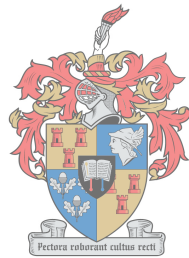


Syllidae Grube, 1850 (Annelida) from southern Africa. A taxonomic update, with a focus on *Syllis* Lamarck, 1818

by

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Safiyya Sedick

Table of contents

DECLARATION	II
TABLE OF CONTENTS	I
ABSTRACT	III
OPSOMMING	IV
ACKNOWLEDGEMENTS	V
LIST OF TABLES	VI
LIST OF FIGURES	VIII
CHAPTER 1: GENERAL INTRODUCTION	1
1.1 ALPHA TAXONOMY AND ITS ROLE IN COSMOPOLITANISM	1
1.2 THE DISINTEGRATION OF COSMOPOLITAN POLYCHAETES	2
1.3 POLYCHAETE TAXONOMY IN SOUTH AFRICA	3
1.4 SYLLIDAE (ANNELIDA)	5
1.5 AIMS	6
CHAPTER 2: DESKTOP REVISION OF SYLLIDAE (ANNELIDA, POLYCHAETA) LISTED IN DAY (1967). .	7
2.1 INTRODUCTION	7
2.2 METHOD AND MATERIALS	10
2.2.1 CREATING THE CHECKLIST	10
2.2.2 ASSIGNING GENERAL SPECIES STATUS	10
2.2.3 LOCAL DISTRIBUTION DATA	11
2.3 RESULTS	13
2.3.1 TAXONOMY	13
2.3.4 GENERAL TAXONOMIC STATUS OF SYLLIDAE	15
2.3.3 LOCAL AND GLOBAL DISTRIBUTION	15
2.4 DISCUSSION	17
CHAPTER 3: SPECIES RICHNESS OF SYLLIDS FROM THREE SITES ON THE SOUTH COAST OF SOUTH AFRICA, WITH NOTES ON GENERAL SYLLID TAXONOMIC AND ECOLOGICAL STATUS	21
3.1 INTRODUCTION	21
3.2 METHODS AND MATERIALS	23
3.2.1 STUDY AREA	23
3.2.2 SAMPLE COLLECTION AND PROCESSING	23
3.2.3 MORPHOLOGICAL IDENTIFICATIONS:	24
3.3 RESULTS	26
3.3.1 SPECIES RICHNESS OF SYLLIDAE (ANNELIDA) AMONG THREE SITES WITH NOTES ON ALIEN STATUS AND SUGGESTIONS FOR FURTHER TAXONOMIC REVISION.	26
.....	48
3.4 DISCUSSION	53
CHAPTER 4: A MORPHOLOGICAL AND MORPHOMETRIC COMPARISON OF SYLLIS ARMILLARIS MÜLLER 1776 AND SYLLIS AMICA QUATREFAGES 1866 FROM SOUTHERN AFRICA AND EUROPE WITH SYLLIS AMICARMILLARIS SIMON, SAN MARTÍN AND ROBINSON 2014 FROM SOUTH AFRICA	57
4.1 INTRODUCTION	57
4.2 METHODS AND MATERIALS	62
4.2.1 MORPHOMETRIC ANALYSIS	62
CHAPTER 4: RESULTS	66
4.3.2 A MORPHOMETRIC ANALYSIS OF SYLLIS ARMILLARIS, SYLLIS AMICA AND SYLLIS AMICARMILLARIS FROM SOUTHERN AFRICA AND EUROPE	66
4.3.2.1 ARE SYLLIS CF. ARMILLARIS AND SYLLIS CF. AMICA FROM SOUTH AFRICA THE SAME AS EUROPEAN CONSPECIFICS?	69

4.3.2.2 ARE <i>SYLLIS</i> CF. <i>ARMILLARIS</i> FROM SOUTH AFRICA AND <i>SYLLIS AMICARMILLARIS</i> SIMILAR?.....	70
4.4 DISCUSSION.....	76
CHAPTER 5: SYNTHESIS.....	80
REFERENCES:	82
APPENDIX	115
AN UPDATED CHECKLIST OF SYLLIDS LISTED IN DAY (1967) WITH NOVEL SPECIES.....	115
TABLE 1.....	144
TABLE 2.....	147

Abstract

Syllidae is a common polychaete family in South African coastal environments but have not been the focus of research since the publication of a comprehensive polychaete identification guide by Day (1967). Further, they are not listed in any local alien species inventories despite several geographically widespread species (with type localities elsewhere) occurring here. Thus, my aim was to update the list of syllids in Day (1967), allocating each species with a general status: alien, indigenous, cryptogenic or with questionable identifications (i.e., species reported without sufficient information, making their taxonomic status uncertain), using recent publications and databases to update species records. This resulted in 29 taxonomic changes and decreased the total number of valid species from 67 to 59. Additionally, >50% have a questionable taxonomic status; ~ 40% were indigenous, 8% casual and 2% potentially alien. Advancements in technology have led to the dissolution of many questionable species into complexes comprising morphologically similar species, often revealing new indigenous species. Thus, the high prevalence of questionable species among records in Day (1967) suggests an underestimation of native and alien syllid diversity. To test this underestimation, three rocky shore sites were sampled along the south coast of South Africa, a reportedly species rich region for polychaetes overall. Collected individuals were identified to species level and assigned a general taxonomic status as before. More than 600 individuals were collected, representing 13 species with 11 more being unidentifiable. Almost 80% of the species identified had a questionable taxonomy, while the remaining was indigenous. Further, the three most abundant unidentifiable species were described, increasing the total number to 62. Species with questionable taxonomy remain dominant and, along with the many unidentifiable species, makes the underestimation of syllid diversity more apparent. The notion that apparently cosmopolitan species actually represent indigenous species was tested by considering three morphologically similar species; the indigenous *Syllis amicarmillaris* and the apparently cosmopolitan *Syllis armillaris* and *Syllis amica*. The aim was to determine whether *S. armillaris*, previously considered common in the region but not collected during my study, and the rare *S. amica* had been identified correctly and are considered as belonging to *S. amicarmillaris*. Fifty individuals from South Africa and Europe were compared morphometrically, based on 46 characters and using Principal Component and Discriminant Function Analyses and pairwise comparisons. These showed that 1) *S. amica* from South Africa is morphologically distinct from *S. amicarmillaris* but similar to specimens from Europe; 2) *S. armillaris* from South Africa is distinct from European conspecifics but morphologically very similar to *S. amicarmillaris*, with only four characters weakly significantly different between them. I therefore recommend that *S. armillaris* from South Africa be referred to as *S. cf. amicarmillaris* and *S. amica* from South Africa as *S. cf. amica*. This shows that two apparently cosmopolitan species have been mis-identified, supporting the the notion that apparently cosmopolitan species actually represent indigenous species. This is especially true for *S. cf. amicarmillaris*. This study adds two more species to the growing list of questionable species in Day (1967).

Opsomming

Syllidae is 'n algemene borselwurm familie wat gevind word in kusomgewings, maar is nie die hoof fokus van navorsing vanaf die volledige borselwurm studie van Day (1967). Verder word hulle nie gelys in enige plaaslike uitheemse inventaris nie, alhoewel daar verskeie geografies wydverspreide spesies voorkom asook dat die soort ligging van die spesies elders is. My doel was om 'n opgedateerde lys van syllids vanaf Day (1967) te genereer, waar elke spesie 'n algemene status toe geken was soos volg: vreemdeling, inheemse of twyfelagtige identifikasies; deur gebruik te maak van onlangse publikasies en databasisse om spesie rekords te kan updateer. Dit het gelei tot 29 taksonomiese veranderinge waar die totale aantal spesies verminder het vanaf 67 tot 59. Verder het > 50% 'n twyfelagtige taksonomiese status ontvang; ~ 40% was inheems, 8% ongereeld en 2% moontlik uitheemse spesies. Bevorderings in tegnologie het gelei tot die ontbinding van talle twyfelagtige spesies in komplekse wat morfologies soortgelyke spesies insluit, wat dikwels nuwe inheemse spesies openbaar. Dus dui die hoë voorkoms van twyfelagtige spesies onder rekords in Day (1967) 'n onderskatting van inheemse en vreemde syllid diversiteit. Om hierdie onderskatting te toets, is drie rotsagtige kusgebiede langs die Suidkus ('n spesies-ryk streek vir borselwurms in geheel) van Suid-Afrika monsters geneem. Versamelde individue is geïdentifiseer volgens spesievlak en 'n algemene taksonomiese status was toegeken soos voorheen. Meer as 600 individue was versamel wat 13 spesies verteenwoordig, terwyl nog 11 spesies onbekendbaar is. Bykans 80% van die geïdentifiseerde spesies het 'n twyfelagtige taksonomie status gehad terwyl die oorblywende spesies as inheems geïdentifiseer was. Verder is die drie mees algehele onbekende spesies beskryf wat die totale aantal spesies tot 62 verhoog. Spesies met 'n twyfelagtige status bly oorheersend in spesiesrykheid en oorvloed, saam met die aansienlike aantal onidentifiseerbare spesies, maak die onderskatting van syllid diversiteit meer duidelik. Met hierdie in gedagte, is die idee dat skynbare kosmopolitiese spesies eintlik inheemse spesies verteenwoordig, dit is getoets deur drie morfologies soortgelyke spesies te oorweeg; die inheemse *Syllis amicarmillaris* en skynbaar kosmopolitiese *Syllis armillaris* en *Syllis amica*. Die doel van die studie was om vas te stel of *S. armillaris*, wat voorheen algemeen in die streek beskou is, maar nie tydens die huidige studie versamel is nie, en die skaarse *S. amica* korrek geïdentifiseer is en word beskou as *S. amicarmillaris*. Vyftig individue van Suid-Afrika en Europa (binne die soort streke van laasgenoemde spesies) is vergelyk met die morfometriese karakters van 46 spesies. Analise van hoofkomponent- en diskriminerende funksie analise en pare vergelykings was gebruik. Die analise het getoon dat 1) *S. amica* van Suid-Afrika morfologies afsondelik is van *S. amicarmillaris*, maar soortgelyk is aan die monsters van Europa; 2) *S. armillaris* vanaf Suid-Afrika is onderskei van Europese spesies, maar morfologies baie soortgelyk aan *S. amicarmillaris* met slegs vier van 16 karakters wat swak betekenisvol verskil tussen hierdie twee groepe. Daarom beveel ek aan dat *S. armillaris* van Suid-Afrika verwys kan word as *S. cf. amicarmillaris* en *S. amica* van Suid-Afrika, verwys as *S. cf. amica*. Dit bied bewyse vir die begrip wat vroeër uitgedruk is en toon dat twee skynbaar kosmopolitiese spesies misidentifiseer is.

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List of tables

Table 2.1 Revised names of the Syllidae (Annelida) listed in Day (1976)

Table 2.2 Local distribution of syllid species among three biogeographic regions: cool temperate west coast (WC), warm temperate south coast (SC) and tropical and subtropical east coast (EC); two temperature transition zones between: the west and south coasts (TZ1) and between the south and east coasts (TZ2) and, Madagascar (MDG)

Table 3.1 Species richness and abundance of syllids at three sites along the south coast of South Africa

Table 3.2 Designation of general status according to definitions in Chapter 2 (Q = Questionable; I = Indigenous) for identified species from Gordons Bay, Danger Point and Mossel on the south coast of South Africa. This includes local and global species records where 'South Africa' refers to the entire coastal region

Table 4.1 Characters used for the morphometric analysis of *Syllis amica*, *Syllis armillaris* and *Syllis amicarmillaris* from the Iziko South African Museum, Museo Nacional de Ciencias Naturales in Madrid (Spain) and fresh specimens collected from the South coast of South Africa

Table 4.2 Number of individuals for *Syllis amica*, *Syllis armillaris* and *Syllis amicarmillaris* used from the Natural history museums in South Africa (Iziko) and Museo Nacional de Ciencias Naturales (MNCN) in Madrid (Spain) that holds *S. armillaris* from Norway (NW) and the fresh specimens collected from the south coast of South Africa (SC)

Table 4.3 Characters selected from the Principal Component Analysis (PCA) that had a weighting of 0.4 or higher in the first five components extracted by the analysis

Table 4.4 Mean \pm Standard deviation (min–max) of measured morphological characters with high loadings (>0.4) in Principal Component Analysis for *Syllis amica*, *Syllis armillaris*, *Syllis amicarmillaris* and *Syllis gracilis* from the Iziko Southern African Museum (Iziko), Museo Nacional de Ciencias Naturales (MNCN) in Madrid (Spain) which includes the single specimen from Norway (NW) and, fresh specimens collected from the South Coast of South Africa (SC)

Table 4.5 Predicted group membership (%) for individuals belonging to *Syllis amica*, *Syllis armillaris*, *Syllis amicarmillaris* and *Syllis gracilis* from the Iziko South African Museum (Iziko), Museo Nacional de Ciencias Naturales (MNCN) in Madrid (Spain), Norway (NW) and the South coast of South Africa (SC)

Appendix 1

Table 1. Comparison of selected morphological characteristics for *Syllis amica*, *Syllis armillaris* and *Syllis amicarmillaris* derived from published literature and, examination of museum and fresh specimens

Table 2. Test statistic and associated significance values for Students t-tests (t-stat), Mann-Whitney (U) and Chi-squared (χ^2) tests performed on measured characters highlighted by the Principal Component Analysis (PCA) as contributing the most to the variation between individuals, for *Syllis armillaris* from the Iziko Southern African Museum and fresh specimens of *Syllis amicarmillaris*

List of Figures

Figure 2.1 Southern Africa showing the Agulhas Current (green) along the east and south coasts of South Africa, the Benguela Current (blue) along the west coast, and the temperature transition zones between Cape Point and Cape Agulhas (TZ1) and, Algoa Bay and the Wild Coast (TZ2) with boundaries indicated by dashed lines

Figure 3.1 South coast of South Africa indicating three sample sites (purple)

Figure 3.2 *Syllis* sp. A: Dorsal view of (I) anterior, showing (II) anterior chaetae (a, b) and pseudosimple chaetae (c, d), (III) midbody chaetae and, (IV) posterior chaetae showing a single, straight, ventral simple chaetiger with pointed tip; (V) aciculae on (a) anterior chaetigers mushroom shaped, midbody (b) distally rounded, (c) rounded on one side, (d) knobbed and (e) distally rounded and hollow on posterior parapodia

Figure 3.3 *Syllis* sp. A: Dorsal view of (I) anterior indicating position of symbiotic protozoans (red arrows); (II) close up of anterior indicating position of pharyngeal tooth (blue arrow) and symbiotic protozoan (red arrow); (III) proventricle; (IV) symbiotic protozoan in anterior intersegmental grooves (red arrow)

Figure 3.4 *Syllis* sp. A: (I) Anterior inferior and pseudosimple chaetae indicating the bidentate teeth on chaetae and gradation of teeth along chaetal blade (red arrow) and, serrated outer edge of pseudosimple chaetae (black arrow); (II) anterior superior chaetiger indicating subequal teeth along chaetal blade (red arrow); (III) mushroom shaped anterior aciculae (blue arrow)

Figure 3.5 *Syllis* sp. A: (I, III) Midbody superior chaetae indicating bidentate teeth and gradation in chaetal blade length (red arrows); (II, V, VI, VII) inferior chaetae indicating chaetae with bidentate teeth and gradation in teeth along chaetal blade (red arrows); (IV, V) aciculae indicating (IV) knobbed and (V) hollow aciculae (blue arrows)

Figure 3.6 *Syllis* sp. A: (I) Posterior inferior chaetae (red arrows) with indentations along chaetal shaft (black arrow) and hollow aciculum (blue arrow); (II) superior chaetae (red arrows) and simple chaetiger (black arrow)

Figure 3.7 *Syllis* sp. D: Dorsal view of (I) anterior, (II) anterior chaetae with solitary subtriangular pseudosimple chaetiger with narrow shaft head, tapering into a sharp point with short spines on outer margin, (III) midbody chaetae with single subtriangle pseudosimple chaetiger with broad shaft head tapering to rounded point, with short spines on outer margin and (IV) posterior chaetae with single, sinuose, bidentate, ventral simple chaetiger with serrated inner margin, (V) aciculae on (a) acute angle on one margin and straight on the other, narrow point, midbody with (b) sickle shape and (c) knob shape and anterior aciculae (d) posterior parapodia with one side curved and the other side straight (pg 44)

Figure 3.8 *Syllis* sp. D: Dorsal view of (I) anterior and (II) whole specimen

Figure 3.9 *Syllis* sp. *D*: Midbody (I) anterior superior chaetae with shorter secondary tooth (red arrow); (II) inferior chaetae indicating bidentate teeth and gradation along chaetal blade (red arrows), (II) indentations along chaetal shaft and pseudosimple chaetiger (black arrows) and (II, III) aciculae with (III) one side curved and the other straight, (II) broad with narrow point (blue arrows)

Figure 3.10 *Syllis* sp *D*: (I, II) Midbody superior chaetae indicating bidentate teeth and gradation along chaetal blade (red arrow), (II) inferior chaetae indicating bidentate teeth, gradation along chaetael blade (red arrows) and indentations along chaetal shafts (black arrow); (II) pseudosimple chaetiger (black arrow); (III, IV) aciculae (blue arrows) (III) knobbed, (IV) sickle-like shape

Figure 3.11 *Syllis* sp. *D*: (I) Posterior superior chaetae indicating bidentate teeth (red arrows) and indentations in chaetal shaft (black arrows); (II) inferior chaetae indicating bidentate teeth and gradation along chaetal blade (red arrows); (III, IV) aciculae with (III) narrow pointed tip, (IV) rounded on one side and curved on the other, almost diamond shaped with two acute angles on either side (blue arrows)

Figure 3.12 *Syllis* sp. *S*: Dorsal view of (I) anterior, (II) anterior chaetae with solitary pseudosimple chaetiger with narrow shaft head and sharp, pointed tip, (III) midbody and (IV) (a) posterior chaetiger with (b) single dorsal, simple chaetiger, straight with thick, rounded tip, (c) ventral simple, chaetiger, thin, pointed with indentations along shaft head, (d) pseudosimple chaetiger with broad shaft head with curved point and, (V) aciculae with (a) anterior aciculae straight, broad, (b) slightly curved on one margin, (c) paddle-shaped, (d,e) midbody distally oblique, (f) bottle-shaped, (g) posteriorly at right angle, (h) distally gently curved, rounded tip to one margin

Figure 3.13 *Syllis* sp *S*: (I) Swollen anterior end, (II) extent of colouration, (III) gradation in colour from anterior (red arrow) to midbody and (IV) anterior end showing shape of palps

Figure 3.14 *Syllis* sp. *S*: (I) Anterior inferior and superior chaetae (red arrows) and, pseudosimple chaetiger (black arrow) and (II) aciculum straight, broad (blue arrow)

Figure 3.15 *Syllis* sp. *S*: (I) Midbody aciculae distally oblique and rounded (red arrow), bottle-shaped (blue arrow) and, (II, III) inferior and superior chaetae indicating bidentate teeth with a gradation along chaetal blade (red arrows) and, indentations in chaetal shaft (black arrows)

Figure 3.16 *Syllis* sp. *S*: (I) Posterior inferior and superior chaetae (red arrows), pseudosimple and simple chaetae (black arrows) and, aciculum distally gently curved with rounded tip toward one margin (blue arrow) and, (II) simple chaetiger (red arrow) and gently rounded aciculum (blue arrow)

Figure 4.1 Morphological features measured of the (I) anterior end, (II) prostomium and palps and, (III) chaetae for *Syllis amica*, *Syllis armillaris*, *Syllis amicarmillaris* and *Syllis gracilis* from South Africa and Europe. Labels for figure are explained in Table 4.1 below

Figure 4.2 Canonical discriminant function displaying five distinct groups of individuals with *Syllis gracilis* Iziko forming cluster 1 (purple), *Syllis armillaris* and *Syllis amicarmillaris* in cluster 2 (red), *Syllis armillaris* from Norway in cluster three (orange), *Syllis armillaris* from Spain in cluster four (black) and, *Syllis amica* from Spain, Iziko and the South Coast of South Africa form cluster five (blue)

Chapter 1: General Introduction

1.1 Alpha taxonomy and its role in cosmopolitanism

Taxonomy is generally defined as the field of science related to the identification, description and classification of taxa (Glasby and Read 1998, Wheeler 2007). Alpha taxonomy is the description and systematic placing of species based solely on their morphological characteristics (Glasby and Read 1998, Wheeler 2007). The evolution of new techniques has allowed us to take a more holistic approach to species descriptions where we are able to detail life history processes and differences at a genetic level (Vogler and Monaghan 2006, Padial et al. 2010). This has contributed to beta taxonomy which is the classification of species based on morphology and additional characters such as physiology and genetics (Glasby and Read 1998, Wheeler 2007). Beta taxonomy allows a closer examination of species that often changes our understanding of the way species are related to each other (Franke 1999, Westheide and Schmidt 2003, Appeltans et al. 2012). However, as taxonomic methodologies become more refined with the development of new technology, new revisions of species are conducted, revealing previously overlooked characters that challenge the validity of species names and descriptions, ultimately changing their systematic placement (Musco et al. 2009, Tirado-Sanchez et al. 2014). Thus, more detailed morphological examinations can often enable the distinction between species that had previously been considered morphologically similar, without the use of molecular data. This is particularly useful when genetic material is unavailable. For example, a revision of the genus *Megalomma* Johansson 1926 in the Mediterranean Sea, using morphological examination only, found that individuals identified as *M. vesiculosum* (Montagu 1813) were misidentified and were actually *M. lanigera* (Grube 1846). Furthermore, *M. neapolitana* (Claparède 1868) was assigned as a junior synonym of *M. lanigera* and two new species were described; *M. messapicum* Giangrande and Licciano 2008 and *M. claparadei* (Gravier 1906) (Giangrande and Licciano 2008). In the present study, only alpha taxonomy will be considered.

Before the 1900s taxonomic studies were often based on limited morphological, distributional and life history information (Knowlton 1993). Taxonomists from regions that lacked documentation of local fauna relied on identification keys from elsewhere in the world where taxa were relatively well documented, such as Europe and North America (Hutchings 1998). Local fauna with similar characteristics to European or North American taxa were consequently identified as such, resulting in many species apparently having cosmopolitan distributions (Hutchings 1998). This often resulted in the lumping together of morphologically similar species into a single nominal species. To further complicate matters, many taxa that were considered indigenous were synonymized with species thought to have a wide distributional range (Knowlton 1993, Klautau et al. 1999, Westheide and Schmidt 2003). Such wide geographic ranges, frequently accompanied by high intra-specific variation, have always been accepted as the result of broad inter-ocean dispersal (Knowlton 1993, Klautau et al. 1999, Westheide and Schmidt 2003). Recent studies have, however, found that this is not always the case and many species exhibit larval dispersal mechanisms, or temperature or salinity tolerances (Knowlton 1993, Klautau et al. 1999, Abbiati and Maltagliati 1996, Westheide and Schmidt 2003, Bickford et al. 2007) that do not allow for such a wide dispersal and distribution (Knowlton 1993, Klautau et al. 1999,

Westheide and Schmidt 2003). This calls into question the status of many apparently cosmopolitan species.

Species that have an apparent cosmopolitan distribution as a consequence of erroneous identification or lumping of morphologically similar species often dissolve into complexes of cryptic or pseudo-cryptic species (i.e., species that are morphologically very similar to each other, but which can be distinguished by new characters) upon taxonomic revision (Klautau et al. 1999, Nygren 2014). Although many apparently cosmopolitan species are really complexes of (pseudo-)cryptic species, some may be truly cosmopolitan through natural migration and dispersal (Orensanz et al. 2002, Pérez-Portela et al. 2013). By contrast, when species have a cosmopolitan distribution because they have been transported outside of their natural range by human activity, they should rather be referred to as introduced or alien (Carlton 1996, Mack et al. 2000, Richardson et al. 2000, Kolar and Lodge 2001, Vermeij 2006, Katsanevakis et al. 2009, Robinson et al. 2016).

1.2 The disintegration of cosmopolitan polychaetes

Polychaetes occur worldwide with many species apparently having a widespread or cosmopolitan distribution (Hutchings 1998, Nygren 2014). However, truly cosmopolitan polychaetes are uncommon and there is often high molecular divergence, usually accompanied by morphological variation, between populations of species that have apparently global distributions (e.g. Barroso et al. 2010, Carr et al. 2011, Nygren and Pleijel 2011, Glasby et al. 2013, Borda et al. 2012, Stiller et al. 2013, Nygren 2014). Several recent studies found that such pseudo-cryptic polychaete species complexes are ubiquitous and that cosmopolitan species are not as common as previously believed (Knowlton 1993, Hutchings 1998, Nygren 2013, Hutchings and Kupriyanova 2017). For example, genetic and morphological examination of the cosmopolitan fire-worm *Eurythoe complanata* (Pallas 1766) sampled from 20 different localities across the Caribbean Sea and Pacific, South Atlantic and Indian oceans showed that this species comprises at least three species; two true cryptic and one pseudo-cryptic species differentiated by the length of the caruncle and the absence of harpoon shaped notochaetae (Barroso et al. 2010). Similarly, morphological and genetic data show that *Perinereis cultifera* (Grube 1840) from the English channel and Algerian Mediterranean coast comprises at least three pseudo-cryptic species, distinguished by the number and morphology of paragnaths (Scaps et al. 2000). Other examples include; *Arenicola defodiens* Cadman and Nelson-Smith 1993 and *Arenicola marina* (Linnaeus 1758) from the North Sea, Wadden Sea and Skagerrak that can be separated by the pattern of annulation of the first head segments (Luttikheizen and Dekker 2010), and *Opehila bicornis* Savigny in Lamarck 1818 and *Ophelia barquii* Fauvel 1927 from the western Mediterranean that can be separated by the number of nephridiopores (Maltagliati et al. 2004). Similarly, *Capitella capitata* (Fabricius 1780) comprises at least 50 pseudo-cryptic species that are distinguished by the shapes of the prostomium, thorax and chaetae (Grassle and Grassle 1977, Méndez et al. 2000, Blake 2009, Blake et al. 2009).

Frequently taxonomic anomalies such as cryptic species are the failure of past taxonomists to consider or make use of obvious (or potentially distinctive) features to characterize taxa (Knowlton 1993, Giangrande 2003). When the taxonomic uncertainties surrounding recognized cryptic species are resolved, the increase in native species diversity may be as much as ten-fold (Knowlton 1993). Furthermore, by recognizing the true

diversity of native species, the role of those cosmopolitan species that have been moved outside of their native ranges (i.e., alien species) can be better understood in ecological communities (Vermeij 1996). For polychaetes, an estimated 292 alien polychaete species across 39 families have been identified, and resolving (pseudo-)cryptic species complexes will make alien polychaetes (and alien species in general) more easily distinguishable from native species (Appeltans et al. 2012, Çinar 2013).

1.3 Polychaete taxonomy in South Africa

Most of our knowledge on local benthic taxa originated in the late 1800s with the international global voyages such as the *Challenger* and *Valdivia*, but it was expanded during the period 1940 – 1980 when the University of Cape Town conducted substantial sampling during their periodic Ecological Surveys (Griffiths et al. 2010). For polychaete taxa, this periodical sampling was reflected in the surge of literature between 1934 and 1980 documenting polychaete fauna in and around southern African waters (e.g. Day 1934, 1939, 1949, 1951, 1953; Day et al. 1954, Day 1958) culminating in the publication of "A monograph on the Polychaeta of southern Africa" (Day 1967). Thereafter, fewer papers on polychaetes were published (e.g. Berrisford 1969, Silberbauer 1969, Knight-Jones and Knight-Jones 1974, Day 1975, Jouin 1975) until the 1990s when interest in this group was renewed (e.g. Schleyer 1991, Kalejta 1993, Nel et al. 1996, Weber and Haig 1997).

Since the 1990's, local studies on polychaetes focused primarily on Spionidae Grube 1850 and Sabellidae Latreille 1825. They infest commercially important molluscs such as oysters and abalone, and the publications detail the invasive nature of these species, their reproduction, and efforts to counteract their infestation in aquaculture (Schleyer 1991, Nel et al. 1996, Simon et al. 2005, Simon et al. 2006, Simon and Booth 2007, Simon et al. 2009, Simon et al. 2010, Boonzaaier et al. 2014, Simon 2015, David and Simon 2014, David et al. 2016; Williams et al. 2016). Comparatively, few recent publications have detailed descriptions of new species from South Africa: *Perinereis namibia* Wilson and Glasby 1993, *Marphysa elityeni* Lewis and Karageorgopoulos 2008, *Pseudopolydora dayii* Simon 2009, *Magelona debeerei* Clarke, Paterson, Florence and Gibbons 2010, *Dipolydora keulderae* Simon 2011, *Laonice antipoda* Sikorski 2011, *Polydora dinthwanya* Simon 2011, *Syllis amicarmillaris* Simon, San Martín and Robinson 2014, *Syllis unzima* Simon, San Martín and Robinson 2014 and *Laonice olgae* Sikorski and Pavlova 2016 (Wilson and Glasby 1993, Simon 2009, Lewis and Karageorgopolous 2008, Clarke et al. 2010, Simon 2011, Sikorski and Pavlova 2016).

Day (1967) is the only comprehensive source of identification for polychaetes in South Africa and is still widely used today. In the introduction to this monograph, the author acknowledges that species with a seemingly widespread distribution, such as *Owenia fusiformis* Delle Chiaje 1844 and *Hydroides norvegica* Gunnerus 1768, may comprise complexes of species while others, like *Diopatra neapolitana* Delle Chiaje 1841, may have been misidentified locally. Investigations of these taxa elsewhere suggested that this prediction was quite accurate. *Hydroides norvegica* was most likely misidentified as the cryptogenic *Hydroides elegans* (Haswell 1883), as the former has only ever been found in the Northern Hemisphere (Ten Hove and Kurpiyanova 2009, Read et al. 2016). *Owenia fusiformis* is considered a cryptic species complex in Australia, southern Brazil, northern North Atlantic Ocean, Persian Gulf and the Yellow sea (Koh and Baud 2001, Koh et al. 2003, Ford and Hutchings 2005, Martin et al. 2006, Parapar and Moreira 2015, Silva and

Lana 2017). *Diopatra neapolitana* is probably also a pseudo-cryptic species complex (Arias et al. 2016). Though Day (1967) only singles out three species, numerous other apparently cosmopolitan species may be found throughout the two-volume monograph.

Recently, more and more researchers are showing that some of the apparently cosmopolitan species in South Africa are actually new indigenous species: the native *M. elityeni*, was previously identified as the cosmopolitan *Marphysa sanguinea* (Montagu 1813) by Day (1967) (Lewis and Karageorgopolous 2008); *Magelona papilicornis* Müller 1858 is a proposed species complex which now includes the indigenous *M. debeerei* (Clarke et al. 2010); and local specimens of the widespread *Perinereis nuntia vallata* (Grube 1857) have been synonymized with the native *P. namibia* (Wilson and Glasby 1993). More recently, *Laonice cirrata* (Sars 1851) was redescribed as *L. antipoda* (Sikorski and Pavlova 2016); while Simon et al. (2017) determined that the apparently cosmopolitan species *Pseudopolydora antennata* (Claparède 1869) is a complex of at least five pseudo-cryptic species, two of them from South Africa. It is therefore likely that many other cosmopolitan species listed in Day (1967) actually represent undescribed, indigenous, species and with its continued use as the primary guide for polychaete identification, there is a risk in continuing to mistake indigenous species for cosmopolitan ones. Therefore, it would be important for us to identify those apparently cosmopolitan species that require revision. In correctly identifying the indigenous species, we would also be making clear the distinction between alien and native species.

Mead et al. (2011a, b) produced the first comprehensive inventories of introduced marine species in South Africa. These lists were created by examining literature and inventories of confirmed introduced marine and estuarine species outside of South Africa but in climatically comparable regions mainly within South America, New Zealand and Australia but also in the northern hemisphere. Mead et al. (2011a, b) considered species that had a reasonably well-resolved taxonomy and discontinuous geographical distributions, while voucher specimens, paleontological, archaeological, historic, biogeographic, genetic and taxonomic records were also examined for those species considered to have a questionable taxonomic status. Species were assigned an alien status according to Chapman (1988), Chapman and Carlton (1991) and Carlton (1996). Consequently, 86 introduced species and 39 cryptogenic marine and estuarine species were listed (Mead et al. 2011a, b). Of the more than 760 polychaete species recorded in South Africa, Mead et al. (2011a, b) listed only ten species. Of these, eight were listed as introduced (*Janua heterostropha* prev. *Janua pagenstacheri* (Montagu 1803), *Neodexiospira brasiliensis* (Grube 1872), *H. elegans*, *Boccardia proboscidea* Hartman 1940, *Alitta succinea* (Leuckart 1847), *Polydora hoplura* Claparède 1869, *Dodecaceria fewkesi* Berkeley and Berkeley, 1954 and, *Ficopomatus enigmaticus* (Fauvel 1923)), and two cryptogenic: *Simplicaria pseudomilitaris* Thiriot-Quévèreux 1965 and the *Capitella* spp complex). It is worthwhile to note that *Neanthes succinea* has been resurrected and re-described from Germany and Asia (Sato 2013, Villalobos-Guerrero and Carrera-Parra 2015) and therefore is worth re-examining in South Africa as it may actually represent an indigenous species.

Recently, Robinson et al. (2016) published a re-assessment of the definitions used to classify introduced species and applied them to the species listed in Mead et al. (2011a, b). This resulted in 89 alien species (instead of 86 in Mead et al. 2011a, b), of which 53 were invasive. Nine polychaete species are listed: three aliens (*J. heterostropha*, *S. pseudomilitaris*, *Polydora* cf. *websteri* Hartman in Loosanoff and Engle, 1943 (a

new addition to the list)), five invasive aliens (*B. proboscidea*, *A. succinea*, *F. enigmaticus*, *N. brasiliensis*, *P. hoplura*), one cryptogenic (*H. elegans*) and one naturalized species (*D. fewkesi*) (Robinson et al. 2016). All of them may be found in Çinar's (2013) global inventory of introduced polychaetes that was also compiled by examining regional publications of alien species lists and polychaete checklists. There are, however, several species listed in Çinar (2013) as alien in other regions that also occur in South Africa but are not considered alien here (cf. Day 1967, Mead et al. 2011a, b; Robinson et al. 2016). For example, *Prionospio sexoculata* Augener 1918, *Heteromastus filiformis* (Claparède 1864), *Thelepus setosus* (Quatrefages 1866) and *Desdemona ornata* Banse 1957 are considered established alien species while *Boccardia polybranchia* (Haswell 1885), *Leitoscoloplos kerguelensis* prev. *Haploscoloplos kerguelensis* (McIntosh 1885) and *Isolda pulchella* Müller in Grube 1858 are classified as cryptogenic, respectively (Çinar 2013). Given that Çinar (2013) compiled the global inventory in a similar manner to Mead et al. (2011a, b), all of the aforementioned species should probably be on the list of alien species in South Africa leading to an underestimate of the number of local alien species .

1.4 Syllidae (Annelida)

A good starting point to investigate the possible underestimation of local and alien diversity in South Africa is with Syllidae. They are common in coastal environments, often forming a substantial part of rocky shore communities (San Martín and Aguado 2014). Syllidae comprises numerous apparently cosmopolitan species, some of which are listed on global species inventories and are meant to occur in South Africa (Aguado et al. 2012, San Martín and Aguado 2014). Syllidae includes five monophyletic sub-families: Anoplosyllinae Aguado and San Martín 2009, Syllinae Grube 1850, Exogoninae Langerhans 1879, Autolytinae Langerhans 1879 and Eusyllinae Malaquin 1893 (Day 1967, Aguado et al. 2012, San Martín and Aguado 2014). Over the last 18 years (2000 – 2017) many publications describe new species belonging to the sub-families Syllinae (92 species), Exogoninae (63 species), Eusyllinae (33 species) and Autolytinae (19 species) (Gil and Musco 2015). These species have been described in places that include but are not restricted to: South America (Nogueira et al. 2001, Fukuda and Nogueira 2006, Paola et al. 2006, Nogueira and Yunda-Guarin 2008, Fukuda et al. 2009), Japan (San Martín and Nishi 2002, Aguado et al. 2006, Aguado et al. 2008), Caribbean Sea (Ruíz-Ramírez and Salazar-Vallejo 2001, Lattig and Martin 2011), Australia (San Martín 2005, San Martín and Hutchings 2006, San Martín et al. 2007), Mediterranean Sea (Abd-Elnaby and San Martín 2010, Musco et al. 2005, Çinar 2015) and Europe (San Martín and Lopez 2000, Parapar et al. 2000, Olivier et al. 2012). The genera with the most new recently (over the last 17 years) described species are *Syllis* Lamarck 1818 (30 species), then *Haplosyllis* Langerhans 1879 (22 species), *Exogone* Örsted 1845 (19 species), *Sphaerosyllis* Claparède 1863 (17 species) and *Branchiosyllis* Ehlers 1887 (13 species) while the remaining genera have up to eight newly described species each (Read and Fauchald 2017). I can therefore predict that diversity within Syllidae is probably also underestimated in South Africa, since so many new species have been described elsewhere over recent years.

The genus *Syllis* belongs to the sub-family Syllinae and is the most common, widespread and species rich genus with at least 140 nominal species (Gil et al. 2017). In South Africa, Day (1967) recorded 19 species, with only one being indigenous (Day 1967). Since Day (1967), only two new native species have been described (Simon et al. 2014). Since the whole family and *Syllis* in particular, of polychaetes have not been

subjected to a thorough taxonomic revision during the last five decades, many more taxonomic changes are expected.

1.5 Aims

The overarching aim of this thesis is to re-assess the native and alien species richness of syllids, and particularly those of *Syllis*, in South Africa. Towards this aim, I will:

- ♣ Create an updated checklist of syllids listed in Day (1967) by updating species names and distributions and by determining whether any of the listed species are possibly part of species complexes
- ♣ Allocate each species on the updated checklist with the corresponding status as indigenous, alien, questionable or cryptogenic, based on recent taxonomic revisions and distributional information, emphasizing those that have an uncertain identity and are most likely members of a species complex
- ♣ Assess the species richness of indigenous and alien syllids at selected sites along the South African coast to determine how well they have been documented in South Africa
- ♣ Describe any new species collected, if any
- ♣ Highlight those species collected from fresh samples that require further examination as a result of their uncertain identity in South Africa and select a common species that may be part of a species complex to clarify their taxonomy using morphometric and morphological approaches

Chapter 2: Desktop revision of Syllidae (Annelida) listed in Day (1967)

2.1 Introduction

Since the turn of this century, many syllid species have been described and others revised worldwide, changing their systematic placing. For example, Anoplosyllinae was erected as a new sub-family, 23 new genera have been erected and over 200 new species have been described (Read and Fauchald 2017). In *Exogone* alone, 48 species have been synonymized with others, 27 new species have been described, nine species are now considered *Nomina dubia* (species with a doubtful name) and one species is classified as *Taxon inquirendum* (an ambiguous species that is impossible to identify or characterize) (Musco and Bellan 2008). This strongly suggests that many of the syllid genera and species listed in Day (1967) require revision. For this reason it is essential that Day (1967) be updated to avoid perpetuating old errors and to highlight those species that have a questionable taxonomy (locally and globally) and include several synonymized species with type localities that are distributed in disjunct regions of the world, suggesting a questionable taxonomic status. Further, an updated species list provides a sound taxonomic foundation upon which to build investigations into areas of research such as alien species distributions and the role they play amongst native species communities (Vermeij 1996).

Çinar's (2013) global inventory of alien polychaetes includes 20 syllid species. Among them, *Exogone africana* Hartmann-Schröder 1974, is native to southern Africa and therefore not considered as potentially alien in South Africa, as it is in the Mediterranean Sea (Zenetos et al. 2010). The remaining syllids on Çinar's (2013) list have type localities elsewhere in the world, and two of these, *Branchiosyllis exilis* Gravier 1900 and *Syllis gracilis* Grube 1840, have both been recorded locally (Day 1967). *B. exilis* is listed as casual along the Pacific coast of the USA, and questionable along the Pacific coast of Mexico and in Panama (Çinar 2013). Locally, it has only ever been found on the east coast of South Africa and in Madagascar (Day 1967). *Syllis gracilis* from Argentina is listed as cryptogenic (Orensanz et al. 2002, Çinar 2013) and has been widely recorded on the west, south and east coasts of South Africa (Day 1967). Even though these species have been recorded locally, they are not listed on any local alien species inventories (cf. Mead et al. 2011a, b, Robinson et al. 2016)

Considering the way in which Mead et al. (2011a, b) compiled their alien species list for South Africa (by only considering species classified as alien in climatically comparable regions), several syllids listed in Day (1967) should probably be included. For example, some have type localities in climatically comparable regions to South Africa suggesting that they may be alien. This therefore implies an underestimation of alien species. For example, 15 species have type localities in the Mediterranean Sea and are widely distributed in tropical and temperate seas (Day 1967). Additionally, alien species often go unrecognized when they do not have any noticeable impacts on the surrounding ecosystem (Ruiz et al. 1997, Bax et al. 2001, Molnar et al. 2008). As a consequence, knowledge surrounding less conspicuous invading organisms is relatively poor while larger more conspicuous species are usually the main concern of studies of invasive species (Ruiz et al.

2000, Giangrande et al. 2001). Syllids are small and have no known noticeable impact on the surrounding environment (e.g. they don't build permanent reefs), making them less conspicuous as alien species, which may have led to them never being considered as alien. Nevertheless, populations that occur in regions outside of their species' locality are not necessarily alien and may actually consist of a species complex (Hutchings and Kupriyanova 2017).

Species that are geographically widespread, occurring in both tropical and temperate climates, are often referred to as cosmopolitan species (Klautau et al. 1999, Hutchings and Kupriyanova 2017). The notion that polychaetes largely differed from other taxa in having large morphological variation was widely accepted by early taxonomists (Knowlton 1993, Klautau et al. 1999, Westheide and Schmidt 2003, Hutchings and Kupriyanova 2017). Conservative views coupled with varying standards of species descriptions (i.e., publication of only species names, very brief descriptions and poor quality of illustrations, if any) resulted in many species having a widespread geographic distribution (Klautau et al. 1999, Hutchings and Kupriyanova 2017). The use of Scanning Electron Microscopy (SEM) along with the recent advancement of molecular taxonomy, morphological descriptions are now being published in immense detail and are often accompanied by molecular data (Hutchings and Kupriyanova 2017). Accordingly, what were once thought to be cosmopolitan taxa have now dissolved into several distinct species that each have a narrow distribution range, and many of which are new indigenous fauna (Klautau et al. 1999, Nygren 2014, Hutchings and Kupriyanova 2017). For example, several syllids listed in Day (1967) have type localities in climatically incomparable regions suggesting that their identifications may be incorrect. Thus, it is possible that indigenous biodiversity has been underestimated.

In South Africa, the distribution of many cosmopolitan and indigenous species follows a general pattern that is strongly influenced by the two major, contrasting ocean currents i.e., the cold temperate Benguela current along the west coast and the tropical and the sub-tropical Agulhas current along the east coast (Awad et al. 2002, Teske et al. 2011). Considering that endemic (i.e., species for which there are no records outside of southern Africa) species were those that only occurred within the political boundaries of South Africa, Awad et al. (2002) determined that the south coast is a region where endemism is highest for polychaetes. Similarly, levels of species richness for polychaetes are also considered to be high in this region and similar to that on the east coast (e.g. 250 species in East London, 330 species in False Bay, 310 species in Mossel Bay) but lowest on the west coast (140 species in Port Nolloth) (Awad et al. 2002). This supports an earlier analysis by Day (1967), who found that the south coast had the highest level of endemism when considering 100 polychaete species with names beginning with A – F. Cape Point and Cape Agulhas had the most endemic species (28 each), followed by Knysna (27) and Port Elizabeth (22) (Day 1967: Fig. 0.1, Page 7). By contrast, species richness is highest along the east coast and lowest along the west and south coasts, which have similar species richness (Day 1967: Fig. 0.1, Page 7). While these two studies are in agreement about the overall distribution of endemic species, the pattern of polychaete species richness differ (Day 1967, Awad et al. 2002). This difference could be attributed to the fact that Day (1967) only included 100 species, as a representative sub-sample, in his analysis whereas Awad et al. (2002) considered 523. Furthermore, it is not clear if these patterns apply equally to all polychaete families. Of the 100 species considered by Day (1967), only 21 syllid species were included. For this reason, it is much more likely that

syllids would adhere to the general pattern for polychaetes described in Awad et al. (2002), than to that in Day (1967).

Given the limited knowledge on species richness, endemism and distribution of syllids in South Africa, their poor taxonomic resolution and their absence from local alien species inventories, it would be worthwhile to update the records listed in Day (1967). In doing so, assigning each species with a general status according to their type localities or to the clarity of their taxonomy will allow us to highlight those species that could potentially be alien or have a questionable taxonomic status that would require further investigation.

Therefore, the specific aims for this chapter are to:

- ♣ Update the taxonomic, ecological and distributional records of Syllidae listed in Day (1967), adding new information from papers published from 1967 to 2017. This will allow me to identify the gaps in knowledge on species richness, endemism and distribution of syllids around southern Africa as well as the extent to which they have been recorded in recent local publications.
- ♣ Assign each species in the updated checklist with a general status as introduced, cryptogenic, questionable or indigenous. In doing so, those species that require further investigation and those that are potentially alien will be highlighted and emphasized.

2.2 Method and Materials

2.2.1 Creating the checklist

Day (1967) defines southern Africa as being the part of the African continent that is south of 24°S latitude and would therefore include the following coastal countries: Angola, Namibia, South Africa and Mozambique but also includes the island of Madagascar. Thus only records from these countries have been considered for this checklist.

Corrected or revised names, type localities, local and global distributional records, and where available, the introduced status outside of South Africa, were taken into consideration, by consulting Day (1967), four online databases (World Polychaete Database (WPD), World Register of Marine Species (WoRMS), Ocean Biogeographic Information System (OBIS) and Encyclopaedia of Life (EOL)) and the wider published literature. Day (1934, 1953, 1957, 1960, 1967) and other local studies that include information about regional distribution, taxonomy, and ecology (e.g. McQuaid and Branch 1984, Hammond and Griffiths 2004, Milne and Griffiths 2014) were consulted to determine and update local distributions. The type of environment and substrate for each species was also considered and was derived from local and global records when available.

2.2.2 Assigning general species status

Each identified species was assigned a status as alien, indigenous or questionable according to the following definitions:

Alien

Presence in a region may be attributed to human actions that allowed them to overcome biogeographical barriers (i.e., human-mediated, extra-range dispersal) (Robinson et al. 2016). Following Mead et al. (2011a, b) species that occur locally may be classified as potentially alien if they were first described outside of the region and have been categorized as alien in climatically comparable regions elsewhere. Alien species are expected to have good global taxonomic resolution but a discontinuous geographical distribution.

Synonym: Introduced.

Alien species are further divided into two sub-categories:

Naturalised Alien

Species that have self-replacing populations over several generations outside of captivity or culture but that have not spread from their point of introduction (Robinson et al. 2016).

Invasive Alien

Species that have self-replacing populations over several generations and have spread from the initial point of introduction (Robinson et al. 2016).

Extralimital

Species whose native range falls within the political boundaries of South Africa, but whose presence in another part of the country is attributable to human transport across fundamental biogeographical barriers (Robinson et al. 2016).

Cryptogenic

Species of unknown origin (Robinson et al. 2016), i.e. whose taxonomy may have been confirmed across its distributional range but whose origin is uncertain.

Questionable

Species with low taxonomic resolution (globally), numerous type localities listed on WPD or WoRMS arising from the synonymization of different species around the world into a single apparently cosmopolitan one, whose identities have not been confirmed and/or for which evidence of cryptic species or species complexes exist in at least part of their range. They are usually reported locally without sufficient information and their taxonomic status is therefore uncertain (Çinar 2013).

Questionable species can further be sub-categorized:

Casual

Species that have only ever been reported once in southern Africa or that Day (1967) refers to as rare or occasional.

Indigenous

Species whose native range is southern Africa but may also occur elsewhere in the world.

Synonym: Native

Where appropriate, species were classified according to their taxonomic status as defined by the International Commission on Zoological Nomenclature (ICZN 2017):

Nomina Dubia

A species name that is unknown or of doubtful application.

Nomina Nuda

A species name that is unavailable because it does not have a valid description or reference.

Incertae Sedis

A species with an uncertain taxonomic position.

2.2.3 Local distribution data

The distribution information for each record in the checklist (Appendix 1) was assimilated from Day (1934, 1953, 1957, 1960, 1967) and local published literature. This distributional information was divided across five biogeographic zones (Fig. 2.1) that are strongly influenced by temperature (Teske et al. 2011). The west coast of South Africa represents a region of cold temperate waters, the south coast warm temperate and east coast tropical and sub-tropical waters (Turpie et al. 2000, Awad et al. 2002, Hutchings et al. 2009, Beal et al. 2012). The transition zones between Cape Point and Cape Agulhas and, Algoa Bay and Wild Coast represent regions where water temperature is highly variable (Teske et al. 2011). Data are presented as the number of syllid species at localities in each of these biogeographic regions.

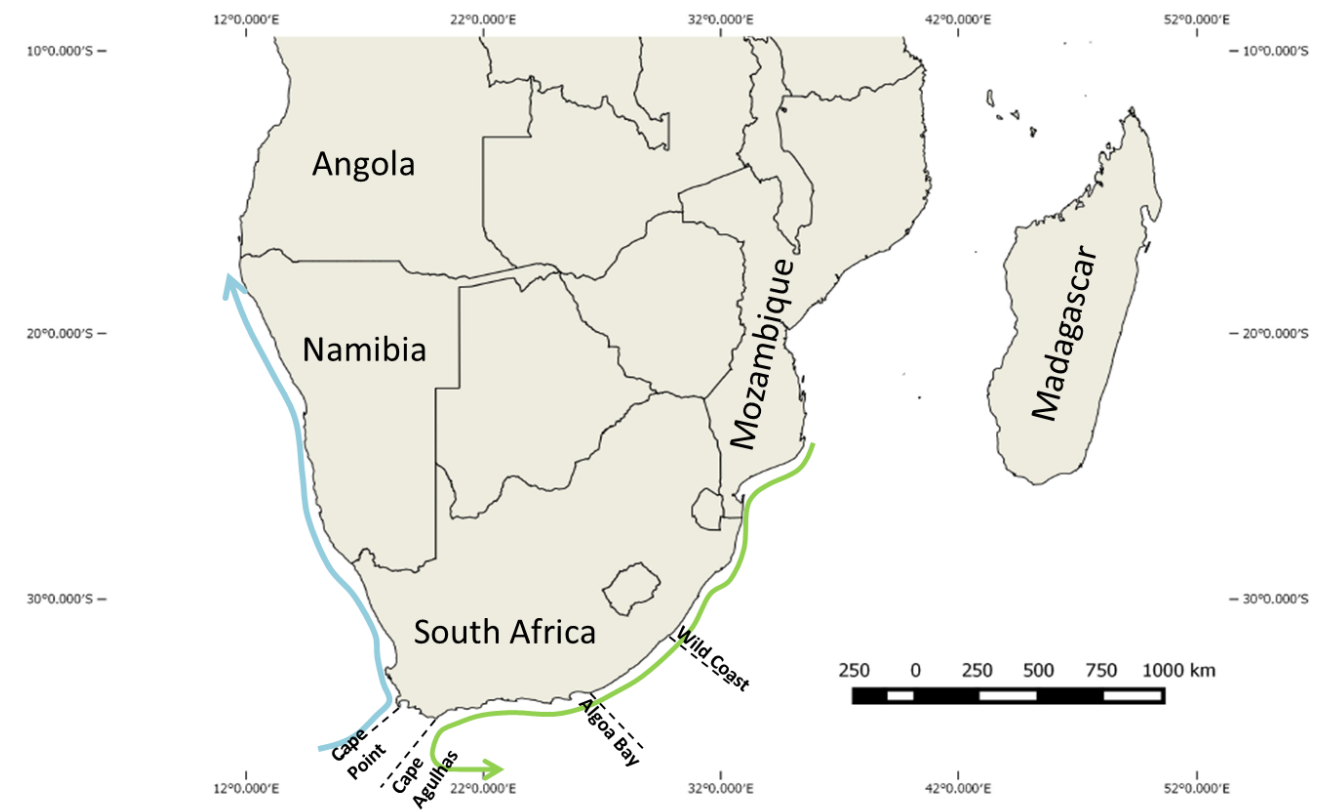


Figure 2.1 Southern Africa showing the Agulhas Current (green) along the east and south coasts of South Africa, the Benguela Current (blue) along the west coast, and the temperature transition zones between Cape Point and Cape Agulhas (TZ1) and, Algoa Bay and the Wild Coast (TZ2) with boundaries indicated by dashed lines.

2.3 Results

The records for each of the species may be found on the updated checklist in Appendix 1.

2.3.1 Taxonomy

After an extensive desktop analysis, 29 taxonomic changes (Table 2.1) were made to the species listed in Day (1967), decreasing the total number of valid species from 67 to 59. Specifically, 12 species have been assigned to different genera, eight were synonymized with others and one sub-genus (*Haplosyllis* Langerhans 1879) was elevated to full genus status. Majority of the changes were made within *Syllis* and *Syllinae*, while the remaining ones were made within *Exogoninae*, *Autolytinae* and *Anoplosyllinae*.

The recently erected sub-family *Anoplosyllinae* and two recently described *Syllinae* (*Syllis unzima* and *Syllis amicarmillaris*) were added to the overall list (Appendix 1). There were also three new records for southern Africa: *Anoplosyllis sexoculata* (Hartmann-Schröder 1962) (*Anoplosyllinae*), and *Exogone africana* and *Exogone dispar* Webster 1879 (*Exogoninae*) (Appendix 1). Among native species *Anguilosyllis capensis* Day 1963, *Irmula spissipes* Ehlers 1913, *Lamellisyllis comans* Day 1960 and *Autolytus bondei* Day 1934) have been categorized as *Incertae sedis* while two more native species (*Exogonoides antennata* Day 1963 and *Autolytus tuberculatus* (Schmarda 1861) are classified as *Nomina dubia*, thus warranting further taxonomic revision (Appendix 1). The non-native species *Pionosyllis malmgreni* McIntosh 1869 is classified as *Nomina nuda* (Appendix 1).

According to the revised classification, *Syllinae* is still the most speciose sub-family, with 24 species across six genera, followed by *Exogoninae* with 13 species (previously 12) belonging to four genera, *Eusyllinae* containing 11 species (previously 9) belong to five genera, and lastly *Autolytinae* with nine species (previously 10) belonging to five genera. *Anoplosyllinae* comprises two species belonging to two genera both formerly classified under *Syllinae*. The three most speciose genera are *Syllis* (10 species), *Exogone* (6 species) and *Trypanosyllis* Claparède 1864 (5 species) while the remaining genera each have less than five species. Twenty species (31%) have a relatively well resolved taxonomy and do not have any synonyms while 23 (33.3%) have up to 20 synonyms and the remaining ones have one synonym each (Appendix 1).

Table 2.1 Revised names of the Syllidae (Annelida) listed in Day (1967).

Original name	Revised name
<i>Alluandella madagascariensis</i> Gravier 1905	<i>Odontosyllis madagascariensis</i> (Gravier 1905)
<i>Autolytus charcoti</i> Gravier 1906	<i>Epigamia charcoti</i> (Gravier 1906)
<i>Autolytus pictus</i> Ehlers 1864	<i>Proceraea picta</i> (Ehlers 1864)
<i>Autolytus prolifer</i> (Müller 1788)	<i>Myrianida prolifera</i> (Müller 1788)
<i>Exogone clavator</i> Ehlers 1913	<i>Exogone heterosetosa</i> Ehlers 1913
<i>Syllis (Typosyllis) armillaris</i> (Müller 1776)	<i>Syllis armillaris</i> (Müller 1776)
<i>Syllis (Haplosyllis) spongicola</i> Grube 1855	<i>Haplosyllis spongicola</i> (Grube 1855)
<i>Syllis (Syllis) gracilis</i> (Grube 1840)	<i>Syllis gracilis</i> (Grube 1840)
<i>Syllis (Haplosyllis) trifalcata</i> Day 1960	<i>Haplosyllis trifalcata</i> (Day 1960)
<i>Syllis (Syllis) longissima</i> Gravier 1900	<i>Syllis gracilis</i> Grube 1840
<i>Syllis (Syllis) amica</i> Quatrefages 1865	<i>Syllis amica</i> (Quatrefages 1865)
<i>Syllis (Langerhansia) anops</i> Ehlers 1897	<i>Typosyllis anops</i> (Ehlers 1897)
<i>Syllis (Langerhansia) ferrugina</i> Langerhans 1881	<i>Paraehlersia ferrugina</i> (Langerhans 1881)
<i>Syllis (Langerhansia) cornuta</i> Rathke 1843	<i>Syllis cornuta</i> (Rathke 1843)
<i>Syllis (Typosyllis) hyalina</i> Grube 1863	<i>Syllis hyalina</i> (Grube 1863)
<i>Syllis (Typosyllis) taprobanensis</i> Willey 1905	<i>Eusyllis ceylonica</i> (Augener 1926)
<i>Syllis (Typosyllis) bouvieri</i> Gravier 1900	<i>Syllis prolifera</i> (Krohn 1852)
<i>Syllis (Typosyllis) variegata</i> Grube 1860	<i>Syllis variegata</i> (Grube 1860)
<i>Syllis (Typosyllis) nigropharyngea</i> Day 1951	<i>Syllis vittata</i> (Grube 1840)
<i>Syllis (Typosyllis) benguellana</i> Day 1963	<i>Typosyllis benguellana</i> (Day 1963)
<i>Syllis (Typosyllis) cirropunctata</i> Michel 1909	<i>Branchiosyllis cirropunctata</i> (Michel 1909)
<i>Syllides longicirrata</i> (Örsted 1845)	<i>Syllides longocirratu</i> s (Örsted 1845)
<i>Sphaerosyllis erinaceus</i> Claparède 1863	<i>Erinaceusyllis erinaceus</i> (Claparède 1863)
<i>Trypanosyllis gemmipara</i> Johnson 1901	<i>Trypanosyllis aeolis</i> (Langerhans 1879)
<i>Pharyngeovalvata natalensis</i> Day 1951	<i>Odontosyllis ctenostoma</i> (Claparède 1868)
<i>Pionosyllis ehlersiaeformis</i> Augener 1913	<i>Paraehlersia ehlersiaeformis</i> (Augener 1913)
<i>Pionosyllis magnidens</i> Day 1953	<i>Nudisyllis magnidens</i> (Day 1953)
<i>Pionosyllis longocirrata</i> Saint-Joseph 1887	<i>Opisthodontia longocirrata</i> (Saint-Joseph 1887)
<i>Procerastea perrieri</i> Gravier 1900	<i>Procerastea nematodes</i> (Langerhans 1884)

2.3.4 General taxonomic status of Syllidae

Among the 59 valid species, 31 are questionable, 22 indigenous, five casual and one potentially alien (Appendix 1). Additionally, two species were classified as *Nomina dubia* and *Nomina nuda*, respectively, and three were classified as *Incertae sedis*. The largest number of questionable (13) and indigenous (12) species and the single potentially alien species all belong to the Syllinae. Exogoninae includes eight questionable species and five indigenous species. Eusyllinae has seven questionable species, three indigenous and two casual species. Autolytinae has four indigenous, one casual and four questionable species. Both species of Anoplosyllinae are categorized as casual. Species categorized as *Incertae sedis* are all indigenous to southern Africa the genera with the most questionable species (excluding those listed as casual) are *Syllis* (six species) and *Exogone* (five species). The most indigenous species belong to *Syllis* (six species) while the remaining genera (i.e., *Autolytus* Grube 1850, *Myrianida* Milne Edwards 1845, *Exogonoides* Day 1963, *Lamellisyllis* Day 1960, *Irmula* Ehlers 1913, *Anguillosyllis* Day 1963, *Trypanosyllis*, *Opisthosyllis* Langerhans 1879, *Haplosyllis* Langerhans 1879, *Sphaerosyllis*, *Spermosyllis* Claparède 1864, *Exogone*, *Odontosyllis* Claparède 1863, *Nudisyllis* Knox and Cameron 1970) all have up to three species each classified as indigenous (Appendix 1).

2.3.3 Local and global distribution

Syllids have been recorded from 51 localities around the southern African coastline. Up to two species occur in all localities, while 33 occur in False Bay, 24 in Table Bay, 14 in Saldanha Bay and eleven in Mossel Bay. The remaining localities include only between three and ten species. In Namibia, Mozambique, and Madagascar there are 14, 12 and ten species respectively. Majority of syllids occur along the west coast of southern Africa and decrease in occurrence toward the south coast (Table 2.2). Four species occur throughout the southern African coast while 20 are restricted to the west coast; seven are restricted to the first transition zone, one is restricted to the south coast, four to the east coast and three to Madagascar. The remaining 20 species either occur on contrasting regions of the coast or have a discontinuous distribution. For example, seven species occur on the west coast, transition zone 1 and along the east coast; three species occur on the west coast, in transition zone 1, the south coast and on the east coast (Table 2.2).

There are no new distributional records, local or global, for 16 indigenous species while the remaining six indigenous species have been recorded outside of southern Africa since Day (1967). Of those species with an apparently widespread global distribution, 13 have an increased global distribution range but no new local records (Appendix 1). Twenty-two valid species have type localities in southern Africa; most (56%) occur along the west coast only, then the south (32%) and east (12%) coasts, with nine species restricted to their type localities. Of the species that have type localities elsewhere in the world, most are from the North Atlantic Ocean (35%), then the Mediterranean Sea (30%), the South Atlantic (8%), the Southern Ocean (8%), South Pacific (8%), Arctic (5%) and lastly Indian Ocean (3%).

Table 2.2 Local distribution of syllid species among three biogeographic regions: cool temperate west coast (WC), warm temperate south coast (SC) and tropical and subtropical east coast (EC); two temperature transition zones between: the west and south coasts (TZ1) and between the south and east coasts (TZ2) and, Madagascar (MDG).

WC	TZ1	SC	TZ2	EC	MDG	Total no. of species
45	36	20	20	29	12	
✓				✓		1
✓	✓			✓		7
✓	✓	✓		✓		3
	✓			✓		1
		✓		✓		1
✓	✓					7
✓		✓		✓		1
✓			✓			1
				✓	✓	1
	✓	✓	✓	✓		1
✓		✓				3
✓			✓	✓		1
✓	✓	✓		✓	✓	2
✓	✓		✓	✓	✓	1
✓	✓	✓	✓	✓		1
✓	✓	✓	✓			1
✓	✓	✓				1
✓		✓			✓	1
✓						20
	✓					7
✓	✓	✓	✓	✓	✓	4
		✓				1
				✓		4
					✓	3

2.4 Discussion

The desktop re-assessment of syllids in South Africa has resulted in a decrease in the total number of valid syllid species from 67 to 59 despite the addition of two new species. This is a consequence of eight species being synonymized and five being considered either invalid, of doubtful identification or of uncertain taxonomic placement.

More than half of the valid species in the updated checklist have been classified as questionable. The strongest determinants of a questionable status were whether the species demonstrated to be a species complex in other locations and/or to show a cosmopolitan distribution. *Syllis gracilis* and *Haplosyllis spongicola* (Grube 1855) have previously been found in southern Africa and have apparent cosmopolitan distributions. Several studies have demonstrated that each species comprises pseudo-cryptic species complexes in at least part of their distribution ranges. For instance, new species were described for each in Spain and the Mediterranean Sea, respectively (Maltagliati et al. 2000, Martin et al. 2003, Lattig et al. 2007, Lattig and Martin 2011, Álvarez-Campos et al. 2017, Cepeda et al. 2017). Individuals belonging to the *S. gracilis* complex were differentiated by morphometric and molecular methods while those belonging to the *H. spongicola* complex were distinguished from each other by morphometric and morphological analyses (Martin et al. 2003, Lattig et al. 2007, Lattig and Martin 2011, Álvarez-Campos et al. 2017, Cepeda et al. 2017). It is therefore probable that *S. gracilis* and *H. spongicola* from southern Africa have been incorrectly identified as the European species being actually new indigenous species. Additionally, it has been suggested that *S. armillaris* from the Ionian Sea, Pacific and Indian Oceans is a complex of morphologically similar species (Lopez et al. 2001, Musco and Giangrande 2005).

Most (78%) questionable species had disjunct distributions in climatically incomparable regions and included several synonymized species from contrasting regions of the world making them potential species complexes. For example, *S. armillaris* has the longest list of synonyms (30) including reports from western Europe (United Kingdom, Norway, France) and South Africa (Table Bay, Cape of Good Hope) (Day 1967, Musco and Bellan 2008). The species with the second largest number of synonyms are *Syllis variegata* Grube 1860 and *Syllis hyalina* Grube 1863 include 20 synonyms each. Species synonymized with *S. hyalina* have type localities in France, Italy, Cuba, Australia, the Mediterranean Sea, Japan, Chile, New Zealand, France, West Africa and Norway, thus representing a disjunct distribution in both tropical and temperate seas (Musco and Bellan 2017). The species synonymized with *S. variegata* span the Red Sea, Gulf of Naples, Australia and France. In South Africa, both of these nominal species are common from the cold temperate west coast to the tropical and sub-tropical east coast (Day 1967) further suggesting that they may be incorrectly identified. *Syllis prolifera* Krohn 1852 and *Syllis cornuta* Rathke 1843 have 17 and 13 synonyms, respectively including species from the Mediterranean, Australia and the West Indies (*S. prolifera*) and Britain, Greenland and New England, USA, (*S. cornuta*) (Musco 2008, Musco and Bellan 2017). Not only are these locations geographically dispersed, but they also represent climatically incomparable regions in temperate and tropical seas (cf. Day 1967, Oug 2001, Çinar 2003, Çinar et al. 2003, Giangrande et al. 2003, Serrano et al. 2006, Aguado and San Martín 2007, Parapar et al. 2009, Mikac and Musco 2010, Magalhes and Bailey-Brock 2014).

In South Africa, *S. prolifera* is widespread throughout the west and east coasts while *S. cornuta* was found at only three localities, Table Bay (west coast), Plettenberg Bay (south coast) and Mozambique (east coast), respectively (Day 1967). Finally, *Syllis amica* Quatrefages 1866 has nine synonyms from the UK, France and Madeira (Portuguese Island) and is widespread throughout temperate North Atlantic, but occurred only along the subtropical and tropical east coast of South Africa (with the exception of one individual from the west coast of South Africa). Considering that all synonymized species are from disparate regions of the world, there is a great chance that they do not really belong to a single species. Furthermore, Day (1967) synonymized several species without any justification, including a large number of European species with apparently cosmopolitan distributions (Hutchings and Kupriyanova 2017), and most likely this also applies to syllids. Many early taxonomists were from Europe (Day 1967, Hutchings and Kupriyanova 2017). Evidence for this can be found in the large number of publications describing European fauna from authors such as Cuvier (1817), Grube (1850), Quatrefages (1866), Malmgren (1867) and monographs published by Fauvel (1923, 1927). This meant that much of their research focused on European taxa and, as a result, species from other regions of the world (e.g. Australia) were identified by using the European species names, resulting in a taxonomic bias amongst cosmopolitan species (Hutchings and Kupriyanova 2017).

In southern Africa, there are five casual syllids that have only been recorded once since Day (1967) (i.e., *S. longocirratu*s, *Procerastea nematodes* Langerhans 1884, *Eusyllis blomstrandii* Malmgren 1867, *Odontosyllis gibba* Claparède 1863). *A. sexoculata* (San Martín and Hutchings 2006) was described after Day (1967), representing a new record but has only ever been recorded in South Africa once and is therefore listed as casual. This number of casual species is considerably high compared to other regions of the world. For example, of 10 alien polychaete species in the Mediterranean Sea, there is only one casual syllid species (Zenetos et al. 2010a, b). This high incidence may be a consequence of the lack of regional studies focusing on syllids or identifying syllids in benthic surveys. If no new information is collected, these syllid species cannot confidently be categorized as alien or that they even occur in South Africa.

In comparison to other polychaete families, Syllidae has an intermediate number of alien species (20 (7%)), whereas Spionidae has 52 (18%) and other taxa such as Glyceridae Grube 1850 and Acoetidae Kinberg 1856 have just one (0.3%) each (Çinar 2013). Çinar's (2013) global inventory lists seven alien syllid species as established in the Mediterranean Sea, Hawai'i and the Pacific coast of the USA. Others were considered questionable (six species), casual (eight) or cryptogenic (two) in the Black Sea, Panama, Pacific coast of Mexico and the USA, Mediterranean Sea and Argentina, although not all species had the same alien statuses throughout their respective distribution ranges. In my study, I identified one potential alien, *Opisthosyllis brunnea* Langerhans 1879 which has a type locality in the North Atlantic Ocean (Portugal), and has a disjunct distribution in the North and South Pacific, and in the South Atlantic Ocean (Musco and Bellan 2008, Appendix 1). In South Africa, *O. brunnea* is widely distributed, occurring along all three coastlines. Nevertheless, it is considered it to be potentially alien because it has been classified as an alien in the Aegean Sea (Çinar and Ergen 2002) and has no synonymized species throughout its distribution range. Further investigation needed to confirm this category.

The total number of questionable and casual species is perhaps an indication of patterns of taxonomic efforts at a regional level. There are more than 176 syllid species in the Mediterranean Sea (Musco and Giangrande 2005), where their taxonomy is reasonably well-resolved. Musco and Giangrande (2005) listed 140 alien polychaetes in the Mediterranean Sea, of which only 1% (10 species) are syllids (Zenetos et al. 2010a, b). Most of the alien syllids are established (6 species) and the remaining four are either questionable or casual (Zenetos et al. 2010a, b). By contrast, in regions where syllid taxonomy may be a little less well resolved, there are disproportionately more questionable or cryptogenic species. For example, Salazar-Vallejo and Londoño-Mesa (2004) listed 132 syllid species from the tropical eastern Pacific Ocean, of which 38 are questionable and three of doubtful identification. Similarly, in southern African, I list a single species, *O. brunnea*, as potentially alien with 31 species classified as questionable. However, the total number of indigenous species for South Africa (22 species) also appears to be comparatively low and is undoubtedly due to the lack of regional taxonomic studies concentrating on syllids. This poor documentation of indigenous syllids in South Africa is highlighted by the large number of questionable species likely representing indigenous species. Considering how understudied syllids are in South Africa, the disproportionately high number of questionable species and the single potentially alien species are in line with regions where syllid taxonomy is not well resolved.

To establish whether there was an expansion of distribution ranges for syllid species in South Africa since Day (1967), local published literature were consulted. An extensive desktop search found a single taxonomic publication focusing on syllids describing two new species (Simon et al. 2014). Furthermore only five other ecological papers reported syllids amongst numerous other taxa. In studying the impacts of sea temperature, substratum type and wave exposure on intertidal communities, McQuaid and Branch (1984) found *S. variegata* in abundance on exposed shores; Teske and Wooldridge (2003) investigated the influence of sediment type and salinity on estuarine macrobenthos and documented one unknown species identified as Syllidae sp.; Hammond and Griffiths (2004) documented the infauna in mussel beds along the west coast of South Africa and found *S. armillaris*, *S. variegata* and *Syllis* sp. in abundance at five out of nine sites. The only study that recorded smaller and less conspicuous syllid species (usually meiofaunal) was that of Hanekom et al. (2009), who conducted an extensive survey of the West Coast National Park. Other than the aforementioned species, they found *Exogone verugera* (Claparède 1868), *A. tuberculatus*, *Myrianida phyllocera* Augener 1918, *Trypanosyllis gemmulifera* Augener 1918, *Odontosyllis polycera* (Schmarda 1861) and *Spermosyllis capensis* Day 1953. This study extended the known distribution only of *A. tuberculatus* (Hanekom et al. 2009). This highlights the fact that amongst the few ecological studies recording syllids, only the relatively larger and more robust species (such as *S. armillaris* or *S. variegata*) are reported.

The overall pattern of syllid richness does not reflect the patterns for polychaetes as determined by Day (1967) but agrees, in part, with that of Awad et al. (2002) (Table 2.2); the largest number of syllid species occurs on the west coast of South Africa and within the first temperature transition zone between Cape Point and Cape Agulhas (Fig. 2.1). The overall pattern of distribution of indigenous syllid species reflects the pattern of species richness determined by this study, but disagrees with the general patterns observed by Day (1967) and Awad et al. (2002) who observed the largest number of indigenous species along the south coast of South Africa. With the way in which Day (1967) had constructed his table, only 21 of 67 syllid

species would have been considered. However, of these, only about seven would have been included in the final analysis, since Day (1967) excluded species with less than three records, thus excluding more than 60% of the syllid species with names starting with A – F. The selection criteria for this table were a means of sub-sampling the more than 5 000 records in Day (1967). Furthermore, Awad et al. (2002) excluded records from outside of South Africa's political borders (i.e., not including records for Mozambique, Namibia and Madagascar) resulting in the exclusion of at least seven syllid species (cf. Day 1967). The taxa with the largest number of records or species would have had the strongest influence on the distribution pattern. It is probably for these reasons that the patterns observed by Day (1967) and Awad et al. (2002) do not necessarily represent the distribution patterns for syllids in South Africa. Additionally, because the information in Table 2.2 was largely derived from John H. Day's publications the pattern observed in his study is likely a reflection of sampling bias as most of his samples were collected along the west coast of South Africa and in False Bay (cf. Day 1953, 1955, 1961, 1963). Further, the general pattern observed across all taxa shows the lowest diversity along the west coast increasing progressively toward Durban before decreasing toward the Mozambique border (Awad et al. 2002). However, some other invertebrate taxa such as chitons contrast the general pattern for invertebrates, in having levels of endemism and species richness that are highest in the transition zones between biogeographic regions, while bivalves had the highest species richness and endemism along the south and east coasts of South Africa (Awad et al. 2002). Other taxa such as ascidians seem to follow this general pattern, showing the lowest species richness and endemism along the west coast of South Africa and the highest along the south coast, steadily decreasing toward the east coast (Awad et al. 2002). From this, it is clear that the general pattern observed by Awad et al. (2002) for all taxa cannot be applied equally; as it is largely dependent on well-documented taxa. This is not the case of syllids and therefore generalized patterns of distribution for polychaetes do not apply to syllids.

Ideally, information derived from taxonomic papers should be used to create a sound checklist that includes confident identifications and confirmed distribution ranges. With confirmation of species identification and distribution, alien statuses can more readily be assigned and the distinction between alien and native species becomes less blurred. The checklist created here identified many species with questionable identifications (31) and, consequently, those that should be targeted for further investigation to reveal possible species complexes and alien species. The scant publications that include syllids also mean that most species do not have updated local distributional ranges. While an extensive regional survey of syllids would be ideal, the considerable costs, time and effort required is substantial. A more parsimonious solution would be to sample a small number of sites to get an idea of the level of species richness and indigenous syllids in South Africa.

Chapter 3: Species richness of syllids from three sites on the south coast of South Africa, with notes on general syllid taxonomic and ecological status

3.1 Introduction

Syllidae is one of the most abundant and speciose families of polychaetes found in benthic communities in coastal environments, becoming substantially less abundant in deeper waters (Aguado et al. 2012, San Martín and Aguado 2014). Species belonging to this family are widespread globally and inhabit a wide range of substrates including rocky shore communities (Fauchald and Jumars 1979, Magnino and Gaino 1998, San Martín 2005, Cacabelos et al. 2007, Mikac and Musco 2010), among which they occur within algae, dead corals and tufts of Bryozoa and hydrozoans, inside calcareous rocks and in coarse sediments but may also be found in finer sediments (San Martín and Aguado 2014, San Martín and Worsfold 2015). Syllids are, however, known to favour algal turf (cf. Fauchald and Jumars 1979, Magnino and Gaino 1998, Oug 2001, San Martín 2005, Serrano et al. 2006, Cacabelos et al. 2007, Mikac and Musco 2010, San Martín and Aguado 2014). Their lengths range from a few millimeters to a few centimeters (San Martín and Aguado 2014, San Martín and Worsfold 2015). South African species range from 2 mm long in *Exogone* to 130 mm in *Syllis*. Syllids are very easily recognized by a well-defined synapomorphic feature, namely the proventricle, which is situated in the anterior to midbody region of the worm (Aguado et al. 2012, San Martín and Aguado 2014, San Martín and Worsfold 2015).

Since the turn of the century, many new syllid species have been described and over the last 12 years alone (2006 – 2017), 33 new syllid species and four new genera have been described globally (Read and Fauchald 2018). More than 30% (12 species) of these were described from the Mediterranean Sea increasing the total number of syllid species to ~190 (Musco and Giangrande 2005, Çinar 2007, Faulwetter et al. 2008, San Martín et al. 2009, Abd-Elnaby and San Martín 2010, Nygren et al. 2010, Abd-Elnaby and San Martín 2011, Del-Pilar-Ruso and San Martín 2012, Çinar 2015). By contrast, in South Africa, there are only 59 valid syllid species (see Chapter 2), with *Syllis amicarmillaris* and *Syllis unzima* the only new species described since *Autolytus capensis*, *Exogone antennata*, *Exogone normalis* Day 1963 and *Typosyllis benguellana* Day 1963 were described (Day 1963, Simon et al. 2014). *Syllis amicarmillaris* and *S. unzima* are also the only species of this genus to be first described in this region (Appendix 1, cf. Day 1967, Simon et al. 2014). It is therefore probable that the actual syllid diversity and species richness in South Africa has been greatly underestimated and that many are yet to be described.

Majority of syllids described in South Africa before 1963 (13 species) have type localities on the west coast, and within the first temperature transition zone between Cape Point and Cape Agulhas. Of the native species described before 1963, only *Sphaerosyllis capensis* Day 1953 has a type locality on the Agulhas Bank while

Opisthosyllis ankylochaeta Fauvel 1921 and *Opisthosyllis laevis* Day 1957 are the only native species that have type localities on the east coast of South Africa (Day 1967). Other than *T. benguellana* that has a type locality in Lamberts Bay on the west coast of South Africa, all syllids described since 1963 have type localities on the south coast of South Africa (Day 1967). The type localities for the most recently described *S. amicarmillaris* and *S. unzima* are both within the Gansbaai area on the south coast, with specimens collected from the outflow paths from two neighbouring abalone farms (Simon et al. 2014). While the presence of *S. amica* and *S. armillaris* outside the aquaculture farms indicate that they may be introduced, a more probable cause for their presence in this region is the abundant nutrients supplied by the outflow path and the ideal environment that it presents. This therefore suggests that there may be a high level of indigenous species in this region. This would be consistent with the general distribution patterns for polychaetes in South Africa described by Awad et al. (2002), who observed the south coast to be the region with the highest number of endemic species and level of species richness. Day (1967) found a similar pattern for native species distribution but found that species richness was highest along the east coast of South Africa (see Chapter 2). However, in Chapter 2 (Table 2.2, Appendix I) showed that highest syllid richness is found on the west coast (45 species) and in the transition zone between False Bay and Cape Agulhas (36 species) with the fewest species occurring on the south coast (20 species) and in Madagascar (12 species), with only one species restricted to the south coast. Considering the sampling bias toward the west coast of South Africa and False Bay (cf. Day 1953, 1955, 1961, 1963) and that the south coast is only moderately to well sampled (Awad et al. 2002, Griffiths et al. 2010), it is therefore probable that many more new indigenous *Syllis* species may be found along the south coast of South Africa.

The majority (67%) of syllid species recorded in South Africa have type localities outside the country, mostly originating from the North Atlantic (27%) and Mediterranean Sea (22%). However, the identities of all, or most, of these apparently cosmopolitan species should be considered questionable as many of them may be members of complexes and most likely represent new indigenous species (see Chapter 2, Appendix 1). *Syllis* is one of the most speciose and common syllid genera and Day (1967) recorded eight valid species (*S. gracilis*, *S. cornuta*, *S. prolifera*, *S. variegata*, *S. vittata*, *S. amica*, *S. hyalina* and *S. armillaris*) in southern Africa. They are mostly listed as common to fairly common with several ecological studies also recording *S. prolifera*, *S. variegata* and *S. armillaris* in the Western Cape Province (McQuaid and Branch 1984, Hammond and Griffiths 2004, Hanekom et al. 2009). These three species, as well as *S. gracilis*, are common along the south coast of South Africa and all have apparently cosmopolitan global distributions and questionable taxonomic status in the region (see Chapter 2, Appendix). It is therefore probable that the South African populations belong to indigenous, undescribed, which in turn suggests an underestimation of native diversity along this stretch of coast.

In this chapter, we investigate syllids at selected sites on the south coast of South Africa where they have previously been recorded to address the following specific aims :

- ♣ To determine species richness of syllids at selected sites along the south coast of South Africa.
- ♣ To assign each identifiable syllid species to one of the following status, indigenous, questionable, cryptogenic, alien and extralimital species, to determine their number and proportion. Those species now classified as *Nomina Dubia*, *Nomina Nuda* and *Incertae sedis* will also be considered.
- ♣ Describe any new species found, if any.

3.2 Methods and Materials

3.2.1 Study Area

The south coast of South Africa forms part of the warm temperate Agulhas bioregion and is that part of the coast where the cold temperate southern Benguela current interacts with the tropical and subtropical Agulhas current (Fig. 2.1; Griffiths et al. 2010, Sink et al. 2011). It is also a region with high levels of diversity and endemism, especially for polychaete taxa (Awad et al. 2002, Griffiths et al. 2010).

3.2.2 Sample collection and Processing

Three rocky shore sites were sampled: Gordons Bay (GB) (34°10'00"S; 18°52'00"E), Danger Point (DP) (19°37'48.54"S; 19°18'8.75"E) and Mossel Bay (MB) (34°10'60"S; 19°18'75"E) (Fig. 3.1). Samples were collected in April and October 2015. At each site 5 – 9 samples (1 – 6 per substrate) were taken along the lower intertidal zone. At GB and DP, samples were collected from foliose algae (3 x GB, 1 x DP), sponge (1 x GB, 1 x DP) and algal turf (i.e., low growing algae that may form thick mats less than 2 cm high) (6 x GB, 5 x DP). The foliose algae and algal turf were examined for meio- and macrofauna and the sponge for sponge epibionts. Only algal turf (5 samples) was collected at MB since it proved to be the best substrate for syllids at Gordon's Bay and Danger Point. A paint scraper was used to scrape 10 x 10 cm quadrats of each substrate off the rocks. Each sample was then placed in a bag containing seawater to be taken back to the lab for processing.

Once in the lab, samples were placed in seawater in sorting trays and sorted under a dissecting microscope (Leica MZ75). Syllids were removed from sorting trays using forceps and relaxed in 7% MgCl₂ before fixing in 4% seawater formalin, and eventually storing in 70% ethanol. Fixed individuals were stained with aqueous methyl green to increase the contrast to better view specimens and morphological features, particularly the chaetae, and examined under either a dissecting microscope or a Leica DM 1000 compound microscope. Photos were taken of preserved specimens using a Leica EC3 camera attached to either microscope.

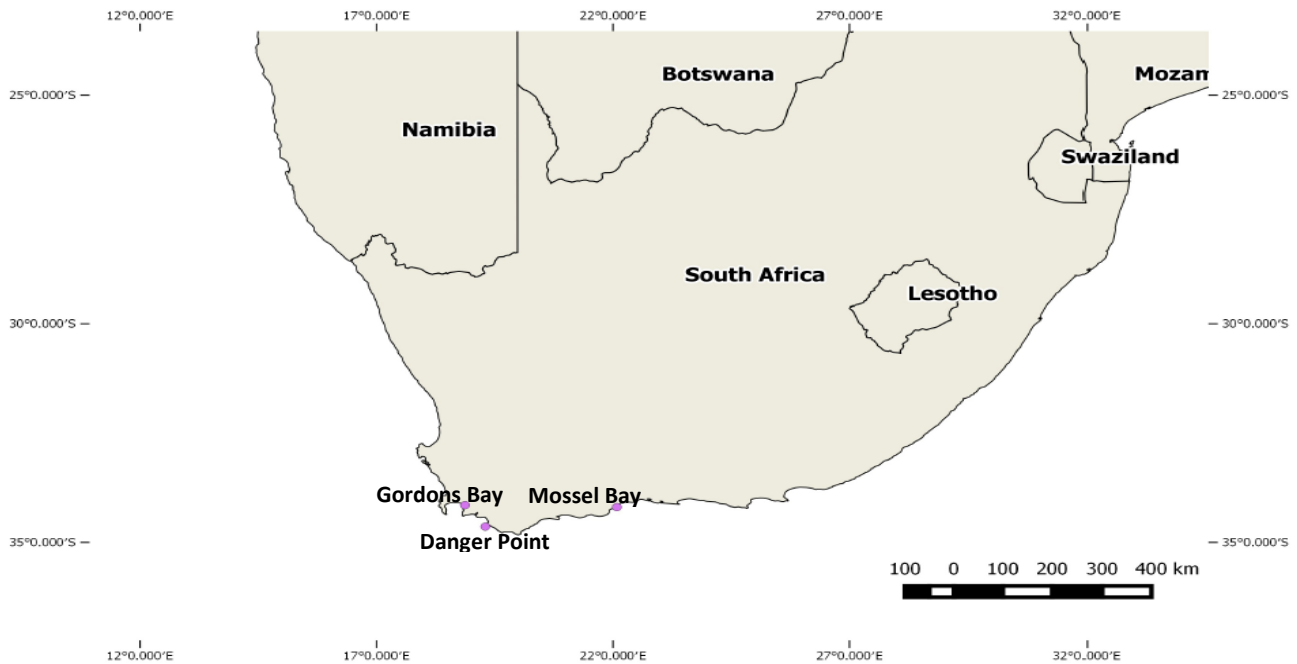


Figure 3.1 South coast of South Africa indicating three sample sites (purple).

3.2.3 Morphological identifications:

All of the individuals were identified to the lowest taxonomic level based on their morphological characteristics according to Day (1967) as a primary reference and more recent publications such as San Martín (1992, 2005), San Martín and Hutchings (2006), San Martín et al. (2013), Simon et al. (2014), and San Martín and Worsfold (2015) for validation.

Syllids have a sub-cylindrical body (ventrally flattened, dorsally convex) with a translucent cuticle and epidermis (Aguado et al. 2012, San Martín and Aguado 2014, San Martín and Worsfold 2015). The main diagnostic features used in the classification of syllids, and which were used in the identifications, include: **Shape of the prostomium:** semicircle to pentagonal or oval; **Number and arrangement of eyes:** Four eyes and two eyespots (which may be absent in some species) in trapezoidal arrangement; **Number of articles in, and position of, antennae:** three antennae (short or long) that may be smooth or jointed with the median antenna positioned in the posterior, middle prostomium or just behind posterior eyes and the lateral antennae positioned on the anterior prostomium in front of anterior eyes; **Shape of palps and degree of separation between left and right palps:** one pair of palps that may be triangular, rounded or oval in shape, palps may be separated from one another, basally fused or fused along the entire length. **Number of tentacular cirri:** one or two pairs of tentacular cirri (short or long; may be altogether absent), smooth or jointed. **Shape of parapodia:** uniramous or biramous; **Number of articles on dorsal cirri:** smooth or jointed, short or long, and may vary in shape; **Presence and length of ventral cirri:** may be absent or fused

to parapodial lobes, may be short, subequal or longer than parapodial lobes; **Shape of pharynx and pharyngeal armature:** pharynx typically straightened but may be coiled in some species, pharyngeal armature may be absent in some species but are typically seen as a single tooth or as a crown of denticles (trepan) on the pharyngeal opening, may sometimes be incomplete and denticles may face toward the anterior or posterior of the pharynx; **Length, shape and number of muscle rows of proventricle:** may be rectangular, squared or barrel shaped, size and number of muscle rows of the proventricle may vary between species (San Martín and Worsfold 2015).

Once specimens were identified, a species list was prepared for all sites. Each species was assigned a general status as Indigenous, Alien or Questionable (see the methods in Chapter 2) and the taxa that required taxonomic revision were highlighted.

Permanent slides were made for undescribed species for which more than 10 specimens were collected and were prepared by placing sections of the parapodia and chaetigers in Aquatex[®] mounting fluid, covering with a coverslip and sealed with clear nail varnish. Morphological line drawings were prepared using a camera lucida. Photographs of specimens were also taken. Associated camera software, Leica LAS EZ V1.5.0, was used to take length and width measurements of specimens on each photo. All other measurements were made by observing the specimens at 40 x magnification.

3.3 Results

3.3.1 Species richness of Syllidae (Annelida) among three sites with notes on alien status and suggestions for further taxonomic revision.

In total, 23 samples comprising 644 syllid polychaetes were collected from Gordons Bay, Danger Point and Mossel Bay. This figure does not include incomplete specimens, stolons and juveniles. The most individuals, for the fewest replicates, were collected at Mossel Bay while the most replicates for the fewest specimens were collected in Gordons Bay (Table 3.1). Thirteen species from seven genera were identified to species level (Table 3.1): four species (three genera) from Gordons Bay; nine (five) from Danger Point; and eight (four) from Mossel Bay. There were also many individuals that could not be identified to species level; four species (for four individuals) at Gordons Bay, one (four) at Danger Point and six (88) at Mossel Bay. When the unidentifiable species across all sites are included, the total number of species collected increases to 24. In total, 14 species were collected at Mossel Bay, ten at Danger Point and eight at Gordons Bay.

Altogether, 548 individuals (84%) were identified to species level with *Syllis* being the most speciose (5 species) and abundant genus, followed by *Exogone* (3 species). The remaining genera were each represented by one species (Table 3.1). *Syllis amicarmillaris* accounted for approximately 54% of all individuals collected, followed by *S. prolifera* (20%), *S. variegata* (14%) and *S. vittata* (5%). *Syllis amicarmillaris*, *S. amica* and *E. naidina* were the only species found at all three sites. *Brania rhopalophora* was found at Gordons Bay and Danger Point only. *Syllis variegata* was found at Danger Point and Mossel Bay, while *E. heterosetosa*, *S. sublaevis*, *E. verugera* and *P. ehlersiaeformis* (prev. *Pionosyllis ehlersiaeformis*) were found at Danger Point only. *Syllis prolifera*, *S. vittata*, *N. magnidens* and *A. maclearanus* were found at Mossel Bay only (Table 3.1).

Based on the definitions outlined in Chapter 2, majority (77%) of the identified species are Questionable (*A. maclearanus*, *B. rhopalophora*, *E. heterosetosa*, *E. naidina*, *E. verugera*, *P. ehlersiaeformis*, *S. prolifera*, *S. amica*, *S. variegata*, *S. vittata*) and are thus in need of revision while the remaining 23% are indigenous (*N. magnidens*, *S. sublaevis*, *S. amicarmillaris*) (Table 3.2). Together, *S. prolifera*, *S. variegata* and *S. vittata* make up 39% of all specimens collected (Table 3.1).

Table 3.1 Species richness and abundance of syllids at three sites along the south coast of South Africa.

Species	Gordons Bay	Danger Point	Mossel Bay
	No. of individuals		
<i>Epigamia</i> Nygren 2004			
<i>Autolytus maclearanus</i> McIntosh 1885 (<i>Incertae sedis</i>)	-	-	3
<i>Brania</i> Quatrefages 1866			
<i>Brania rhopalophora</i> (Ehlers 1897)	1	2	-
<i>Exogone</i> Örsted 1845			
<i>Exogone heterosetosa</i> McIntosh 1885	-	11	-
<i>Exogone naidina</i> (Örsted 1845)	2	1	6
<i>Exogone verugera</i> (Claparède 1868)	-	1	-
<i>Nudisyllis</i> Knox and Cameron 1970			
<i>Nudisyllis magnidens</i> (Day 1953)	-	-	6
<i>Paraehlersia</i> San Martín 2003			
<i>Paraehlersia ehlersiaeformis</i> (Augener 1913)	-	1	-
<i>Sphaerosyllis</i> Claparède 1863			
<i>Sphaerosyllis sublaevis</i> Ehlers 1913	-	3	-
<i>Syllis</i> Lamarck 1818			
<i>Syllis amicarmillaris</i> Simon, San Martín & Robinson 2014	6	225	62
<i>Syllisamica</i> (Quatrefages 1865)	1	2	2
<i>Syllis prolifera</i> (Krohn 1852)	-	-	110
<i>Syllis Variegata</i> (Grube 1840)	-	6	72
<i>Syllis Vittata</i> (Grube 1840)	-	-	25
Unknown species			
Incomplete specimens	9	6	16
Stolon	-	8	1
Juvenile	-	4	-
<i>Syllis</i> sp. 1	-	-	1
<i>Syllis</i> sp. 2	-	4	-
<i>Syllis</i> sp. 3	1	-	-
<i>Syllis</i> sp. 4	1	-	-
<i>Syllis</i> sp. 5	1	-	-
<i>Syllis</i> sp. 6	1	-	-
<i>Brania</i> sp.	-	-	1
<i>Syllis</i> sp. A	-	-	17
<i>Syllis</i> sp. B	-	-	2
<i>Syllis</i> sp. D	-	-	16
<i>Syllis</i> sp. S	-	-	51

Table 3.2 Designation of general status according to definitions in Chapter 2 (Q = Questionable; I = Indigenous) for identified species from Gordons Bay, Danger Point and Mossel on the south coast of South Africa. This includes local and global species records where ‘South Africa’ refers to the entire coastal region.

Species	Local records	Global records	Status
<i>Autolytus Maclearanus</i> (<i>Epigamia incertae sedis</i>)	Saldanha Bay, Table Bay, Port Alfred	Sub-Antarctic Indian Ocean, Chile, New Zealand	Q
<i>Brania rhopalophora</i>	Namibia: Swakopmund, Lüderitz, Walvis Bay; South Africa: Table Bay, False Bay, Mossel Bay	Hawaii, New Zealand and the Sub-Antarctic Islands	Q
<i>Exogone heterosetosa</i>	Namibia: Walvis Bay; South Africa	Antarctic Ocean, Southern South America, Australia, New Zealand, Tristan Da Cunha	Q
<i>Exogone naidina</i>	Saldanha Bay, Table Bay, False Bay	Apparently Cosmopolitan	Q
<i>Exogone verugera</i>	Namibia: Lüderitz; South Africa: Saldanha Bay, Table Bay, Seapoint, False Bay	Mediterranean Sea, North Sea, Sweden, UK, Spain, Portuguese EEZ, Morocco, Greenland, Canada, Gulf of Saint Lawrence, Bay of Fundy, Gulf of Maine, North Carolina, Gulf of Mexico, Japanese Sea, Hawaii, Southern California, Australia	Q
<i>Nudisyllis magnidens</i>	False Bay	South Africa only	I
<i>Paraehlersia ehlersiaeformis</i>	Namibia: Swakopmund; South Africa: False Bay, Cape Agulhas, Jeffreys Bay	New Zealand	Q
<i>Sphaerosyllis sublaevis</i>	Saldanha Bay, False Bay, Cape Agulhas	Chile, Australia, India	I

<i>Syllis amicarmillaris</i>	South west and west coast of South Africa: west and east Walker Bay and in Saldanha Bay	SA only	I
<i>Syllis amica</i>	Namibia: Diaz Point; South Africa: Oatland Point (False Bay), Danger Point, Mossel Bay, Durban, Port St. John	North Atlantic Ocean	Q
<i>Syllis prolifera</i>	Mozambique: Inhaca Island; Madagascar, Namibia; South Africa: Lamberts Bay, Saldanha Bay, Table Bay, False Bay, Algoa Bay, Durban Bay	Apparently cosmopolitan	Q
<i>Syllis variegata</i>	Mozambique; Namibia: Lüderitz; South Africa: Port Nolloth, Zout River, Groen River, Lamberts Bay, Paternoster, Saldanha Bay, Table Bay, Oudekraal, False Bay: St. James, Kleinmond; Danger Point, Cape Agulhas, Still Bay, Mossel Bay, Storms river, Algoa Bay, Port Alfred, East London, the Haven, Qolora, Richards Bay	Apparently cosmopolitan	Q
<i>Syllis vittata</i>	Namibia: Sinclair's Island, Lüderitz; South Africa: Lamberts Bay, Table Bay, False Bay, Cape Agulhas, Mossel Bay, Richards Bay	North Atlantic Ocean	Q

3.3.2 A description of three previously undescribed species of *Syllis* from the south coast of South Africa

Here I describe the three most abundant unidentified species collected in this study, and for which the best material was available. Specimens of the remaining 14 unidentified species were too few, or in too poor condition to enable proper descriptions.

SYSTEMATICS

Order: Phyllodocida Dales 1962

Family: Syllidae Grube 1850

Subfamily: Syllinae Grube 1850

Genus: *Syllis* Lamarck 1818

Syllis sp. A
(Figures 3.2 – 3.6)

MATERIAL EXAMINED:

Holotype: Complete specimen (algal turf, lower intertidal, rocky shore); Coll. S. Sedick, October 2015, Mossel Bay (34°10'60"S; 19°18'75"E).

Paratypes: Two complete specimens; October 2015. One specimen with permanent slides of the anterior, mid-body and posterior parapodia; October 2015. Data as for Holotype.

DESCRIPTION:

Holotype cylindrical, short and broad, 2.86 mm long for 44 chaetigers, 0.306 mm wide without parapodia at mid-proventricle, tapering toward posterior. In living and preserved specimens, anterior segments light pink to light brown, two thin dark brown bars running across the dorsum at anterior and posterior margins of anterior segments; median transverse bands in some segments (Figs 3.2 I, 3.3 I). Oval prostomium, two pairs of red eyes in wide trapezoidal arrangement (Fig.3.3 I). Palps separate, broadly triangular rather than long; antennae, tentacular and dorsal cirri distinctly articulated (Figs. 3.2 I). Lateral antennae longer than palps, 20 articles long, arising from anterior prostomium, in front of anterior pair of eyes. Median antenna in line with posterior eyes, 16 articles long. Peristomium shorter than subsequent segments, two pairs of tentacular cirri, dorsal pair with 22 articles, ventral pair with 16 (Figs 3.2 I, 3.3 I). Dorsal cirri slender, cirriform, alternate in length, subequal to or longer than body width, long dorsal cirri 25 articles long, shorter dorsal cirri 10 articles long in anterior, dorsal cirri with 25, 21; 14, 15 and 17, 17 articles on left and right parapodia of chaetigers 1 to 3, respectively. Ventral cirri short, not extending beyond parapodial lobe, digitiform. Parapodia with up to nine, seven, and six compound chaetae in anterior, mid-body and posterior respectively (Figs 3.4, 3.5, 3.6). Heterogomph falcigers minutely to strongly bidentate along length of body, secondary tooth well separated from the primary tooth, chaetal blades of medium length, dorso-ventral gradation in blade length (Figs 3.4 I, II, 3.5, 3.6). One or two pseudosimple chaetae present on anterior, midbody and posterior

parapodial lobes (Figs 3.2 II, 3.4 I). Pseudosimple chaetae broad with narrow, rounded tip, short spines on margin of shaft head, or narrow with thicker, more rounded tip, short spines on margin of shaft head (Figs 3.2 II, 3.4 I). Posterior simple dorsal chaetae straight, pointed tip, solitary, ventral posterior chaetae gently curved (Figs 3.2 IV, 3.6 II), bidentate. Up to three aciculae per parapodium anteriorly, two in mid-body, one or two aciculae in posterior parapodia. Anterior aciculae mushroom shaped (Fig. 3.2 V a), mid-body of three types (distally rounded (Fig. 3.2 V b), rounded on one side (Fig. 3.2 V c), knobbed shaped (Fig. 3.2 V d)), posteriorly only distally rounded, hollow (Fig. 3.2 V e) (Figs 3.4 III, 3.5 IV, V, 3.6 I). Pharynx eight chaetigers long, anterior dorsal tooth teardrop shaped, positioned at anterior margin, proventricle seven chaetigers long, 23 rows of muscles (Figs 3.2 I, 3.3 I, II, III). Two anal cirri, about 16 articles long.

VARIATION:

Individuals may be 2.3 – 5.2 mm for 34 – 53 chaetigers long. Pigmentation may extend from prostomium to anterior segments and or midbody in some individuals. Lateral antennae with 14 – 20 articles, median antenna with 18 – 21 articles. Dorsal tentacular cirri with 17 – 30 articles, ventral tentacular cirri with 13 – 20. Shorter dorsal cirri with 8 – 14 articles, longer dorsal cirri with 19 – 30 articles. Anterior parapodia with 7 – 10 chaetae each, 7 – 9 in midbody, 6 – 8 in posterior. Pseudosimple chaetae may be present only in anterior or only in midbody or throughout the length of the animal. Pharynx usually 5 – 8 chaetigers long, up to 11 chaetigers long in larger individuals, proventricle 5 – 8 chaetigers long. Anal cirri 14 – 22 articles long.

REMARKS:

Syllis sp. A is characterized by light pink to light brown colouration on prostomium and anterior segments with dark bars along anterior and posterior margins of anterior chaetigers that fade progressively toward the posterior of the animal, in living and newly preserved specimens. It also has superior anterior chaetae with short spines and distally hollow aciculae on posterior parapodia. The colour pattern of this species is similar to specimens of *Syllis gracilis*, *Syllis vittata* and *Syllis prolifera* as described in Day (1967) and, *Syllis unzima* and *Syllis corallicola* Verrill 1900 (San Martín 1992, Licher 1999, Simon et al. 2014). All have dark cross bars on anterior or midbody segments which may vary in extent, frequency and colour within each species (Day 1967, San Martín 1992, Licher 1999, Simon et al. 2014). *Syllis* sp. A is similar to *S. gracilis* and *S. prolifera* in having bidentate or minutely bidentate chaetae while *S. vittata*, *S. unzima* and *S. corallicola* have unidentate, distally hooked chaetae and short, stout inferior chaetae with short spines along one margin, respectively (Day 1967, San Martín 1992, Licher 1999, Simon et al. 2014). The new species has broad, triangular palps with dorsal cirri that are 25 articles long whereas *S. vittata* has larger distinctly separate palps that are long and narrow, with long dorsal cirri up to 40 articles long (Day 1967).

Syllis sp. A differs from *S. gracilis* by being an order of a magnitude shorter (2.86 mm and 35 mm respectively), but with dorsal cirri that are approximately 1.5 times as long as in the latter (25 articles and 16 articles respectively) (Day 1967, Licher 1999, Maltagliati et al. 2004, Álvarez-Campos et al. 2017). In *Syllis* sp. A, pseudosimple chaetae are broad or narrow with rounded tips and have short spines on one margin but in *S. gracilis* compound chaetae are replaced by Y-shaped pseudosimple chaetae in midbody (Day 1967, Licher 1999, Maltagliati et al. 2004, Álvarez-Campos et al. 2017).

Syllis sp. A closely resembles Day's (1967) description of *S. prolifera* but differs in that it has long distinctly separate palps with a more quadrangular prostomium, and ventral cirri that extend beyond the parapodial lobe. Day (1967) does not describe simple chaetae or aciculae for *S. prolifera*. *Syllis* sp. A also closely resembles Licher's (1999) description of *Syllis prolifera* from the Mediterranean Sea, Aegean Sea and the North Atlantic with respect to the globular shape of the palps, the strongly bidentate chaetae with fine spines along one margin of the shaft head, a dorso-ventral gradation in blade length and width, and ventral simple chaetae that are s-shaped and bidentate. *S. prolifera* differs from *Syllis* sp. A in that specimens have no colour pattern, shorter spines on the margin of superior chaetal blades, thicker solitary simple dorsal chaetae and aciculae that are more anvil shaped than round (Day 1967, Licher 1999).

Syllis sp. A is similar to *S. unzima* in having distally hollow aciculae (Simon et al. 2014). The new species differs from *S. unzima* in that it is slender and short, has transverse bars that only extend into the midbody region and distally hollow aciculae are present on posterior parapodia only (Simon et al. 2014). *Syllis* sp. A also lacks distally hooked chaetae that are bidentate instead of unidentate (Simon et al. 2014). *Syllis* sp. A differs from *S. corallicola* in the light pink to dark brown, rather than red, transverse bars that are not accompanied by double circles as in *S. corallicola* (San Martín 1992). The new species also differs in having dorsal and ventral simple chaetae that are curved and bidentate instead of straight (San Martín 1992).

Based on morphological observations and comparisons with known species, I suggest this morphotype be formally described as a new species.

EPIBIOTIC PROTOZOANS

Protozoans are present around the posterior prostomium on dorsum, and in grooves between dorsal cirri of *Syllis* sp. A (Fig. 3.3 IV). Their presence in these grooves may extend as far as posterior segments of the individual but are mostly concentrated around anterior segments. Álvarez-Campos et al. (2014) also found that protozoans were present in intersegmental furrows positioned close to the base of parapodia of *S. prolifera* from the Spanish Mediterranean coast. Protozoans have previously been mistaken for papillae in *S. prolifera* (as *S. microoculata* (Hartmann-Schröder, 1965)) from Hawai'i. *Typosyllis macropectinans* Hartmann-Schröder, 1982, *S. magdalena* Wesenberg-Lund, 1962 and *S. elongata* (Johnson 1901) also have protozoans present on the ventral side of posterior segments; around the prostomium; and on nuchal organs, mouth opening and on anterior dorsal cirri, respectively. The presence of these protozoans do not appear to impair or harm these syllids although ciliate protozoans have been observed to have degrading effects on crustaceans (Morado et al. 1999, Gómez-Gutiérrez et al. 2003, Álvarez-Campos et al. 2014)

HABITAT:

Algal turf, lower intertidal, rocky shore.

DISTRIBUTION:

Mossel Bay, South Africa

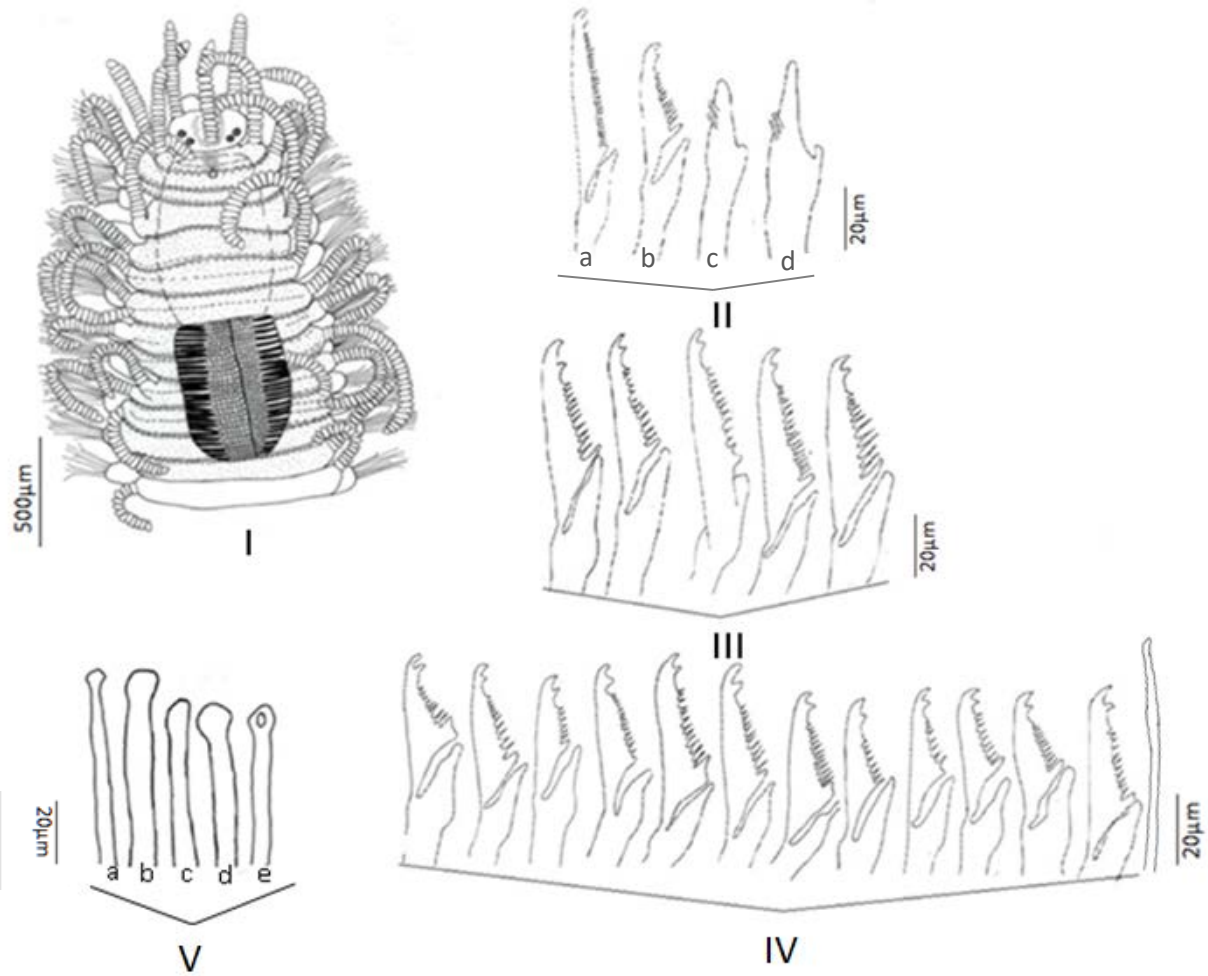


Figure 3.2 *Syllis* sp. A: Dorsal view of (I) anterior, showing (II) anterior chaetae (a, b) and pseudosimple chaetae (c, d), (III) midbody chaetae and, (IV) posterior chaetae showing a single, straight, ventral simple chaetiger with pointed tip; (V) aciculae on (a) anterior chaetigers mushroom shaped, midbody (b) distally rounded, (c) rounded on one side, (d) knobbed and (e) distally rounded and hollow on posterior parapodia.

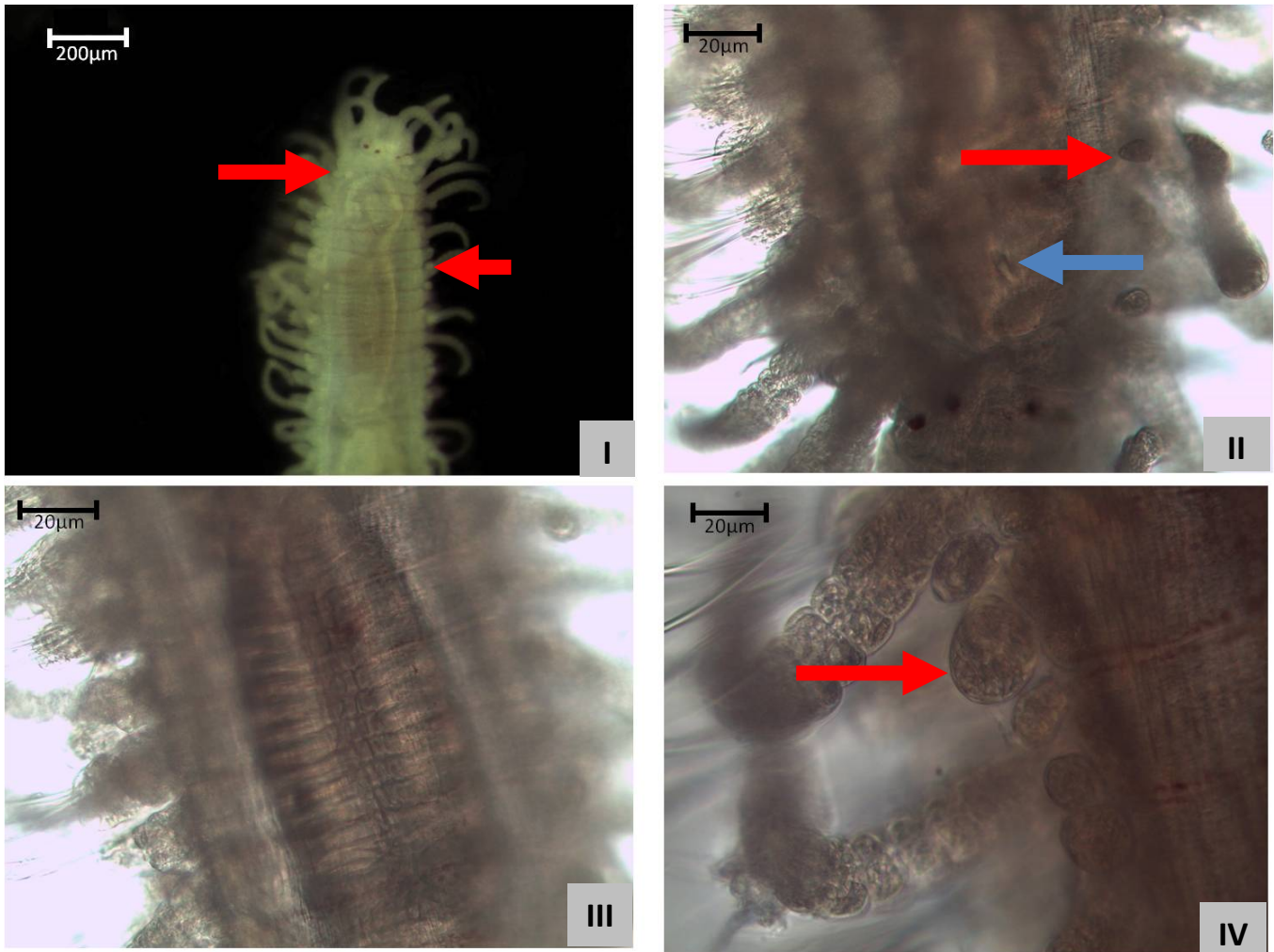


Figure 3.3 *Syllis* sp A: Dorsal view of (I) anterior indicating position of symbiotic protozoans (red arrows); (II) close up of anterior indicating position of pharyngeal tooth (blue arrow) and symbiotic protozoan (red arrow); (III) proventricle; (IV) symbiotic protozoan in anterior intersegmental grooves (red arrow).

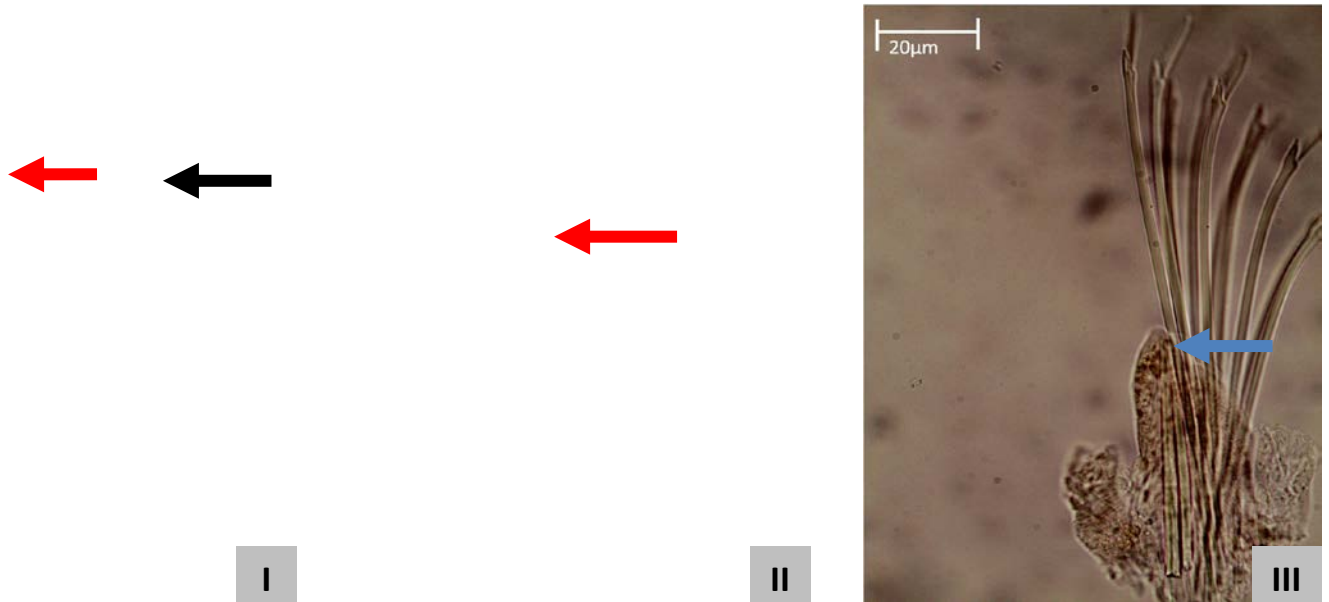


Figure 3.4 *Syllis* sp. A: (I) Anterior inferior and pseudosimple chaetae indicating the bidentate teeth on chaetae and gradation of teeth along chaetal blade (red arrow) and, serrated outer edge of pseudosimple chaetae (black arrow); (II) anterior superior chaetiger indicating subequal teeth along chaetal blade (red arrow); (III) mushroom shaped anterior aciculae (blue arrow).

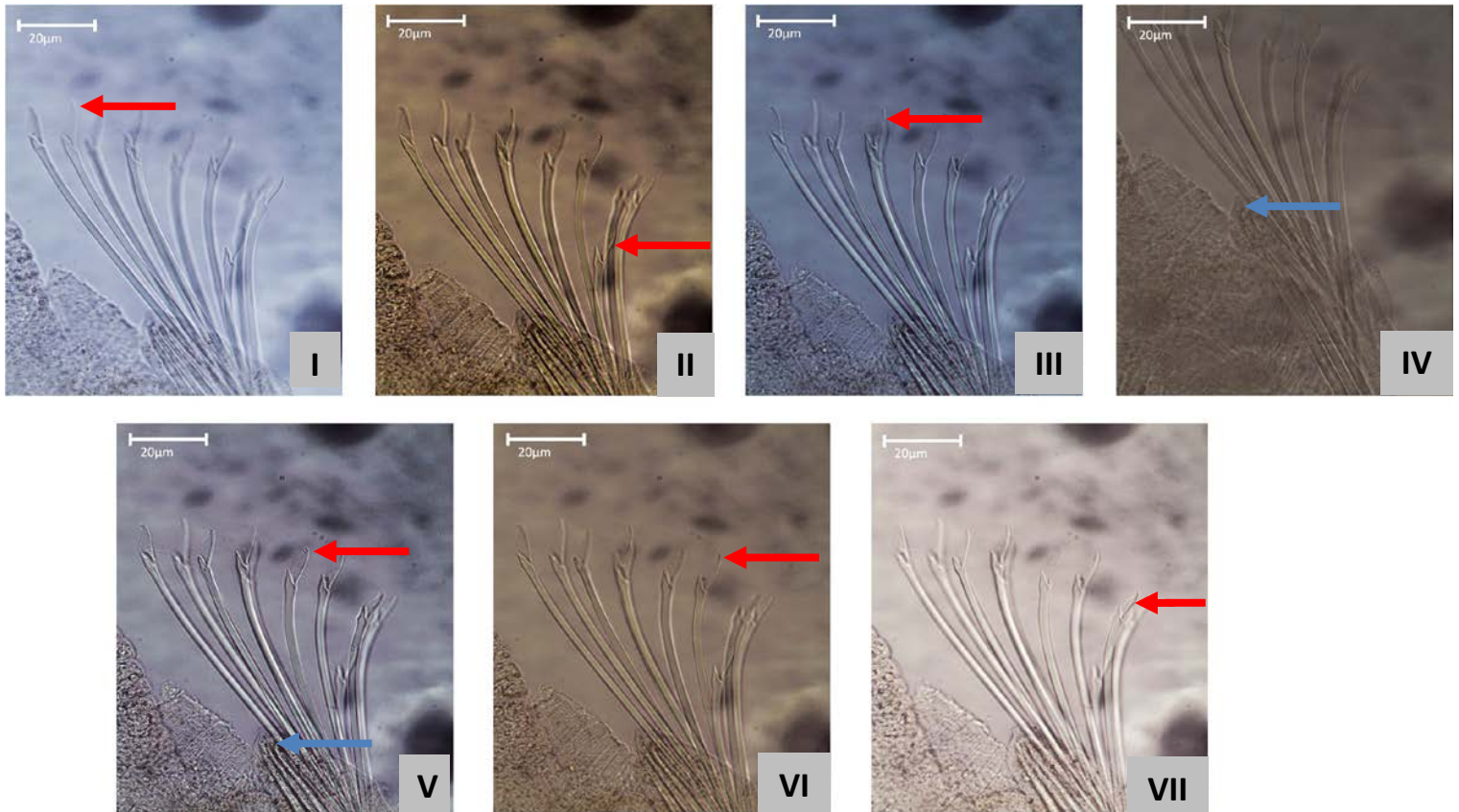


Figure 3.5 *Syllis* sp. A: (I, III) Midbody superior chaetae indicating bidentate teeth and gradation in chaetal blade length (red arrows); (II, V, VI, VII) inferior chaetae indicating chaetae with bidentate teeth and gradation in teeth along chaetal blade (red arrows); (IV, V) aciculae indicating (IV) knobbed and (V) hollow aciculae (blue arrows).

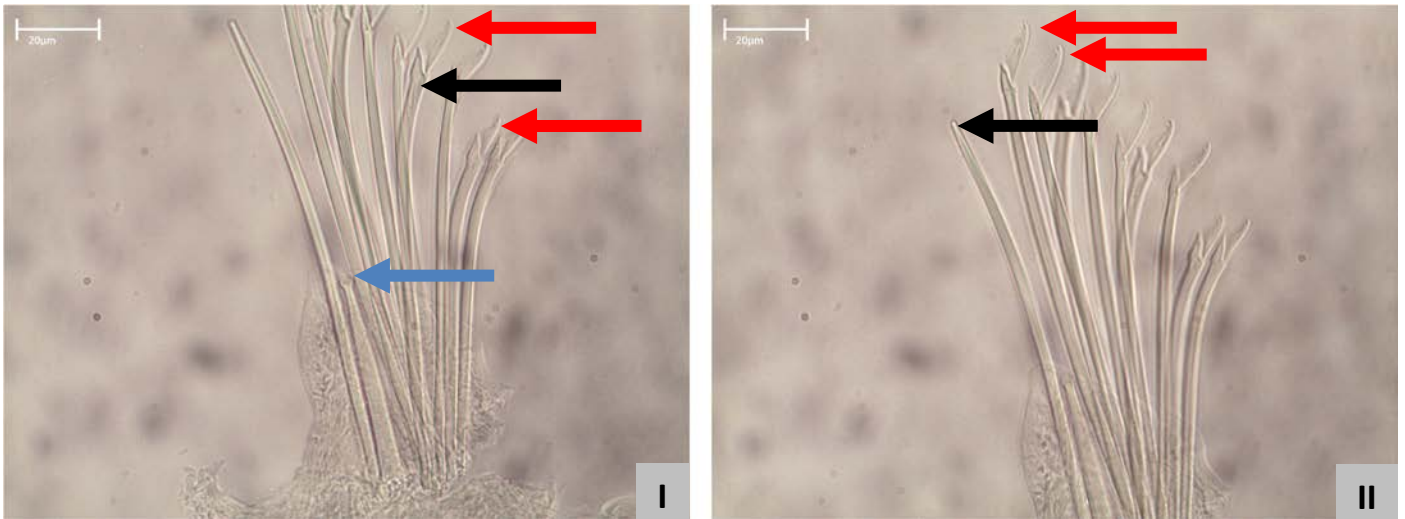


Figure 3.6 *Syllis* sp. A: (I) Posterior inferior chaetae (red arrows) with indentations along chaetal shaft (black arrow) and hollow aciculum (blue arrow); (II) superior chaetae (red arrows) and simple chaetiger (black arrow).

Syllis sp. *D*
(Figures 3.7 – 3.11)

MATERIAL EXAMINED:

Holotype: Complete specimen (algal turf, lower intertidal, rocky shore); Coll. S. Sedick, October 2015, Mossel Bay (34°10'60"S; 19°18'75"E).

Paratypes: Four complete specimens; one specimen with slides of anterior, mid-body and posterior parapodia. Data as for Holotype.

Other material examined: Seven complete specimens; October 2015. Three incomplete specimens; October 2015. Data as for Holotype.

DESCRIPTION:

Holotype subcylindrical, in cross section midbody and posterior slightly wider than anterior, 4.25 mm long for 53 chaetigers, 0.4 mm wide at middle proventricle, without parapodia, tapered at pygidium (Figs 3.8 I, II). No colour pattern in live and preserved specimens (Fig. 3.8 I, II). Prostomium oval. Two pairs of red eyes, round, equal size, in trapezoidal arrangement (Figs 3.7 I, 3.8 I). Palps triangular, longer than broad, separate, slightly longer than prostomium. Median and lateral antennae, dorsal and tentacular cirri distinctly articulated. Lateral antennae shorter than median antenna but longer than prostomium, originating in front of anterior pair of eyes, 12 articles long (Figs 3.7 I, 3.8 I). Median antenna longer than palps and prostomium, originating between posterior pair of eyes, 18 articles long. Peristomium similar in length to subsequent segments, two pairs of tentacular cirri, dorsal pair with 16 articles, slightly longer than ventral pair with 13 articles (Figs 3.7 I, 3.8 I). Dorsal cirri subequal to body width or slightly longer, longest dorsal cirri 21 articles long anteriorly, short dorsal cirri with 12 articles anteriorly, first three pairs of dorsal cirri with 19, 19; 15, 16 and 15, 13 articles on left and right parapodia of chaetigers 1 to 3, respectively. Ventral cirri shorter than parapodial lobes, digitiform. Anterior parapodia with up to 10 compound chaetae, 7 – 8 on mid-body parapodia, up to 5 chaetae on posterior parapodia. Heterogomph falcigers strongly or minutely bidentate throughout, primary and secondary teeth perpendicular or at an angle to main shaft, secondary tooth well separated from primary tooth, moderately long, thin spines on margin, secondary tooth shorter, equal or subequal to primary tooth (Figs 3.7 II, III, IV, 3.9 I, II, 3.10 I, II, 3.11 I, II). One or two pseudosimple chaetae, sub-triangular in shape, on anterior and midbody parapodia, shaft head broad, tapering to rounded point, or narrow shaft head, tapering into sharper point, short spines on outer margin edge (Figs 3.7 II, III, 3.9 II, 3.10 II). Single posterior dorsal simple chaeta straight, thin, pointed. Posterior ventral simple chaetae are thin, sinuose in shape, bidentate with serrated inner edge (Fig 3.7 IV). Up to three aciculae anteriorly of one type; acute angle on one margin. broad with narrow point (Figs 3.7 V d, 3.9 II). Two aciculae in midbody; broad, round, sickle-shaped (Fig. 3.7 V b) and knob-shaped (Fig. 3.7 V c), respectively (Figs 3.10 III, IV). One or two posteriorly; rounded on one margin and straight on other (Fig. 3.7 V a), almost diamond shaped with two acute angles on either side (Figs 3.11 III, IV). Pharynx about 8 chaetigers long, anterior conical dorsal tooth

distinctly back from anterior margin (Figs 3.7 I, 3.8 I). Proventricle about 10 chaetigers long, 37 muscle rows. Two anal cirri, 11 articles long.

VARIATION:

Individuals may be 2.5 – 7.1 mm for 48 – 58 chaetigers in length. Two smaller eyespots sometimes on anteriormost region of prostomium, well in front of the anterior eyes. Lateral antennae with 8 – 13 articles, median antennae with 16 – 19 articles (up to 18 and 23 articles, respectively) in larger individuals. Dorsal tentacular cirri with 11 – 18 articles or with 21 articles in larger individuals, ventral tentacular cirri with 8 – 14 articles or 18 – 25 articles in larger individuals. Anterior dorsal cirri range from 10 – 29 articles, 8 – 30 in mid-body. Anterior chaetae with 7 – 12 chaetae per parapodium, 6 – 10 in mid-body, posterior with 4-8. Pseudosimple chaetae may be present along entire length of animal. Up to four aciculae anteriorly, two or three in mid-body, one or two in posterior. Length of pharynx 6 – 8 chaetigers or 10 – 12 in larger individuals. Anal cirri with 7 – 14 articles.

REMARKS:

Syllis sp. *D* is recognized by its strongly bidentate chaetae with the primary and secondary tooth each perpendicular to the main shaft, ventral simple chaetae that are thin, sinuose and bidentate with a serrated edge along one margin. Pseudosimple chaetae also have a fine serrated edge along one margin in anterior parapodia. The pharyngeal tooth is distinctly back from the anterior margin. Individuals have a visibly narrower anterior and slightly wider midbody and posterior that taper towards the pygidium.

This species is most similar to *S. hyalina* and *S. variegata* from South Africa (Day 1967), and *S. prolifera* from the Mediterranean Sea (Álvarez-Campos et al. 2014). *Syllis* sp. *D* resembles *S. hyalina* and *S. prolifera* with respect to the strongly bidentate compound chaetae with primary and secondary teeth perpendicular to the main shaft but with shorter spines on the chaetal blade (Day 1967, Álvarez-Campos et al. 2014). *Syllis* sp. *D* also resembles *S. hyalina* in having two ocular specks positioned on the anteriormost prostomium (Day 1967). This new species resembles *S. prolifera* with respect to the short spines along the margin of the superior chaetal shaft head (Álvarez-Campos et al. 2014). *Syllis* sp. *D* is similar to *S. variegata* in the length of the proventricle, up to ten segments (Day 1967). Dorsal cirri of *Syllis* sp. *D* are of medium length (12 – 21 articles) compared to *S. hyalina* (6 – 12 articles) and *S. prolifera* (22 – 27 articles). *Syllis* sp. *D* differs from *S. hyalina* in that it is much smaller with longer antennae and proventricle (Day 1967). The new species is different from live specimens of *S. prolifera* and *S. variegata* in the distinct lack of a colour pattern on body (Day 1967). *Syllis* sp. *D* has shorter antennae and longer proventricle with a greater number of muscle rows. Individuals of *Syllis* sp. *D* are short, with a shorter pharynx and dorsal cirri that are more similar in length to the width of the body than *S. variegata* (Day 1967).

S. prolifera from the Mediterranean Sea is the only one of the aforementioned species that has a pharyngeal tooth that is distinctly back from the anterior margin as in *Syllis* sp. *D*, a character that is also similar to *S.*

unzima, *S. bussettonensis* (Hartmann-Schröder 1982), *S. antoniae* Salcedo-Oropeza, San Martín and Solís-Weiss 2012, *S. rubicunda* Aguado, San Martín and Nishi 2008 and *S. vivipara* Krohn 1869 (Licher 1999, Aguado et al. 2008, Salcedo-Oropeza et al. 2012, Simon et al. 2014). *S. bussettonensis* and *Syllis* sp. D n. sp. both have strongly bidentate chaetae and similarly shaped aciculae (Licher 1999) but *Syllis* sp. D is smaller, with palps that are narrow and longer than the prostomium, shorter antennae and a straight, long pharynx. *Syllis* sp. D and *S. antoniae* are alike in the length of the pharynx and the general shape of the posterior ventral simple chaetae (Salcedo-Oropeza et al. 2012) but vary in that *Syllis* sp. D is shorter, has an oval prostomium and distinctly articulated dorsal cirri. *Syllis* sp. D and *S. rubicunda* are similar in their bidentate chaetae and pharyngeal tooth that is slightly removed from the anterior pharyngeal margin (Aguado et al. 2008) but the former has a slender tapered body, is transparent with short, thinner dorsal cirri. *Syllis* sp. D differs from *S. vivipara* by having bidentate chaetae of median length (San Martín 1992).

After morphological observations and comparisons with known species, I recommend that this morphotype be formally described as a new species.

HABITAT:

Algal turf, lower intertidal, rocky shore.

DISTRIBUTION:

Mossel Bay, South Africa.

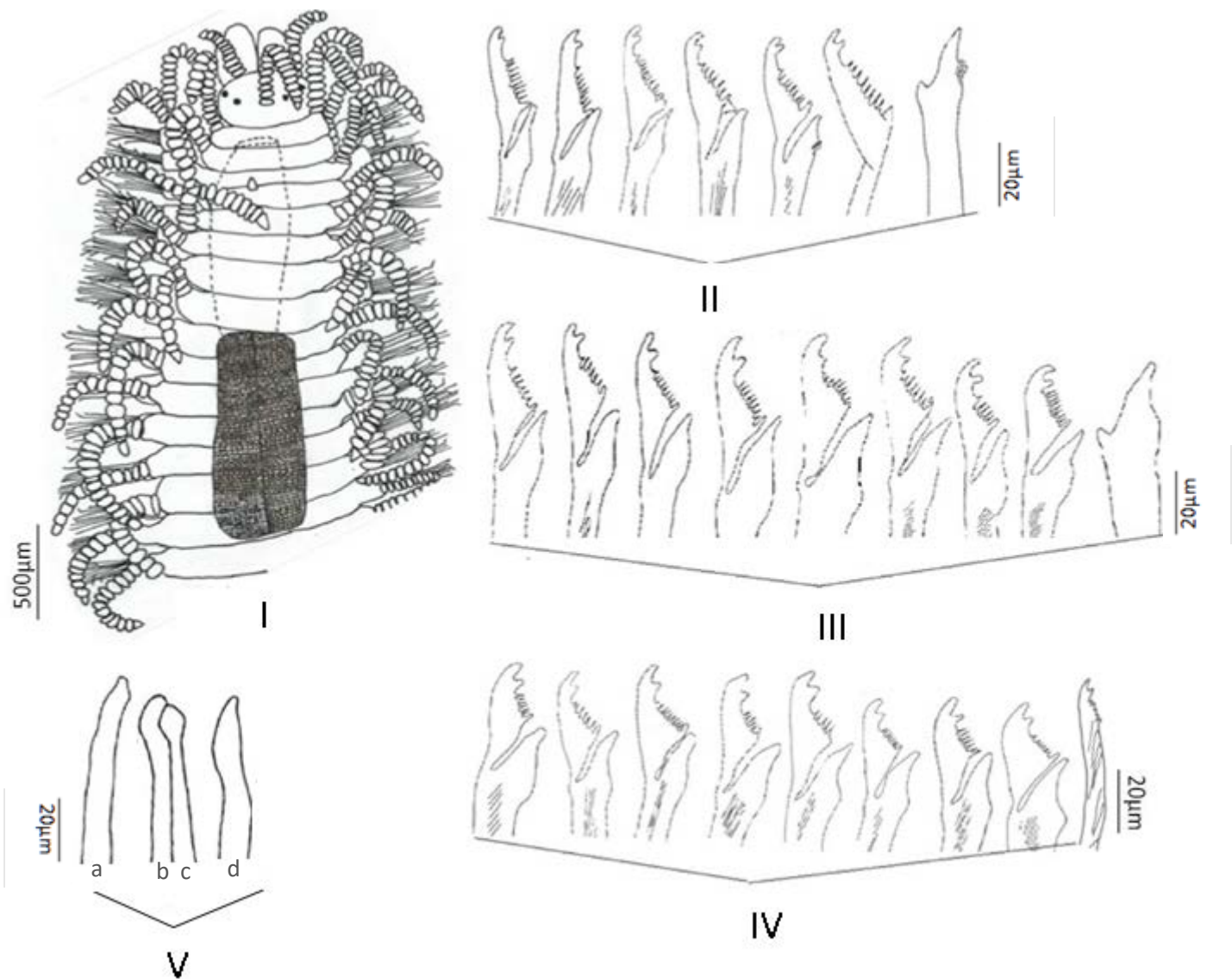


Figure 3.7 *Syllis* sp. *D*: Dorsal view of (I) anterior, (II) anterior chaetae with solitary subtriangular pseudosimple chaetiger with narrow shaft head, tapering into a sharp point with short spines on outer margin, (III) midbody chaetae with single subtriangle pseudosimple chaetiger with broad shaft head tapering to rounded point, with short spines on outer margin and (IV) posterior chaetae with single, sinuose, bidentate, ventral simple chaetiger with serrated inner margin, (V) aciculae on (a) acute angle on one margin and straight on the other, narrow point, midbody with (b) sickle shape and (c) knob shape and anterior aciculae (d) posterior parapodia with one side curved and the other side straight.

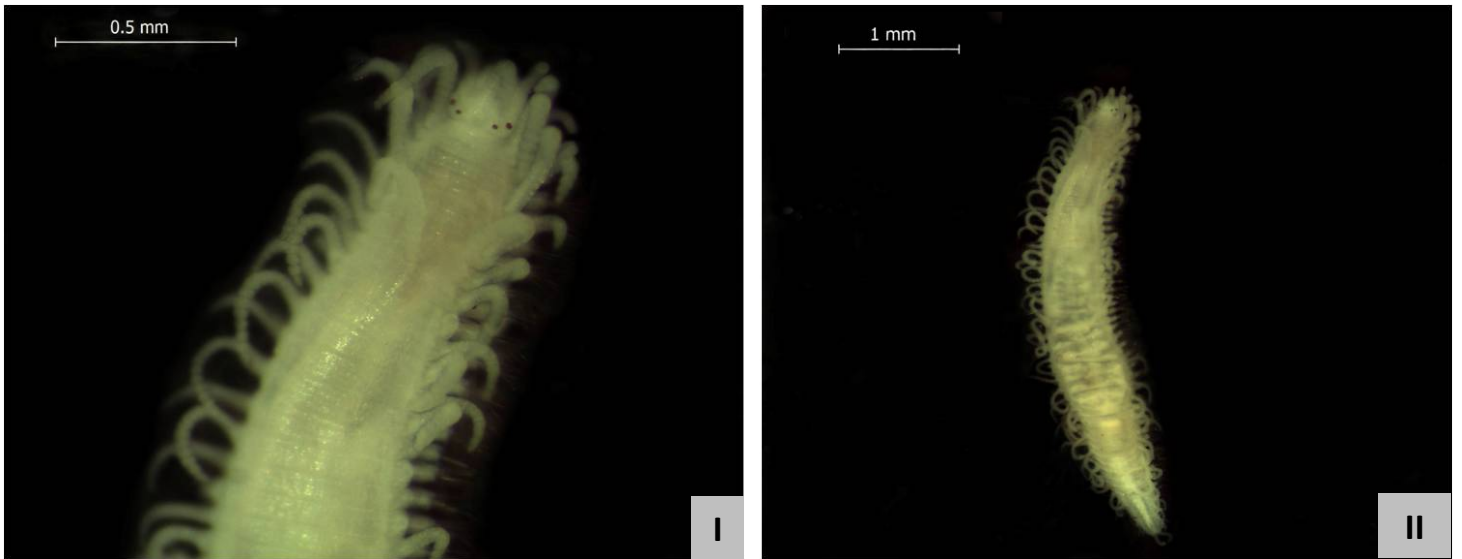


Figure 3.8 *Syllis* sp. *D*: Dorsal view of (I) anterior and (II) whole specimen.

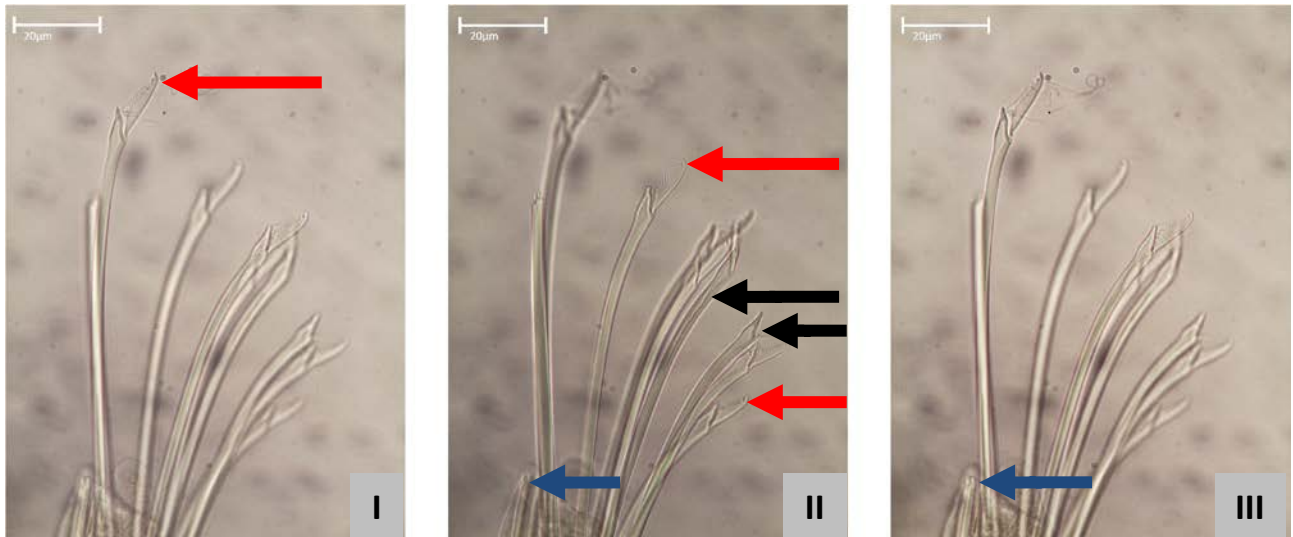


Figure 3.9 *Syllis* sp. *D*: Midbody (I) anterior superior chaetae with shorter secondary tooth (red arrow); (II) inferior chaetae indicating bidentate teeth and gradation along chaetal blade (red arrows), (II) indentations along chaetal shaft and pseudosimple chaetiger (black arrows) and (II, III) aciculae with (III) one side curved and the other straight, (II) broad with narrow point (blue arrows).

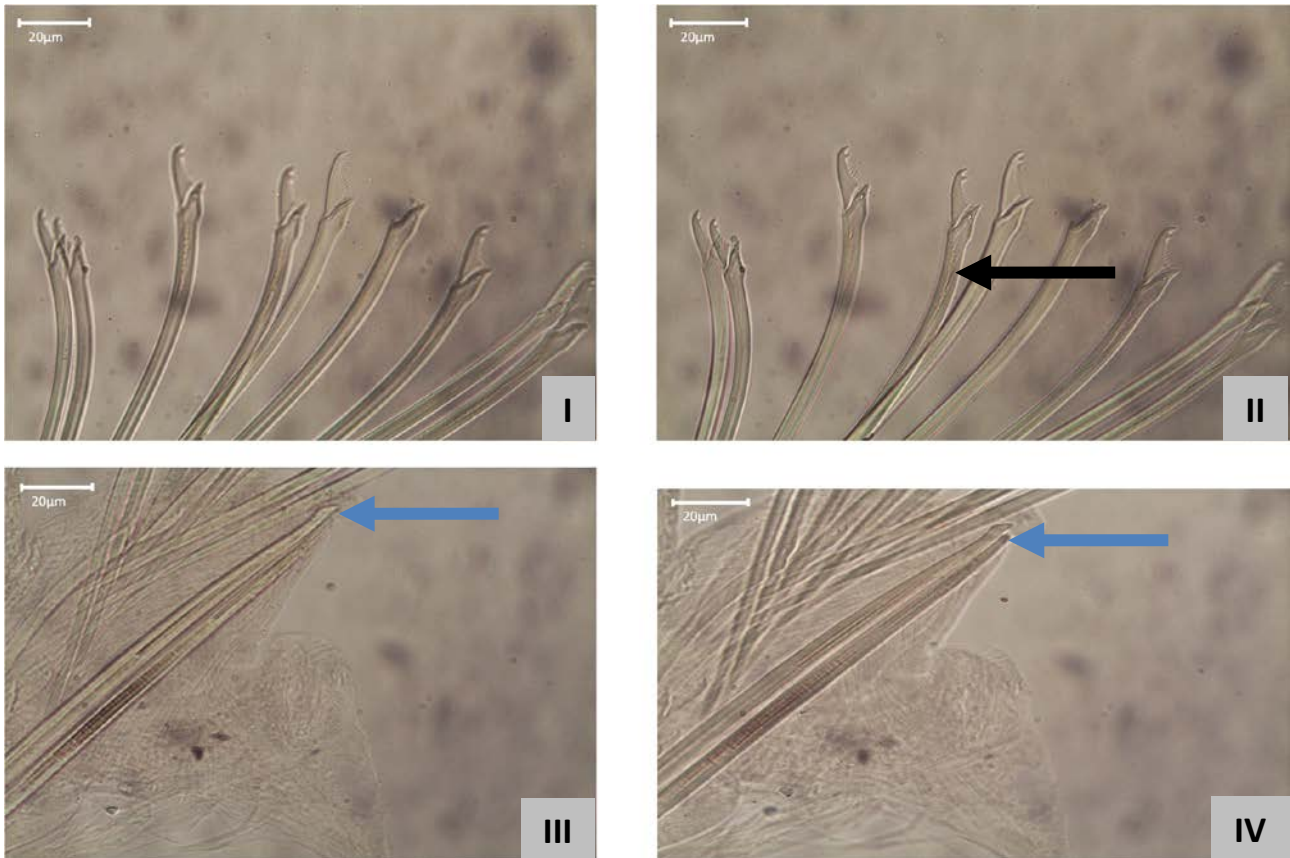


Figure 3.10 *Syllis sp D*: (I, II) Midbody superior chaetae indicating bidentate teeth and gradation along chaetal blade (red arrow), (II) inferior chaetae indicating bidentate teeth, gradation along chaetael blade (red arrows) and indentations along chaetal shafts (black arrow); (II) pseudosimple chaetiger (black arrow) ; (III, IV) aciculae (blue arrows) (III) knobbed , (IV) sickle-like shape.

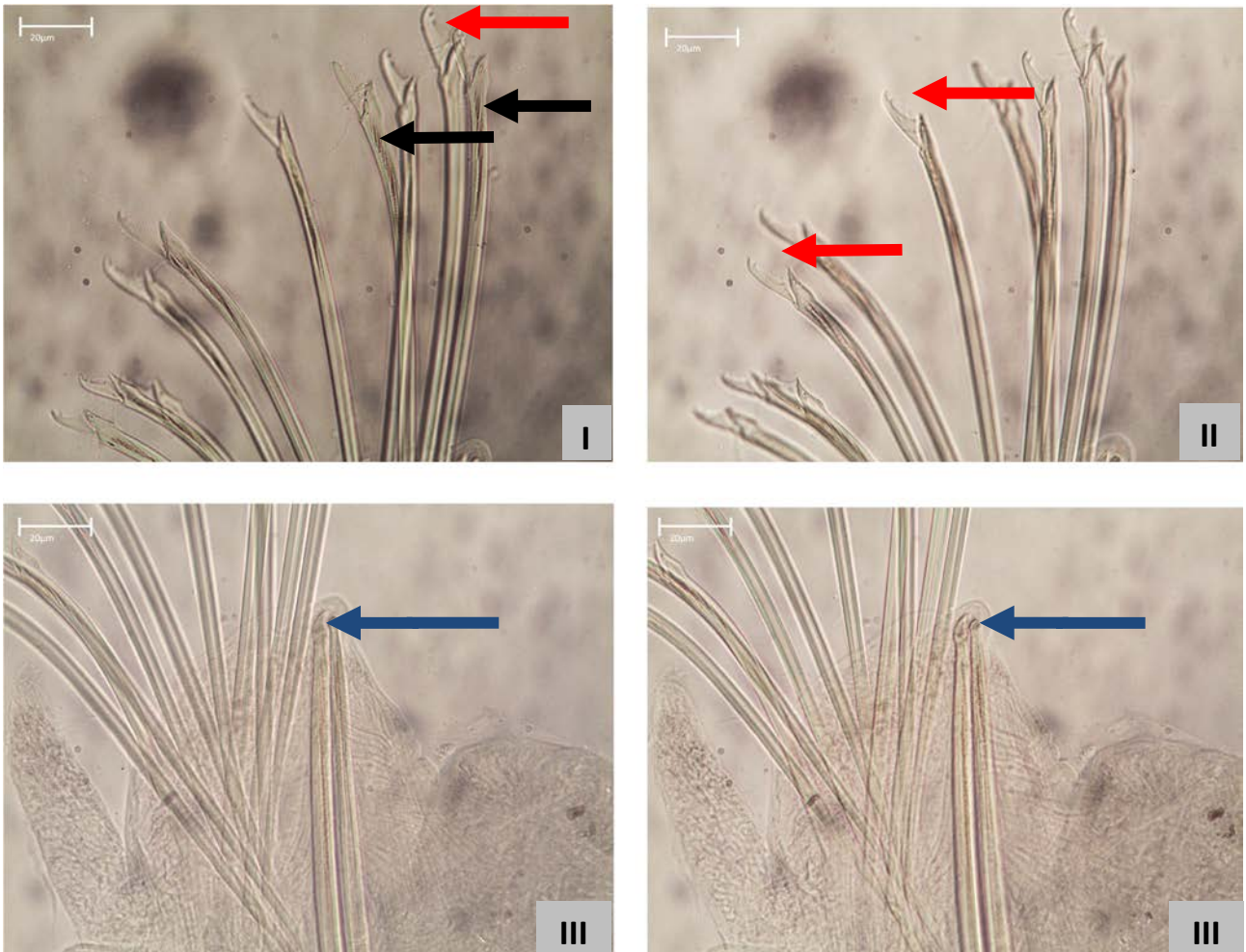


Figure 3.11 *Syllis* sp. *D.*: (I) Posterior superior chaetiger indicating bidentate teeth (red arrow) and indentations in chaetal shaft (black arrows); (II) inferior chaetae indicating bidentate teeth and gradation along chaetal blade (red arrows); (III, IV) aciculae with (III) narrow pointed tip, (IV) rounded on one side and curved on the other, almost diamond shaped with two acute angles on either side (blue arrows).

Syllis sp. S
(Figures 3.12 – 3.16)

MATERIAL EXAMINED:

Holotype: Complete specimen (algal turf, lower intertidal, rocky shore); Coll. S. Sedick; October 2015; Mossel Bay (34°10'60"S; 19°18'75"E).

Paratypes: Four complete specimens; one specimen with slide of anterior, mid-body and posterior parapodia; October 2015. Data as for Holotype.

Other material examined: 15 complete specimens in 70% ethanol. Data as for Holotype.

DESCRIPTION:

Holotype cylindrical, dorsally swollen, appearing rounder in cross section anteriorly than posteriorly, becoming less swollen toward posterior (Fig. 3.13 I). Species robust, 5.95 mm for 61 chaetigers, 0.393 mm wide at middle proventricle, without parapodia. Live and preserved specimens, dark brown, almost completely opaque, pigmentation on prostomium and anterior segments, fading in colour toward posterior (Figs 3.12 I, 3.13 II, III). Prostomium oval, two pairs of red similarly-sized round eyes, trapezoidal arrangement (Figs 3.12 I, 3.13 II, IV). Palps separate, broadly triangular, similar in length to prostomium. Median and lateral antennae, dorsal and tentacular cirri distinctly articulated. Lateral antennae longer than palps, arising from anterior prostomium, 17 articles (Fig. 3.12 I). Median antenna longer than palps and prostomium, originating behind posterior eyes, 23 articles (Fig. 3.12 I). Peristomium shorter than subsequent segments, two pairs of tentacular cirri, dorsal pair longer than ventral pair, 20 articles, ventral pair with 18 articles. Dorsal cirri shorter or subequal to body width, long dorsal cirri 27 articles anteriorly, 22 articles in mid-body, short dorsal cirri 13 articles anteriorly, 10 articles in mid-body, dorsal cirri with 27, 25; 11, 18; 21, 19 articles on left and right parapodia of chaetigers 1 to 3, respectively. Ventral cirri short, not extending beyond parapodial lobes. Anterior parapodia with 13 compound chaetae, ten in mid-body, eight in posterior. Heterogomph falcigers unidentate or minutely bidentate, moderately long, thin spines on chaetal blade, fine spines on basal margin (Figs 3.12 II, III, IV, 3.15 II, III, 3.16 I). Up to three pseudosimple chaetae on anterior, mid-body and posterior parapodia, broad, narrow rounded tip (Figs 3.12 IV, 3.14 I, 3.16 I) or narrow with wide pointed tip (Figs 3.12 IV, 3.14 I). Posterior ventral simple chaetae solitary, thin and pointed; posterior solitary dorsal simple chaetae straight, thicker, rounded tip (Figs 3.16 I, II). Up to three aciculae anteriorly; paddle shaped; slightly curved on one margin; straight, broad (Figs 3.12 I, 3.15 II). Two aciculae in mid-body; distally oblique; bottle-shaped (Figs 3.12 V, 3.15 I). One or two aciculae in posterior; right angle; distally gently curved, rounded tip toward one margin (Figs 3.12 V, 3.16 I). Pharynx five chaetigers long, anterior tooth, proventricle eight chaetigers long, about 26 rows of muscles (Fig. 3.12 I). Two anal cirri, 14 articles long.

VARIATION:

About 1.8 – 9.1 mm long for 49 – 61 chaetigers. Dark chocolate to light brown pigmentation that may extend to inner dorsal margins of palps. Intersegmental brown bars, starting just after proventricle, fading toward posterior. Lateral antennae 13 – 17 articles, median antennae 17 – 20 articles. Dorsal tentacular cirri 14 – 17, 22 – 24 articles in larger individuals. Ventral tentacular cirri 13 – 17 articles. Longer anterior dorsal cirri 6 – 12 articles in smaller individuals or 10 – 13 in larger individuals, short anterior dorsal cirri 15 – 17 articles in smaller individuals or 17 – 27 in larger individuals. Long midbody dorsal cirri 8 – 10 articles in smaller individuals or 5 -20 in larger individuals, short midbody chaetae 13 – 19 articles in smaller individuals or 19 – 34 in larger individuals. Anterior compound chaetae 8 – 12 per parapodium or 6 – 7 in smaller individuals, 6 – 9 in midbody, 5 – 8 in posterior for small and large animals. Pseudosimple chaetae may be present in anterior and mid-body only, or along the length of the body. Pharynx 6 - 8 chaetigers long, proventricle 5 – 8. Anal cirri 9 – 16 articles.

REMARKS:

Live individuals of *Syllis* sp. *S* are characterized by a dark brown prostomium and anterior region which is also distinctly rounded dorsally. This species is similar to *S. amicarmillaris*, *S. amica*, *S. gracilis*, *Syllis* sp. *A* and *Syllis* sp. *D* in that they are the only *Syllis* species in South Africa with pseudosimple chaetae (Day 1967, Licher 1999, Simon et al. 2014). *Syllis* sp. *S* differs from live specimens of *S. amicarmillaris* in the distinct brown colour, longer tentacular cirri and, longer dorsal cirri and unidentate chaetae (Simon et al. 2014). *Syllis* sp. *S* resembles *Syllis* sp. *D* in the length of the antennae and number of aciculae along the length of the body but the new species differs from *Syllis* sp. *D* in having an anterior pharyngeal tooth close to the anterior margin of the pharynx and unidentate or minutely bidentate chaetae. *Syllis* sp. *S* resembles *S. gracilis* in the shape of superior anterior chaetae but this new species differs from *S. gracilis* in the dark chocolate colour that extends into the midbody region and pseudosimple chaetae that are broad with narrow tips or narrow with broad tips (Day 1967, Licher 1999, Maltagliati et al. 2004, Álvarez-Campos et al. 2017). *Syllis* sp. *S* and *Syllis magdalena* Wesenberg-Lund 1962 are similar in their chocolate brown colour only (Licher 1999). *Syllis* sp. *S* differs from *S. magdalena* in having palps that are broadly triangular and similar in length to the prostomium, a short pharynx and proventricle with fewer muscle rows, unidentate chaetae and a prostomium that is attached to the peristomium rather than separated by a transversal pit (Licher 1999).

After morphological observation and comparisons with known species, I suggest this morphotype be formally described as a new species.

HABITAT:

Algal turf, lower intertidal, rocky shore.

DISTRIBUTION:

Danger Point and Mossel Bay, South Africa

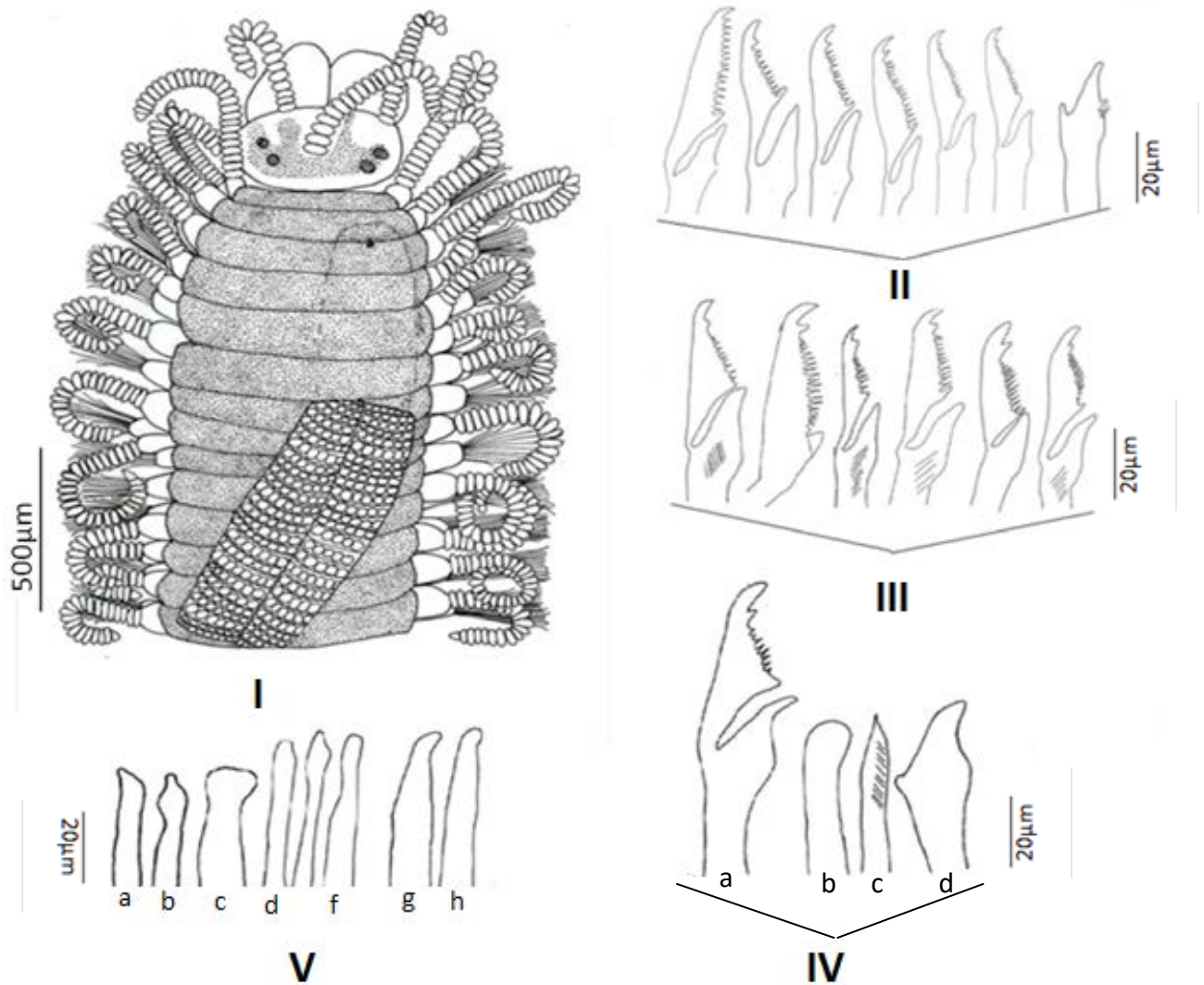


Figure 3.12 *Syllis* sp. S: Dorsal view of (I) anterior, (II) anterior chaetae with solitary pseudosimple chaetiger with narrow shaft head and sharp, pointed tip, (III) midbody and (IV) (a) posterior chaetiger with (b) single dorsal, simple chaetiger, straight with thick, rounded tip, (c) ventral simple, chaetiger, thin, pointed with indentations along shaft head, (d) pseudosimple chaetiger with broad shaft head with curved point and, (V) aciculae with (a) anterior aciculae straight, broad, (b) slightly curved on one margin, (c) paddle-shaped, (d,e) midbody distally oblique, (f) bottle-shaped, (g) posteriorly at right angle, (h) distally gently curved, rounded tip to one margin.



Figure 3.13 *Syllis* sp S: (I) Swollen anterior end, (II) extent of colouration, (III) gradation in colour from anterior (red arrow) to midbody and (IV) anterior end showing shape of palps.

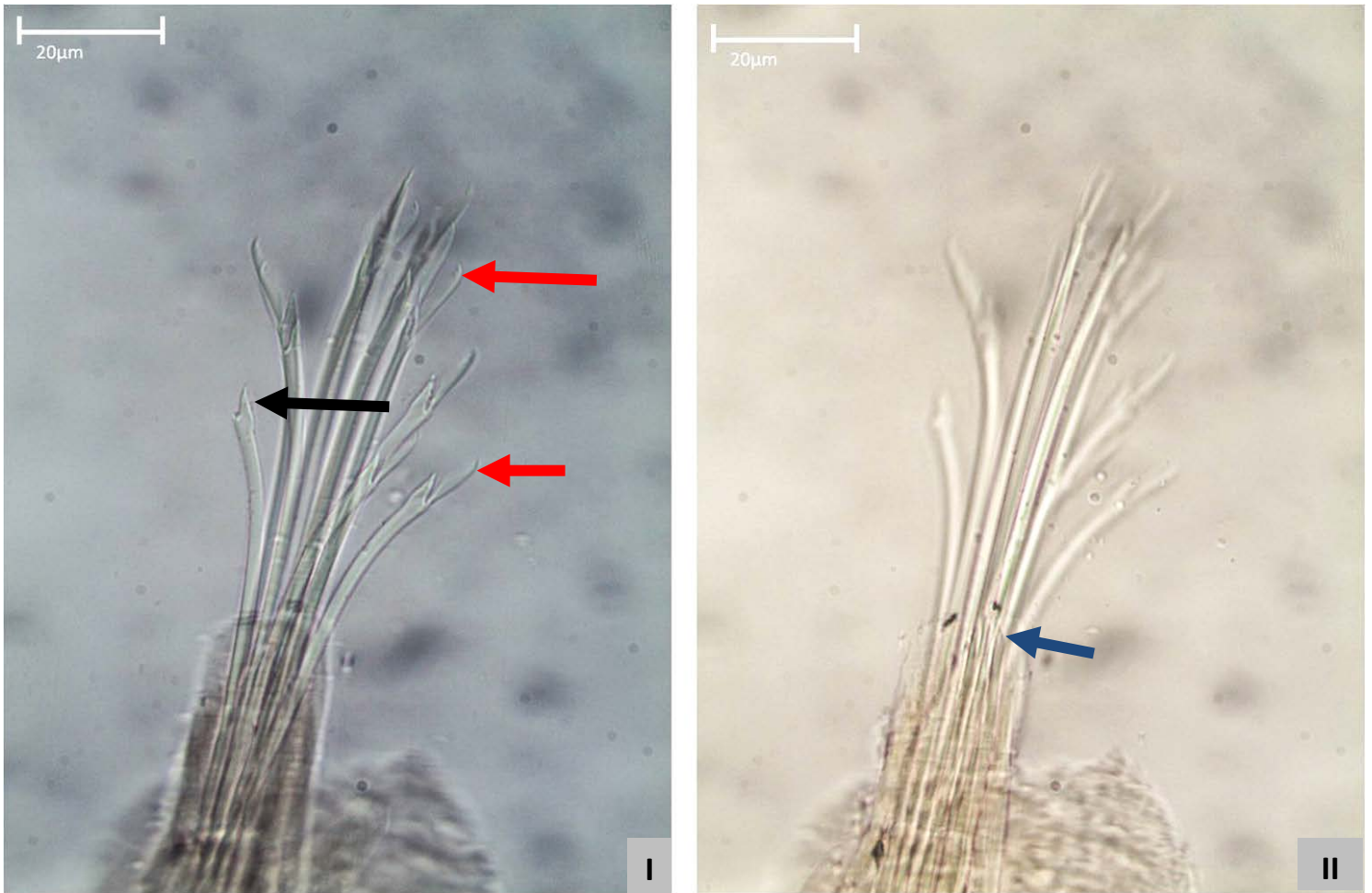


Figure 3.14 *Syllis* sp. S: (I) Anterior inferior and superior chaetae (red arrows) and, pseudosimple chaetiger (black arrow) and (II) aciculum straight, broad (blue arrow).

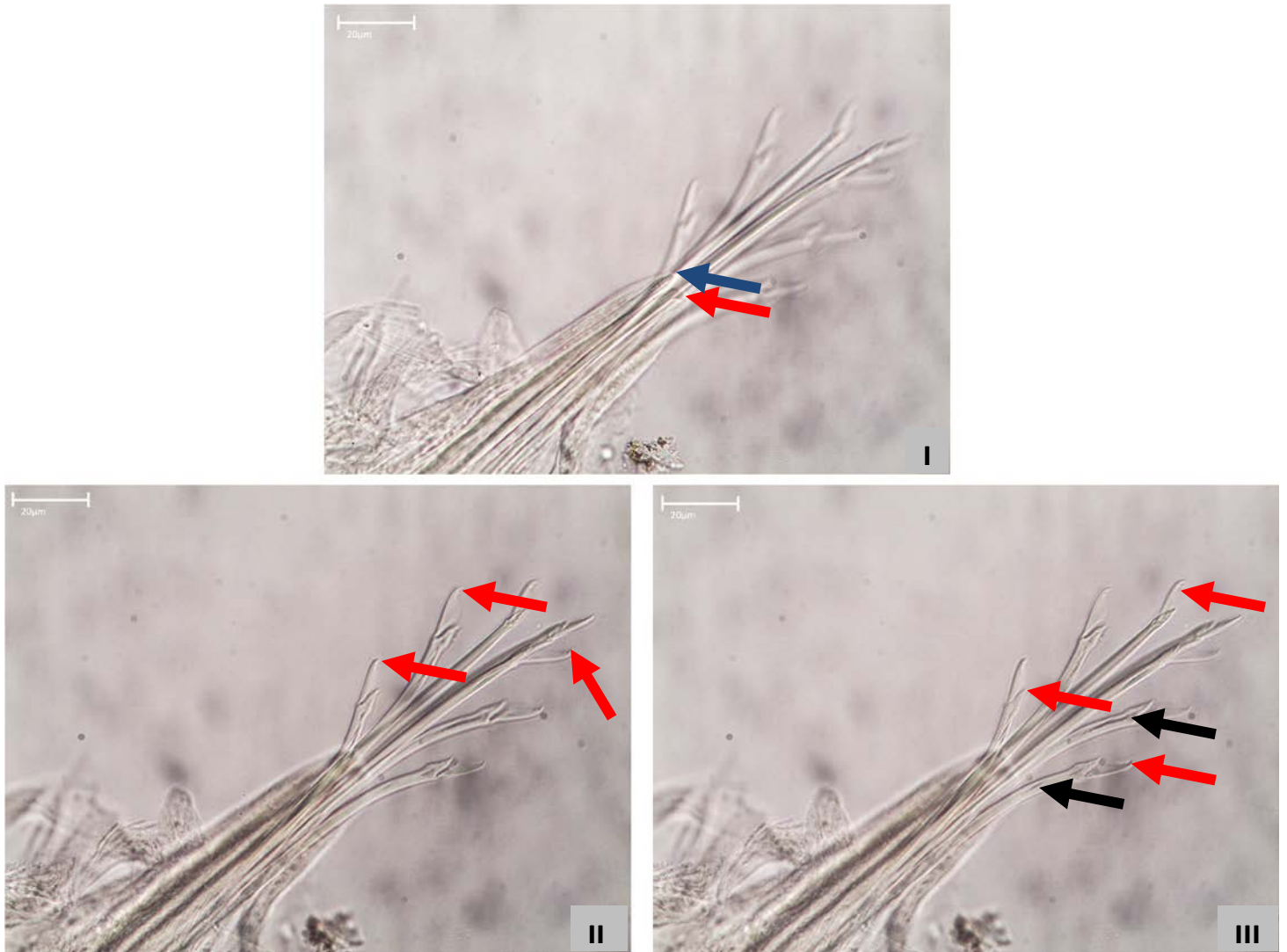


Figure 3.15 *Syllis* sp. S: (I) Midbody aciculae distally oblique and rounded (red arrow), bottle-shaped (blue arrow) and, (II, III) inferior and superior chaetae indicating bidentate teeth with a gradation along chaetal blade (red arrows) and, indentations in chaetal shaft (black arrows).

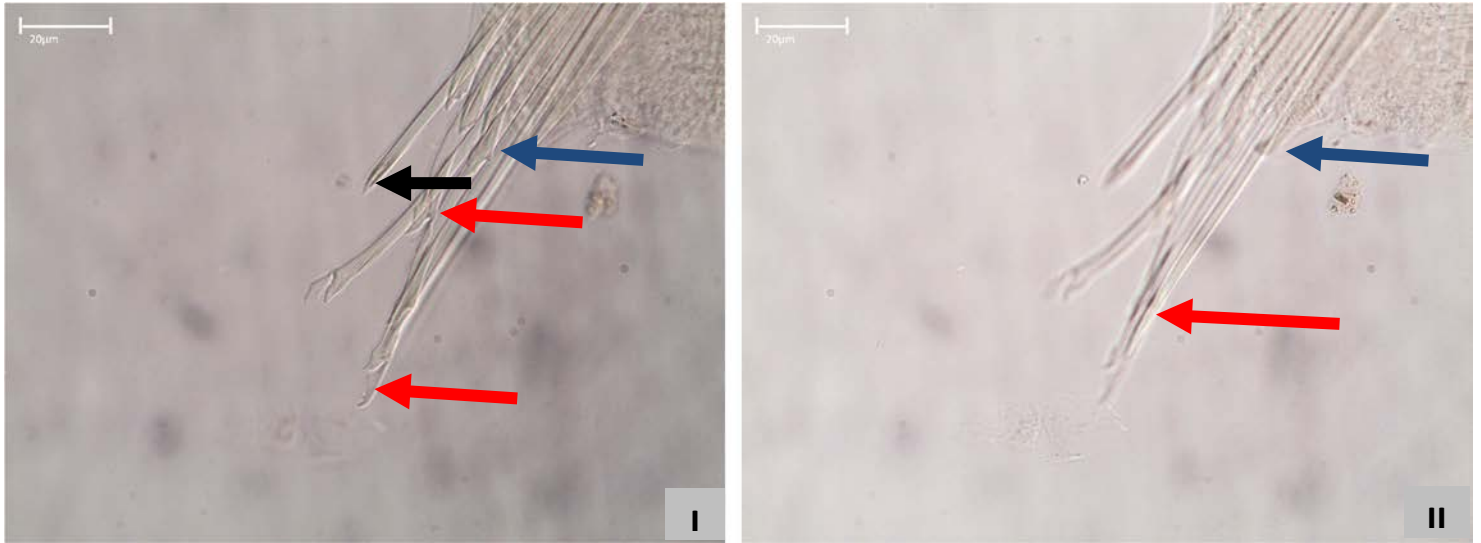


Figure 3.16 *Syllis* sp. S: (I) Posterior inferior and superior chaetae (red arrows), pseudosimple and simple chaetae (black arrows) and, aciculum distally gently curved with rounded tip toward one margin (blue arrow) and, (II) simple chaetiger (red arrow) and gently rounded aciculum (blue arrow).

3.4 Discussion

Overall, 13 species (seven genera) were identified from three sites; four from Gordons Bay, nine from Danger Point and eight from Mossel Bay. There were also many unidentifiable species that, if added to the total, would increase the number of species across all sites to as much as 24 if all the species really are new. This increases the total number of species to seven at Gordons Bay, ten at Danger Point and 14 at Mossel Bay. Previously, Day (1967) reported 29 and ten syllid species in False Bay and Mossel Bay, respectively. Further, most (77%) of the identified species had a questionable taxonomic status. This means that each of these putative species may be a member of a complex of morphologically similar species, some of which may be native (i.e., differ from other species within the complex and, therefore, undescribed), thereby potentially increasing the number of native syllids as much as ten-fold. This supports my hypothesis that: the overall syllid richness and the number of native syllid species has been slightly underestimated, especially at selected sites along the south coast of South Africa.

The numbers of syllid species that could be identified in this study were seven times less than what was reported for False Bay, two less than what was reported in Mossel Bay and one more species than what was reported at Danger Point. The numbers reported for False Bay by Day (1967) include species recorded at several localities across the entire bay whereas I considered only one site within the bay. This may explain the comparatively low numbers found there.

In the introduction to this chapter I suggest that differences in syllid richness between Day (1967) and Awad et al. (2002) are due to a sampling bias but, the results of this chapter do not seem to support this statement. Griffiths et al. (2010) found that most benthic samples have been collected from the west and southwest coasts of South Africa, especially in localities such as Table Bay, Lamberts Bay, Saldanha Bay, Langebaan lagoon and False Bay, which could account for high species richness recorded in the region. However, for syllids, some sites such as Table Bay (24 species) and Saldanha Bay (14 species) have higher syllid richness than others such as Lamberts Bay (nine species) and Langebaan Lagoon (three species) that have syllid species richness similar to that at south coast sites (Day 1967). A more recent assessment of Langebaan Lagoon and Saldanha Bay reveal seven and four syllid species, respectively (Hanekom et al. 2009). Thus even though the sampling effort at these west coast sites has been high, the level of syllid richness is not consistent across sites and, quite possibly over time. This may be a characteristic of the prevailing environment (e.g. wave exposure, algal cover), which is explored further elsewhere in the discussion. After sampling at selected sites along the south coast, the number of syllid species on the south coast now seems more comparable to the west coast and has revealed that the numbers of syllids on the south coast are still considerably low. The overall low level of syllid richness highlighted in this study along the south coast of South Africa is consistent with the patterns found in Chapter 2. This contrasts patterns observed by Awad et al. (2002) where species richness was highest along the south coast of South Africa and lowest on the east coast. The syllid richness observed in this chapter also contradicts the pattern in Day (1967) where syllid richness is highest on the east coast. As Awad et al. (2002) represents a more general pattern, one that may not even include syllids, it is unsurprising that it does not align with the results of this chapter. However, the consistently low level of syllid richness observed in Day (1967) is surprising,

considering the west coast (and False Bay) sampling bias prevalent in JH Day's publications (cf. Day 1953, 1955, 1961, 1963). It is therefore possible that the pattern observed by Day (1967) for polychaetes in general may actually be a true reflection of syllid species richness. Having said that, this pattern is strongly dependent on the method of sample collection and analysis, as many syllids are meiofaunal and are often omitted from typical macrofaunal studies.

The low taxonomic resolution of syllids in South Africa is highlighted by the fact that more than 50% (11) of all collected species could not be identified to species level. The three most abundant of these are described in this chapter and together, these three proposed new species make up more than 20% of all individuals collected at Mossel Bay (Table 3.1). It is not unusual to come across new syllid species even in regions where syllid taxonomy is relatively well resolved. For example, San Martín (2005), San Martín and Hutchings (2006) describe 37 new species from Australia, Noguiera et al. (2001) described five new species from Brazil and Abd-Elnaby and San Martín (2010) described one new species from the eastern Mediterranean Sea. Of the 37 species described by San Martín (2005) and, San Martín and Hutchings 2006, four of them are re-descriptions of European species that had previously been mis-identified. I therefore predict that with an increase in investigations in South Africa, many more new syllid species will be described.

The poor understanding of species richness of indigenous species is further exacerbated by the fact that 77% of the species that could be identified are classified as questionable. Of these questionable species *S.cf. prolifera*, *S. cf. variegata* and *S. cf. vittata* were the most abundant. These species may represent local members of species complexes that comprise several morphologically similar species for two reasons. Firstly, apparently cosmopolitan species such as these often consist of large species complexes and it is highly likely that the local representatives are actually new indigenous species (Klautau et al. 2013). For example, *M. elityeni* and *Laonice antipoda* are recently described indigenous species belonging to the *Marphysa sanguinea* and *Laonice cirrata* species complexes, respectively (Lewis and Karageorgopolous 2008, Sikorski and Pavlova 2016). *Marphysa sanguinea* and *L. cirrata* are apparently cosmopolitan species that had previously been mis-identified by Day (1967) (Lewis and Karageorgopolous 2008, Sikorski and Pavlova 2016). Secondly, all three of these species are found in climatically incomparable regions both locally (across all three biogeographic regions) and globally. *S.cf. prolifera* and *S.cf. variegata* are distributed in the Mediterranean, Caribbean Sea, English Channel, Australia and New Zealand while *S. vittata* is distributed throughout the North Atlantic Ocean with South Africa as its only locality in the southern hemisphere (Appendix 1). Taken together, the many unidentified species collected in this study, the many species with a questionable taxonomic status that may be local representatives of species complexes (10 species), and the disproportionately low number of native species collected from the three sample sites (three species), imply that the number of indigenous species along the south coast of South Africa has been underestimated.

I was expecting to find a number of species previously listed as fairly common to common throughout southern Africa including at Mossel Bay and in False Bay, namely *S. cf. armillaris*, *S.cf. gracilis*, *Trypanosyllis cf. zebra* (Grube 1860), *T. cf. gemmulifera*, *Amblyosyllis cf. formosa* (Claparède 1863) and *Odontosyllis cf. polycera* (Schmarda 1861) (Day 1967). However, they were not among the species collected and there may

be several reasons for their absence. The first may be related to the nature of the substrate sampled. Majority of the samples were collected from algal turf and fewer samples from foliose algae, soft sediment and sponge. While very little to no information is available for syllids along the south coast of South Africa recent ecological investigations have documented *S. cf. armillaris* along the west coast of South Africa. Hammond and Griffiths (2004) found *S. cf. armillaris* in relatively high abundances in mussel beds at five out of nine sites near Groenriver mouth on the west coast of South Africa making up 48%, 6%, 9%, 54% and 18% of the total abundance at each site, respectively. High abundance of syllids was observed at more sheltered sites while *S. cf. armillaris*, a more robust species, was the only species found in a high abundance at more exposed sites (Hammond and Griffiths 2004). Hanekom et al. (2009) also found *S. cf. armillaris* present, but not common, in Saldanha Bay and Langebaan Lagoon, but in soft substrata. It is possible that I did not find *S. armillaris* as I did not collect samples from mussel beds. Also, my selected sample sites were in more sheltered areas compared to where *S. cf. armillaris* was found on the west coast. Furthermore, even though several substrates were sampled at Gordons Bay, very few species were collected. This may be a result of the type of environment that this locality presents in that it has very low algal cover and is often very cobbled in large areas along the beach (pers. obs). Therefore, in addition to substrate, the type of beach or shore plays a role in the number of species that may be found there.

Another possible explanation for the absence of these supposedly common species from the collected samples may be related to the accuracy with which I could identify species using the identification key for the region. The descriptions in Day (1967) are sometimes brief and provide little detail, and in some instances may simply be inaccurate. Furthermore, it sometimes appears that Day (1967) frequently used the original descriptions of apparently cosmopolitan species in his monograph rather than re-describing the species that he had examined. For example, as it is not characteristic for *S. cf. armillaris* (Müller 1776), the description of this species in Day (1967) does not indicate the presence of pseudosimple chaetae. Yet specimens of *S.cf. armillaris* lodged at the Iziko South African museum by John Day have these pseudosimple chaetae (pers. obs). Such inaccurate descriptions of species could have serious consequences for the identification of specimens and will be explored more extensively in Chapter 4.

This study also enlarges the distribution for 77% of identified species: *S. amicarmillaris*, *S.cf. amica*, *E. cf. naidina*, *E. cf. verugera*, *S. sublaevis*, *S.cf. prolifera*, *N. magnidens*, *P.cf. ehlersiaeformis*, *B. cf. rhopalophora* and *A. cf. maclearanus*. For example, according to Day (1967), *S. cf. amica* only occurred on the tropical and subtropical east coast, while I found it more than a thousand kilometres to the south west, at Gordons Bay, Danger Point and Mossel Bay. Similarly, *A. cf. maclearanus*, known from the cold temperate west coast of South Africa, was here found more than five hundred kilometres to the south east at Mossel Bay. Such large shifts in distribution range for these species suggest that they may have been introduced to these regions. However, considering their small size and low abundance, it is more likely that individuals may have been previously overlooked.. Finally, it is also possible that these individuals from the south coast may represent different species to those identified by Day (1967) from the east and west coasts of South Africa, which may also link back to the inadequacy of descriptions, as mentioned above. Recently Simon et al. (2017) found that although specimens from the south and northeast coasts of South Africa all conformed to the description of *Pseudopolydora antennata* Claparède 1869 in Day (1967), they actually represented two independent,

easily distinguishable, species. This will be considered further in Chapter 4 in relation to *S. cf. amica*, an apparently cosmopolitan species with a questionable taxonomic status in South Africa.

Syllis amicarmillaris was by far the most abundant species at all three sites, accounting for slightly more than half of the specimens collected. Although I have presented some possible reasons for the absence of *S.cf. armillaris* from all three sampling sites, its absence is still peculiar as Day (1967) lists the species as being “very common and widely distributed” throughout southern Africa, including in the sites sampled here. Here I suggest that the specimens identified by Day (1967) may in fact be what has since then been described as *S. amicarmillaris*. The same might apply to *S. cf. amica* (found at all of the sampling sites) that has a similar chaetal shape to *S. amicarmillaris* (Simon et al. 2014) and that has a doubtful widespread global distribution and questionable taxonomic status in South Africa (Chapter 2). This will be further explored in Chapter 4.

This study revealed three indigenous species, three undescribed morphospecies that have been proposed to be formally described as new species, eleven species that I was unable to identify and ten species with a questionable taxonomic status that could represent new indigenous species that have previously been misidentified. Although this emphasizes the great potential for the underestimation of syllid richness at the sampled sites on the south coast, syllid species richness on the south coast is still considerably low in comparison to the west coast and agrees with geographic patterns of species richness observed by Day (1967). This low species richness contrasts the general pattern for all marine taxa and for polychaetes in general, as described by Awad et al. (2002) who found the highest levels of species richness and endemism along the south coast of South Africa. A possible reason for this may be that the collected samples were restricted to a few substrates, which may explain the observed level of species richness. While a general re-assessment of syllid diversity throughout South Africa is needed, this study provides a sound base upon which to build further investigations into the family.

Chapter 4: A morphological and morphometric comparison of *Syllis armillaris* Müller 1776 and *Syllis amica* Quatrefages 1866 from southern Africa and Europe with *Syllis amicarmillaris* Simon, San Martín and Robinson 2014 from South Africa

4.1 Introduction

Several species, including syllids, with apparently cosmopolitan distributions are now recognized as being complexes of similar but distinct species (Knowlton 1993, Klautau et al. 1999, Nygren 2014). For example, *Haplosyllis spongicola* was widely accepted as a cosmopolitan species with high morphological variability, particularly in the length of the dorsal cirri and the shape of the chaetae (Martín et al. 2003, Lattig et al. 2007). However, *H. spongicola* should be considered a pseudo-cryptic species complex; morphological examination and morphometric analyses of 28 populations of *H. spongicola* worldwide suggested that the inter-population variability among most morpho-types was high enough to suggest several species and even a second genus (Martín et al. 2003). Based on these analyses and using some of the specimens from Martín et al. (2003), Lattig et al. (2007) later re-described *H. spongicola* from Spanish Seas and described two new species, *Haplosyllis carmenbrittoae* Lattig, San Martín and Martín 2007 from the Canary Islands and *Haplosyllis granulosa* (Lattig, San Martín and Martín 2007) (Lattig and Martín 2009) from Spanish and western Mediterranean Seas. Since then, the number of new species described within the genus *Haplosyllis* has already reached a total of 36 species, three times more than at the time *H. spongicola* was considered cosmopolitan (Lattig and Martín 2009). Similarly, molecular analyses revealed that *Syllis gracilis* from marine and freshwater environments along the Italian coast displayed enough genetic divergence to be considered a cryptic species complex (Maltagliati et al. 2000). More recently, Álvarez-Campos et al. (2017) demonstrated that individuals identified as *S. gracilis* from the Mediterranean Sea, North Atlantic Ocean and the North and South Pacific Oceans can be separated by molecular and morphological evidence and is thus a pseudo-cryptic species complex comprising up to eight distinct lineages. Although both nominal species have been recorded in South Africa (Day, 1967), neither study included specimens from there.

Species complexes have also been suggested for other species such as *Syllis armillaris* (Lopez et al. 2001, Musco and Giangrande 2005, Mikac and Musco 2010) and *Branchiosyllis exilis* (Mikac and Musco 2010, Góngora-Garza et al. 2011, Álvarez-Campos et al. 2012) separated solely on morphology, and *Trypanosyllis krohnii* separated by molecular methods (Álvarez-Campos et al. 2012). Individuals within these apparent complexes from different localities are often morphologically different and usually have characters that distinguish them from the nominal species. For *S. armillaris*, the extent to which chaetal blades may or may not become more spindle-shaped towards the posterior of the worm, the number of teeth on chaetal blades

and the presence of stout pseudosimple chaetae in midbody differentiate between at least three morphotypes (Musco and Giangrande 2005). Similarly, individuals of *B. exilis* examined from five widely disparate locations differ in the long, slender dorsal cirri, dorso-ventral gradation of chaetal blade length and length of distal and proximal teeth of chaetal blades, providing enough support to group specimens from Australia, Panama and Cuba together while specimens from the Mediterranean Sea and the Phillipines formed a second group (Álvarez-Campos et al. 2012). While *T. krohnii* has not been recorded in South Africa, *S. cf. armillaris* and *B. exilis* were reported as locally widespread (Day 1967). The evidence provided here and the fact that the worldwide distributed populations of these species have been resolved into smaller, more locally distributed populations of distinct species in other regions of the world, suggests that these and other widespread species present in South Africa may also be local populations of a different species (see also Chapter 2).

Of particular interest to me are *S. armillaris* and *S. amica* and their close resemblance to the recently described *Syllis amicarmillaris*. In Chapter 3, *S. amicarmillaris* was identified as the overall most abundant species collected, while *S. armillaris* was unexpectedly absent even though it was previously reported as very abundant in the intertidal around southern Africa (Day 1967, Hammond and Griffiths 2004). *Syllis amicarmillaris* is so named for its resemblance in body plan to *S. armillaris* and its resemblance in chaetal characters to *S. amica* (Simon et al. 2014). *Syllis amicarmillaris* resembles *S. armillaris* in having an elongated, cylindrical, tapered body, stout dorsal cirri and relatively long pharynx and proventricle. *Syllis armillaris* differs from *S. amicarmillaris* in that the superior chaetae in the former species are much longer and narrower with a minute secondary tooth while inferior chaetae are wider with broader blades, and the absence of sinuous, bidentate, ventral simple chaetae. Moreover, the most obvious and probably most important distinction between these two species is the absence of pseudosimple chaetae along the length of the body in *S. armillaris*. *Syllis amicarmillaris* resembles *S. amica* in the presence of similarly shaped pseudosimple chaetae on midbody parapodia only. The differences between these two species are more obvious in that *S. amica* has much longer dorsal cirri, a shorter pharynx and proventricle and larger, more rounded palps (Day 1967). However, the questionable taxonomic status of *S. armillaris* and *S. amica* in South Africa (Chapter 2, Appendix) raises the possibility that they may have been incorrectly assigned and are actually *S. amicarmillaris*. Furthermore, *S. armillaris* is also the species with the most synonymized species (30 species), as determined in Chapter 2.

This idea is reinforced by the fact that *S. armillaris* probably represents a complex of species as described above (Lopez et al. 2001, Musco and Giangrande 2005, Mikac and Musco 2010). This species was originally described from Arctic waters by O.F. Müller (1776). As was common in many early taxonomic studies, the description highlighted only characters that the author considered distinctive and lacked sufficient detail of other morphological characters that could potentially contribute to distinguishing the species. Consequently, the description for *S. armillaris* only mentions; subdepressed, lens-shaped, conical feet (Müller 1776). Fauvel (1923) later re-described the species based on individuals from the English Channel, Atlantic Ocean, Mediterranean Sea and North Sea as being long and thin with numerous segments, having four red eyes and two ocular specks, long antennae, a pharynx with a large tooth and crown of 10 soft papillae, a long proventricle, short fusiform dorsal cirri and chaetae with a marked secondary tooth that becomes short in the

mid-body and chaetae taking on a more hooked appearance in midbody. Individuals may be yellow, uniformly pink or with pink transverse lines (Fauvel 1923). The description in Day (1967) generally agrees with that in Fauvel (1923) but differs in having chaetae with longer blades and sometimes having a minute secondary tooth in anterior and posterior chaetigers. Day (1967) does not mention hook-shaped chaetae or length of antennae.

More recent re-descriptions of *S. armillaris* include Licher (1999) and Musco and Giangrande (2005). However, these descriptions do not provide much clarity on this species complex either. Specimens that Licher (1999) examined from Europe, the Arctic, Mediterranean Sea, Pacific Ocean, South Atlantic Ocean (excluding South Africa) and Tasmanian Sea have; two intermittent transverse lines along the anterior region; bidentate or minutely bidentate chaetae with long chaetal blades that are not hooked in mid-body, and short antennae and dorsal cirri. Licher's (1999) description does not completely match those of Fauvel (1923) or Day (1967), except perhaps with respect to chaetal length in the latter. Musco and Giangrande's (2005) re-description of *S. armillaris* from the Ionian Sea corresponds well with that of Licher (1999). Specimens have a brownish pigmentation with no distinctive colour marks and longer anterior and posterior chaetal blades (Musco and Giangrande 2005). In this way it is also similar to the description by Day (1967). These descriptions and re-descriptions suggest at least two morphologically different groups for *S. armillaris* with specimens examined by Fauvel (1923) forming one group and those examined by Licher (1999), Musco and Giangrande (2005) and Day (1967) forming another. This, along with its apparently cosmopolitan status, suggests that closer morphological examination of other morpho-types from different regions around the world will reveal several new species belonging to this complex.

Syllis amica was first described by Quatrefages in 1866 from the coasts of France and England. It was described as being long and relatively wide, with palps that are long, broad and fused along most of their length, dorsal cirri that are twice as long as the body is wide and weakly articulated, chaetae that are short, curved and basally broad, and pseudosimple chaetae that are broad and obliquely truncate (Quatrefages 1866). Fauvel (1923) later re-described specimens from Ireland, the Atlantic Ocean and the Mediterranean Sea as being either dark, colourless, pale pink or brown; elongated and uniform in width; having long basally fused palps; a pharynx with a long anterior tooth; dorsal cirri that are almost fusiform and sub-equal to body width; two kinds of chaetae in the mid-body: curved and unidentate or obliquely truncate; and a proventricle that is yellow or red. This re-description conforms to the original description in the shape of the midbody chaetae but differs in the length of the dorsal cirri, pigmentation and fusion of palps (Fauvel 1923). Day (1967) describes *S. amica* as being long with stout dorsal cirri that are subequal to body width, having short chaetae that are either unidentate or minutely bidentate, and having pseudosimple chaetae with an obliquely truncate shaft head. This description corresponds with that of Fauvel (1923), but Day (1967) does not mention fusion of the palps, the pharyngeal tooth or pigmentation. Lee and Rho (1992) described specimens from Japan as whitish yellow with palps that are fused at the base, having a red pharynx with a large anterior tooth, long dorsal cirri, bidentate compound chaetae that become shorter and thicker in midbody region and pseudosimple chaetae that are twice as wide as compound chaetae and with a blunt sharp tip. This re-description of *S. amica* is most similar to Fauvel (1923). Specimens examined by Licher (1999) from the South Atlantic (West Africa, South Africa (Simonstown)), the North Atlantic (Gulf of Saint Malo) and the

Aegean Sea are long, with large palps, long dorsal cirri that are distinctly jointed, bidentate or minutely bidentate chaetae that are curved and twice as thick in the midbody than anterior region, and pseudosimple chaetae that are distally oblique. This description fits well with that of Quatrefages (1866). This again, suggests at least two morphologically different groups for *S. amica* with descriptions by Fauvel (1923), Day (1967) and Lee and Rho (1992) forming one group and descriptions by Quatrefages (1866) and Licher (1999) forming another. Its widespread distribution throughout the North Atlantic and Mediterranean Sea, with South Africa as its only locality in the Southern Hemisphere (see Appendix 1), again suggests that further investigation will reveal a number of new species belonging to this species complex.

Despite the similarity between these three species, specimens of *S. cf. amica* and *S. cf. armillaris* previously collected in South Africa, including specimens recorded by Day (1967), were not examined when describing *S. amicarmillaris* (see Simon et al. 2014). Given that several apparently cosmopolitan species recorded locally in Day (1967) have proved to be indigenous species (e.g., *Marphysa elityeni* Lewis and Karageorgopolous 2008, *Magelona debeeri* Clarke, Paterson, Florence & Gibbons 2010, *Pseudopolydora eriyali* Simon, Sato-Okoshi and Abe 2017 and *Pseudopolydora uphondo* Simon, Sato-Ojoshi and Abe 2017), it is possible that *S. cf. amica* and or *S. cf. armillaris* recorded locally may actually be the species described as *S. amicarmillaris*. Alternatively, *S. amica* and *S. armillaris* from South Africa could represent previously undescribed native species. Finally, if the South African *S. cf. amica* and *S. cf. armillaris* does not correspond with *S. amicarmillaris*, but instead match the descriptions of these species from their type localities, they may represent two alien species in South Africa.

To resolve this issue, *S. cf. amica* and *S. cf. armillaris* from South Africa need to be examined and compared with specimens from their respective type regions and with *S. amicarmillaris*. Preferably comparisons such as these should be made using genetic analysis but this may be difficult if comparisons rely on specimens from museum collections. The extraction and amplification of DNA from especially soft-bodied organisms that have been fixed in formalin and stored in ethanol for long periods is difficult; even if it is possible, the results may not be very reliable (Wandeler et al. 2007). Thus, to disentangle potential species complexes, detailed morphological examinations need to be conducted. By re-describing species, diagnostic features are highlighted allowing further comparisons, and being useful as a basis for eventual investigations into the complex and the geographic range of the involved species (Lopez et al. 2001). For species that appear very similar, qualitative descriptions may prove insufficient in detecting differences. In such instances, an alternative way of isolating diagnostic characteristics and ultimately improving our understanding of the distinction between species is through morphometric analyses that take a quantitative approach, comparing the size and shapes of characters or features statistically (Rohlf 1990, Rouse and Pleijel 2001, Garraffoni and Camargo 2006, Costa-Paiva and Paiva 2007, Martin et al. 2017). Principal Component and Discriminant Function analyses can then be used to reduce the number of variables from the original, usually very large, dataset to a smaller set of variables that can then be used to group similar individuals (Clarke and Warwick 2001, Landau and Everitt 2004, Martin et al. 2017). This allows taxonomists to judge whether particular features are different enough to establish them as diagnostic and essentially use them as a basis for further investigations into phylogenetic relationships (Bookstein 1982, Garraffoni and Camargo 2006). This approach has been used to successfully unravel at least one species complex within Syllidae; Martin et al. (2003) and

Lattig et al. (2007) used morphometrics to disambiguate part of the *H. spongicola* complex. They identified chaetal characters, main fang length, proventricle length, number of articles on dorsal cirri and number of articles on antennae as distinguishing factors (Lattig et al. 2007). Populations from Florida and Jamaica, Puerto Rico and the Bahamas, Mexico and Easter Island, Taiwan, Sumatra and Vietnam each formed separate groups, representing distinct species (Martin et al. 2003, Lattig et al. 2007).

- ♣ The main aim of this study is therefore to use morphometric analyses to determine whether the individuals reported as *Syllis* cf. *amica* and *Syllis* cf. *armillaris* from South Africa really belong to these species or correspond to *Syllis amicarmillaris* .
 - I will therefore compare the specimens of *Syllis* cf. *amica* and *Syllis* cf. *armillaris* from South Africa with the European conspecifics.
 - If they differ, I will compare them with *Syllis amicarmillaris* to disambiguate their characteristic morphological traits.
 - If they do not differ, the analysis will establish which features allow them to be morphologically distinguished from *S. amicarmillaris*
 - If these species differ from the European conspecifics and, *S. amicarmillaris*, then they are most likely new indigenous species.

4.2 Methods and Materials

4.2.1 Morphometric Analysis

A total of 46 length and width measurements (Table 4.1, Fig. 4.1) of the body, antennae, cirri and chaetae (Martin et al. 2003, Lattig et al. 2007) were taken for 55 specimens; 21 of *S. cf. armillaris*, 19 of *S. cf. amica*, 10 of *S. amicarmillaris*. Five individuals of *S. cf. gracilis* were included as a control (Table 4.2). All individuals measured were complete specimens selected at random. Several photos of each specimen were taken using a dissecting microscope (Leica MZ75) or at 40 x magnifications using a Leica DM 1000 compound microscope with a Leica EC3 camera attached to either microscope. Software associated with the camera attached to the microscope, Leica LAS EZ V1.5.0, was used then to measure the appropriate features on each photo. Counts of the number of articles of dorsal and tentacular cirri, and median and lateral antennae were made by examining specimens at 40 x magnifications (Table 4.1). Categorical data for the presence (or absence) of pseudosimple chaetae and the shape of ventral posterior chaetae were collected by examining specimens at 40x magnification (Table 4.1). Individuals lacking a given character due to mechanical breakage or an incomplete feature were omitted from the analysis for that character only. These measurements made up a data set that was used for the multi-variate analyses.

The Principal Component Analysis was run in SPSS version 24 on a standardized matrix i.e., the correlation matrix, using varimax rotation to decrease the number of variables characterizing *S. amica*, *S. armillaris*, *S. amicarmillaris* and *S. gracilis* and determine which, if any, of the measured variables may be used to distinguish these four species from one another. The species were numbered from 1 – 8: *S. amica* (Namibia, Saldanha Bay, False Bay), *S. armillaris* (Namibia, False Bay) and *S. gracilis* (Namibia, Hawai'i) from the Iziko Southern African Museum numbered 1 – 3, respectively; *S. amica* (South Bay of Biscay, France), *S. armillaris* (Galicia, Spain) and *S. armillaris* (Norway) numbered 4 – 6, respectively; and fresh specimens of *S. amica* collected from the south coast of South Africa (Danger Point, Mossel Bay) and *S. amicarmillaris* (Danger Point, Mossel Bay) numbered 7 – 8, respectively. Individuals from the Museo Nacional de Ciencias Naturales in Madrid (Spain) were coded as MNCN, although the single individual from Norway was coded NW; individuals from the Iziko Southern African Museum were coded IZIKO and fresh specimens collected from the south coast of South Africa were coded SC.

Sixteen components with an eigenvalue > 1 were extracted, accounting for 80.08% of the variance. According to Landau and Everitt (2004), individual components that account for less than an overall average of 5% variance of extracted components are negligible; thus only the first five components were considered when determining which characters contributed the most to species separation. The characters selected from the rotated component matrix were those that had a weighting of 0.4 or higher within each of the five components (Landau and Everitt 2004). The regressional scores for these components were run through a Discriminant Function Analysis which is a predictor model that derives a set of rules or parameters that group individuals together based on a set of *a priori* defined groups. This determines whether any of the individuals group together based on the reduced set of variables and how well they fit into these predefined groups. This distinction between each species was graphically represented by a canonical analysis and in the form of a

table The more similar the individuals are, the closer they are placed on the graph. *A priori* groups were assigned a percentage (or number value out of the total number of individuals) that fit the parameters of the group and their suggested re-assignment (or predicted group membership) if they did not fall within the parameters of the predefined group.

Those characters with high loadings (>0.4) in the PCA were compared between *S. armillaris* Iziko and *S. amicarmillaris* to test for any significant differences. Using XLSTAT in Microsoft Excel, the data were tested for normality. The characters for which the data had a normal distribution, a Students t-test was performed and, when data did not have a normal distribution, a Mann-Whitney test of significance was performed. For categorical data, contingency tables were constructed and a Chi² test performed.

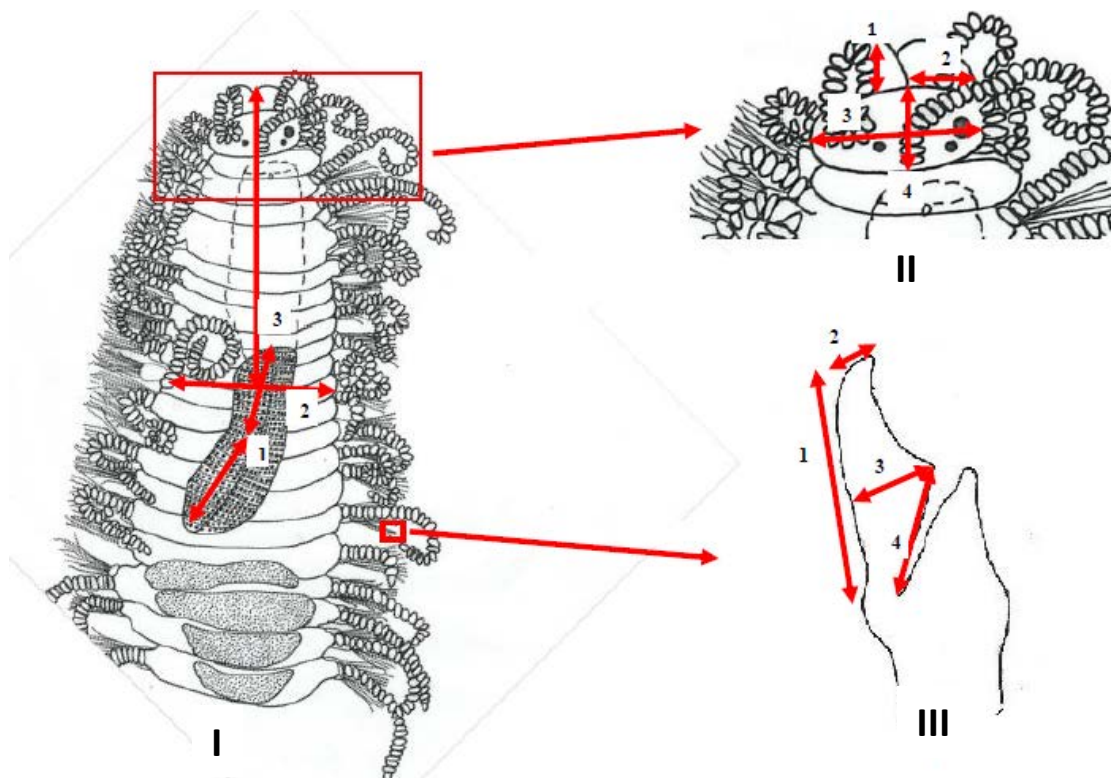


Figure 4.1 Morphological features measured of the (I) anterior end, (II) prostomium and palps and, (III) chaetae for *Syllis amica*, *Syllis armillaris*, *Syllis amicarmillaris* and *Syllis gracilis* from South Africa and Europe. Labels for figure are explained in Table 4.1 below.

Table 4.1 Characters used for the morphometric analysis of *Syllis amica*, *Syllis armillaris* and *Syllis amicarmillaris* from the Iziko South African Museum, Museo Nacional de Ciencias Naturales in Madrid (Spain) and fresh specimens collected from the South coast of South Africa.

Character number	Measurements	
Soft tissue		
1	Length from palps to chaetiger 10 (mm)	(Fig. 4.1 I 3)
2	Width at chaetiger 10 (mm)	(Fig. 4.1 I 2)
3	Length of proventricle (mm)	(Fig. 4.1 I 1)
4	Length of palps (\bar{x} ; mm)	(Fig. 4.1 II 1)
5	Width of palps at base (\bar{x} ; mm)	(Fig. 4.1 II 2)
6	Length of prostomium (mm)	(Fig. 4.1 II 4)
7	Width of prostomium (mm)	(Fig. 4.1 II 3)
41	Length of median antennae (\bar{x} no. of articles)	
42	Length of lateral antennae (\bar{x} no. of articles)	
43	Length of dorsal tentacular cirri (\bar{x} no. of articles)	
44-45	Length of dorsal cirri on chaetiger 1-10 (\bar{x} no. of articles; max/min)	
Anterior, Mid-body and Posterior chaetae (mm)		
8-13	Length of chaetae (max/min)	(Fig. 4.1 III 1)
14-19	Length of primary tooth on compound chaetae (max/min)	(Fig. 4.1 III 2)
20-25	Length of secondary tooth on compound chaetae (max/min)	
26-31	Width of chaetiger at base 1 (max/min)	(Fig. 4.1 III 4)
32-37	Width of chaetiger at base 2 (max/min)	(Fig. 4.1 III 3)
Categorical data		
38	Simple chaetae	0=absent; 1=sub-triangular; 2=y-shaped
39	Shape of posterior ventral simple spines	0= absent ; 1=s-shaped; 2=straight; 3= gently curved
40	No. of teeth on posterior ventral simple spines	0=none; 1=unidentate; 2=bidentate

Table 4.2 Number of individuals for *Syllis amica*, *Syllis armillaris* and *Syllis amicarmillaris* used from the Natural history museums in South Africa (Iziko) and Museo Nacional de Ciencias Naturales (MNCN) in Madrid (Spain) that holds *S. armillaris* from Norway (NW) and the fresh specimens collected from the south coast of South Africa (SC).

<i>Syllis amica</i>						
Collection	Locality	No. individuals	Of	Date collection	of	Accession Number
Iziko	False Bay, South Africa	2		29/09/1954		A20799
	Saldanha Bay, South Africa	3		17/02/1969		Unknown
	Namibia	1		21/02/2001		A21512
MNCN	South Bay of Biscay, France	10		07/2009		16.01/6974
SC	Danger Point, South Africa	2		09/2015		
	Mossel Bay, South Africa	1		10/2015		
<i>Syllis armillaris</i>						
Collection	Locality	No. individuals	Of	Date collection	of	Accession Number
Iziko	False Bay, South Africa	7		Unknown		A20176
	Mowe Bay, Namibia	2		01/06/1969		A20175
	Kunene, Namibia	1		Unknown		A20176
MNCN	Galicia, Spain	10		06/09/1987		16.01/14085
	Altafjord, Norway	1		11/06/2005		16.01/1123
<i>Syllis amicarmillaris</i>						
Collection	Locality	No. individuals	Of	Date collection	of	Accession Number
SC	Danger Point, South Africa	5		09/2015		
	Mossel Bay, South Africa	5		10/2015		
<i>Syllis gracilis</i>						
Collection	Locality	No. individuals	Of	Date collection	of	Accession Number
Iziko	Kunene, Namibia	2		Unknown		A20090
	Luderitz, Namibia	2		16/11/1969		A20149
	Honolulu, Hawai'i	1		09/11/1968		A20091

Chapter 4: Results

4.3.2 A morphometric analysis of *Syllis armillaris*, *Syllis amica* and *Syllis amicarmillaris* from southern Africa and Europe

Bartlett's test of sphericity was significant ($r=1608.076$; $p<0.001$), indicating that a factor analysis is appropriate and that the sample was chosen at random. However, the KMO measure of sampling adequacy is less than 0.6 ($p= 0.283$) indicating that the data sample size might have been too small and that results should be interpreted cautiously. Based on 46 variables, the Principal Component Analysis isolated 16 components that have eigenvalues >1 that together accounted for 80.08 % of the total variability. The first five components account for just 11.54%, 11.19%, 7.59%, 6.88% and 5.47%, respectively (42.66% total). The remaining components each accounted for less than 5% of the variation with the minimum value being 0.011%. Five characters on the first component, four on the second, three on the third, four on the fourth and three on the fifth were selected for the analyses (Table 4.3). The soft tissue characters i.e., palp and prostomium length and width, load strongly on component one but more robust features such as length of secondary tooth on midbody chaetae, number of articles on dorsal cirri and antennae are the primary variables loading strongly onto components one and two that discriminate between species.

In the Discriminant Function Analysis, the first function coefficient accounted for 49 % of the variance between each of the assigned groups (*S. amica* Iziko, *S. armillaris* Iziko, *S. gracilis* Iziko, *S. amica* MNCN, *S. armillaris* MNCN, *S. armillaris* NW, *S. amica* SC, *S. amicarmillaris* SC) and the second 30.3%, together accounting for 79.3% of the variation. Furthermore, Wilks Lambda revealed that the group means, and consequently the individual species groups, were all significantly different from one another ($p < 0.001$). However, visualization on a canonical discriminant function analysis based on these two functions suggests five separate clusters (Fig. 4.2). Cluster 1 comprises only *S. gracilis*, the control, which grouped separately from the remaining clusters (Fig. 4.2), confirming that the characters chosen for the analysis are strong enough to separate individuals into their respective groups.

Table 4.3 Characters selected from the Principal Component Analysis (PCA) that had a weighting of 0.4 or higher in the first five components extracted by the analysis.

Measured characters	PC1	PC2	PC3	PC4	PC5
Length of palps (mm)	0.84 4	-	-	-	-
Palp width at base (mm)	0.86 1	-	-	-	-
Length of prostomium (mm)	0.83 0	-	-	-	-
Width of prostomium (mm)	0.84 7	-	-	-	-
Length of the secondary tooth on midbody chaetae (mm)	0.44 3	-	-	-	-
Number of articles on median antennae (\bar{x})	-	0.83 5	-	-	-
Number of articles on lateral antennae (\bar{x})	-	0.76 2	-	-	-
Number of articles on short dorsal cirri (\bar{x})	-	0.84 6	-	-	-
Number of articles on long dorsal cirri (\bar{x})	-	0.73 8	-	-	-
Length of inferior chaetae on midbody (mm)	-	-	0.55 2	-	-
Shape of posterior ventral spines	-	-	0.88 0	-	-
Number of teeth on ventral posterior spines	-	-	0.84 6	-	-
Length from palps to chaetiger 10 (mm)	-	-	-	0.62 9	-
Width of worm at chaetiger 10 (mm)	-	-	-	0.83 4	-
Length of proventricle (mm)	-	-	-	0.83 3	-
Width of anterior chaetae at base 1 (mm)	-	-	-	0.40 0	-
Length of anterior inferior chaetae (mm)	-	-	-	-	0.84 0
Width of posterior chaetae at base 1 (mm)	-	-	-	-	0.86 2
Presence (or absence) and shape of pseudosimple chaetae	-	-	-	-	0.40 0

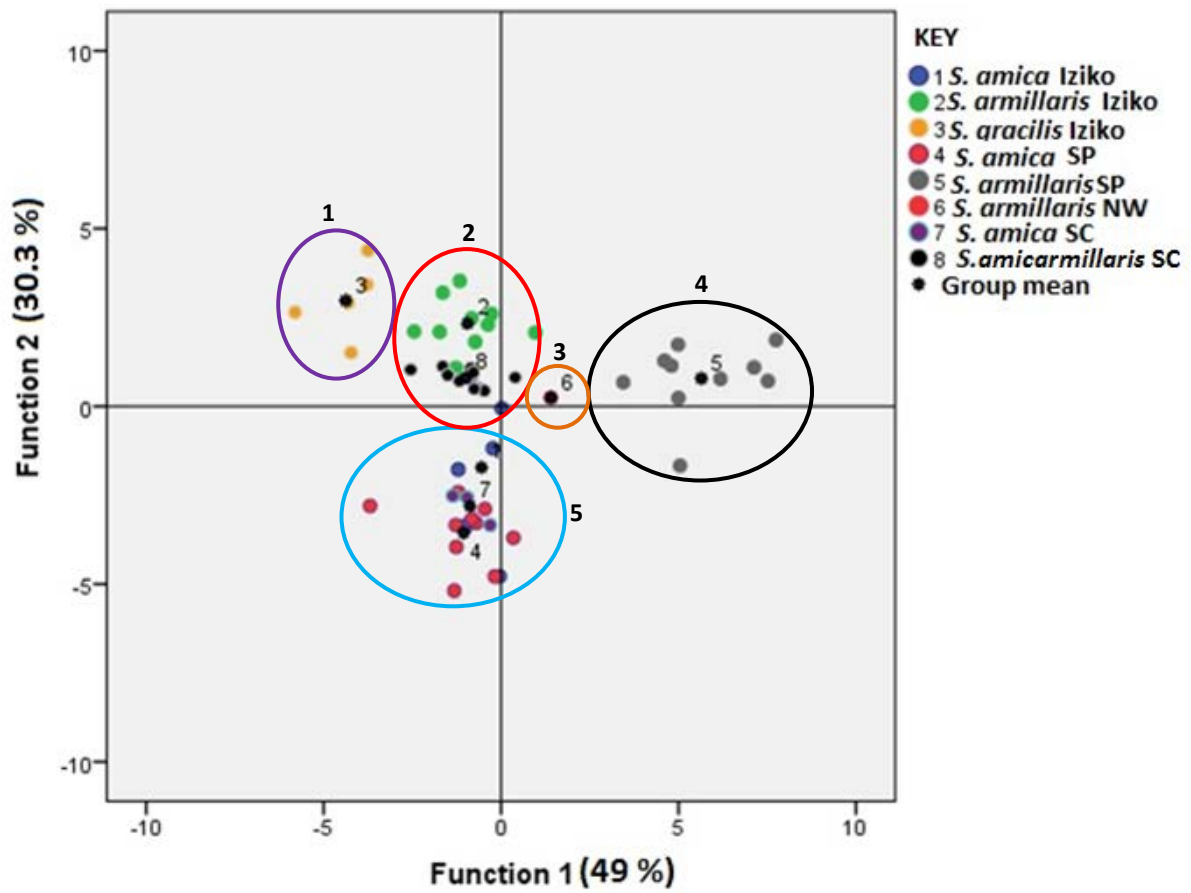


Figure 4.2 Canonical discriminant function displaying five distinct groups of individuals with *Syllis gracilis* Iziko forming cluster 1 (purple), *Syllis armillaris* and *Syllis amicarmillaris* in cluster 2 (red), *Syllis armillaris* from Norway in cluster three (orange), *Syllis armillaris* from Spain in cluster four (black) and, *Syllis amica* from Spain, Iziko and the South Coast of South Africa form cluster five (blue).

4.3.2.1 Are *Syllis cf. armillaris* and *Syllis cf. amica* from South Africa the same as European conspecifics?

Syllis cf. armillaris

Syllis cf. armillaris Iziko is grouped separately from European conspecifics; where *S. cf. armillaris* Iziko forms part of cluster 2, *S. armillaris* MNCN forms cluster 4 and *S. armillaris* NW forms cluster 3 (Fig. 4.2). This provides strong evidence that European conspecifics are different from the specimens from South Africa. Considering the characters that may separate these groups, *S. cf. armillaris* Iziko differs from specimens from Spain most obviously in having; one or two pseudosimple chaetae on anterior to midbody parapodia, broadly triangular palps that are shorter than in European specimens, shorter dorsal cirri, fewer anterior chaetae per parapodium, a longer pharynx and proventricle and they are shorter with fewer chaetigers (Table 4.4, Appendix Table 1). *S. armillaris* MNCN is characterized by narrow, long palps, a wide, long prostomium, a long, distinct secondary tooth on all chaetae, and longer, narrower chaetal blades on falcigers than specimens from South Africa (Table 4.4). The single individual of *S. armillaris* from Norway grouped separately from *S. armillaris* from Spain and South Africa, forming cluster 3 (Fig. 4.2). The specimen from Norway has a shorter palp length, prostomium width and length and, length from the palps to chaetiger 10 (Table 4.4, Appendix Table 1). The proventricle of this specimen is also approximately half the size of specimens from Spain and chaetae have no secondary tooth. Median and lateral antennae are also longer but dorsal cirri are shorter than the specimens from Spain (Table 4.4). According to the predicted group membership individuals of *S. armillaris* Iziko and NW have all been correctly classified (100%) whereas 90% of *S. armillaris* MNCN are correctly classified and 10% (1 individual) was re-assigned to *S. amica* SC. Despite the re-classification of one individual, morphological comparisons and the DFA (and predicted group membership) strongly suggest that *S. armillaris* from South Africa, Spain and Norway are separate species (Table 4.5).

Syllis cf. amica

Specimens of *S. cf. amica* from Europe and South Africa (south and west coast) show a high degree of overlap, together forming cluster 5. There are several characters that make individuals belonging to each of these groups of *S. amica* similar. These similarities can be observed in the maximum values for each character measurement whereas the ranges for these measurements are wide and varied. For example, the width of individuals at chaetiger 10 is similar in all groups; Iziko (0.016 – 5.5 mm), MNCN (2.6 – 5.77 mm) and SC (4.1 – 5.68 mm); no. of articles on lateral antennae; Iziko (21 – 27), MNCN (12 – 25), SC (12 – 21); and length of dorsal cirri; Iziko (19 – 43), MNCN (21 – 41), SC (35 – 40). Similarly, the differences between these groups could also be seen in the maximum measurements for each character with ranges that are wide-ranging, especially in preserved specimens. The lengths of the palps are longest, and with the largest range, in the preserved specimens; Iziko (0.012 – 1.86 mm) and MNCN (0.009 – 1.74 mm) specimens and,

smallest in the fresh samples of *S. amica* SC (0.85 – 1.75 mm); palp widths differ, are longest and have the largest range in Iziko specimens (0.012 – 1.73 mm) and are similar in MNCN (0.01 – 1.49 mm) specimens and fresh specimens of *S. amica* SC (1.01 – 1.47 mm) (Table 4.4). Prostomium widths are different in all three groups; widest in *S. amica* MNCN (0.8 – 3.21 mm), half of this in Iziko specimens (0.02 – 1.62 mm) and narrowest in SC specimens (0.97 – 1.19 mm). Lengths from palps to chaetiger 10 are longest in *S. amica* Iziko (0.05 – 13.1 mm) then MNCN (7.2 – 12.1 mm) and SC (8.95 – 10.4 mm). Midbody chaetae of *S. amica* Iziko have a distinct secondary tooth whereas those of the other groups are unidentate (Table 4.4). The DFA shows that the characters that distinguish between species could classify only 50% (three individuals) of *S. amica* Iziko from the west coast of southern Africa correctly, while one specimen each overlap with *S. amica* MNCN (South Bay of Biscay) and *S. armillaris* MNCN (Galicia), respectively, and even with *S. armillaris* Iziko (Table 4.5). None of the individuals belonging to the three *S. amica* groups overlap with *S. amicarmillaris* thereby confirming that they are distinct species. Several of the soft tissue characters overlap among the three *S. amica* groups making it difficult to separate them.

4.3.2.2 Are *Syllis* cf. *armillaris* from South Africa and *Syllis amicarmillaris* similar?

Cluster 2 groups *S. cf. armillaris* from South Africa and *S. amicarmillaris* together closely, with one individual of *S. cf. armillaris* overlapping with *S. amicarmillaris* (Fig. 4.2). *S. cf. armillaris* from South Africa and *S. amicarmillaris* are grouped together mostly along Function 1 (Fig. 4.2). *S. amicarmillaris* and *S. cf. armillaris* Iziko both have pseudosimple chaetae that are sub-triangular and s-shaped ventral posterior chaetae that are bidentate in *S. amicarmillaris* and unidentate in *S. cf. armillaris*. The two groups separate on Function 2 (Fig. 4.2). To explore the characters that might be driving the separation of these species, the characters identified by the PCA analysis as contributing to the variability among species were compared using pairwise comparisons. The presence or absence of the pseudosimple chaetae was not included in the analysis as all individuals examined, possessed pseudosimple chaetae. A t-test showed that the length of the proventricle ($t=-2.171$, $p<0.05$) and palps ($t=-2.11$, $p<0.05$) were significantly different between *S. cf. armillaris* Iziko and *S. amicarmillaris*. This can be seen in *S. cf. armillaris* Iziko having 20 % fewer muscle rows on the proventricle with a shorter and smaller range (Table 4.4.); *S. amicarmillaris* (7.6 – 19.8 mm) and *S. cf. armillaris* (5.81 – 17.1 mm). The length of the palps is larger in *S. amicarmillaris* (0.7 – 2.01 mm) than in *S. cf. armillaris* (0.6 – 1.7). A Mann-Whitney U test revealed the prostomium length ($U=23.5$, $p<0.05$) and the width of posterior chaetae at base 1 measurement ($U=77$, $p<0.05$) to be significantly different between the two species. The length of the prostomium is similar in both species; *S. amicarmillaris* (2.07 – 3.3mm) and *S. cf. armillaris* (1.4 – 3.22 mm) but width of posterior chaetae is larger in *S. amicarmillaris* (0.00593 – 0.0121) than *S. cf. armillaris* (0.0072 – 0.0107). However, although these characters are significantly different between the species groups, they are only just so, with p-values that range from 0.043 – 0.049 (Appendix, Table 2). There were no significant differences between the two species for any of the remaining 12 characters (Appendix Table 2).

According to the predicted group membership all individuals belonging to *S. cf. armillaris* and *S. amicarmillaris*, respectively, had been grouped correctly (100%) despite the single overlapping individual

(Fig. 4.2). This indicates that although *S. armillaris* and *S. amicarmillaris* closely resemble each other, the analysis could not confirm that they are a single species. However, three of the four features that make *S. cf. armillaris* different from *S. amicarmillaris* are predominantly soft tissue characters; length of the proventricle, palps and prostomium, and one chaetal characteristic, the width of posterior chaetae. The results of the pairwise comparison present weak evidence for differences between characters belonging to these two species. Further, the morphological similarities between *S. cf. amica* and *S. amicarmillaris* far outweigh the difference between them. This therefore means that the South African *S. cf. armillaris* may actually be the recently described *S. amicarmillaris*.

Table 4.4 Mean \pm Standard deviation (min–max) of measured morphological characters with high loadings (>0.4) in Principal Component Analysis for *Syllis amica*, *Syllis armillaris*, *Syllis amicarmillaris* and *Syllis gracilis* from the Iziko Southern African Museum (Iziko), Museo Nacional de Ciencias Naturales (MNCN) in Madrid (Spain) which includes the single specimen from Norway (NW) and, fresh specimens collected from the South Coast of South Africa (SC).

Measured characters	<i>Syllis amicarmillaris</i>	<i>Syllis armillaris</i>			<i>Syllis amica</i>			<i>Syllis gracilis</i>
	SC	Iziko	MNCN	NW	Iziko	MNCN	SC	Iziko
Average palp length (mm)	1.4705 \pm 0.4057 (0.748 - 2.015)	1.086 \pm 0.407 (0.60 - 1.69)	1.738 \pm 1.22 (0.009 - 4.435)	1.54	1.23 \pm 0.66 (0.012 - 1.86)	1.134 \pm 0.626 (0.0085 - 1.745)	1.39 \pm 0.48 (0.85 - 1.75)	1.15 \pm 0.71 (0.013 - 1.76)
Average palp width (mm)	1.277 \pm 0.476 (0.142 - 1.8)	0.965 \pm 0.347 (0.6045 - 1.535)	1.705 \pm 1.01 (0.0724 - 4.115)	1.715	1.03 \pm 0.624 (0.0125 - 1.735)	0.936 \pm 0.516 (0.01 - 1.49)	1.29 \pm 0.24 (1.015 - 1.47)	1.87 \pm 1.76 (0.012 - 4.77)
Prostomium length (mm)	2.81 \pm 0.421 (2.07 - 3.3)	2.117 \pm 0.706 (1.44 - 3.22)	3.637 \pm 1.745 (2.11 - 8.34)	3.18	1.93 \pm 1.045 (0.023 - 3.14)	2.01 \pm 0.502 (0.8 - 2.49)	2.75 \pm 0.53 (2.26 - 3.31)	2.23 \pm 1.36 (0.025 - 3.49)
Prostomium width (mm)	1.25 \pm 0.233 (0.979 - 1.7)	1.129 \pm 0.483 (0.382 - 1.73)	1.927 \pm 1.166 (0.598 - 4.93)	1.42	0.88 \pm 0.62 (0.02 - 1.62)	1.43 \pm 0.73 (0.8 - 3.21)	1.11 \pm 0.12 (0.97 - 1.19)	1.63 \pm 1.54 (0.012 - 4.18)
Length from palps to chaetiger 10 (mm)	11.463 \pm 2.87 (8.26 - 15.9)	10.125 \pm 3.39 (6.54 - 16.8)	13.283 \pm 3.27 (6.39 - 16.82)	10.7	9.3 \pm 4.97 (0.048 - 13.15)	9.116 \pm 1.45 (7.2 - 12.1)	9.6 \pm 0.73 (8.95 - 10.4)	10.84 \pm 1.66 (8.93 - 12.7)
Width at chaetiger 10 (mm)	5.52 \pm 1.21 (3.86 - 7.1)	4.29 \pm 1.495 (2.79 - 7.33)	5.01 \pm 1.37 (1.96 - 6.47)	4.97	3.56 \pm 2.03 (0.016 - 5.5)	3.88 \pm 0.84 (2.6 - 5.77)	5.14 \pm 0.9 (4.1 - 5.68)	4.98 \pm 1.22 (3.83 - 6.49)
Length of proventricle (mm)	13.787 \pm 4.64 (7.56 - 19.8)	9.536 \pm 4.094 (5.81 - 17.1)	10.22 \pm 4.45 (1.4 - 15.7)	5.95	6.68 \pm 4.06 (0.05 - 12.8)	7.62 \pm 1.65 (5.18 - 10.1)	5.43 \pm 0.98 (4.63 - 6.52)	12.14 \pm 3.34 (7.89 - 16.52)
Length of inferior anterior chaetae (mm)	0.00577 \pm 0.00290 (0.00147 - 0.0106)	0.00664 \pm 0.003 (0.00122 - 0.0108)	0.004026 \pm 0.00225 (0.00145 - 0.0072)	0.00278	0.0076 \pm 0.0026 (0.0036 - 0.011)	0.0035 \pm 0.0023 (0.001 - 0.0078)	0.006 \pm 0.001 (0.0051 - 0.0064)	0.0122 \pm 0.0164 (0.00233 - 0.413)

Length of anterior chaetae at base 1* measurement (mm)	0.00336 ± 0.00058 (0.00251 - 0.00415)	0.00307 ± 0.000542 (0.00234 - 0.00378)	0.00251 ± 0.0009 (0.0004 - 0.0034)	0.00294	0.0036 ± 0.0013 (0.0025 - 0.0061)	0.0028 ± 0.001 (0.002 - 0.004)	0.00326 ± 0.001 (0.0028 - 0.0042)	0.003 ± 0.0005 (0.0026 - 0.0039)
Length of inferior midbody chaetae (mm)	0.00964 ± 0.00404 (0.00239 - 0.014)	0.00741 ± 0.00432 (0.00126 - 0.0119)	0.0039 ± 0.0038 (0.00158 - 0.011)	0.00374	0.0061 ± 0.0042 (0.00136 - 0.0112)	0.005 ± 0.002 (0.0024 - 0.009)	0.0088 ± 0.0026 (0.0058 - 0.0105)	0.012 ± 0.0018 (0.0094 - 0.014)
Length of secondary tooth on midbody chaetae (mm)	0.00165 ± 0.00066 (0.00118 - 0.00212)	0.00136 ± 0.000254 (0.000936 - 0.00166)	0.0054 ± 0.00527 (0.00124 - 0.0144)	No secondary tooth	0.00147**	No secondary tooth	No secondary tooth	0.0016 ± 0.00016 (0.00144 - 0.00176)
Length of posterior chaetae at base 1 measurement (mm)	0.00756 ± 0.00197 (0.00593 - 0.0121)	0.0083 ± 0.001 (0.0072 - 0.0107)	0.008 ± 0.003 (0.00086 - 0.012)	0.00768	0.0077 ± 0.0024 (0.0052 - 0.012)	0.006 ± 0.001 (0.0045 - 0.008)	0.007 ± 0.001 (0.006 - 0.0082)	0.03 ± 0.032 (0.065 - 0.071)
Presence and shape of pseudosimple chaetae	Sub-triangular	Sub-triangular	None	None	Obliquely truncate	Obliquely truncate	Obliquely truncate	Y-shaped
Shape of ventral posterior spines	S-shaped	Straight/ Gently curved/ S-shaped	Straight/Gently curved/ S-shaped	Gently curved	Gently curved	Straight/ Gently curved	Gently curved	Gently curved/ S-shaped
Number of teeth on ventral posterior chaetae	Bidentate	None/ Unidentate	None/Unidentate/Bidentate	Bidentate	Unidentate	Unidentate	Unidentate	Bidentate
Median antennae (no. of articles)	14.1 ± 3.755 (7 - 18)	11.3 ± 6.67 (7 - 18)	13.3 ± 5.67 (11 - 21)	17	16.83 ± 14.61 (19 - 37)	12.3 ± 11.24 (11 - 25)	28.67 ± 8.08 (20 - 36)	10.4 ± 6.58 (10 - 17)
Lateral antennae (no. of	12.8 ± 2.6	11.05 ± 4.23	12.15 ± 1.6	14	11.75 ± 13.02	(14.05 ± 6.01)	17.67 ± 4.93	9.8 ± 5.73

articles)	(9 - 15.5)	(9.5 - 15)	(10 - 15.5)		(21 - 27)	(12 - 25)	(12 - 21)	(10 - 15)
Dorsal cirri (min) (no. of articles)	10.3 ± 2.58 (4 - 13)	11.1 ± 3.66 (7 - 19)	11.1 ± 2.33 (10 - 15)	9	10.5 ± 7.01 (21 - 27)	12.8 ± 2.44 (8 - 16)	16 ± 4.58 (12 - 21)	8.8 ± 1.64 (7 - 11)
Dorsal cirri (max) (no. of articles)	20.1 ± 4.5 (11 - 28)	21 ± 3.26 (17 - 28)	24.6 ± 3.2 (20 - 30)	22	28.5 ± 16.22 (19 - 43)	30.5 ± 5.27 (21 - 41)	37.3 ± 2.52 (35 - 40)	19 ± 2 (17 - 22)

*Please refer to Figure 4.1

Table 4.5 Predicted group membership (%) for individuals belonging to *Syllis amica*, *Syllis armillaris*, *Syllis amicarmillaris* and *Syllis gracilis* from the Iziko South African Museum (Iziko), Museo Nacional de Ciencias Naturales (MNCN) in Madrid (Spain), Norway (NW) and the South coast of South Africa (SC).

	<i>S. amica</i> Iziko	<i>S. armillaris</i> Iziko	<i>S. gracilis</i> Iziko	<i>S. armillaris</i> MNCN	<i>S. amica</i> MNCN	<i>S. armillaris</i> NW	<i>S. amica</i> SC	<i>S. armillaris</i> SC
<i>S. amica</i> Iziko	50	16.7	0	16.7	0	0	16.7	0
<i>S. armillaris</i> Iziko	0	100	0	0	0	0	0	0
<i>S. gracilis</i> Iziko	0	0	100	0	0	0	0	0
<i>S. armillaris</i> MNCN	0	0	0	90	0	0	10	0
<i>S. amica</i> MNCN	0	0	0	0	100	0	0	0
<i>S. armillaris</i> NW	0	0	0	0	0	100	0	0
<i>S. amica</i> SC	0	0	0	0	0	0	100	0
<i>S. amicarmillaris</i>	0	0	0	0	0	0	0	100

4.4 Discussion

The morphometric analysis confirmed that the populations of *S. cf. armillaris* from South Africa and Europe correspond to distinct species thereby proving that another apparently cosmopolitan species has been incorrectly identified here. However, the evidence supporting a separation between the South African specimens *S. cf. armillaris* and *S. amicarmillaris* is very weak. By contrast, the morphometric analysis clearly separates the South African *S. cf. amica* from *S. amicarmillaris* confirming they are different species. *Syllis cf. amica* closely resembles specimens of *S. amica* from Europe, with a large amount of overlap. Further morphological, and possibly genetic, examination is required to determine whether they are actually different species.

Syllis amica, *S. armillaris* from South Africa and *S. amicarmillaris* are similar in body plan and chaetal characteristics. The most obvious character shared between them being the presence of one or two broad pseudosimple chaetae. These pseudosimple chaetae are absent in Day's (1967) description of *S. armillaris* and in the description of the European species by Fauvel (1923). While latter seems accurate, the former was most likely a mistake. Other similarities between these three species include the width of the anterior and posterior chaetae. The differences between *S. amica*, and *S. armillaris* and *S. amicarmillaris* are greater and more evident than between the latter two species. The shape of the palps, prostomium, number of articles in antennae and dorsal cirri are the features that drive the separation of *S. amica* from *S. armillaris* and *S. amicarmillaris* from South Africa. Number of articles in median and lateral antennae and dorsal cirri of *S. amica* are almost twice as long as the short, fusiform antennae and dorsal cirri of *S. armillaris* and *S. amicarmillaris* (Table 4.4). The shape of the palps are ovoid and rounded in *S. amica* and may sometimes have a narrow base whereas the palps in *S. armillaris* and *S. amicarmillaris* are triangular and short, often with a wide base. The prostomium in *S. amica* is often sub-pentagonal whereas it is ovoid in *S. armillaris* and *S. amicarmillaris*. From this, it is clear that *S. amica* is a separate species from *S. armillaris* and *S. amicarmillaris*. The separation between *S. armillaris* and *S. amicarmillaris* is less clear. Other than the aforementioned similarities, *S. armillaris* and *S. amicarmillaris* also have midbody chaetae that are similar in length and anterior chaetae that are similar in width. This is reflected in the proximity of these species and the single overlapping individual displayed on the graphical presentation on the DFA, suggesting that these individuals may actually belong to the same species. However, the predicted group membership provides contrasting results and shows that individuals have been correctly assigned, suggesting that *S. armillaris* and *S. amicarmillaris* are separate species. Furthermore, four (length of proventricle, length of palps, length of prostomium, width of posterior chaetae) of the 16 characters highlighted by the PCA were weakly significantly different between these two species groups. Three of these characters are soft tissue (length of the proventricle, length of palps, length of prostomium) with at least one of these characters (length of proventricle) considered a distinguishing character. However, all of the specimens of *S. armillaris* have been in preservative, some for nearly 50 years and could therefore have been subjected to uneven shrinking as a result of fixation. This may have affected soft tissue characters measured for this species and consequently, the overall statistical result. I therefore suggest that *S. armillaris* from South Africa should be referred to as *S. cf. amicarmillaris* rather than *S. armillaris*. Examination of additional material may provide a better defined result.

Preservation and fixation techniques are known to affect the morphology of soft-bodied animals (e.g. Nishikawa and Terazaki 1996, Black and Dodson 2003). Amongst polychaetes, this has been demonstrated in Sabellidae (Costa-Paiva et al. 2007) and Nereididae (Oliviera et al. 2010) where the manner of fixation or preservation made specimens shorter and wider, or thicker and elongated, or narrower and flatter than living specimens. From this, it is clear that the soft tissue of polychaetes may be affected during preservation. Specimens of *S. cf. amicarmillaris* examined from the Iziko Southern African Museum are more than 40 years old and this may account for the consistently, and sometimes significantly, lower mean values for soft tissue characters in these samples compared to the fresh samples of *S. amicarmillaris*. Additionally, previous studies have shown that some morphological features in polychaetes may vary with size and this should be considered when performing statistical analyses (Lu and Fauchald 1998, Costa-Paiva and Paiva 2007, Marin et al. 2017). For example, Martin et al. (2017) found that more than 50% of the measured characters of *Oxydroma humesi* (Pettibone 1961) were size dependant and, this was accounted for by dividing the size dependant characters by the length of the worm. In doing so, they were able to differentiate between two populations of *O. humesi* and describe a new species; *O. okupa* Martin, Meca and Gil 2017 from the Iberian Peninsula. Therefore, a manner of solving the problem of uneven shrinking of soft tissue characters due to fixation may be by correcting for size dependant characters.

By contrast, *S. cf. amicarmillaris* and *S. armillaris* from South Africa had similar values for chaetal measurements, features that are not susceptible to shrinkage as a result of preservation. For example, length of prostomium for fresh specimens of *S. amicarmillaris* was found to be significantly different and is nearly twice the length recorded for preserved specimens of *S. cf. amicarmillaris* whereas average width of anterior chaetae at base 1 measurement (Fig. 4.1 III(4)) is 0.0036 and 0.00307 mm respectively (Table 4.4). Lattig et al. (2007) recommend that the length of the proventricle is of better use in identification when considering preserved specimens. Taking into account the long time that *S. cf. amicarmillaris* has been preserved and the multivariate analysis, the characters that may be used to differentiate between *S. amicarmillaris* and *S.cf. amicarmillaris* are the length of the proventricle and the width of the posterior chaetae.

In 1977, Ben-Eliahu defined three morphological groups of *S. armillaris* that are outlined in the introduction, which includes the 'true *armillaris*' morpho-type. Two additional morpho-types are outlined in the introduction to which Fauvel (1923), Day (1967), Licher (1999), Lopez et al. (2001), and Musco and Giangrande (2005) adhere. Based on the criteria outlined by Ben-Eliahu (1977) and on the information that I have collected on *S. cf. amicarmillaris* in this study, I could not categorize it in any of the morphological groups outlined by Ben-Eliahu (1977) nor the two morpho-types outlined in the introduction to this chapter. While *S. cf. amicarmillaris* has long posterior chaetal blades that would classify it as 'true *armillaris*' it also has pseudosimple chaetae that are absent from this group. However, the last morpho-type defined by Ben-Eliahu (1977) has a reduced number of chaetae in midbody with chaetal blades becoming fused and beginning to resemble an ypsiloid shape; posterior chaetae are longer and bidentate. While *S. cf. amicarmillaris* does not have ypsiloid pseudosimple chaetae, it is the presence of pseudosimple chaetae that would make it much more similar to Ben-Eliahu's (1977) morpho-type 3. Thus, while the original description of *S. armillaris* does not have

pseudosimple chaetae, *S. cf. amicarmillaris* can still be placed within the greater species complex. The presence and shape of pseudosimple chaetae may be a feature that distinguishes a new species and I am certainly not the first person to find pseudosimple chaetae on specimens purported to be *S. armillaris*, a species that is actually characterized by the absence of this feature. Musco and Giangrande (2005) discovered ypsiloid pseudosimple spines on specimens similar to '*S. armillaris*' from Belize and they eventually described it as *Syllis mayeri* Musco and Giangrande 2005. It is unclear whether recent ecological studies conducted locally (i.e. Hammond and Griffiths 2004, Hanekom et al. 2009) collected specimens that really conformed to the description of *S. armillaris*, or if they are *S. cf. amicarmillaris* or *S. amicarmillaris* or a different species since the specimens were not lodged at the museum and consequently not available for comparison.

Syllis amica is clearly distinct from both *S. amicarmillaris* and *S. cf. amicarmillaris* (discussed elsewhere) but there is considerable overlap among preserved and fresh specimens from South Africa and museum specimens from Europe (Table 4.5). This could be attributed mainly to the high morphological variability within the *S. amica* Iziko group. While all of the specimens examined conformed to the description in Day (1967) by having obliquely truncate pseudosimple chaetae, dorsal cirri that are sub-equal to body width and short chaetae in midbody that are either unidentate or minutely bidentate, other characters differed. For example, the shape of the prostomium for some individuals was broad and almost square while others had an open trapezoidal shape; the palps were basally fused or fused for most of their length and appeared triangular in some but more ovoid in others; the dorsal cirri were either short and stout or long and thin; some individuals were long and narrow while other individuals were short and wide. The sometimes large morphological differences may exceed any possible variation that may exist interspecifically and may be the reason there is a large amount of overlap with other species groups, suggesting that there may be more than one species. This is evidenced by the fact that half of the individuals were not classified within their nominal species by the Discriminant Function Analysis (Table 4.5). Day (1967) states that *S. amica* has only ever been found on the east coast of South Africa but fresh specimens were collected from the south coast, while the specimens held at the Iziko Southern African museum were collected only from the west coast. Consequently, I was unable to examine any individuals of *S. amica* upon which the description in Day (1967) was based. I could therefore not confirm that *S. amica* from the east coast of South Africa is the same as those individuals from the west or south coasts of South Africa that I examined. In the introduction to this chapter, two morphotypes are suggested for this species based on the available descriptions. However, none of the specimens of *S. amica* that I examined from South Africa can be placed in any of these morphotypes. The high variation in some morphological features could also be an artefact of the small sample sizes, particularly among the South African samples, or an effect of preservation of the comparatively large number of museum specimens (compared to the relatively few fresh specimens) used in this analysis. Considering the results from the DFA and the similarity between South African and European specimens and, the morphological overlap (and high variability) observed within the *S. amica* Iziko group it is possible that there may be several species included here. The use of more directly comparable materials (i.e., fresh specimens of all populations) may present a more defined result...

Uneven shrinking owing to fixation of specimens that have been held in museums for extended periods may

compromise the results when newly collected and museum specimens are compared directly in a single analysis. Having said that, the use of morphometrics in taxonomic studies concerning polychaetes (even though rarely used) often provide clear results using both recently collected specimens and specimens that had been stored in museum collections for up to 50 years (cf. Martin et al. 2003, Ford and Hutchings 2005, Lattig et al. 2007). By contrast, my study showed distinct differences among specimens that had been recently collected and those that had been received from museums, while the museum specimens also showed higher variability in measurements of soft-tissue characters. Thus the poor resolution found in this study may have been a consequence of the comparatively small sample size compared to the aforementioned studies combined with the effects of uneven shrinkage. I examined 55 individuals with only 13 being fresh specimens while the remaining preserved specimens are more than 40 years old (Table 4.2). This was fewer than the 63 to 190 specimens examined by Martin et al. (2003), Ford and Hutchings (2005), Lattig et al. (2007) and Martin et al. (2017). Despite the smaller sample size and comparatively larger number of preserved specimens used in this study, the morphometric analysis provided a clear result for some comparisons. The *Syllis* cf. *amicarmillaris* are different from the European specimens, while those of *S. cf. amica* collected in South Africa are clearly different from *S. cf. amicarmillaris* and *S. amicarmillaris*. However, the analysis was less effective at resolving the placement of *S. cf. amicarmillaris* from South Africa, which might correspond to the recently described *S. amicarmillaris*, or that of *S. amica* from South Africa that may be a new species. In this regard, morphometric analysis is an effective tool that helps support the qualitative views of the taxonomist, but the power of the analysis increases with the correction of size-dependent measurements and sample size.

The present study has shown conclusively that specimens identified by John Day as *S. armillaris* had been identified incorrectly and may be *S. amicarmillaris*. Furthermore, this study provides evidence that specimens that match the description of *S. amica* according to Day (1967) are very similar to, but probably not the same as the specimens from within the native range of the species. These results contribute to the increasing number of studies showing that some of the apparently cosmopolitan species listed in Day (1967) and as present in South Africa represent new indigenous species. Together, Wilson and Glasby (1993), Lewis and Karageorgopolous (2008), Clarke et al. (2010), Sikorski and Pavlova (2016) and Simon et al. (2017) have added six new species to South Africa's indigenous fauna replacing five apparently cosmopolitan species that were all listed in Day (1967) (viz., *Perinereis nuntia vallata*, *Marphysa sanguinea*, *Magelona papilicornis*, *Laonice cirrata* and *Pseudopolydora antennata*). Thus, the continued use of Day (1967) when identifying apparently cosmopolitan species may lead to continued incorrect identifications and the ultimate underestimation of native diversity.

Chapter 5: Synthesis

“It is depressing that the number of taxonomists is decreasing at a time when our appreciation of marine biological diversity is just starting to develop” (Gibbons et al. 1999). It has taken more than five decades for taxonomic records of South African syllids to be updated and this supports the opinions of Gibbons et al. (1999) and similar sentiments expressed by Griffiths et al. (2010) regarding local fauna and flora. More taxonomists need to be trained and employed to effectively establish consistent species databases for, not only South African, but global marine biodiversity. Without it, we run the risk of perpetuating old mistakes. The two monographs published by Fauvel (1923, 1927) on French fauna and the two-volume monograph, published by Day (1967), on the identification of polychaetes in South Africa are good examples of this. Day (1967) as a whole has not been updated since it was published, most likely as a result of few publishing polychaete taxonomists over recent decades, yet continues to be used as the primary source of identification for polychaetes in South Africa. The monograph includes many species that are considered cosmopolitan, and often the descriptions (including the associated figures) have too little detail to assign an accurate identification as a consequence of limited technology. Consequently many species that are actually native are mis-identified as species that are apparently wide spread. This is supported by the fact that several publications discrediting the reporting of some of the apparently cosmopolitan polychaetes occurring in South Africa have been published over the last decade.

A desktop update of the records of syllids in Day (1967) reveals that more than half of the species have a questionable taxonomy often as a result of their apparently cosmopolitan status (Chapter 2). These apparently cosmopolitan species often consist of large species complexes resulting in a possible underestimation of native species richness. Further, resolving the status of apparently cosmopolitan species and confirming their identification informs management strategies. By doing so, there is also a clear distinction between alien and native species and management plans can be implemented to control, monitor or eradicate alien species in local species communities. Thus far, one potentially alien syllid has been identified (*Opisthosyllis brunnea*) and requires further investigation into its local distribution range and potential impacts (Chapter 2).

It is also clear from Chapter 2 that the taxonomic state and overall knowledge of syllids in South Africa is poor. This is reflected in the literature, in that few studies identifying syllids have been published over the last 50 years. Additionally, all of these studies are ecological except, for the most recent publication describing two new species by Simon et al. (2014). It may also be seen in the 17 species that I was unable to identify using Day (1967) and the subsequent description of three species that I propose to formally describe as new (Chapter 3). Half of the species on the updated list of syllids occurring in South Africa are also considered questionable, possibly representing indigenous species. This means that the actual richness of syllids in South Africa is likely twice or three times larger than what we think it is; serving to highlight its clear underestimation in the region.

The use of morphometric and morphological comparisons to disambiguate species identifications proved

100% effective in this study (Chapter 4). Using this method I was able to confirm that South African specimens of the apparently cosmopolitan *Syllis armillaris* were morphologically very similar to the native *Syllis amicarmillaris* (Chapter 4), with only four out of 16 characters being significantly different between them. This study also showed that the specimens attributed to *Syllis amica* from South Africa belong to a separate species from *S. amicarmillaris* but are morphologically similar to the European specimens (Chapter 4) with several features that overlap. However, there are some noticeable differences between these three groups that suggest that they may be different species. Additionally, this study also showed that the ratio of preserved and fresh samples used in such analyses should be considered carefully, as preserved specimens may be subject to uneven shrinking over time which may influence the results. Even more so, the results indicate that more comparable materials (i.e., fresh specimens) or a more appropriate method of comparison should be used. For instance, if comparable materials are unavailable then a more robust statistical method should be considered to account for the sometimes large differences between the size of preserved and fresh specimens. Alternatively, if fresh specimens for these species are found, then genetics may provide a clear result. Furthermore, the validity of the results would also depend on sample size and on the size-range of the specimens considered in the analyses (Chapter 4). For these reasons, I suggest that *S. armillaris* from South Africa be referred to as *S. cf. amicarmillaris* while *S. amica* from South Africa should be referred to as *S. cf. amica*. In doing so, these add to the growing number of apparently cosmopolitan species in Day (1967) that have been mis-identified and are actually new indigenous species.

Ecologists require sound identifications to build a complete picture of the regional (and global) biodiversity. For taxonomists, this seems like an impossible task as species are being discovered faster than they can be described. More taxonomists and, more collaboration between taxonomists and ecologists are needed. If identification guides like Day (1967) are consistently updated through a collaborative effort, we can mitigate future problems. This can be accomplished by considering one family at a time and by consulting with experts at various institutions around the country (or worldwide) that may have specimens in their personal collections and or databases. Further, given that syllids are such common species, the problem of apparently cosmopolitan species possibly representing new indigenous species could perhaps extend to other taxa. With this in mind, the gross underestimation of biodiversity of the region becomes more apparent. The disintegration of apparently cosmopolitan species across taxa may reveal that the actual biodiversity of marine species is several times its current value.

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Appendix

An updated checklist of syllids listed in Day (1967) with novel species

The information for the updated checklist was mainly derived from four online databases (see 2.2 above) and the wider literature was used to supplement this. References were only provided in the remarks section of each record where appropriate. The references used for the checklist are in the reference list. The names for species that have been synonymized with previously described species have been listed beneath their senior synonyms therefore only senior synonyms are listed. When species were recorded along the entire coastline of South Africa, i.e. the west, south and east coast, the local distribution was listed as South Africa, otherwise specific locations are given. Distribution outside of South Africa will be assigned according to region or country but where a region has a coastline in more than one sea or ocean, or if a species is found in one specific locality within a region, this will be specified. For example: France has a coastline in the Mediterranean Sea and the Atlantic Ocean, so the region within France was specified in parenthesis, i.e., France (Port Vendres, Normandy). The type localities of the senior synonyms (thus nominal species) are highlighted in bold. The Mediterranean Sea refers to all of the countries that have boundaries in the Mediterranean Sea. This includes; Algeria, Libya, Egypt, Israel, Lebanon, Syria, Turkey, Greece, Italy, France and Spain. It also includes records in the Adriatic and Aegean Seas. Habitat type refers to the type of environment in which the species has been recorded including substrate type when available.

SYSTEMATICS

Order: Phyllodocida Dales 1962

Family: Syllidae Grube 1850

Sub-Family: Anoplosyllinae Aguado and San Martín 2009

Genus: *Anoplosyllinae* Claprède 1868

Anoplosyllis sexoculata (Hartman-Schröder 1962)

Syllides sexoculata Hartman-Schröder 1962

Type locality: Chile

Local distribution: Namibia

Global distribution: Southern Chile; Australia: Victoria, New South Wales

Habitat: Occur interstitially in fine to coarse sand on algae and on colonies of sabellariids, intertidally to about 20 m.

Remarks: *Anoplosyllis sexoculata* has a disjunct distribution with a type locality and distribution in the East South Pacific, in the West South Pacific and a single locality in the South Atlantic. San Martín and Hutchings (2006) list Namibia as part of its distribution but there are no other records in southern Africa to confirm this,

nor is *A. sexoculata* listed in Day (1967). Here, it is listed as a new record for southern Africa.

Local status: Casual

Genus: *Syllides* Örsted 1845

*Syllides longocirratu*s (Örsted 1845)

Syllis (*Syllides*) *longocirrata* Örsted 1845

Type locality: Norway

Local distribution: South Africa: False Bay

Global distribution: English Channel; France: Roscoff; Ireland; Sweden; United Kingdom; Mediterranean Sea; Gulf of Maine

Habitat: Typical of the intertidal zone and shallow waters until a depth of ~46 m in sand and mud

Remarks: Day (1967) listed *S. longocirratu*s as being rare with only two individuals recorded in False Bay (Day 1960). *S. longocirratu*s is largely distributed in the temperate waters of the eastern North Atlantic and at one locality in the western North Atlantic. It is found in the cold temperate waters of South Africa which is the only locality in the South Atlantic outside of its general distributional range.

Local status: Casual

Sub-Family: *Autolytinae* Langerhans 1879

Genus: *Autolytus* Grube 1850

Autolytus bondei Day 1934

Type locality: St. James (South Africa)

Local distribution: South Africa: False Bay

Habitat: Collected from plankton

Remarks: This record is based on a single specimen collected from plankton and there are no other recent local or global records for this species.

Local status: Indigenous

Autolytus maclearanus McIntosh 1885

Autolytus gibber Ehlers 1897

Type locality: Kerguelen Islands

Local distribution: South Africa: Saldanha Bay, Table Bay, Port Alfred

Global distribution: Sub-Antarctic Indian Ocean; Chile; New Zealand

Habitat: Shallow waters, up to 99 m; volcanic mud

Remarks: Day (1967) lists this species as being occasional. The distribution for *A. maclearanus* is in the southern region of the Indian, Atlantic and Pacific Oceans. Additionally, the fact that it is originally from the subantarctic volcanic Kerguelen Islands in the southern Indian Ocean makes its presence in South Africa dubious.

Local status: Questionable

Autolytus tuberculatus (Schmarda 1861)

Cirrotyllis tuberculata Schmarda 1861

Type locality: Cape of Good Hope (South Africa)

Local distribution: South Africa: Table Bay, False Bay, Jeffreys Bay

Habitat: Shallow waters, up to 99 m. Common on hydroids.

Remarks: Common in the Western Cape. *A. tuberculatus* was recently recorded in a survey of the West Coast National Park (Hanekom et al. 2009).

Local status: Indigenous

Genus: *Epigamia* Nygren 2004

Epigamia charcoti (Gravier 1906)

Autolytus (Regulatus) charcoti Gravier 1906

Type locality: Antarctica

Local distribution: Namibia; South Africa: Table Bay, False Bay, Jeffreys Bay, Algoa Bay

Global distribution: New Zealand

Habitat: Shallow waters, up to 99 m.

Remarks: *Epigamia charcoti* can be found in the Southern Ocean, Atlantic Ocean and Pacific Ocean. Locally, it is found in harbours that experience frequent international shipping (Table Bay and Algoa bay) and where considerable numbers of aliens have previously been found (Peters et al. 2014).

Local status: Questionable

Genus: *Myrianida* Milne Edwards 1845

Myrianida phyllocera Augener 1918

Type locality: Lüderitz (Namibia)

Local distribution: South Africa: Langebaan Lagoon, Kommetjie, False Bay, Jeffreys Bay, Algoa Bay

Habitat: Intertidal and shallow waters up to 99 m.

Remarks: Was recently found in Langebaan Lagoon, extending its distribution range northwards along the west coast and presenting a new record (Hanekom et al. 2009). No records exist outside of southern Africa.

Local status: Indigenous

Myrianida prolifera (Müller 1788)

Autolytus agassizii Quatrefages 1866

Autolytus ehbiensis Saint Joseph 1887

Autolytus hesperidum Claparède 1868

Autolytus prolifer (Müller 1788)

Autolytus prolifera (Müller 1788)

Crithida prolifera (Müller 1788)

Nereis prolifera Müller 1788

Type locality: Norway

Local distribution: South Africa: Table Bay, False Bay, Mossel Bay, Durban Bay

Global distribution: Ireland; North Sea; United Kingdom; English Channel; France: Dinard, Roscoff, Wimeraeux; Portuguese EEZ; Madeira; Spain; Mediterranean Sea; Gulf of Saint Lawrence; Gulf of Maine; Bay of Fundy; Gulf of Mexico; Georgia (USA)

Habitat: Shallow waters up to 99 m depth, most common from 0 – 5 m. Found in association with hydroids, algae and seagrasses. Also found on small cliffs and overhangs (3 – 8) and on bare rock (0 – 15 m). Absent in deeper waters ~600 m.

Remarks: *Myrianida prolifera* is distributed throughout the eastern North Atlantic from Ireland and the North Sea to Spain; in the western North Atlantic from the Gulf of Saint Lawrence to the Gulf of Mexico. It is also found in the North Pacific (Georgia) with South Africa being the only locality in the South Atlantic.

Local status: Questionable

Myrianida pulchella Day 1953

Type locality: St. James (South Africa)

Local distribution: South Africa: Cape Agulhas, Durban Bay

Habitat: Intertidal, type of sediment not stated in original description

Remarks: Day (1967) lists this species as rare.

Local status: Indigenous

Genus: *Proceraea* Ehlers 1864

Proceraea picta (Ehlers 1864)

Autolytus (Proceraea) picta Ehlers 1864

Autolytus pictus Ehlers 1864

Myrianida picta Ehlers 1864

Type locality: Croatia (Adriatic Sea)

Local distribution: Angola; South Africa: Table Bay, False Bay; Mozambique: Inhaca Island

Global distribution: Ireland; United Kingdom; English Channel; France: Roscoff, Wimereaux; Portuguese EEZ; Madeira; Spain; Morocco; Mediterranean Sea; Australia

Habitat: Intertidal to shallow waters (up to 99 m), in association with hydroids and algae.

Remarks: Outside of the Mediterranean, *P. picta* is distributed in the eastern North Atlantic from Ireland to Morocco; at one locality in the South Pacific Ocean (Australia) and in southern Africa in the South Atlantic Ocean. The general distribution of this species is disjunct and most likely represents a species complex. Also, since Day (1967) is uncertain about the South African record, local records of *P. picta* need to be re-examined.

Status: Questionable

Genus: *Procerastea* Langerhans 1884

Procerastea nematodes (Langerhans 1884)

Procerastea perieri Gravier 1900

Type locality: Madeira (Portugal)

Local distribution: South Africa: Saldanha Bay

Global distribution: Sweden; North Sea; English Channel; France: Saint-Vaast-la-Hogue, Roscoff; Portuguese EEZ; Spain; Mediterranean Sea; Falkland Islands; Santa Catalina Island; California; United States of America

Habitat: Feeds on hydroids growing just below the low tide mark; typical of shallow waters, up to 99 m.

Remarks: *Procerastea nematodes* is distributed in the eastern North Atlantic from Sweden to Spain; in the North Pacific it is found in Santa Catalina and the USA; and South Africa and the Falkland Islands represent the only localities in the South Atlantic. Thus the distribution of this species is dispersed across localities which are far apart. Even though Day (1967) recorded this at only one site but lists it as being locally abundant. It has not been recorded locally since.

Local status: Casual

Sub-Family: Eusyllinae Malaquin 1893

Genus: *Amblyosyllis* Grube 1857

Amblyosyllis formosa Claparède 1863

Amblyosyllis algefnae Viguié 1886

Amblyosyllis plectorhyncha Marenzeller 1874

Amblyosyllis dorsigera Claparède 1864

Amblyosyllis immatura Langerhans 1879

Amblyosyllis lineata Grube 1863

Gattiola spectabilis Johnston 1865

Pterosyllis dorsigera Claparède 1863

Pterosyllis formosa Claparède 1863

Pterosyllis plectorhyncha Marenzeller 1874

Thylaciphorus hessii Quatrefages 1866

Type locality: Normandy (France)

Local distribution: Madagascar; South Africa: Lamberts Bay, Saldanha Bay, Table Bay, Mossel Bay

Global distribution: Mediterranean Sea; Ireland; United Kingdom; France: Wimereux, Roscoff; English Channel; Spain; Portuguese EEZ; Madeira; Japan

Habitat: Bare rock and in association with algae at 0 – 15 m; may be absent in deeper waters (> 99 m)

Remarks: The type locality and general distribution for this species is in the temperate North Atlantic but can also be found in the Pacific Ocean (Japan). Its distribution in South Africa is on the cold temperate west coast and warm temperate south coast and also in the subtropical region of Madagascar.

Local Status: Questionable

Genus: *Eusyllis* Malmgren 1867

Eusyllis assimilis Marenzeller 1875

Eusyllis monilicornis Saint-Joseph 1887

Type locality: Mediterranean Sea

Local distribution: Saldanha Bay

Global distribution: Australia; New Zealand; Japan; Ireland; English Channel; Canada; Gulf of Mexico

Habitat: Present in shallow waters in association with hard substrata, muddy sand, calcareous algae, coralligenous concretions. Absent in deeper waters (> 200 m).

Remarks: *Eusyllis assimilis* is recorded at localities in the North and South Atlantic and Pacific Oceans, presenting a widespread but disjunct distribution. Individuals belonging to this species from the Mediterranean and the Pacific differ from the type specimen in that they have a complete denticled pharyngeal arc (Brusa et al. 2013) suggesting that *E. assimilis* may be a complex of species. In southern Africa, it has only been found at one locality.

Local status: Questionable

Eusyllis blomstrandii Malmgren 1867

Type locality: Spitsbergen (Arctic)

Local distribution: Angola

Global distribution: Arctic; Japan; Mediterranean Sea; Bay of Fundy; Belize; Canada; Caribbean Sea; English Channel; France: Wimereux, Roscoff; Ireland; North Sea; Spain; United Kingdom; Ireland; Portuguese EEZ

Habitat: Typical of the intertidal and deeper waters in association with Bryzoa, Hydrozoa, filamentous algae on exposed rocks and muddy sand. May be absent in deeper waters (> 100 m)

Remarks: This species has a discontinuous distribution in the eastern and western Atlantic i.e., the Caribbean Sea and the Bay of Fundy. *E. blomstrandii* has only been recorded at one locality and has not been recorded in southern Africa since 1934.

Local status: Casual

Eusyllis ceylonica Augener 1926

Typosyllis taprobanensis Willey 1905

Type locality: Sri Lanka EEZ

Local distribution: South Africa: Still Bay, Jeffreys Bay

Habitat: Shallow waters (1- 99 m)

Remarks: This species has one synonym from the Gulf of Mannar which also falls within the Sri Lankan EEZ. *E. ceylonica* is known only from its type locality and no other records outside of its type locality other

than South Africa exist. Day (1967) lists the species as *Syllis* (*Typosyllis*) *cf. taprobanensis* along with an uncertain record of the species in the Western Cape.

Local status: Questionable

Genus: *Nudisyllis* Knox and Cameron 1970

Nudisyllis magnidens (Day 1953)

Pionosyllis magnidens Day 1953

Type locality: Lamberts Bay (South Africa)

Local distribution: South Africa: False Bay

Habitat: Intertidal; typically in association with algae.

Remarks: There are no other records outside of South Africa.

Status: Indigenous

Genus: *Odontosyllis* Claparède 1863

Odontosyllis ctenostoma (Claparède 1868)

Odontosyllis virescens Marenzeller 1874

Pharyngeovalvata natalensis Day 1951

Type locality: Mediterranean Sea

Local distribution: Angola; South Africa: Table Bay, False Bay, Richards Bay

Global distribution: Mediterranean Sea; United Kingdom; Ireland; English Channel; France: Roscoff, Wimereux; Portuguese EEZ; Spain

Habitat: Found in the intertidal region

Remarks: Augener (1918) originally recorded *O. ctenostoma* from Angola but Day (1967) lists *O. ctenostoma* as having no southern African records. *Pharyngeovalvata natalensis* Day 1951 was synonymised with *O. ctenostoma* by San Martín and Hutchings (2006). It was first recorded in South Africa when a single incomplete specimen was collected from a commercial trawler in False Bay at depth (72 m) and Day (1960) mentions that the specimen bore a close resemblance to *O. ctenostoma* but has a characteristic pharynx. One individual of *P. natalensis* was recorded in Table Bay and Richards Bay, respectively (Day 1967). Both locations are large harbours that are open to regional and international shipping where large numbers of alien species have previously been recorded (Peters et al. 2014). It is therefore possible that *O. ctenostoma* may be an alien species, or, given its uncertain history in southern Africa and the fact that it hasn't been recorded since, it may be mis-identified.

Local status: Questionable

Odontosyllis gibba Claparède 1863

Syllis brevicornis Grube 1863

Type locality: Normandy (France)

Local distribution: Mozambique: Inhaca Island

Global distribution: Mediterranean Sea; Red Sea; United Kingdom; English Channel; France: Wimereux, Roscoff; Spain

Habitat: Typical of the rocky shore but may also be present in deeper waters (~ 600 m)

Remarks: Its local distribution is based on the collection of a single specimen (Day 1967). Furthermore, its type locality and general distribution is in the temperate North Atlantic Ocean but is found in the tropical waters of Mozambique.

Status: Casual

Odontosyllis polycera (Schmarda 1861)

Odontosyllis suteri Benham 1915

Procome polycera (Schmarda 1861)

Syllis polycera Schamrda 1861

Trypanosyllis occipitalis Hutton 1904 in Augner 1913

Type locality: Table Bay (South Africa)

Local distribution: Mozambique; Madagascar; Namibia: Lüderitz; South Africa: Port Nolloth; Lamberts Bay; False Bay; Kleinmond; Arniston; Mossel Bay; Buffels River; Storms River; Port Elizabeth

Global distribution: New Zealand

Habitat: Intertidal to deep waters (499 m)

Remarks: Day (1967) lists this species as being fairly common in southern Africa as its local distribution suggests. *O. polycera* was recently recorded in a survey of the West Coast National Park and noted as being present in Saldanha Bay and Langebaan Lagoon (Hanekom et al. 2009), well within its known distribution range.

Local status: Indigenous

Odontosyllis madagascariensis (Gravier 1905)

Alluaudella madagascariensis Gravier 1905

Type locality: Madagascar

Habitat: Intertidal

Remarks: *O. madagascariensis* is known only from its original record (Gravier 1905)

Local status: Indigenous

Genus: *Opisthodonta* Langerhans 1879

Opisthodonta longocirrata (Saint-Joseph 1887)

Parapionosyllis longocirrata (Saint-Joseph 1887)

Pionosyllis longocirrata Saint-Joseph 1887

Pionosyllis morenoae San Martín 1984

Type locality: Dinard (France)

Local distribution: Langebaan Lagoon, Table Bay, Simonstown (False Bay)

Global distribution: English Channel; France: Roscoff; Western Mediterranean Sea; Spain

Habitat: Intertidal and shallow waters up to 100 m.

Remarks: Day (1953) was only able to identify two individuals, collected one each from Simonstown (False Bay) and Langebaan Lagoon, to genus level and listed them as *Pionosyllis* sp. In 1960, he identified the species as *Pionosyllis longocirrata* (Saint-Joseph 1887), when he collected three more specimens from an experimental plate and wooden frame submerged in Table Bay harbour. *Pionosyllis longocirrata* (Saint-Joseph 1887) was later revised as *Opisthodonta longocirrata* by McIntosh (1908). The distribution and type locality for *O. longocirrata* are in the North Atlantic with South Africa being its only locality in the South Atlantic.

Local status: Questionable

Genus: *Paraehlersia* San Martín 2003

Paraehlersia cf. *ehlersiaeformis* (Augener 1913)

Pionosyllis ehlersiaeformis Augener 1913

Type locality: Sharks Bay (Australia)

Local distribution: Namibia: Swakopmund; South Africa: False Bay, Cape Agulhas, Jeffreys Bay

Global distribution: New Zealand

Habitat: Found in mucus tubes attached to hydroids, algae, coralline concretions and seagrasses. Surf zone: Pelagic and interstitial; up to 100 m depth.

Remarks: Day (1967) lists *P. ehlersiaeformis* as being fairly common in southern Africa. Its type locality and distribution are in the South Pacific Ocean with South Africa as its only South Atlantic localities. Furthermore, Day (1967) lists this record as *Pionosyllis* cf. *ehlersiaeformis* and noted that his specimens differed from Augener's (1913, 1918) description in the absence of a bidentate posterior simple chaetiger and a weaker secondary tooth on compound chaetae. San Martín et al. (2009) suggest that records of *P. ehlersiaeformis* from South Africa are doubtful, and that the species requires revision locally.

Local status: Questionable

Paraehlersia ferrugina (Langerhans 1881)

Ehlersia ferrugina Langerhans 1881

Langerhansia ferrugina (Langerhans 1881)

Syllis (Ehlerisa) ferrugina (Langerhans 1881)

Syllis (Langerhansia) ferrugina (Langerhans 1881)

Syllis (Langerhansia) ferruginosa (Langerhans 1881)

Syllis ferrugina (Langerhans 1881)

Typosyllis (Ehlersia) ferrugina (Langerhans 1881)

Typosyllis (Langerhansia) ferrugina (Langerhans 1881)

Type locality: Canary Island; Puerto de la Cruz; Tenerife Island; Spain

Local distribution: Angola; South Africa: Lamberts Bay, Saldanha Bay, Table Bay, False Bay

Global distribution: Gulf of Mexico, North Carolina, the Mediterranean Sea: Adriatic Sea, Aegean Sea, Israel, Italy; European waters: Ireland, Bay of Biscay, Portuguese EEZ; New Zealand

Habitat: Found on coral and in sediments, common on algae and seagrasses; typical of the rocky shore and shallow waters.

Remarks: The numerous synonyms and several type localities along with its widespread distribution suggest that *P. ferrugina* could be a complex of species (San Martín et al. 2009).

Local status: Questionable

Sub-Family: *Exogoninae* Langerhans 1879

Genus: *Brania* Quatrefages 1866

Brania furcelligera (Augener 1913)

Grubea furcelligera Augener 1913

Type locality: Western Central Australia (Geraldton)

Local distribution: South Africa: Table Bay, False Bay

Global distribution: New Zealand and Islands of the tropical Pacific

Habitat: Found in shallow waters (up to 99 m) in association with algae, corals, sand and seagrasses.

Remarks: South Africa is the only record for this species in the Atlantic Ocean.

Local Status: Questionable

Brania pusilla (Dujardin 1851)

Exogone pusilla Dujardin 1851

Grubea pusilla (Dujardin 1851)

Grubeosyllis pusilla (Dujardin 1851)

Type locality: Saint Malo (France)

Local distribution: Namibia: Lüderitz

Global distribution: Mediterranean Sea; North Sea; United Kingdom; English Channel; France: Roscoff, Wimereux; Bay of Biscay; Portuguese EEZ; Australia

Habitat: Intertidal to ~200 m depth but becomes rare in waters deeper than 40 m. Found on all hard substrates, seagrasses, algae, calcareous concretions, also in coarse to fine sand.

Remarks: A single specimen was collected by Augener (1918) and is considered doubtful by Day (1967). Furthermore, *B. pusilla* has a discontinuous distribution in the North and South Atlantic Ocean as well as the Pacific Ocean.

Local status: Questionable

Brania rhopalophora (Ehlers 1897)

Grubea rhopalophora Ehlers 1897

Type locality: Chile: **Tierra del Fuego**, Cape Horn

Local distribution: Namibia: Swakopmund, Lüderitz, Walvis Bay; South Africa: Table Bay, False Bay, Danger Point, Mossel Bay

Global distribution: Hawai'i; New Zealand; Sub-Antarctic Islands

Habitat: Intertidal and shallow waters up to 99 m.

Remarks: Day (1967) listed this species as being fairly common. This species was originally recorded locally by Augener (1918) from the intertidal and from shallow water dredgings at Swakopmund and Lüderitz, respectively. *B. rhopalophora* has a discontinuous distribution with a single locality in the North and South Pacific Ocean, and South Atlantic and Sub-Antarctic region.

Local status: Questionable

Genus: *Exogone* Örsted 1845

Exogone africana Hartmann-Schröder 1974

Exogone verugera africana Hartmann-Schröder 1974

Type locality: Lüderitz (Namibia)

Local distribution: Angola (Not recorded in Day (1967))

Global distribution: Mediterranean Sea; Brazil: Paraíba, Pernambuco, Espírito Santo, São Paulo; Hawai'i; Japan; Australia: Queensland, New South Wales, Western Australia

Habitat: Intertidal and shallow waters up to 81 m, in algae, on stones and rocks

Remarks: *Exogone africana* was first described as a sub-species of *Exogone verugera* which is also found in South Africa. *E. africana* is very similar to *E. brevi antennata*, *E. dispar* and *E. verugera* and young individuals of the species can easily be confused (San Martín 2005). For example, the only difference between *E. verugera* and *E. africana* is that the former species lacks dorsal cirri on the second chaetiger (San Martín 2005). There are also several ways in which *E. dispar* is similar to *E. africana* (e.g., number of muscle rows in proventricle, length of pharynx, number of aciculae, morphology of simple chaetae), the only differences being a median antenna that is distinctly longer than the lateral antennae, and more spinulated falciger blades (Paresque et al. 2014). Furthermore, *E. africana* has been classified as an alien in the Mediterranean Sea (Turkey and Egypt) with the most likely vector of introduction being shipping, however, while their population numbers show an increase in Turkey their impact is still uncertain (Abd-Elnaby and San Martín 2010, Çinar and Dagli 2012). The distribution of this species is discontinuous and spans the North and South Pacific Ocean, and the North and South Atlantic. Further, there are no recent records for this species in southern Africa and therefore *E. africana* is listed here as a new record for southern Africa, expanding its distribution further North along the west coast of Africa. Individuals of *E. verugera* from South Africa were likely not examined before the publication of *E. africana* thus it is possible that *E. verugera* may actually be *E. africana*.

Local status: Indigenous

Exogone dispar (Webster 1879)

Exogone (exogone) dispar (Webster 1879)

Paedophylax dispar Webster 1879

Paedophylax longicpes Verrill 1880

Type locality: Virginia (USA)

Local distribution: Not recorded in Day (1967)

Global distribution: Arctic; North Sea; Spain; Mediterranean Sea; Mexico; Panama; Brazil: Paraíba, Pernambuco, Espírito Santo, São Paulo; Caribbean Sea; Trinidad and Tobago; Galapagos Islands; China; Japan; Western Australia

Habitat: Intertidal (rocky shores) to deeper waters (~157 m) in sediments, from mud to coarse sand, broken shells, inside corals, amongst algae and seagrasses. May be absent in deeper waters (~600 m).

Remarks: The distribution of this species is largely cosmopolitan and it is found in three major oceans; North Eastern Atlantic from the Arctic to Spain and from Mexico to the Islands of Trinidad and Tobago, the the North Western Atlantic; the North Pacific (China and Japan); and the south Indian Ocean in Western Australia. There are no recent records for this species in southern Africa nor is this species listed in Day (1967), however, San Martín (2005) listed South Africa as forming part of *E. dispar*'s recorded distribution. Here, *E. dispar* is listed as a new record for southern Africa.

Local Status: Questionable

Exogone heterosetosa Ehlers 1913

Exogone anomalochaeta Benham 1921

Exogone clavator Ehlers 1913

Exogone heterochaeta Augener 1913

Exogone turqueti Gravier 1906

Type locality: Marion Island

Local distribution: Namibia to Jeffreys Bay

Global distribution: Antarctic Ocean; South America; Australia; New Zealand; Tristan Da Cunha

Habitat: Found in shallow waters, up until about 600 m depth, on all substrates including volcanic sand, mud, sand, gravel, dead corals, algae, sponges.

Remarks: *Exogone clavator*, previously thought to be an indigenous species to South Africa, was synonymised with *E. heterosetosa* by Hartman-Schröder (1974). Day (1967) lists *E. clavator* as common around southern Africa and found from Namibia on the North west coast of southern Africa to Jeffrey's Bay on the east coast of southern Africa. *E. heterosetosa* has a discontinuous distribution in the South Atlantic and the Southern Ocean. World register of Marine Species (WoRMS) lists *E. clavator* as a subjective synonym of *E. heterosetosa* (Gil and Musco 2014) and, given the widespread, disjunct distribution of *E. heterosetosa* and the fact that there are no records for the species in southern Africa, *E. clavator* should be re-examined.

Local status: Questionable

Exogone naidina (Örsted 1845)

Exogone (exogone) naidina Örsted 1845

Exogone gemmifera Pagenstecher 1862

Exogone kefersteinii Claparède 1863

Gossia longiseta Quatrefages 1866

Paedophylax levis Bobretzky 1870

Schmardiya chauseyana Quatrefages 1866

Syllis longiseta Gosse 1855

Type locality: Denmark

Local distribution: South Africa: Saldanha Bay, Table Bay, False Bay

Global distribution: North Sea; Ireland; United Kingdom; English Channel; France: Chausey Isles, Normandy, Roscoff, Wimereux; Spain; Black Sea; Mediterranean Sea; Caribbean Sea; Bering Sea; Japan; United States of America: North Carolina; Australia; Tropical West Africa

Habitat: Intertidal to shallow waters (up to 99 m), on algae, fine to coarse sand, seagrasses. May be absent in deeper waters (> 200 m).

Remarks: *Exogone naidina* has an extensive distribution and is found in the eastern North Atlantic from the North Sea to Tropical West Africa (Day 1967) and at one locality in the western North Atlantic (Caribbean Sea); it is found in the North Pacific at three localities and a single locality in the South Pacific (Australia); South Africa is the only locality in the South Atlantic.

Local status: Questionable

Exogone normalis Day 1963

Type locality: Agulhas Bank (South Africa)

Local distribution: South Africa: Table Bay, Mossel Bay, Jeffreys Bay

Habitat: Recorded from sand and, sand with broken shells at depths of up to 100 m

Remarks: There are no records outside of South Africa for this species

Local status: Indigenous

Exogone verugera (Claparède 1868)

Exogone (Exogone) verugera (Claparède 1868)

Paedophylax brevicornis Webster & Benedict 1887

Paedophylax veruger Claparède 1868

Type locality: Gulf of Naples (Italy)

Local distribution: Namibia: Lüderitz; South Africa: Saldanha Bay, Table Bay, Seapoint, False Bay

Global distribution: Mediterranean Sea; North Sea; Sweden; United Kingdom; Spain; Portuguese EEZ; Morocco; Greenland; Canada; Gulf of Saint Lawrence; Bay of Fundy; Gulf of Maine; North Carolina; Gulf of Mexico; Japanese Sea; Hawaii; Southern California; Australia

Habitat: Intertidal and shallow waters up to 99 m

Remarks: *Exogone verugera* was recorded in a recent survey of the West Coast National Park and noted as being present in Saldanha Bay, confirming its local distribution (Hanekom et al. 2009). Globally, this species is distributed in the eastern North Atlantic from the North Sea to Morocco; in the western North Atlantic from Greenland to the Gulf of Mexico; and in the North (Japanese Sea, Hawai'i, Southern California) and South (Australia) Pacific Ocean. Southern Africa is the only locality in the South Atlantic Ocean. This species has a very widespread and disjunct distribution with localities that are very far apart, i.e., Southern Carolina and Greenland; and Greenland and Hawai'i which also present very different climatic conditions. Furthermore, *E. africana* was a subspecies of *E. verugera* but has since been elevated to species level. It is possible that species of *E. verugera* were not examined before the publication of *E. africana* and therefore they may be synonymous.

Local status: Questionable

Genus: *Erinaceusyllis* San Martín 2005

Erinaceusyllis erinaceus (Claparède 1863)

Sphaerosyllis (sphaerosyllis) erinaceus Claparède 1863

Sphaerosyllis erinaceus Claparède 1863

Type locality: Normandy (France)

Local distribution: Walvis Bay (Namibia) to Lamberts Bay (South Africa)

Global distribution: Arctic; North Sea; Ireland; United Kingdom; English Channel; France (Roscoff); Mediterranean Sea; Gulf of Maine; Bay of Fundy; Caribbean Sea; North West Japanese Sea

Habitat: Intertidal to deeper waters (up to 199 m)

Remarks: Day (1967) lists this species as having a continuous distribution from Walvis Bay (Namibia) to Lamberts Bay. *E. erinaceusyllis* has a widespread and scattered distribution from the cold, temperate waters of the Arctic and North Sea to the warm waters of the Caribbean and Mediterranean Sea's.

Local status: Questionable

Genus: *Spermosyllis* Claparède 1864

Spermosyllis capensis Day 1953

Type locality: Langebaan Lagoon (South Africa)

Global distribution: Brazil

Habitat: Intertidal.

Remarks: *Spermosyllis capensis* was recently again recorded in Langebaan Lagoon (Hanekom et al. 2009).

Local status: Indigenous

Genus: *Sphaerosyllis* Claparède 1863

Sphaerosyllis capensis Day 1953

Sphaerosyllis hystrix capensis Day 1953

Type locality: Cape Agulhas (South Africa)

Local distribution: South Africa: Saldanha Bay, Plettenberg Bay, Port Elizabeth

Habitat: Intertidal and deeper waters up to 199 m; in muddy sand, coralline algae and dead coral.

Remarks: Individuals of this species have been recorded in European waters but are considered uncertain as there are no re-descriptions of the species outside of South Africa (Musco and Bellan 2008).

Local status: Indigenous

Sphaerosyllis semiverrucosa Ehlers 1913

Type locality: False Bay (South Africa)

Local distribution: Namibia; South Africa: Table Bay

Habitat: Shallow waters (up to 99 m) in muddy sand

Remarks: *Sphaerosyllis semiverrucosa* was recorded in New South Wales, Australia in the late 1970's (Hutchings and Rainer 1979) but no other local or global records exist for this species.

Local status: Indigenous

Sphaerosyllis sublaevis Ehlers 1913

Type locality: False Bay (South Africa)

Local distribution: South Africa: Saldanha Bay, False Bay, Cape Agulhas

Global distribution: Chile; Australia; India

Habitat: Shallow waters, up to 99 m.

Remarks: *Sphaerosyllis sublaevis* is found in the cold temperate waters of South Africa but has a global distribution in the tropical waters of the South Pacific and Indian Oceans.

Local status: Indigenous

Sub-Family: Syllinae Rioja 1925

Genus: *Branchiosyllis* Ehlers 1887

Branchiosyllis cirropunctata (Michel 1909)

Syllis (*Typosyllis*) *cirropunctata* Michel 1909

Syllis cirropunctata Michel 1909

Typosyllis (*Typosyllis*) *cirropunctata* (Michel 1909)

Typosyllis cirropunctata (Michel 1909)

Type locality: Gulf of Naples (Italy)

Local distribution: Mozambique

Global distribution: Mediterranean Sea; Central Pacific; Australia: South Western and South Australia

Habitat: Intertidal to shallow water, associated with algae.

Remarks: Day (1967) recorded a single specimen of *B. cirropunctata* which is the only record for southern Africa. Furthermore, Licher (1999) and San Martín et al. (2008) erroneously classified *Syllis cirropunctata* (a synonym of *B. cirropunctata*) as *B. exilis* from the Spanish Mediterranean Sea as these species have a

similar colour pattern. However, they determined that the latter species could be distinguished from *B. exilis* by the absence of falcigers with protuberances on the head of the shaft (Álvarez-Campos et al. 2012).

Local status: Questionable

Branchiosyllis exilis (Gravier 1900)

Branchiosyllis abbranchiata Hartman-Schröder 1965

Branchiosyllis fuscoturata (Augener 1922)

Branchiosyllis uncinigera (Hartman-Schröder 1960)

Syllis (Ehlersia) nitida Verrill 1900

Syllis (Typosyllis) plessisi Rullier 1972

Syllis exilis Gravier 1900

Syllis fuscoturata (Augener 1922)

Syllis grandigularis Verrill 1900

Trypanosyllis uncinigera Hartman-Schröder 1960

Typosyllis fuscoturata (Augener 1922)

Type locality: Red Sea

Local distribution: Madagascar, South Africa: Tongaat, Isipingo, Inyoni rocks

Global distribution: Mediterranean Sea; Portuguess EEZ; Spain; Bermudas; Gulf of Mexico; Caribbean Sea; West Indies; Hawai'i; United states of America (Pacific); California; Mexico (Pacific); Panama; Samoa Islands,

Habitat: Nearshore reefs, shallow waters, rocky shore and subtidal; usually in association with algae, bare sediment, epifauna and encrusted cliffs. May be absent in deeper waters (15 – 600 m). May also be found in association with a range of sponges and ophiurids.

Remarks: Most species belonging to the genus *Branchiosyllis* have a narrow range of distribution in that they are found in the Caribbean Sea and Pacific Ocean, including the Indo-Pacific region (San Martín et al. 2008, Álvarez-Campos et al. 2012). *B. exilis* is the only species that has been reported worldwide circumtropically (San Martín et al. 2008, Álvarez-Campos et al. 2012). Çinar (2013) lists *B. exilis* as cryptogenic in the USA and questionable in Panama and Mexico. Álvarez-Campos et al. (2012), found small differences between specimens of *B. exilis* from different localities. For example, individuals from Cuba, Australia and Panama are similar to individuals documented from the Galapagos Islands and Indonesia in that they have slender, large dorsal cirri with 30 – 40 articles while those from the Mediterranean Sea and the Phillipines have dorsal cirri with 15 – 25 articles. Specimens from the Mediterranean Sea, Cuba, Australia and the holotype (Djibouti) have bidentate blades with a dorso-ventral gradation in falciger length where the dorsal-most blades have a distal tooth that is equal or slightly larger than the proximal tooth and the ventral-most chaetae have a distal tooth that is larger than the proximal tooth. Specimens from Panama and the Phillipines have bidentate blades that are all similar in length with the distal and proximal tooth all equal in size. Álvarez-Campos et al. (2012) suggest that though the dissimilarities may not be enough to classify them as a distinct species, it is suggestive of a complex of similar species (San Martín 2008, Álvarez-Capós et al. 2012). The description published in Day (1967) does not provide sufficient detail to adequately compare characteristics with the re-description in Álvarez-Campos et al. (2012) but there are

similarities between the two. In Day (1967), the length of the pharynx agrees with the re-description in that it is shorter than the proventricle with an anterior dorsal tooth, there is no indication of whether there is a crown of ten soft papillae surrounding the anterior tooth as in the re-description. Furthermore, the re-description refers to bidentate compound chaetae anteriorly and in mid-body, and unidentate falcigers posteriorly with curved tips and distally curved shafts with small spines (Álvarez-Campos et al. 2012). Day (1967) refers to fairly long, minutely bidentate blades anteriorly and the rest of the body with short unidentate blades. It is quite possible, given the similarities and the southern African distribution in tropical waters, that the species in Day (1967) may actually be *B. exilis* but museum specimens need to be examined to confirm this.

Local Status: Questionable

Genus: *Haplosyllis* Langerhans 1879

Haplosyllis spongicola (Grube 1855)

Haplosyllis (*Syllis*) *hamata* (Claparède 1868)

Haplosyllis hamata (Claparède 1868)

Haplosyllis maderensis Czerniavsky 1881

Haplosyllis oligochaeta

Haplosyllis palpata Verrill 1900

Haplosyllis spongicola tentaculata Marion 1877

Haplosyllis spongicola var. *spongicola* (Grube 1855)

Hemisyllis dispar Verrill 1900

Nereis teticola Dalle Chiaje 1828

Syllis (*Haplosyllis*) *hamata* Claparède 1868

Syllis (*Haplosyllis*) *spongicola* Grube 1855

Syllis hamata Claparède 1868

Syllis oligochaeta Bobretzky 1870

Syllis setubalensis McIntosh 1855

Syllis spongicola Grube 1855

Syllis spongicola tentaculata Marion 1879

Type locality: Mediterranean Sea

Local distribution: Angola; South Africa: Western Cape and Durban; Madagascar

Global distribution: Apparently cosmopolitan, typically in tropical and temperate seas; Mediterranean and European Atlantic waters.

Habitat: Found in association with different marine sponge species but are also found in association with numerous hard substrates such as coral, bare rock, in terrigenous and carbonate sediment and on algae. Typically in the intertidal but can also be found at depths of up to 600 m.

Remarks: *Haplosyllis spongicola* may be part of a cryptic species complex where several distinct species of the *Haplosyllis* genus had been erroneously described as *H. spongicola* (e.g. Martin et al. 2003, Paola et al. 2006, Lattig et al. 2007, Lattig and Martin 2011, Cepeda et al. 2017). Consequently, Lattig et al. (2007) suggested that records of *H. spongicola* outside of the Mediterranean and European seas (i.e., other temperate and tropical records) need to be reviewed. This statement has been supported by Lattig and Martin (2011) and Cepeda et al. (2017) who described new species belonging to this complex from the Indian Ocean and Red Sea and, Saudi Arabian Red Sea, respectively.

Local status: Questionable

Haplosyllis trifalcata (Day 1960)

Syllis (*Haplosyllis*) *trifalcata* Day 1960

Type locality: False Bay (South Africa)

Local distribution: South Africa: False Bay

Habitat: Found in shallow waters (1-99 m).

Remarks: The only specimen found to date is the type specimen collected by Day (1960) in False Bay.

Local status: Indigenous

Genus: *Opisthosyllis* Langerhans 1879

Opisthosyllis ankylochaeta Fauvel 1921

Type locality: Madagascar

Local distribution: Madagascar

Global distribution: New Caledonian Islands (South Pacific)

Habitat: Intertidal, in coral reefs.

Remarks: No other records for this species exist in southern Africa besides the original record.

Local status: Indigenous

Opisthosyllis brunnea Langerhans 1879

Type locality: Madeira (Portugal)

Local distribution: Mozambique; South Africa: False Bay to Durban Bay

Global distribution: Mediterranean Sea; Portuguese EEZ; Spain; Caribbean Sea; Gulf of Mexico; Panama; Somalia; Japan; Korea; Australia: New South Wales, Queensland, Western Australia

Habitat: Intertidal (rocky shore) to shallow water (up to 99 m); associated with corals, algae, sponges and other biological concretions

Remarks: *Opisthosyllis brunnea* has a wide, discontinuous distribution in the North and South Atlantic, in the Indian Ocean and Pacific Ocean. Furthermore, it has been classified as alien in the Aegean Sea (Çinar and Ergen 2003)

Local status: Potentially alien

Opisthosyllis laevis Day 1957

Type locality: Mozambique

Local distribution: Madagascar

Global distribution: Red Sea

Habitat: Intertidal

Remarks: Given that Mozambique and Madagascar are disjunct from the Red Sea, it is possible that *O. laevis* is an alien in the Red Sea.

Local status: Indigenous

Genus: *Syllis* Lamarck 1818

Syllis benguellana Day 1963

Typosyllis benguellana Day 1963

Type locality: Lamberts Bay (South Africa)

Local distribution: South Africa: Lamberts Bay

Habitat: Typically found in coastal sediments and shallow waters but can be found in waters up to 99 m deep. Found in coarse white sand and shells.

Remarks: *Syllis benguellana* has been observed as locally abundant in its type locality (Day 1967). To date, only a single specimen has been collected from coastal sediments in the Red Sea (Abd-Elnaby 2014) and in Hong Kong (Che et al. 1998); no other records for this species exist outside of its type locality in South Africa. The *S. benguellana* specimen identified by Abd-Elnaby (2014) does not correspond wholly with Day (1963) in that the specimen from the Red Sea has bidentate chaetae instead of unidentate chaetae and three aciculae instead of two aciculae anteriorly (Abd-Elnaby 2014).

Local status: Indigenous

Syllis cf. amica (Quatrefages 1866)

Type locality: South Africa: **Danger Point**, Oatland Point

Local distribution: Namibia: Diaz Point (Lüderitz); South Africa: Saldanha Bay, False Bay, Mossel Bay

Habitat: Intertidal, algal turf

Remarks: Day (1976) records *S. amica* along the East coast of South Africa but specimens lodged at the Iziko South African Museum are from the west coast of South Africa. Further, specimens of *S. cf. amica* were collected on recent field trips to the south coast of South Africa. Morphometric analyses show that fresh specimens of *S. cf. amica* from the south coast of South Africa, historical specimens from the Iziko South African Museum, European specimens and fresh specimens of *S. amicarmillaris* from the south coast of South Africa are all distinct. Morphological assessment of these individuals confirms the statistical analysis and clear morphological differences can be seen between individuals from each collection. This implies that *S. cf. amica* may be an undescribed species, new to South Africa. However, few specimens were used in the analyses and additional specimens need to be collected and examined

Local status: Indigenous

Syllis amicarmillaris Simon, San Martín and Robinson 2014

Type locality: Danger Point (South Africa)

Local distribution: South Africa: Gordons Bay (False Bay), Gans Bay, Saldanha Bay, Mossel Bay

Habitat: Common in sediments within the effluent outflow path from abalone (*Haliotis midae*) farms and less so on the surface of abalone grown in offshore longline culture system. Typical of the lower intertidal on algal turf, foliose algae and sponge.

Remarks: A recently described species that was found in abundance at three localities (Gordons Bay, Danger Point, Mossel Bay) along the south coast of South Africa extending the distribution eastward. *S. amicarmillaris* is morphologically similar to *S. amica* and *S. armillaris* in chaetal characteristics and body plan, respectively. Morphological and morphometric analyses reveal that *S. amicarmillaris* is closely morphologically similar to *S. armillaris* from South Africa but is a separate species from *S. amica*.

Local status: Indigenous

Syllis cf. amicarmillaris Simon, San Martín and Robinson 2014

Type locality: Danger Point (South Africa)

Local distribution: South Africa: Mossel Bay

Habitat: Intertidal, algal turf, foliose algae, sponge

Remarks: *S. armillaris* is widely distributed and can be found in the Atlantic, Pacific and Indian Oceans. Locally, Day (1967) records *S. armillaris* throughout South Africa from Namibia to Mozambique. This apparently cosmopolitan distribution in addition to its numerous synonyms is suggestive of a species complex (López et al. 2001, Musco and Giangrande 2005). Morphometric analysis of specimens of *S. armillaris* from the Iziko South African Museum, European specimens from Spain and Norway, close to its type locality, reveals that individuals identified as *S. armillaris* by Day (1967) are distinct from European specimens but are closely morphologically similar to *S. amicarmillaris*. Morphological analysis corresponds with the statistical analysis and shows that individuals of *S. armillaris* from the Iziko South African Museum are more similar to *S. amicarmillaris* than the description of *S. armillaris* in Day (1967). This suggests that individuals of *S. cf. amicarmillaris* are undescribed indigenous species that form part of a species complex. However, specimens lodged at the Iziko South African Museum were mainly collected from the west coast of southern Africa and *S. armillaris* was not found in recent sample collections from the south coast of South Africa where Day (1967) records this species as very common and widespread. Additional samples should be collected at a larger number of sites and compared.

Local status: Indigenous

Syllis cornuta Rathke 1843

Ehlersia (Syllis) cornuta (Rathke 1843)

Ehlersia cornuta (Rathke 1843)

Langerhansia cornuta (Rathke 1843)

Syllis (Ehlersia) cornuta Rathke 1843

Syllis (Langerhansia) cornuta Rathke 1843

Syllis (Typosyllis) cornuta Rathke 1843

Syllis (Typosyllis) harti (Berkeley & Berkeley 1938)

Syllis cornuta collingsii McIntosh 1908

Syllis fabricii Malmgren 1867

Syllis pallida Verrill 1875

Typosyllis (Ehlersia) cornuta (Rathke 1843)

Typosyllis (Langerhansia) cornuta (Rathke 1843)

Typosyllis cornuta (Rathke 1843)

Type locality: Norway

Local distribution: Mozambique; South Africa: Table Bay, Plettenberg Bay

Global distribution: Hawai'i; Mediterranean Sea; European waters: North Sea, English Channel, France, United Kingdom, Sweden; Canada (Gulf of Saint Lawrence); Greenland (Arctic Ocean); Bay of Fundy; New England (USA); Gulf of Mexico; Belize; Caribbean Sea; Panama

Habitat: Found in association with sediments and with algae; typical of the rocky shore and nearshore reefs but can also be found in deeper waters up to 1 000 m.

Remark: Noted as being fairly common in southern Africa (Day 1967). *S. cornuta* has a type locality and general distributional range in the cold temperate waters of the North-eastern Atlantic. It also occurs in the western North Atlantic and is distributed as far south as Panama with two additional, disjunct, locations in the North Pacific (Hawai'i) and South Atlantic (South Africa).

Local status: Questionable

***Syllis gracilis* Grube 1840**

Syllis (Syllis) gracilis Grube 1840

Syllis (Syllis) longissima Gravier 1900

Syllis brachycirris Grube 1857

Syllis buchholziana Grube 1877

Syllis longissima Gravier 1900

Syllis mixtasetosa Bobretzky 1870

Syllis navicellidens Czerniavsky 1881

Syllis nigrovittata Czerniavsky 1881

Syllis palifica Ehlers 1901

Syllis quadridentata Czerniavsky 1881

Syllis vancaurica Grube 1868

Type locality: Gulf of Naples (Italy)

Local distribution: Namibia; Madagascar; South Africa: False Bay (St. James), Gans Bay, Mossel Bay, Algoa Bay, Port Alfred, Murrumbene Estuary, Durban Bay; Mozambique: Inhaca Island

Global distribution: Apparently cosmopolitan, typically in temperate and tropical seas

Habitat: Common on all kinds of hard substrata and sediments, especially amongst algae, coral, sponges and calcareous concretions. Found from the intertidal to 300m depth, encrusting rocks as well as small cliffs and overhangs.

Remarks: *Syllis gracilis* is noted as being fairly common in Southern Africa (Day 1967). A pseudo-cryptic

species complex exists where several distinct species of the genus *Syllis* have mistakenly been described as *S. gracilis* (e.g. Maltagliati et al. 2000, Álvarez-Campos et al. 2017). Moreover, *S. gracilis* is listed as cryptogenic in Argentina (Orensanz et al. 2002, Çinar 2013)

Local status: Questionable

Syllis hyalina Grube 1863

Pionosyllis hyalina (Grube 1863)

Syllis (*Typosyllis*) *hyalina* Grube 1863

Syllis (*Typosyllis*) *hyalina juanensis* Augener 1922

Syllis (*Typosyllis*) *melanopharyngea* Augener 1918

Syllis (*Typosyllis*) *tristanensis* Day 1954

Syllis borealis Malmgren 1867

Syllis macrocola Marenzeller 1874

Syllis pellucida Ehlers 1864

Syllis simillima Claparède 1864

Syllis tristanensis Day 1954

Syllis velox Bobretzky 1870

Typosyllis (*Syllis*) *hyalina* (Grube 1863)

Typosyllis (*Syllis*) *velox* (Bobretzky 1870)

Typosyllis (*Syllis*) *hyalina* (Grube 1863)

Typosyllis aciculata orientalis Imajima 1966

Typosyllis hyalina (Grube 1863)

Typosyllis melanopharyngea (Augener 1918)

Typosyllis orientalis Imajima & Hatman 1967

Typosyllis taltalensis Hartmann-Schröder 1962

Typosyllis tristanensis Day 1954

Type locality: Croatia (Adriatic Sea)

Local distribution: Southern Africa: False Bay to Angola, Mossel Bay; Mozambique; Madagascar

Global distribution: Mediterranean Sea; Black Sea; North Sea; Norway; Ireland; Bay of Biscay; Portuguese EEZ; Gulf of Maine; Gulf of Mexico; Caribbean Sea; West Africa; Tristan da Cunha; New Zealand; Chile: Juan Fernandez islands; Hawai'i

Habitat: Found in association with algae, vermetid tubes, sponges, sandy and muddy sediments as well as corals in nearshore reef systems. Typical of intertidal and subtidal zones. *S. hyalina* is also recorded from seamounts and knolls. **Remarks:** This species has a type locality in the Mediterranean Sea and a widespread discontinuous distribution which includes the north and south of both the Pacific and Atlantic Oceans.

Local status: Questionable

Syllis prolifera Krohn 1852

Gnathosyllis zonata Haswell 1886

Pionosyllis prolifera (Krohn 1852)

Syllis (Typosyllis) bouvieri Gravier 1900

Syllis (Typosyllis) prolifera Krohn 1852

Syllis (Typosyllis) zonata (Haswell 1833)

Syllis armandi Claparède 1864

Syllis bouvieri Gravier 1900

Syllis fiumensis Ehlers 1864

Syllis lussinensi Grube 1863

Syllis nigrans Bobretzky 1870

Syllis zonata (Haswell 1833)

Typosyllis (Syllis) nigrans (Bobretzky 1870)

Typosyllis (Syllis) prolifera (Krohn 1852)

Typosyllis bouvieri (Gravier 1900)

Typosyllis nigrans (Bobretzky 1870)

Typosyllis prolifera (Krohn 1852)

Typosyllis zonata (Haswell 1833)

Type locality: Mediterranean Sea

Local distribution: Mozambique: Inhaca Island; Madagascar; Namibia; South Africa: Lamberts Bay, Saldanha Bay, Table Bay, False Bay, Algoa Bay, Durban Bay

Global distribution: Black Sea; Red Sea; Port-Vendres; Gulf of Aden; Gulf of Mexico; Caribbean Sea; Trinidad and Tobago; Cuba; West Indies; United Kingdom; English Channel; Ireland; Italy; Portuguese EEZ; Spain; Australia: Port Jackson; New Zealand

Habitat: Found on bare rock and in association with algae in intertidal, subtidal and deeper waters but may be absent in waters deeper than 99 m.

Remarks: *Syllis prolifera* is an apparently cosmopolitan species that has a large number of synonyms and is distributed throughout the North Atlantic and at two disjunct localities in the South Atlantic and South Pacific Ocean.

Local status: Questionable

Syllis unzima Simon, San Martín and Robinson 2014

Type locality: Gans Bay (South Africa)

Local distribution: South Africa: Walker Bay, Kleinzee

Habitat: Found on cultured *Holothuria scabra*; on oyster (*Crassostrea gigas*) and foliose coralline algae within the effluent outflow path from an abalone farm, respectively.

Remarks: Recently described species.

Local status: Indigenous

Syllis variegata Grube 1860

Isosyllis armoricana (Claparède 1863)

Syllis (Typosyllis) variegata Grube 1860

Syllis (Typosyllis) variegata variegata Cognetti 1954
Syllis armoricana Claparède 1863
Syllis aurantiaca Claparède 1868
Syllis hexagonifera Claparède 1864
Syllis nigropunctata Haswell 1886
Syllis oblonga Keferstein 1862
Syllis sardai San Martín 1992
Syllis schmardiana Haswell 1886
Syllis variegata profunda Cognetti 1954
Those fusiformis Kinberg 1886
Typosyllis (Syllis) aurantiaca (Claparède 1868)
Typosyllis (Syllis) variegata (Grube 1860)
Typosyllis (Typosyllis) variegata (Grube 1860)
Typosyllis armoricana (Claparède 1860)
Typosyllis aurantiaca (Claparède 1868)
Typosyllis cirromaculata Hartmann-Schroder 1960
Typosyllis variegata (Grube 1860)
Typosyllis variegata profunda (Cognetti 1954)

Type locality: Croatia (Adriatic Sea)

Local distribution: Namibia: Lüderitz; Mozambique; South Africa: Port Nolloth, Zout River, Groen River, Lamberts Bay, Paternoster, Saldanha Bay, Langebaan Lagoon, Table Bay, Oudekraal, False Bay: St. James, Kleinmond, Danger Point, Cape Agulhas, Still Bay, Mossel Bay, Storms river, Algoa Bay, Port Alfred, East Londo, the Haven, Qolora, Richards Bay.

Global distribution: North Sea; Ireland; France: Port-Vendres, Normandy; English Channel; Spain; United Kingdom; Gulf of Mexico; Caribbean Sea; Cuba; Panama; Mediterranean Sea; Red Sea; Australia: Port Jackson; New Zealand

Habitat: Intertidal, subtidal and nearshore reefs but may be found in deeper waters (1500 m); also known from seamounts and knolls. Found in association with algae and encrusting cliffs, coralligenous sediments, muddy detritic bottoms, animal and vegetal calcareous grounds, vermetid reefs and corals.

Remarks: *Syllis variegata* is an apparently cosmopolitan species widespread throughout southern Africa and around the globe. Its widespread and discontinuous distribution and numerous synonyms suggest a possible species complex.

Local status: Questionable

Syllis vittata Grube 1840

Syllis (Typosyllis) vittata Grube 1840
Syllis aurita (Claparède 1864)
Syllis buskii McIntosh 1908
Syllis nigropharyngea Day 1951
Typosyllis (Syllis) vittata (Grube 1840)
(Typosyllis) (Typosyllis) vittata (Grube 1840)
Typosyllis vittata (Grube 1840)

Typosyllis vitatta (Grube 1840)

Type locality: Mediterranean Sea

Local distribution: Namibia: Sinclair's Island, Lüderitz; South Africa: Lamberts Bay, Table Bay, False Bay, Cape Agulhas, Mossel Bay, Richards Bay

Global distribution: North Atlantic Ocean: UK EEZ, English Channel, North West Italy, Spain

Habitat: Typically, intertidal and shallow waters (up to 99 m) but also known from seamounts and knolls.

Remarks: Day (1951) previously described this species as the indigenous *S. nigropharyngea* but was later synonymized by Licher (1999) as the cosmopolitan *S. vittata*. This species has only ever been recorded in the North Atlantic Ocean and Mediterranean Sea with South Africa as the only region outside of the North Atlantic where *S. vittata* has been recorded.

Local status: Questionable

Syllis sp. A

Type locality: Mossel Bay (South Africa)

Local distribution: Known only from its type locality.

Habitat: Algal turf, lower intertidal, rocky shore.

Remarks: A new record for southern Africa.

Local Status: Indigenous

Syllis sp. D

Type locality: Mossel Bay (South Africa)

Local distribution: Known only from its type locality.

Habitat: Algal turf, lower intertidal, rocky shore.

Remarks: Recently described species that is listed here as a new record for southern Africa.

Local Status: Indigenous

Syllis sp. S

Type locality: Danger Point (South Africa)

Local distribution: South Africa: Mossel Bay

Habitat: Algal turf, lower intertidal, rocky shore.

Remarks: Recently described species that is listed here as a new record for southern Africa.

Local Status: Indigenous

Genus: *Trypanosyllis* Claparède 1864

Trypanosyllis aeolis Langerhans 1879

Trypanosyllis (Trypanedenta) gemmipra Johnson 1901

Trypanosyllis gemmipara Johnson 1901

Trypanosyllis misakiensis Izuka 1906

Type locality: Madeira Island (Portugal)

Local distribution: South Africa: Durban to Mozambique: Delgoa Bay

Global distribution: Mediterranean Sea; Portuguese EEZ; Spain; Canary Islands; Australia; Washington State; Japanese EEZ

Habitat: Intertidal (rocky shore) and shallow waters in sediments, algae, seagrasses, calcareous concretions, dead corals and sponges. May be absent in deeper waters (>50 m)

Remarks: Its distribution within southern Africa corresponds with its circumtropical distribution but its presence in Washington State and Japan is questionable. Day (1967) lists *T. aeolis* as being occasional. There are no recent records of this species in South Africa.

Local Status: Questionable

Trypanosyllis ankyloseta Day 1960

Type locality: False Bay (South Africa)

Local distribution: Known only from its type locality.

Habitat: Found at depth (42 m) on a sandy and rock bottom.

Remarks: To date, only a single specimen has been collected (Day 1960).

Status: Indigenous

Trypanosyllis gemmulifera Augener 1918

Type locality: Swakopmund (Namibia)

Local distribution: South Africa: Hondeklip Bay, Langebaan lagoon, Lamberts Bay Saldanha Bay, Table Bay, Oudekraal, False Bay, Mossel Bay, Algoa Bay

Habitat: Typically found in the intertidal but may be found in shallow waters up to 99 m.

Remarks: *Trypanosyllis gemmulifera* is regarded as being fairly common in southern Africa by Day (1967) and was recently found in Langebaan Lagoon, well within its distributional range (Hanekom et al. 2009).

Local status: Indigenous

Trypanosyllis prampramensis Augener 1918

Type locality: Ghana

Local distribution: South Africa: Kommetjie, Table Bay, False Bay, Still Bay

Habitat: Intertidal

Remarks: Day (1967) mentions that the occasional specimen is found off the coast of South Africa.

Furthermore, no records have been found outside of its type locality in Tropical West Africa and temperate South Africa.

Local status: Questionable

Trypanosyllis zebra Grube 1860

Syllis rubra Grube 1857

Syllis zebra Grube 1860

Trypanosyllis krohnii Claparede 1864

Type locality: Adriatic Sea

Local distribution: South Africa: Kommetjie, False Bay to Port Shepstone; Mozambique; Madagascar

Global distribution: West Indies; France: Port-Vendres, Roscoff; English Channel; Ireland; North Sea; UK; Spain; Portuguese EEZ; Mediterranean Sea; Gulf of Mexico; Caribbean Sea; Cuba

Habitat: Common on all substrates, including algae, calcareous concretions, sponges, dead corals, bryozoans, hydroids, ascidians, sand, silty clay and gravel. Present in the intertidal and subtidal, up to 100 m. May be absent in deeper waters (> 100 m).

Remarks: *Trypanosyllis zebra* is an apparently cosmopolitan species that is found in warm temperate regions and has type localities in the warmer waters of the Mediterranean Sea. It is distributed worldwide in regions that are tropical such as the Caribbean Sea and cold temperate such as the North Sea whereas in southern Africa *T. zebra* is found in warm temperate (i.e., False Bay) and subtropical and tropical waters (i.e. Mozambique and Madagascar).

Status: Questionable

Genus: *Typosyllis* Langerhans 1879

Typosyllis anops Ehlers 1897

Langerhansia anops (Ehlers 1897)

Syllis (ehlersia) anops Ehlers 1897

Syllis gracilis Schmarda 1864

Type locality: Punta Arena (Chile); Cape Horn (Chile); Cape of Good Hope (South Africa)

Local distribution: South Africa: Table Bay, False Bay, East London

Global distribution: Antarctica, Kerguelen Islands, New Zealand, Australia, South China

Habitat: Shallow waters, up to 99 m.

Remarks: *Syllis gracilis* Schmarda 1864 was originally described from the Cape of Good Hope but is now considered a subjective synonym of *T. anops*. This species was originally described from the South Pacific and is distributed in the cold waters of the Antarctic and Sub-Antarctic and at one locality in the North Pacific. The warm temperate waters of the South coast of South Africa are the only South Atlantic localities.

Local status: Questionable

Incertae Sedis

Genus: *Anguillosyllis* Day 1963

Anguillosyllis capensis Day 1963

Type locality: Agulhas Bank (South Africa)

Local distribution: Angola, South Africa: Table Bay, Plettenberg Bay

Global distribution: Papua New Guinea

Habitat: Sand and mud in deep (183 m) to very deep waters (> 5655 m)

Remarks: *Anguillosyllis capensis* displays morphological features that are characteristic of both Exogoninae (complete fusion of palps, single pair of tentacular cirri) and Eusyllinae (lacks a pharyngeal tooth, dorsal cirri are long and filiform) but cannot be confidently placed in either sub-family (Aguado and San Martín 2008).

Local status: Indigenous

Genus: *Irmula* Ehlers 1913

Irmula spissipes Ehlers 1913

Type locality: Simonstown (South Africa)

Remarks: *Irmula spissipes* has been found in ecological studies from the Mediterranean Sea and India (Sukumaran and Devi 2009). Since there are no taxonomic re-descriptions of this species from European waters it has been suggested that their presence outside of their type locality should be considered doubtful (Musco 2008).

Local Status: Indigenous

Genus: *Lamellisyllis* Day 1960

Lamellisyllis comans Day 1960

Type locality: False Bay (South Africa)

Local distribution: Known only from its type locality.

Habitat: Typically found in shallow water (8 – 12 m) associated with rocks and sand.

Remarks: To date, the holotype is the only known specimen for this species and genus. This species has characteristics that resemble Autolytinae (presence of nuchal epaulettes) and Eusyllinae (epigamic reproduction) but cannot be placed in either sub-family (Aguado and San Martín 2008)

Local status: Indigenous

Nomina dubia

Genus: *Exogonoides* Day 1963

Exogonoides antennata Day 1963

Type locality: Agulhas Bank (South Africa)

Local distribution: South Africa: Plettenberg Bay

Habitat: Sand, mud and rock at a depth range of up to 99 m

Remarks: No specimens have been collected outside of South Africa. Aguado and San Martín (2008) suggest that *E. antennata* be considered *nomina dubia* since the pharynx and the proventricle of the holotype and paratype could not be examined. They also suggest that the holotype and paratype could actually be one specimen with the holotype being the anterior of the animal and the paratype the posterior of the animal. Since the pharynx and proventricle are key characters in identifying species belong to Syllidae, the description, and by extension the species, would become invalid as there is no way to confirm the identity of the species.

Local status: *Nomina dubia*

Nomina nuda

Genus: *Pionosyllis* Malmgren 1867

Pionosyllis malmgreni McIntosh 1869

Type locality: United Kingdom

Local distribution: South Africa: Saldanha Bay, Table Bay, False Bay

Global distribution: North Atlantic Ocean

Habitat: Intertidal

Remarks: Upon examination of the original description and drawings of *P. malmgreni* by McIntosh (1869), San Martín et al. (2014) suggest that the species be synonymised with *Megasyllis procera* Hartman 1965. However, there is no way to confirm this since the type specimens for this species seem to be lost. The type locality and distribution for this species is in the North Atlantic Ocean and locally, is found in two harbours that experience considerable boat traffic, and where alien species have previously been found (Peters et al. 2014).

Local status: Nomen nudum

Table 1. Comparison of selected morphological characteristics for *Syllis amica*, *Syllis armillaris* and *Syllis amicarmillaris* derived from published literature and, museum and fresh specimens.

	<i>Syllis amica</i>						<i>Syllis amicarmillaris</i>		<i>Syllis armillaris</i>						
	Japan (Lee and Rho 1992)	Arctic, Mediterranean Sea, Pacific, South Atlantic (Licher 1999)	South Bay of Biscay (MNCN)	West Coast of South Africa (Iziko)	East Coast of South Africa (Day 1967)	South Coast of South Africa	West and South Coast of South Africa (Simon et al. 2014)	South Coast of South Africa	South Africa and Mozambique (Day 1967)	West and East coast of South Africa (Iziko)	Galicia, Spain (MNCN)	Norway (MNCN)	Ionian Sea (Musco and Giangrande 2005)	Pacific and Indian Oceans (Lopez et al. 2001)	Europe, Arctic, Mediterranean Sea, Pacific, South Atlantic, Tasmanian Sea (Licher 1999)
Length (mm)	-	45	2-14	10-19	20-60	7-18	32	2-23	25 - 35	3-12	14-27	3.059	24	15-21	25.5
Width (mm)	-	-	0.3-0.6	0.2-0.6	-	0.4-0.6	0.47	0.4-0.7	-	0.3-0.7	0.2-0.7	0.5	0.53	0.14-0.29	0.6
No. of chaetigers	-	185	87-116	113-171	-	131-155	181	48-126	-	-	-	93	155	24-124	142
Colour pattern	Whitish yellow	-	N/A	N/A	-	None	None	None	-	N/A	N/A	N/A	Brownish with colour marks	No colour pattern	Anterior with two transverse lines, intermittent
Shape of prostomium	Sub-globular, broader than long	Oval	Broadly oval	Oval	-	Oval to sub-hexagonal	Oval	Oval	-	Oval, broader than long	Oval	Oval, broad	Oval	Oval, wider than long	Sub-hexagonal
No. of eyes	4	4	4	4	-	4	4	4	-	4	-	4	4	4	4
Arrangement of eyes	Trapezoidal, anterior eyes larger than posterior eyes	Trapezoid	Trapezoid	Trapezoid	-	Trapezoidal to open trapezoidal	Trapezoidal	Trapezoidal	-	Trapezoidal	-	Widely trapezoidal	Open trapezoidal	-	Wide trapezium
Presence of ocular specks	Yes	-	None	None	-	None	None	Yes	Yes	Yes	None	None	-	-	-

Shape of palps	Subtriangular, fused at base	Voluminous	Broadly triangular, distinctly separate	Longer than broad, triangular, separate	-	Triangular, longer than broad, separate	Triangular	Triangular, distinctly separate	Large, projecting	Broadly triangular, distinctly separate to triangular, longer than broad, fused at base	Distinctly separate, triangular, becoming narrower toward the point of the triangle	Small, triangular, broad base	Long, triangular, fused at bases	-	Rounded
Lateral antennae (No. of articles)	14-18	13-14	13-17	11-28	-	12-20	16	9-16	-	10-15	9-16	14	10-12	11-12	11
Median antennae (No. of articles)	23-30	16-19	24	9-29	-	20-36	19	7-18	-	7-20	6-21	17	13-14	16	13
Dorsal tentacular cirri (No. of articles)	19-25	16-19	14-24	10-27	-	19-28	13	12-24	-	12-15	12-23	18	15	20-25	11-12
Dorsal cirri (No of articles)	16-25	18-24	11-24	6-35	15-25	12-40	12-19	9-28	8-12	7-22	9-30	9-22	7-9	8-12	8-10
Shape of ventral cirri	-	Thumb-shaped	Short, subequal	Digitiform	-	Short, digitiform	Short, digitiform	Short, digitiform	-	Short, digitiform	Slender, short, digitiform	Short, slender, digitiform	-	Short	Thumb-shaped
Compound chaetae	Bidentate	Bidentate, sub-bidentate	Unidentate or minutely bidentate	Unidentate or minutely bidentate	Unidentate or minutely bidentate	Unidentate or minutely bidentate	Bidentate	Bidentate with weaker secondary tooth, minutely bidentate	-	Unidentate or minutely bidentate	Unidentate or minutely bidentate	Unidentate or minutely bidentate	Bidentate, minutely bidentate	Minutely bidentate	Bidentate, sub-bidentate
Anterior: No. of chaetae (per bundle)	-	-	9-11	9-15	-	10-13	12-14	8-14	-	5-11	8-14	11	10-11	18	9
Midbody: No. of	-	-	7-9	5-10	-	7	6-8	9	-	7-10	9-12	9	4-5	5	8

chaetae (per bundle)															
Posterior: No. of chaetae (per bundle)	-	-	5-8	5-7	-	5	up to 5	4-7	-	3-5	4-8	7	-	3	3-4
Presence of pseudosimpl e chaetae	-	Yes	Yes	Yes	Yes	Yes	Yes	Yes	-	Yes	No	No	-	-	No
Shape of ventral simple chaetae	-	Slender, slightly curved, subdistal with fine spines	Gently curved, bidentat e	Gently curved, unidentate	-	Gently curved, unidentate	Sinuose, bidentate	S-shaped, bidentate	-	S-shaped, bidentate	Gently curved, unidentate	Gently curved, unidentate	-	-	-
Pharynx: No. of segments	6-7	5-6	10-13	7-19	5	9-11	9-10	7-15	-	8-13	7-10	Everted	9	14	8-9
Proventricle: Length (No. of chaetigers)	-	10.-16	7-11	6-14	-	6	10	9-15	-	8-15	7-13	12	7	8-10	-
Proventricle: Number of muscle rows	-	38-42	35-40	35-46	-	31-34	45-50	33-50	40	40	28-43	31	37	42	37-38
Anal cirri: No. of articles	-		7-15	15-27	-	14-22	18	8-15	-	-	9-19	21	-	-	10-12

Table 2. Test statistic and associated significance values for Students t-tests (t-stat), Mann-Whitney (U) and Chi-squared (χ^2) tests performed on measured characters highlighted by the Principal Component Analysis (PCA) as contributing the most to the variation between individuals, for *Syllis armillaris* from the Iziko Southern African Museum and fresh specimens of *Syllis amicarmillaris*.

Measured characters	Test statistic			Significance value
	t-stat	U	χ^2	(P(T<=t)) two tail
Length of palps (mm)	-2.115	-	-	0.049
Palp width at base (mm)	-1.674	-	-	0.114
Length of prostomium (mm)	-	23.500	-	0.045
Width of prostomium (mm)	-0.719	-	-	0.485
Length of the secondary tooth on midbody chaetae (mm)	-0.600	-	-	0.656
Number of articles on median antennae (\bar{x})	-	38.500	-	0.405
Number of articles on lateral antennae (\bar{x})	-	36.500	-	0.324
Number of articles on short dorsal cirri (\bar{x})	-	56.500	-	0.657
Number of articles on long dorsal cirri (\bar{x})	0.511	-	-	0.616
Length of inferior chaetae on midbody (mm)	-	32.000	-	0.183
Shape of posterior ventral spines	-	-	0.556	0.456
Number of teeth on ventral posterior spines	-	-	0.556	0.456
Length from palps to chaetiger 10 (mm)	-0.953	-	-	0.353
Width of worm at chaetiger 10 (mm)	-2.016	-	-	0.060
Length of proventricle (mm)	-2.171	-	-	0.044
Width of anterior chaetae at base 1 (mm)	-1.121	-	-	0.277
Length of anterior inferior chaetae (mm)	0.657	-	-	0.520
Width of posterior chaetae at base 1 (mm)	-	77.000	-	0.043