

A new species in the *Spirobranchus kraussii* complex (Annelida: Serpulidae) from Australia

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ABSTRACT. The blue coral-worm *Spirobranchus kraussii* (Baird, 1864) (Annelida: Serpulidae) was originally described from South Africa and reported as a widely distributed Indo-Pacific species, however it is now recognized as a complex of regionally distributed species. Molecular studies led to the description of taxa within the monophyletic *S. kraussii* complex including *S. lirieneae* Brandão & Brasil, 2020 (Brazil), *S. sinuspersicus* Pazoki, Rahimian, Struck, Katouzian & Kupriyanova, 2020 (Arabian (Persian) Gulf), *S. akitsushima* Nishi, Abe, Tanaka, Jimi & Kupriyanova, 2022 (Japan), *S. bakau* Sivananthan, Shantti, Kupriyanova, Quek, Yap & Teo, 2021 (Singapore), and *S. manilensis* Sivananthan, Sivalingam, Kupriyanova, Quek, Yap & Teo, 2022 (Philippines). *Spirobranchus kraussii* was reported (as *Pomatoleios kraussii*) as an intertidal belt-forming species from mid-20th century in Queensland, Australia. Here, this species was described as *Spirobranchus straughanae* sp. nov. as a result of the analysis of historic specimens from the Australian Museum and newly obtained DNA sequences of *cytb* and *18S*. Phylogenetic analyses revealed seven well-supported clades within the complex and *S. straughanae* sp. nov. was recovered as sister group to *S. lirieneae*. Genetic distances between *S. straughanae* sp. nov. and other species ranged from 12.8% to 25.6% (p-distance) and 17.3% to 46.6% (Kimura 2-parameter), reinforcing its status as a distinct species. Morphologically, *S. straughanae* sp. nov. differs from congeners in the complex by opercular characteristics, tube morphology, and glandular distribution. The talon can be used to differentiate taxa, but its structure varies significantly. Peduncular wing patterns and chaetal morphology further distinguish species within the complex. The findings underscore the importance of integrative approaches to resolution of species boundaries in the *S. kraussii* complex.

Keywords: integrative taxonomy, systematics, species complex, *cytb*, 18S

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Introduction

The family Serpulidae Rafinesque, 1815 (Annelida) comprises a diverse group of primarily marine annelid worms inhabiting calcareous tubes typically attached to hard substrates. A distinctive feature of these animals is the operculum — a plug-like structure borne on a modified radiole that closes the tube entrance when the animal retracts. Members of this family are distributed worldwide, occurring in environments ranging from coastal areas to the deep sea (Rouse *et al.*, 2022). *Spirobranchus* Blainville, 1818 is the second largest serpulid genus after *Hydroides* Gunnerus, 1768, encompassing 41 nominal species (Read & Fauchald, 2025). Although easily recognizable by their opercula with calcareous endplates and lateral wing-like peduncular projections, *Spirobranchus* spp. show a significant intraspecific variability (Willette *et al.*, 2015) often overlapping with interspecific variability (Simon *et al.*, 2019; Kupriyanova *et al.*, 2022), which makes morphological distinction problematic.

Within the genus, the *Spirobranchus kraussii* complex forms a distinct group characterized by the absence of collar chaetae in adults, flat or concave calcified opercular endplates without external ornamentation but with an internal talon, and tubes with flat projections over the entrance. The nominal species was described by Baird (1864) based on intertidal gregarious worms collected in Western Cape Province, South Africa as *Placostegus cariniferus* var. *kraussii*, supposedly an African variety of New Zealand's *Placostegus cariniferus* (Gray, 1843). Pixell (1913) established the monotypic genus *Pomatoleios* with *P. crosslandi* from Tanzania. The name *Pomatoleios crosslandi* was initially widely reported throughout the Indo-Pacific (Fauvel, 1932: India; Monro, 1933: South Africa; Day, 1934: South Africa; Okuda, 1937: Japan; Rioja, 1947: Gulf of California and Mexico; Pillai, 1960: Sri Lanka; and Mohammad, 1971: Kuwait) being included in the list of Indian Ocean species by Hartman (1974).

However, after Day (1955) examined the type material of *Placostegus cariniferus* (transferred to *Spirobranchus* by Ehlers, 1907), *Placostegus cariniferus* var. *kraussii* and *Pomatoleios crosslandi* in Natural History Museum, London (NHM), he suggested that the African material belongs to the same species. He maintained *Spirobranchus cariniferus* as a valid New Zealand species, raised South-African *P. cariniferus* var. *kraussii* to a full species and synonymized tropical African *P. crosslandi* with warm temperate *P. kraussii*. Subsequently the name *P. kraussii* was commonly used in Indo-Pacific reports (Imajima & Hartman, 1964: Japan; Pillai, 1965: Philippines, as *P. kraussii* var. *manilensis*; Straughan, 1969: Hawaii; Mohammad, 1974; 1975: Kuwait; Crisp, 1977: Kuwait; Uchida, 1978: Japan; Tromp, 1978: Panama; Miura & Kajihara, 1984: Japan; Bailey-Brock, 1987: Hawaii; Ishaq and Mustaqim, 1996: Pakistan; Nishi, 1993: Japan; Wehe & Fiege, 2002: Suez Canal; Bastida-Zavala, 2008: Panama). It was listed by ten Hove and Kupriyanova (2009) as a widely distributed species, forming intertidal aggregations in the Indo-Pacific. Although Hartman (1959) accepted the synonymization, both *P. crosslandi* and *P. kraussii* remained in use for over a decade, even being used together by Morgans (1959) and Stephenson and Stephenson (1972), seemingly referring to the same South African species.

Ten Hove and Kupriyanova (2009: 77–78) briefly mentioned potential synonymy of the genus *Pomatoleios* with *Spirobranchus*, but the synonymy was formally proposed by Pillai (2009: 48). He argued that the absence of collar chaetae in *Pomatoleios* was not sufficient to separate the genera because juvenile *Pomatoleios* possess collar chaetae. Pazoki *et al.* (2020) provided genetic support for this hypothesis by showing that the multiple species previously lumped into *Pomatoleios kraussii* form a well-supported clade nested in a monophyletic *Spirobranchus* clade.

The name *S. kraussii* was subsequently used by Chan *et al.* (2014) for a population from Singapore and by Bastida-Zavala *et al.* (2017) for worms from Hawaii. Interestingly, Bastida-Zavala and Sánchez-Ovando (2021) reported both *S. crosslandi* and *S. cf. kraussii* from Pacific Panama with little explanation. Hutchings and Kupriyanova (2018) stressed that “cosmopolitan” distributions attributed to shallow water polychaete taxa is a result of taxonomic problems in the group. Notable exceptions are neo-cosmopolitan distributions *sensu* Darling and Carlton (2018) resulting from human-mediated translocations. Therefore, identity of specimens collected far from type locality needs confirmation. Simon *et al.* (2019) were first to question the wide distribution of *Spirobranchus kraussii*. They redescribed the species based on syntypes and freshly collected material from the type locality in South Africa (Western Cape Province) and the Eastern part of its distribution (KwaZulu-Natal). The sequences of the South African populations were also compared with those from specimens collected in distant localities of the reported *S. kraussii* range: Honshu, Japan (*Spirobranchus* sp. 1), Hawaii (*S.* sp. 2), Kuwait (*S.* sp. 4) and northern Queensland, Australia (*S.* sp. 3). The study confirmed that *S. kraussii* is restricted to warm temperate ecoregion of South Africa and the name was used for a complex of regionally distributed undescribed species.

After *S. kraussii* re-description in Simon *et al.* (2019), *S. cariniferus* was included in the *S. kraussii* complex and new species had been described. Brandão and Brasil (2020) described *S. lirianae* from Brazil, using morphological data. *Spirobranchus* sp. 4 *sensu* Simon *et al.* (2019) from intertidal aggregations in tropical Kuwait was described as *S. sinuspersicus* Pazoki, Rahimian, Struck, Katouzian & Kupriyanova, 2020; *S.* sp. 1 from warm temperate intertidal aggregations in Honshu, Japan was described as *S. akitsushima* Nishi, Abe, Tanaka, Jimi & Kupriyanova, 2022, whereas *S.* sp. 5 and *S.* sp. 6 were suggested as other unnamed species from tropical Okinawa, Japan by Kobayashi and Goto (2021). A species from mangroves of tropical Singapore was described as *S. bakau* Sivananthan, Shantti, Kupriyanova, Quek, Yap & Teo, 2021. Sivananthan *et al.* (2022) also raised *S. kraussii* var. *manilensis* to full species, *S. manilensis* Sivananthan, Sivalingam, Kupriyanova, Quek, Yap & Teo, 2022, based on examination of the type material, but no freshly collected material was available. Thus, currently the complex includes seven named species, while *S.* sp. 2 from Hawaii, *S.* sp. 3 from tropical Australia, *S.* sp. 5, and *S.* sp. 6 from tropical Okinawa, Japan remain undescribed. The taxonomic status of *S. crosslandi* from tropical western coast of Africa remains uncertain.

In Australia, the *S. kraussii* complex was initially briefly mentioned by Endean *et al.* (1956a, 1956b) who reported *P. crosslandi* (being unaware of the synonymization by Day,

1955) as a species sporadically occurring in high numbers only under sheltered rocks, mainly in northern Queensland. In her first taxonomic account of Australian serpulids, Dew (1959) referred the species mentioned by Endean *et al.* (1956a) to *Pomatoleios kraussii*, but did not examine any specimens. Guiler (1960) followed Endean *et al.* (1956a, 1956b), using the name *P. crosslandi* when referring to a rocky shore species in Queensland. Knox (1960) already mentioned *P. kraussi* (sic!) from subtropical Queensland, although mistakenly used the name *P. kraussii* to refer to Australian population and *P. crosslandi* to South African population. Straughan (1967) was the first to examine specimens, to provide a short diagnosis of *P. kraussii* in Queensland, and to report its distribution from Cape Bedford down to Dunwich, Queensland.

A collection of *Spirobranchus* species under the name *Pomatoleios kraussii* from northern Queensland apparently examined by Straughan (1967) is deposited at the Australian Museum. Interestingly, since the Straughan (1967) study, there were no reports of this taxon until fresh material was collected and sequenced by Simon *et al.* (2019). The aim of this study was to formally describe and name the species of the *S. kraussii* complex from Queensland reported as *S. sp. 3* in Simon *et al.* (2019), providing its phylogenetic position within the complex.

Material and methods

Morphological analysis

The study was based on the material of *Spirobranchus* cf. *kraussii* deposited at the Australian Museum collection. Part of this material was examined by Straughan (1967), and even though she did leave notes in the vials with specimens, she reported no AM registration numbers in her publication.

Individuals were removed from tubes and cleaned with a fine artist brush. Opercula of 10 specimens were dissected and cleared with glycerin to expose the talon or kept overnight in lysis solution with proteinase K, from Bioline Isolate II Genomic DNA kit, to digest soft tissue leaving only calcareous structures. Specimens were stained for two minutes with 0.5% methyl green in distilled water to reveal patterns of ventral thoracic shields and other glandular clusters. Microscope pictures were taken on a dissecting microscope. For scanning electron microscopy (SEM) observations, specimens were dehydrated in a series of ethanol at 80%, 90%, and 100%, mounted on aluminum stubs, coated with gold-palladium sputter, and observed under a JEOL 6480LA scanning electron microscope at Microscopy Unit at Macquarie University, Sydney.

DNA extraction, amplification and sequencing

We added new DNA sequence data (*cytb* and *18S rRNA*) to those of *Spirobranchus* sp. 3 from Mission Beach, Queensland, Australia provided in Simon *et al.* (2019; Fig. 1). Unpublished *cytb* sequences from Brazilian specimens of *S. lirianae* were also included, and sequences from other species of the *S. kraussii* complex were sourced from GenBank (Table 1).

Posterior abdominal segments were dissected, and total DNA extraction was done using Bioline Isolate

II Genomic DNA kit according to the manufacturer's protocol. The anterior fragments of *18S rRNA* gene (approximately 1100 bp) were amplified with the primers TimA (AMCTGGTTGATCCTGCCAG) and 1100R2 (CGGTATCTGATCGTCTTCGA) from Nören and Jordelius (1999). The *cytb* gene fragments (approximately 400 bp) were amplified with the same primer pair as in Halt *et al.* (2009), *Cytb424F* (GGWTAYG TWYTWCCWTGR GGWCARAT) from Boore and Brown (2000) and *cobr825* (AARTAYCAYTCYGGYTTRATRTG) from Burnette *et al.* (2005). The PCR conditions for *18S* were initial denaturation at 94°C for 3 min, 40 cycles of denaturation at 94°C for 30 sec, annealing at 57°C for 30 sec, and extension at 72°C for 30 sec, with final extension at 72°C for 3 min. For *cytb*, initial denaturation was 94°C for 5 min, followed by 45 cycles with denaturation at 94°C for 30 sec, annealing at 47°C for 30 sec, and extension at 72°C for 1 min, with final extension at 72°C for 4 min.

PCR products were sent for Sanger sequencing to Macrogen™ in South Korea. The resulting sequence chromatograms were reviewed and manually corrected using Geneious Prime 2024.0.7 (<https://www.geneious.com>). BLAST search (Altschul *et al.*, 1990) was used to verify if the appropriate gene regions had been targeted. The *18S* and *cytb* sequences were aligned separately using the MUSCLE algorithm in MEGA X software (Hillman *et al.*, 2022), and edited in Aliview software (Larsson, 2014).

Data analyses

The final trimmed analyzed dataset included 27 *18S* sequences 773 bp long and 36 *cytb* sequences 297 bp long. Sequences of *18S* from *S. lirianae* specimens and of one of *S. bakau* specimens were not obtained (Table 1). The *cytb* and *18S* datasets were concatenated with FASconCAT v.1.11 (Kück and Longo, 2014) resulting in a dataset 1070 bp long.

The phylogenetic relationships were inferred using Maximum Likelihood (ML) analysis in IQ-TREE (Minh *et al.*, 2020). Nucleotide substitution models selected using the Bayesian Information Criterion (BIC) in ModelFinder (Kalyaanamoorthy *et al.*, 2017) were HKY+I+G4 for *cytb* and TNE+I for *18S*. Branch support was estimated using 1000 ultrafast bootstraps (Hoang *et al.*, 2018). Analyses of individual *cytb* and *18S* datasets were performed to verify if *18S* data absent from seven individuals would affect tree topologies. Pairwise genetic distances for *cytb* sequences were calculated (Table 2) using both the p-distance and Kimura 2-parameter models in MEGA X (Kumar *et al.*, 2018).

Results

Order Sabellida Levinsen, 1883

Family Serpulidae Rafinesque, 1815

Genus *Spirobranchus* de Blainville, 1818

Spirobranchus straughanae sp. nov.

urn:lsid:zoobank.org:act:04AE171B-1428-4D1C-AE29-027D5DB44792

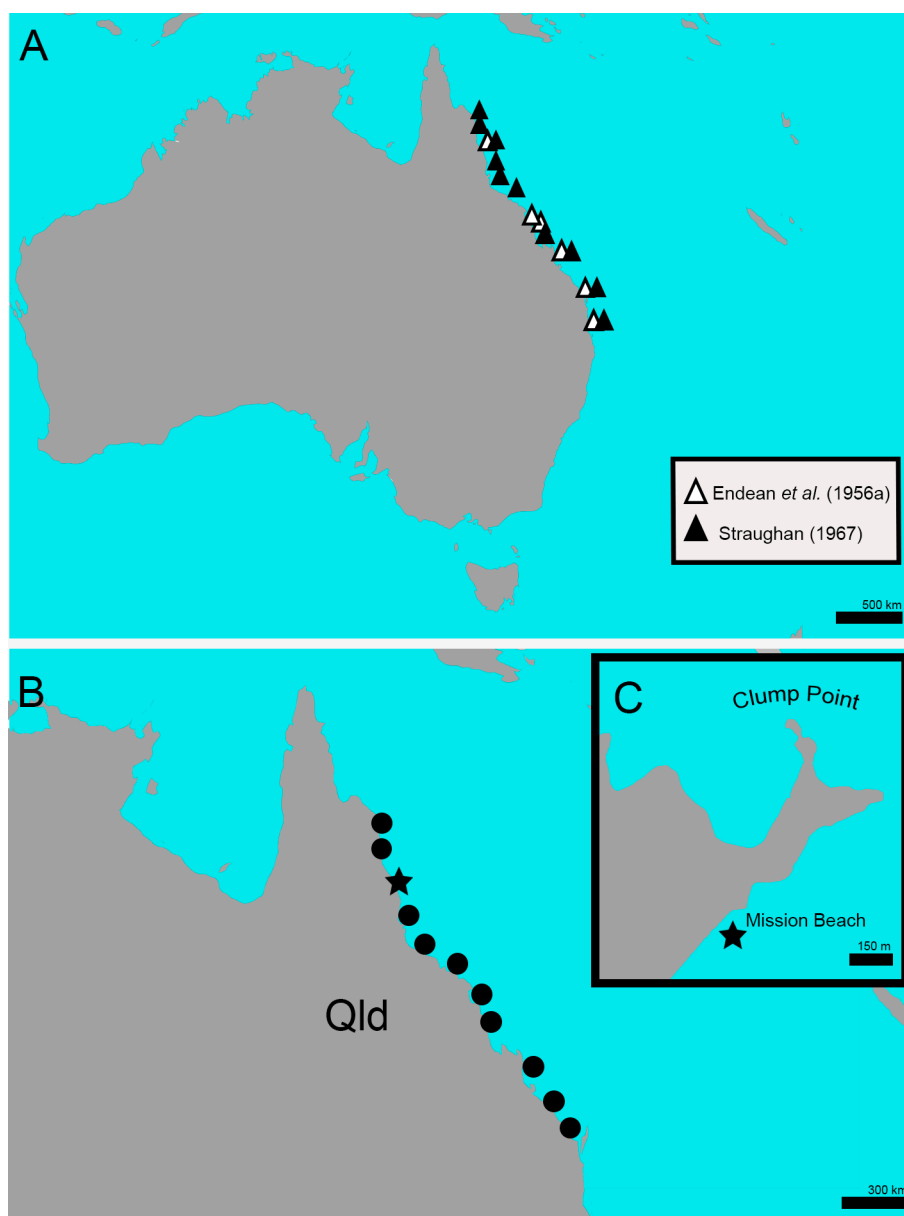


Figure 1. Map showing distribution of *S. straughanae* sp. nov. A. Records from previous studies. B. Collection sites of specimens used in the present study. Star indicates type locality. C. Detail of type locality in Mission Beach.

Pomatoleios crosslandi – Endean *et al.*, 1956a, 1956b (name only); Guiler, 1960 (name only)

Pomatoleios kraussi (sic!) – Knox, 1960 (name only)

Pomatoleios kraussii – Dew, 1959 (name only); Straughan, 1967: 235 (Qld, diagnosis, distribution)

Spirobranchus sp. 3 – Simon *et al.*, 2019 (DNA sequences only)

Type material. Holotype: AM W.48305, Australia, Queensland, Mission Beach, Clump Point, under rocks in shallow subtidal zone (17°52'S, 146°07'E), leg E. Kupriyanova, 07/11/2015, 95% ethanol. Paratypes: W.48301 (1 spec.), W.48302 (1 spec.), W.48303 (1 spec.), W.48304 (1 spec.), W.48306 (1 spec.), W.48307 (1 spec.), W.48309 (1 spec.). Same locality as for holotype.

Additional material. W.15039 (several spec.) Queensland, Yorkeys Knob, north of Cairns (16°49'S, 145°43'E), 15/01/1965; W.198110 (several spec.) Queensland,

Townsville (19°15'S, 146°49'E); W.201723 (several spec.) Queensland, Hervey Bay, Point Vernon (25°15'S, 152°49'E), 23/10/1976; W.201727 (several spec.) Queensland, Townsville (19°15'S, 146°49'E), 8/02/1950; W.27387 (1 spec.) Queensland, Townsville, Kissing Point (19°14'S, 146°48'E), 2/12/1963; W.30231 (8 spec.) Queensland, Cairns, Yorkeys Knob, Breakwater (16°52'S, 145°49'E), 11/2001; W.33887 (1 spec.) Queensland, Cairns, Wharf 4 (16°52'S, 145°49'E), 19/11/2001; W.3843 (several spec.) Mackay, Shoal Point (21°8'S, 149°11'E), 1965; W.3844, Cairns, Pretty Beach (16°36'S, 145°31'E), 7/02/1964; W.3867 (several spec.), Ross River Creek, Townsville (19°15'S, 146°49'E), 4/08/1964; W.3868 (1 spec.) Queensland, Burnett Heads (24°46'S, 152°25'E), 09/1963; W.3869 (6 spec.) Queensland, Moreton Bay, Scarborough, Reef Point (27°12'S, 153°7'E), 5/1962; W.3872 (2 spec.) Queensland, river mouth, Bundaberg (24°52'S, 152°21'E),

Table 1. Terminals used in phylogenetic analysis with registration numbers and collection localities. *The voucher is named *Spirobranchus* sp. 3 by Simon *et al.* (2019). Abbreviations: BA = Bahia, PE = Pernambuco, KZN = KwaZulu-Natal, WCP = Western Cape Province; CBM-ZW = Natural History Museum and Institute, Chiba, Japan, MZUSP = Zoology Museum, University of São Paulo, Brazil, SAM = South Australian Museum, ZRC.ANN = Zoological Reference Collection, Department of Zoology, University of Singapore, ZUTC = Zoological Museum of the University of Tehran, Iran.

Species	Registration numbers	Collection locality	<i>Cytb</i> Accession numbers	<i>18S</i> Accession numbers	Source
<i>S. straughanae</i> sp. nov.	AM W.48301	Qld, Australia	MK308648	MK308662	*Simon <i>et al.</i> (2019)
<i>S. straughanae</i> sp. nov.	AM W.48302	Qld, Australia	MK308647	MK308663	*Simon <i>et al.</i> (2019)
<i>S. straughanae</i> sp. nov.	AM W.48303	Qld, Australia	PV562148	PV588023	This study
<i>S. straughanae</i> sp. nov.	AM W.48304	Qld, Australia	PV562149	PV588024	This study
<i>S. lirianeeae</i>	MZUSP8185	BA, Brazil	PV562150	—	This study
<i>S. lirianeeae</i>	MZUSP8182	BA, Brazil	PV562151	—	This study
<i>S. lirianeeae</i>	MZUSP8187	PE, Brazil	PV562152	—	This study
<i>S. lirianeeae</i>	MZUSP8192	PE, Brazil	PV562153	—	This study
<i>S. lirianeeae</i>	MZUSP8190	PE, Brazil	PV562154	—	This study
<i>S. lirianeeae</i>	MZUSP8186	PE, Brazil	PV562155	—	This study
<i>S. kraussii</i>	AM W.49196	WCP, South Africa	MK308644	MK308659	Simon <i>et al.</i> (2019)
<i>S. kraussii</i>	AM W.49197	WCP, South Africa	MK308645	MK308660	Simon <i>et al.</i> (2019)
<i>S. kraussii</i>	AM W.49199	WCP, South Africa	MK308646	MK308661	Simon <i>et al.</i> (2019)
<i>S. kraussii</i>	AM W.49191	WCP, South Africa	MK308650	MK308665	Simon <i>et al.</i> (2019)
<i>S. kraussii</i>	AM W.49192	KZN, South Africa	MK308651	MK308666	Simon <i>et al.</i> (2019)
<i>S. kraussii</i>	AM W.49193	KZN, South Africa	MK308652	MK308667	Simon <i>et al.</i> (2019)
<i>S. sinuspersicus</i>	ZUTC.6810	Iran	MN372434	MN372441	Pazoki <i>et al.</i> 2020
<i>S. sinuspersicus</i>	ZUTC.6809	Iran	MN372435	MN372442	Pazoki <i>et al.</i> 2020
<i>S. sinuspersicus</i>	ZUTC.6808	Iran	MN372436	MN372443	Pazoki <i>et al.</i> 2020
<i>S. sinuspersicus</i>	ZUTC.6778	Iran	MN372437	MN372444	Pazoki <i>et al.</i> 2020
<i>S. cariniferus</i>	—	New Zealand	JX144867	JX144808	Smith <i>et al.</i> (2012)
<i>S. cariniferus</i>	—	New Zealand	JX144868	JX144807	Smith <i>et al.</i> (2012)
<i>S. cariniferus</i>	—	New Zealand	JX144869	JX144813	Smith <i>et al.</i> (2012)
<i>S. cariniferus</i>	—	New Zealand	JX144870	JX144811	Smith <i>et al.</i> (2012)
<i>S. akitsushima</i>	CBM-ZW 1127	Kamakura, Japan	LC661622	LC661650	Nishi <i>et al.</i> (2022)
<i>S. akitsushima</i>	CBM-ZW 1128	Kamakura, Japan	LC661623	LC661651	Nishi <i>et al.</i> (2022)
<i>S. akitsushima</i>	CBM-ZW 1129	Kamakura, Japan	LC661624	LC661652	Nishi <i>et al.</i> (2022)
<i>S. akitsushima</i>	CBM-ZW 1130	Kamakura, Japan	LC661625	LC661653	Nishi <i>et al.</i> (2022)
<i>S. bakau</i>	ZRC.ANN.0484	Singapore	MW767138	MW767146	Sivananthan <i>et al.</i> (2021)
<i>S. bakau</i>	ZRC.ANN.0485	Singapore	MW767139	MW767147	Sivananthan <i>et al.</i> (2021)
<i>S. bakau</i>	ZRC.ANN.0486	Singapore	MW767140	MW767148	Sivananthan <i>et al.</i> (2021)
<i>S. bakau</i>	ZRC.ANN.0487	Singapore	MW767141	MW767149	Sivananthan <i>et al.</i> (2021)
<i>S. bakau</i>	ZRC.ANN.0481	Singapore	MW767142	MW767150	Sivananthan <i>et al.</i> (2021)
<i>S. bakau</i>	ZRC.ANN.0482	Singapore	MW767143	MW767151	Sivananthan <i>et al.</i> (2021)
<i>Spirobranchus</i> sp. 2	AM W.45327	Hawaii	MK308655	MK308670	Simon <i>et al.</i> (2019)
<i>Spirobranchus</i> sp. 5	—	Okinawa, Japan	LC604689	LC604685	Kobayashi & Goto (2021)
<i>Spirobranchus</i> sp. 5	—	Okinawa, Japan	LC604690	—	Kobayashi & Goto (2021)
<i>Spirobranchus</i> sp. 5	—	Okinawa, Japan	LC625520	—	Kobayashi & Goto (2021)
<i>Spirobranchus</i> sp. 5	—	Okinawa, Japan	LC625521	—	Kobayashi & Goto (2021)
<i>Spirobranchus</i> sp. 6	—	Okinawa, Japan	LC604691	LC604686	Kobayashi & Goto (2021)
<i>Spirobranchus</i> sp. 6	—	Okinawa, Japan	LC604692	—	Kobayashi & Goto (2021)
<i>Spirobranchus</i> sp. 6	—	Okinawa, Japan	LC625532	—	Kobayashi & Goto (2021)
<i>Spirobranchus</i> sp. 6	—	Okinawa, Japan	LC625533	—	Kobayashi & Goto (2021)
<i>S. triqueter</i>	SAM E3534	Sweden	OQ427481	DQ317121	Kupriyanova <i>et al.</i> (2006; 2023)
<i>S. schmardai</i>	AM W.51857	NSW, Australia	ON457553	ON221935	Kupriyanova <i>et al.</i> (2022)
<i>Galeolaria hystrix</i>	—	New Zealand	JX144861	JX144799	Smith <i>et al.</i> (2012)

Table 2. Mean genetic distances for *cytb* sequences of the *Spirobranchus kraussii* complex species based on pairwise distance (p-distance) and Kimura's 2-parameter model. K2P values are shown above the diagonal and p-distance values are shown below it.

	<i>S. sp. 2</i>	<i>S. sp. 5</i>	<i>S. sp. 6</i>	<i>S. lirianee</i>	<i>S. sinuspersicus</i>	<i>S. cariniferus</i>	<i>S. bakau</i>	<i>S. akitsushima</i> sp. nov.	<i>S. straughanae</i>	<i>S. kraussii</i>
<i>S. sp. 2</i>	—	0.40338	0.36082	0.00378	0.43563	0.47922	0.29369	0.33594	0.17922	0.32653
<i>S. sp. 5</i>	0.23282	—	0.36977	0.42289	0.45495	0.37932	0.23252	0.37181	0.43959	0.36376
<i>S. sp. 6</i>	0.21348	0.21799	—	0.37500	0.46537	0.35973	0.29599	0.04974	0.33770	0.32171
<i>S. lirianee</i>	0.00375	0.23973	0.21769	—	0.45756	0.47471	0.33956	0.33361	0.17335	0.33297
<i>S. sinuspersicus</i>	0.24345	0.24658	0.24830	0.24916	—	0.45756	0.49321	0.43489	0.46332	0.43855
<i>S. cariniferus</i>	0.25843	0.22603	0.21769	0.25589	0.24916	—	0.39299	0.36557	0.46609	0.43663
<i>S. bakau</i>	0.19101	0.15411	0.19048	0.20875	0.25589	0.22896	—	0.33558	0.39639	0.32241
<i>S. akitsushima</i>	0.20599	0.21918z	0.04422	0.20539	0.23906	0.21886	0.20539	—	0.30778	0.38264
<i>S. straughanae</i> sp. nov.	0.13109	0.24315	0.20068	0.12795	0.24916	0.25589	0.22559	0.19192	—	0.35295
<i>S. kraussii</i>	0.19476	0.21918	0.20068	0.19529	0.24579	0.24579	0.20202	0.22222	0.20539	—

13/06/1962; W.3873 (1 spec.) Queensland, Pinalba (25°16'S, 152°49'E), 09/1963; W.3874 (1 spec.) Queensland, Ross River, Townsville (19°15'S, 146°49'E), 2/12/1963; W.3876 (3 spec.), Queensland, Half Tide, Mackay (21°17'S, 149°17'E), 5/08/1963; W.3877 (1 spec.) Queensland, Hervey Bay, Point Vernon (25°15'S, 152°49'E), 14/04/1964; W.3878 (several spec.) Queensland, Tannum Sands (23°56'S, 151°22'E), 05/1963; W.3879 (9 spec.) Queensland, Hervey Bay, Point Vernon (25°15'S, 152°49'E), 22/07/1962; W.3880 (2 spec.) Queensland, Port Curtis, Barney Point (23°50' S, 151°16' E), 25/05/1963; W.3881 (several spec.) Queensland, Yepoon (23°7'S, 150°44'E), 29/11/1963; W.3882 (several spec.) Queensland, Townsville, Kissing Point (19°14'S, 146°48'E), 2/12/1963; W.3883 (1 spec.) Queensland, Moreton Bay, North Stradbroke Island, Dunwich (27°30'S, 153°24'E), 6/06/1960; W.3884 (2 spec.) Queensland, Hervey Bay, Point Vernon (25°15'S, 152°49'E), 21/06/1962; W.3885 (2 spec.) Queensland, Bowen, Ross Bay (19°59'S, 148°16'E), 1/12/1963; W.4060 (several spec., including 10 spec. sorted and dissected to expose talons) Queensland, Innisfail, Flying Fish Point (17°29'S, 146°4'30"E), 17/01/1965; W.4066 (3 spec.) Queensland, Port Douglas (16°29'S, 145°27'E), 17/01/1965; W.4067 (2 spec.) Queensland, Cairns, Pretty Beach (16°36'S, 145°31'E), 13/01/1965; W.41813 (several spec.) Townsville, Kissing Point (19°14'S, 146°48'E), 1984; W.41860 (several spec.) Townsville, Kissing Point (19°14'S, 146°48'E), 1984.

Diagnosis. Funnel-shaped opercular endplate and 2-3 talon teeth. Posterior abdominal region covered by glandular clusters.

Description.

Size. Holotype: incomplete specimen, 7 mm long; thorax 1 mm; width at opercular endplate 0.9 mm. Paratypes: incomplete specimens, 5 – 9 mm long; thorax 1 mm; (n = 7, mean = 6.57 mm); width at opercular endplate 0.8 – 0.9 mm (n = 7, mean = 0.82 mm). Longest measured individual (W.41813, Figs. 2A–2B), with 45 abdominal chaetigers, total length 12 mm, width at opercular endplate 0.8 mm.

Tube. Aggregated tubes (Fig. 2A), white, sometimes internally and laterally blueish. Triangular to trapezoidal in cross-section, lumen circular. One or two keels present trough tube length, with a narrow furrow between them. Keels extending from tube mouth, forming a pointed or flat projection (Fig. 2A). Transverse striations present.

Radiolar crown. Two radiolar lobes arranged in circles. Each lobe with 19 radioles, connected by inter-radiolar membrane for up to half their length. Color faint cream in preserved material, except for dark brown bands alternating along achis. Radioles rectangular in cross-section, inner side with two rows of filiform pinnules. Pinnules distally shorter along radioles. Tips of radioles smooth, filiform and about same size as distal pinnules (Figs. 5A–B). Dorsal radioles longer than ventral ones. Paired black spots with ocellar clusters present in some fixed individuals, 4 to 6 pairs per radiole.

Mouth parts. Two thin, smooth flat lips. Dorsal lips with lateral extensions forming a pair of lateral filiform palps (Fig. 4D), often brown-coloured, about as long as proximal pinnules. Palps symmetrical, same size and shape on both sides, without a lip fold. Inner margin of palps and lips densely ciliated (Fig. 4D). Ventral lips forming a flap along inner side at base of radiolar lobe.

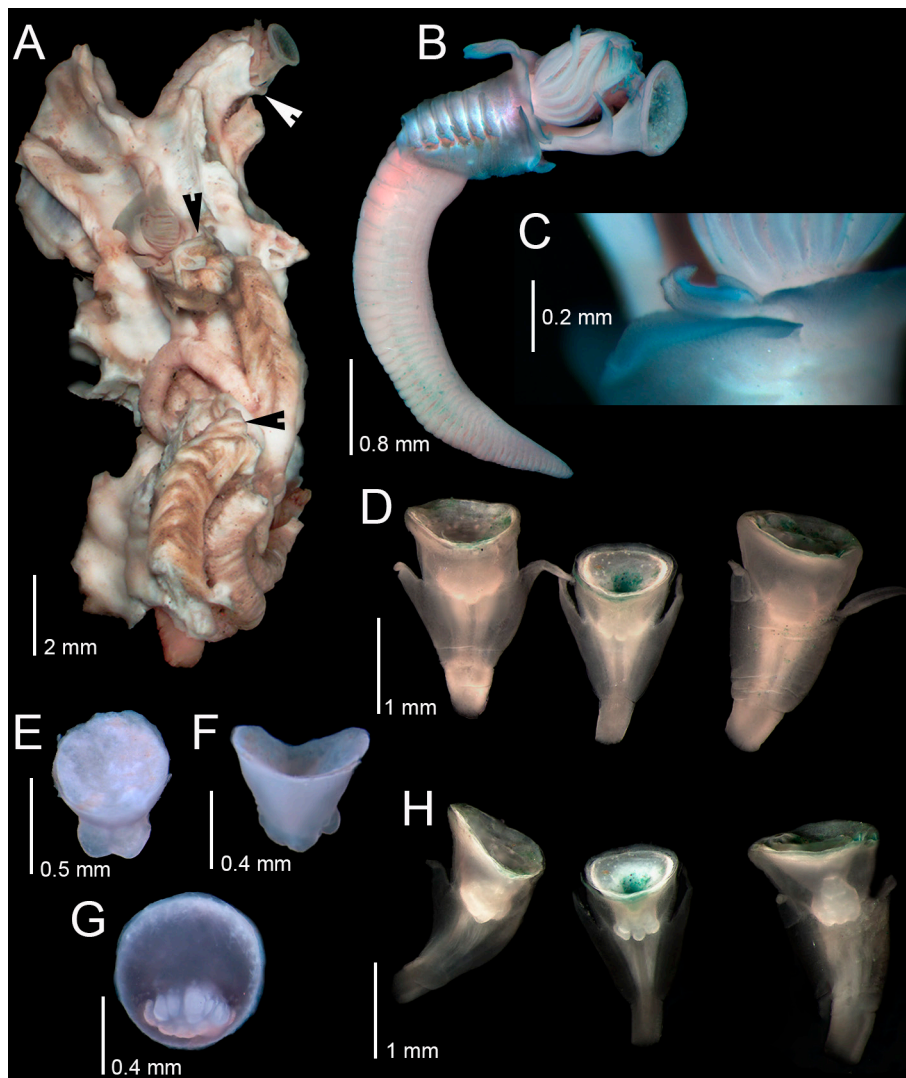


Figure 2. *Spirobranchus straughanae* sp. nov. A. Fragment of a tube cluster, arrows pointing to tube mouths (AM W.41813). B. Complete specimen removed from tube, lateral view (AM W.41813). C. Detail of collar lobes and tonguelet, lateral view (AM W.41813). D. Three dissected opercula (AM W.4060). E – G. Dissected opercular endplate removed from soft tissue (AM W.4060). E. Superior view with two-teeth talon. G. Ventral view with three-teeth talon showing protrusions. H. Same opercula as in D, cleared with glycerin.

Peduncle. Smooth, triangular in cross-section, inserted slightly left to mid-dorsal line (Fig. 2B, D). Pair of smooth triangular distal peduncular wings, tapering towards rounded tips, not reaching tip of operculum (Fig. 2D). Constriction present at wings base (Fig. 2D).

Operculum. Opercular ampulla funnel-shaped, covered with white calcareous deeply concave opercular endplate, without ornamentation, circular in top view (Fig. 2B, D–H). Talon embedded in opercular ampulla (Fig. 2D, H), ending in two or three same-sized unequally rounded teeth (Fig. 2E–G), smooth or with distal protrusions (Fig. 2G).

Collar and thoracic membranes. Three-lobed collar extending to margins of inter-radiolar membranes (Fig. 4A–C). Dorso-lateral lobes long, rounded with smooth edges, mid-ventral lobe round to triangular, reaching near crown top, inserted between radiolar lobes. Dorso-lateral lobes continuous with thoracic membranes, forming a short ventral apron covering first abdominal segment. Inner surface of collar lobes covered with dense, evenly sparse tufts of cilia (Fig. 4C). Bilobed tonguelets present between collar lobes

(Fig. 2C), inner lobe round and outer lobe leaf-shaped, twice as long as inner lobe, with a smooth rim. Tonguelet lobes with cilia along edge (Fig. 4E).

Thorax. Six uncinigerous chaetigers (Figs. 2B, 3A–C). Collar chaetae absent in adults, juveniles sometimes with slim limbate collar chaetae. Notopodial lobes conical, partially covered with neuropodia (Figs. 4B, 5A). Thoracic chaetae limbate, serrated when seen under higher magnification, arranged in two fascicles of different lengths per notopodium, with inferior thinner chaetae and superior thicker chaetae (Fig. 5A). Neuropodial lobes rectangular (Figs. 3A, 4B), partially covering next neuropodia, all bearing straight transverse tori of similar size along thorax. Thoracic uncini saw-shaped, with nine curved teeth, and flat, rounded to spatulate anterior peg (Fig. 5B). Parapodial lobes approach each other posteriorly, forming a ventral triangular depression (Fig. 4B–C).

Abdomen. One to four achaetous segments anteriorly (Fig. 4A). Number of chaetigers varying from 30 to 45 ($n = 16$). Abdomen approximately three times longer than thorax (Fig.

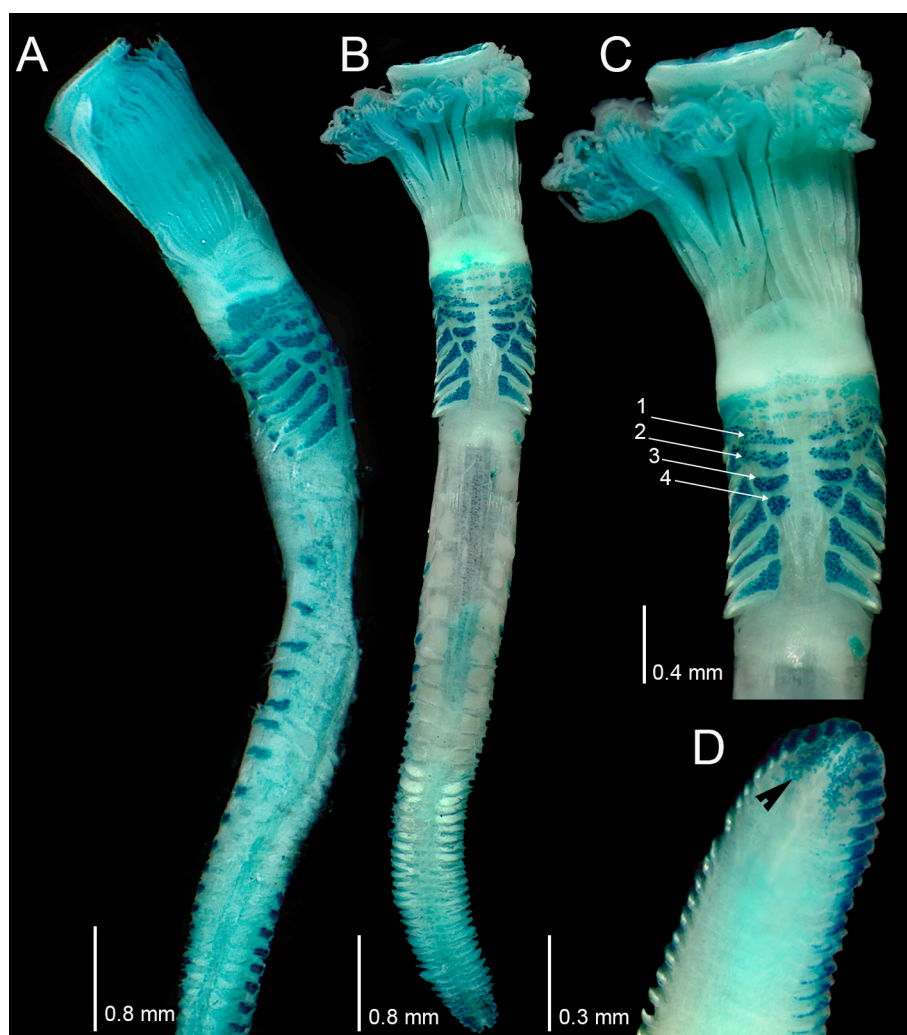


Figure 3. Glandular distribution patterns in *S. straughanae* sp. nov. (AM W.4060) stained with methyl green. A. Lateral view of thoracic and abdominal neuropodia. B. Ventral view showing glandular pattern in triangular depression region. C. Close-up view of triangular depression region. Numbers 1 – 4 represent pairs of ventral shields. D. Posterior region of abdomen, arrow pointing to dorsal glandular clusters anterior to pygidium.

2B, 4B), with larger anterior chaetigers, the posterior third with densely packed, much shorter chaetigers (Fig. 4B). Notopodial uncini smaller than thoracic ones, saw-shaped, with 10–13 teeth and somewhat flat or gouged anterior peg (Fig. 5E). On posterior chaetigers, uncini sometimes saw-to-rasp (Fig. 5E). Two to four neuropodial chaetae per fascicle, true trumpet-shaped (Fig. 5C), abruptly bent, each with two distal rows of denticles separated by a groove (Fig. 5E) and a lateral filiform projection serrated with minute teeth. Pygidium bilobed, with terminal anus (Fig. 3D).

Glandular clusters (Fig. 3). Ventral collar lobe bearing numerous glandular patches, less dense ventrally than on lateral lobes forming horizontal bands (Fig. 3A–C). Thorax with four pairs of shields, not fused medially (Fig. 3B–C). First and second pairs as faint bands of about the same size, marked by scattered glandular spots. Third and fourth pairs shorter than second pair, third round- to square-shaped and fourth pair round- to diamond-shaped (Fig. 3C). Thoracic neuropodia covered with glandular clusters (Fig. 3A–C), each forming a triangular patch (Fig. 3B–C) with a circular terminal spot (Fig. 3A). Glandular clusters absent on apron. Abdomen with notopodia covered bearing glandular bands

around tori (Fig. 3A), denser posteriorly, near fecal groove rim. Dense dorsal glandular coverage near pygidium (Fig. 3D).

Habitat. Intertidal to shallow subtidal, under sheltered rocks.

Type-locality. Clump Point, Mission Beach, Queensland, Australia

Distribution. Tropical to subtropical along North Queensland coast from Cape Bedford to Dunwich (15°S to 27°S), becoming less common southwards to Point Vernon (lat. 25°S) (Endean *et al.*, 1956a, 1956b; Straughan, 1967; present study).

Etymology. The species is named after Dr. Dale Straughan, who first examined specimens and provided taxonomic information about this taxon (as *Pomatoleios kraussii*) in Australia.

Remarks

Morphology. Comparisons of relevant characters for *S. straughanae* sp. nov. and other species in the complex are provided in Table 3. Apart from juveniles, individuals from the same populations were variable in size, but body length

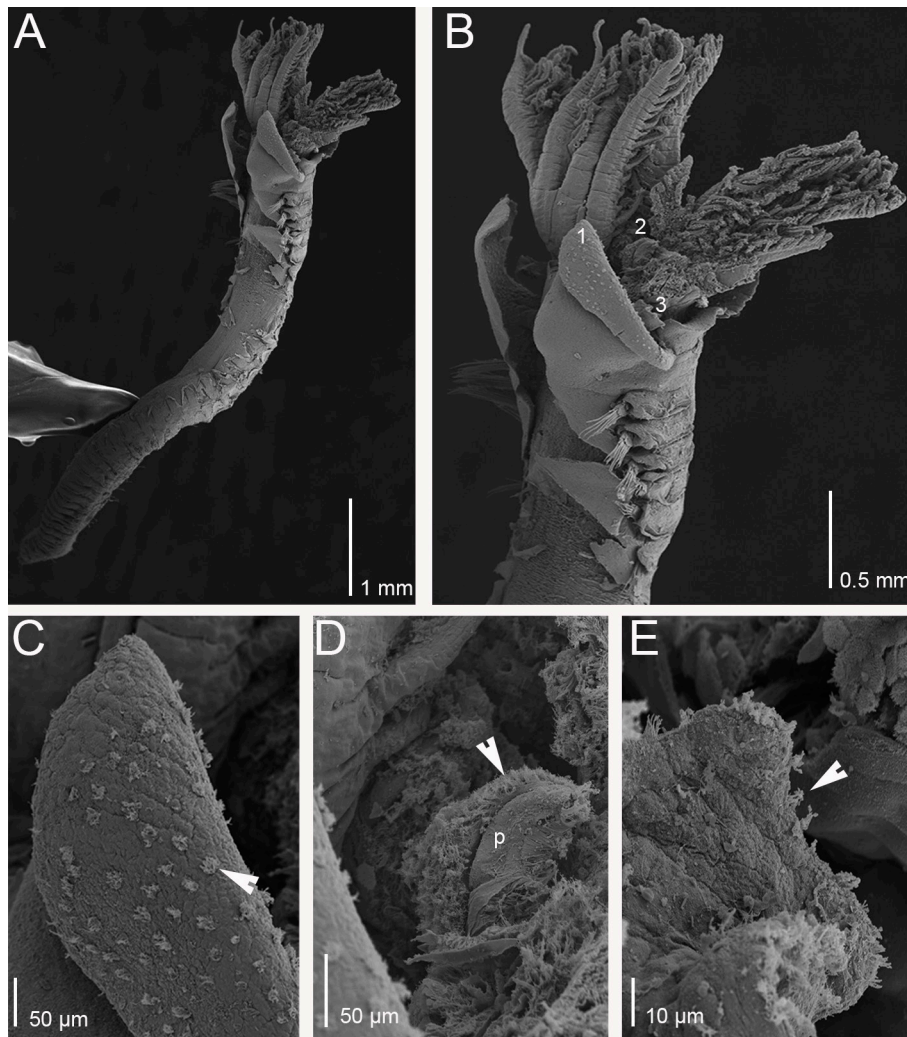


Figure 4. SEM images of *S. straughanae* sp. nov. (AM W.4060). A. Complete specimen in dorsolateral view. B. Detail of thorax. Numbers 1, 2 and 3 are regions seen in detail on C – E. C. Collar inner margin showing tufts of cilia. D. Inner crown region showing one palp (p) with densely ciliated edge. E. Tonguelet outer lobe showing tufts of cilia positioned along the rim. All arrows point to cilia.

could have been affected by fixation conditions. The body size is worth mentioning when comparing *S. straughanae* sp. nov. to other *S. kraussii* complex species, as *S. kraussii* is significantly larger (reaching 31 mm) than *S. straughanae* sp. nov. reaching 12 mm. Sivananthan *et al.* (2021) mentioned that *S. bakau* is similar in size to the syntypes of *S. kraussii*, though the latter could be juveniles or specimens contracted due to dehydration (Simon *et al.*, 2019). *Spirobranchus bakau* length range is 3–14 mm (Sivananthan *et al.*, 2021), meaning the new species size is similar to that of specimens found in Tanzania (Pixell, 1913), Philippines (Pillai, 1965; Sivananthan *et al.*, 2022), China (Fiege & Sun, 1999), Turkey (Çinar, 2006), Hong Kong (Sun *et al.*, 2012), Persian Gulf and Gulf of Oman (Pazoki *et al.*, 2020), and Singapore (Sivananthan *et al.*, 2021). Additionally, *S. lirianee* with adults measuring around 13 mm (ICB pers. obs.) should be considered part of this group, although Brandão and Brasil (2020) did not specify its size.

Tube morphology in the new species was not remarkably different from that of other species in the *S. kraussii* complex, but both one pointed longitudinal keel and two keels forming a flat projection over the tube mouth were observed. Single-keeled tubes seem to be more common in younger specimens.

Faint blue coloration similar to that observed in *S. lirianee* and *S. akitsushima* was present in some preserved specimens of *S. straughanae* sp. nov. Sivananthan *et al.* (2021) reported a wider variation within tubes of *S. bakau*, with winged median keels and presence of lateral keels, not observed in *S. straughanae* sp. nov.

A number of new characters have been proposed in descriptions of new species in the *S. kraussii* complex. Although opercular morphology is simple compared to that of other *Spirobranchus* species, specimens in the *S. kraussii* complex possess variable talons. Descriptions of talon morphology are not consistent in the literature (Simon *et al.*, 2019). *Spirobranchus straughanae* sp. nov. is similar to *S. lirianee*, *S. sinuspersicus* and *S. kraussii* in possessing talons ending in teeth, but opercula in *S. kraussii* and *S. sinuspersicus* present a shallower concavity, not funnel-shaped. The talon in *S. sinuspersicus* is short, not extending deep into the opercular ampulla, with 2–3 teeth. In *S. kraussii* the talon goes deeper into the ampulla than in *S. sinuspersicus* and 10 small teeth are present (termed protrusions in Pazoki *et al.*, 2020 and followed by Sivananthan *et al.*, 2021 and Nishi *et al.*, 2022). The major difference between *S. straughanae* sp. nov. and *S. lirianee* is the number of

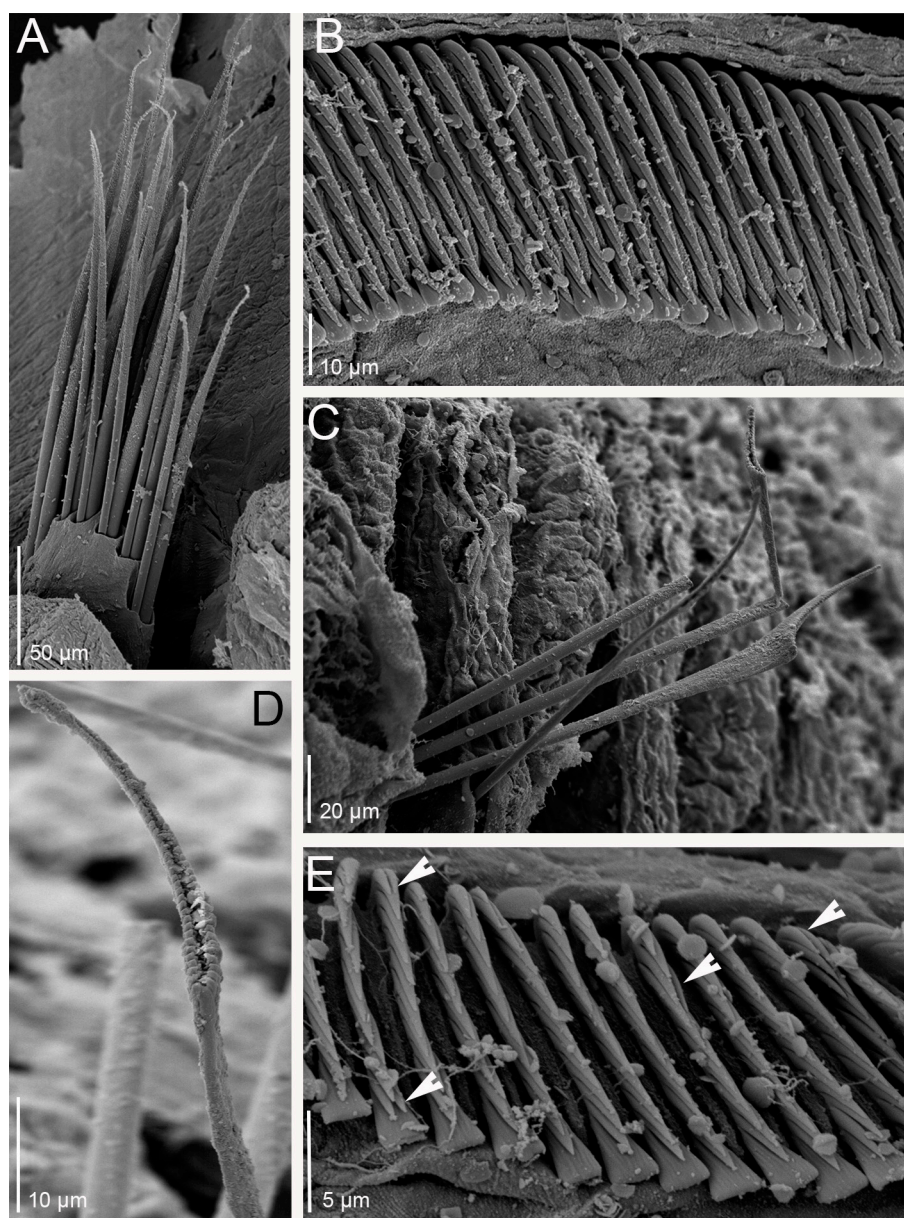


Figure 5. SEM images of *S. straughanae* sp. nov. chaetae (AM W.4060). A. Thoracic notopodial limbate chaetae. B. Thoracic uncini. C. Abdominal neuropodial true trumpet-shaped chaetae. D. Detail of a true trumpet-shaped chaeta. E. Abdominal uncini, arrows pointing at double toothed rows.

talon teeth, 2-3 in *S. straughanae* sp. nov. and usually 3-5 in *S. lirianaeae*. Furthermore, different degrees of the talon development were observed, including bifid smooth talons in smaller individuals, which suggests ontogenetic variability of this character. *Spirobranchus bakau* and *S. manilensis* have elongated talons, the former being peg-like and the latter somewhat rectangular (Sivananthan *et al.*, 2021, 2022). Nishi *et al.* (2022) reported that *S. akitsushima* either has very short talons or lacks them at all.

Pazoki *et al.* (2020) classified peduncular wings pattern in *S. sinuspersicus* as “V”-shaped when wings start at the peduncular basis, and “Y”-shaped when the wings start in the middle of peduncle. However, Nishi *et al.* (2022) suggested that in *S. akitsushima* the shape of peduncular wings could vary depending on the fixation method. Following this classification, in *S. straughanae* sp. nov. peduncular wings are “Y”-shaped, as in most species in the complex apart

from *S. sinuspersicus* and some specimens of *S. akitsushima*.

Juveniles in the *S. kraussii* complex have limbate collar chaetae that are usually shed as animals age, so they are absent in adults. Adult specimens of *S. bakau* often retain collar chaetae (Sivananthan *et al.*, 2021), but in *S. straughanae* sp. nov. adults with collar chaetae were not observed. Uncini from species of the complex also share some subtle similarities, as *S. sinuspersicus* shows double teeth in saw-shaped uncini, not only close to the peg as known for some *Spirobranchus* spp. (ten Hove & Kupriyanova, 2009), but also in the middle of an uncinus. The same was observed for *S. straughanae* sp. nov., but only in the abdomen.

Glandular clusters were useful in distinguishing specimens of the *S. kraussii* complex from *S. giganteus*, *S. minutus* and *S. sp.* (as *S. tetracerus*) in Brazil (Brandão & Brasil, 2020), but glandular distribution patterns are poorly

known for serpulids. Here, *S. straughanae* sp. nov. presented a pattern similar to that observed in *S. lirianeeae* with minor differences: in *S. lirianeeae*, ventral collar region and the apron are medially covered with glandular clusters that are absent in *S. straughanae* sp. nov. The first pair of ventral thoracic glandular shields on the triangular depression area in *S. straughanae* sp. nov. is distinct, whereas in *S. lirianeeae* there is only a band of scattered spots. The subsequent ventral shields are conspicuous in members of *S. lirianeeae*, the second and third pairs are wider than fourth, and all are nearly square to rectangular in shape, often with a fifth pair is present. In *S. straughanae* sp. nov., the first two pairs of ventral shields are less defined in comparison to those in *S. lirianeeae*, the second pair being oblique compared to the horizontal shields in the latter, while the third and fourth pairs are more rounded compared to those in *S. lirianeeae*. In *S. straughanae* sp. nov. the fifth pair of glandular shields and glandular coverage of apron (both present in *S. lirianeeae*) were not observed. Finally, the new species presents glands covering the dorsum on the posterior abdomen near the pygidium, not observed in *S. lirianeeae*.

Phylogenetic analyses. The results of ML analyses using the concatenated dataset are presented in Figure 6. The analysis inferred nine well-supported species: 1) *S. cariniferus* (New Zealand, bs 100), 2) *S. akitsushima* (Japan, bs 93), 3) *S. bakau*

(Singapore, bs 97), 4) *S. sinuspersicus* (Persian Gulf, bs 100), 5) *S. kraussii* (South Africa, bs 100), 6) *S. straughanae* sp. nov. (Qld, Australia, bs 98), 7) *S. sp. 5* (Japan, bs 100), 8) *S. sp. 6* (Japan, bs 93) and 9) *S. lirianeeae* including *S. sp. 2* (Brazil and Hawaii, bs 98). The relationship between the Hawaiian *S. sp. 2* sequence and *S. lirianeeae* from Brazil will be addressed in another study. *Spirobranchus lirianeeae* sequences were recovered as sister taxon of *S. straughanae* sp. nov., but with low support (bs 69). The clade *S. straughanae* sp. nov. + *S. lirianeeae* was recovered as sister clade to *S. kraussii* (bs 88). Monophyly of the *Spirobranchus kraussii* complex was well-supported (bs 100), with well supported relationships within the clade formed by *S. bakau*, *S. sinuspersicus*, *S. kraussii*, *S. straughanae* sp. nov., *S. lirianeeae* and *S. sp. 5* (bs 97). The unnamed *S. sp. 5* formed a clade with *S. bakau* (bs 98) and *S. sp. 6* formed a clade with *S. akitsushima*. These relationships were identical to the results in Nishi et al. (2022).

The inter-specific genetic distances of *cytb* sequences of the *S. kraussii* complex species used for phylogenetic reconstruction were measured using two parameters (Table 2). P-distance values, excluding the new species, ranged 0.4–25.8%, the lowest distance being between *S. lirianeeae* and *S. sp. 2*, whereas the highest being between *S. sp. 2* and *S. cariniferus*. It is worth mentioning that 0.4% is unusually low, whereas the second lowest p-distance

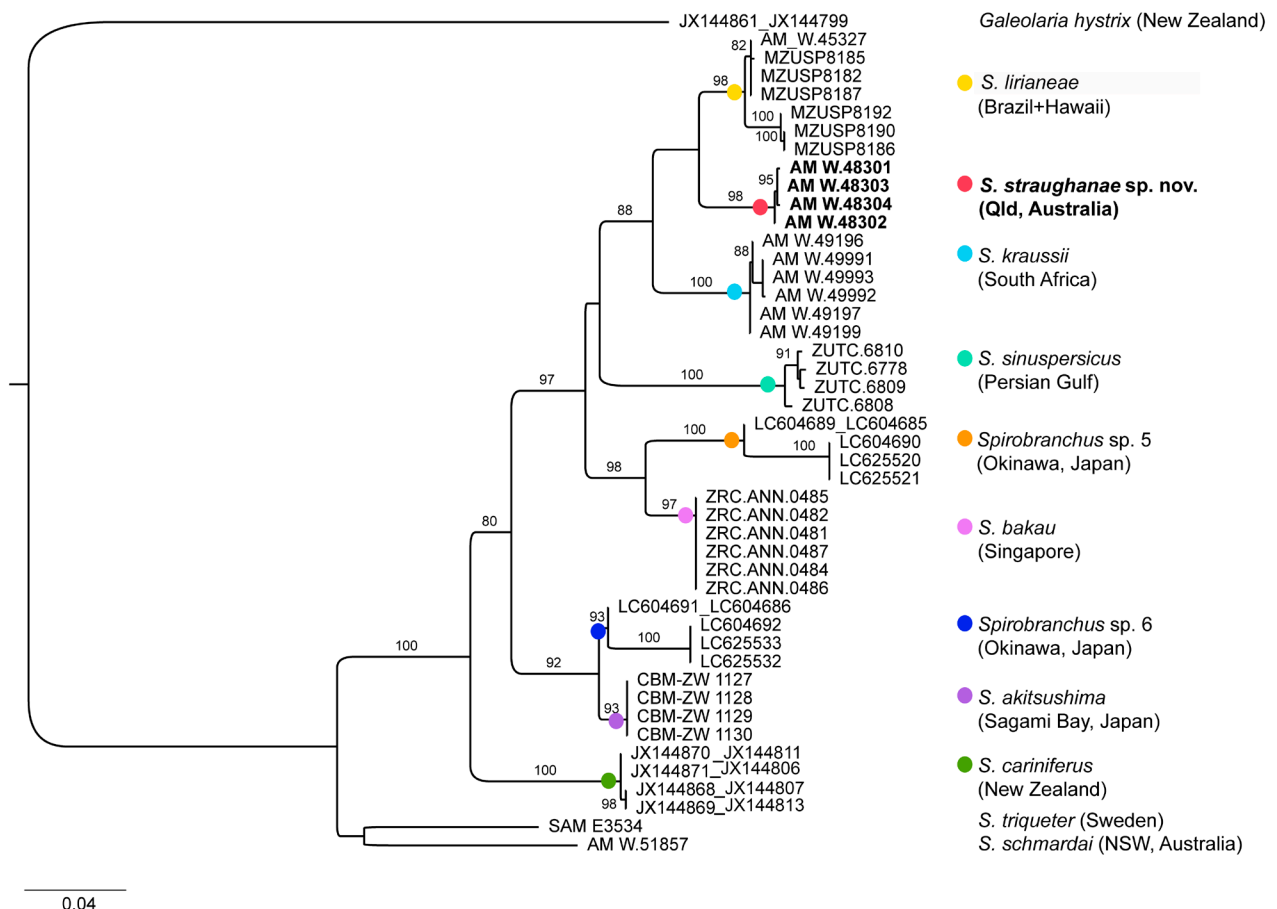


Figure 6. Phylogram of the maximum likelihood analysis for the concatenated (*cytb* + *18S*) sequence dataset. Terminals named using museum registrations numbers or, when not available, Genbank accession numbers. Numbers above nodes are bootstrap values. Only bootstrap values >80 are shown.

Table 3. Morphological comparison among species of the *S. kraussii* complex.

	<i>S. straughanae</i> sp. nov.	<i>S. akitsushima</i>	<i>S. bakau</i>	<i>S. cariniferus</i>	<i>S. kraussii</i>	<i>S. lirianeae</i>	<i>S. manilensis</i>	<i>S. sinuspersicus</i>
Total length of adults (mm)	7–12	5–12	3–14	~6–15	31	5–13	8–18	15
No. of abdominal chaetigers	30–45	30–60	27–45	~21–88	~70	~46	38–41	~41
Achaetous abdominal segments	anterior 1–4 segments	anterior 2–3 segments	anterior 1–3 segments	anterior 1–3 segments	anterior to mid-abdomen	at least 1st segments	anterior 1–3 segments	anterior 1–2 segment
Peduncular wings shape	y-shaped	y or v-shaped	v-shaped	v-shaped	y-shaped	y or v-shaped	v-shaped	v-shaped
Peduncular wings tips	tapering to round tip	not fringed, rarely bilobed	tapering or with truncated	tapering to round tip	smooth and pointed	tapering to round tip	tapering	tapering, rarely fringed
Peduncle insertion	left	left	left	left	left	left	left	central
Opercular endplate	funnel-shaped	slightly concave	slightly concave	flat to slightly concave	slightly concave	funnel-shaped	deeply concave	flat to slightly concave
Talon	2–3 teeth, smooth or with protrusions	absent, no protrusions or with a rounded swelling	peg-like structure extending into ampulla, bifid or trifid	?	short, extending into ampulla, 10 teeth	short, extending into ampulla, 3–5 teeth	extending into ampulla, with a series of tooth-like serrations along the edge	circular, with 2 or 3 small protrusions
Thoracic uncini	saw- and saw-to-rasp-shaped	saw-shaped	saw-to-rasp-shaped	?	saw-shaped	saw-shaped	?	saw- and saw-to-rasp-shaped
Tonguelets	bi-lobed, outer lobe leaf-shaped, inner lobe, with twice as long, with cilia along edge	folded, leaf-like	bi-lobed, triangular	?	?	bi-lobed, outer and inner lobe leaf-shaped, with outer twice as long, with fringed rim	bi-lobed	bi-lobed, triangular
Collar chaetae in adults	absent	absent	frequently present	absent	absent	absent	absent	absent
Number of ventral shields	4	?	?	5	?	4–5*	?	?

Table 3. *Continued...*

Table 3. Continued.

	<i>S. straughanae</i> sp. nov.	<i>S. akitsushima</i>	<i>S. bakau</i>	<i>S. cariniferus</i>	<i>S. kraussii</i>	<i>S. lirianee</i>	<i>S. manilensis</i>	<i>S. sinuspersicus</i>
Shape of ventral shields	1st pair undefined; 2 nd pair long, oblique and round; 3 rd round - to square-shaped; 4th pair round- to diamond-shaped	?	?	?	?	1st pair as scattered spots; 2nd – 4th pairs trapezoidal to square-shaped; 5th pair, if present, as small spots	?	?
Source	This study	Nishi <i>et al.</i> , 2022	Sivananthan <i>et al.</i> , 2021	This study	Simon <i>et al.</i> , 2019	Brandão & Brasil, 2020; *updated in this study	Sivananthan <i>et al.</i> , 2021, 2022	Pazoki <i>et al.</i> , 2020

found between *S. akitsushima* and *S. sp. 6*. (4%) is also unusual since other low values started at 15%. The overall values were also observed by Nishi *et al.* (2022) under the same parameters. The p-distance between *Spirobranchus straughanae* sp. nov. and the other *S. kraussii* complex species ranged 12.8–25.6%, with the lowest distance to *S. lirianee* and the largest to *S. cariniferus*. Regarding the Kimura 2 parameter, values excluding *S. straughanae* sp. nov. ranged 0.4–49.3%, the lowest distance being between *S. lirianee* and *S. sp. 2*, the highest being between *S. bakau* and *S. sinuspersicus*. Similar to p-distance, the K2P distances between *S. lirianee*/S. sp. 2 and *S. akitsushima*/S. sp. 6 were unusually low, whereas overall low values excluding these were at least 23%, similar to those observed by Palero *et al.* (2018). The distance between *Spirobranchus* sp. nov. and the other *S. kraussii* complex species ranged 17.3–46.6%, with the lowest distance to *S. lirianee* and the highest to *S. cariniferus*. Intra-specific distance among *S. straughanae* sp. nov. specimens was 0.34–0.67% (p-distance) and 0.34–0.7% (K2P), whereas the closest related congeners presented similar values: *S. lirianee* excluding *S. sp. 2* was 0.3–4.7% (p-distance) and 0.34–5.4% (K2P), while *S. kraussii* was 0.34–2% (p-distance) and 0.34–2.1% (K2P). Similar values were observed for intra- and interspecific genetic distance among other Serpulidae genera (Sun *et al.*, 2016; Styan *et al.*, 2017).

Discussion

The present study results show that the populations of *S. cf. kraussii* in Queensland belong to a species that is not only genetically (see Simon *et al.*, 2019), but also morphologically distinct from *S. kraussii* and other members of the *S. kraussii* complex. This is not surprising given that species of shallow-water (intertidal to low subtidal) genus *Spirobranchus* initially reported as widely distributed almost invariably turn out to be species complexes when reviewed (e.g., ten Hove, 1994; Fiege & ten Hove, 1999; Simon *et al.*, 2019; Kupriyanova *et al.*, 2022). In their review of serpulid taxonomy, ten Hove and Kupriyanova (2009) mentioned five nominal *Spirobranchus* species (*S. corniculatus* (Grube, 1862), *S. gardineri* Pixell, 1913, *S. giganteus* (Pallas, 1766), *S. polytrema* (Philippi, 1844) and *S. tetraceros* (Schmarda, 1861)) as likely species complexes. Since the initial confirmation of the species complex status of nominal *S. kraussii* by Simon *et al.* (2019), every analyzed population collected in the localities remote from South Africa resulted in a description of a new species (Pazoki *et al.*, 2020; Sivananthan *et al.*, 2021, 2022; Nishi *et al.*, 2022; this study).

Spirobranchus straughanae sp. nov. is the eighth species described in the *S. kraussii* complex and more species are likely to be discovered. Currently, *Spirobranchus* sp. 2 *sensu* Simon *et al.* (2019) from Hawaii is being investigated as an occurrence of the Atlantic *S. lirianee* in the Pacific Ocean, whereas *S. sp. 5* and *S. sp. 6 sensu* Kobayashi and Goto (2021) from Japan await further studies within a broader review of the complex. The status of the tropical Tanzanian *S. crosslandi* remains to be clarified with a combination of morphological and molecular data.

Finally, a mysterious intertidal species from the *Spirobranchus kraussii* complex was introduced to and

established in the eastern Mediterranean in the 1980s. This species was reported as *Pomatoleios kraussii* (Ghobashy *et al.*, 1986, 1990; Shalla & Holt, 1999; Belal & Ghobashy, 2014; Egypt; Ben-Eliahu & ten Hove, 1992; Israel; Çinar, 2013; Türkiye) based on the assumption that the nominal species is widely distributed in the Indo-Pacific. The species was found in large densities on both sides of the Suez Canal in Egypt (Shalla & Holt, 1999; Belal & Ghobashy, 2014) and thus was regarded as a Lessepsian migrant. However, a species under the name *S. kraussii* has not been reported from the Red Sea, therefore, the vector, origin, and identity of this species remain unknown. It could have been introduced from the Arabian (Persian) Gulf as shown for *S. arabicus* Monro, 1937 (Kupriyanova *et al.*, 2025). If so, the source population is likely to belong to *S. sinuspersicus*, but testing this hypothesis requires a study using DNA data.

While reporting *P. crosslandi* in Australia, Endean *et al.* (1956a, 1956b) described its distribution as north Queensland, becoming more common further north, from Point Vernon (25°S) to White Cliffs (20°S), while occurring less predominantly, as far south as Scarborough, north of Brisbane. Unfortunately, Endean *et al.* (1956a, 1956b) did not provide a list with registered occurrences of this species. Dew (1959) cited Endean *et al.* (1956a) when recorded *P. kraussii* but did not specify its distribution. Knox (1960) included a map of the region sampled by Endean *et al.* (1956a, 1956b) and added two question marks north of the known range, without explaining their significance or geographic names, thus describing the distribution of *P. kraussii* (sic!) as subtropical in Queensland.

Guiler (1960) referred to Endean *et al.* (1956a, 1956b) for information on the distribution of *P. crosslandi* but reported its range spanning from latitudes 10°S to 25°S, not providing geographic names. This contrasts with Endean *et al.* (1956a, 1956b), where the northernmost study site was at latitude 16°S. Moreover, Guiler (1960) stated that the species did not extend south of Point Vernon (25°S), despite Endean *et al.* (1956a) mentioning its presence in Scarborough (27°S). Therefore, information presented in Guiler (1960) is not reliable to ascertain that the species occurs as far north as Cape Bedford (15°S), as later reported by Straughan (1967).

Within its Australian range, Endean *et al.* (1956a, 1956b) mentioned “*P. crosslandi*” as a dominant species in intertidal, low-salinity zones under sheltered rocks. The type series of *S. straughanae* sp. nov. collected by EKK in Mission Beach was found in the same habitat as described by Endean *et al.* (1956a, 1956b), but no large aggregations or intertidal belts were observed. Species in the *S. kraussii* complex typically build intertidal belt-forming aggregations on rocky shores (Simon *et al.*, 2019; Pazoki *et al.*, 2020; Nishi *et al.*, 2022; Sivananthan *et al.*, 2022), whereas *S. bakau* found in mangroves is an exception (Sivananthan *et al.*, 2021). Brandão and Brasil (2020) recorded only solitary individuals of *S. lirianeeae*, but in later collections by ICB, small intertidal aggregations with around 20 tubes were observed. It is difficult to determine the gregarious nature of *S. straughanae* sp. nov. based on the museum material because individually fixed specimens could have been removed from aggregations.

Based on our morphological and molecular results, we assume that Endean *et al.* (1956a, 1956b) and Guiler (1960) referred to the species herein described as *S. straughanae* sp. nov. when they reported *P. crosslandi* in Queensland, and

so did Dew (1959) and Knox (1960) when they mentioned *P. kraussii* and *P. kraussi* (sic!), respectively. Whether *S. straughanae* sp. nov. is the only species of the *S. kraussii* complex in Australia remains to be seen.

The results herein highlight the importance of integrative taxonomic studies and standardized methods in unraveling cryptic diversity in marine invertebrates. Future research should focus on expanding sampling and molecular analyses across the Indo-Pacific to resolve the status of undescribed taxa. Ecological and developmental studies are needed to understand intraspecific variation in diagnostic features such as talon morphology, tube structure, and aggregation behavior within *Spirobranchus* species.

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