Research Article

Not out of Africa: *Spirobranchus kraussii* (Baird, 1865) is not a global fouling and invasive serpulid of Indo-Pacific origin

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Abstract

A common intertidal belt-forming serpulid *Spirobranchus kraussii* (Baird, 1865) was originally described from South Africa and subsequently reported from tropical and subtropical localities, mainly in the Indo-Pacific and Mediterranean Sea. It generally is assumed that the wide distribution of the nominal species is a result of human-mediated translocations. Here we provide a detailed illustrated re-description of *S. kraussii* based on the historical types and material freshly collected in South Africa from the type locality (Western Cape Province) and Eastern part of the country (KwaZulu-Natal Province). The description is accompanied by DNA sequence data (cyt b and 18S). Phylogenetic analysis of DNA sequences of specimens collected in South Africa, as well as farther afield in Australia, Japan, Hawaii, and Kuwait reveal several genetically distinct regionally distributed lineages. Closer comparative examination of morphological characters and environmental requirements reported in populations around the world has provided further evidence to reject the accepted status of this species as widespread in the Indo-Pacific. We conclude that *Spirobranchus kraussii* is a warm temperate/subtropical intertidal species restricted to South African coasts. It belongs to a globally distributed complex including some tropical fouling and invasive species. Further study into taxonomy and invasion ecology of this complex, especially in the Mediterranean, is needed.

Key words: non-indigenous species, introduced, species complex, cyt b, 18S

Introduction

Polychaetes were assumed to have naturally wide, or even cosmopolitan, distribution ranges for much of the twentieth century (e.g., Hartman 1959; Day 1967). However, recent studies overwhelmingly demonstrate that “cosmopolitan” taxa usually represent complexes of either similar morphospecies or cryptic (only genetically distinct) species (see Nygren 2014; Hutchings and Kupriyanova 2018 for reviews; Nygren et al. 2018). The exceptions are the wide distributions resulting from artificial translocation of organisms beyond their natural ranges, i.e., as non-indigenous species (NIS) (e.g., Ben-Eliahu and ten Hove 1992; Çinar 2006,
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2013; Bastida-Zavala 2008; Link et al. 2009; Mead et al. 2011). In a global review, Çinar (2013) listed 292 polychaete species that have been recorded as NIS. Amongst these are 46 species of Serpulidae that include nominal species for which a non-indigenous status has been confirmed in at least parts of their distributions, for example, Ficopomatus enigmaticus (Fauvel, 1923) in the USA (e.g., Bastida-Zavala 2008; Pernet et al. 2016) and Hydrodoides dianthus (Verrill, 1873) in Japan, China, USA and Brazil (Link et al. 2009; Sun et al. 2017). The list also includes taxa, such as Hydrodoides brachyacantha Rioja, 1941, that have since been proved to be a complex of morphologically similar species with distinct distributions (Sun et al. 2016). The situation is further complicated when assumed NIS turn out to be complexes of species, of which some may be non-indigenous (e.g., F. enigmaticus, Styan et al. 2017; H. dianthus, Sun et al. 2017). Thus, there is a danger of not only overestimating the distribution ranges of species, but also incorrectly assigning species with the status of “non-indigenous” if identifications are not confirmed with thorough taxonomic investigations.

A suspiciously widespread serpulid in the list of Çinar (2013) that requires further investigation (Hutchings and Kupriyanova 2018) is the intertidal belt-forming Spiobranchus kraussii (Baird, 1865). This species was first described as Placostegus cariniferus var. kraussii by Baird (1865), as a South African variety of Placostegus cariniferus (Gray, 1843) from New Zealand (originally described as a vermetid mollusc Vermetus cariniferus Gray, 1843). The type locality is indicated as Cape of Good Hope and the type material is held in the Natural History Museum, London (NHM). Nearly 50 years later, Pixell (1913) established a monotypic genus Pomatoleios, characterised by the absence of collar chaetae, with the type species Pomatoleios crosslandi and the type locality Ras Changani and Chwaka, off Tanzania. P. crosslandi from Eastern Africa was later reported from localities such as Madras, India (Fauvel 1932), South Africa (Monro 1933; Day 1934), Onagawa Bay, Honshu, Japan (Okuda 1937) and even Topolobampo, Gulf of California, Mexico (Rioja 1947). The latter record has not been confirmed and is not mentioned in Bastida-Zavala’s (2008) overview though the latter mentions “Pomatoleios sp.” from Pacific Panama.

During a visit to the NHM (British Museum) John Day examined the type material of Placostegus cariniferus from New Zealand, P. cariniferus var. kraussii from South Africa and Pomatoleios crosslandi from Eastern Africa (Day 1955). He concluded that P. cariniferus var. kraussii was distinct from P. cariniferus, thus elevating the South African taxon to full species status. He also referred the South African species to Pomatoleios owing to the absence of collar chaetae and synonymised P. crosslandi with P. kraussii as they “proved to be identical” (Day 1955). Although this synonymisation was accepted by Hartman (1959), both names continued to be used for more than a decade, with Morgans (1959) and Stephenson
and Stephenson (1972) using both names in the same publications when presumably referring to one and the same species in South Africa.

The acceptance of the name *Pomatoleios kraussii* was similarly slow when applied in the north-western Indo-Pacific. *P. crosslandi* was recorded in Sri Lanka (Pillai 1960) and Hartman herself included this species in a list of polychaetes in the northern Indian Ocean (Hartman 1974). However, in 1971 *P. kraussii* was reported from Sri Lanka (Pillai 1971) and Kuwait (Mohammad 1971), after which the name became widely used in the Arabian (Persian) Gulf (e.g., Mohammad 1974, 1975; Crisp 1977; Wehe and Fiege 2002). Ishaq and Mustaquim (1996) claim the first find of *P. kraussii* in Pakistan and remarked that the descriptions by Day (1955, 1967) conform to that of their specimens, except for the number of teeth on the thoracic uncini.

*Pomatoleios kraussii* has been reported as a Lessepsian migrant in the Suez Canal and eastern Mediterranean Sea, including Turkey (e.g., Ghabashy et al. 1986, 1990; Ben-Eliahu and ten Hove 1992; Shalla and Holt 1999; Çinar 2006; Belal and Ghabashy 2014).

In the Pacific Ocean, Knox (1960) identified two intertidal belt-forming species that we presently both place in the genus *Spirobranchus: Pomatoleios kraussii* [sic!] on the subtropical coasts of Queensland, Australia, and *Pomatoceros cariniferus* on the transitional warm temperate and cold temperate New Zealand shores. However, he added to the confusion by using the name *P. kraussii*, with a South African type locality, for a Northern Australian taxon, and *P. crosslandi* for the species on the subtropical and warm temperate shores of East and South Africa. Pillai (1965) reported *P. kraussii* var. *manilensis* from Manila, Philippines, while Straughan (1967) again used the name *P. kraussii* for specimens from Queensland, presumably following Knox (1960). Even further afield, Imajima and Hartman (1964), Uchida (1978), Miura and Kajihara (1984) and Nishi (1993) used this name for specimens from Japan from warm temperate Sagami Bay, Honshu to tropical Okinawa, while Straughan (1969a, b) and Bailey-Brock (1987) reported it from Hawaii, and Chan et al. (2014) most recently described larval settlement of “*S. kraussii*” from Singapore.

Pillai (2009) synonymised the genus *Pomatoleios* with *Spirobranchus* arguing that the absence of collar chaetae was not enough to separate the two genera since some juvenile *Pomatoleios* possess collar chaetae. He also reported *Spirobranchus kraussii* from Abu Dhabi (Pillai 2009), based on a sample deposited in Natural History Museum (NHM ANEA 2009.23).

The reported distribution of nominal *S. kraussii* covering temperate, subtropical and tropical regions appears to be too wide to be natural. Hutchings and Kupriyanova (2018) suggested that wide distributions in marine annelids are suspicious and have to be proven rather than taken for granted. Thus, the taxon is either a complex of morphologically similar species with restricted distributions or a very successful invader. Here we take
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Figure 1. Map of Southern Africa, showing the ecoregions and westernmost edge of distribution. Spirobranchus kraussii occurs from Cape of Good Hope in South Africa to Xai Xai in Mozambique, with abundance decreasing northwards in the Natal Ecoregion, and particularly in the Delagoa Ecoregion. WC: Western Cape, EC: Eastern Cape; KZN: KwaZulu-Natal.

the first step towards unravelling this problem by providing a thorough re-description of real S. kraussii based on historical syntypes and material freshly collected in South Africa both from the type locality (Western Cape Province) and the Eastern part of its distribution (KwaZulu-Natal). The fresh material from South Africa is accompanied by DNA sequence data. The latter have been compared with sequences obtained from specimens collected in several distant localities of the reported range of the nominal S. kraussii. In addition, we compared morphology of specimens from South Africa with some key descriptions from other regions to gauge the congruence among specimens from the apparent wide range of the species.

Materials and methods

Sample collection and preservation

The type locality for Spirobranchus kraussii (Cape of Good Hope) is now within the Table Mountain National Park Marine Protected Area. Thus, samples were collected from rocks in the upper intertidal of Muizenberg (False Bay), just outside the boundary of the park, and further afield from rocks and rock pools in the upper intertidal at Danger Point (Walker Bay) in the Western Cape Province of South Africa. These locations fall within the western part of the warm temperate Agulhas Ecoregion (Figure 1) where mean annual temperatures range from 14 to 16 °C, although summer
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Temperatures can exceed 18 °C (Sink et al. 2012; Smit et al. 2013). Samples were transported live to the laboratory where they were stored in seawater until processed. Worms were removed from tubes by carefully cracking with cutting pliers. Worms were anaesthetized in 7% MgCl₂ in tap water, then either fixed in 4% formaldehyde in seawater for 24 hrs, rinsed in distilled water and stored in 70% ethanol or fixed directly in 96% ethanol. Additional samples collected from Park Rynie, KwaZulu-Natal (30°18′S; 30°43′E, collected by J. Kara, 8/26/2016) were used for molecular analyses only and fixed directly to 96% ethanol. This location falls within the subtropical Natal Ecoregion (Figure 1), where annual temperatures range from 20 to 25 °C (Sink et al. 2012; Smit et al. 2013). Opercula were removed from worms from Danger Point and Muizenberg and cleaned in a weak solution of household bleach (final concentration of 0.6% sodium hypochlorite) to expose the talon.

Worms in tubes were photographed in situ with a Samsung S6 Edge smartphone or an Olympus TG 5 digital camera. To record variation in colour, live worms were photographed with the Olympus TG5 digital camera, on the macro (stacking) setting. Photographs of the fixed worms and talon were taken with a Leica EC3 camera attached to a Leica MZ 75 stereomicroscope and stacked with Helicon Focus (version 6.8.0). Body length measurements (from tip of radioles to end of pygidium), thoracic width, opercular length and width were taken from digital photographs using the LasEs software (Version 3.3.0 2016). Tube openings were measured with a Tork Craft manual caliper.

For scanning electron microscopy, specimens were dehydrated through two washes in 100% ethanol of 10 minutes each, then one wash in a 1:1 mixture of 100% ethanol and hexamethyldisalazane (HMDS) for 15 minutes and finally two washes in HMDS for 30 minutes each. The HMDS was then poured off and the specimens left overnight for residual HMDS to evaporate off. Specimens were sputter-coated with gold palladium and viewed on a Zeiss Merlin scanning electron microscope at the Stellenbosch University Central Analytical Facility.

Type material of Spirobranchus kraussii and S. kraussii var. manilensis from the Natural History Museum of London (abbreviated as NHM) and additional specimens of S. kraussii from the Iziko Museum of Cape Town (abbreviated as IZIKO) were examined. Old South African material of S. kraussii present in the Zoological Museum Copenhagen and Naturalis (Leiden) agreed in detail with our fresh material (see Taxonomical remarks). Specimens collected in this study were deposited at Iziko and Australian Museum, Sydney, Australia (abbreviated as AM).

Extraction, amplification, and sequencing

Freshly collected material from South Africa, as well as from Australia, Japan, Kuwait, and Hawaii, USA was used for the molecular part of the study.
Table 1. Collection information and GenBank accession numbers of specimens used in this study. All specimens are deposited in the collections of the Australian Museum (AM), KZN = KwaZulu-Natal, Qld = Queensland, SA = South Australia.

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carried out at the Australian Museum Center of Wildlife Genomics. All vouchers were examined and deposited in the collections of Australian Museum, Sydney (Table 1). Genomic DNA was extracted from posterior parts of abdomens using a DNeasy Blood and Tissue Kit (Qiagen, Dusseldorf, Germany) according to the manufacturer’s protocol. Stock DNA was diluted 1:10 with deionized water to produce template strength DNA for Polymerase Chain Reactions (PCR).

A combination of mitochondrial (cytochrome b) and ribosomal (18S) genes were used to check for concordance between these types of markers. Each of these markers evolves at a different rate and thus provides a different level of resolution. The 18S rRNA genes (approximately 1800 bp) were amplified by PCR in two overlapping fragments, one of approximately 1100 bp with the primers TimA (AMCTGGTTGATCCCTGCCAG) and 1100R2 (CGGTATCTGATCGTCTTCGA) from Nóren and Jordelius (1999); the other of approximately 1300 bp using 18s2F (GTTGCTGCAGTTAAA) and 18s2R (ACCTTGTTAGCTGTTTTACTTCCTC) from Kupriyanova et al. (2006). The 18S fragments were combined using BioEdit (Hall 1999). The Cyt b gene fragments (approximately 350 bp) were amplified with the primer pair Cytb424F (GGWTAYGTWTCCWTGRGGWCARAT) and cobr825 (AARTAYCAYTCYGGYTTRATRTG) (Halt et al. 2009). PCR conditions were as follows: an initial denaturation step at 94 °C for 3 min (18S and Cyt b), 40 cycles at 94 °C for 30 s (18S) resp. 45 cycles at 94 °C for 1 min (Cyt b), 52 °C for 30 s (18S) resp. 50 °C for 30 s (Cyt b), 72 °C for 30 s (18S) resp. 72 °C for 1 min (Cyt b), with a final extension at 72 °C for 5 min (18S) resp. 8 min (Cyt b). PCR products were sequenced by Macrogen TM, South Korea. Sequences were edited and aligned using Codon Code Aligner. A BLAST search confirmed the correct gene regions had been
amplified (Altschul et al. 1990) and the new sequences were submitted to GenBank.

Two sequence datasets were analysed. The first dataset included Cyt b of 15 specimens of *Spirobranchus cf. kraussii* collected in South Africa (type locality in Western Cape Province and another locality in Kwazulu-Natal), tropical Australia, Hawaii, Kuwait and temperate Japan, together with sequences of the outgroup species *S. cariniferus* from New Zealand and *Galeolaria caespitosa* from Australia downloaded from GenBank. Collection information and GenBank accession numbers of specimens used in this study are found in Table 1.

The combined analysis concatenated sequences of the 18S (1616 bp) and Cyt b (347 bp) gene fragments of the same specimens. Both datasets were aligned separately using ClustalX v2.1 (Larkin et al. 2007) with default settings (15 gap opening penalty and 6.66 gap extension penalty) and combined using BioEdit v7.0.5.3 (Hall 1999). The genes were separated as different partitions in the analyses. Best-fit models of nucleotide substitution identified using the Bayesian information criterion (BIC) as implemented in jModeltest v2.1.9 (Darriba et al. 2012) were HKY+F+G4 for Cyt b and K2P+I for 18S.

Phylogenetic trees were constructed with maximum-likelihood implemented in IQ-TREE v1.4.4 (Nguyen et al. 2015) with 1000 ultrafast bootstrap replicates (Minh et al. 2013).

### Results

**Order SABELLIDA**

**Family SERPULIDAE** Rafinesque, 1815

**Genus *Spirobranchus*** Blainville, 1818

**Spirobranchus kraussii** (Baird, 1865)

(Figures 2–6)

**Synonymy**

*Placostegus cariniferus* var. *Kraussii* Baird, 1865: 14–15 ("Promontorio Bonae Spei" = Cape of Good Hope; material studied); Hartman 1959: 585 (regarded as subspecies, *Placostegus cariniferus Kraussii*, see *Pomatoleios kraussii*).

*Placostegus caeruleus* Schmarda, 1861 [partim]: 29–30, pl. 21 fig. 178 (Cape of Good Hope, SA; the New Zealand material mentioned is questionable (Day 1967: 801, *Pomatoceros caeruleus*) and most probably belongs to *Spirobranchus cariniferus* (Gray, 1843), *fide* Glasby and Read 1998: 348); Möörch 1863: 417 (copy of Schmarda’s description); Hartman 1959: 585 (see *Pomatoceros caeruleus*).

*Vermilia caerulea* [partim]: de Quatrefages 1866: 512–513 (change of genus only, copy of Schmarda’s diagnosis)

*Vermilia* (*Placostegus*) *caerulea* [partim]: Hutton 1878: 326 (translation of Schmarda’s diagnosis)

*Pomatoceros caeruleus* [partim]: Day 1934: 80 (Table Bay, SA, and see below; name only, but not the synonym *Pomatoceros strigiceps* given, referring to New Zealand material); 1975: 204–205 (Cape of Good Hope specimens only; discussion of possible, and in our present view, partly mistaken synonymy of *Placostegus caeruleus* and *Pomatoceros strigiceps*); Hartman 1959: 586 (Cape of Good Hope material only).
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Pomatoleios crosslandi: Monro 1933: 508 (Still Bay, SA; name only); Day 1934: 80 (St. James, Port Alfred, Durban, all SA; diagnosis); 1951: 65 (KwaZulu-Natal, SA; diagnosis); Day et al. 1952: 389, 406 (several localities Knysna estuary, common to abundant; name); Eyre et al. 1938: 90–91, 95, 100, 111, pl. 10 (East London, SA; lower balanoid zone); Eyre and Stephenson, 1938: 30–31, 36 (Durban, lower balanoid zone); Stephenson et al. 1938: 6, 9, 13, 15, pl. 1 (Port Elizabeth, name only); Morgans 1959: figs 4, 6 (False Bay, SA; name only); Stephenson and Stephenson 1972: 32, 103–106, 110, 122, 130, 155, figs 8.7, 8.10, Plate 4 (South Africa; dominant on south and east coasts, mid-littoral zone, figure of mass of tubes).

Pomatoleios kraussii: Day 1955: 449 (Cape Point, St. James, Arniston, Still Bay, Storms River, Jeffrey’s Bay, Port Elizabeth, Kleinemonde (as Kleinmond), East London, Qolora, all SA; synonymy of Pomatoleios crosslandi by comparison of type material of both taxa; elevation of var. kraussii to full specific rank by comparison with New Zealand material of Placostegus cariniferus Gray, 1843); 1962: 654 (KwaZulu-Natal, SA; and see below; name only); 1967: 800–801 fig. 38.3.a–f (Cape, KwaZulu-Natal, SA; Mozambique; description); 1969, 1974: 65 (False Bay, SA to Maputo Bay (as Delagoa Bay) in Mozambique and see below; name in key); Hartman 1959: 587 (South Africa); Kirkegaard 1959: 108 (False Bay, SA; diagnosis); 1988: 89 (name only); Morgans 1959: 398–411 (False Bay, SA; belt-forming, name only, in error P. crosslandi in figs 4 and 6); Day et al. 1970: 34 (False Bay; name); Day et al. 1971: 211, 213 (Cape Agulhas, SA; name only); Stephenson and Stephenson 1972: 154, fig. 8.43 (Mozambique; as P. kraussi [sic], name only); Zibrowius 1973: 72–73 (False Bay; diagnosis, discussion; his records of Togo, Liberia for the time being are regarded as doubtful); ten Hove 1979: 290–291 (discussion of biotic factors leading to belt forming in e.g., Pomatoleios); Hartmann-Schröder 1974: 201–202 (Knysna Estuary SA to Xai Xai just north of Maputo Bay Mozambique; diagnosis); Moldan et al. 1979: 61, 62 (Cape south coast, name only); McQuaid and Branch 1984: 149 (warm sites on Cape Peninsula; name only); McQuaid et al. 1985: 117 (Cape Peninsula, sometimes forming large colonies in lower balanoid zone, name only); ten Hove and van den Hurk 1993: 34–35 (belt-forming); Branch et al. 1994, 1999, 2007: 52, fig. 23.4; 2010: 74, fig. 29.9 (South Africa to Mozambique; diagnosis); Bustamante 1994: Thesis Chapter 1, Appendix 1 (Cape Infanta, Mossel Bay, Tsitsikamma, Port Elizabeth, Dwesa, Balito Bay, all SA, not at Cape Vidal, SA, or Inhaca Island, Mozambique; name only); Bustamante and Branch 1996: 347 (south and east coasts, sheltered sites, name only); Bustamante et al. 1997: 126, 128 (Port Elizabeth, low intertidal on sheltered shores, name only), 129 (Port Elizabeth, mid intertidal on exposed shores, name only); Sink et al. 2005: 88, 90 (Natal and Maputoland regions of KwaZulu-Natal, mid-shore, name only); Hutchings et al. 2006: 21, 23 (Port Elizabeth harbour wall, 0 m, name only); Kemp et al. 2009: 23 (Still Bay and Arniston, cementing stone walls of intertidal fish traps, name only); Spirobranchus kraussii: Allanson et al. (2014): 23 (Knysna, on artificial rocky shores, name only); Branch et al. 2016: 74, fig. 29.9 (South Africa to Mozambique; diagnosis).

Tropical East Africa

? Pomatoleios crosslandi: Pixell, 1913: 85–86, pl. 9 fig.10 (description; Ras Shangani and Chwaka, Zanzibar); Hartman 1959: 587 (Indian Ocean; see Pomatoleios kraussii).

? Pomatoceros coeruleus [sic]: Fauvel 1919: 464 (Tuléar, Madagascar; diagnosis, hardly to be attributed without check of material).

? Pomatoceros caeruleus: Day 1934: 80 [partim]: (Madagascar; name only, but not the synonym Pomatoceros striigiceps given, referring to New Zealand material).

? Pomatoleios kraussii: Day 1955: 449 (synonymizing P. crosslandi; Zanzibar, Ras Shangani, Chwaka); 1962: 654 (Dar-es-Salaam, Tanzania; name only); 1967: 800–801 (Madagascar); 1969: 65 (tropical east Africa; name in key); Plante 1963: 187, 195, 197 (Tuléar, Madagascar; name only); 1965: e.g., 231–249, pl. 4–5, 7 (same; species from quiet water and low turbidity); Picard 1967: 20 (Tuléar; name, infra- and mid-littoral); ten Hove 1973: 5–6, fig. 34 (Madagascar; figure of talonate operculum).

Material studied

South Africa, Western Cape Province, Cape of Good Hope, collected by C. Krauss, 1840.9.30.28 (Syntypes: NHM, 15 complete, 10 incomplete specimens);

**Figure 2.** Spirobranchus kraussii tube structure. A) Clump of tubes from Muizenberg. Arrow shows blunt flap over tube mouth, arrowheads indicate pointed flaps. B) Tubes in situ in Danger Point with pointed flaps over tube mouth. C) Mouth of empty tube of syntype (NHM 1840.9.30.28). D) Dorsal view of tube in C, arrow indicating blunt flap over mouth opening (note brown deposit on inner wall). Scale bars: A 5 mm, C and D 2 mm. Photo by C. Simon.

Dale Brook, False Bay (34°7'30.45"S; 18° 27'12.19"E), collected by J.R. Grindley, 30 May 1961 (IZIKO MB-A020011; 9 specimens, 1 complete); Muizenberg, False Bay (34°6'44.74"S; 18°27'59.71"E), upper intertidal rocks and retaining wall, collected by C. Simon and E. Dirksen 19 November 2017 (IZIKO SAM-A086844, 16 complete specimens, 3 incomplete specimens); Danger Point (34°37'25.77"S; 19°19'9.88"E), mid intertidal rock pools, collected by H. van Niekerk and C. Simon 10 April 2017 (IZIKO SAM-A086845, 19 complete specimens, IZIKO SAM-A086846, clump of intact tubes; AM W.49196-49201, 6 specimens); St. James, False Bay, Kysten [coast], legit Th. Mortensen (1930, probably label error for 1929); identified by ten Hove 1988 Pomatoleios kraussii; reexamined April 2018 (3 large specimens, Naturalis coll. nr. ZMA V.Pol. 3639, exchange from Zoological Museum Copenhagen); Simonstown, False Bay, Galathea Sta. 172, 16 January 1951, identified by H. Zibrowius (1973) (cluster with 175 specimens, reexamined HAtH August 2018; ZMC NHMD 237841). Additional specimens: 3 specimens processed for SEM: Danger Point (34°37'25.77"S; 19°19'9.88"E), mid intertidal rock pools, collected by H. van Niekerk and C. Simon 10 April 2017.

**Material studied for comparison**

*Spirobranchus kraussii* var. *manilensis*, Philippines, Manila Bay, Binakayan (Paratypes: NHM, 4 complete specimens: 1966.33.34/43), from on and among farmed oysters.

**Description** (Based mainly on material from Muizenberg and Danger Point. Details of syntypes (1840.9.30.28) included in square brackets where relevant.)

TUBE: white blueish (fixed specimens) or greenish blue (Figure 2A, B). Lining of fresh tubes white to blueish (Figure 2B), but may be brown in old
**Figure 3.** *Spirobranchus kraussii*, live (A, B, D) and preserved (C) specimens from Muizenberg, showing variations in colouration. A) Radiolar crown with broad white band at base, B) Radiolar crown with orange pinnules, C) Blue pigment on edge of thoracic membrane and lateral collar lobes, extending into peduncle, D) radiolar crown with alternating white and golden brown bands and blue collar and pigmented spots (? radiolar eyes; arrows). Operculum regenerating end plate (large arrow). Scale bars: A–D 2 mm. Photo by C. Simon.

Tubes that may have been dried out (Figure 2D). Subcircular with flattened top in cross-section, lumen circular (Figure 2B, C). Internal tube opening (minimum, *mean*, maximum) 2–2.4–2.9 mm (SD = 0.34, n = 14). Outer tube opening 2.9–3.6–4.2 mm (SD = 0.44, n = 14) [outer tube opening 2.6 mm, lumen 2.1 mm]. Two keels giving tube a flat top extending over mouth of tube forming blunt or rounded to pointed flap (Figure 2A, D; arrows and arrowheads, respectively).

Radiolar Crown: In live and preserved specimens base of radioles (including inter-radiolar membrane) usually dark (brown, black, blue, grey) (Figures 3A, C, D, 4A, B), sometimes with white line along margin, one individual with bright yellow line. Radioles usually with alternating bands of light brown (gold or beige) and white (Figures 3A, D, 4A). Widths of bands vary. Few may have (partly) bright orange radioles (Figure 3B).
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Figure 4. Spirobranchus kraussii, preserved specimens from Danger Point. A) Dorsal view of anterior, B) Ventral view of anterior, C) Lateral view of anterior, D) Lateral view of posterior, E) Dorsal view of mouth. Abbreviations: aaz, achaetous abdominal zone; ac, abdominal chaetae; ap, apron; lcl, lateral collar lobe; mb, inter-radiolar membrane; mo, mouth; op, operculum; pa, palp; pd, peduncle; pw, peduncle wing; tf, terminal filament; tm, thoracic membrane; tn, tonguelet; v, ventral surface; vel, ventral collar lobe. Scale bars: A–C 2 mm, D and E 0.5 mm. Photo by C. Simon (A–D), H. van Niekerk (E).
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Pigment fades slightly after preservation. Crown composed of two lobes arranged in semicircles, each with 16–24 [11–13] radioles (n = 38 [10]), proximally connected by inter-radiolar membrane for about half of their length. Radioles rectangular in cross-section, external side smooth, inner side with two rows of pinnules becoming shorter distally, absent from the terminal filaments (Figure 4A, B), which are equal in size to the proximal (longer) pinnules. Prostomial eyes absent. We were unable to ascertain if the 3 to 4 pairs of pigmented areas per radiole contained ocelli or not (Figure 3D). Stylodes absent (Figures 3D, 4A, B).

MOUTH PARTS: Two thin, smooth lips, dorsal lip with median notch and pair of filiform palps (Figure 4E).

PEDUNCLE: Smooth, subtriangular in cross section, inserted just below left of radiolar lobe (Figure 4A), near medial line. Pair of smooth lateral wings with pointed tips, do not extend beyond operculum (Figure 4A). No constriction. Pseudoperculum absent. Colouration variable; ventral surface white with irregular or even black stripes (Figure 4C), dorsally dark purple-blue, grey-blue or white. Colouration extending into lateral wings.

OPERCULUM: Funnel-shaped (Figure 3D), continuing into peduncle without a constriction; rim varies in thickness. Opercular endplate slightly concave, calcareous, without ornamentation, blue-grey, circular to ovoid as seen from top (Figures 3C, 4A); 1.4–1.9–2.6 mm (SD = 0.2, n = 36) long, 1.2–1.7–2.1 mm (SD = 0.2, n = 36) wide. Talon embedded in opercular ampulla (Figure 5, see also Taxonomical remarks).

COLLAR AND THORACIC MEMBRANES: Three-lobed collar high (Figure 4B), extending to margin of inter-radiolar membrane, dorso-lateral lobes shorter, edge entire; continuous with thoracic membranes, forms apron across 1 to 2, but up to 5 abdominal chaetigers (Figure 4A–C). Pairs of small, wart-like protuberances of collar chaetiger absent; tonguelets between

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Figure 5. Spirobranchus kraussii, opercular endplate. A) lateral view, dorsal edge facing left, B) dorsal view, C) underside. Arrows indicate talon. Scale bars: 0.5mm. Photo by C. Simon.
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**Figure 6.** *Spirobranchus kraussii*, SEM micrographs of A) chaetae from sixth thoracic chaetiger (insert: close up of chaetae showing fibres), B) abdominal chaetae in posterior, C) row of thoracic uncini, D) row of anterior abdominal uncini, E) posterior abdominal uncini. Scale bars: A 20 μm (insert 2 μm), B–D 10 μm, B insert 20 μm. Photo by C. Simon.

ventral and lateral collar lobes present (Figure 4A, C). Collar light to dark brown or blue (Figures 3C, D, 4A, B).

**THORAX:** Six uncinigerous chaetigers (Figure 4B, C). Collar chaetae absent in adults, juveniles not observed. Thoracic chaetae limbate, of two sizes, finely serrated (Figure 6A). *Apomatus*-chaetae absent. Uncini along entire thorax saw-shaped, with 10 or 11 curved teeth, excluding anterior-most gouged peg (Figure 6C). Thoracic tori of similar size along thorax, approaching each other posteriorly leaving a ventral depression (Figure 4B).

**ABDOMEN:** 1 or 2 achaetous segments anteriorly (Figure 4B, C), number of chaetigers varies 40–70–93 (SD = 10, n = 37) [47–65]. Uncini saw-shaped with gouged peg, 9–11 teeth in uncini from anterior and posterior abdomen, about half size of thoracic uncini (Figure 6D, E). Abdominal chaetae true trumpet-shaped, abruptly bent (Figure 6B), distally with 2 rows
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of denticles, separated by groove, only present for last 5–25 [9–19] chaetigers; not present on all chaetigers once they appear (Figure 4D). Two or three per fascicle. Capillary chaetae absent throughout. Dorsum light to dark brown, venter colourless (beige) to brown (Figure 4D), sometimes grey or blue.

SIZE: length 15–22–31 mm (SD = 4.8, n = 37) [9.6–11.7 mm], width of thorax 0.5–1.8–2.9 (SD = 0.82, n = 37), radioles and operculum accounting for 11.6–17.1–26.4 % (SD = 4.3, n = 30) [12.9–19%] of body length.

DISTRIBUTION: South Africa: Western Cape Province (south coast only), Eastern Cape Province, KwaZulu-Natal; southern Mozambique

ECOLOGY: Low to upper intertidal, often in rock pools.

**Taxonomic remarks**

In our synonymy we have followed the practical approach of authors such as Day (1955, 1967) and Zibrowius (1973) in regarding the older name Placostegus caeruleus Schmarda, 1861 as not fitting for the Cape material. Day (1967) tried to restrict the use of the name Pomatoceros caeruleus (Schmarda, 1861) to material from New Zealand. In his opinion Schmarda’s original record from “Cape of Good Hope” is very doubtful, being different from the New Zealand material. Later, Zibrowius (1973) pointed out that an older name was available for the New Zealand populations, Vermetus cariniferus Gray, 1843, nowadays recognized as Spirobranchus cariniferus. Though we accordingly synonymized a number of records under the specific epithet caeruleus with Spirobranchus kraussii sensu stricto, this certainly cannot be applied to all “caeruleus”. After the original combination of a Cape taxon and one from New Zealand under the name Placostegus caeruleus by Schmarda (1861), the specific epithet caeruleus (caerulea, in error coeruleus, mainly under the genus Pomatoceros) has been used over 50 times in the literature, from localities as far apart as North Carolina, South Africa, Vietnam, the Philippines, Australia and New Zealand. A full revision falls outside the scope of this paper, but the name has been used for what we now regard as Spirobranchus americanus (Day, 1973) (e.g., by Neff 1971, North Carolina); S. cariniferus (Gray, 1843) (e.g., Knox 1954, New Zealand); S. kraussii sensu lato (e.g., Fauvel 1930, India); S. corniculatus (= Pomatoceros davaoensis Treadwell, 1942, reidentified to Pomatoceros caeruleus by Hartman 1956); we may have overlooked other erroneous uses of caeruleus. After 1970 the name has hardly been used, and with over 100 records “kraussii” is the prevailing reference to this taxon. Given the utterly confused and confusing use of the name caeruleus, stability will be served with the use of the better defined names cariniferus and kraussii.

Specimens deposited in NHM by Krauss, becoming syntypes after examination by Baird (1865), and those deposited at the Iziko Museum of Cape Town about 120 years later, are in poor condition. In syntypes, the
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Tips of the radioles are damaged, making observations of the terminal filaments nearly impossible. The collar and thoracic membranes are damaged in almost all the specimens examined, and all abdomens are flattened. However, the syntypic and old and fresh topotypic specimens show several similarities (Supplementary material Table S1), including shape (sub-circular) and diameter of tube, the proportion of the radioles not connected by the inter-radiolar membrane (~ half), the shape of the peduncle with a pair of smooth distal wings (the operculum was missing from all syntypes examined so structure could not be confirmed), the presence of a high collar ventrally extending almost to the margin of the radiolar crown, an apron over anterior abdominal chaetigers, and arrangement of true trumpet chaetae and the proportion of the body made up by the crown. However, the syntypic specimens are half to a third the length of the fresh material, although the numbers of abdominal chaetigers are similar to those of the smaller specimens among the fresh material. This difference in body size may be a consequence of prolonged storage in suboptimal conditions, the more so since the description by Baird (1865) suggests that the specimens had dried out and then been rehydrated. Additionally, the numbers of radioles per lobe are also lower than reported by Day (1934) and on recently collected specimens. However, ten Hove and Kupriyanova (2009) do not consider this a reliable character since radioles are difficult to count accurately; ventral radioles may be small while the dorsal-most radiole may be folded inwards and be hidden beneath the peduncle. Furthermore, the well-defined achaetous abdominal zone present in the fresh material could not be detected in the syntypic material; instead the anterior of the abdomen is quite stretched.

The recently collected samples conform with general descriptions provided by Day (1934, 1967) in relation to shape and colour of the tubes, body size, peduncle and opercular shape, the extent to which the radioles are united by the inter-radiolar membrane, the presence of bare terminal filaments, shape of thoracic membranes and ventral apron, absence of collar chaetae, shape of thoracic chaetae and uncini and shape of abdominal trumpet chaetae (Table S1). However, the descriptions differ from the specimens examined here with respect to the colour of the radioles (banded blue and white in Day (1967), but usually light brown and white in current study), and number of teeth on thoracic uncini (8–10 in Day (1967), 10 or 11 in current study). Furthermore, descriptions by Day (1934, 1967) do not indicate the distribution of the abdominal chaetae, although the figure suggests that they are absent from anterior chaetigers.

Although the specimens examined here conform, in a general way, to the description of Pomatoleios crosslandi by Pixell (1913), there are some differences (Table S1). In the latter description, the terminal filaments are nearly half the length of the free radioles and the largest specimens...
examined were only 14 mm long, compared to a maximum of 31 mm in the South African specimens (Day 1967, current study). Additional diagnostic characters that are not given by Pixell (1913), but which could contribute to better evaluating the similarities and differences among the specimens include: the colour and shape of the tubes, the colour of the specimens, and maybe the arrangement of the abdominal chaetae.

Characters shared by specimens identified as *S. kraussii* in other parts of the world include: shape of the operculum (slightly concave, unadorned), arrangement of radioles in two semi-circles, and absence of collar chaetae in adults (Table S1) (Pixell 1913; Pillai 1960, 1965, 2009; Bailey-Brock 1987; Ishaq and Mustaquim 1996; Fiege and Sun 1999; Çınar 2006; ten Hove and Kupriyanova 2009; Belal and Ghobashy 2012; Sun et al. 2012). There are, however, several points of differences among these descriptions (Table S1, characters underlined). The tube is described or illustrated as triangular in cross-section, with a median keel, in specimens from Sri Lanka, Manila, Hawaii, Hong Kong and Suez Bay (Pillai 1960, 1965; Bailey-Brock 1987; Belal and Ghobashy 2012; Sun et al. 2012; Bastida-Zavala et al. 2017), but having two longitudinal ridges or flattened dorsal ridge extending as a flap over the tube mouth in specimens from Hainan, Turkey and Abu Dhabi (Fiege and Sun 1999; Çınar 2006; Pillai 2009), as they do in the South African specimens. However, in both material from False Bay (SA) as well as from Karwar Harbour (India) some smaller tubes with only a single keel have been observed by one of us (HAtH); these tubes thus are triangular in cross-section, amidst tubes with two longitudinal keels, and (sub)trapezoidal in cross-section. The robustness of tube shape in cross-section as a diagnostic character should anyhow be tested more thoroughly since Li et al. (2016) showed that in *Hydroides elegans* the tube is more circular at low temperatures, but with two keels at elevated temperatures.

In most specimens of *S. kraussii*, including those from South Africa, the proportion of the radioles free from the inter-radiolar membrane is approximately half, but is as much as 66% to 75% in those from Manila (Pillai 1965), and as little as 33% in those from Turkey (Çınar 2006). Similarly, the length or height of the collar, usually up to the margin of the inter-radiolar membrane in the South African specimens, may be shorter than (Pillai 1960, 1965), or extend to well beyond (Pixell 1913), the membrane. Additionally, the specimens differ with respect to the distribution of the abdominal trumpet chaetae; these are present only in the posterior-most chaetigers in the specimens from South Africa, but in all others where the distribution is described, they first appear in the anterior abdomen, continuing to the posterior chaetigers where they may even be accompanied by capillary chaetae (Pillai 1965, 2009; Ishaq and Mustaquim 1996; ten Hove and Kupriyanova 2009; Belal and Ghobashy 2012). Collar chaetae were reported only in juveniles of specimens from
Hawaii and Abu Dhabi (Bailey-Brock 1987; Pillai 2009). Finally, the specimens also show great variability in overall body size. Specimens from South Africa, Manila, Pakistan and Suez Bay have a maximum body size ranging from 20 mm to 35 mm (Pillai 1965; Ishaq and Mustaquim 1996; Belal and Ghabashy 2012; current study), but in those from Tanzania, Hainan, Turkey and Hong Kong, the size ranges from 10 mm to 14 mm (Pixell 1913; Fiege and Sun 1999; Çinar 2006; Sun et al. 2012). Furthermore, the diameter of the tubes of specimens from Hawaii (Bailey-Brock 1987) was less than half those of larger specimens from South Africa, and smaller specimens from Hong Kong (Sun et al. 2012). Finally, the two to three segments comprising the achaetous abdominal zone present in the specimens from South Africa (current study) is absent in some specimens (ten Hove and Kupriyanova 2009; Belal and Ghabashy 2012) but not mentioned in any other descriptions consulted here.

The presence or absence of a talon, a calcareous extension of the opercular endplate reaching into the peduncle (ten Hove 1973 fig. 34; ten Hove and Kupriyanova 2009) is not consistently reported in descriptions of *S. kraussii*. A talon was dissected out of six specimens of the recently collected South African material, and was present in all older material from Table Bay examined by one of us (HAtH). Talons have also been recorded in specimens from Manila (Pillai 1965), Madagascar (ten Hove 1973), Hawaii and the Pacific coast of Panama (Bailey-Brock 1987; Bastida-Zavala 2008) and Suez Bay (Belal and Ghabashy 2012), but were absent from specimens from Hong Kong (Sun et al. 2012). A talon was not mentioned in specimens from Sri Lanka (Pillai 1960), Pakistan (Ishaq and Mustaquim 1996), Hainan, China (Fiege and Sun 1999), Turkey (Çinar 2006) and Abu Dhabi (Pillai 2009). In addition, one of us (HAtH) has kept extensive records of this feature in material examined over the last four decades and found talons present in specimens identified as *S. kraussii* from Kuwait, Australia (Western Australia, Northern Territory, Queensland), and the Mediterranean coast of Israel. He did, however, find that it may not be consistently present; for example, of the 18 specimens of *S. cf. kraussii* examined from Kuwait, 16 had talons. The variability and taxonomic significance of this character still needs to be determined, just as that of other characters mentioned before. This is particularly important as most diagnoses and descriptions in the literature are based on one specimen, at best a few.

**Distribution remarks**

Day (e.g., 1934, 1951, 1955, 1967, 1969, 1974) recorded *Spirobranchus kraussii* along the south and east coasts of South Africa and as far north as Maputo (Delagoa) Bay in south Mozambique while Hartmann-Schröder (1974) reports it from Xai-Xai, north of Maputo Bay (Figure 1).
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recently it was not found in Cape Vidal in northern KwaZulu-Natal or in southern Mozambique (Bustamante 1994), and was present in decreasing abundance from the southeastern coast to southern KwaZulu-Natal and finally Maputoland in the north (i.e., north of Cape Vidal; cf. Bustamante et al. 1997; Sink et al. 2005). Southern Mozambique should therefore probably be considered the edge of its northern distribution.

Ecological remarks
The coasts of South Africa are bordered by the warm, southwest flowing Agulhas Current in the south and east, and the cold, north flowing Benguela Current on the west coast (e.g., Stephenson and Stephenson 1972; Teske et al. 2011; Smit et al. 2013). The coastline of southern Africa can be divided into four ecoregions with different sea surface temperatures; the cold temperate Southern Benguela ecoregion on the west coast north of Cape Point, warm temperate Agulhas ecoregion on the south coast from east of Cape Point to north of East London in the Eastern Cape Province, the subtropical Natal ecoregion with a northern boundary in the region of Cape Vidal in northern KwaZulu-Natal and the tropical Delagoa ecoregion to the north, although transition zones are sometimes also recognized between the different regions (Figure 1; Teske et al. 2011; Sink et al. 2012; Smit et al. 2013). The distribution of S. kraussii from Cape Point to southern Mozambique therefore falls within the bioregions experiencing warm temperate and subtropical conditions, petering out towards the tropical ecoregion.

Although Day (1934, 1951, 1955, 1967, 1974) recorded S. kraussii as common in the low to high intertidal, the actual zone occupied and abundance on different shores depends on wave exposure (Morgans 1959; McQuaid and Branch 1984; McQuaid et al. 1985; Bustamante 1994; Bustamante and Branch 1996; Bustamante et al. 1997; Sink et al. 2005). On shores that are sheltered or semi-sheltered from strong wave action, S. kraussii is very abundant on the low shore, where it may be the most abundant animal taxon present (Bustamante and Branch 1996; Bustamante et al. 1997). By contrast, these authors also showed that on more exposed shores, the species is usually more abundant in the mid-shore. Spirobranchus kraussii has never been recorded in the subtidal in South Africa (see Hutchings et al. 2006, Supplementary Table S1, p. 21).

Results of molecular analyses
The results of a Maximum Likelihood analysis based on Cyt b dataset are shown in Figure 7. The nominal Spirobranchus kraussii was recovered as a monophyletic clade with five clades within it. The well-supported (0.99) clade of South African S. kraussii sensu stricto included a well-supported (0.92) group combining material from eastern part of the country and formed
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Figure 7. Maximum Likelihood tree based on mitochondrial cyt b DNA sequence data. Values at nodes represent bootstrap values. KZN: KwaZulu-Natal.

Discussion

This study provides the first detailed description of Spirobranchus kraussii sensu stricto from the type locality and thus, arguably from its natural range in southern Africa. Specimens from South Africa and localities in eastern Mediterranean and Suez Canal, tropical east Africa, the Arabian (Persian) Gulf, Sri Lanka, Australasia, and Hawaii share the presence of a simple...
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unadorned operculum with a concave endplate and the absence of collar chaetae in adults. These obvious “easily recognizable” characters undoubtedly contributed to the perceived wide distribution of the taxon. However, the literature-based comparisons of the present study have identified differences (Table S1) such as tube shape, distribution of abdominal chaetae, absence/presence of a talon and achaetous abdominal zone, and body size among groups of specimens from localities worldwide. In fact, the specimens of *S. kraussii* sensu stricto from South Africa do not show a perfect fit with any of the descriptions of specimens attributed to this species within its supposed extended or invasive range.

The results of the molecular part of the study, albeit preliminary, also reject the hypothesis that the nominal morphospecies *S. kraussii* is a single species with a natural wide distribution in the Indo-Pacific or a global invader. Instead, our results strongly suggest that this taxon is a complex of morphologically similar and closely related genetically distinct species with regionally restricted distributions. Five clades representing specimens from 1) South Africa, 2) Hawaii, 3) Queensland, Australia, 4) Japan, and 5) Kuwait suggest a natural phylogeographic pattern resulting from allopatric speciation. Thus, henceforth all *S. kraussii* outside of SA are undescribed and unnamed species and for the time being should be referred to as *S. cf. kraussii*.

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**Figure 8.** Maximum Likelihood tree based on combined nuclear 18S and mitochondrial cyt b DNA sequence data. Values at nodes represent bootstrap values. KZN: KwaZulu-Natal.
S. kraussii is a large species complex, the distribution of the real S. kraussii is apparently restricted to the south to eastern coasts of South Africa. Moreover, we argue that although it is not impossible, it is unlikely that this species would be an invasive alien capable of expanding its range via human-mediated translocations. The improbability of S. kraussii being a successful invasive species is highlighted if its potential spread is considered within the context of the framework for biological invasions (Blackburn et al. 2011). A species has to go through several stages and overcome a number of barriers to become an established or invasive alien (Blackburn et al. 2011, Figure 1). However, the ecological preferences of S. kraussii in its native range suggest that successful spread of the species from South Africa is unlikely.

The first stage in an invasion pathway is transport via some vector that requires the species to overcome a major geographical barrier. The hypothetical spread of S. kraussii has been attributed to shipping through hull fouling (e.g., Crisp 1977; Coles et al. 1999; Çinar 2013). South Africa lies on various major shipping routes and is the documented recipient of several NIS via hull fouling (e.g., Mead et al. 2011), but could as easily be a donor of such species (e.g., Lee and Chown 2009). However, transport via hull fouling can only occur if a species readily settles on artificial surfaces such as ships’ hulls and remain attached throughout the journey to the recipient region (O’Brien et al. 2017). Spirobranchus kraussii has been recorded in False Bay, Mossel Bay and Port Elizabeth (Day 1967; McQuaid and Branch 1984; Bustamante 1994) which are all active shipping hubs in South Africa (Peters et al. 2017). However, S. kraussii was not recorded in the fouling communities on experimental plates suspended in the subtidal, nor as a surface fouler on ships, in False Bay or Table Bay, including ships that had travelled only from other ports in South Africa (Millard 1951; Henschel et al. 1990; Jurk 2011). Thus, this species does not (readily) settle on artificial substrates. In fact, the only reports of S. kraussii settling on artificial structures in South Africa has been on retaining or harbour walls, albeit in low densities, in Port Elizabeth, Knysna and Muizenberg (Hutchings et al. 2006; Allanson et al. 2014; this study). Therefore, we argue that transport via hull fouling could be difficult and reject the idea that S. kraussii could have been spread as a hull fouler from South Africa. It might be also be possible that larvae had been transported via ballast water, another common vector of transportation for polychaetes (e.g., Çinar 2013), to the recipient regions where they established fouling communities. It must, however, be noted that there are no records of serpulid larvae in ballast water (e.g., Carlton and Geller 1993).
Spirobranchus cf. kraussii has been reported as a fouler of artificial substrates in Suez Canal, Eastern Mediterranean (e.g., Shalla and Holt 1999; Emara and Belal 2004; Çinar 2006), and Mumbai Harbour, India (e.g., Swami and Udhayakumar 2010), thus supporting suggestions that species morphologically similar to S. kraussii have indeed been transported via hull fouling. By contrast, in other parts of its extended range S. cf. kraussii populations are reported as preferentially settling on natural rather than artificial substrates (Pillai 1960: Sri Lanka; Crisp 1977: Arabian (Persian) Gulf; Bailey-Brock 1987: Hawaii; Ishaq and Mustaquim 1996: Pakistan; Fiege and Sun 1999: South China Sea; Sun et al. 2012: Hong Kong; Belal and Ghobashy 2012: Suez Bay). In Japan, Miura and Kajihara (1984) contrast the life histories of fouling serpulid Hydroides ezoensis and non-fouling S. cf. kraussii in Sagami Bay, Honshu and there is only one published report of the taxon (id. Hiromi Uchida) incidentally and sparsely settling on artificial substrates in Kii Peninsula (Raveendran and Harada 2001). In addition, Nishi (1993) examined the ecology of S. cf. kraussii in tropical Japan (Okinawa), reporting that the animals form a well-defined intertidal zone and easily settle on concrete piers and vertical walls. Chan et al. (2014) examined larval settlement inducers in what they called tropical fouling serpulid S. kraussii living on mangrove roots in Singapore. Finally, Bastida-Zavala et al. (2017) found only one specimen of S. cf. kraussii in Hawaii after extensive surveys of fouling plates on the United States coasts. Such wide variability of ecological requirements again points to a species complex.

The Suez Canal linking the Red Sea and eastern Mediterranean Sea has been suggested as another vector for the transport of S. kraussii (e.g., Ben-Eliahu and ten Hove 1992; Shalla and Holt 1999; Çinar 2006; Belal and Ghobashy 2012). Thus, if S. kraussii does occur along the coast of the Red Sea, its spread into the Suez Canal and beyond by passive means, as suggested by Belal and Ghobashy (2012), is conceivable. The only records for nominal S. kraussii for the Red Sea are from within the Gulf of Suez and a single location immediately south of the gulf (Belal and Ghobashy 2012, 2014; see also Perry et al. 2018 for list of Spirobranchus species recorded in the region). Thus, it is conceivable that an NIS matching the description of S. kraussii transported via shipping became established in the northern parts of the Red Sea before spreading through the Suez Canal. The reverse possibility cannot be excluded either. In the case of S. cf. kraussii, anti-Lessepsian migration (after invasion following ship transport to the Eastern Mediterranean) might be more likely than the more commonly occurring Lessepsian migration. Furthermore, the descriptions of specimens from Turkey (Çinar 2006) and the Levant coast of the Mediterranean (Ben-Eliahu and ten Hove 1992, 2011) were not detailed enough to determine whether these represented the same species as those from the Gulf of Suez.
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(Belal and Ghabashy 2012), but it is very unlikely that either belong to S. kraussii sensu stricto from South Africa. Comparative molecular analysis of DNA sequences of populations worldwide with those from the Suez Bay and eastern Mediterranean is needed to determine the origin of the latter population.

After successful transportation the NIS can become established in the recipient region if it can survive and reproduce there (Blackburn et al. 2011). Important environmental variables that affect an organism’s distribution and abundance in a particular area include seawater temperature, wave exposure (which may also influence zonation), and substrate suitability (e.g., McQuaid et al. 1985; Bustamante et al. 1997; Perry et al. 2018). Most global records for S. cf. kraussii, including the synonymized Pomatoleios crosslandi, are from tropical or sub-tropical regions of the Indo-Pacific (e.g., Day 1967; Pillai 1960, 1965, 2009; Straughan 1967, 1969a, b; Crisp 1977; Bastida-Zavala et al. 2017) or eastern Mediterranean (e.g., Ben-Eliahu and ten Hove 1992; Belal and Ghabashy 2012). By contrast, S. kraussii sensu stricto occurs mostly in warm temperate and subtropical regions of South Africa and is less common in the more tropical northern KwaZulu-Natal and southern Mozambique, the apparent northern limit to its distribution (cf. Bustamante 1994; Sink et al. 2005; Smit et al. 2013). Similarly, the preference for natural rocky substrates in the intertidal zone within sheltered habitats by S. kraussii sensu stricto is shared by many (e.g., Straughan 1967, 1969a, b; Miura and Kajihara 1984; Ishaq and Mustaquim 1996; Bustamante et al. 1997; Shalla and Holt 1999; Belal and Ghabashy 2012), but not all, populations ascribed to this species. For example, on more sheltered shores, S. kraussii is most abundant in the low shore in South Africa, but S. cf. kraussii is most abundant in high intertidal in Hawaii (cf. Straughan 1969a; Bustamante and Branch 1996; Bustamante et al. 1997). Furthermore, in Australia, high densities of S. cf. kraussii occur subtidally as foulers of water intake pipes of industrial cooling systems (Straughan 1968), while in Turkey the taxon is found on both natural and artificial substrates, particularly in polluted habitats of harbours (Çinar 2006). These incongruences in temperature and habitat preferences provide additional evidence that S. kraussii sensu stricto is not as widespread as it is currently assumed and again points to the existence of a species complex, rather than a single widespread species.

The final stage in the invasive pathway is the expansion of the species from the point of establishment (Blackburn et al. 2011) as demonstrated along the Suez Canal and through the eastern Mediterranean where populations of nominal S. kraussii have been increasing in number and spread (cf. Shalla and Holt 1999; Emara and Belal 2004; Çinar 2006; Ben-Eliahu and ten Hove 2011; Belal and Ghabashy 2012, 2014). There are no reports of expanding populations of this nominal taxon from other
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Multiple locations within its proposed Indo-Pacific range. Again, this contradicts the idea of a single, widespread NIS, and instead suggests that at least one species in the S. kraussii complex is indeed a successful invader in the Mediterranean, being either a Lessepsian migrant from the Red Sea or hull fouler introduced from some other location in the Indo-Pacific. The former scenario is less likely because of the lack of established populations of S. cf. kraussii in the Red Sea.

In conclusion, we argue that a combination of morphological characters and ecological requirements with preliminary molecular data have provided enough evidence to reject the currently accepted status of Spirobranchus kraussii as a single widespread species in the Indo-Pacific and a Lessepsian migrant invading eastern Mediterranean. Clarifying the taxonomic and invasive status of all the species within the S. kraussii complex throughout its proposed wide range is beyond the scope of this study. However, here we have provided a solid foundation of morphological and molecular data on S. kraussii sensu stricto against which specimens from other locations can be compared.

Acknowledgements

CAS thanks the staff at the Scanning Electron Microscopy (Central Analytical Facilities, Stellenbosch University) for technical assistance and the National Research Foundation (Incentive Funding) for research funds. We thank Dr Danny Eibye-Jacobsen (ZMC) for the loan of material and critical evaluation of its date of collection, and two anonymous reviewers whose comments and suggestions improved the paper.

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