A new record of a cryptogenic *Dipolydora* species (Annelida: Spionidae) in South Africa

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Abstract

In this study we report a new record of a cryptogenic polychaete from southern Africa. The species was found inhabiting sand tubes in intertidal sand flats in the Knysna Estuary on the southern coast of South Africa. Morphological comparisons using light and scanning electron microscopy showed extensive taxonomic similarities with *Dipolydora socialis* described from other localities and from museum vouchers. In addition, 18S rRNA and COI barcodes were generated for the species. Genetic analysis of the assembled polydorid dataset corroborated the morphological data in delineating the species as a taxonomic unit with >99% genetic similarity to available sequences of *D. socialis* in the GenBank database. *Dipolydora socialis* has been reported as having a widespread distribution, and since it can reside within tubes associated with fouling communities or as a shell borer, several vectors may have been responsible for its global spread and introduction to southern Africa. Finally, considering the many cryptic complexes that are currently being uncovered within polychaetes, including spionids, future taxonomic studies should incorporate additional genetic data from other regions of the world to determine whether *D. socialis* may also be part of a larger species complex.

Introduction

Marine invasions are recognized as one of the greatest threats to global biodiversity (Costello *et al.*, 2010). Although the study of marine invasive species formally began in the 1970s, research on this field in southern Africa has only recently developed but is important due to the region's status as a biodiversity hotspot (Griffiths *et al.*, 2009). In South Africa, at least 96 marine non-indigenous species (NIS) have been recorded; these include 55 that are invasive, and nine polychaete species (Miza *et al.*, 2019). However, it is likely that the number of non-indigenous polychaete species identified in the region is underestimated, as evidenced by recent studies (e.g. Williams *et al.*, 2017; Malan *et al.*, 2020; van Rensburg *et al.*, 2020). Polychaetous annelids are frequent members of the non-indigenous marine fauna across the globe, likely due to factors that make them prone to introductions (Çinar, 2013), as well as biological mechanisms that enhance invasion success (Papacostas *et al.*, 2017). For example, many polychaetes exhibit r-selected life history strategies where they produce numerous planktonic larvae that can spend months in the water column, which in turn facilitates uptake into ballast water (Carlton & Gellar, 1993). In addition, tubiculous (tube-dwelling) polychaetes (e.g. Spionidae and Serpulidae) can foul the hulls of ships, exist as symbionts of hull fouling organisms such as barnacles and sponges and bore into the shells of commercially reared molluscs, the latter of which is a major component of South Africa's aquaculture industry (Çinar, 2013; David *et al.*, 2014).

Spionidae forms a significant component of the known non-indigenous polychaetes (Çinar, 2013), and many, especially members of the *Polydora*-complex (i.e. nine genera defined by an enlarged fifth chaetiger with modified spines (Walker, 2011)), can be extremely destructive if they successfully invade a habitat. For example, the tube-dwelling spionid *Boccardia proboscidea* invaded a sewage outfall area in Argentina, producing biogenic reefs that excluded other organisms from the impacted area (Jaubet *et al.*, 2011). Polychaetes such as *B. proboscidea* are considered examples of invasive ecosystem engineers (IEEs) that could have major ecological impacts through habitat modification (Guy-Haim *et al.*, 2018). It is therefore imperative that non-indigenous polychaetes be identified as early as possible to facilitate management before they become problematic, a major goal of rapid assessment surveys (e.g. David & Krick, 2019; Pederson *et al.*, in press). However, this is complicated by the fact that polychaetes are known to exhibit high levels of cryptic diversity (Carr *et al.*, 2011; Nygren, 2014; Nygren *et al.*, 2018; Malan *et al.*, 2020) and many species that were once considered 'cosmopolitan' may actually be part of cryptic complexes (Hutchings & Kupriyanova, 2018). Many purported species complexes result from limited investigations to distinguish species or poor taxonomic practices (i.e. they represent pseudo-cryptic species complexes; see Nygren, 2014). In contrast, true cryptic species are reproductively isolated but show strikingly similar morphologies and can only be distinguished genetically or through reproductive crosses (Rice *et al.*, 2008; Struck *et al.*, 2018; Struck & Cerca De Oliveira, 2019).

A recent survey of intertidal fauna in the Knysna Estuary on the southern coast of South Africa (Figure 1A) revealed an unknown spionid worm inhabiting sediment tubes (Figure 1B). The species could not be identified using the taxonomic monograph of Day (1967), but preliminary investigation using light microscopy tentatively identified the worm as *Dipolydora* cf. *socialis* based on the key provided by Blake (1996) (see Williams *et al.*, 2017). *Dipolydora socialis* (Schmarda, 1861) inhabits sediment but can also be associated with colonial invertebrates such as sponges and molluscs (e.g. Sato-Okoshi & Takatsuka, 2001; Williams, 2001; David & Williams, 2012a), or as a borer in molluscan shells (Blake, 1971). The species is considered cryptogenic i.e. 'not demonstrably native or introduced' (Carlton, 1996; Schwindt *et al.*, 2020), along the Pacific coast of North America and Atlantic coast of South America and in Australia (Boyd *et al.*, 2002; Orensanz *et al.*, 2002; Hayes *et al.*, 2005). The taxonomic history of *D. socialis* is complicated, with the species having undergone numerous taxonomic revisions, the most significant of which was a synonymization with another *Dipolydora* species, *Dipolydora carunculata* (Radashevsky, 1993) (Blake, 1996), a designation which was later rejected due to insufficient evidence (Manchenko & Radashevsky, 2002). In this study we utilize morphological and molecular data to investigate the presence of *D. socialis* in southern Africa.

Materials and methods

Sediment samples were collected from the intertidal region within the Knysna Estuary, Western Cape Province, South Africa (34°3'57''S 23°3'17''E) on 21 January 2015. During collection, sandy tubes were processed individually, and all fragments per tube were interpreted as an individual undergoing architomic division. Samples were sorted, anaesthetized in 7% $MgCl_2$ and either fixed in 4% formalin in seawater and then stored in 70% ethanol, or directly in 96% ethanol. Photographs of whole animals were taken through an Olympus SZ61 microscope using a Canon Powershot S3 IS camera. For morphological comparison, additional *Dipolydora socialis* specimens were obtained from Discovery Bay, Hong Kong and Rhode Island, USA (specimens collected by J. Williams). Voucher specimens from Chile (type locality) (USNM 1006390), Philippines (USNM 187534), Brazil (USNM 1022162) and Taiwan (USNM 1022160) from the National Museum of Natural History were also examined. Specimens were compared morphologically using both light microscopy (Leica Microsystems) and scanning electron microscopy (SEM) (FEI Quanta 450). For SEM preparations, worms were dehydrated in an ascending ethanol series (75%, 80%, 85%, 90%, 95%) for 10 min each and in 100% three times for 15 min each. Specimens were critically point dried over CO_2 (Samdri-795 Critical Point Dryer), mounted on an aluminium stub with sticky tape and coated with gold (EMS-550 Sputter Coater).

For genetic analyses, genomic DNA from two South African specimens (referred to previously as *Dipolydora* cf. *socialis*) was extracted using the DNeasy blood and tissue DNA extraction kit (QIAGEN, Hilden, Germany), following the manufacturer's protocol. A ~800 bp fragment of the 18S rRNA gene and a ~710 bp fragment of cytochrome c oxidase I (COI) gene were amplified using the polymerase chain reaction (PCR) and the forward and reverse primer pairs from Teramoto *et al.* (2013) and the Dorid_COI.3F and Dorid_COI.3R primers from Williams *et al.* (2017). Cycling parameters for 18S rRNA included initial denaturation of 95°C for 4 min, followed by 40 cycles of 95°C for 30 s, annealing 55°C for 30 s, extension 72°C for 30 s, and final extension 72°C for 7 min. Cycling parameters for the COI gene followed the conditions outlined by Williams *et al.* (2017).

Amplified PCR products were verified on a 2% agarose gel stained with ethidium bromide and purified using a gel clean-up kit (QIAGEN, Hilden, Germany). Amplicons were sequenced by GeneWiz (South Plainfield, NJ, USA) using the forward primers and Big Dye Terminator Cycle Sequencing. Sequence data generated were deposited into the GenBank database for archiving (accession nos. MT019828 & MT019829 and MT040509 & MT040510).

The generated sequence data were first compared with the GenBank database using the BLASTn tool to determine initial similarity indices. COI and 18S rRNA datasets were then compiled using archived polydorid sequences from GenBank. *Dipolydora* cf. *socialis* sequences from South Africa were obtained from Williams *et al.* (2017) based on a tentative identification prior to the present study (accession nos. KY677859, KY677899, KY002976), whereas the North American COI sequence was based on a single individual sampled from Massachusetts, USA (David & Krick, 2019) (accession no. MK189200). The archived 18S rRNA gene sequences for *Dipolydora* cf. *socialis* (Williams *et al.*, 2017) were sampled from the same locality as those from the current study. Both datasets were aligned using the Clustal W alignment algorithm in BioEdit ver. 7.0.5.3 (Hall, 1999) and edited by eye. Genetic relatedness among taxa was assessed by calculating pairwise uncorrected p-distances in MEGAX (Kumar *et al.*, 2018). In addition, a Maximum likelihood phylogenetic tree was also constructed in MEGAX with 1000 bootstrap to determine cladal support, using the General Time Reversible (GTR) evolutionary model as determined by AICc index in jModelTest2 (Darriba *et al.*, 2012). All trees were edited and visualized in FigTree ver. 1.4.3 (Rambaut, 2007). Voucher specimens were deposited at the Iziko South Africa Museum (SAM) and the National Museum of Natural History (USNM, Smithsonian Institution).

Results

SYSTEMATICS

Order SPIONIDA sensu Rouse & Fauchald, 1997
Family SPIONIDAE Grube, 1850
Genus Dipolydora Verrill, 1881
Dipolydora socialis (Schmarda, 1861)
Figures 1C, D, 2

Abbreviated synonymy (main taxonomic sources provided)

Leucodore socialis Schmarda, 1861: 64, figures a–c, pl. 26, figure 209

Polydora caeca var. *magna* Berkeley, 1927: 419; Pettibone, 1967: 11.

Polydora magna Berkeley & Berkeley, 1936: 473;, 1952: 21.

Polydora socialis plena Berkeley & Berkeley, 1936: 469; 1953: 20–21.

Polydora socialis Hartman, 1941: 310–311, pl. 48, figures 41–42; 1969: 147; Hartmann-Schröder, 1962: 137–139, figures 167–168; 1965: 209–211, figures 200–203; Blake, 1971: 20–23, figures 13–14; 1975: 215, figures 237–238; 1979: 607–609; 1981: 950; 1983: 264; Carrasco, 1974: 194–196, figures 27–32; Light, 1977: 71; 1978: 179–181, figure 180; Sato-Okoshi & Okoshi, 1997: 486; Blake & Kudenov, 1978: 248–250, figure 38d–e; Johnson, 1984: 6–28 to 6–30, figures 6–19 and 6–20.

Polydora plena Foster, 1971: 24–25, figures 22–29.

Polydora neocardalia Hartman, 1961: 96–98, pl. 14, figures 1–4; 1969: 141, 2 figures; Lissner *et al.*, 1986: appendix D; Steinhauer & Imamura, 1990: figure 1.

Dipolydora socialis Blake, 1996: 189–192, figure 4.34; Williams, 2001: 442–445, figures 7–8; Walker, 2009: 39, 133; 2011: 52; Schwindt *et al.*, 2020: tables 1, S1.
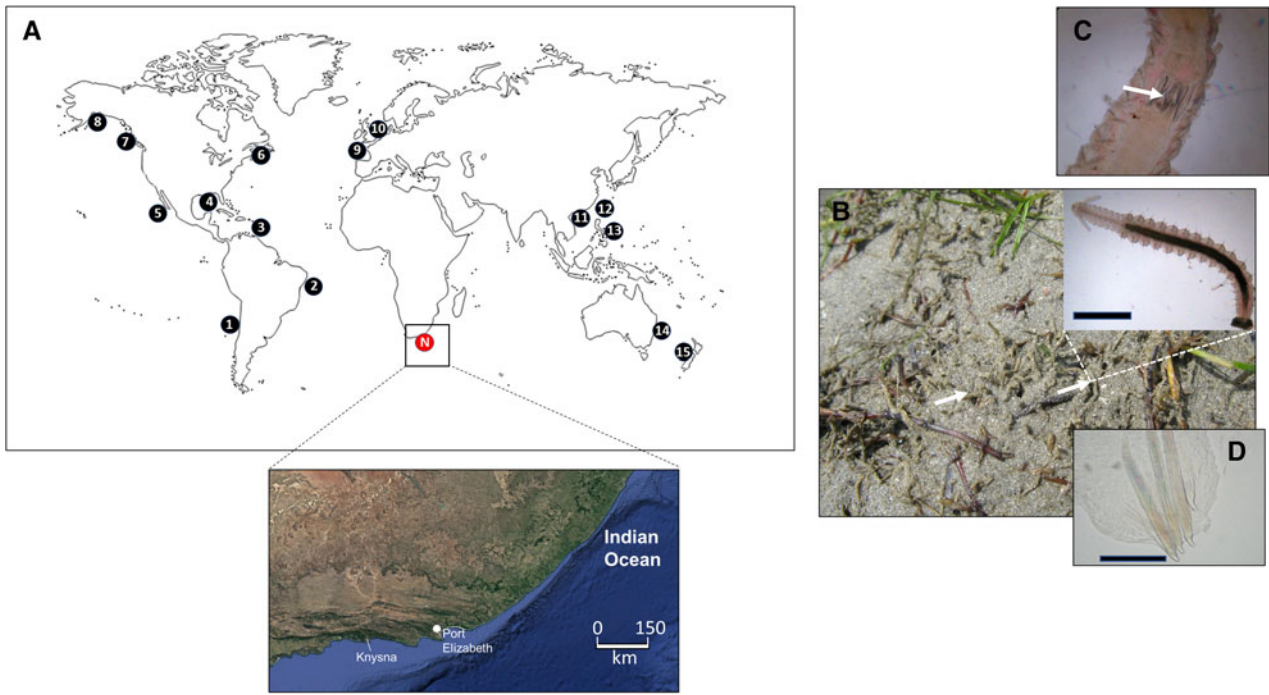
Fig. 1. (A) Map showing global distribution of *Dipolydora socialis* based on reports from the literature: 1 – Chile (type locality), 2 – Brazil, 3 – Trinidad & Tobago, 4 – Gulf of Mexico, 5 – Humboldt & Bodega Bay, California, 6 – Rhode Island, USA, 7 – British Columbia, Canada, 8 – Gulf of Alaska, 9 – Iberian Peninsula (Spain), 10 – Germany & Black Sea, 11 – Hong Kong, 12 – Taiwan, 13 – Philippines, 14 – New South Wales, Australia, 15 – New Zealand. 'N' represents the first southern African population of *D. socialis* found in the current study. **(B)** Colony of sand tubes constructed by *D. socialis* in the intertidal zone at the Knysna Estuary; inset photo shows a microscopic image of a live *D. socialis* with a recently regenerated anterior end (scale bar: 600 μm). **(C)** Microscopic image showing the mid-region of *D. socialis* with the visible gizzard identified (white arrow). **(D)** Microscopic image of the modified spines on the enlarged fifth chaetiger (scale bar: 100 μm).
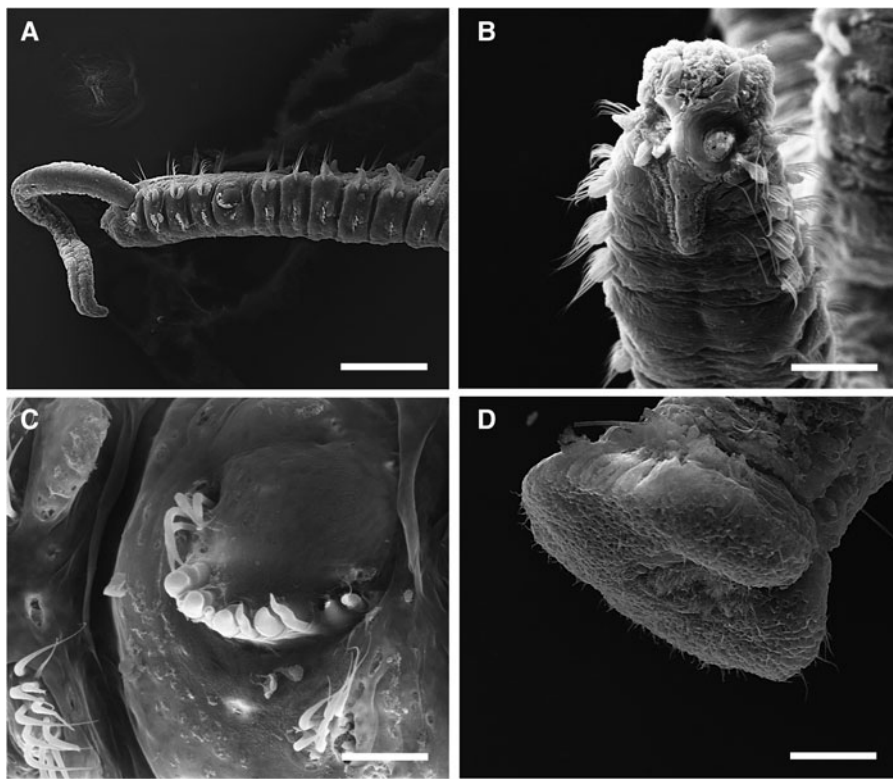

Fig. 2. Scanning electron micrograph (SEM) plates of *Dipolydora socialis* showing (A) lateral view of anterior chaetigers, (B) dorsal view with palps removed showing caruncle and nuchal organ, (C) modified fifth chaetiger with spines and (D) pygidium with tufts of cilia in the centre. Scale bars: A, 250 μm, B, 150 μm, C, 25 μm, D, 50 μm.

Dipolydora cf. *socialis* Williams *et al.*, 2017: 107, 109–113, figures 1–5, tables 2, 3.
?*Dipolydora socialis* Abd Elnaby, 2019, figure 8.

Specimens examined. Knysna, Western Cape Province, South Africa (34°3′57″S 23°3′17″E) from sediment, January 2015,

coll. C. Simon and F. Smith (8 specimens, destroyed for molecular analyses, 5 complete specimens SAM A089093 and 4 specimens on 2 SEM stubs USNM 1620898); Discovery Bay, Lantau Island, Hong Kong (22°18′0.74″N 114°01′0.84″E), from burrows in gastropod shells inhabited by hermit crabs, 8 June 2004, coll. J. Williams (2 specimens destroyed for molecular analyses,

Table 1. Morphological comparison of *Dipolydora socialis* from selected geographic regions

	USA (MA/RI/CA)	PH	BR	HK	TW	[a]CH	SA
Prostomium	Bifid	Strongly bifid	Bifid	Bifid	Bifid	Bifid	Bifid
Caruncle	Extends to chaetigers 4–9	Extends to chaetigers 3–5	Extends to chaetiger 6	Extends to chaetiger 5	Extends to chaetigers 4–5	Extends to chaetiger 7–9	Extends to the end of 3rd chaetiger
5th chaetiger	4–5 spines with sub-terminal protuberance	5 falcate spines with sub-terminal protuberance	5 spines with sub-terminal protuberance	4–5 simple spines	4–5 simple spines	4 simple spines with subterminal protuberance	5 spines with sub-terminal protuberance
Branchiae	Begins on chaetiger 8	Begins on chaetigers 8–10	Begins on chaetiger 8	Begins on chaetiger 7/8	Begins on chaetiger 8	Begins on chaetiger 8	Begins on chaetiger 8
Pygidum	Tri-lobed; can be fused to form continuous lobe	Large ventral lobe, 2 smaller dorsal lobes	Continuous lobe with notch	Continuous lobe with notch	Terminal segments damaged	Posterior regions damaged	Continuous lobe with notch
Substrates	Associated with sediment; shells of various molluscs & gastropods (RI)	Sediment tubes in the crevices of gastropod shells	Associated with muddy *Diopatra* tubes	Associated with hermit crab shells	Associated with shells of *Crassostrea gigas*	Associated with shells of *Ostrea chilensis*	Silty sediment tubes
Hooded hooks	Begins on chaetiger 7	Begins on chaetiger 7	Begins on chaetiger 7	Begins on chaetiger 7	Begins on chaetiger 7	Begins on chaetiger 7	Begins on Chaetiger 7
Gizzard	Chaetiger 16	Chaetiger 16	Chaetiger 15	Chaetiger 16	Chaetiger 16	Chaetiger 16	Chaetiger 16
Reference	Blake (1971); Blake (2006); Present study	Williams (2001)	Present study	Present study	Present study	Present study	Present study

PH, Philippines; BR, Brazil; HK, Hong Kong; TW, Taiwan; *CH, Chile; SA, South Africa.
[a]Type locality.

3 specimens in ethanol USNM 1620899); Pettaquamscutt River, Narragansett, Rhode Island, USA (41°26′57.6″N 71°27′2.0″W), from burrows in *Crepidula fornicata*, 16 October 1998, coll. J. Williams (3 specimens destroyed for molecular analyses); Rowes Wharf, Boston, MA, USA from mudtubes on *Ostrea edulis*, July 2018, coll. J. Carlton & A. David (2 specimens); Sombrero Island, Philippines, July 1997 (USNM 187534, 10 specimens); Pontal do Sul, Parana, Brazil, August 1998, coll. V. Radashevsky (USNM 1022162, 11 specimens); Hsiangshan, Taiwan, July 1999, coll. V. Radashevsky (USNM 1022160, 3 specimens); Chiloe Island, Chile, February 1998, coll. W. Sato-Okoshi & M. Takatsuka (USNM 1006390, 4 specimens).

Description of South African specimens. Whole specimens, 100–180 chaetigers in length. Prostomium bifid, extends as a caruncle to the end of chaetiger 3, surrounded by rows of sensory cilia (Figure 2A, B). Palps long and extend posteriorly to chaetigers 10–12 with ventral food groove lined by frontal cilia (other ciliary groups not observed because not fixed originally for SEM; see Worsaae, 2001). Eyes and body pigmentation absent, brown pigmentation along feeding groove on palps present in some preserved specimens. Chaetiger 1 with noto- and neurochaetae, chaetigers 2–4 and 6 with two rows of capillary notochaetae and neurochaetae. Hooded hooks with curved shaft without constriction with an angle of 45° between apical tooth and main fang; no observable changes in angle in subsequent chaetigers. Hooded hooks begin on chaetiger 7; 3–4 per fascicle, accompanied by 1–2 capillary chaetae; companion chaetae not present from chaetiger 10. Branchiae small, beginning on chaetiger 8 for all specimens examined (Figure 2A). Branchiae decrease in length after

chaetiger 10; absent on terminal chaetigers. Chaetiger 5 enlarged; approximately twice the size of preceding and succeeding chaetigers, with 4–5 simple stout spines (Figure 1D) accompanied by dorsal bundle of geniculate chaetae and ventral fascicle of capillaries (Figure 2C), spines falcate-shaped with subterminal protuberance and alternating row of companion chaetae. Posterior notopodial spines present as fine needle-like capillaries. Conspicuous gizzard beginning in chaetiger 16, extending for ∼2 chaetigers with longitudinal muscles; only observable under light microscopy (Figure 1C). Pygidium disc-shaped with dorsal notch and tuft of cilia in the centre (Figure 2D).

Remarks. Morphologically, *Dipolydora* cf. *socialis* specimens from South Africa were almost indistinguishable from *Dipolydora socialis* reported from several geographic regions, including the type locality, except for slight variations such as caruncle extension and overall shape of the pygidium (see Table 1). During initial identification, regeneration of anterior segments was observed in 40% of worms collected (Figure 1B inset), with a maximum of eight anterior chaetigers regenerated; in addition, at least five individual fragments were regenerating both anterior and posterior ends simultaneously.

Genetic barcoding. DNA barcoding using the sequence data available from GenBank corroborated morphological analyses in identifying the specimens as *Dipolydora socialis*. Overall genetic distances of the in-group taxa ranged from 0.000–0.047 for the 18S rRNA marker and 0.000–0.224 for the COI marker. The maximum intraspecific distance for *D. socialis* specimens were 0.000 for the 18S rRNA marker and 0.015 for the COI marker with
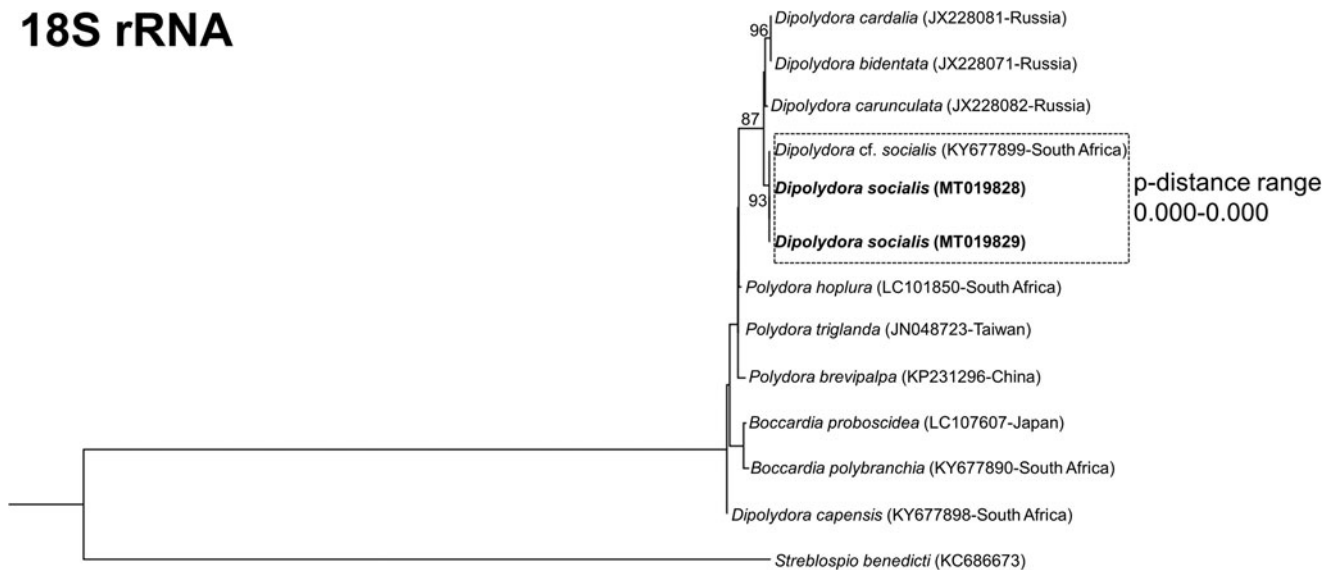
18S rRNA

Fig. 3. Maximum likelihood phylogenetic tree showing phylogenetic position of *Dipolydora socialis* relative to other polydorid taxa based on 18S rRNA barcode data. Codes adjacent to taxa represent GenBank accession codes and numbers above and below branch nodes represent bootstrap support based on 1000 replications. Nodes without bootstrap support represent clades where bootstrap values are less than 50. Sequences in bold font are those generated in the present study.

COI

Fig. 4. Maximum likelihood phylogenetic tree showing phylogenetic position of *Dipolydora socialis* relative to other polydorid taxa based on COI barcode data. Codes adjacent to taxa represent GenBank accession codes and numbers above and below branch nodes represent bootstrap support based on 1000 replications. Nodes without bootstrap support represent clades where bootstrap values are less than 50. Sequences in bold font are those generated in the present study.

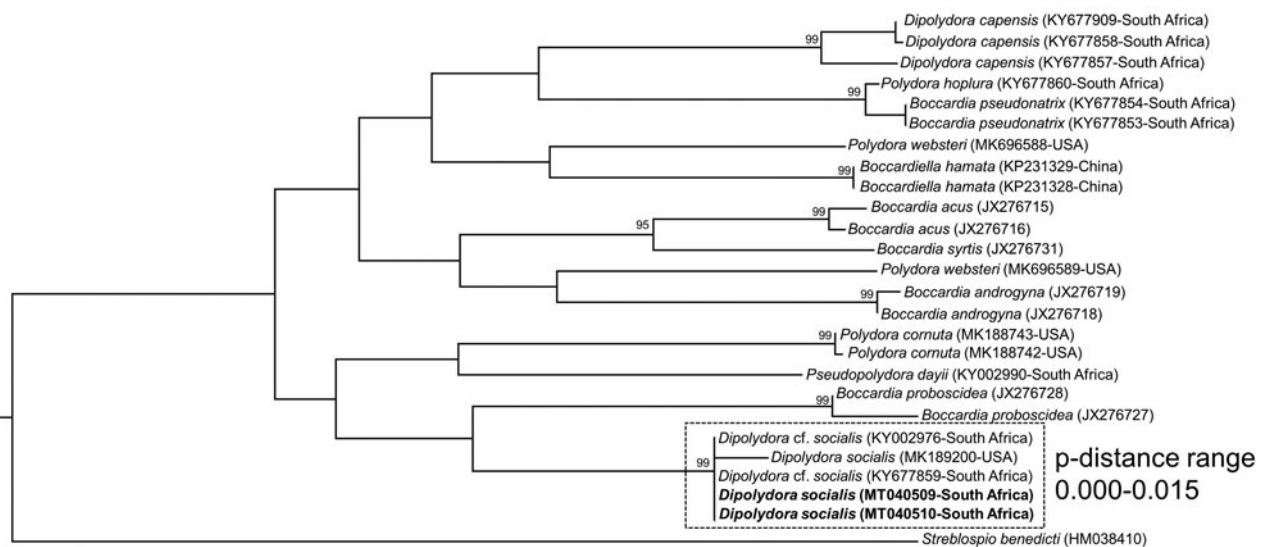the species forming a distinct clade with high bootstrap support (Figures 3 & 4). For the 18S rRNA dataset, *D. socialis* also exhibited low genetic distances with *D. cardalia* (0.009) and *D. carunculata* (0.007).

Discussion

Thus far, seven *Dipolydora* species have been recorded in South Africa: *D. capensis* (Day, 1955), *D. normalis* (Day, 1957), *D. keulderae* (Simon, 2011), *D.* cf. *giardi* (Mesnil, 1896), *D. armata* (Langerhans, 1880), *D. flava* (Claparède, 1870) and *D. caeca* (Oersted, 1843), with only the first three species native to the region (Day, 1967; Simon, 2011). The status of the remaining species as native or non-native has not been confirmed. In this study,

we show that the specimens identified tentatively as *Dipolydora* cf. *socialis* in South Africa by Williams *et al.* (2017) and those from this study exhibit extensive genetic and morphological similarities with the supposedly cosmopolitan spionid, *D. socialis*. It should be noted that although we confirmed reciprocal monophyly of specimens from the east coast of North America and South Africa, sequence data from type locality (Chile) were not available for inclusion in the analysis. The samples examined do share extensive similarities in traditional taxonomically informative traits across different populations, most notably the visible gizzard at chaetigers 15–22, a distinctive trait of the species (Blake, 1996; Walker, 2009, Table 1). Despite these similarities, some variability does exist. For example, South African specimens had a maximum of 180 chaetigers whereas Blake (1996) reported worms

from California having up to 400 chaetigers. Although intraspecific variation in size may reflect environmental differences and is a common feature across marine invertebrate taxa (e.g. Zakas & Rockman, 2014), this should be investigated further, as pseudocryptic species complexes are common among polychaetes (Nygren, 2014). This makes it particularly difficult to determine the taxonomic importance of size in this group. Furthermore, other variations detected, such as length of the caruncle, may be linked either to intraspecific variation in size, or reflect interspecific variation (Simon *et al.*, 2019*a*). Without genetic data from a wider distribution, we cannot confirm whether *D. socialis* is (1) a single widespread species (e.g. as shown for *Polydora hoplura*, Sato-Okoshi *et al.*, 2017) or (2) a member of a complex of cryptic species of which one or more may be widespread (as suggested for *Spirobranchus kraussii*, Simon *et al.*, 2019*b* and *Ficopomatus enigmaticus*, Yee *et al.*, 2019). A recent study by Abe & Sato-Okoshi (2021) focusing on specimens in northeastern Japan lends support to the latter hypothesis as the authors also morphologically confirmed *D. socialis* there, but the18S rRNA sequence exhibited relatively high genetic divergence from *D. socialis* sequences from South Africa (including those analysed in the present study). Therefore, until sequence data are obtained from morphologically confirmed specimens from additional sites, the most parsimonious option for referring to the South African specimens is using the nominal name, *D. socialis*.

We found interspecific genetic variation between *D. socialis* and *D. carunculata* to be an order of magnitude lower than that of the other pairwise comparisons. Both species also showed similarities in taxonomically informative traits based on Radashevsky's (1993) description of *D. carunculata* and a museum specimen of *D. carunculata* that was analysed separately (David unpublished data). Blake (1996) synonymized *D. carunculata* as *D. socialis*, regarding these differences as intraspecific variation and extending the apparent distribution of *D. socialis* to the Sea of Japan. However, this synonymy was later rejected by Manchenko & Radashevsky (2002) who argued that Blake (1996) did not consider morphological variation in relation to the ecology of each population. Considering the results from our study, we suggest that the status of *D. carunculata* with *D. socialis* as distinct species be re-evaluated with additional morphological and molecular data or reproductive crosses (e.g. Rice *et al.*, 2008).

In this study, we also confirm architomy in *D. socialis* by observing fragmenting worms along with regenerating anterior (Figure 1B inset) and posterior ends of smaller fragments, prior to anaesthetization. Although architomic division has been reported before in *D. socialis* based on lab experiments (Stock, 1964) this is the first field observation of the phenomenon in the species. Asexual reproduction via architomy has thus far only been recorded from six spionids, including *D. socialis* (Blake, 2006; David & Williams, 2012*b*; Whitford & Williams, 2016). Stock (1964) found that *D. socialis* can regenerate a maximum of eight chaetigers which was also confirmed from field observations in this study. Such a reproductive strategy in a nonindigenous species has important management implications since it may facilitate rapid establishment of the species in the introduced range (David & Williams, 2012*b*). *Dipolydora socialis* also offers a potentially effective model system to study anterior and posterior regeneration in a single species that inhabits both soft and calcareous substrates. Investigating whether regeneration rates vary across these habitats (calcareous substrate *vs* sediment) would provide valuable insights into the polymorphisms of spioniform worms.

Dipolydora socialis may have been transported to southern Africa, and Knysna Estuary in particular, via multiple vectors

(see review in Papacostas *et al.*, 2017). Firstly, the species is known to produce planktotrophic larvae that could survive for months in the water column (Blake & Arnofsky, 1999) and could therefore have been transported to South Africa in ballast water. Secondly, there are multiple harbours and marinas in Knysna Estuary (Claassens *et al.*, 2020), so the species could have arrived as an epibiont of hull fouling invertebrates such as sponges from an unidentified population elsewhere in the country. Finally, for many years, Knysna Estuary was a hub for oyster farming that relied on regular importation of oyster spat and movement of oysters (Haupt *et al.*, 2010; Williams *et al.*, 2016). Given that the species has been reported as a shell borer (Blake, 1971) and shell fouler (Sato-Okoshi & Takatsuka, 2001), it may have arrived as a hitchhiker, even though it has not been reported on farmed molluscs in South Africa. Another record of *D. socialis* on the African continent was recently provided by Ab Elnaby (2019); however, the description lacked critical taxonomic details and the images provided were not of sufficient quality to allow for accurate species delineation. As that study also lacked genetic data, we regard the Egyptian report as dubious.

In Australia, Walker (2009) reported *D. socialis* producing thick tube colonies which may cause geophysical alterations in the environment that could negatively affect other organisms. Similarly, in Bodega Harbor, California, historical colonization of sediment by *D. socialis* resulted in the extirpation of native fauna and the establishment of an 'alternative' community dominated by *D. socialis* and *B. proboscidea* (Bowles, 2013). Thus, *D. socialis* provides another example of a spionid that could be considered an ecosystem engineer, one with potential negative impacts in non-native regions. Finally, if *D. socialis* does have shell-boring capabilities, it could become established on shellfish farms which are known to serve as potential source populations for invasive polychaetes (David, 2015; Williams *et al.*, 2016). Shell borers are known to negatively impact molluscs, including causing an energetic burden, reducing shell strength and lowering growth rates of hosts (Nel *et al.*, 1996; Clements *et al.*, 2018; Spencer *et al.*, 2020). Consequently, we recommend that future monitoring on the South African coast include explicit searches for this species as this will provide much-needed information on the extent of its distribution and its natural history in the region.

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