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Descriptions of three new species of South African Syllidae Grube, 1850 (Polychaeta) and range confirmation of *Syllis amicarmillaris* Simon, San Martín & Robinson, 2014

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Abstract. The understanding of South African polychaetes has greatly benefited from John Day's seminal contributions, particularly his 1967 monograph. However, many of the species he documented were described as non-endemic or cosmopolitan. Some of these may in fact represent distinct species, leading to an underestimation of the true diversity of Southern African polychaetes. This study examines four species belonging to the highly diverse and morphologically variable family Syllidae. Three of these were previously identified as *Syllis prolifera*, *Syllis variegata*, and *Paraehlersia ferruginea* based on Day's monograph. Detailed morphological analyses and comparisons with Day's material reveal that these specimens represent new species, which are described and illustrated here. The fourth species was identified as *Syllis amicarmillaris* following Simon *et al.* (2014), despite its occurrence approximately 250 km from the type locality. Our observations confirm that this population corresponds to *S. amicarmillaris*, with the only noted differences being related to the smaller size of our specimens, compared to the type description. Our results suggest that syllid diversity in South African waters is likely underestimated, and that further expanding molecular sampling—especially within syllid species complexes—will be essential to uncover hidden diversity and clarify species boundaries.

Keywords. South Africa, Annelida, diversity, *Syllis*, *Paraehlersia*.

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Introduction

The knowledge of polychaetes in South Africa and adjacent areas was significantly advanced by the eminent polychaetologist John Day. His extensive series of contributions on the coastal areas of Southern Africa culminated in the influential *Monograph of Polychaeta of Southern Africa* (Day 1967a, 1967b). However, many species documented in this monograph are not endemic to the region, instead showing ‘cosmopolitan’ distributions (Simon *et al.* 2022). Recent research suggests that several of these supposedly cosmopolitan species may actually represent complexes of morphologically similar species (e.g., Hutchings & Kupriyanova 2018). Consequently, the real diversity of Southern African polychaetes has likely been significantly underestimated (Simon *et al.* 2022).

Moving forward, it is crucial for non-taxonomists, who often need to identify polychaetes in their research, to recognize that nearly half the species listed in Day’s monograph should be considered pseudo-cosmopolitans or unresolved cosmopolitans (*sensu* Darling & Carlton 2018). They may actually comprise local cryptic species (e.g., Simon *et al.* 2019; Kara *et al.* 2023), whose descriptions in Day’s monograph should be used with caution. Moreover, characters and tools (particularly those based on genetics) allowing species identifications and classifications have evolved over time, leading to thorough revisions of diagnostic characters for many taxa, notably within the family Syllidae Grube, 1850 (Martin *et al.* 2021).

Species descriptions within Syllidae have traditionally relied on morphological characters, with the barrel-shaped proventricle —a muscular structure associated with the gut— serving as key diagnostic feature (Rouse *et al.* 2022). Nevertheless, the family is exceptionally large and morphologically diverse, encompassing a wide range of species —from minute meiofaunal to very long forms— distributed globally across virtually all marine environments (Martin *et al.* 2021). Unsurprisingly, modern observational methods, coupled with molecular techniques, have uncovered numerous cryptic or pseudo-cryptic complexes, hidden among what were considered ‘cosmopolitan’ species (e.g., Nygren 2014; Hutchings & Kupriyanova 2018). The complexity of the family underscores the need to re-examine many of these so-called cosmopolitan species, particularly in regions such as South Africa, where only five new species have been described since the publication of the seminal Day monograph (Simon *et al.* 2014; Sedick & Simon 2019).

The present study focuses on four species of South African Syllidae from two genera: *Syllis* Savigny in Lamarck, 1818 (Syllinae), likely the most species-rich genus within the family, and *Paraehlersia* San Martín, 2003 (Eusyllinae), a small genus with only nine recognized species (Martin *et al.* 2021; San Martín *et al.* 2023; Prado & San Martín 2024; Read & Fauchald 2025). Among the species of *Syllis*, two were previously identified as the ‘cosmopolitan’ *S. prolifera* Krohn, 1852 and *S. variegata* Grube, 1860, following Day (1967a), by Sedick (2018). However, recent studies proved that *S. prolifera* was a species complex (del Olmo *et al.* 2024), while the same was suggested for *S. variegata* (San Martín 2003). The third species was tentatively identified as *S. amicarmillaris* Simon, San Martín & Robinson, 2014 by Sedick (2018). However, this species was described from Atlantic-influenced coasts of South Africa (Simon *et al.* 2014), while our material was collected in the region influenced by the Indian Ocean. As for the species of *Paraehlersia*, it was initially identified only to the genus level by Arturo Álvarez-Aguilar, based on materials collected about 110 km east of Mossel Bay (Álvarez-Aguilar and Simon, unpublished data). In turn, Day (1967a) had only reported *Paraehlersia ferruginea* (Langerhans 1881), which was originally described from Canary Islands and appears to be widely distributed in North Atlantic temperate and tropical waters (San Martín 2003; Prado & San Martín 2024). However, these reports have also been suggested to

comprise a species complex (San Martín 2003). Therefore, in this study we are providing detailed descriptions and illustrations of these four South African species, and we discuss their actual taxonomic status.

Material and methods

Samples were collected on the South African coast of the Indian Ocean by scraping 10×10 cm of algal turf on rocky shores at the lower intertidal in Mossel Bay in 2015, and with a manual box corer in intertidal soft sediments at Knysna Estuary in 2021. Samples were sieved through a 500 µm pore size mesh and the specimens in the retained substrate were sorted under a stereo microscope Leica MZ75, relaxed in 7% MgCl₂ in tap water, fixed in a 4% formalin seawater solution, and stored in 70% ethanol.

Morphological features were examined under either a dissecting microscope Zeiss Stemi 2000C or a Nikon Eclipse e200 compound microscope and photographed with Euromex CMEX10pro digital cameras attached to either microscope, using the software ImageFocusAlfa by Euromex (© 2014–2023). For light microscopy observations, selected specimens were placed on a slide with a drop of glycerin, covered, and sealed with transparent nail enamel. For Scanning Electron Microscope (SEM) observations, selected specimens were prepared using standard SEM procedures (Martin *et al.* 2003). SEM images were taken with a Hitachi TM3000 TABLETOP microscope at the SEM Service of the CEAB-CSIC. Figure plates were composed in Adobe Photoshop 2024 (25.11.0 release). Specimens were deposited at the Biological Collections of the Center for Advanced Studies of Blanes (CEAB) and the Iziko South African Museum, Cape Town (SAM). Additionally, the material originally identified by Day was borrowed from SAM, mostly collected during University of Cape Town (UCT) Ecological Surveys. Specimen measurements are indicated as those for the holotype, with the variability in paratypes between brackets.

Results

Taxonomic account

Phylum Annelida Lamarck, 1809
Class Polychaeta Grube, 1850
Subclass Errantia Audouin & Milne-Edwards, 1832
Order Phyllodocida Dales, 1962
Suborder Nereidiformia Glasby, 1993
Family Syllidae Grube, 1850
Subfamily Syllinae Grube, 1850
Genus *Syllis* Savigny in Lamarck, 1818

Syllis kikeballesterosi sp. nov.

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Figs 1–4

Syllis prolifera (Grube, 1860) – Sedick 2018: 136–137.

non *Syllis* (*Typosyllis*) *prolifera* – Krohn 1852: 66. — Day 1967a: 248, fig. 12.3g–i.

Etymology

The species name ‘*kikeballesterosi*’ is dedicated to our esteemed colleague and dear friend, Enric “Kike” Ballesteros, an exceptional naturalist and ecologist. Kike passed away on November 27, 2024, after courageously battling an aggressive illness. True to his passion for marine life, he continued diving and exploring the underwater world he cherished until his final days.

Type material

Holotype

SOUTH AFRICA • complete specimen; Mossel Bay; [34°11'11" S](#), [22°09'38" E](#); Apr.–Oct. 2015; Safiyya Sedick leg.; intertidal algal turf; fixed in 4% seawater formalin, preserved in 70% ethanol; SAM-A089287.

Paratypes

SOUTH AFRICA • 10 complete specimens, 9 anterior fragments, 3 posterior fragments; same collection data as for holotype; SAM-A089288 • 7 entire specimens; same collection data as for holotype; CEAB AP 998A • 2 specimens, prepared for light microscopy; same collection data as for holotype; CEAB AP 998B • 2 specimens, prepared for SEM; same collection data as for holotype; CEAB AP 998C.

Other material examined

SOUTH AFRICA • 1 incomplete, 5 complete specimens; Glencairn False Bay, station FAL128S; [34°9'41" S](#), [18°25'53" E](#); 17 Feb. 1953; subtidal; fixed in 4% seawater formalin, preserved in 70% ethanol; SAM-MB-A020804 • 3 complete specimens; Saldanha Bay, UCT Ecological Survey, station SB246C; [33°4.1" S](#), [17°59.7" E](#); 4 May 1960; fixed in 4% seawater formalin, preserved in 70% ethanol; SAM-MB-A060290 • 4 complete specimens; West Coast Dredge, UCT Ecological Survey, station WCD41Q; [33°6'29.99" S](#), [17°56'42" E](#); 2 May 1960; subtidal; fixed in 4% seawater formalin, preserved in 70% ethanol; SAM-MB-A069907 • 1 incomplete specimen; KwaZulu-Natal, Tongaat Beach; [29°36'53.35" S](#), [31°9'27.3" E](#); 1946; intertidal; fixed in 4% seawater formalin, preserved in 70% ethanol; SAM-MB-A020805.

Description

Body short, thin, narrow, 3.3 (3.3–4.2) mm long, 0.4 (0.32–0.53) mm wide, with 38 (34–53) chaetigers, with two dark, fine, transversal lines dorsally in anterior segments (Fig. 1A, E–F). Prostomium small, roughly sub-pentagonal (Fig. 1A–B, E–G), with four eyes in trapezoidal arrangement; eyespots not seen. Palps short, separate, triangular, fused at base (Figs 1A–B, G, 3B). Median antenna with 12 articles, lateral antennae with 15, 1.2 and 1.4 times as long as prostomium and palps, respectively (Figs 1A–B, F–G, 3A–B). Dorsal tentacular cirri with 25 articles, ventral tentacular cirri with 15–16 (Figs 1B–G, 3A–B). Tentacular segment narrower than subsequent ones, with a short occipital flap (Figs 1A–B, F, 3A–B). Dorsal cirri long, narrow, as long as body width (Figs 1A–E, 3A–B). Dorsal cirri of chaetiger 1 with 23 articles, 16 in chaetiger 2, 21 in chaetiger 3, and 16–18 (short) and 18 (long) in midbody chaetigers (Figs 1A–G, 3A). Parapodial lobes short, conical, distal papillae absent (Figs 2A–B, 3A, D–E). Ventral cirri shorter than parapodial lobes, lanceolated in few anterior segments (Figs 2A, 3B), then digitiform all along body (Fig. 3B, D–E). Compound chaetae with heterogomph shaft with few, short subdistal spines; blades bidentate, with sub-distal teeth smaller than distal ones, slight dorso-ventral gradation in length, and serration with spines of moderate size, all similar in size in dorsal chaetae, progressively longer towards basis in ventral-most chaetae (Figs 2A–G, 4A–B). Anterior parapodia with 10–11 compound chaetae, with blades 27 µm long (dorsal) and 22 µm long (ventral) (Figs 2A, C–D, 3D, 4A). Midbody parapodia with 10–11 compound chaetae, blades 23 µm long (dorsal), 20 µm long (ventral) (Figs 2B, E–F, 3E, 4B). Posterior parapodia with eight compound chaetae, blades 18 µm long (dorsal), 12 µm long (ventral) (Fig. 2B, G). Dorsal simple chaetae straight, with pointed tips, lacking marginal spines distally (Figs 2H, 4C); ventral simple chaetae bidentate, with well-marked teeth directed laterally (subdistal one slightly smaller than distal one) and a few short, well-marked marginal spines distally (Figs 2I, 4D–E). Four aciculae on anterior parapodia, one thinner with subdistal swelling and pointed tip, three drumstick-shaped (Fig. 2J), reducing in number to two, drumstick-shaped in midbody and posterior segments (Fig. 2K); aciculae of posterior parapodia thicker than in anterior parapodia, one thicker than the other (Fig. 2K). Pharynx similar in length and width to proventricle, extending for

six segments, with pharyngeal tooth near opening, but in slightly posterior position (Fig. 1A–B, E–F). Proventricle occupying six segments, short, wide, with 23 muscular rows (Fig. 1A–B, E–F). Pygidium with two anal cirri of similar length, with 15–18 articles; pygidial appendix digitiform (Figs 1A, D–E, H, 3C).

Distribution

Southern coast of South Africa (Mossel Bay). Day (1967a) reported *S. (T.) prolifera* as ranging from Namibia to Mozambique, a span that crosses four distinct biogeographical zones from cool temperate to tropical waters. However, considering the results highlighted in del Olmo *et al.* (2024) for the Mediterranean lineages and our own observations, such an extensive distribution is highly improbable for a single species. This may also apply to *S. kikeballesterosi* sp. nov., whose precise distribution would require further targeted sampling to be accurately assessed.

Remarks

The putative cosmopolitan species *S. prolifera* has recently been revealed to be a complex of pseudocryptic species containing at least five different lineages within the western Mediterranean Sea and Gulf of Cadiz (del Olmo *et al.* 2024). Comparing our specimens with all these different lineages is beyond the scope of our paper. However, there are evident differences in the length pattern of the first five dorsal cirri (Table 1), as well as in the shape of midbody and posterior chaetae, which shows marginal spines always longer and thicker in our specimens (Fig. 4A–B) compared with the those in the Mediterranean lineages (del Olmo *et al.* 2024).

The original types of *S. prolifera* described in Krohn (1852) are lost according to Licher (1999), who defined and described the neotype for specimens collected in the type locality, Villefranche-sur-Mer (French Mediterranean). San Martín (2003) also included the species as reported in the Iberian peninsula, and the description perfectly agrees with that in Licher (1999), with only a slight difference in the length pattern of the anterior appendages, with the 5th dorsal cirri being slightly shorter (Table 1). According to these two authors, the European *S. prolifera* and the specimens described by Day (1967a) are longer (10.5 mm and 10–20 mm, respectively) than our specimens (3.6–4.2 mm long). The specimens in Day (1967a) have palps shorter than our specimens, while both the European and Day (1967a) specimens have much longer antennae (32 and 27 articles in median antenna, 20 and 16 in lateral antenna, respectively) than our specimens (12 and 15). San Martín (2003) reported the presence of a small papilla in the parapodial lobes and digitiform ventral cirri (absent and lanceolated in our specimens), blades of compound chaetae with both teeth similar in size (subdistal tooth smaller than distal one in our specimens), up to five narrow aciculae with blunt tips in anterior chaetigers, reducing in number and becoming drumstick shaped in posterior segments (three aciculae in anterior segments, also reducing in number towards posterior segments, but always being drumstick shaped in our specimens; Fig. 2K).

However, the description of *S. prolifera* in Day (1967a) is presumably based on specimens reported from four studies (Day 1951, 1953, 1957, 1963). We could examine material that can be linked conclusively to the first and the last of these, in addition to material collected during other University of Cape Town Ecological Surveys from Saldanha Bay and dredging off the west coast in May 1960. Our observations reveal that these specimens represent three taxa, all different from our new species.

The worms collected in False Bay —MB-A020804, a station number listed in Day (1960), although not included as a collection site for the species— and Saldanha Bay —station MB-A060290— match the description in Day (1967a). They usually have 3–4 aciculae in anterior parapodia, decreasing to 2–3 in mid parapodia, with at least 2–3 having pointed tips and at least one a slightly bent tip; the dorsal simple chaetae are similar in shape to those in our species, but the tip is minutely bidentate, while the ventral

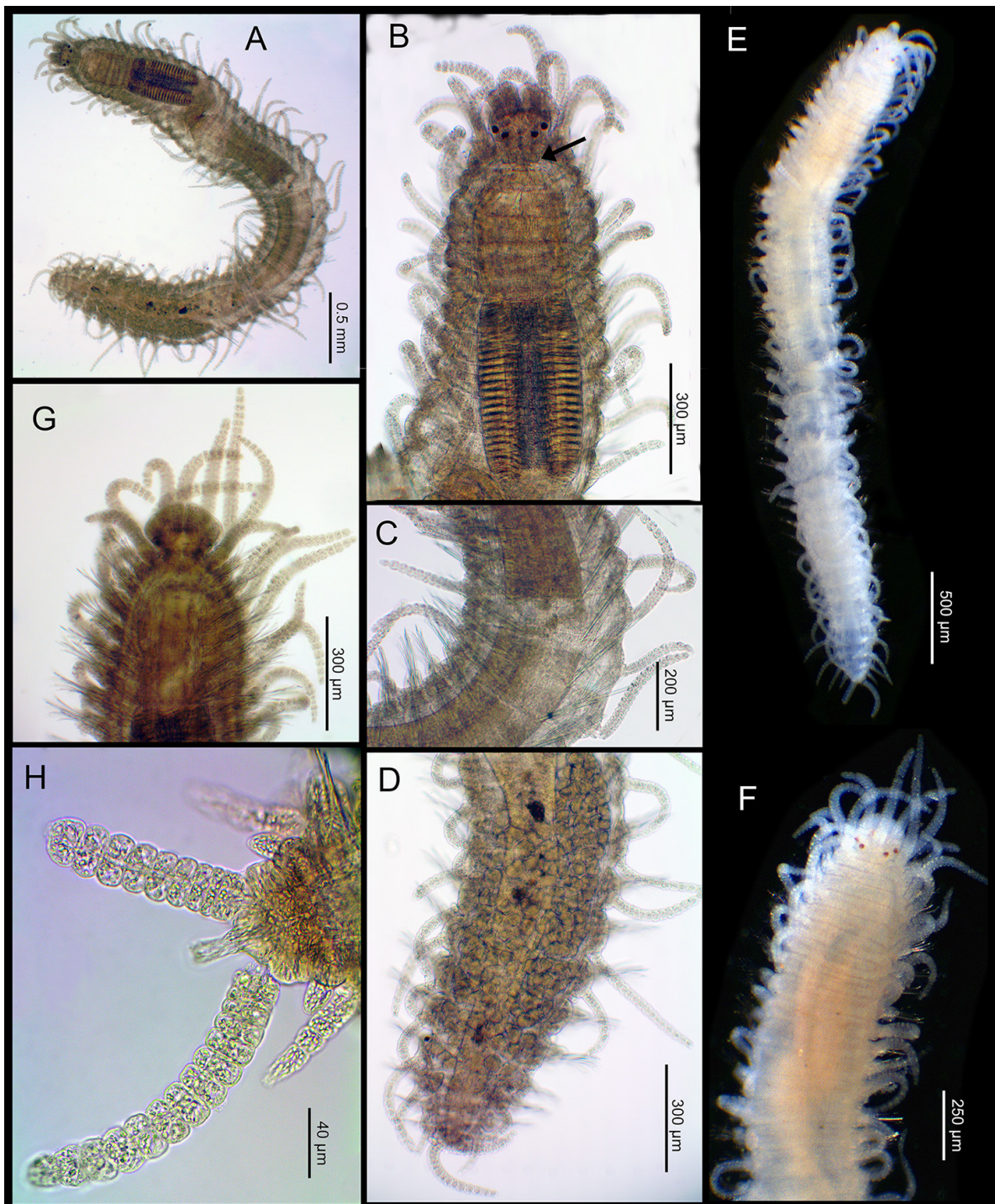


Fig. 1. *Syllis kikeballesterosi* sp. nov., paratype (CEAB AP 998B). **A.** Entire body, dorsal view. **B.** Anterior end, dorsal view showing the short occipital flap (black arrow). **C.** Midbody, dorsal view. **D.** Posterior end, dorsal view. **E.** Entire body, dorsal view. **F.** Anterior end, dorsal view. **G.** Anterior end, ventral view. **H.** Detail of posterior end, ventral view.

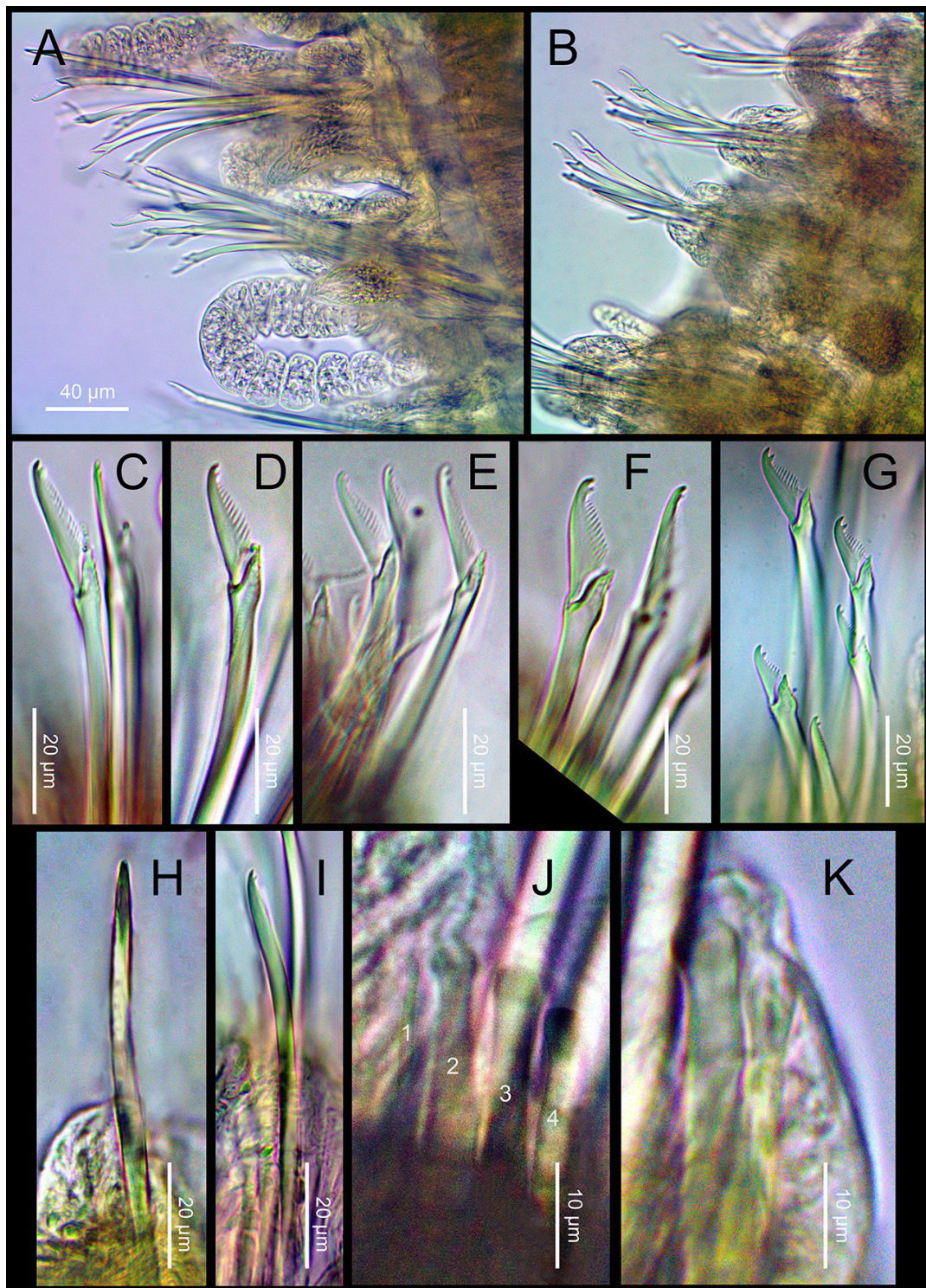


Fig. 2. *Syllis kikeballesterosi* sp. nov., paratype (CEAB AP 998B). **A.** Midbody parapodia. **B.** Posterior parapodia. **C.** Dorsal compound chaetae, anterior parapodium. **D.** Ventral compound chaeta, same parapodium as C. **E.** Dorsal compound chaetae, midbody parapodium. **F.** Ventral compound chaetae, same parapodium as E. **G.** Compound chaetae, posterior parapodium. **H.** Dorsal simple chaeta. **I.** Ventral simple chaeta. **J–K.** Aciculae. **J.** Anterior parapodium, indicated by numbers. **K.** Posterior parapodium.

simple chaeta is strongly bidentate, and the posterior falcigers include some with short, strongly bidentate blades – similar to those shown in Day (1967a: fig. 12.3.f).

Specimens from West Coast Dredges —station MB-A069907; reported, but not described, in Day (1963)— are similarly sized to our species, but have 4–5 aciculae, including some straight aciculae and some with strongly bent tips, and very robust falcigers. They also have what looks like simple chaetae through loss of blade. Although these might correspond to falcigers having lost the blades, these are the only specimens consistently showing these simple chaetae. Furthermore, these specimens were collected from depths greater than 1000 m, and are therefore unlikely to be the same species occurring in intertidal or subtidal waters.

The specimen from KwaZulu-Natal —station MB-A020805; Day (1951)— is quite slender (but still bigger than our species), has very fine dorsal cirri, and lacks dorsal stripes of pigment across the anterior region, showing a diffuse brown pigmentation pattern instead.

Two species of *Syllis* having drumstick-shaped aciculae have been described from the studied region, including *Syllis unzima* Simon, San Martín & Robinson, 2014 and *Syllis zahri* Sedick & Simon, 2019

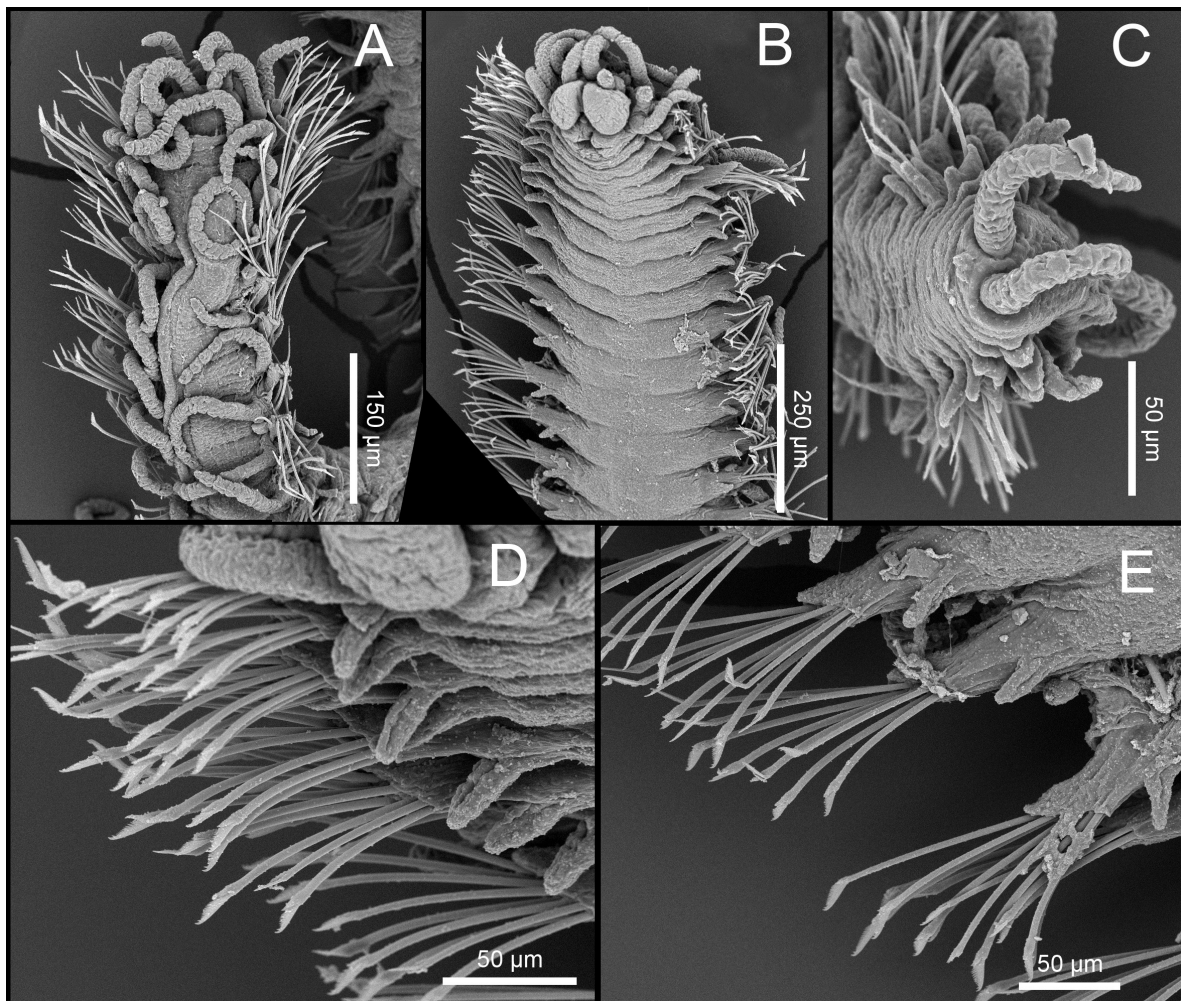


Fig. 3. *Syllis kikeballesterosi* sp. nov., paratype (CEAB AP 998C). **A.** Anterior end, dorsal view. **B.** Anterior end, ventral view. **C.** Pygidium, ventral view. **D.** Anteriormost parapodia, ventral view. **E.** Midbody parapodia, ventral view.

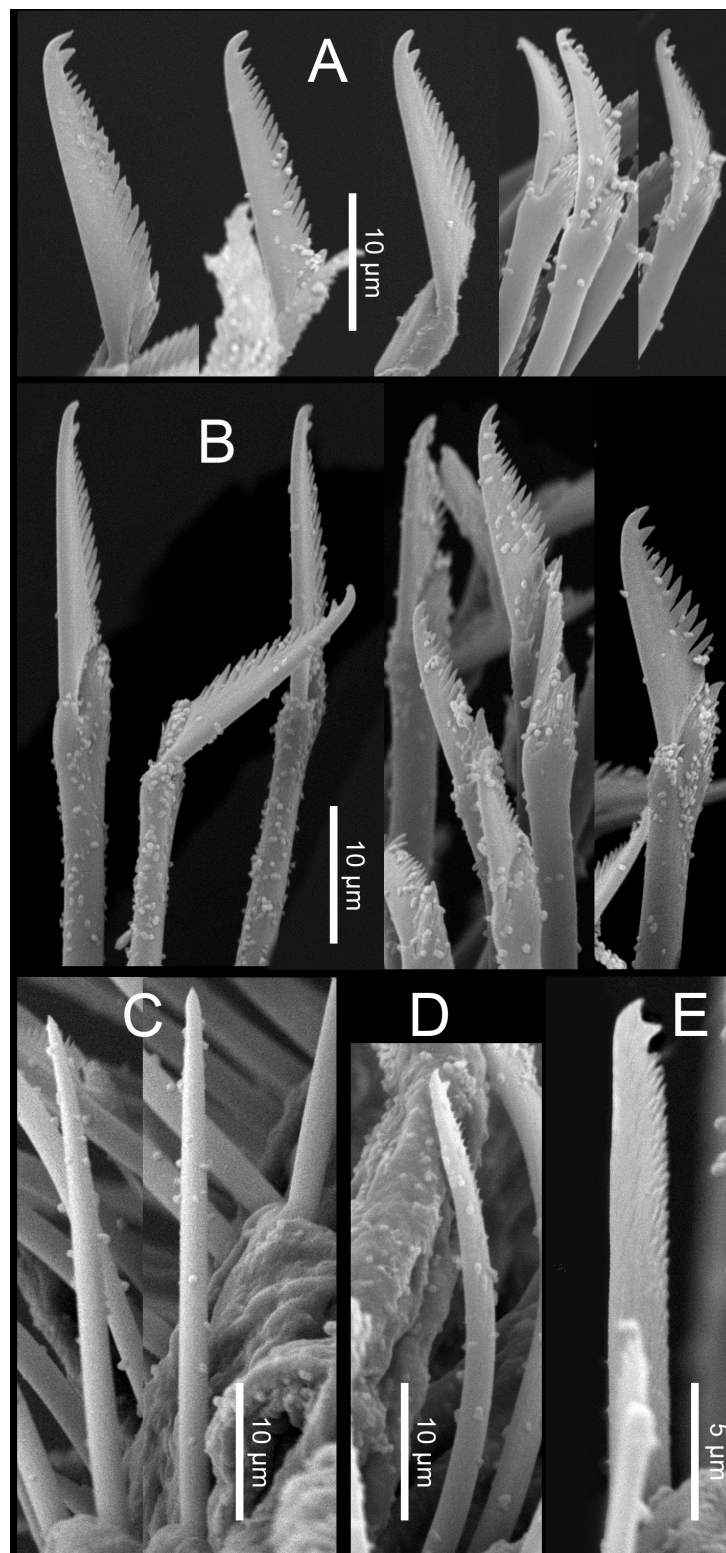


Fig. 4. *Syllis kikeballesterosi* sp. nov., paratype (CEAB AP 998C). **A.** Compound chaetae, anterior parapodia. **B.** Compound chaetae, midbody. **C.** Dorsal simple chaetae, posteriormost parapodia. **D.** Ventral simple chaetae, posteriormost parapodia. **E.** Detail of the tip of a ventral simple chaeta, posteriormost parapodia.

Table 1. Alternating length pattern of antennae, dorsal tentacular cirri, and first five anterior dorsal cirri in the *Syllis prolifera* complex, the neotype in Licher (1999), the specimen in San Martín (2003), and the five lineages in del Olmo *et al.* (2024), compared to *Syllis kikeballesterosi* sp. nov. CA: central antennae; LA: lateral antennae; DTC: dorsal tentacular cirri; DC1–DC5: dorsal cirri from chaetigers 1 to 5. Length relationships expressed as: very short (s) < short (S) < long (l) < very long (L).

	CA	LA	DTC	DC1	DC2	DC3	DC4	DC5
Lineage 1	S	s	L	S	L	S	s	S
Lineage 2	S	s	l	S	l	L	S	L
Lineage 3	S	s	L	s	S	l	L	S
Lineage 4	l	s	L	s	L	S	s	l
Lineage 5	s	s	L	s	S	L	S	s
<i>Syllis prolifera</i> (neotype)	l	s	l	L	S	l	L	S
<i>Syllis prolifera</i> (San Martín, 2003)	l	s	l	L	S	l	L	s
<i>Syllis kikeballesterosi</i> sp. nov.	s	S	L	L	S	l	l	S

(Simon *et al.* 2014; Sedick & Simon 2019). These also share with our new species the characteristic color pattern formed by dark transversal bands on each anterior segment. *Syllis unzima* also has the pharyngeal tooth in the anterior margin in a slightly posterior position but differs in having unidentate compound chaetae with long spines on margin, unidentate ventral simple chaetae, proventricle shorter than pharynx (extending for four chaetigers), reproducing by viviparity, and living as symbiont with holothurians. *Syllis zahri* differs in having the pharyngeal tooth close to pharyngeal anterior margin, two types of pseudo-simple chaetae formed by loss of blade and enlargement of shaft in different regions of the body, dorsal simple chaetae with rounded tip, and ventral simple chaetae unidentate, with smooth margin.

Other species of *Syllis* show drumstick-shaped aciculae and a pharyngeal tooth placed slightly backwards from anterior margin. Among them, *Syllis vivipara* Krohn, 1869 from the Mediterranean Sea, Atlantic Ocean, and Caribbean Sea, *Syllis proluxa* Ehlers, 1901 from South America, and *Syllis escribanoi* San Martín, Lucas & Westheide, 2021 from China, show either some or all chaetae unidentate (Hartman 1964; San Martín 2003; San Martín *et al.* 2021). *Syllis rubicunda* Aguado, San Martín & Nishi, 2006 from Japan, *Syllis antoniae* Salcedo-Oropesa, San Martín & Solís-Weiss, 2012 from the Mexican Pacific, and *Syllis busseltonensis* (Hartmann-Schröder, 1982), *Syllis similisunzima* San Martín, Lucas & Hutchings, 2023, and *Syllis thylacine* San Martín, Lucas & Hutchings, 2023 from Australia, all have bidentate chaetae. *Syllis rubicunda* differs in having broad dorsal cirri and a distinctive red or orange color pattern (Aguado *et al.* 2006). *Syllis antoniae* lacks a dorsal color pattern and the long dorsal cirri have more than 60 articles, are about 3× as long as body width, and alternate with short cirri with ca 30 articles (Salcedo-Oropesa *et al.* 2012). *Syllis busseltonensis* also lacks dorsal color pattern, the pharynx is narrower than proventricle, each occupying 3–5 segments, the dorsal simple chaetae are bidentate and have a subdistal marginal serration, and the ventral simple chaetae are slender and lack distal serration (San Martín *et al.* 2023). *Syllis similisunzima* has a color pattern with dark transversal bands, but differs in having long midbody dorsal cirri with >30 articles, twice as long as body width, and alternating with short cirri with ca 20 articles, distally bilobed parapodial lobes, 7–8 chaetae per parapodium with subdistal tooth markedly smaller than distal one, bidentate dorsal simple chaeta with subdistal marginal serration, and ventral simple chaetae bidentate, smooth (San Martín *et al.* 2023). *Syllis thylacine* has a dorsal color pattern with segmental transverse reddish bands on posterior margins of each

segment and a lateral spot at bases of each cirrophore, midbody dorsal cirri alternating from similar to body width (20 articles) to longer than body width (up to 30 articles), bidentate compound chaetae with subdistal teeth similar or larger than distal one, bidentate dorsal simple chaetae with subdistal marginal serration, bidentate smooth ventral simple chaetae, and longer pharynx and proventricle (7–8 segments, 32 muscle cell rows) (San Martín *et al.* 2023).

Syllis pseudohyalina sp. nov.

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Figs 5–8

non *Syllis* (*Typosyllis*) *variegata* Grube, 1860 – Day 1967a: 248, fig. 12.3j–i.

non *Syllis variegata* Grube, 1860 – Day 1960: 308, in part. — Sedick 2018: 137–138.

Etymology

The species name ‘*pseudohyalina*’ refers to the close similarity with the Mediterranean *Syllis hyalina*, by adding the prefix ‘*pseudo*’ coming from the Greek word ‘*pseudos*’ (ψεύδος), meaning ‘false’ or ‘deceptive’, being commonly used to reflect something that resembles another thing but is not genuinely that thing.

Type material

Holotype

SOUTH AFRICA • entire specimen; Mossel Bay; [34°11'11" S, 22°09'38" E](#); Apr.–Oct. 2015; Safiyya Sedick leg.; intertidal algal turf; fixed in 4% seawater formalin, preserved in 70% ethanol; SAM-A089289.

Paratypes

SOUTH AFRICA • 3 entire specimens, 1 regenerating posterior end, 1 lacking posterior region; same collection data as for holotype; SAM-A089290 • 2 specimens, prepared for light microscopy; same collection data as for holotype; CEAB AP 1001A • 2 specimens, prepared for SEM; same collection data as for holotype; CEAB AP 1001B.

Other material examined

SOUTH AFRICA • 3 incomplete specimens; West Coast Dredge, UCT Ecological Survey, station WCD19J; [33°5'35.9988" S, 17°54'29.9982" E](#); 29 Apr. 1959; fixed in 4% seawater formalin, preserved in 70% ethanol; SAM-MB-A069882 • 4 complete specimens, 5 incomplete specimens; West Coast Dredge, UCT Ecological Survey, station WCD8G; [34°9'18" S, 18°17'30.0012" E](#); 24 Mar. 1959; fixed in 4% seawater formalin, preserved in 70% ethanol; SAM-MB-A069870 • 1 incomplete specimen; Saldanha Bay, UCT Ecological Survey, station SB189M; [33°1.1" S, 18°0.3" E](#); 30 Apr. 1959; fixed in 4% seawater formalin, preserved in 70% ethanol; SAM-MB-A060274.

Description

Body long, 3.6 (3.1–7) mm long, 0.46 (0.35–0.5) mm wide, with 49 (33–74) chaetigers (Figs 5A, 7A). Prostomium small, usually with two pairs of eyes, anteriormost half size of posterior; figured specimen being aberrant in having right posterior eye divided in two (Fig. 5A–B). Palps triangular, as long as prostomium, fused at bases (Figs 5A–B, 7B–C). Median antenna with 24 articles, lateral ones with 16–19 articles (Figs 5A–B, 7B–C). Dorsal tentacular cirri shorter than median antenna, longer than lateral, with 22 articles, ventral tentacular cirri with 14 articles (Figs 5B, 7A–C). Tentacular segment shorter than subsequent ones, partly covering posterior end of prostomium (Figs 5A–B, 7B). Nuchal organs not seen. Dorsal cirri thick, fusiform, distally tapering, similar in length, all along body, alternating long

and short at midbody, longer ones slightly longer than body width, with 24 articles at chaetiger 1, 16 at chaetiger 2, 17 at chaetiger 3, 27 at chaetiger 4, 12–13 (short), and 18–20 (long) at midbody chaetigers (Figs 5A, 7A–D). Parapodial lobes short, conical (Fig. 7C, F–G). Ventral cirri conical to pyriform in anterior segments, digitiform in mid- and posterior body, as long as parapodial lobes (Figs 6J–K, 7C–D). Compound chaetae with heterogomph shaft with few, short subdistal spines becoming thicker in midbody and posterior chaetigers; falciger blades bidentate, with subdistal teeth slightly smaller than distal one all along body, and few straight, thick marginal spines slightly longer at bases (Figs 6A–G, 8A–E). Anterior parapodia with nine compound chaetae, blades 27 μm (dorsal) and 22 μm (ventral) (Figs 6A–B, 7B–C, F, 8A). Midbody parapodia with 6–7 compound chaetae, blades 23 μm (dorsal), 20 μm (ventral) (Figs 6C–D, 7D, G, 8B–C). Posterior parapodia with 4–5 compound chaetae, blades 17.5–26.3 μm (dorsal), 12.5–14.2 μm (ventral), with some short blades markedly thinner than others (Figs 6E–G, 7E, 8D–E). Dorsal simple chaetae straight, bidentate, with teeth directed upwards, subdistal teeth slightly smaller than distal ones, with few short subdistal spines (Figs 6H, 8F), ventral simple chaetae curved, bidentate, with teeth directed laterally, both of similar size, with few short subdistal spines (Figs 6I, 8G). Four aciculae in anterior parapodia, one clearly thinner than others, with 90° bent tip, two straight with round, truncated end, and one with pointed oblique tip; two aciculae in midbody parapodia, thick, with pointed oblique tips, one clearly more oblique than other, both slightly protruding from acicular lobe; single acicula in posteriormost segments, with slightly inflated, oblique tips, slightly protruding from acicular lobes (Figs 6L–N, 7F). Pharynx short, red color, extending over 9–10 segments, with pharyngeal tooth located at opening, slightly posterior (Fig. 5B). Proventricle very

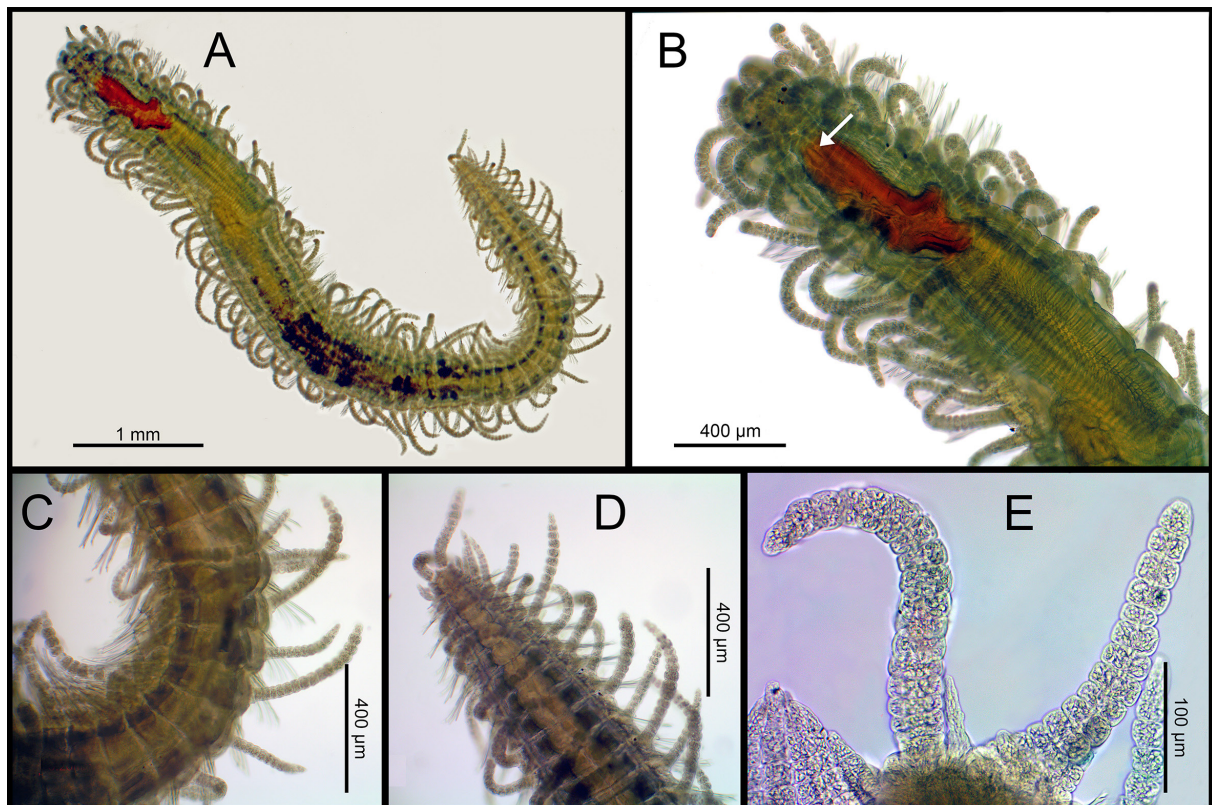


Fig. 5. *Syllis pseudohyalina* sp. nov., paratype (CEAB AP 1001A). **A.** Entire body, dorsal view. **B.** Anterior end, dorsal view (white arrow pointing at pharyngeal tooth). **C.** Midbody, dorsal view. **D.** Posterior end, dorsal view. **E.** Detail of pygidium, ventral view.

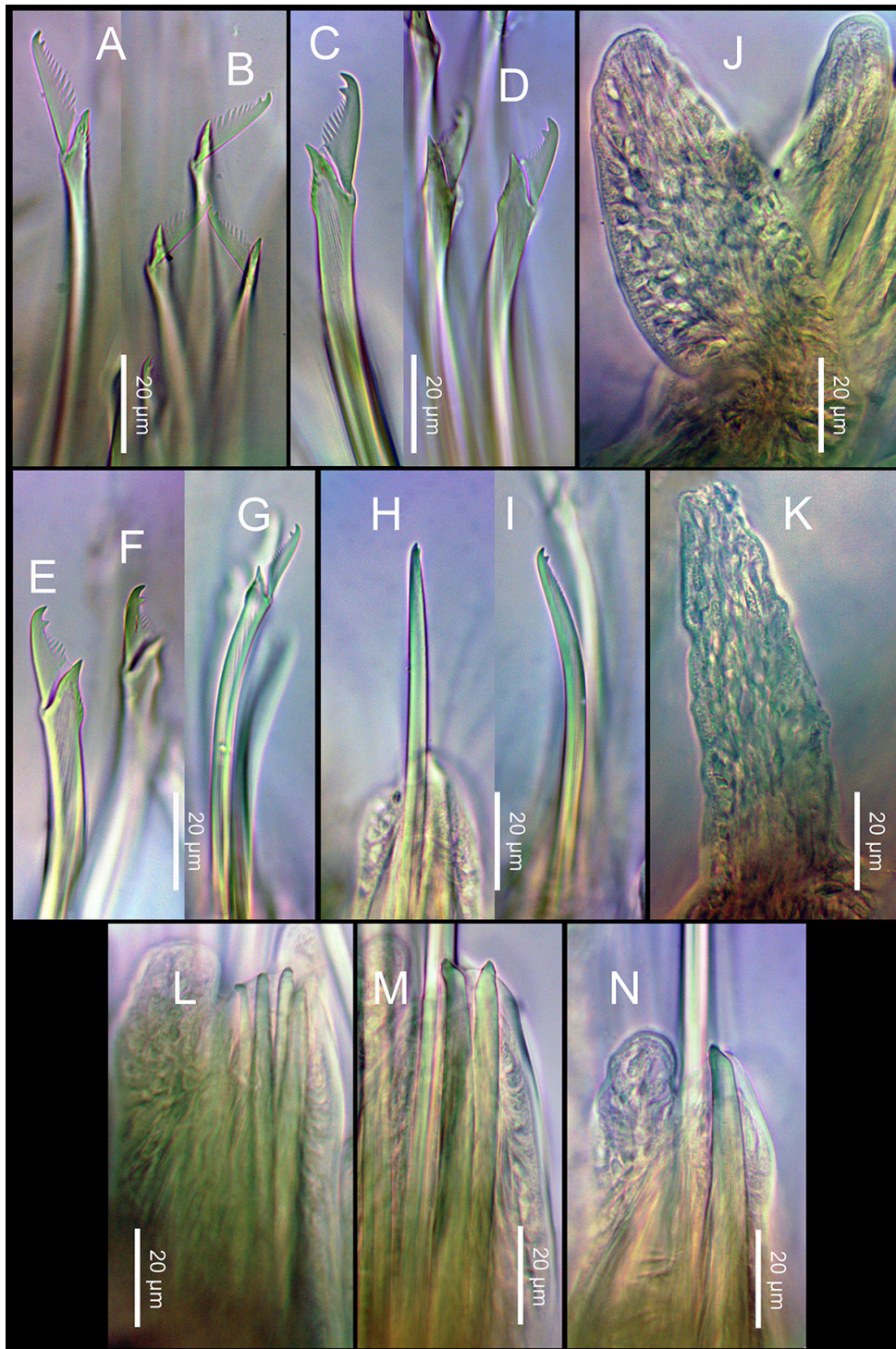


Fig. 6. *Syllis pseudohyalina* sp. nov., paratype (CEAB AP 1001A). **A.** Long compound chaetae, anterior parapodia. **B.** Short compound chaetae, anterior parapodia. **C.** Long compound chaetae, midbody parapodia. **D.** Short compound chaetae, midbody parapodia. **E.** Long, thick compound chaetae, posterior parapodia. **F.** Short, thick compound chaetae, posterior parapodia. **G.** Short, thin compound chaetae, posterior parapodia. **H.** Dorsal simple chaetae. **I.** Ventral simple chaetae. **J.** From anterior parapodia. **K.** From posterior parapodia. **L–N.** Aciculae. **L.** From anterior parapodia. **M.** Ventral cirri, midbody parapodia. **N.** Ventral cirri, posterior parapodia.

long, extending along 11–12 segments, with 45 (42–51) muscular rows (Fig. 5A–B). Pygidium small; 2 anal cirri with 14–17 articles; pygidial appendix only one, digitiform (Figs 5A, D–E, 7E).

Distribution

South African coast. Western Cape Province: off southwestern and southern (Mossel Bay) coasts.

Remarks

Our specimens most closely resemble *Syllis hyalina* Grube, 1863, originally described from the Mediterranean (Grube 1863; San Martín 2003). Both species lack body color—despite some specimens of *S. hyalina* have been reported as having dark transversal bands in anterior segments (San Martín 2003)—, have only falcigerous bidentate chaetae with the subdistal teeth similar in shape and size to the distal, and have the posterior acicula slightly protruding from the acicular lobe, slightly inflated distally, and having an oblique tip. However, the Mediterranean *S. hyalina* is longer (21 vs 6–7 mm) and has more chaetigers (110 vs 74), robust palps longer than prostomium (triangular, shorter than prostomium), shorter antennae (median: 7–15 articles, lateral: 11–12 articles vs median: 24, lateral: 16–19), dorsal tentacular cirri as long as median antenna (shorter than median antenna), ventral cirri longer than parapodial lobes (as long as parapodial lobes), and the pharynx lacking color and being slightly longer than proventricle, which shows 33 muscular rows (reddish, shorter, with 42 muscular rows in our specimens).

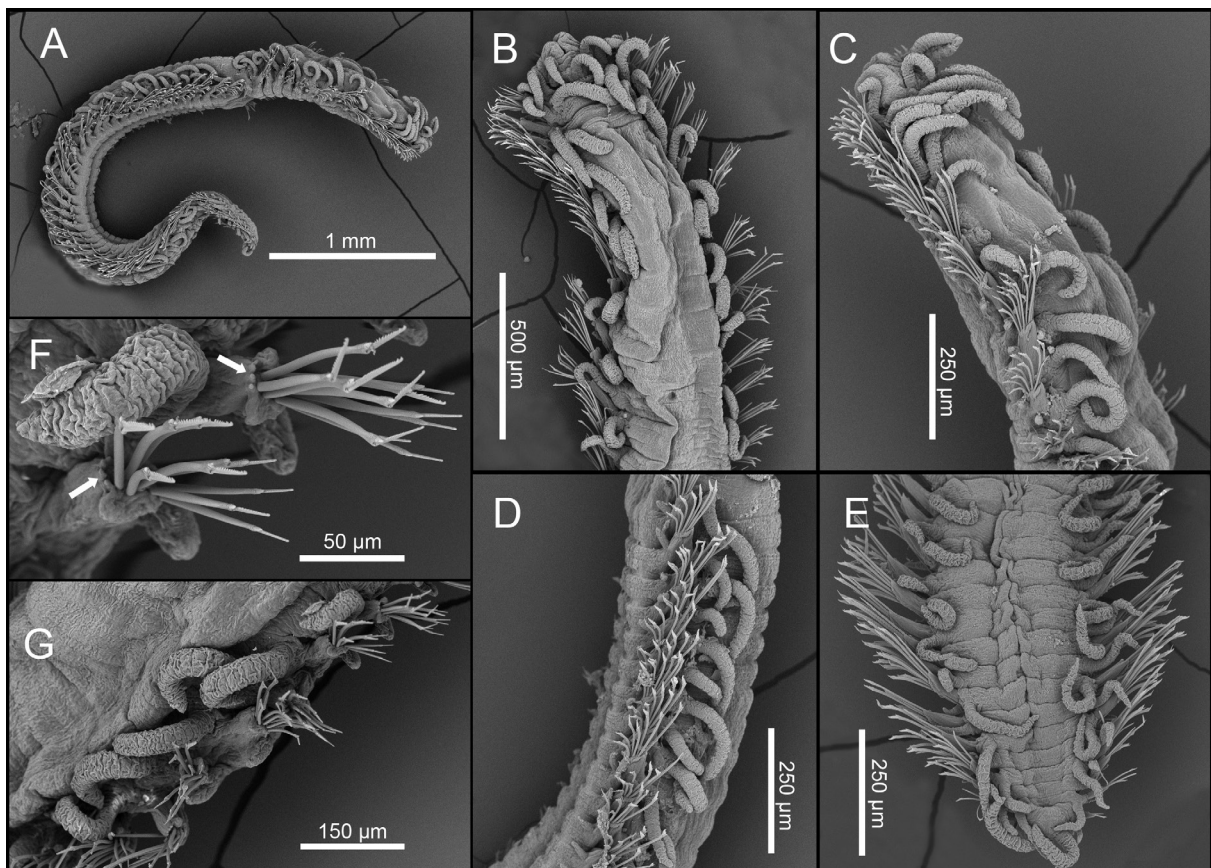


Fig. 7. *Syllis pseudohyalina* sp. nov., paratype (CEAB AP 1001B). **A.** Entire specimen, lateral view. **B.** Anterior end, dorsal view. **C.** Anterior end, lateral view. **D.** Midbody, lateral view. **E.** Posterior end, dorsal view. **F.** Anterior parapodia, with arrows pointing to protruding tips of aciculae. **G.** Midbody parapodia.

Our specimens also resemble *Syllis armillaris* (O.F. Müller, 1776) and *Syllis malaquini* Ribeiro, Ponz-Segrelles, Helm, Egger & Aguado, 2020 in overall body shape (Müller 1776; Ribeiro *et al.* 2020). However, *S. armillaris* differs in having the blades of the midbody compound chaetae with the distal tooth smaller and with short marginal spines (both teeth similar in size, marginal spines similar to anterior chaetae in our specimens). Moreover, *S. malaquini* shows a characteristic color pattern consisting of dark lines on the dorsum of each segment, including peristomium, and dark stain on the anterior region of prostomium (absent in our specimens) and dorsal simple chaetae with a distal notch (bidentate in our specimens) (Ribeiro *et al.* 2020).

The specimens reported as *Syllis* (*Typosyllis*) *hyalina* in Day (1967a), despite being briefly described and illustrated, show marked differences with *S. pseudohyalina* sp. nov. (e.g., in having a very short proventricle), but also differ from the Mediterranean *S. hyalina*. Day (1967a) suggested that they might be juveniles of *S. variegata*, which is a Mediterranean species most likely absent in South Africa. Therefore, further sampling is required to clarify the taxonomic status of the specimens attributed to *S. (T.) hyalina* by Day (1967a).

Day (1967a) cites Day (1953, 1960) as sources for his report of *S. variegata*. None of the material examined by Day (1953) was available, but we examined three of the 22 samples reported in Day (1960) as *S. variegata*. That paper, however, does not include a description of these specimens, which,

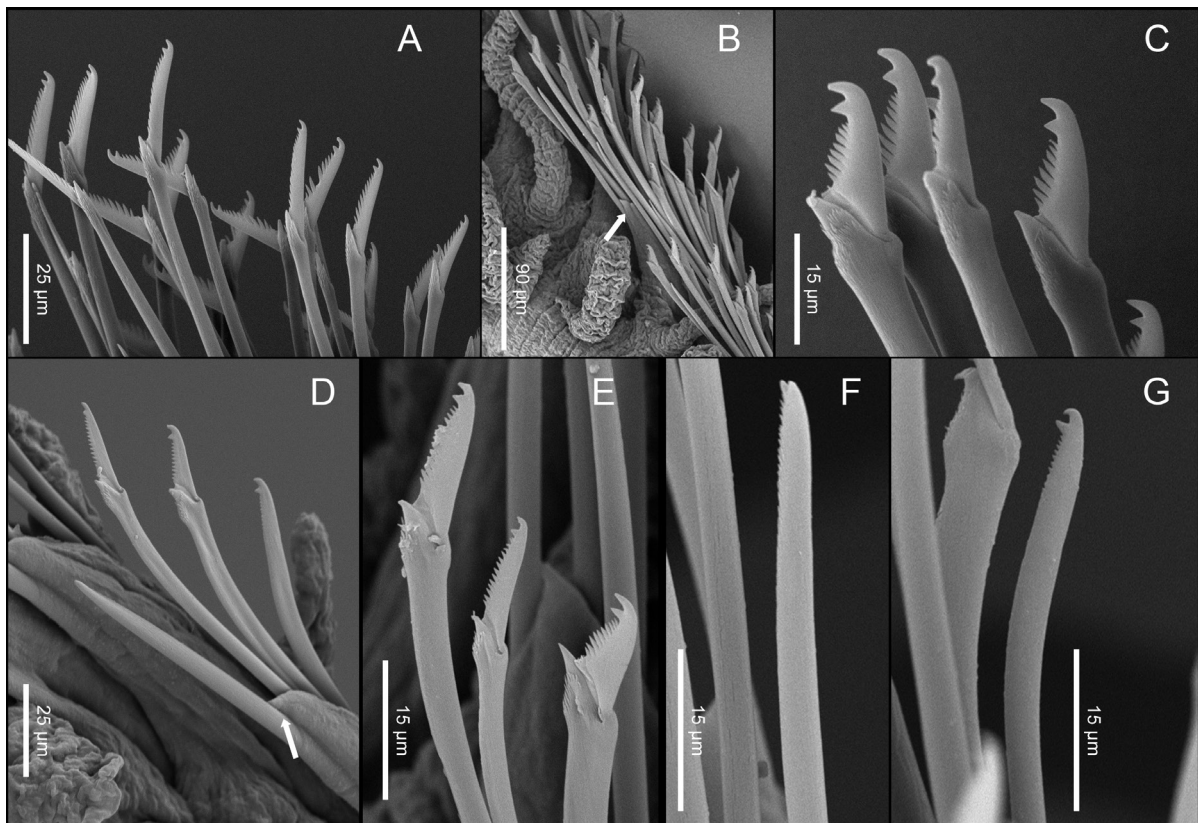


Fig. 8. *Syllis pseudohyalina* sp. nov., paratype (CEAB AP 1001B). **A.** Compound chaetae, anterior segments. **B.** Compound chaetae, midbody, white arrows pointing to protruding tips of aciculae. **C.** Detail of thick and thin blades of compound chaetae, midbody. **D.** Compound chaetae, posterior parapodia. **E.** Detail of blades of compound chaetae, posterior parapodia. **F.** Tip of dorsal simple chaetae. **G.** Tip of ventral simple chaetae.

upon examination, did not match the description of *S. variegata* in Day (1967a). Although smaller, our specimens, initially identified as *S. variegata* by Sedick (2018), more closely resemble this material (SAM MB-A060274; SAM MB-A069882; SAM MB-A069870) than the description in Day (1967a). *Syllis variegata*, as redescribed in San Martín (2003) and reported in Day (1967a), is much longer (15 mm and 40 mm long, respectively) than our South African specimens (6–7 mm), although the complete specimens collected by Day (1960) and examined here were all shorter than 40 mm long. However, the Mediterranean *S. variegata* and our specimens agree in having the midbody dorsal cirri as long as or shorter than body width, while these are longer than body width in Day's (1967a) *S. variegata*. Furthermore, both the Mediterranean and Day's (1967a) *S. variegata* have the anterior dorsal cirri longer than body width (similar or shorter in our specimens). Moreover, the Mediterranean *S. variegata* shows a characteristic reddish transversal ∞ pigmentation pattern in each anterior segment that progressively disappears in midbody and posterior segments (San Martín 2003), Day's (1967a) specimens have a broken brown bar pattern (with three bars on each segment) also in anterior region and disappearing posteriorly, while our specimens and those we examined from Day (1960) lack pigmentation. This absence of pigmentation is unlikely due to fading, as specimens matching the description of *S. variegata* according to Day (1967a) are still strongly pigmented after being in 95% ethanol for a year (C. Simon, personal observation). The single acicula of posterior parapodia in the Mediterranean *S. variegata* has a straight pointed tip that clearly protrudes from the parapodial lobe (San Martín 2003), while our specimens show the single posterior acicula slightly protruding from the acicular lobe and having an oblique tip. Moreover, our specimens show slightly longer antennae (median: 24 articles, lateral: 16–18) than the Mediterranean (17–18 and 12–13, respectively) and Day's (1967a) specimens (16 and 12, respectively), and the pharynx is shorter than the proventricle (extending through 9–10 segments) and shows a characteristic red color, while it is longer than the proventricle (extending through 11–12 segments). Some of the 1959 specimens collected in Day (1960) have up to five aciculae in anterior chaetigers, with 1–2 with a pointed oblique tip. Moreover, while the red pharynx is between 9–11 chaetigers long, the proventricle was up to 16 chaetigers long, a difference that may be size related. Therefore, neither our specimens nor those described by Day (1967a), belong to *S. variegata*. Our observations also confirm that our specimens differ from those found by Day (1967a) and belong to a different species, with the taxonomy of the latter requiring further efforts to be accurately assessed.

Syllis amicarmillaris Simon, San Martín & Robinson, 2014
Figs 9–12

Syllis amicarmillaris Simon, San Martín & Robinson, 2014: 736–738, figs 7–11.

Syllis amicarmillaris – Sedick 2018: 137–138.

Material examined

SOUTH AFRICA • 3 entire specimens, 4 lacking posterior end; Mossel Bay; 34°11'11" S, 22°09'38" E; Apr.–Oct. 2015; Safiyya Sedick leg.; intertidal algal turf; fixed in 4% seawater formalin, preserved in 70% ethanol; CEAB AP 1003A • 2 specimens, prepared for light microscopy; same collection data as for preceding; CEAB AP 1003B • 2 specimens, prepared for SEM; same collection data as for preceding; CEAB AP 1003C.

Other material examined

SOUTH AFRICA • 17 complete specimens; Saldanha Bay, Lynch Point, UCT Ecological Survey, station SB155X; 33°2'52.774" S, 18°0'45.186" E; 22 Sep. 1957; fixed in 4% seawater formalin, preserved in 70% ethanol; SAM-MB-A060395.

Description

Body long, thick, 8–9.5 mm long 0.6–0.7 mm wide, with 74–90 chaetigers (Figs 9A–B, 11A–B). Prostomium small, with four eyes, with two eyespots in anterior position (Figs 9A–D, 11A, C). Palps triangular (Fig. 9A–D). Median antenna with 15 articles, lateral ones with 11 articles (Figs 9C–D, 11C). Tentacular segment with dorsal (13 articles) and ventral (11 articles) tentacular cirri (Fig. 9C–D, 11C). Dorsal cirri of chaetiger 1 with 15–16 articles, 13–16 in chaetiger 2, 16 in chaetiger 3, and 6–7 (short) and 10–11 (long) in midbody and posterior chaetigers (Figs 9A–F, 11C–E). Parapodial lobes short, with rounded ends (Figs 9G–I, 11C–F). Ventral cirri short, lanceolate with round tips, slightly distally bilobed (Figs 9G–I, 11D, F–H). Compound chaetae heterogomph, bidentate, with very small proximal tooth, and moderately long spines on margin, all similar throughout, with some dorso-ventral and antero-posterior gradation in length (Figs 10A–D, 12A–D, G). Anterior parapodia with 6–9 compound chaetae, blades 36 μm (long), progressively decreasing dorso-ventrally to 17 μm (short) (Figs 10A, 12A). Midbody parapodia with 5–7 compound chaetae, blades 28 μm (long) progressively decreasing to 17 μm (short), with 5–6 segments showing 2–3 pseudo-simple chaetae by loss of blade and with shafts slightly thicker than compound chaetae, not present in all parapodia (Figs 10B–E, 12B–E). Posterior parapodia with 6–10 compound chaetae, blades 28 μm (long), 19 μm (short) (Figs 10F–G, 12F–G). Dorsal simple chaetae straight (Figs 10H, 12H–J), ventral simple chaetae sinuous (Figs 10I, 12K). Three aciculae in

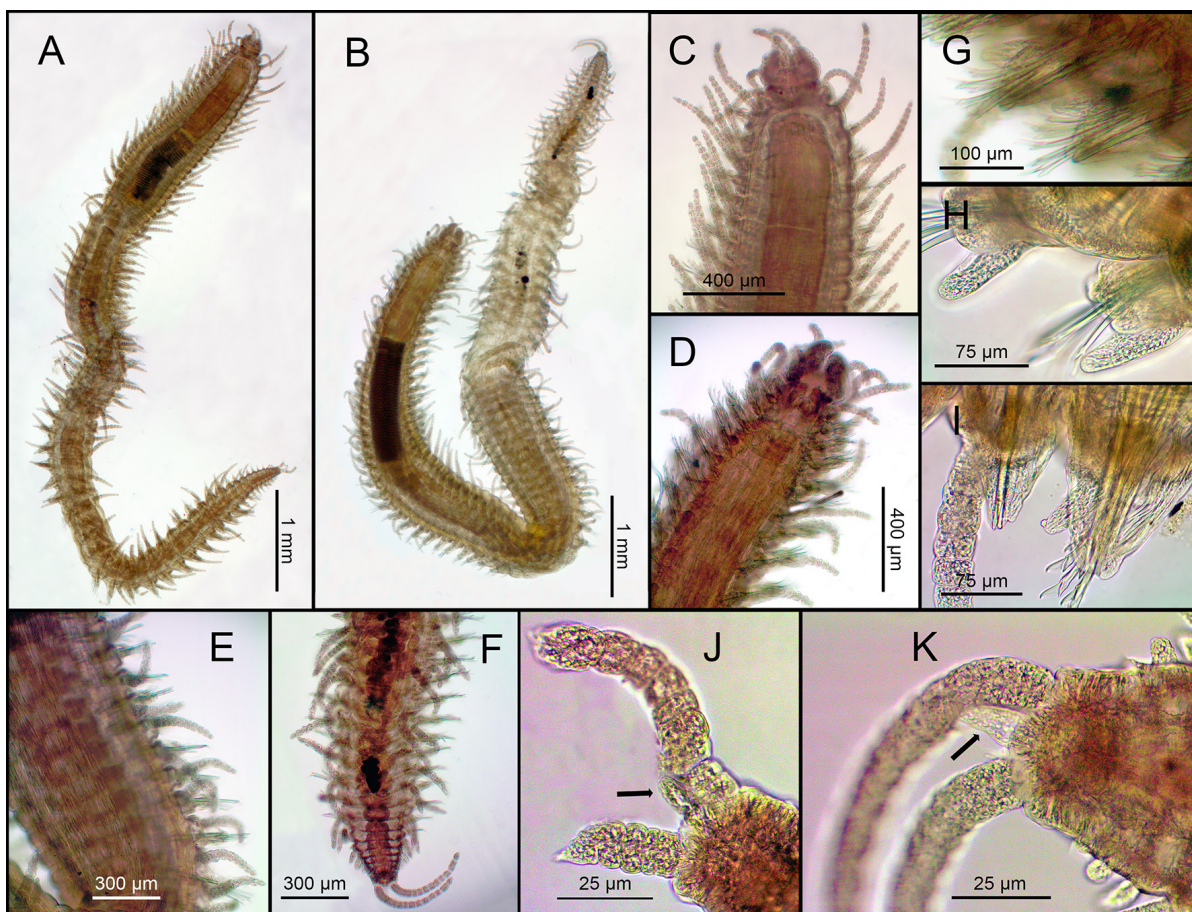


Fig. 9. *Syllis amicarmillaris* Simon, San Martín & Robinson, 2014 (CEAB AP 1003B). **A.** Entire body, dorsal view. **B.** Entire body ventral view. **C.** Anterior end, dorsal view. **D.** Anterior end, ventral view. **E.** Midbody parapodia, ventral view. **F.** Posterior end, dorsal view. **G.** Anterior ventral cirri. **H.** Midbody ventral cirri. **I.** Posterior ventral cirri. **J–K.** Detail of pygidium, black arrows pointing at middle stylus.

anterior parapodia (two with oblique tip, one with acuminate, pointed, straight tip); two in midbody parapodia (one acuminate, one oblique); one in posterior parapodia, with oblique tips, thicker than anterior ones, slightly protruding from parapodial lobes (Figs 10J–L, 12E). Pharynx long, extending over 8–10 segments, with small, conical tooth on anterior margin (Fig. 9A–D). Proventricle similar in length to pharynx, extending through 10–11 segments, with about 41–45 muscle cell rows (Fig. 9A–B). Pygidium with two long anal cirri with 16 articles and a digitiform median appendix (Figs 9A–B, F, J–K, 11B, G–H).

Distribution

South African coasts. Western Cape Province: west (Saldanha Bay), south-west (west and east Walker Bay – type locality) and south (Mossel Bay).

Remarks

The specimens collected at Mossel Bay fully agree with the morphology the types of *S. amicarmillaris* (Simon *et al.* 2014). Both have similar body shapes and lack pigmentation, have heterogomph, bidentate

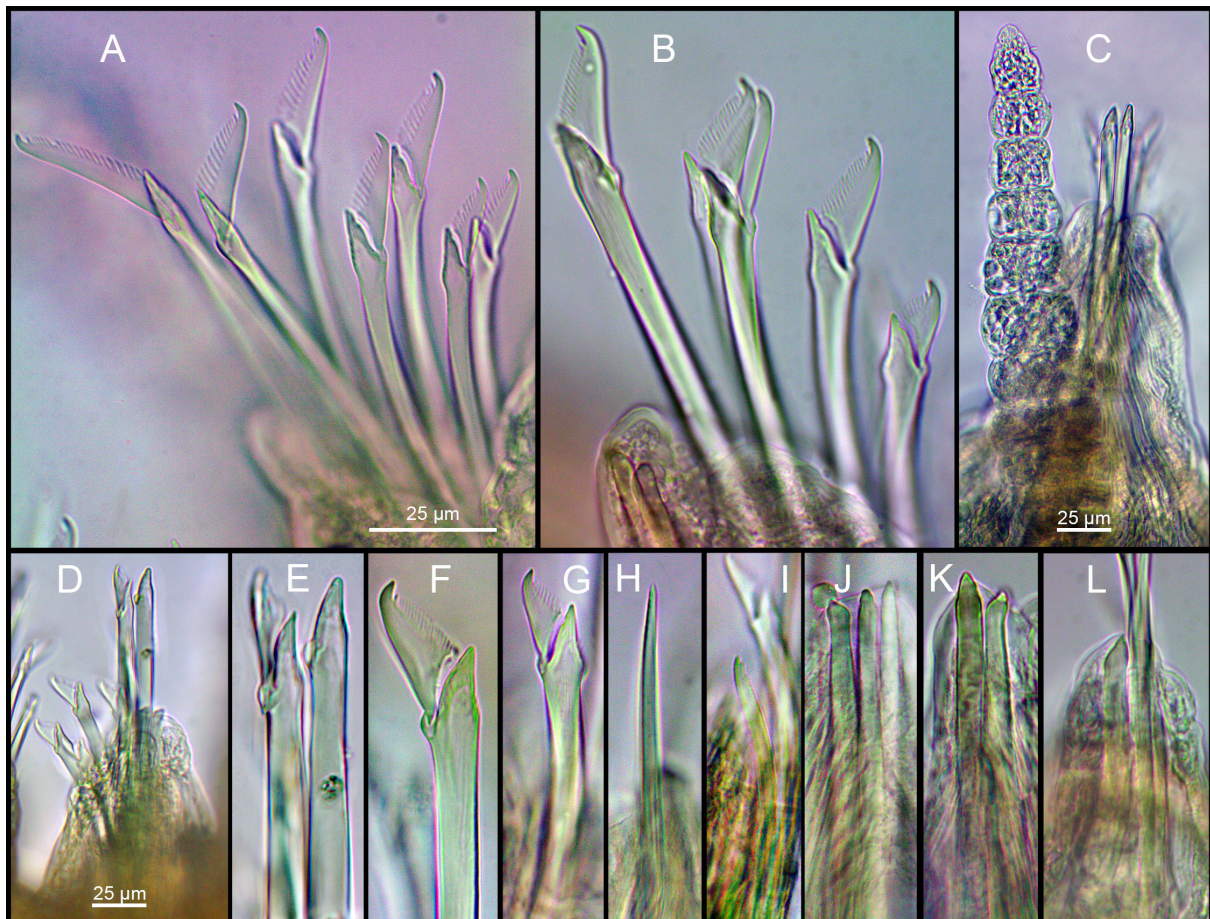


Fig. 10. *Syllis amicarmillaris* Simon, San Martín & Robinson, 2014 (CEAB AP 1003B). **A.** Compound chaetae, anterior parapodia. **B.** Compound chaetae, midbody parapodia. **C–D.** Midbody parapodia with simple chaetae due to blade loss. **E.** Detail of thick midbody chaetae with and without blade. **F.** Long chaeta, posterior parapodia. **G.** Short chaeta, posterior parapodia. **H.** Dorsal simple chaetae. **I.** Ventral simple chaetae. **J–L.** Aciculae. **J.** Anterior parapodia. **K.** Midbody parapodia. **L.** Posterior parapodia. All scales same as A, except C–D.

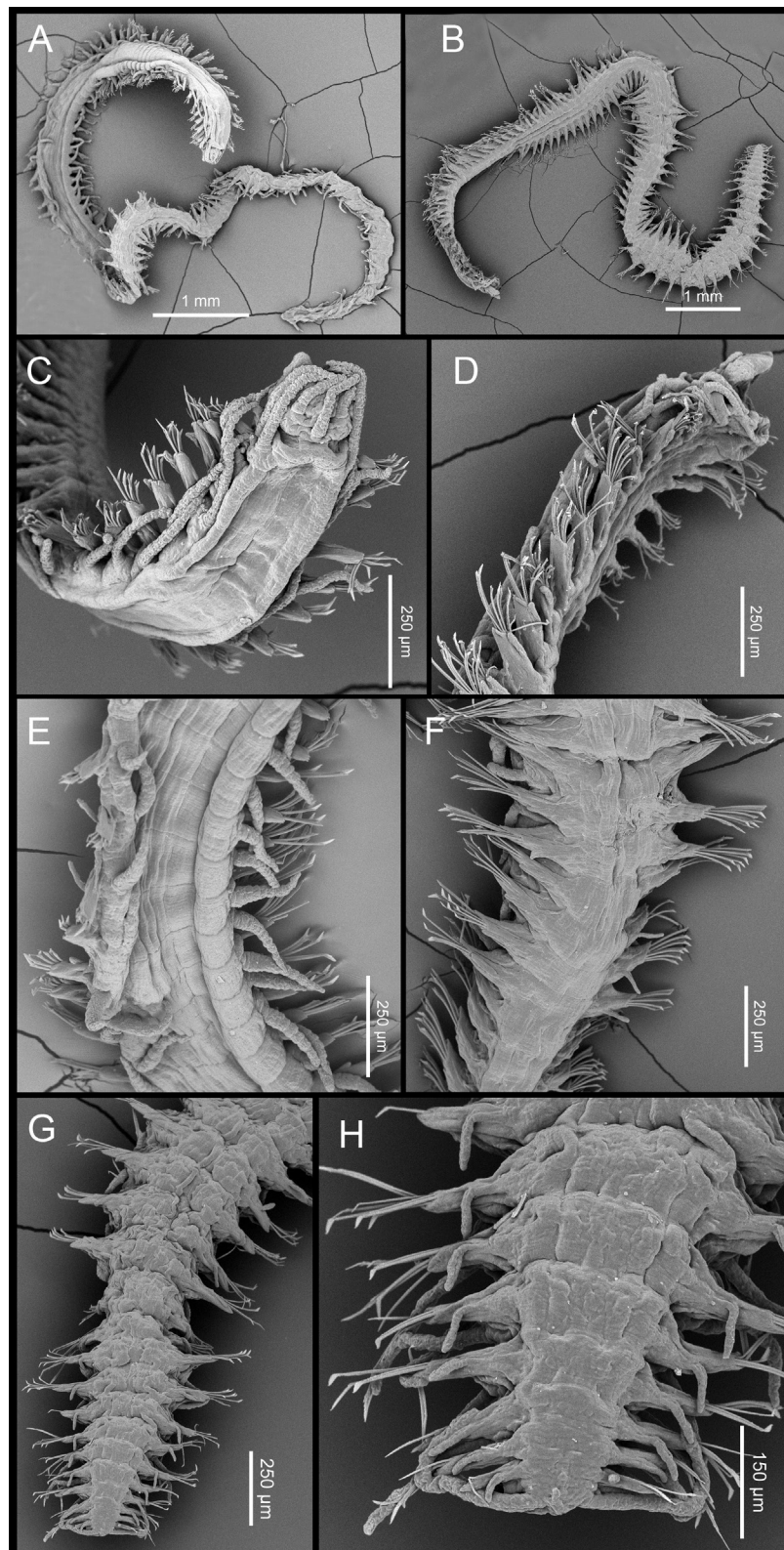


Fig. 11. *Syllis amicarmillaris* Simon, San Martín & Robinson, 2014 (CEAB AP 1003C). **A.** Entire specimen, dorsal view. **B.** Entire specimen lateral view. **C.** Anterior end, dorsal view. **D.** Anterior end, lateral view. **E.** Midbody, dorsal view. **F.** Midbody, lateral view. **G.** Posterior end, ventral view. **H.** Pygidium, ventral view.

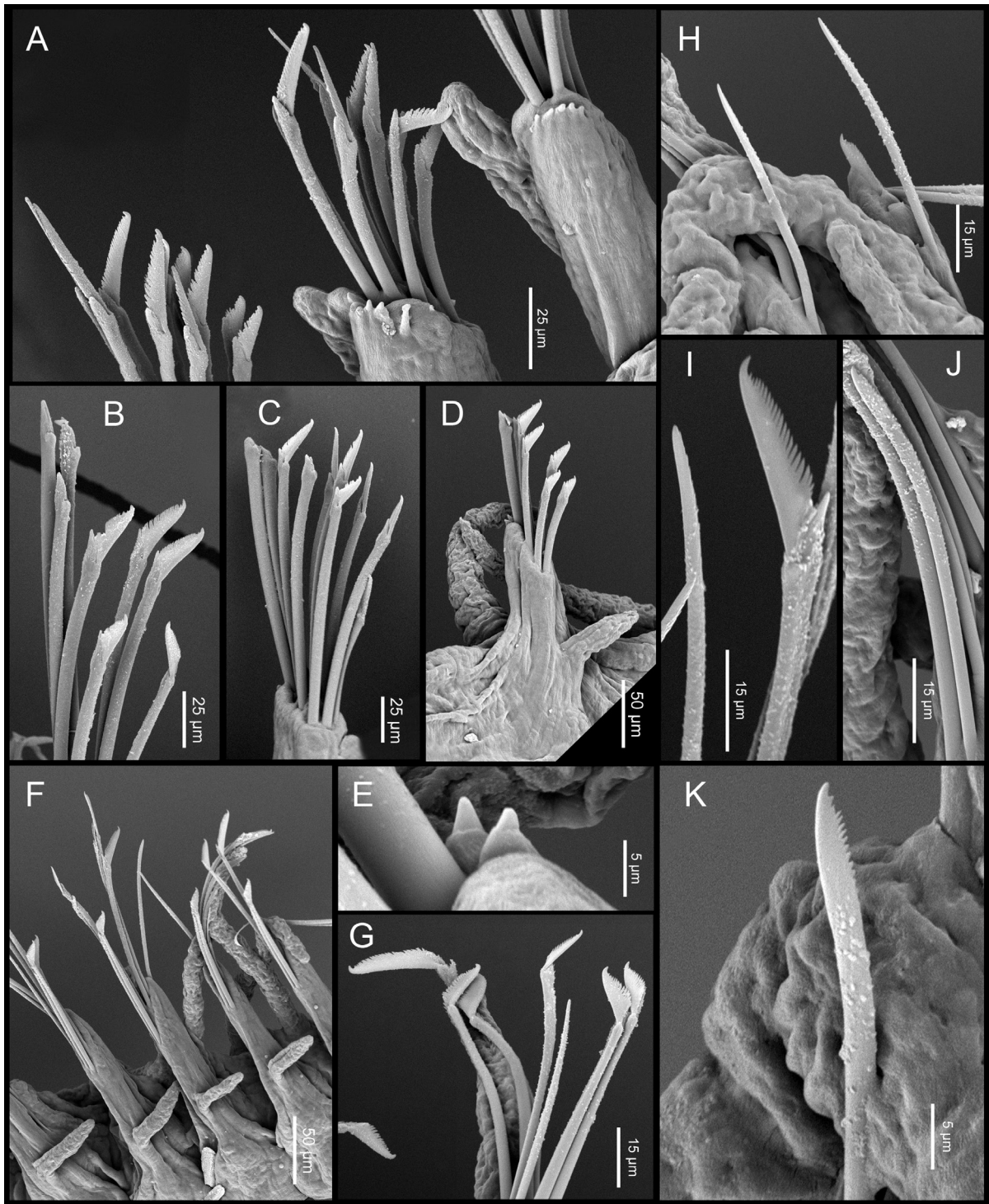


Fig. 12. *Syllis amicarmillaris* Simon, San Martín & Robinson, 2014 (CEAB AP 1003C). **A.** Compound chaetae, anterior segments. **B–D.** Midbody compound chaetae with three (B), two (C), and none (D) lacking blade. **E.** Detail of protruding tips of aciculae in D. **F.** Posterior parapodia. **G.** Compound chaetae, a posterior parapodia. **H.** Dorsal simple chaetae. **I.** Tip of dorsal simple chaetae. **J.** Ventral simple chaetae. **K.** Tip of ventral simple chaetae.

compound chaetae with small proximal tooth, show midbody pseudo-simple chaetae by loss of blade and enlargement of shaft, have sinuous ventral simple chaetae, long pharynx extending over 8–10 segments, and proventricle equal in length with pharynx extending over 10–11 segments with a similar number of muscular rows. The only observed differences are likely caused by the differences in size, as the types of *S. amicarmillaris* are longer (32 mm vs 8–9.5 mm in our specimens). Therefore, the number of chaetigers is higher (181 vs 74–90) and the midbody dorsal cirri have more articles (12–19 vs 9–10). Also, the number of parapodia bearing pseudo-simple chaetae is smaller in our specimens, with these chaetae being sometimes present in the parapodia of one side of a segment and absent in that of the other side. Moreover, when present, its number may vary in the two parapodia of the same segment.

Samples identified as *S. variegata* collected in 1957 as part of the UCT Ecological Survey in Saldanha Bay, and possibly identified by John Day, were in fact *S. amicarmillaris*. These specimens could not be linked to any publications, but they are unlikely to have been used to develop the description of *S. variegata* owing to the presence of the short dorsal cirri and pseudo-simple chaetae that are characteristic for *S. amicarmillaris*.

The original description of *S. amicarmillaris* includes populations distributed along the South African coast from Walker Bay (the type locality) to Saldanha Bay (Simon *et al.* 2014), a distance of approximately 350 km. Although Mossel Bay is somewhat closer to Walker Bay (approximately 260 km away), this geographic distance could still act as a barrier to gene flow. Nonetheless, the available morphological evidence does not support a clear distinction between these populations. Further molecular analyses are needed to determine whether the specimens from Walker Bay and Mossel Bay represent geographically separated populations of a single species or whether speciation has already occurred. Additionally, while Day (1960) reported *S. variegata* from Mossel Bay—three lots of which matching with *S. pseudohyalina* sp. nov.—Day (1953) also listed Danger Point as a locality for *S. variegata*. However, this site is in Walker Bay, very close to the type locality of *S. amicarmillaris*. These partly overlapping and potentially conflicting records by Day add further confusion to the taxonomic and biogeographic picture of polychaetes from South African coasts, highlighting the need for more detailed morphological and genetic studies to resolve these issues.

Subfamily Eusyllinae Malaquin, 1893

Genus *Paraehlersia* San Martín, 2003

Paraehlersia knysnaensis sp. nov.

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Figs 13–16

non *Syllis* (*Langerhansia*) *ferruginea* Langerhans, 1881 – Day 1967a: 244, fig 12.20–r.

Etymology

The species name ‘*knysnaensis*’ is dedicated to the type locality at Knysna Estuary, South Africa.

Type material

Holotype

SOUTH AFRICA • entire specimen; Knysna Estuary, Railway; 34°2′23.65″ S, 23°2′6.49″ E; Jul. 2021; Arturo Álvarez-Aguilar and Danne Pretorius leg.; intertidal, soft sediments; fixed in 4% seawater formalin, preserved in 70% ethanol; SAM–A089279.

Paratypes

SOUTH AFRICA • 2 anterior fragments; Knysna Estuary, Railway; 34°2'23.65" S, 23°2'6.49" E; Jul. 2021; CEAB AP 1006A • 2 entire specimens; same collection data as for preceding; Jul. 2021; CEAB AP 1006B • 2 entire specimens, 3 anterior fragments; same collection data as for preceding; May 2021; SAMC-A089213 • 1 entire specimen; same collection data as for preceding; Jan. 2021; SAM-A089280 • 1 specimen, prepared for SEM; same collection data as for preceding; Jan. 2021; CEAB AP 1006C • 1 specimen lacking posterior end; Bollard Bay; 34°2'37.33" S, 23°3'59.65" E; Jul. 2021; SAM-A089281 • 5 entire specimens, 2 anterior fragments; Reserve; 34°3'31.80" S, 23°2'2.18" E; Jul. 2021; SAM-A089282 • 1 anterior fragment; The Point; 34°2'21.32" S, 23°0'45.01" E; Jan. 2021; SAM-A089283 • 1 entire specimen, 1 in two fragments; Thesen Island Bridge; 34°2'39.01" S, 23°2'52.19" E; May 2021; SAMC-A089232 • 1 entire specimen, 1 specimen stolonizing; Ashmead; 34°2'39.01" S, 23°2'52.19" E; May 2021; SAM-A089291 • 1 entire specimen; same collection data as for preceding; Jan. 2021; SAM-A089285 • 1 entire specimen; Brenton; 34°3'31.80" S, 23°2'2.18" E; Jan. 2021; SAM-A089286 • 1 specimen prepared for SEM; same data as for preceding; Jul. 2021; CEAB AP 1006D • 1 entire specimen; Thesen Island Bridge; 34°2'39.01" S, 23°2'52.19" E; Jan. 2021; SAM-A089284 • 2 specimens prepared for light microscopy; same data as for preceding; Jul. 2021; CEAB AP 1006E.

Other material examined

SOUTH AFRICA • 1 complete, 3 incomplete specimens (2 stolonizing); Saldanha Bay, UCT Ecological Survey, station SB183N; 33°2'30"S, 17°58'42"E; 29 Apr. 1959; fixed in 4% seawater formalin, preserved in 70% ethanol; SAM-MB-A060273 • 1 incomplete specimen; False Bay, Oatland Point, UCT Ecological Survey; station FAL149V; 34°11'48"S, 18°27'16"E; 12 Mar. 1953; SAM-MB-A020798.

Description

Body long and thin, but highly variable in length, 6.52 (4.1–12) mm long, 0.36 (0.31–0.73 mm wide, with 59 (55–65) chaetigers (Figs 13A–B, 15A–B). Prostomium small, oval to sub-pentagonal, with four eyes and two anterior ocular spots (Figs 13B–D). Palps large, triangular, $\frac{2}{3}$ as long as prostomium, fused at bases, with a distinct groove (Fig. 13A–D). Lateral and median antennae pseudo-articulated (Figs 13B, D, 15C–D). Tentacular segment shorter than following ones (Figs 13D, 15C–D). Dorsal tentacular cirri pseudo-articulated, slightly longer than ventral one, as long as median antenna; ventral tentacular cirri pseudo-articulated (Figs 13B–D, 15C–D). Dorsal cirri slender, elongated, whip-shaped, alternating long and short all along body, smooth except first that is slightly pseudo-articulated distally (Figs 13B–F, 15C–F). Dorsal cirri of chaetiger 1 as long as body width, of chaetiger 2 $\frac{1}{3}$ of body width, of chaetiger 3 $\frac{1}{3}$ of body width, of chaetiger 4 half of body width (Figs 13C–D, 15C), then alternating $\frac{1}{3}$ and half body width along most of body (Figs 13E, 15E), to as long and half body width in posteriormost segments (Figs 13F, 15G). Anterior dorsal cirri with a short sub-cirral papilla at bases of cirrophores and a fossa between cirrophore and papilla (Fig. 16A). Parapodial lobes conical with round tips (Figs 13B–F, 15C–F). Ventral cirri as long as parapodial lobes, anterior ones lanceolate, with round tips, posterior and midbody triangular with elongated tips (Figs 13H–I, 15B, D, F, H). Anterior parapodia with 20–30 compound chaetae mostly falcigers; 4–6 spinigers of two lengths; number of chaetae reducing towards posterior segments (Figs 14A, 16B, G, K). Anterior parapodia with falcigers with short, bidentate blades, most dorsal 18 μ m long, most ventral 14 μ m, with a very small subdistal tooth, and few thick marginal spines (Figs 14A–B, 16B–D); spinigers long, filiform, 2–3 with blades ca 90 μ m long, 2–3 with blades ca 50 μ m long, distally bifid, visible only under SEM, with short marginal spines (Figs 14A, C, 16B, E). Midbody parapodia compound chaetae with 5–10 falcigers, ca 15–17 μ m long, similar to anterior ones in mid-anterior parapodia (Fig. 16H), progressively changing to show two different forms: thick, $\frac{2}{3}$ as thick as thin, with subdistal tooth much larger than distal one (Figs 14D, 16I–J) and thin, with subdistal tooth slightly larger than distal one (Figs 14E, 16I); all with few thick marginal spines;

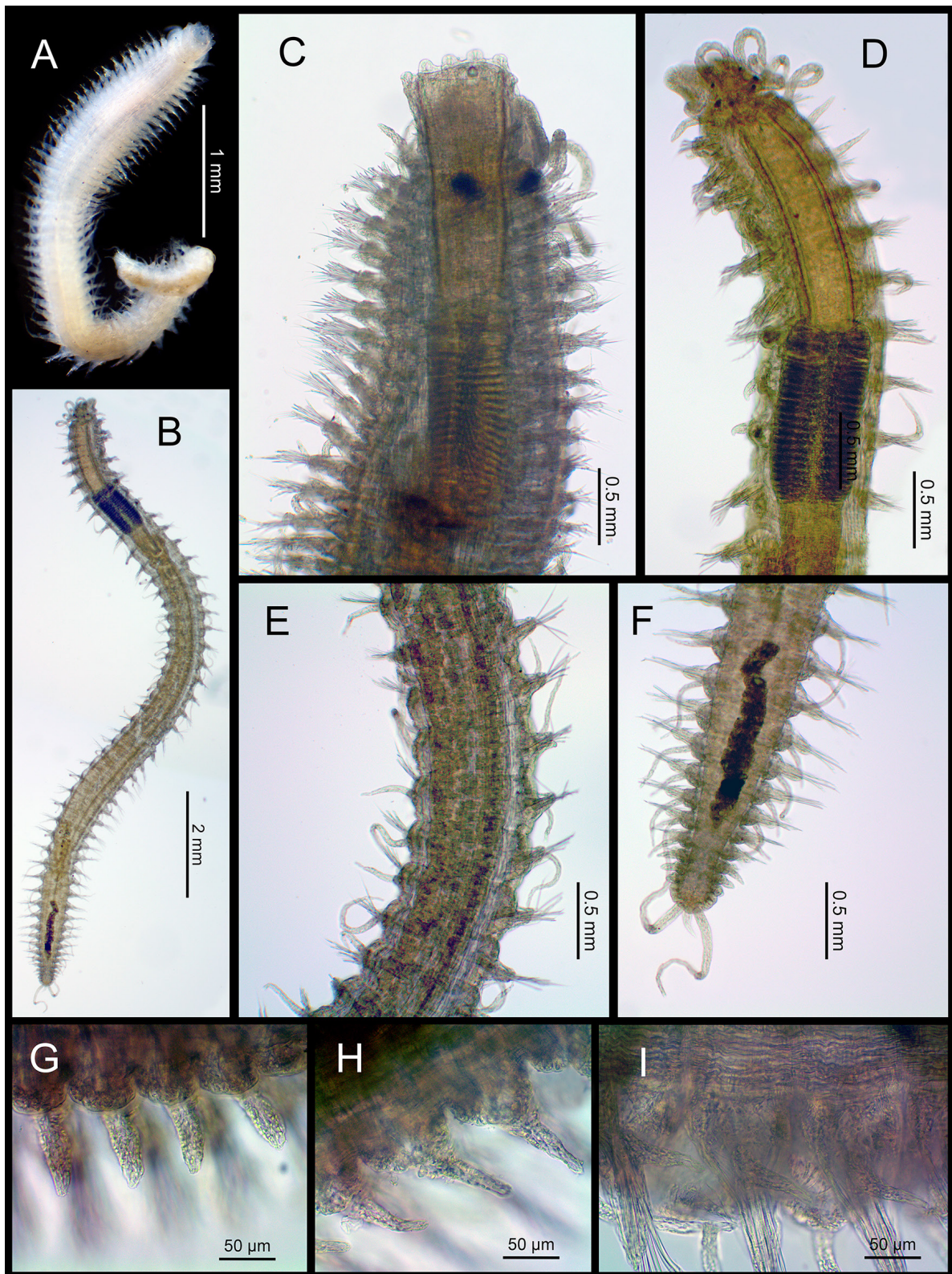


Fig. 13. *Paraelhersia knysnaensis* sp. nov., paratype (CEAB AP 1006E). **A.** Entire body, ventral view with everted pharynx. **B.** Entire body, dorsal view. **C.** Anterior end, ventral view with everted pharynx. **D.** Anterior end, dorsal view. **E.** Midbody parapodia, dorsal view. **F.** Posterior end, dorsal view. **G.** Anterior ventral cirri. **H.** Midbody ventral cirri. **I.** Posterior ventral cirri.

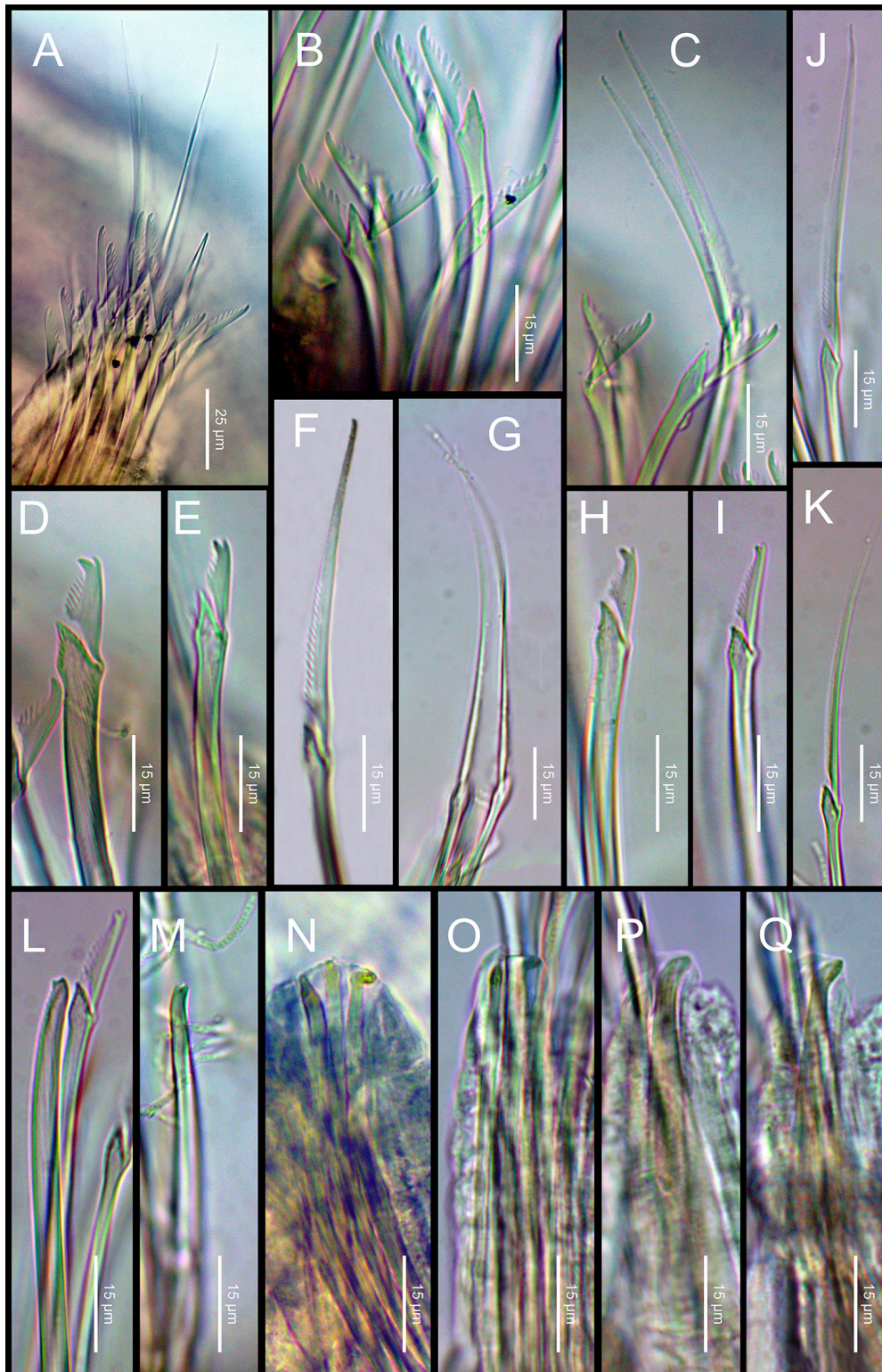


Fig. 14. *Paraelhersia knysnaensis* sp. nov. Paratype (CEAB AP 1006E). A–C. Anterior parapodia. A. Chaetal bundle. B. Falcigers. C. Short spinigers. D–G. Midbody parapodia. D. Thick falciger. E. Thin falciger. F. Short spiniger. G. Long spinigers. H–M. Posterior parapodia. H. Thick falciger. I. Thin falciger. J. Short spiniger. K. Long spiniger. L. Dorsal simple chaetae. M. Ventral simple chaetae. N–Q. Aciculae. N. Anterior parapodia. O. Midbody parapodia. P–Q. Posterior parapodia.

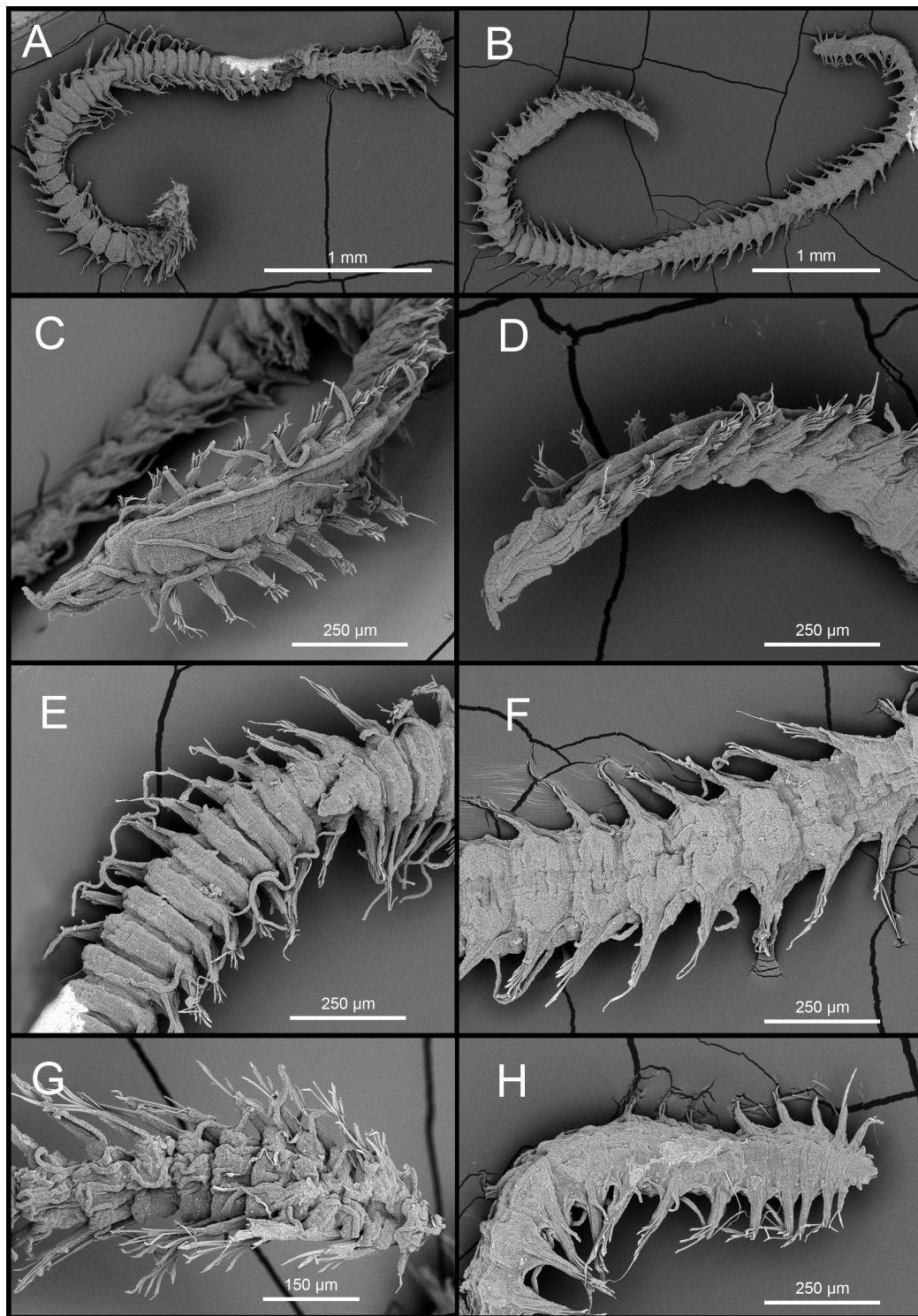


Fig. 15. *Paraelhersia knysnaensis* sp. nov. (A, E, G. CEAB AP 1006C. B–D, F, H. CEAB AP 1006D). **A.** Entire specimen, dorsal view. **B.** Entire specimen, ventral view. **C.** Anterior end, dorsal view. **D.** Anterior end, lateral view. **E.** Midbody, dorsal view. **F.** Midbody, ventral view. **G.** Posterior end, dorsal view. **H.** Posterior end, ventral view.

2–4 spinigers of two lengths similar to anteriormost parapodia (Figs 14D–G, 16F–G). Posterior parapodia with 3–5 falcigers, 15–17 μm long and varying in thickness; thick $\frac{1}{4}$ as thick as thin, with subdistal tooth much larger than distal one (Figs 14H, 16L), thin with subdistal tooth slightly smaller than distal one (Figs 14I, 16L); all with few thick spines on margin (Figs 14H–I, 16L); two spinigers of similar length (60–65 μm), similar in shape to anteriormost parapodia, apparently unidentate (Figs 14K, 16K, M). Dorsal simple chaetae on most posterior segments, slightly curved, with slightly serrated margin, distally bidentate, both teeth short, broad, upwards directed (Figs 14L, 16N–O); ventral simple chaetae on most posterior segments, markedly bidentate, both teeth acute,

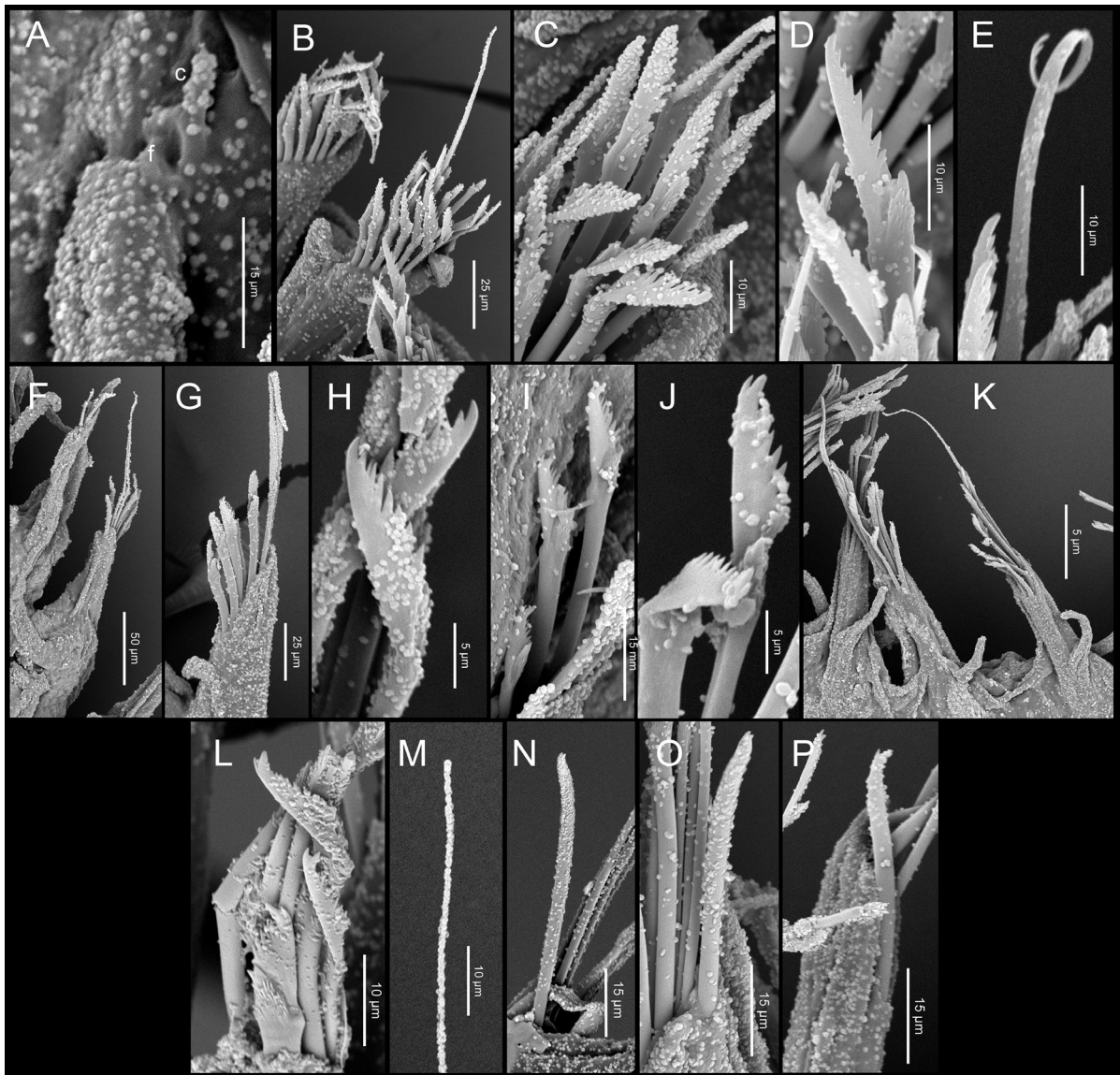


Fig. 16. *Paraelhersia knysnaensis* sp. nov., paratype (CEAB AP 1006C). **A.** Basis of anterior dorsal cirri, showing the fossa (f) and appendix (c). **B.** Anterior parapodia. **C.** Falcigers, anterior parapodia. **D.** Detail of falciger, anterior parapodia. **E.** Tip of spiniger, anterior parapodia. **F–G.** Midbody parapodia. **H.** Falcigers, mid-anterior parapodia. **I–J.** Falcigers, mid-posterior parapodia. **K.** Posteriormost parapodia. **L.** Falcigers, posteriormost parapodia. **M.** Tip of spiniger, posteriormost parapodia. **N–O.** Dorsal simple chaetae. **P.** Ventral simple chaetae.

large, subdistal slightly longer than distal one, apparently smooth (Figs 14M, 16P). Three aciculae in anterior parapodia, two straight with slightly inflated, acuminate tip, one with round tip bent in oblique angle (Fig. 14N); two aciculae in midbody parapodia, one straight with slightly inflated, acuminate tip and one with round tip bent in oblique angle (Fig. 14O); one acicula in posterior parapodia, with round tip bent in oblique angle (Fig. 14P–Q). Pharynx with a small pharyngeal tooth close to anterior margin, similar in size (Fig. 13C) or slightly longer (Fig. 13B, D) than proventricle, extending through 6–7 segments; proventricle through 4–7 segments with 26 (25–27) muscular rows. Pygidium small, triangular, with two very long, smooth, whip-shaped anal cirri; pygidial appendix triangular (Figs 13B, F, 15G–H).

Distribution

South Africa. Western Cape Province: west coast (Saldanha Bay, False Bay) and southern coast (Knysna Estuary).

Remarks

Paraehlersia knysnaensis sp. nov. differs from all previously known species in the genus in having two types of spiniger chaetae (long and short) and falciger blades with the distal tooth much longer than the subdistal one in anterior parapodia, while all other species have spinigers with either a graduating length or with similar lengths and falcigers with both teeth similar in size. Also, *P. knysnaensis* has two types of falcigers (thin, with teeth of similar size and thick, with subdistal tooth much larger than distal one) in midbody posterior parapodia, while all other species have only falcigers corresponding to the thick type, with subdistal tooth either slightly or much larger than distal one.

Paraehlersia pamela Prado & San Martín, 2024, from the Alboran Sea, shares with *P. knysnaensis* sp. nov. the shape of simple chaetae and aciculae, as well as the small size of the pharyngeal tooth, but *P. pamela* has a shorter body (3.52 mm and 4.1–12 mm long, respectively) and the pharynx is longer than proventricle (similar in size or slightly longer in our species) (Prado & San Martín 2024).

Paraehlersia ferrugina (Langerhans, 1881), from the Canary Islands, has the ventral simple chaetae with subdistal tooth much longer than distal one and up to eight aciculae with truncated tips in anterior region (San Martín 2003), while the subdistal tooth in the ventral simple chaetae is only slightly longer and the aciculae are not so numerous and have rounded tips in *P. knysnaensis* sp. nov. *Paraehlersia ferrugina* was also reported from South Africa by Day (1967a), but the specimens differ from *P. knysnaensis* in shape of falciger and spiniger chaetae. *Paraehlersia ferrugina* was first reported from South Africa in Day (1960), which did not include any illustration or descriptive notes —only a mention that it was a new record for the country. Day (1967a) cited only his earlier work (Day 1960) as the reference for this identification. We have examined this material and it matched *P. knysnaensis* in all diagnostic features. Notably, the shape of both falcigers and spinigers were inaccurately represented in Day (1967a). In particular, the marginal teeth of anterior falcigers, as well as those at the base of posterior falcigers, are significantly more pronounced than depicted.

Paraehlersia articulata (Kudenov & Harris, 1995), from the Santa Barbara Channel (California), has aciculae with diamond shaped tips (round in *P. knysnaensis* sp. nov.) and a proventricle with slightly less muscular cell rows (22–24 vs 25–27) (Kudenov & Harris 1995).

Paraehlersia longichaetosa Fukuda, Centurión, Nogueira & San Martín, 2012, from offshore Banco Sarmiento (Argentina), has filiform dorsal cirri (whip-shaped in *P. knysnaensis* sp. nov.), ventral cirri shorter than parapodial lobes (equally long in *P. knysnaensis*), bidentate ventral simple chaetae with a clear distal serration (smooth in *P. knysnaensis*), and single posterior acicula with irregularly inflated tips (round, bent at oblique angle in *P. knysnaensis*) (Fukuda *et al.* 2012).

Paraehlersia martapolae Fukuda, Centurión, Nogueira & San Martín, 2012, from São Paulo (Brazil), has ventral cirri shorter than parapodial lobes (similar in length in *P. knysnaensis* sp. nov.), pharynx longer than proventricle, through 9–12 segments (similar in size to proventricle, through 6–7 segments in *P. knysnaensis*), and proventricle shorter than pharynx, extending through 5–6.5 segments with 21–24 muscular rows (as long as proventricle, through 4–5 segments, with 25–27 muscular rows in *P. knysnaensis*) (Fukuda *et al.* 2012).

Paraehlersia dionisi (Núñez & San Martín, 1991), from the Canary Islands, has dorsal simple chaetae with heavily serrated margin (slightly serrated margin in *P. knysnaensis* sp. nov.), aciculae with rounded tip ending in a lateral, short mucron (with round, non-mucronate tip in *P. knysnaensis*), and proventricle shorter than pharynx, extending through seven segments and with 30 muscular rows (similar in length to pharynx, extending through 4–5 segments, and 25–30 muscular rows in *P. knysnaensis*) (Núñez & San Martín 1991).

Paraehlersia kawesqar Soto & San Martín, 2018, from Concepción Channel (Chile), has ventral cirri shorter than parapodial lobes (similar in length to parapodial lobes in *P. knysnaensis* sp. nov.), acicula distally acuminate (with round tip, bent in oblique angle in *P. knysnaensis*), pharynx shorter than proventricle extending through 7–9 segments (similar, 6–7 segments in *P. knysnaensis*), proventricle extending through 14–15 segments (4–5 in *P. knysnaensis*) (Soto & San Martín 2018).

Paraehlersia ehlersiaeformis (Augener 1913), from Shark Bay (Australia), has ventral cirri shorter than parapodial lobes (longer than parapodial lobes in *P. knysnaensis* sp. nov.), dorsal simple chaetae slightly truncated (bidentate in *P. knysnaensis*), ventral simple chaetae with proximal tooth slightly hooked (both teeth acute in *P. knysnaensis*), acicula in anterior parapodia with acuminate or lancet-shaped tip (round in *P. knysnaensis*) and solitary with oblique tip in midbody and posterior parapodia (straight, with rounded tip in *P. knysnaensis*), pharynx longer than proventricle (similar in *P. knysnaensis*), and proventricle with 21–22 muscular rows (25–27 in *P. knysnaensis*) (San Martín & Hutchings 2006).

Discussion

The discovery and description of *S. kikeballesterosi* sp. nov., *S. pseudohyalina* sp. nov., *S. amicarmillaris*, and *P. knysnaensis* sp. nov. contribute significantly to our understanding of syllid polychaete biodiversity in South Africa, further evidence that the real number of indigenous polychaete species reported to date along Southern African coasts has been significantly underestimated (Simon *et al.* 2022). These new records and species descriptions enhance the taxonomic resolution within the group and provide insights into morphological variations across species and biogeographical distribution patterns.

The description of *S. kikeballesterosi* sp. nov. highlights the need to reassess records of the widely reported but now discredited cosmopolitan species *S. prolifera* (del Olmo *et al.* 2024). The South African specimens differ clearly morphologically from the Mediterranean taxa, particularly in the shape of chaetae and dorsal cirri patterns. Detailed comparison with historical material cited by Day (1951, 1953, 1957, 1963, 1967a) reveals that these older records comprise at least three distinct taxa, none of which matching the newly described species. Furthermore, *S. kikeballesterosi* also differs from all other known regional and global species of *Syllis* sharing the presence of drumstick-shaped aciculae and pigmentation pattern. Taken together, these findings clearly support our description of *S. kikeballesterosi*.

Syllis pseudohyalina sp. nov. closely resembles *S. hyalina*, a Mediterranean species, but differs in body size, appendage proportions, chaetal morphology, and internal organs (e.g., the reddish pharynx and shorter proventricle). While it also shares similarities with *S. armillaris* and *S. malaquini*, it can be distinguished by the shape of the falcigers and the absence of a pigmentation pattern. Some specimens previously reported by Day (1967a) as *S. (T.) hyalina* and *S. variegata* had already raised doubts about their identity, but our study confirms that these historical records likely represent at least two distinct

taxa, neither of which corresponds to our new species. Specimens attributed to *S. variegata* by Day (1960, 1967a) differ from both the Mediterranean type and our material in pigmentation, cirri length, acicula morphology, and internal anatomy, suggesting a need to reassess their identity. In contrast, the South African material described here shares a closer resemblance with the examined material from Day (1960) than with Day's (1967a) formal descriptions. These results not only support the description of *S. pseudohyalina* but also help clarifying the confusion surrounding earlier records from South Africa, emphasizing the importance of detailed morphological re-evaluation of historical material to correctly assess local syllid diversity.

The confirmation of the presence of *S. amicarmillaris* in Mossel Bay aligns with previous records (Simon *et al.* 2014) and suggests a broader distribution spanning the Southern African coasts, from the southeast to southwest as previously shown for two species of nereidids (Kara *et al.* 2018, 2020). While our specimens are smaller than those in the original description, the observed morphological differences are likely attributable to size variation rather than taxonomic divergence.

The description of *P. knysnaensis* sp. nov. adds a new member to the genus, distinguished by its unique chaetal morphology, including two distinct spiniger types and falciger blades with pronounced tooth differentiation. Comparisons with all other species of *Paraehlersia* reveal a combination of diagnostic traits that unequivocally supports its description as a new species. Additionally, our study also confirms that some morphological traits of specimens previously identified as *P. ferruginea* were misinterpreted by Day (1967a) and, upon re-examination, can be confidently assigned to our new species.

Overall, our results support previous findings (e.g., Simon *et al.* 2019, 2022; Kara *et al.* 2023) in highlighting the rich yet understudied diversity of polychaetes along the Southern African coasts. This is particularly evident among syllids, where several currently reported species—including, but not limited to those newly described in this study—may have been misidentified or may represent cryptic complexes. These taxonomic uncertainties underscore the need for further research, particularly—yet not exclusively—through integrative approaches that combine detailed morphology with molecular data.

Additionally, by re-examining material cited in several of John Day's works, we have revealed discrepancies between the specimens he reported and his formal descriptions in Day (1967a), with some nominal species likely encompassing multiple taxa. These inconsistencies undoubtedly reflect a broader trend by many early taxonomists, who often accepted high levels of intraspecific variation in supposedly cosmopolitan, globally widespread species (Hutchings & Kupriyanova 2018). As such, re-evaluating the specimens examined by Day—especially those designated as widespread or 'cosmopolitan'—using both morphological and molecular tools is essential for refining and updating the taxonomy of South African polychaetes.

Conclusion

This study enhances the understanding of syllid polychaetes in South Africa by describing three new species—*S. kikeballesterosi* sp. nov., *S. pseudohalina* sp. nov., and *P. knysnaensis* sp. nov.—and extending the known distribution of *S. amicarmillaris* along the South African Indian Ocean coast. These findings emphasize the need for continued taxonomic research in understudied marine ecosystems, particularly in regions where syllid diversity remains poorly documented.

The discovery of these new species reinforces the growing evidence that many polychaetes previously considered cosmopolitan may instead comprise cryptic species complexes. This study highlights the importance of reassessing species boundaries using modern taxonomic tools, such as detailed morphological analyses and scanning electron microscopy, which were essential in distinguishing the newly described taxa. Although suitable material for molecular analyses was unavailable for the new

species described here, we acknowledge that the integration of molecular data has become a powerful and widely accepted tool for species delimitation, and this is particularly true in Syllidae (e.g., Moreno-Martin *et al.* 2023; del Olmo *et al.* 2024; Álvarez-Campos *et al.* 2025). Therefore, future acquisition of fresh material will be important to test the species hypotheses proposed in this work through combining our careful morphological descriptions with molecular analyses.

Our results strongly suggest that syllid biodiversity in South African waters is likely higher than previously recognized, warranting further investigation. In this context, prioritizing molecular sampling—especially within Syllidae, which contains numerous species complexes—will be crucial for resolving hidden diversity and refining our understanding of species boundaries in the region.

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References

- Aguado M.T., San Martín G. & Nishi E. 2006. Two new species of Syllidae (Polychaeta) from Japan. *Scientia Marina* 70 (S3): 9–16.
- Álvarez-Campos P., Lattig P., Turon M., San Martín G., Buckley D., Britayev T.A., Martin D. & Machordom A. 2025. Evolution of *Haplosyllis* (Syllidae, Annelida) with emphasis on the Indo-Pacific Region and the *djiboutiensis* species complex. *Zoologica Scripta* 54: 684–707. <https://doi.org/10.1111/zsc.12730>
- Audouin J.V. & Milne-Edwards H. 1832. Classification des Annélides et description de celles qui habitent les côtes de la France. *Annales des Sciences naturelles, Paris* 27: 337–347.
- Augener H. 1913. Polychaeta I. Errantia. In: Michaelsen W. & Hartmeyer R. (eds) *Die Fauna Südwest-Australiens. Ergebnisse der Hamburger südwest-australischen Forschungsreise 1905*. Vol. 4. Lieferung 5. Gustav Fischer, Jena.
- Dales R.P. 1962. The polychaete stomodeum and the inter-relationships of the families of Polychaeta. *Proceedings of the Zoological Society of London* 139: 389–428. <https://doi.org/10.1111/j.1469-7998.1962.tb01837.x>
- Darling J.A. & Carlton J.T. 2018. A framework for understanding marine cosmopolitanism in the Anthropocene. *Frontiers in Marine Science* 5: 293. <https://doi.org/10.3389/fmars.2018.00293>
- Day J.H. 1951. The Polychaete fauna of South Africa. Part I. The intertidal and estuarine Polychaeta of Natal and Mosambique. *Annals of the Natal Museum* 12: 1–67.
- Day J.H. 1953. The Polychaete fauna of South Africa. Part 2. Errant species from Cape shores and estuaries. *Annals of the Natal Museum* 12: 397–441.
- Day J.H. 1957. The Polychaete fauna of South Africa. Part 4. New species and records from Natal and Moçambique. *Annals of the Natal Museum* 14: 59–129.
- Day J.H. 1960. The Polychaete fauna of South Africa. Part 5. Errant species dredged off Cape coasts. *Annals of the South African Museum* 45: 261–373.

- Day J.H. 1963. Polychaete fauna of South Africa. Part 7. Species from depths between 1000 and 3300 metres west of Cape Town. *Annals of the South African Museum* 46: 353–371.
- Day J.H. 1967a. *A Monograph on the Polychaeta of Southern Africa. Part 1. Errantia*. Vol. 656. Trustees of the British Museum of Natural History, London.
- Day J.H. 1967b. *A Monograph on the Polychaetes of Southern Africa. Part 2. Sedentaria*. Vol. 656. Trustees of the British Museum of Natural History, London.
- del Olmo I., Roma–Cavagliani J., Martín–Hervás M.d.R., Langeneck J., Cervera J.L. & Álvarez-Campos P. 2024. Integrative taxonomy in *Syllis prolifera* (Annelida, Syllidae): from a unique cosmopolitan species to a complex of pseudocryptic species. *Invertebrate Systematics* 38: IS24004. <https://doi.org/10.1071/IS24004>
- Fukuda M.V., Centurion R., Nogueira J.M.M. & San Martín G. 2012. Two new species of *Paraehlersia* San Martín, 2003 (Polychaeta, Syllidae) from the Atlantic Coast of South America. *Zootaxa* 3264: 38–52. <https://doi.org/10.11646/zootaxa.3264.1.2>
- Glasby C.J. 1993. Family revision and cladistic analysis of the Nereidoidea (Polychaeta : Phyllodocta). *Invertebrate Taxonomy* 7: 1551–1573. <https://doi.org/10.1071/IT9931551>
- Grube A.E. 1850. Die Familien der Anneliden. *Archiv für Naturgeschichte, Berlin* 16: 249–364.
- Grube A.E. 1860. Beschreibung neuer oder wenig bekannter Anneliden. Beitrag: Zahlreiche Gattungen. *Archiv für Naturgeschichte, Berlin* 26: 71–118.
- Grube A.E. 1863. Beschreibung neuer oder wenig bekannter Anneliden. Sechster Beitrag. *Archiv für Naturgeschichte, Berlin* 29: 37–69.
- Hartman O. 1964. Polychaeta Errantia of the Antarctica. *Antarctic Research Series* 3: 1–131. <https://doi.org/10.1029/AR003>
- Hutchings P.A. & Kupriyanova E. 2018. Cosmopolitan polychaetes – fact or fiction? Personal and historical perspectives. *Invertebrate Systematics* 32: 1–9. <https://doi.org/10.1071/IS17035>
- Kara J., Macdonald A.H.H. & Simon C.A. 2018. Integrative taxonomic methods reveal an incorrect synonymisation of the South African *Pseudonereis podocirra* (Schmarda) as the widespread *Pseudonereis variegata* (Grube) from Chile. *Invertebrate Systematics* 32: 1282–1297. <https://doi.org/10.1071/is18016>
- Kara J., Santos C.S.G., Macdonald A.H.H. & Simon C.A. 2020. Resolving the taxonomic identities and genetic structure of two cryptic *Platynereis* Kinberg species from South Africa. *Invertebrate Systematics* 34: 618–636. <https://doi.org/10.1071/is19072>
- Kara J., Molina–Acevedo I.C., Macdonald A., Zanol J. & Simon C. 2023. A closer look at the taxonomic and genetic diversity of endemic South African *Marphysa* Quatrefages, 1865. *PeerJ* 11: e16665. <https://doi.org/10.7717/peerj.16665>
- Krohn A. 1852. Ueber die Erscheinungen bei der Fortpflanzung von *Syllis prolifera* und *Autolytus prolifer*. *Archiv für Naturgeschichte, Berlin* 18: 66–76.
- Kudenov J.D. & Harris L.H. 1995. Family Syllidae Grube, 1850. In: Blake J.A., Hilbig B. & Scott P.H. (eds) *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel*. Vol. 5: 1–97. Santa Barbara Museum of Natural History, Santa Barbara.
- Lamarck J.B. 1809. *Philosophie zoologique, ou exposition des considérations relatives à l'histoire naturelle des Animaux; à la diversité de leur organisation et des facultés qu'ils en obtiennent; aux causes physiques qui maintiennent en eux la vie et donnent lieu aux mouvements qu'ils exécutent; enfin, à celles qui produisent, les unes le sentiment, et les autres l'intelligence de ceux qui en sont doués*. Dentu, Paris.

- Lamarck J.B. 1818. *Histoire naturelle des Animaux sans Vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels, enfin, l'exposition des principes fondamentaux de la zoologie*. Vol 5. Déterville & Verdrière, Paris.
- Langerhans P. 1881. Ueber einige canarische Anneliden. *Nova Acta der Kaiserlichen Leopoldinisch-Carolinischen Deutschen Akademie der Naturforscher, Halle* 42: 93–124.
- Licher F. 1999. Revision der Gattung *Typosyllis* Langerhans, 1879 (Polychaeta: Syllidae). Morphologie, Taxonomie und Phylogenie. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 551: 1–336.
- Martin D., Britayev T.A., San Martín G. & Gil J. 2003. Inter-population variability and character description in the sponge associated *Haplosyllis spongicola* complex (Polychaeta: Syllidae). *Hydrobiologia* 496: 145–162. <https://doi.org/10.1023/A:1026184529208>
- Martin D., Aguado M.T., Fernández-Álamo M.A., Britayev T.A., Böggemann M., Capa M., Faulwetter S., Fukuda M.V., Helm C., Petti M.A.V., Ravara A. & Teixeira M.A.L. 2021. On the diversity of Phyllodocida (Annelida: Errantia), with a focus on Glyceridae, Goniadidae, Nephtyidae, Polynoidae, Sphaerodoridae, Syllidae, and the holoplanktonic families. *Diversity* 13: 131. <https://doi.org/10.3390/d13030131>
- Moreno-Martin P., Mourin M., Verdes A. & Alvarez-Campos P. 2023. Morphological and molecular study of Syllinae (Annelida, Syllidae) from Bermuda, with the description of five new species. *Royal Society Open Science* 10: 230638. <https://doi.org/10.1098/rsos.230638>
- Müller O.F. 1776. *Zoologicae Danicae Prodrum, seu Animalium Daniae et Norvegiae indigenarum characteres, nomina et synonyma imprimis popularium*. Hallageriis, Havniae [Copenhagen].
- Núñez J. & San Martín G. 1991. Two new species of Syllidae (Polychaeta) from Tenerife (Canary Islands, Spain). In: Proceedings of the Third International Polychaete Conference. *Bulletin of Marine Science* 48: 236–241.
- Nygren A. 2014. Cryptic polychaete diversity: a review. *Zoologica Scripta* 43: 172–183. <https://doi.org/10.1111/zsc.12044>
- Prado A. & San Martín G. 2024. Syllidae (Annelida) from the Alborán Sea (Western Mediterranean), with the description of a new species of *Paraehlersia* San Martín, 2003. *Zootaxa* 5437: 87–104. <https://doi.org/10.11646/zootaxa.5437.1.5>
- Read G. & Fauchald K. 2025. World Polychaeta Database. Available from <http://www.marinespecies.org/polychaeta> (accessed 17 September 2025).
- Ribeiro R.P., Ponz-Segrelles G., Helm C., Egger B. & Aguado M.T. 2020. A new species of *Syllis* Grube, 1850 including transcriptomic data and an updated phylogeny of Syllinae (Annelida: Syllidae). *Marine Biodiversity* 50: 31. <https://doi.org/10.1007/s12526-020-01046-y>
- Rouse G.C., Pleijel F. & Tilic E. 2022. *Annelida*. Oxford University Press, Oxford.
- Salcedo-Oropesa D.L., San Martín G. & Solís-Weiss V. 2012. The genus *Syllis* (Polychaeta: Syllidae: Syllinae) in the southern Mexican Pacific, with the description of two new species and three new records. *Zootaxa* 3263: 47–62. <https://doi.org/10.11646/zootaxa.3263.1.2>
- San Martín G. 2003. Annelida, Polychaeta II: Syllidae. In: Ramos M.A., Alba J., Bellés X., Gosálbez J., Guerra A., Macpherson E., Serrano J. & Templado J. (eds) *Fauna Iberica*. Vol. 21. CSIC, Madrid.
- San Martín G. & Hutchings P. 2006. Eusyllinae (Polychaeta: Syllidae) from Australia with the description of a new genus and fifteen new species. *Records of the Australian Museum* 58: 257–370.

- San Martín G., Lucas Y. & Westheide W. 2021. The hidden worms on the beach: interstitial Syllidae (Annelida) from the Indo-Pacific. *Proceedings of the Biological Society of Washington* 134: 149–195. <https://doi.org/10.2988/0006-324x-134.1.149>
- San Martín G., Lucas Y. & Hutchings P.A. 2023. The genus *Syllis* Savigny in Lamarck, 1881 (Annelida: Syllidae: Syllinae) from Australia (Part 3): new species and redescription of previously described species. *Zootaxa* 5230: 251–295. <https://doi.org/10.11646/zootaxa.5230.3.1>
- Sedick S. 2018. Syllidae Grube, 1850 (Annelida) from southern Africa. A taxonomic update, with a focus on *Syllis* Lamarck, 1818. PhD Thesis, Stellenbosch University, South Africa.
- Sedick S. & Simon C. 2019. Three new species of *Syllis* Savigny in Lamarck, 1818 (Annelida: Syllidae) from the south coast of South Africa. *Zootaxa* 4688: 585–598. <https://doi.org/10.11646/zootaxa.4688.4.10>
- Simon C.A., San Martín G. & Robinson G. 2014. Two new species of *Syllis* (Polychaeta: Syllidae) from South Africa, one of them viviparous, with remarks on larval development and vivipary. *Journal of the Marine Biological Association of the United Kingdom* 94: 729–746. <https://doi.org/10.1017/S0025315413001926>
- Simon C.A., van Niekerk H.H., Burghardt I., ten Hove H. & Kupriyanova E. 2019. Not out of Africa: *Spirobranchus kraussii* (Baird, 1865) is not a global fouling and invasive serpulid of Indo-Pacific origin. *Aquatic Invasions* 14: 221–249. <https://doi.org/10.3391/ai.2019.14.2.06>
- Simon C.A., Kara J., Clarke D.T. & Sedick S. 2022. Revisiting ‘A monograph on the Polychaeta of southern Africa’: establishing taxonomic research priorities in southern Africa. *African Journal of Marine Science* 44: 83–100. <https://doi.org/10.2989/1814232X.2022.2041094>
- Soto E.H. & San Martín G. 2018. New reports and a new species of Syllidae (Annelida) from Chilean Patagonia. *Journal of the Marine Biological Association of the United Kingdom* 98: 1599–1607. <https://doi.org/10.1017/S0025315417001242>

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