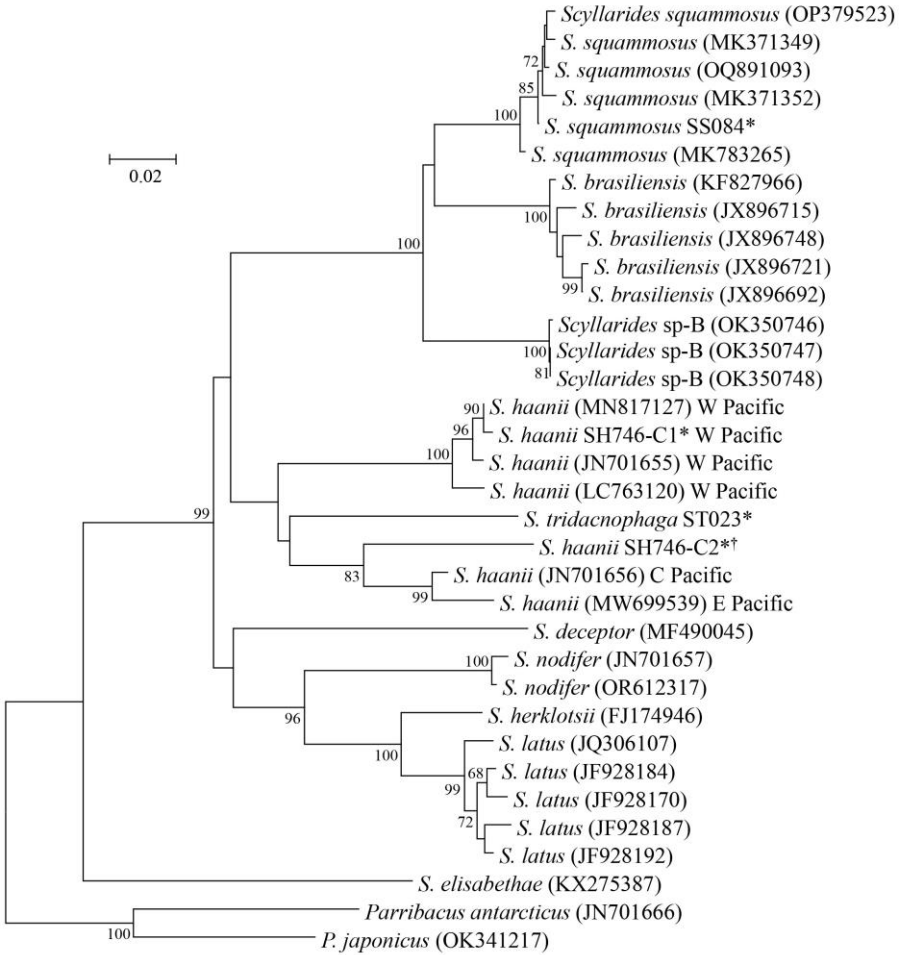


Fig. 2. Neighbor-joining tree based on K2P distances between selected COI haplotypes of the genus *Scyllarides* and two outgroup species of *Parribacus*. Accession numbers are shown in the parenthesis. Bootstrap values of > 60 % (out of 1050 replicates) are shown at the nodes. Specimens carrying asterisk are *Scyllrides* species analyzed in the present study. †determined as nuclear mitochondrial pseudogene (NUMT). Essentially the same tree topology was obtained when the NUMT sequence was excluded.

latter as Type 3. Since the fifth pereiopod with exopod is often broken in the plankton sample, the position of the fourth and fifth pereiopod bases can be used as an alternative character. The fourth pereiopod is located at the most posterior edge of the thorax in Type 2, while the fifth pereiopod is located at the most posterior edge of the thorax in Type 3. According to these characteristics, mid- to final stage phyllosoma larvae of *S. herklotsii, S. latus, S. nodifer*, *S. squammosus*, *Scyllarides* sp-B, and *Scyllarides* sp-C belong to Type 2 (Michel 1968, 1971; Robertson 1969; Johnson 1971b, c, 1977; Crosnier 1972; Berry 1974; Sekiguchi 1990; Palero et al. 2016; Chow et al. 2022), and those of *S. aequinoctialis*, *S. astori*, *S. elizabethi*, and *S. haanii* belong to Type 3 (Johnson 1968a, 1970, 1971a; Robertson 1969; Berry 1974; Johnson and Knight 1975; Konishi et al. 2024). It is unlikely that the larvae of *S. astori* and *S. roggenveeni* are successfully transported to the central to western Pacific, as the adult distribution of *S. astori* and *S. roggenveeni* is restricted to the tropical west coast of the Americas and the Galapagos Islands (Holthuis 1991; Webber and Booth 2007; Azofeifa-Solano et al. 2016; Carbajal-López, et al. 2017) and Easter Island (Holthuis 1991; Webber and Booth 2007), respectively.

Johnson (1971b) reported mid- to final stage *Scyllarides* phyllosoma larvae collected from Hawaiian waters (20°–29° N, 155°–170° W) and

Table 4. Mean K2P (%) distance between samples of the genus *Scyllarides* for 16S rDNA (above diagonal) and COI (below diagonal).

Scyllarides samples	1	2	3	4	5	6	7	8	9	10	11	12
1. *S. brasiliensis*	—	6.59	*	10.45	11.05	10.89	12.39	10.05	4.06	11.88	4.47	10.72
2. *S. deceptor*	19.64	—	*	6.10	6.21	7.85	8.34	6.19	7.42	7.52	9.68	3.23
3. *S. elisabethae*	24.21	24.92	—	*	*	*	*	*	*	*	*	*
4. *S. haanii*[§]	18.33	18.23	24.94	—	0.54	10.12	9.99	9.83	11.77	7.27	12.84	8.70
5. *S. haanii*[†]	18.93	14.13	22.60	9.02	—	9.89	10.08	9.70	12.45	7.27	13.92	9.22
6. *S. herklotsii*	19.92	16.63	21.28	15.46	12.29	—	2.77	4.96	13.62	11.82	13.96	10.52
7. *S. latus*	20.21	16.06	22.03	17.45	12.38	5.27	—	6.24	14.03	10.90	14.78	10.09
8. *S. nodifer*	19.28	17.00	22.59	17.72	13.90	11.60	11.19	—	11.44	10.04	12.81	8.27
9. *S. squammosus*	7.66	19.32	23.14	16.68	16.72	17.83	18.91	18.46	—	13.74	4.59	9.19
10. *S. tridacnophaga*	17.78	16.44	25.22	13.89	10.97	16.13	17.37	18.05	18.77	—	13.04	9.16
11. *Scyllarides* sp-B	8.49	20.83	23.18	16.80	17.26	17.85	17.75	19.10	7.54	19.01	—	10.22
12. *Scyllarides* sp-C	*	*	*	*	*	*	*	*	*	*	*	—

[§]western Pacific; [†]central + eastern Pacific. A clone sequence (SH746-C2) determined as NUMT in *S. haanii* (SH746) is not included for calculating K2P. *No data.

identified them as *S. squammosus*, since it was believed that only this species of the genus was distributed in the Hawaiian Islands and these larvae were in morphological agreement with *S. squammosus* phyllosoma larvae from New Caledonia reported by Michel (1968, 1971). Although adult *S. haanii* has been confirmed to occur in Hawaii (Morin and MacDonald 1984), the phyllosoma larva of *S. haanii* recently found by Konishi et al. (2024) was Type 3. The phyllosoma larvae of *S. squammosus* from the western Pacific reported in subsequent studies (Sekiguchi 1990; Palero et al. 2016; Chow et al. 2022) are all in morphological agreement with those of Johnson (1971b, 1977). However, the detection of *Scyllarides* sp-B and -C by Chow et al. (2022) indicates the presence of cryptic *Scyllarides* species in the Pacific. It is noteworthy that the collection sites of *Scyllarides* sp-B phyllosoma larvae were in Hawaiian waters (25°–31° N, 170° W) (see Chow et al. 2022) close to those of *Scyllarides* phyllosoma larvae reported by Johnson (1971b, 1977), and Chow et al. (2022) found no *S. squammosus* phyllosoma larva in this area. In light of these, *Scyllarides* phyllosoma larvae reported by Johnson (1971b, 1977) may be *Scyllarides* sp-B as suggested by Chow et al. (2022), and the population referred to as *S. squammosus* in the Hawaiian Islands may be *Scyllarides* sp-B. Genetic and morphological analyses of adult specimens of "*S. squammosus*" from Hawaiian Islands are necessary to address this issue.

The *Scyllarides* sp-C phyllosoma larva, collected just off the coast of the central Japanese archipelago, was the final stage (Chow et al. 2022) and was expected to settle in the nearby coastal area. As only *S. haanii and S. squammosus* are thought to be distributed in Japanese waters (Holthuis 1991; Webber and Booth 2007), no research has been conducted on the morphological and genetic diversity of these species. An extensive survey of *Scyllarides* species in Japan and the adjacent waters is necessary to find the parental species of *Scyllarides* sp-C phyllosoma larva.

Hidaka et al. (2022) observed large nucleotide sequence variation in COI of *S. haanii* (K2P ranging from 0.6 to 11.3 %), suggesting the presence of a cryptic species. We also observed large nucleotide sequence divergence between the western and central plus eastern Pacific *S. haanii*, supporting Hidaka et al. (2022). Genetic and morphological analyses of larger numbers of adult *S. haanii* specimens from across the Pacific may be needed to further investigate population structure.

Scheltema (1971) first coined the term "teleplanic

larvae" for long-lived pelagic larvae and exemplified 10 gastropod species having teleplanic larvae. *Scyllarides* phyllosoma larvae require 8 to 9 months to complete development (Robertson 1969), as do those of *Panulirus* (Kittaka and Kimura 1989; Yamakawa et al. 1989; Matsuda and Yamakawa 2000; Matsuda et al. 2006), which deserve to be teleplanic larvae. Pollock (1992) speculated that the teleplanic larvae of three North Pacific palinurid species (*Panulirus japonicus* from Northeast Asia, *P. marginatus* from Hawaii, and *P. interruptus* from the west coast of North America) share the same North Pacific wide circulation route but settle at different locations. Nevertheless, none of the phyllosoma larvae of these three species have been found in other waters (Johnson 1956; Johnson 1968b, 1971a, b, c; Phillips and McWilliam 1989; Polovina and Moffitt 1995; Minami et al. 2001; Funes-Rodríguez et al. 2015; Chow et al. 2006). Pronghorn spiny lobster (*P. penicillatus*) is the only species with a Pacific-wide distribution for both adults and the larvae (Johnson 1968b, 1971a, b, c, 1974; Holthuis 1991; Minami et al. 2001; Chow et al. 2011). However, Johnson (1974) doubted that even long-lived phyllosoma larvae would succeed in crossing the Eastern Pacific Barrier, and subsequently, complete genetic isolation between the western and eastern Pacific populations of *P. penicillatus* was found (Chow et al. 2011; Abdulah, et al. 2014; Iacchei et al. 2016). In addition, *P. japonicus*, *P. marginatus*, *P. interruptus* (and *P. gracilis*), and *P. pascuensis* are endemic to Northeast Asia, Hawaii, the west coast of North (and central) America, and Easter Island, respectively, despite their long-lived pelagic larvae. The geographic distributions of these *Panulirus* species appear to correspond well with those of *S. squammosus*, *Scyllarides* sp-B, *S. astori*, and *S. roggeveeni*, respectively, suggesting that similar mechanisms govern the retention and dispersal of the long-lived phyllosoma larvae of these palinurid and scyllarid species.

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