Heteroscleromorph demosponge taxonomy and diversity of the Amathole region (Eastern Cape, South Africa)

By

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Thesis presented for the Degree of Doctor of Philosophy in the Department of Biodiversity and Conservation Biology, University of the Western Cape.

March 2021

FINAL

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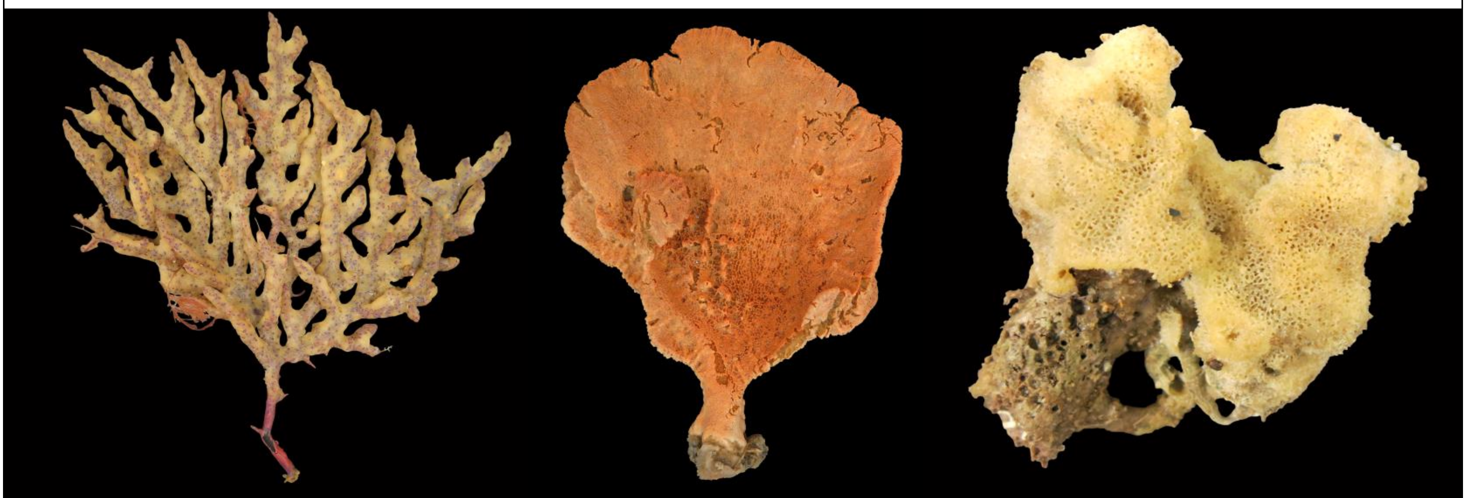

UNIVERSITY of the WESTERN CAPE

forestry, fisheries & the environment

Department: Forestry, Fisheries and the Environment REPUBLIC OF SOUTH AFRICA

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Keywords

Indian Ocean

South Africa

Eastern Cape

Amathole region

Systematics

Taxonomy

Diversity

Biogeography

Porifera

Sponges

Abstract

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PhD Thesis, Department of Biodiversity and Conservation Biology, University of the Western Cape.

Sponges are functionally important and ubiquitous components of the global marine benthos. South Africa accounts for roughly 4% of the global marine sponge diversity, comprising 374 described species and seven varieties/forms, with elevated apparent endemism (59.3%). However, an estimated 900 sponge species are thought to be undescribed, and much work is needed to update and expand our knowledge of the South African sponge fauna.

The Amathole region is situated offshore of the Amathole District, around the city of East London, on the south-east coast of South Africa. This area has been historically unexplored and was thus the focus of the *Imida* Frontiers Project initiated in 2015, under the auspices of the African Coelacanth Ecosystem Programme (phase IV). As a component of this larger project, the research presented here focuses exclusively on the diversity, depth distribution and biogeographic affinities of the heteroscleromorph demosponge fauna.

This study included 474 specimens, from four expeditions comprising 48 sites across depths of 3–229 m. Non-random-stratified sampling was undertaken during two cruises onboard the R/V *Ellen Khuzwayo* in 2016, with 457 specimens collected from 42 sites using an epibenthic dredge. An additional 11 specimens were included from three dredge sites in 2015, as were six specimens from three SCUBA sites sampled by the Coral Reef Research

Foundation in 1999. Underwater visual surveys were undertaken onboard the R/V *Phakisa* using a Remotely Operated Vehicle during two expeditions in 2017, with *in situ* images used for species accounts.

The Amathole region was found to support elevated heteroscleromorph demosponge diversity, with the fauna dominated by two orders (Poecilosclerida, Tetractinellida), and three families (Geodiidae, Isodictyidae, Latrunculiidae). Of the 74 species obtained, 47 were known, while 27 are likely new to science. Twenty-three species were further described, eight as new. This study also documented an additional 35 species and 11 genera for South Africa, and three genera for the Indian Ocean. Consequently, the number of marine sponge species from South Africa will increase to 410 with six varieties/forms. Assemblages did change with depth, and taxa-specific depth restrictions were observed. However, low average similarities and a relatively high number of unique species were indicative of heterogeneity within each depth zone, possibly driven by habitat type. Species richness peaked in the mesophotic zone, which was likely an artefact of the collection effort. Finally, faunal affinities were primarily with southern Africa, with additional influence from the Western Indian Ocean region. Species were shared with every ecoregion in South Africa, but the fauna was most similar to that found in the Agulhas and southern Benguela ecoregions.

Findings were limited by the exclusion of aspiculate demosponges, and specimens from the other classes, as well as under-sampling in the shallow and sub-mesophotic depth zones. Nevertheless, this study supports the position of the region within the Algoa to Amathole Ecologically or Biologically Significant Marine Area, and formation of the Amathole Offshore Marine Protected Area in 2019. Sixty-three (85%) of the recorded species fall within the latter, and thus receive some level of protection.

March 2021

Declaration

I declare that *Heteroscleromorph demosponge taxonomy and diversity of the Amathole region (Eastern Cape, South Africa)* is my own work, that it has not been submitted for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

Robyn Pauline Payne March 2021

Signed:

Acknowledgements

Financial support was provided by the African Coelacanth Ecosystem Programme (DST-NRF), with bursary funding provided by the South African National Research Foundation (NRF). I gratefully acknowledge Prof. Sven Kerwath (Principal Scientist) and Dr Denham Parker, from the Department of Forestry, Fisheries and the Environment (DFFE), for enabling and facilitating my participation in the *Imida* Frontiers Project.

More specifically, I would like to express my gratitude to my supervisors: Dr Toufiek Samaai (DFFE) and Prof. Mark J. Gibbons (University of the Western Cape), for their ongoing assistance, guidance and advice. Dr Samaai has particularly served as my patient mentor, and has given me unrestricted access to the sponge specimens in his care, while allowing me various opportunities to participate in sampling trips, conferences and courses. His enthusiasm for sponge taxonomy is infectious, and I am forever indebted to him for introducing me to this remarkable group.

The resources for specimen collection and processing were largely provided by DFFE, while the captain and crew of the R/V *Ellen Khuzwayo* are warmly thanked for their expertise. Imtiyaaz Malick, now based at the South African Environment Observation Network, cheerfully helped me sort numerous dredge samples at sea, for which I am extremely appreciative. Lori Bell Colin and Dr Patrick Colin, of the Coral Reef Research Foundation (CRRF), are thanked for collections of specimens made in South Africa, and the provision of specimens through Dr Michelle Kelly (NIWA, Auckland, New Zealand). Collections by the CRRF were made under contract to the United States National Cancer Institute Contract no. N01–CM–27704. The Government of South Africa granted the CRRF permits for collection and they were made through the cooperation of Prof. Michael Davies-Coleman, then at Rhodes University. The underwater visual surveys undertaken onboard the R/V *Phakisa* were carried out by a skilled core team comprising Prof. Kerwath, Dr Parker, Ryan Palmer (South African Institute for Aquatic Biodiversity: NRF-SAIAB), Dr Kerry Sink (South African National Biodiversity Institute), Nick Riddin (formerly NRF-SAIAB), Thor Eriksen (NRF-SAIAB), Siseko Benya (NRF-SAIAB) and Luther Adams (University of Cape Town: UCT). I am grateful to all those involved, mentioned or not, whose contributions made this research possible.

My sincerest thanks go to Liesl Janson (DFFE), who spent many hours processing sponges with me in the lab, and has served as both a friend and source of support. A word of thanks is also extended to Winston April (DFFE) for his help with the histology, as well as Miranda Waldron (UCT) and Dr Wayne Florence (Iziko South African Museum) for access to, and assistance with, scanning electron microscopes. This thesis would not have been achievable without the use of the World Porifera Database, and the editors are gratefully acknowledged for providing continued access to data and key taxonomic papers.

Countless people brightened my days at DFFE – thank you for your friendship, life lessons and a sense of community!

Although this process was challenging, I feel privileged to have been given the opportunity to pursue this degree. This would not have been possible without the unconditional love and support from my family: my parents, grandparents and two sisters. To my parents, Michael and Lyn Payne, you have given me everything and I dedicate this thesis to you.

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'I learned that such a work was expected from me, and I was the more easily induced to undertake it from a belief that no other naturalist was likely to devote his time to illustrate a comparatively limited and isolated class of organized beings, obscure in character, and possessed of less interest than attaches to almost every other. The class may be said to occupy at present a piece of debateable land, lying between the confines of the two organic kingdoms, — too poor and barren to be an object of contest with the subjects of either, and readily relinquished to the occupation of any eccentric borderer who may find his pleasure in cultivating an intimacy with its rude tenantry. This is not an easy task, for there is so much that is common to them, and each adapts itself so readily to circumstances and assumes a new mask, that it requires a tact, to be gained only by some experience, to recognize them under their guises; while we labour, perhaps in vain, to devise phrases which shall aptly pourtray to others the characteristics of objects that have no fixed shape, and whose distinctive peculiarities almost cheat the eye.'

– Johnston (1842)

1.1 The Phylum Porifera

The phylum Porifera comprises exclusively aquatic, largely filter-feeding, sessile metazoans that possess choanocytes, a differentiated inhalant and exhalant aquiferous system with exterior pores, high cellular motility with totipotent capabilities, and often siliceous or calcitic spicules (Hooper & van Soest 2002; van Soest *et al.* 2012). Considered the oldest extant metazoans on Earth, and possible sister-group to all other multicellular animals (Feuda *et al.* 2017; Simion *et al.* 2017; Nielsen 2019), the evolutionary and ecological success of sponges is attributed to their simple but highly adaptable bauplan, and incorporation of symbiotic microbes (Gaino *et al.* 1995; van Soest *et al.* 2012; Carballo & Bell 2017). Consequently, they are ubiquitous in benthic ecosystems today (van Soest *et al.* 2012).

Sponges are functionally important components of the global marine benthos, and can be considered key ecosystem engineers (de Goeij *et al.* 2017; Folkers & Rombouts 2020), according to their role in benthic and pelagic processes, as well as associations with other organisms (Bell 2008). Some species can modify the substrate as preliminary stabilisers that bind rubble and aid reef regeneration (Wulff 2001; Rasser & Riegl 2002), while others are bioeroders that remove fragments from calcareous substrata, contributing to both reef-associated sediment and carbonate cycling (Glynn & Manzello 2015; Schönberg *et al.* 2017; Meyer *et al.* 2019). As efficient filter-feeders, sponges play an important role in benthic-pelagic coupling, while also retaining and transforming dissolved organic matter into bioavailable forms, accessible to higher trophic levels, via the 'sponge loop' pathway (de Goeij *et al.* 2013; de Goeij *et al.* 2017; Folkers & Rombouts 2020; Pawlik & McMurray 2020). These processes are often facilitated by a diverse symbiotic microbial community (Pita *et al.* 2018), which can comprise up to 35% of the host's biomass, and include bacteria, archaea, unicellular algae, fungi and viruses, together forming the sponge holobiont (Webster

& Taylor 2012; Webster & Thomas 2016). Sponges likewise provide microhabitats for macroscopic organisms, in terms of hosting endobionts (Papatheodoulou *et al.* 2019), and acting as a settlement surface (Turon *et al.* 2000), while also enhancing predation protection (Bell 2008). They also serve as a food source (Wulff 2006; Pawlik *et al.* 2018; Fitt 2020; Maschette *et al.* 2020), and can be used as tools by other animals (Mann *et al.* 2008; Wild *et al.* 2019). Moreover, they play an important role in spatial competition, which is often chemically mediated (de Voogd *et al.* 2004; Wulff 2006). Finally, high-density sponge aggregations have been found to increase structural complexity and enhance biodiversity, while often supporting commercially important species, and thus comprise vulnerable habitats that require legal protection (Hogg *et al.* 2010; Maldonado *et al.* 2015; Powell *et al.* 2018). Globally, the ecological importance of sponges is high, but underappreciated (Bell 2008). However, this is likely to change in the future, as sponges are expected to benefit under projected climate change scenarios, and dominate certain ecosystems, including coral reefs (Bell *et al.* 2013; Schönberg *et al.* 2017; Bell *et al.* 2018; Pawlik & McMurray 2020).

From an anthropogenic perspective, sponges played an important role in early civilizations, starting at least 5 000 years ago (Pronzato & Manconi 2008). They were used for household, hygienic, medical and artistic purposes (Voultsiadou 2007; Hogg *et al.* 2010; Voultsiadou 2010; Jesionowski *et al.* 2018). Nowadays, human interest is largely based on the ability of sponges and/or their microbial symbionts to produce secondary metabolites that have potential pharmaceutical applications (Mehbub *et al.* 2014; Davies-Coleman *et al.* 2019). Furthermore, sponges may act as a source of bio-inspiration for the development of advanced materials (Li *et al.* 2020), lead to a greater understanding of animal evolution (Rennard *et al.* 2018; Colgren & Nichols 2019), and may be used as bioindicators and bioremediators of pollution (Orani *et al.* 2018; Wyllia *et al.* 2018). Presently, sponge research is primarily driven by biodiscovery and conservation (Hooper & van Soest 2002; van Soest *et al.* 2012).

To date, 9 349 sponge species are known to exist worldwide, in four classes: Calcarea, Demospongiae, Hexactinellida and Homoscleromorpha (van Soest *et al.* 2020a). Of these 9 087 (97%) are marine, with the majority belonging to the class Demospongiae (82%, van Soest *et al.* 2020a). However, our knowledge of global marine sponge diversity is incomplete, with roughly 30% of species known, and an additional 17 000 thought to exist (Appeltans *et al.* 2012). Although rudimentary (Wörheide *et al.* 2005), global sponge diversity patterns are consistent with those reported for other marine animal groups, and increased species richness is observed in the tropics (van Soest *et al.* 2012). However, this is biased according to collection and taxonomy efforts, and is not evident at lower spatial and taxonomic levels (van Soest *et al.* 2012). Due to their sessile nature and limited larval dispersal (Maldonado 2006), sponges often occur in local areas of endemism (Bell *et al.* 2015), with most information on global sponge diversity generated in regional studies (van Soest *et al.* 2012). Thus, further research is needed on the sponge fauna of understudied geographic areas, including South Africa (Bell *et al.* 2015; Schönberg 2017).

1.2 South Africa's Marine Biodiversity

The Exclusive Economic Zone (EEZ) around mainland South Africa comprises roughly one million km^2, and extends to a maximum depth of 5 700 m, with only 25% of the seafloor found in depths less than 1 000 m (Griffiths *et al.* 2010; Sink *et al.* 2019e). Situated at the confluence of the Atlantic and Indian oceans, South Africa has contrasting geological and oceanographic settings along each coast (Sink *et al.* 2019e). The oceanographic regime is dominated by two major current systems, including the cold Benguela Current which flows northward along the west coast (Atlantic Ocean), and the warm Agulhas Current which flows vigorously southward along the east coast (Indian Ocean) (Griffiths *et al.* 2010). This variability drives the division of marine biota into three main biogeographic shelf provinces, including the cold-temperate southern Benguela (west coast), the warm-temperate Agulhas (south coast) and subtropical Natal-Delagoa (east coast), with boundaries located at Cape Point (Western Cape) and Mbashe (Eastern Cape) (Sink *et al.* 2019b) (Fig. 1A).

The wide range of environmental settings has resulted in elevated ecosystem diversity, species diversity and endemism levels (Gibbons *et al.* 1999; Sink *et al.* 2019e). To date, 150 marine ecosystem types have been documented in South Africa, in six ecoregions, including four on the continental shelf (southern Benguela, Agulhas, Natal, Delagoa), and two in the deep ocean (Southeast Atlantic Deep Ocean, Southwest Indian Deep Ocean), as defined by Sink *et al.* (2019b) (Fig. 1A). Approximately 87% of these ecosystem types receive some level of protection from the newly expanded Marine Protected Area (MPA) network, which increased the number of MPA's from 26 to 42 (including the Prince Edward Islands MPA) in 2019 (Sink *et al.* 2019d). This recent expansion increased protection around the South African mainland from less than 0.5% to 5.4% (Sink *et al.* 2019d). Currently, South Africa is leading marine biodiversity conservation in Africa, and is only exceeded in the Western Indian Ocean region by the Seychelles (26%), with all other countries protecting less than 2% (Sink *et al.* 2019d).

Over 13 000 marine species occur in South Africa, with richness increasing from west to east (Awad *et al.* 2002; Sink *et al.* 2019e). The number of range-restricted species and richness is also elevated in areas situated at, or adjacent to, biogeographic boundaries (Awad *et al.* 2002; Acuña & Griffiths 2004; Scott *et al.* 2012). However, this may be an artefact, as they also correspond to areas of enhanced sampling and shipping activity (Awad *et al.* 2002; Acuña & Griffiths 2004; Scott *et al.* 2012; Griffiths & Robinson 2016).

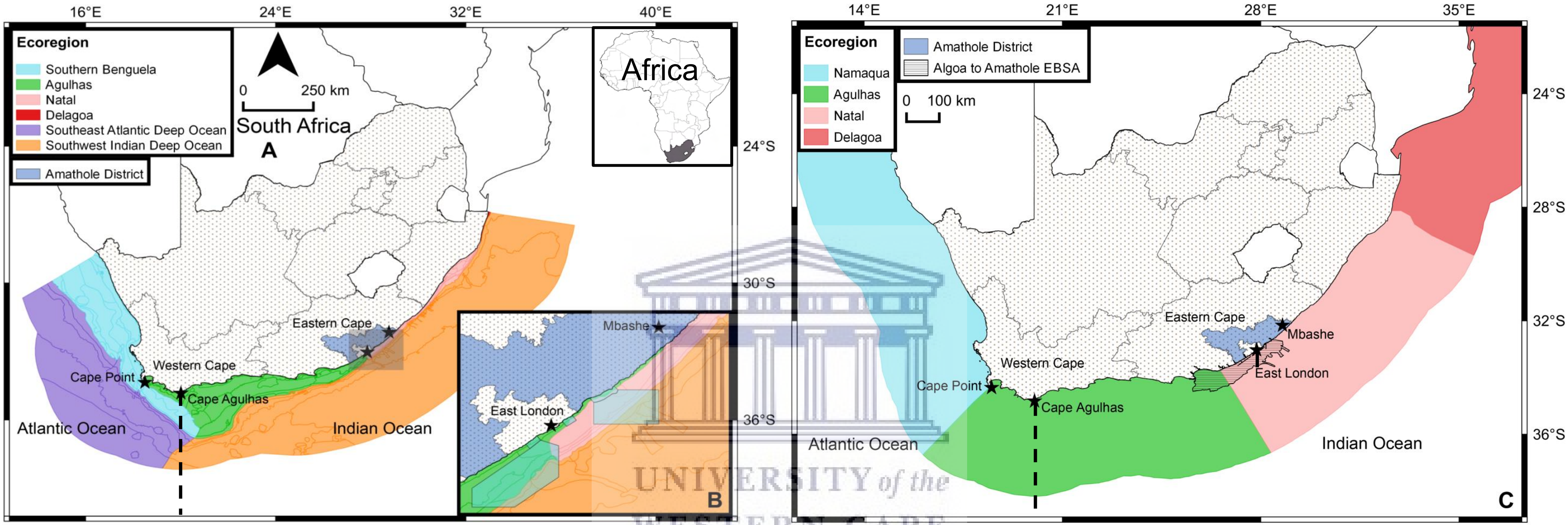

Figure 1: Maps of South Africa with place names mentioned in the text, depicting both national (**A**, Sink *et al.* 2019b) and global (**C**, Marine Ecoregions of the World: MEOW, Spalding *et al.* 2007) marine ecoregions, with the latter used by the World Porifera Database (van Soest *et al.* 2020a). The Amathole region is located in the transitional Agulhas-Natal ecoregion boundary zone (**B**) or in the Natal ecoregion (**C**) depending on the biogeographic classification system used. The Marine Protected Areas (light blue blocks) depicted in **B** are further detailed in Figure 3. Generated using QGIS v.2.6.1.

Nonetheless, an estimated 26 to 33% of South African species are considered endemic, with the highest endemicity consistently reported for the Agulhas ecoregion (south coast) (Gibbons *et al.* 1999; Awad *et al.* 2002; Costello *et al.* 2010; Griffiths *et al.* 2010; Griffiths & Robinson 2016; Sink *et al.* 2019e). Although possibly due to geographical isolation from other warm temperate regions, levels may be inflated as this ecoregion is situated exclusively within South Africa's territory and farthest from the political boundaries (Awad *et al.* 2002; Griffiths *et al.* 2010; Griffiths & Robinson 2016). Nevertheless, at the global scale, these marine endemicity levels are similar to Australia (28%), and are only exceeded by Antarctica (45%) and New Zealand (51%) (Costello *et al.* 2010). Possibly explained by the relative geographical isolation of South Africa (Costello *et al.* 2010; Griffiths & Robinson 2016), and contrasting ocean current systems detailed above (Procheş & Marshall 2002), these values should be interpreted with caution as they are subject to the degree of taxonomic knowledge and sampling effort, both locally and in adjacent areas (Gibbons *et al.* 1999; Griffiths & Robinson 2016). Thus, the poorer levels of taxonomic research in the wider African region likely artificially inflate apparent rates of endemism in South Africa (Gibbons *et al.* 1999; Griffiths *et al.* 2010; Scott *et al.* 2012; Griffiths & Robinson 2016). In addition, much of South Africa's marine diversity remains unexplored, especially smaller and more taxonomically challenging taxa, and the biota of under-sampled deep-sea environments (Gibbons *et al.* 1999; Griffiths *et al.* 2010). As of 2010, undescribed species were estimated at 38% for South Africa, with at least 7 500 additional marine species needing description in order to bring the state of taxonomic knowledge up to European levels (Costello *et al.* 2010; Griffiths *et al.* 2010). South Africa has also not been immune to the global, progressive loss of taxonomic expertise (Gibbons *et al.* 1999), with the country comprising a low number of experts (roughly two per taxon), and outdated guides for major taxa (Costello *et al.* 2010). The majority of work is carried out by part-time/retired taxonomists or postgraduate students

(Gibbons *et al.* 1999; Griffiths *et al.* 2010; Sink *et al.* 2019e). For example, as of 2010, an estimated 31 marine taxonomists were active, with only five employed as full-time systematists (Griffiths *et al.* 2010). The current situation is dire, with most of the remaining taxonomic expertise in South Africa expected to be lost within the next five years (Sink *et al.* 2019a).

Despite South Africa's status as a developing nation, and seemingly current lack of taxonomic expertise, marine biodiversity knowledge exceeds that of any other African country (Griffiths 2005; Griffiths *et al.* 2010; McQuaid 2010). This is largely due to the history of marine biological exploration in South Africa (Sink *et al.* 2019e), which can be divided into three eras (Costello *et al.* 2010; Griffiths *et al.* 2010; Sink *et al.* 2019e). The first 'colonial' era was characterised by exploratory studies, with the earliest marine collections undertaken in the late 18th century, followed by those carried out during global ocean expeditions, such as the HMS *Challenger* Expedition (1872–1876) (Gibbons 1995; Griffiths *et al.* 2010). During this period, specimens collected from the colonies were deposited in European museums, where they were catalogued and described, often in monographs (Costello *et al.* 2010; Griffiths *et al.* 2010). The second 'descriptive' era was characterised by regional studies, initiated by an increased availability of research resources (Costello *et al.* 2010). Roughly spanning from the start of the 20th century to 1970, prominent marine taxonomists, such as J.D.F. Gilchrist and K.H. Barnard, catalogued and/or described most of the common marine invertebrates and fish (Griffiths *et al.* 2010). The third and current 'modern' era is characterised by large-scale multidisciplinary studies instigated by the development of new technologies (Costello *et al.* 2010), with research shifting to phylogenetic and biological questions of ecological understanding (Griffiths *et al.* 2010). Thus, from the 1970's, taxonomic research has been largely neglected, with much of the species knowledge today from work conducted in the 'descriptive' era, which is now outdated and inaccessible to non-experts (Sink *et al.* 2019e). Sponge research in South Africa follows these general periods and trends. However, taxonomic work on this group is currently ongoing.

1.3 South African Sponge Research

Research on South African sponges spans over two centuries, with most work of the late 18th and 19th centuries based on small incidental collections housed in European institutions. Initiated by the description of at least one species by Esper in 1797, it was more than four decades later when Bowerbank (1845, 1864) and Haeckel (1870, 1872) described the first calcareous sponges. At the same time, Ehlers (1870) re-investigated Esper's material, while Carter (1871) described a new tetillid. Subsequently, Bowerbank (1873) described a further two species, both of which were disputed by Gray (1873). Noteworthy contributions were later made by Carter (1874, 1875b, 1879, 1881, 1882a, 1882b, 1882c, 1885), founded on his examination of South African material retained at the British Museum of Natural History (currently the Natural History Museum, London). Additional species descriptions and records were also provided by Vosmaer (1880), from material in the Leyden Museum (now the Naturalis Biodiversity Center, Leiden). The extensive collections carried out by the global HMS *Challenger* Expedition (1872–1876) led to the discovery of 13 new 'Monaxonida' from mainland South Africa (Dendy & Ridley 1886; Ridley & Dendy 1886, 1887). Sollas (1886, 1888) worked on the 'Tetractinellid' sponges from this expedition, but no specimens of this group were collected from South Africa, and he resorted to describing a single species from unrelated South African material that had been purchased from a dealer. The final work of the 19th century was conducted by Lendenfeld (1889a), who provided an account of the 'horny' sponges from South Africa.

The 20th century was characterised by the enhanced effort of international sponge taxonomists to document the South African sponge fauna from opportunistic collections and larger expeditions, augmented by considerable material provided by researchers based in South Africa. One such researcher was John D.F. Gilchrist, who was appointed as Government Fisheries Biologist in 1895/1896 (Gibbons 1995; Day 2000; Brown 2003). Originally from England, and South Africa's first resident marine biologist, he investigated the fisheries potential of the country, while also collecting numerous marine invertebrates, which were sent to experts for identification and/or description (Day 2000; Brown 2003). The sponges were examined by Kirkpatrick (1901, 1902, 1903a, 1903b), who described over 30 new species, including the first hexactinellids and lithistids from South Africa. Kirkpatrick (1913) later documented an additional hexactinellid from material received from Louis Péringuey, the Director of the South African Museum. Further additions to the fauna resulted from continued work on the aforementioned smaller opportunistic collections (Topsent 1905; Baer 1906), and other earlier expeditions. For example, the SS *Valdivia* Expedition or Deutsche Tiefsee Expedition (1898–1899) led to the discovery of numerous new species, including a hexactinellid (Schulze 1904), 17 tetractinellids (Lendenfeld 1907), and a few calcareous sponges (Urban 1908, 1909). Conversely, only a few species were described as a result of the South Polar ship *Gauss* Expedition or Deutsche Südpolar Expedition (1901–1903) (Hentschel 1914; Brøndsted 1931). Stephens (1915) worked on sponges collected from the south-west coast of South Africa during the Scottish National Antarctic Expedition (1902–1904), and noted the absence of shared species with those documented earlier by Kirkpatrick.

The next two decades were dominated by research undertaken by Burton (1926, 1929, 1931, 1933a, 1933b, 1936), which also included the description of a single species collected from South Africa during the HMS *Discovery* Expedition (1901–1904) (Burton 1932). Some of Burton's later publications were based on samples provided by T. Allan Stephenson, an English marine biologist who was appointed to the Chair of Zoology at the University of Cape Town (UCT, South Africa) in 1931 (Day 2000; Brown 2003). Like Gilchrist, Stephenson was interested in marine invertebrates, but focused on intertidal communities, possibly due to the fact that he lacked access to a research vessel (Brown 2003). Nevertheless, Stephenson organised a survey of the entire coastline of southern Africa, consisting of nearly 50 sites, which was carried out from 1931 to 1940 (Adamson & Stephenson 1939; Day 2000). From about 1937, he was assisted in this endeavour by John H.O. Day, who later became the Head of the Zoology Department at UCT in 1946/1947 (Day 2000; Brown 2003). Day wanted to expand Stephenson's intertidal work offshore to the edge of the continental shelf, which he realised by hiring fishing trawlers from about 1948, and acquiring a small antiquated ship in 1957 (Day 2000). Ensuing collections and resultant samples provided by Day, formed the basis of the work undertaken by Lévi (1960, 1963, 1967) and Borojević (1967). Lévi (1963) described over 30 new poecilosclerids, while providing an initial tally of the South African sponge fauna: 16 Calcarea, 180 Demospongiae and six Hexactinellida. Later describing eight new tetractinellids, Lévi (1967) also provided a taxonomic key for this group, while Borojević (1967) described five new calcareous sponges. In the interim, Lévi (1964a) additionally documented and described several deep-water sponges collected largely off the South African east coast during the *Galathea* II, Danish Deep Sea Expedition (1950–1952). Roughly 20 years later, Uriz (1984, 1985, 1987, 1988, 1990) conducted work on deep-water sponges that had been trawled from fishing grounds largely comprising the soft-bottomed continental shelf and slope off Namibia. As part of these Benguela surveys, at least one collection station was located just offshore of the Namibian-South African border. Thus, several species are considered shared between

Namibia and the South African west coast (which fall into the same ecoregion), including a dense population of the sponge *Suberites dandelenae* Samaai & Maduray, 2017.

At the end of the 20th century, and into the 21st century, numerous overseas researchers revised various taxa[1], often based on museum material, which collectively enhanced our knowledge of the South African sponge fauna. Perhaps the most internationally significant advancement was the completion of the *Systema Porifera*, a comprehensive guide to the classification of sponges, which was developed by 45 researchers from 17 countries over roughly six years (Hooper & van Soest 2002). This encyclopaedia includes re-descriptions of certain South African species (e.g. *Lithochela conica* Burton, 1929), in addition to work by the first sponge taxonomist of South African nationality (Samaai & Kelly 2002). After completing earlier sponge studies (Samaai 1998; Samaai *et al.* 1999), Toufiek Samaai continued with a doctorate focussing on latrunculids (Samaai 2002). Concentrated work on this family in South Africa was initiated by the first marine biodiscovery programme centred at a South African university (Rhodes) (Davies-Coleman *et al.* 2019), with taxonomic research prolific and ongoing (Samaai *et al.* 2003, 2004a, 2004b, 2006, 2009a, 2012; Parker-Nance *et al.* 2019; Samaai *et al.* 2020a). Subsequent additions to the South African sponge fauna arose from video-based biological surveys (Schleyer & Celliers 2005; Schleyer *et al.* 2006), single-species descriptions (Samaai *et al.* 2009b), and extensive collections along the coastline. In 2005, Samaai & Gibbons collected 65 shallow-water demosponge species along the west coast, while Maduray (2013) documented 83 deep-water sponges trawled offshore of

[1]For example, genus *Polymastia*: Boury-Esnault 1987; genus *Acarnus*: van Soest *et al.* 1991; genus *Rhabderemia*: van Soest & Hooper 1993; genus *Mycale*: Hajdu 1995; a few poecilosclerid families: Desqueyroux-Faúndez & van Soest 1996; family Microcionidae: Hooper 1996; genus *Guitarra*: Carballo & Uriz 1998; genus *Lophophysema*: Tabachnick & Lévi 1999; genus *Clathria*: Hooper *et al.* 2000; genus *Petromica*: Muricy *et al.* 2001; family Guitarridae: Uriz & Carballo 2001; genus *Petromica*: List-Armitage & Hooper 2002; genus *Clathrina*: Klautau & Valentine 2003; genus *Tethya*: Ribeiro & Muricy 2011; genus *Placospongia*: Becking 2013; family Polymastiidae: Plotkin *et al.* 2017; class Calcarea: van Soest & de Voogd 2018, and genus *Penares*: Sim-Smith & Kelly 2019.

the west and south coasts. Recently, Samaai *et al.* (2019) detailed 33 shallow-water demosponges collected from the north-east coast, including the first homosclerophorid from South Africa.

Sponge research in South Africa during the 21st century has become increasingly multidisciplinary, with studies exploring larger ecological topics, including the domestic distribution of demosponges, patterns of diversity and endemism (Samaai 2006), as well as species richness along a bathymetric gradient (Samaai *et al.* 2010). Innovative technologies, such as gene sequencing, have also enabled the resolution of taxonomically-challenging taxa (Samaai *et al.* 2017b), and the characterisation of sponge-associated bacterial communities (Matobole *et al.* 2017; Waterworth *et al.* 2017). Finally, some of the latest work comprises the correction of several South African sponge species names (Ribeiro & Muricy 2011; Samaai *et al.* 2017a; Sim-Smith & Kelly 2019; Samaai *et al.* 2020b; van Soest *et al.* 2020b). General findings from this extensive history of South African sponge research, which pertain to this study, are further discussed below.

1.4 Current State of South African Sponge Knowledge

Based largely on the World Porifera Database (van Soest *et al.* 2020a), an updated marine sponge species list is provided for South Africa (Appendix A). Currently, the sponge fauna comprises four classes, seven subclasses, 23 orders, 71 families, 152 genera, 374 species and seven varieties/forms (Table 1). Accounting for roughly 4% of the global marine sponge diversity, it is dominated by the class Demospongiae, subclass Heteroscleromorpha, and orders Poecilosclerida (44.7%) and Tetractinellida (23.3%) (Fig. 2). This is especially evident in the abundance of poecilosclerids in past studies (Lévi 1963; Samaai & Gibbons 2005; Maduray 2013; Samaai *et al.* 2019). Of this order, the family Latrunculiidae is most studied in South Africa, initiated largely by chemical biodiscovery research (Davies-Coleman *et al.*

2019, see Section 1.3). Indeed, the country is a diversity hotspot for this family (Samaai *et al.* 2004a), and comprises two endemic genera: *Cyclacanthia* and *Tsitsikamma*. Another three genera are also endemic, including *Lithobactrum* (order Tetractinellida), *Lithochela* (order Poecilosclerida) and *Waltherarndtia* (order Axinellida), all of which are monospecific (van Soest *et al.* 2020a). Of the 374 species and seven varieties/forms present, 220 (58.8%) and six (85.7%) are apparent endemics respectively. Together, 59.3% are apparent endemics, which is consistent with the 57% previously reported by Samaai (2006). Although much higher than proposed by earlier studies (3.5%, Gibbons *et al.* 1999; 8.8%, Griffiths *et al.* 2010), this level is comparable to those documented for other immobile marine benthic invertebrates in South Africa, including anemones (46%, Laird 2013) and bryozoans (57%, Boonzaaier 2017). Possibly due to the sessile nature and limited larval dispersal of this phylum (van Soest *et al.* 2012), in addition to the prevailing environmental conditions (as detailed in Section 1.2), this endemism level is more likely exaggerated due to the lack of taxonomic knowledge and sampling effort, both in South Africa, and in adjacent areas (Gibbons *et al.* 1999; Griffiths & Robinson 2016). The global community of sponge scientists comprises roughly 300 members (less than 150 specialists) from 72 counties, with most located in Europe (41.8%), and least in Africa (1.5%) (Schönberg 2017). Thus, the current state of marine sponge diversity knowledge in South Africa is poor (Gibbons *et al.* 1999; Samaai 2006; Griffiths *et al.* 2010), with an estimated 900 undescribed species (Griffiths *et al.* 2010), and roughly 1 000 unaccesioned lots at the Iziko South African Museum (Boonzaaier 2017). Presently, any relatively intensive collection effort leads to the discovery of new species and records, as well as range extensions (e.g. Samaai & Gibbons 2005; Maduray 2013; Samaai *et al.* 2019). Taxonomic work is hampered by inaccessible, outdated and/or non-English literature, in addition to the historical deposition of South African sponge type material in European museums. Furthermore, although sponges are included in field guides for South Africa

(Branch *et al.* 2010; Samaai *et al.* 2018), and the Western Indian Ocean (Kelly 2011), identifying characteristics are largely based on morphology, with spicules and skeletal structures excluded. This, in combination with the need for a microscope for accurate identification, makes sponges inaccessible to non-specialists, including ecologists and community scientists, and often leads to misidentifications.

The sponge fauna of South Africa varies with depth (Samaai *et al.* 2010; Maduray 2013), and the diversity of species, morphology and colour decrease with increasing depth (Samaai *et al.* 2010). Conversely, the mean depth range of species increases with depth, with at least some of the deep-water sponges derived from the bathyal fauna, with low rates of recruitment and/or survival (Samaai *et al.* 2010).

Sponge assemblages also differ according to location, and three distinct groups that correspond to the west, south and east coasts have been identified (Lévi 1963; Samaai 2006; Maduray 2013; Samaai *et al.* 2019). With boundaries located at Cape Point and East London (Samaai 2006), these groups coincide well with the main biogeographic shelf provinces/ecoregions as defined by Sink *et al.* (2019b). These boundaries are not impassable (Burton 1932), due to the complex oceanographic regime, and some species are shared by neighbouring provinces/ecoregions (Maduray 2013). Interestingly, these species often demonstrate intraspecific variation according to the different environmental conditions experienced along each coast (e.g. silica concentration), and those on the west coast occasionally contain silica formations (e.g. in the *Guitarra flamenca* Carballo & Uriz, 1998 holotype), or have much larger/thicker spicules than their conspecifics from the south and/or east coast (Uriz 1988). Alternatively, intraspecific variation might also be due to the age/size of the specimen(s) examined (Samaai *et al.* 2017b).

Table 1: Taxa composition summary of marine sponges from the South African Exclusive Economic Zone (EEZ), excluding the Prince Edward Islands. Extracted from Appendix A. Values in parentheses indicate the number of currently accepted endemic genera, species and/or varieties and forms.

Class	Subclass	Order	# Families	# Genera	# Species	# Varieties & Forms
	Calcaronea	Leucosolenida	6	12	29 (15)	-
	Calcinea	Clathrinida	3	5	8 (5)	-
Calcarea	**2**	**2**	**9**	**17**	**37 (20)**	**-**
	Heteroscleromorpha	Agelasida	1	1	1	-
		Axinellida	3	11 (1)	15 (11)	-
		Biemnida	2	3	7 (5)	1
		Bubarida	1	2	4 (3)	-
		Clionaida	1	2	10 (3)	-
		Haplosclerida	5	7	27 (11)	-
		Merliida	1	1	1	-
		Poecilosclerida	18	39 (3)	138 (89)	-
		Polymastiida	1	3	5 (3)	-
		Scopalinida	1	1	1	-
		Suberitida	2	9	18 (9)	1 (1)
		Tethyida	2	4	6 (4)	1 (1)
		Tetractinellida	10	26 (1)	68 (46)	4 (4)
		Trachycladida	1	1	1	-
	Keratosa	Dendroceratida	2	3	3 (1)	-
		Dictyoceratida	4	11	18 (7)	-
	Verongimorpha	Chondrillida	1	1	1	-
		Verongiida	2	2	3 (1)	-
Demospongiae	**3**	**18**	**58**	**127 (5)**	**327 (193)**	**7 (6)**
	Amphidiscophora	Amphidiscosida	1	2	3 (3)	-
	Hexasterophora	Lyssacinosida	2	5	6 (3)	-
Hexactinellida	**2**	**2**	**3**	**7**	**9 (6)**	**-**
	-	Homosclerophorida	1	1	1 (1)	-
Homoscleromorpha	**-**	**1**	**1**	**1**	**1 (1)**	**-**
Total	**7**	**23**	**71**	**152 (5)**	**374 (220)**	**7 (6)**

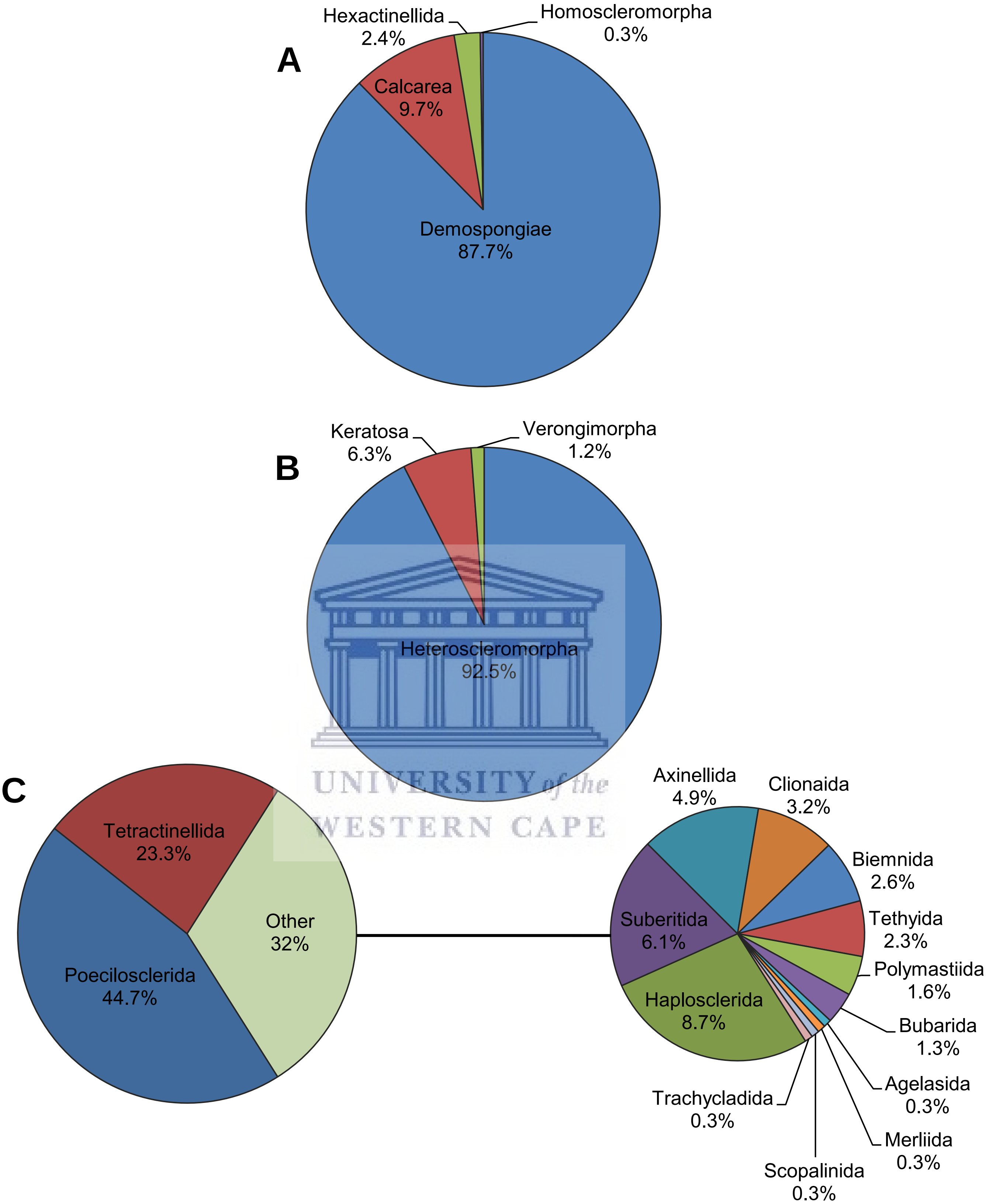

Figure 2: Taxa composition of marine sponges from the South African Exclusive Economic Zone (EEZ), excluding the Prince Edward Islands, including all classes (**A**), subclasses of the dominant class Demospongiae (**B**), and orders of the dominant subclass Heteroscleromorpha (**C**). Values represent a combination of species, varieties and forms.

Nonetheless, the sponge fauna on the west coast has cold-temperate affinities, with low species richness and high levels of dominance (Stephens 1915; Samaai & Gibbons 2005; Samaai 2006). For example, *Suberites dandelenae* Samaai & Maduray, 2017 comprises a sizeable biomass, and extends into Namibia, where the sponge fauna has similar affinities (Uriz 1988, 1990; Samaai *et al.* 2017b). The south coast sponge fauna has warm-temperate affinities, with the highest species richness and endemism, especially around Cape Town, which could be attributed to its position near a biogeographic boundary (Cape Point), but is more likely due to disproportionately intense sampling effort (Samaai 2006). Both of these coasts show little to no faunal links with the Antarctic sponge fauna (Downey *et al.* 2012). Finally, the sponge fauna on the east coast has subtropical affinities, with additional recruitment from the Indo-Pacific (Samaai 2006; Samaai *et al.* 2019). This coast has been historically underworked (Samaai 2006; Griffiths *et al.* 2010), with further sampling required, especially at the biogeographic boundaries (Samaai 2006; Samaai *et al.* 2019). One such area of interest, adjacent to the Mbashe boundary, is the Amathole region.

1.5 Study Area: the Amathole Region

The Amathole region is situated offshore of the Amathole District, around the city of East London (33.03 S, 27.85 E), which is located in the Eastern Cape Province, on the south-east coast of South Africa. Coastal waters in the region are influenced by fluvial input from several prominent rivers (e.g. Great Fish, Great Kei, Mbashe), with the oceanographic regime dominated by the major western boundary Agulhas Current system, which comprises of waters from the Mozambique Channel, east Madagascar and the South Indian Ocean gyre (Lutjeharms 2007; Goschen *et al.* 2012). This warm, vigorous current flows southward, largely constrained at the shelf break which is at a depth of roughly 110 m off East London, where it reaches maximum velocity (Lutjeharms 2007; Meyer *et al.* 2013; de Wet 2013;

Dlamini 2017). Here, the continental shelf is steep and narrow (maximum width of 23 km), widening towards the south (de Wet 2013; Dlamini 2017), with the subsequent deflection of the current driving inshore upwelling which extends southwards from Mbashe to the eastern edge of Algoa Bay (Schumann *et al.* 1988; Lutjeharms *et al.* 2000; Goschen & Schumann 2011; Russo *et al.* 2019). The strong subsurface thermal front which persists at Mbashe, as described by Beckley & van Ballegooyen (1992), supports the designation of this location as a province/ecoregion boundary in the national marine biogeographic classification system devised by Sink *et al.* (2019b).

According to this national classification (Sink *et al.* 2019b), the Amathole region is located in the transitional Agulhas-Natal ecoregion boundary zone (Fig. 1B). Alternatively, it is located in the Natal ecoregion as defined by the global Marine Ecoregions of the World (MEOW) biogeographic classification system devised by Spalding *et al.* (2007) (Fig. 1C), which is utilized by the World Porifera Database (van Soest *et al.* 2020a). Nevertheless, this area supports a high habitat, ecosystem and species diversity, and forms part of the Algoa to Amathole Ecologically or Biologically Significant Marine Area (EBSA) (Fig. 1C) (Massie *et al.* 2019; online EBSA Portal). Habitat types include unconsolidated sediment, mesophotic reefs, rhodolith beds, fluvial fans, submarine canyons and an undocumented shipwreck (Dingle & Robson 1985; de Wet 2013; Dlamini 2017; Parker *et al.* 2017; Button 2018; Adams *et al.* 2020).

Numerous ecosystem types occur within the region, some of which are considered threatened due to their limited spatial extent and the evidence of degradation (e.g. Amathole Hard Shelf Edge, Amathole Lace Corals, Kei Fluvial Fan, Kei Reef Mosaic) (Sink *et al.* 2019b; Sink *et al.* 2019c; Sink *et al.* 2019d), as well as by the presence of several alien species (Robinson *et al.* 2020). These ecosystems are dominated by algae, corals, and sponges (Button 2018). They also support many overexploited linefish species such as the red steenbras (*Petrus rupestris* (Valenciennes, 1830)), seventy-four (*Polysteganus undulosus* (Regan, 1908)), red stumpnose (*Chrysoblephus gibbiceps* (Valenciennes, 1830)), dageraad (*Chrysoblephus cristiceps* (Valenciennes, 1830)) and black musselcracker (*Cymatoceps nasutus* (Castelnau, 1861)), most of which are endemic to South Africa (Button 2018; van der Bank *et al.* 2019). Furthermore, the first living coelacanth (*Latimeria chalumnae* Smith, 1939) was captured by a trawler near East London in 1938, with this area also boasting the first and shallowest records of reef-building cold-water corals from South Africa (Parker *et al.* 2017). Protection in the Amathole region comprises the coastal Amathole MPA (247 km^2) which was established in 2011, and consists of three smaller areas (Gxulu, Gonubie and Kei). In 2019, the Amathole Offshore MPA (4 206 km^2) was declared as an extension of the previous Gxulu and Kei coastal areas (Sink *et al.* 2019d).

1.6 Study Purpose and Scope

The Amathole region has been historically understudied due to precarious sea conditions and the absence of large-scale fisheries and marine mining (Button 2018; Russo *et al.* 2019; Adams *et al.* 2020). Thus, the multidisciplinary and multi-institutional *Imida* Frontiers Project was initiated in 2015, under the auspices of the African Coelacanth Ecosystem Programme (ACEP, phase IV), with the purpose of combining bathymetric and geophysical surveys of benthic habitat with ecological surveys and predictive modelling, to determine the spatial distribution of ecologically sensitive areas and their associated species. As a component of this larger project, this study aims to investigate the diversity, depth distribution and biogeographic affinities of the heteroscleromorph demosponge fauna (i.e. having spicules) from the Amathole region. Aspiculate demosponges, and specimens from the other three poriferan classes (Calcarea, Hexactinellida, Homoscleromorpha), are excluded from this study due to time constraints. The four main objectives are as follows:

I) To identify the heteroscleromorph demosponge fauna, and compile a species list.

II) To describe/re-describe a subset of heteroscleromorph demosponge species.

III) To investigate variation (e.g. composition and species richness) in heteroscleromorph demosponge assemblages according to a bathymetric gradient.

IV) To investigate biogeographic affinities, based on known heteroscleromorph demosponge fauna.

Founded on the previous research undertaken on the sponge fauna of South Africa, as detailed in the sections above, four main findings are expected:

I) **The heteroscleromorph demosponge fauna will be diverse, and dominated by the order Poecilosclerida.** According to the national marine biogeographic classification system devised by Sink *et al.* (2019b), the Amathole region is located in the transitional Agulhas-Natal ecoregion boundary zone, with biogeographic boundaries in South Africa previously found to be sites of increased range-restricted species and richness (Awad *et al.* 2002; Acuña & Griffiths 2004; Scott *et al.* 2012). Moreover, the Amathole region comprises high habitat and ecosystem diversity, which has been shown to increase species richness (Schlacher *et al.* 2007; Hewitt *et al.* 2008; Sanciangco *et al.* 2013). The South African sponge fauna is dominated by the order Poecilosclerida (44.7%), which is further evidenced in the abundance of this taxon in past studies (Lévi 1963; Samaai & Gibbons 2005; Maduray 2013; Samaai *et al.* 2019).

II) **New species and records, as well as range extensions, will be discovered.** The current state of marine sponge diversity knowledge in South Africa is poor (Gibbons *et al.* 1999; Samaai 2006; Griffiths *et al.* 2010), especially regarding the fauna of the understudied east coast (Samaai 2006; Griffiths *et al.* 2010), and at biogeographic boundaries (Samaai 2006;

Samaai *et al.* 2019). Presently, any relatively intensive collection effort leads to the discovery of new species and records, as well as range extensions (e.g. Samaai & Gibbons 2005; Maduray 2013; Samaai *et al.* 2019), with this the first focused sampling undertaken in the Amathole region.

III) **Heteroscleromorph demosponge assemblages will demonstrate a significant difference in composition according to depth zone (shallow, mesophotic and sub-mesophotic). Species richness will decrease with depth.** The sponge fauna of South Africa has previously been shown to vary with depth (Samaai *et al.* 2010; Maduray 2013), with species richness decreasing with increasing depth (Samaai *et al.* 2010).

IV) **Heteroscleromorph demosponge faunal affinities will be primarily with southern Africa, with additional influence from the Western Indian Ocean region.** Due to their sessile nature and limited larval dispersal (Maldonado 2006), most sponges occur in local areas of endemism (van Soest *et al.* 2012; Bell *et al.* 2015), which is evidenced by the elevated level of apparent endemism in South Africa (59.3%). The Amathole region is located on the south-east coast, with the oceanographic regime dominated by the major western boundary Agulhas Current system, which comprises of waters from the Mozambique Channel, east Madagascar and the South Indian Ocean gyre (Lutjeharms 2007; Goschen *et al.* 2012). Thus, the heteroscleromorph demosponge fauna will likely have an additional influence from the Western Indian Ocean region, as found for the east coast, which has subtropical affinities with supplementary recruitment from the Indo-Pacific (Samaai 2006; Samaai *et al.* 2019). Previous research has shown little to no faunal links between the South African and Antarctic sponge fauna (Downey *et al.* 2012).

2.1 Collection

Material was collected from the continental shelf and slope of the Amathole region (see Section 1.5 in Chapter 1). A total of 474 heteroscleromorph demosponge specimens were included in this study, from four expeditions comprising 48 sites across depths of 3–229 m (Fig. 3, Table 2). Seven, 36, and five sites were located in the shallow (1–30 m), mesophotic (31–150 m) and sub-mesophotic (>150 m) depth zones respectively, following Lesser *et al.* (2018).

Non-random-stratified sampling was undertaken during two cruises onboard the R/V *Ellen Khuzwayo* (African Coelacanth Ecosystem Programme (ACEP) IV *Imida* Frontiers Project, voyage 151: 16 February–4 March 2016, voyage 159: 22 August–11 September 2016), with selected sites including locations of known recreational fishing activity and/or elevated structural complexity as identified by sonar. A single site from voyage 159 was situated outside the Amathole region, in Algoa Bay (No. 48 or Station 3920, Fig. 3C), but was included in this study as it falls within the Agulhas ecoregion (Fig. 1) and forms part of the Algoa to Amathole Ecologically or Biologically Significant Marine Area (EBSA) (Fig. 1C) (Massie *et al.* 2019; online EBSA Portal). Sponges were collected using an epibenthic dredge, with 271 specimens amassed from 23 dredges during voyage 151, and 186 specimens amassed from 19 dredges during voyage 159 (Fig. 4). Specimens were frozen on collection for later processing, a curation method that preserves *in situ* colour (Hooper 1996). A substrate sample was collected from each dredge where possible, and described according to the Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) classification scheme (Althaus *et al.* 2015). However, substrate collection and accurate classification was sporadic, with dredge samples likely representing a combination of substrate types found within the heterogeneous region (Rees 2009). Thus, substrate type did not feature in the analyses below, but was included in species accounts.

An additional 17 specimens were included in this study, from two previous collections carried out in the Amathole region. Three dredges deployed from the R/V *Ellen Khuzwayo* (voyage 131) in 2015 yielded 11 specimens, while six specimens were included from three sites sampled in 1999 by the Coral Reef Research Foundation (CRRF) via SCUBA, on behalf of the United States National Cancer Institute shallow-water collection programme (Parker-Nance *et al.* 2019).

Underwater visual surveys were undertaken onboard the R/V *Phakisa* using a Remotely Operated Vehicle (ROV; Seaeye Falcon 12177) during two expeditions (20 January–9 February 2017 and 3–21 May 2017), with 100 dives completed (~3 642 min, Fig. 5). For further details on deployment see Button (2018). Where possible, *in situ* sponge images were used for species accounts, with the associated data for each dive mentioned in this study found in Table 3.

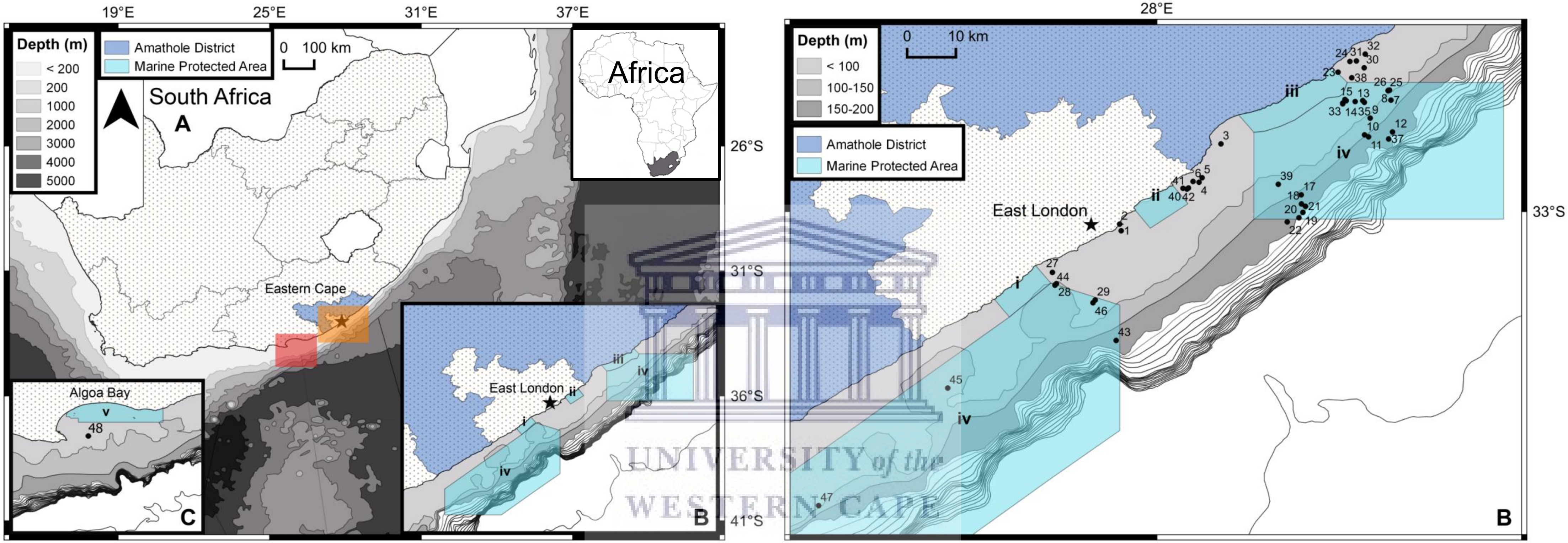

Figure 3: Maps illustrating sponge collection sites (•), within the South African context (**A**), the Amathole region (**B**) and at a single location outside the Amathole region (**C**, No. 48 or Station 3920). Numbers correspond to sites detailed in Table 2. Marine Protected Areas include the Amathole (i: Gxulu, ii: Gonubie, iii: Kei), Amathole Offshore (iv, recent extensions of i and iii) and Addo Elephant National Park (v) (Sink *et al.* 2019d). Generated using QGIS v.2.6.1.

Table 2: Sponge collection sites, where depth zone is denoted by the symbols S (shallow: 1–30 m), M (mesophotic: 31–150 m) and SM (sub-mesophotic: >150 m) following Lesser *et al.* (2018).

Expedition	No.	Date	Grid	Site/Station	Position (start)	Position (end)	Method (# sponges)	Duration (min)	Depth (m) Zone	Substrate
CRRF	1	8-Feb-1999	-	ELondon 1 (Lighthouse Reef)	33.0425º S 27.9210º E	-	SCUBA 1	-	23 S	Rock, amongst rocky reef comprising of boulders and sand
	2	11 & 14-Feb-1999	-	EL Harb 1 (Orient Pier)	33.0278º S 27.9175º E	-	SCUBA 2	-	3–5 S	Rock, near cement wall
	3	12-Feb-1999	-	Cintsa 1	32.8500º S 28.1417º E	-	SCUBA 3	-	16–17 S	Rock, amongst reef comprising of rounded rock and sand
R/V *Ellen Khuzwayo* VOY 131	4	24-Feb-2015	-	491	32.9350º S 28.0933º E	-	Dredge 5	-	55 M	-
	5	27-Feb-2015	-	492	32.9250º S 28.1000º E	-	Dredge 1	-	39 M	-
	6	27-Feb-2015	-	Unknown	32.9333º S 28.0800º E	-	Dredge 5	-	<55 M	-
ACEP *Imida* Frontiers Project R/V *Ellen Khuzwayo* VOY 151	7	21-Feb-2016	Ellen 151–10	3716	32.7531º S 28.5177º E	32.7547º S 28.5207º E	Dredge 34	24	78 M	Cobbles, Shell hash
	8	21-Feb-2016	Ellen 151–11	3717	32.7309º S 28.5145º E	32.7276º S 28.5198º E	Dredge 3	33	87 M	Rock, Pebble, Coarse sand with shell fragments
	9	22-Feb-2016	Ellen 151–15	3721	32.7929º S 28.4718º E	32.7967º S 28.4705º E	Dredge 1	17	90 M	Coral Rubble, Coarse sand with shell fragments
	10	22-Feb-2016	Ellen 151–16	3722	32.8300º S 28.4593º E	32.8327º S 28.4573º E	Dredge 33	9	87 M	-
	11	22-Feb-2016	Ellen 151–18	3724	32.8345º S 28.4682º E	32.8361º S 28.4635º E	Dredge 13	11	76 M	-

Expedition	No.	Date	Grid	Site/Station	Position (start)	Position (end)	Method (# sponges)	Duration (min)	Depth (m) Zone	Substrate
ACEP *Imida* Frontiers Project R/V *Ellen Khuzwayo* VOY 151	12	22-Feb-2016	Ellen 151–19	3725	32.8236º S 28.5211º E	32.8198º S 28.5158º E	Dredge 14	14	199 SM	-
	13	23-Feb-2016	Ellen 151–26	3732	32.7563º S 28.4385º E	32.7613º S 28.4302º E	Dredge 4	11	56 M	Rock, Rhodoliths
	14	23-Feb-2016	Ellen 151–28	3734	32.7613º S 28.4110º E	32.7632º S 28.4091º E	Dredge 3	2	68 M	-
	15	23-Feb-2016	Ellen 151–30	3736	32.7543º S 28.4188º E	32.7568º S 28.4152º E	Dredge 6	6	45 M	Rhodoliths
	16	23-Feb-2016	Ellen 151–31	3737	32.7517º S 28.4159º E	32.7529º S 28.4143º E	Dredge 2	3	31 M	Rock, Coquina
	17	24-Feb-2016	Ellen 151–33	3739	32.9629º S 28.3193º E	32.9636º S 28.3185º E	Dredge 17	3	94 M	-
	18	24-Feb-2016	Ellen 151–34	3740	32.9831º S 28.3197º E	32.9846º S 28.3176º E	Dredge 18	6	104 M	Shell hash
	19	24-Feb-2016	Ellen 151–35	3741	33.0019º S 28.3229º E	33.0068º S 28.3136º E	Dredge 1	12	194 SM	-
	20	24-Feb-2016	Ellen 151–36	3742	33.0137º S 28.3142º E	33.0172º S 28.3063º E	Dredge 32	12	204 SM	-
	21	24-Feb-2016	Ellen 151–38	3744	32.9883º S 28.3285º E	32.9932º S 28.3229º E	Dredge 1	7	151 SM	-
	22	24-Feb-2016	Ellen 151–39	3745	33.0229º S 28.2883º E	33.0316º S 28.2797º E	Dredge 39	10	122 M	-
	23	28-Feb-2016	Ellen 151–64	3770	32.6912º S 28.4008º E	32.6876º S 28.4045º E	Dredge 1	10	25 S	Shell hash, River-borne detritus

Expedition	No.	Date	Grid	Site/Station	Position (start)	Position (end)	Method (# sponges)	Duration (min)	Depth (m) Zone	Substrate
ACEP *Imida* Frontiers Project R/V *Ellen Khuzwayo* VOY 151	24	28-Feb-2016	Ellen 151–74	3780	32.6674º S 28.4269º E	32.6640º S 28.4309º E	Dredge 3	9	28 S	Boulders, Rock, Shell hash
	25	29-Feb-2016	Ellen 151–83	3789	32.7321º S 28.5112º E	32.7303º S 28.5119º E	Dredge 1	7	83 M	-
	26	29-Feb-2016	Ellen 151–84	3790	32.7312º S 28.5121º E	32.7252º S 28.5101º E	Dredge 8	9	85 M	-
	27	2-Mar-2016	Ellen 151–101	3807	33.1347º S 27.7689º E	33.1604º S 27.7762º E	Dredge 14	23	33 M	-
	28	2-Mar-2016	Ellen 151–102	3808	33.1597º S 27.7777º E	33.1616º S 27.7778º E	Dredge 22	20	39 M	-
	29	2-Mar-2016	Ellen 151–105	3811	33.1959º S 27.8636º E	33.1962º S 27.8622º E	Dredge 1	9	74 M	-
ACEP *Imida* Frontiers Project R/V *Ellen Khuzwayo* VOY 159	30	26-Aug-2016	Ellen 159–1	3813	32.6816º S 28.4585º E	32.6869º S 28.4617º E	Dredge 20	10	55–52 M	Rock, Coquina/Shell hash, Pebble
	31	26-Aug-2016	Ellen 159–2	3814	32.6663º S 28.4412º E	32.6714º S 28.4397º E	Dredge 6	10	29–35 M	Boulders, Shell hash, Pebble
	32	26-Aug-2016	Ellen 159–3	3815	32.6511º S 28.4609º E	32.6581º S 28.4653º E	Dredge 6	10	38–43 M	Rock, Coquina/Shell hash, Pebble, Coarse sand with shell fragments
	33	27-Aug-2016	Ellen 159–19	3831	32.7596º S 28.4116º E	32.7604º S 28.4105º E	Dredge 2	4	47 M	Rock, Rhodoliths
	34	27-Aug-2016	Ellen 159–20	3832	32.7597º S 28.4110º E	32.7587º S 28.4119º E	Dredge 23	5	45 M	Rock
	35	28-Aug-2016	Ellen 159–21	3833	32.7580º S 28.4589º E	32.7577º S 28.4554º E	Dredge 9	9	62–58 M	Rock, Coquina/Shell hash

Expedition	No.	Date	Grid	Site/Station	Position (start)	Position (end)	Method (# sponges)	Duration (min)	Depth (m) Zone	Substrate
	36	28-Aug-2016	Ellen 159–22	3834	32.7541º S 28.4553º E	32.7531º S 28.4533º E	Dredge 8	4	54–52 M	Rock
	37	29-Aug-2016	Ellen 159–33	3845	32.8392º S 28.5126º E	32.8344º S 28.5192º E	Dredge 1	15	229–222 SM	Boulders, Shell hash, Coral Rubble
	38	30-Aug-2016	Ellen 159–44	3856	32.7035º S 28.4311º E	32.6998º S 28.4358º E	Dredge 2	10	45–53 M	Rock, Rhodoliths
	39	30-Aug-2016	Ellen 159–49	3861	32.9395º S 28.2685º E	32.9363º S 28.2757º E	Dredge 30	12	90 M	Shipwreck, Shell hash, Coarse sand with shell fragments
	40	31-Aug-2016	Ellen 159–58	3870	32.9485º S 28.0577º E	32.9478º S 28.0588º E	Dredge 8	3	29 S	Boulders, Shell hash, Pebble
ACEP *Imida* Frontiers Project R/V *Ellen Khuzwayo* VOY 159	41	31-Aug-2016	Ellen 159–60	3872	32.9501º S 28.0665º E	32.9478º S 28.0698º E	Dredge 7	5	41 M	Shell hash
	42	31-Aug-2016	Ellen 159–61	3873	32.9476º S 28.0699º E	32.9458º S 28.0731º E	Dredge 3	6	42–44 M	Shell hash, Coarse sand with shell fragments
	43	2-Sep-2016	Ellen 159–64	3876	33.2856º S 27.9099º E	33.2826º S 27.9134º E	Dredge 18	10	103 M	Coquina/Shell hash, Coral Rubble
	44	3-Sep-2016	Ellen 159–81	3893	33.1632º S 27.7746º E	33.1625º S 27.7753º E	Dredge 18	3	36 M	Shell hash
	45	4-Sep-2016	Ellen 159–85	3897	33.3910º S 27.5374º E	33.3902º S 27.5398º E	Dredge 7	10	78 M	Boulders, Cobbles, Shell hash, Pebble
	46	5-Sep-2016	Ellen 159–97	3909	33.2020º S 27.8586º E	33.1949º S 27.8610º E	Dredge 8	12	76–65 M	Cobbles, Rock, Shell hash, Pebble
	47	6-Sep-2016	Ellen 159–101	3913	33.6515º S 27.2519º E	33.6463º S 27.2583º E	Dredge 2	10	82 M	Rock, Coquina/Shell hash, Pebble, Coarse sand with shell fragments

Expedition	No.	Date	Grid	Site/Station	Position (start)	Position (end)	Method (# sponges)	Duration (min)	Depth (m) Zone	Substrate
ACEP *Imida* Frontiers Project R/V *Ellen Khuzwayo* VOY 159	48	8-Sep-2016	Ellen 159–108	3920	33.9948º S 25.8891º E	33.9930º S 25.8917º E	Dredge 8	5	22–24 S	Rock, Coquina/Shell hash

Table 3: Remotely Operated Vehicle (ROV; Seaeye Falcon 12177) dive sites for images used in this study. All dives below were carried out onboard the R/V *Phakisa* within the mesophotic depth zone (31–150 m, Lesser *et al.* 2018).

Date	Dive	Position (start)	Position (end)	Duration (min)	Depth (m)
21-Jan-2017	R2	33.1529º S 27.7821º E	33.1578º S 27.7655º E	-	37–40
5-Feb-2017	R23	33.1562º S 27.7888º E	33.1540º S 27.7893º E	34	65–66
8-Feb-2017	R38	33.1592º S 27.7623º E	33.1605º S 27.7610º E	35	38–43
9-Feb-2017	R43	33.1511º S 28.0060º E	33.1599º S 27.9970º E	67	79–80
5-May-2017	R49	32.7510º S 28.4220º E	32.7603º S 28.4159º E	66	44–47
18-May-2017	R87	32.7252º S 28.4348º E	32.7327º S 28.4309º E	34	46–49
19-May-2017	R88	33.1161º S 28.0634º E	33.1245º S 28.0531º E	31	83–85

Figure 4: Sponges were primarily collected onboard the R/V *Ellen Khuzwayo* using an epibenthic dredge.

Figure 5: Underwater visual surveys were carried out onboard the R/V *Phakisa*, using a Remotely Operated Vehicle (ROV; Seaeye Falcon 12177), and revealed high habitat diversity within the Amathole region.

2.2 Taxonomic Procedure

After a sample number was assigned (TS–; accession prefix for the personal collection of Dr Toufiek Samaai, Department of Forestry, Fisheries and the Environment, Cape Town, South Africa), and digital colour photographs were taken, the macroscopic features of each specimen were described following Boury-Esnault & Rützler (1997). Thereafter, a small tissue sample was taken for genetic analysis (to supplement the work of Ngwakum (2019)), and sponge-associated barnacles were sent to Andrew Hosie of the Western Australian Museum for identification. Excess frozen material from larger specimens was sent to Prof. Denzil Beukes (School of Pharmacy) and Prof. Edith Antunes (Department of Chemistry), from the University of the Western Cape, for chemical biodiscovery research. Findings from these independent studies/research groups will not be discussed in detail, but may be incorporated into later publications. Two further sub-samples were collected for dissociated spicule suspensions and thick-section mounts, which were made according to the procedures described by Hooper (1996) and Boury-Esnault & Rützler (1997). Any remaining material was preserved in 96% ethanol.

Spicules were prepared by dissolution of tissue fragments in nitric acid, followed by two consecutive washes with distilled water and a single wash with 96% ethanol. Spicules were permanently mounted on slides with Entellan® slide mountant, and measured using an OMAX A35140U camera with ToupView software. Dimensions were based on 15 measurements, and are given as minimum–*mean*–maximum length × width (µm) in the text, unless otherwise stated. Comparative spicule dimensions from other specimens obtained in this study, and from the literature where possible, were included to determine the level of intraspecific variability following Samaai & Gibbons (2005). For scanning electron microscopy (SEM), spicule extracts were mounted on film negative fixed to aluminium stubs and either sputter-coated with gold-palladium or left uncoated. Subsequently, images were taken at the Iziko South African Museum with a Hitachi TM4000Plus, or at the University of Cape Town Electron Microscope Unit using an FEI Nova NanoSEM 230 equipped with a field emission gun. Such microscopy was necessary to reveal small but important spicule variations that confer specific identity (Anđus *et al.* 2016).

To examine the skeletal structure, hand-cut perpendicular sections (including both ectosomal and choanosomal regions) of each specimen were made and stored in 96% ethanol. Thereafter, sections were embedded in paraffin wax after being processed through a series of dehydrating and cleaning agents (Table 4). Using a microtome, a segment of ~30–90 µm was cut from each section and the wax was removed using a xylene wash. The segments were then mounted on a slide with Entellan, examined and photographed using the equipment and software mentioned previously. To produce figures, digital images were edited and combined on a black background using Photoshop CS5 and PowerPoint.

Each species account is largely based on a single specimen (shown in bold in Chapter 3, Section 3.2). For new species, this specimen will become the holotype in the future formal description. The symbol (▲) denotes new species throughout, with provisional etymology provided for those described in Chapter 3. The classification of taxa follows the online World Porifera Database (van Soest *et al.* 2020a), based on the *Systema Porifera* (Hooper & van Soest 2002), with revision by Morrow & Cárdenas (2015).

Table 4: Microwave 5mm/2 layer method for sponge specimen histology processing.

	Step	Time (min)	Temperature (°C)	Pressure (mBar)	Agent
Dehydrate	1. Fixation	105	50		70% ethanol
	2. Flushing	2	37		60% ethanol
	3. Rinsing	30	45		Absolute alcohol
	4. Ethanol	45	55		Absolute alcohol
Clean	5. Xylene	90	50		Xylene
	6. Isopropanol	20	60		Isopropanol
Dry	7. Vaporization	1.5		600	N/A
Harden for wax	8. Wax Impregnation	140	70	995–150	N/A

2.3 Registration of Type and General Material

Primary and secondary type materials of new species, and additional material, will be housed in the Iziko South African Museum (Cape Town), with accession numbers (prefix SAMC) provided once deposited. Voucher samples will also be kept in the collection of Dr Toufiek Samaai, presently of the Department of Forestry, Fisheries and the Environment (DFFE), Oceans and Coasts Branch. Other abbreviations used in the species accounts include NHMUK (accession prefix for the Natural History Museum, London, UK [formerly British Museum of Natural History, with accession prefixes BMNH, BM (NH), NHM, London]), MNCN (Museo Nacional de Ciencias Naturales de Madrid, Spain), MNHN (Muséum National d'Histoire Naturelle, Paris, France) and NIWA (National Institute of Water and Atmospheric Research, Greta Point, Wellington [formerly New Zealand Oceanographic Institute, NZOI]).

2.4 Depth Analyses

To determine whether the sponge fauna of the Amathole region was influenced by depth (shallow, mesophotic, sub-mesophotic; as defined above), Bray-Curtis similarity coefficients based on a presence/absence (non-detection) matrix of the species found at each site were calculated using PRIMER v.6.1.11 (Plymouth Routines in Multivariate Ecological Research; Clarke & Gorley 2006). Presence/absence data were used in preference to "abundance" or another measure of quantity, owing to the fragmentary nature of many sponges, and other potential inaccuracies resulting from dredge sampling, including uneven catchability (Schlacher *et al.* 2007; Przeslawski *et al.* 2015). One-way analysis of similarity (ANOSIM) and non-metric multidimensional scaling (nMDS) ordination routines were performed to assess and visualise the sponge faunal (dis)similarities between sites, by the factor depth. ANOSIM is an approximate equivalent of ANOVA, enabling a non-parametric test for statistically significant differences in the sponge assemblage composition between sample groups specified by an *a priori* factor (Clarke & Gorley 2006), in this case depth, with the significance of this statistical test assigned here at the 5% level. SIMPER (similarity percentage analysis) is an exploratory analysis which indicates the species principally responsible for differences within/between sets of samples (Clarke & Gorley 2006), and was thus used to assess the extent of similarity both within and between the depth zones, while also identifying the species contributing to the observed (dis)similarity. PRIMER software was also used to generate Michaelis-Menton species accumulation curves to determine whether the sampling effort had been sufficient to accurately document the heteroscleromorph demosponge diversity in the Amathole region, overall and in each depth zone. Higher taxa (genus, family, order) were represented by percentage contribution per depth zone.

2.5 Biogeographic Analysis

To comment on the biogeographic affinities of the sponge fauna from the Amathole region, it was compared to that of surrounding areas at the realm, province and ecoregion level, as classified by Spalding *et al.* (2007). This global marine biogeographic classification system was utilized, following the World Porifera Database (van Soest *et al.* 2020a) and van Soest *et al.* (2012), with the South African ecoregions updated according to the detailed national classification devised by Sink *et al.* (2019b) (Fig. 1A). The percentage similarity between surrounding areas and the Amathole region was assessed by calculating the ratio of shared species (previously known sponge species documented from this study) between any area and the Amathole region, and the total number of previously known species recorded from the Amathole region, following Xavier & van Soest (2007). Further analyses were not feasible, due to the scarcity of data available in the surrounding areas, even at the fundamental level of accessible, comprehensive and updated sponge species lists. As stated on the website itself (van Soest *et al.* 2020a), presently no regional sponge species lists can be reliably extracted from the World Porifera Database.

3.1 Systematics

A total of 474 heteroscleromorph demosponges were collected from the Amathole region (Eastern Cape, South Africa), comprising 74 species (Table 5, Appendix B). There were representatives of 11 orders, two suborders, 34 families, four subfamilies, 53 genera, and nine subgenera.

The orders Poecilosclerida (32 species) and Tetractinellida (22 species) were most speciose, together accounting for 72.9% of all species (Fig. 6). The orders Axinellida and Biemnida were also relatively well represented, with five species documented each, while Bubarida and Tethyida had three and two species respectively. The remaining five orders comprised only one species each. The fauna was dominated by the family Geodiidae (order Tetractinellida; nine species), followed by Isodictyidae and Latrunculiidae (order Poecilosclerida; four species each), with the remainder of the families having three species or less. Over half (52.7%) of the species represent a single genus each. However, four species were designated to *Isodictya*, while three species each were designated to the genera *Erylus*, *Mycale*, *Penares*, *Phorbas* and *Tsitsikamma*. Two species each were designated to the genera *Biemna*, *Characella*, *Geodia*, *Guitarra*, *Iophon*, *Myxilla*, *Rhabderemia* and *Sollasipelta*. Of the 74 species obtained, 47 (63.5%) were known and could be included in the biogeographic analysis. Twenty-seven (36.5%) species were compared to congeners found in South Africa and/or adjacent regions and were found to differ, or represent the first record of a genus in South Africa and/or the Indian Ocean, and thus are likely new to science. Both unique (only recorded from a single site, de Voogd & Cleary 2008), and common species were present in the collection. For example, a single specimen of *Acarnus claudei* van Soest, Hooper & Hiemstra, 1991 was collected from one site, while 66 specimens of *Pachastrella caliculata* Kirkpatrick, 1902 were collected from 25 sites.

Table 5: Heteroscleromorph demosponges from the Amathole region (Eastern Cape, South Africa). Taxa are in alphabetical order with classification following the World Porifera Database (van Soest *et al.* 2020a), based on the *Systema Porifera* (Hooper & van Soest 2002), with revision by Morrow & Cárdenas (2015). The symbols (▲) and (*) denote new and South African endemic species respectively, while South African endemic genera are underlined. The abbreviation TL denotes type locality. Depth values are from this study only, with additions from the taxonomic literature included in the species accounts where possible. The data below will only be added to the South African marine sponge species list (Appendix A) after publication.

	No. of Specimens	**Site/Station (s)**	**Depth (m)**	**Distribution**
Phylum Porifera Grant, 1836 **Class Demospongiae Sollas, 1885** **Subclass Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012** **Order Axinellida Lévi, 1953** Family Axinellidae Carter, 1875a				
1. *Axinella* sp. ▲	10	7, 10, 11, 17, 30, 43	52–103	Amathole region
2. *Phakellia* sp. ▲	8	3, 4, 27, 28, 31, 41, 45	16–78	Amathole region
Family Raspailiidae Nardo, 1833				
3. *Didiscus* cf. *placospongioides* Dendy, 1922	1	44	36	Cargados Carajos/Tromelin Island (TL), Madagascar
Subfamily Plocamioninae Hooper, 2002b				
4. *Lithoplocamia longioxea* **sp. nov.** ▲	2	20	204	Amathole region
Subfamily Thrinacophorinae Hooper, 2002b				
5. *Ceratopsion microxephora* (Kirkpatrick, 1903)*	15	7, 28, 30, 35, 36, 39, 44, 46	36–90	South Africa
 Order Biemnida Morrow, 2013 Family Biemnidae Hentschel, 1923				
6. *Biemna* sp. ▲	26	7, 10, 12, 14, 17, 20, 22, 26, 27, 28, 30,	33–204	Amathole region

	No. of Specimens	Site/Station (s)	Depth (m)	Distribution
		39, 45, 46, 47		
7. *Biemna sigmodragma* Lévi, 1963*	6	4, 5, 27, 28	33–55	South Africa
8. *Sigmaxinella* sp. ▲	1	10	87	Amathole region
Family Rhabderemiidae Topsent, 1928				
9. *Rhabderemia indica* Dendy, 1905	1	39	90	South India & Sri Lanka (TL), Gulf of Aden, Red Sea, Gulf of Thailand
10. *Rhabderemia spirophora* (Burton, 1931)*	2	30, 32	38–55	South Africa
Order Bubarida Morrow & Cárdenas, 2015 Family Bubaridae Topsent, 1894				
11. *Bubaris amatholensis* **sp. nov.** ▲	2	21, 29	74–151	Amathole region
Family Desmanthidae Topsent, 1893				
12. *Paradesmanthus macphersoni* (Uriz, 1988)	3	7, 30, 43	52–103	Namibia, South Africa
13. *Petromica (Petromica) tubulata* (Kirkpatrick, 1903)*	3	39, 46	65–90	South Africa
Order Clionaida Morrow & Cárdenas, 2015 Family Placospongiidae Gray, 1867				
14. *Placospongia* sp. ▲	3	6, 24, 27	28–33	Amathole region
Order Haplosclerida Topsent, 1928 Family Petrosiidae van Soest, 1980				
15. *Petrosia (Strongylophora) durissima* (Dendy, 1905)	12	12, 15, 17, 18, 20, 22, 34, 39, 43	45–204	South India & Sri Lanka (TL), Philippines, Bismarck Sea, Madagascar, Seychelles, South Africa (?)
Order Merliida Vacelet, 1979 Family Hamacanthidae Gray, 1872				
16. *Hamacantha (Vomerula) esperioides* (Ridley & Dendy, 1886)	1	20	204	South Africa (TL), Namibia, Uruguay-Buenos Aires Shelf
Order Poecilosclerida Topsent, 1928 Family Acarnidae Dendy, 1922				
17. *Acarnus claudei* van Soest, Hooper & Hiemstra, 1991*	1	48	22–24	South Africa

	No. of Specimens	Site/Station (s)	Depth (m)	Distribution
18. *Iophon regium* **sp. nov.** ▲	2	10	87	Amathole region
19. *Iophon ferrugineum* **sp. nov.** ▲	2	10, 20	87–204	Amathole region
Family Coelosphaeridae Dendy, 1922				
20. *Forcepia (Forcepia) mucosa* **sp. nov.** ▲	12	7, 10, 11, 15, 31, 34, 35, 39, 44	29–90	Amathole region
21. *Histodermella natalensis* (Kirkpatrick, 1903)*	1	43	103	South Africa
Family Crambeidae Lévi, 1963				
22. *Crambe acuata* (Lévi, 1958)	3	15, 33, 34	45–47	Red Sea (TL), Kenya, Seychelles, Madagascar, South Africa, Namibia
23. <u>*Lithochela*</u> *conica* Burton, 1929*	4	7, 44	36–78	South Africa
Family Crellidae Dendy, 1922				
24. *Crella (Grayella) erecta* (Lévi, 1963)*	3	1, 30, 34	23–55	South Africa
Family Dendoricellidae Hentschel, 1923				
25. *Fibulia ramosa* (Ridley & Dendy, 1886)	1	30	52–55	South Africa (TL), Namibia, Prince Edward Islands, Uruguay-Buenos Aires Shelf (?)
Family Esperiopsidae Hentschel, 1923				
26. *Amphilectus informis* (Stephens, 1915)*	1	40	29	South Africa
Family Guitarridae Dendy, 1924				
27. *Coelodischela* cf. *diatomorpha* Vacelet, Vasseur & Lévi, 1976	2	22	122	Madagascar (TL), Philippines
28. *Guitarra flamenca* Carballo & Uriz, 1998	5	2, 32, 38, 48	3–53	Namibia (TL), South Africa
29. *Guitarra indica* Dendy, 1916	2	3, 11	16–76	Western India
Family Hymedesmiidae Topsent, 1928				
30. *Phorbas* sp. ▲	1	10	87	Amathole region
31. *Phorbas clathratus* (Lévi, 1963)*	2	10, 36	52–87	South Africa
32. *Phorbas mollis* (Kirkpatrick, 1903)*	8	7, 11, 28, 31, 34, 40, 42	29–78	South Africa
Family Isodictyidae Dendy, 1924				
33. *Isodictya compressa* (Esper, 1797)	2	3, 24	16–28	TL unknown, Norway (?), Greenland (?), North America (?), Antilles (?), East India (?), South Africa
34. *Isodictya elastica* (Vosmaer, 1880)	17	2, 6, 27, 28, 31, 32, 34, 40, 44	3–45	South Africa (TL), Namibia

	No. of Specimens	Site/Station (s)	Depth (m)	Distribution
35. *Isodictya grandis* (Ridley & Dendy, 1886)*	4	4, 40, 42, 44	29–55	South Africa
36. *Isodictya multiformis* (Stephens, 1915)*	6	6, 7, 10, 24, 34, 46	28–87	South Africa
Family Latrunculiidae Topsent, 1922				
37. *Cyclacanthia* sp. ▲	5	16, 34, 41	31–45	Amathole region
38. *Tsitsikamma* sp. 1 ▲	7	30, 34, 41, 44	36–55	Amathole region
39. *Tsitsikamma* sp. 2 ▲	9	6, 16, 27, 30, 33, 34, 41	31–55	Amathole region
40. *Tsitsikamma* sp. 3 ▲	2	30, 43	52–103	Amathole region
Family Mycalidae Lundbeck, 1905				
41. *Mycale* sp. 1 ▲	17	7, 8, 10, 13, 26, 32, 39, 40, 43	29–103	Amathole region
42. *Mycale* sp. 2 ▲	4	10, 13, 39	56–90	Amathole region
43. *Mycale (Aegogropila) meridionalis* Lévi, 1963*	13	6, 7, 10, 26, 27, 28, 34, 40, 41, 42, 43	29–103	South Africa
Family Myxillidae Dendy, 1922				
44. *Ectyonopsis flabellata* (Lévi, 1963)*	1	10	87	South Africa
45. *Myxilla (Burtonanchora) sigmatifera* (Lévi, 1963)	1	18	104	South Africa (TL), Namibia
46. *Myxilla (Myxilla) lissotylota* **sp. nov.** ▲	4	7, 10, 11	76–87	Amathole region
Family Tedaniidae Ridley & Dendy, 1886				
47. *Hemitedania* sp. ▲	8	7, 10, 11, 39, 41, 48	22–90	Amathole region, Algoa Bay
48. *Tedania (Tedania) tubulifera* Lévi, 1963*	2	10, 28	39–87	South Africa
Order Scopalinida Morrow & Cárdenas, 2015 Family Scopalinidae Morrow, Picton, Erpenbeck, Boury-Esnault, Maggs & Allcock, 2012				
49. *Svenzea* sp. ▲	11	9, 10, 15, 20, 26, 36, 39, 43, 46	45–204	Amathole region
Order Suberitida Chombard & Boury-Esnault, 1999 Family Suberitidae Schmidt, 1870				
50. *Homaxinella abnorma* **sp. nov.** ▲	11	10, 27, 28, 31, 34, 38, 43, 44	29–103	Amathole region
Order Tethyida Morrow & Cárdenas, 2015				

	No. of Specimens	Site/Station (s)	Depth (m)	Distribution
Family Hemiasterellidae Lendenfeld, 1889b				
51. *Hemiasterella vasiformis* (Kirkpatrick, 1903)*	4	7, 28, 39	39–90	South Africa
Family Tethyidae Gray, 1848				
52. *Tethya magna* Kirkpatrick, 1903	4	8, 44, 45, 48	22–87	South Africa (TL), Australia
Order Tetractinellida Marshall, 1876 **Suborder Astrophorina Sollas, 1887** Family Ancorinidae Schmidt, 1870				
53. *Holoxea massa* **sp. nov.** ▲	11	18, 22, 39	90–122	Amathole region
54. *Stelletta capensis* Lévi, 1967*	1	32	38–43	South Africa
55. *Stryphnus progressus* (Lendenfeld, 1907)	6	10, 12, 22, 39	87–199	South Africa (TL), Vema Seamount
Family Geodiidae Gray, 1867				
Subfamily Erylinae Sollas, 1888				
56. *Erylus amorphus* Burton, 1926*	3	19, 20	194–204	South Africa
57. *Erylus gilchristi* Burton, 1926*	9	20, 22	122–204	South Africa
58. *Erylus polyaster* Lendenfeld, 1907*	3	7, 22	78–122	South Africa
59. *Pachymatisma* sp. ▲	3	7, 10, 35	58–87	Amathole region
60. *Penares alatus* (Lendenfeld, 1907)*	4	17, 36, 39, 43	52–103	South Africa
61. *Penares* cf. *intermedius* (Dendy, 1905)	25	17, 18, 22, 23, 30, 39, 43	25–122	South India & Sri Lanka (TL), Eastern India, Kenya, Tanzania
62. *Penares orthotriaena* Burton, 1931	12	15, 17, 22, 34, 36, 39, 43, 48	22–122	South Africa (TL), Mozambique
Subfamily Geodiinae Gray, 1867				
63. *Geodia labyrinthica* (Kirkpatrick, 1903)*	2	7	78	South Africa
64. *Geodia libera* Stephens, 1915	3	45	78	South Africa (TL), Vema Seamount
Family Macandrewiidae Schrammen, 1924				
65. *Macandrewia* cf. *auris* Lendenfeld, 1907*	1	20	204	South Africa
Family Neopeltidae Sollas, 1888				
66. *Sollasipelta cavernicola* (Vacelet & Vasseur, 1965)	4	11, 17, 20, 25	76–204	Madagascar
67. *Sollasipelta thoosa* (Lévi, 1964)	6	7, 11, 17, 18, 22	76–122	Mozambique (TL), Kenya
Family Pachastrellidae Carter, 1875a				
68. *Characella* sp. 1 ▲	11	7, 10, 11, 15, 30, 35, 36, 39	45–90	Amathole region

	No. of Specimens	Site/Station (s)	Depth (m)	Distribution
69. *Characella* sp. 2 ▲	11	20	204	Amathole region
70. *Pachastrella caliculata* Kirkpatrick, 1902*	66	4, 7, 8, 10, 11, 12, 14, 17, 18, 20, 22, 26, 27, 28, 30, 31, 34, 35, 36, 37, 39, 43, 44, 45, 46	29–229	South Africa
Family Theonellidae Lendenfeld, 1903				
71. *Theonella* sp. ▲	7	7, 11, 17, 18, 30	52–104	Amathole region
Family Vulcanellidae Cárdenas, Xavier, Reveillaud, Schander & Rapp, 2011				
72. *Poecillastra* sp. ▲	5	7, 17	78–94	Amathole region
Suborder Spirophorina Bergquist & Hogg, 1969 Family Scleritodermidae Sollas, 1888				
73. *Aciculites spinosa* Vacelet & Vasseur, 1971	2	22	122	Madagascar
74. *Microscleroderma hirsutum* Kirkpatrick, 1903	1	34	45	South Africa (TL), Western Arabian Sea

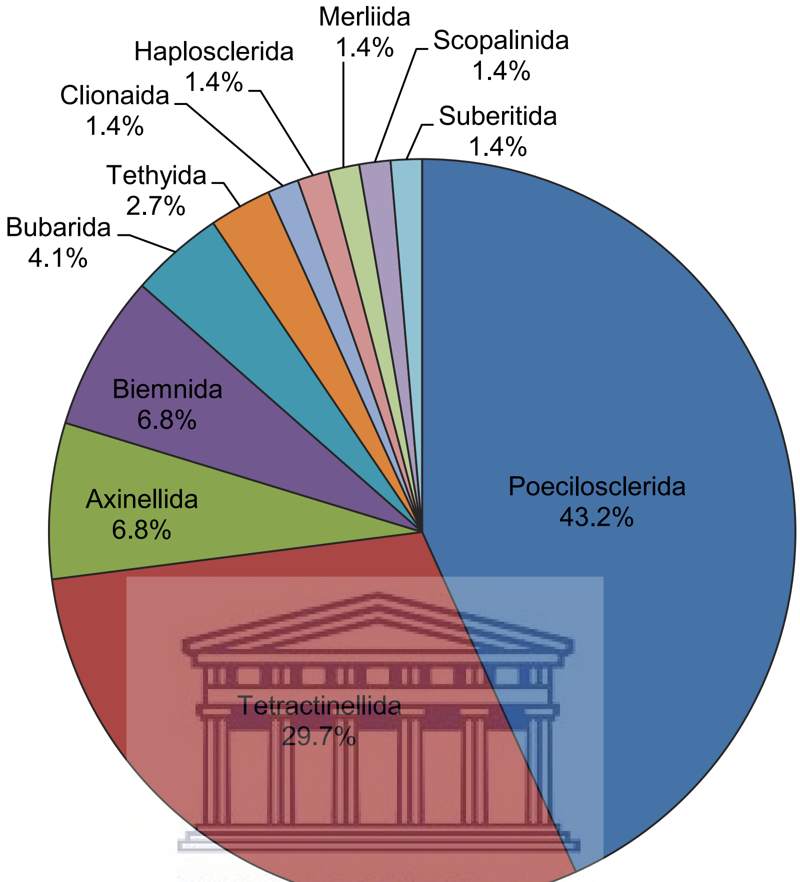

Figure 6: Taxonomic order composition of the heteroscleromorph demosponges from the Amathole region (Eastern Cape, South Africa).

Of the 47 known species, 39 had been described and/or previously documented from South Africa. Twenty-five of these are currently considered endemic, with one species found in the South African endemic genus *Lithochela*, while six species—*Biemna sigmodragma* Lévi, 1963, *Ceratopsion microxephora* (Kirkpatrick, 1903), *Crella (Grayella) erecta* (Lévi, 1963), *Histodermella natalensis* (Kirkpatrick, 1903), *Phorbas clathratus* (Lévi, 1963) and *Phorbas mollis* (Kirkpatrick, 1903)—represent the first records since their original description(s). The remaining eight known species—*Guitarra indica* Dendy, 1916, *Penares* cf. *intermedius* (Dendy, 1905), *Rhabderemia indica* Dendy, 1905, *Aciculites spinosa* Vacelet & Vasseur, 1971, *Coelodischela* cf. *diatomorpha* Vacelet, Vasseur & Lévi, 1976, *Didiscus* cf. *placospongioides* Dendy, 1922, *Sollasipelta cavernicola* (Vacelet & Vasseur, 1965) and *Sollasipelta thoosa* (Lévi, 1964)—represent new species records for South Africa, while the last five also represent the first records of these genera in South Africa. Finally, this was the first record of *Aciculites spinosa* since its original description.

Of the 27 new species, one and three were found in the South African endemic genera *Cyclacanthia* and *Tsitsikamma* respectively. A further eight species that were designated to the genera *Bubaris*, *Hemitedania*, *Lithoplocamia*, *Placospongia*, *Characella*, *Holoxea* and *Svenzea*, represent the first records of these genera in South Africa, while the latter three also represent the first records of these genera in the Indian Ocean.

3.2 Descriptions

For the purposes of this study, the taxonomic descriptions of only 23 heteroscleromorph demosponge species from the Amathole region are given below. Of these, 15 are re-described from fresh material and eight are described as new (denoted as **sp. nov. ▲**).

Phylum Porifera Grant, 1836

Class Demospongiae Sollas, 1885

Subclass Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012

Order Axinellida Lévi, 1953

Family Raspailiidae Nardo, 1833

Subfamily Plocamioninae Hooper, 2002b

Genus *Lithoplocamia* Dendy, 1922

Type species: *Lithoplocamia lithistoides* Dendy, 1922 (by monotypy).

Diagnosis. Raspailiidae with a secondary basal reticulate skeleton lacking any trace of axial compression, formed by (sub)isodictyal tracts of acanthostrongyles or acanthotylostrongyles (from Hooper 2002b).

***Lithoplocamia longioxea* sp. nov. ▲**

(Fig. 7A–F, Table 6)

Material examined. TS 4018 (BD15-Spg1(21)), TS 4039 (BD15-Spg1(42)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–36, Station 3742 (33.0137º S, 28.3142º E–33.0172º S, 28.3063º E, Eastern Cape, South Africa), 204 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 12 min, 24 February 2016.

Description. Massive fragment (Fig. 7A). Length 7 cm, width 4 cm and thickness 1 cm. Surface smooth and slippery, irregular random oscules (~1 mm) and subcircular ostia (<1 mm) throughout. Texture firm and dense, not compressible, brittle. Colour *in situ* dark brown, in preservative beige. Sticky to slimy exudate present in life.

Skeleton. Choanosomal skeleton comprises a dense sub-isodictyal reticulation of acanthostrongyles, with no axial compression (Fig. 7B). Ill-defined radial to plumose tracts (~130 µm across) of choanosomal styles ascend to surface (Fig. 7C), protruding slightly. Ectosome consists of sparse bouquets of oxeas surrounding protruding choanosomal spicules, supporting a dermal membrane often worn away.

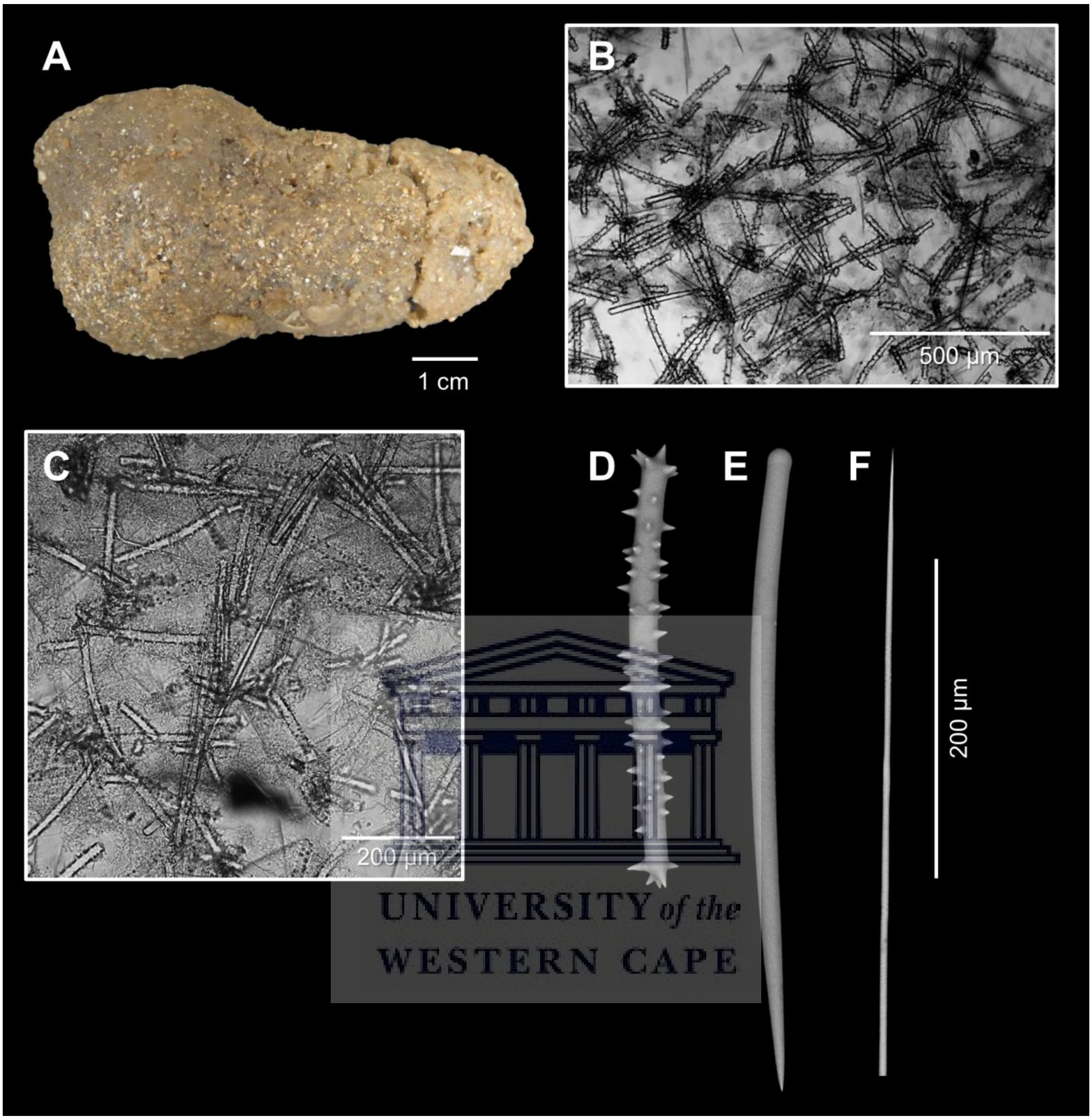

Figure 7: *Lithoplocamia longioxea* **sp. nov.** ▲. A, specimen TS 4018. B, choanosomal skeleton. C, style tract. D, acanthostrongyle. E, style. F, oxea apex.

Table 6: Comparative spicule dimensions and known location, form and depth for the accepted species of *Lithoplocamia* Dendy, 1922 occurring in the Indian Ocean according to van Soest *et al.* (2020a). Spicule dimensions expressed in µm, with specimens from this study (TS) given as minimum–*mean*–maximum length × width, n = 15.

Species	Acanthostrongyles	Styles	Oxeas	Location/Form/Depth (m)
1. *Lithoplocamia indica* Pulitzer-Finali, 1993 (Orig. Descrip.)	190–260 × 13–18	-	-	North Kenya Banks/lobate, roughly conical/110
2. *Lithoplocamia lithistoides* Dendy, 1922 (Orig. Descrip.)	170 × 20	350 × 18	400 × 4	Seychelles & Mauritius/massive, encrusting, hemispherical/ 71–183
Hooper (2002b) (Re-description of NHMUK 1921.11.7.68)	122–226 × 12–24	252–427 × 9–14	322–435 × 3–5	Mauritius/massive/183
3. *Lithoplocamia minor* Pulitzer-Finali, 1993 (Orig. Descrip.)	115–165 × 7–9	210–250 × 7–8	-	Mombasa/massive, exterior dark orange, interior light orange/12–14
4. *Lithoplocamia tuberculata* Pulitzer-Finali, 1993 (Orig. Descrip.)	155–170 × 15–20	-	-	North Kenya Banks/hemispherical, tuberculated/110–244
5. *Lithoplocamia longioxea* sp. nov. ▲ (TS 4018)	210–*227*–244 × 14–*18*–21	361–*385*–422 × 14–*18*–24	525–*674*–779 × 3–*5*–6	Amathole region (Eastern Cape, South Africa)/massive fragment, dark brown/204
TS 4039	225–*254*–278 × 15–*18*–21	385–*443*–497 × 16–*18*–20	593–*712*–815 × 3–*4*–6	Amathole region (Eastern Cape, South Africa)/thickly encrusting, dark brown/204

Spiculation. Megascleres. Acanthostrongyles with thick straight spines on the shaft and both apices, straight to slightly curved: 210–*227*–244 × 14–*18*–21 µm (excluding spines), n = 15 (Fig. 7D). Styles smooth, straight to slightly curved, with slightly pronounced rounded heads, hastate : 361–*385*–422 × 14–*18*–24 µm, n = 15 (Fig. 7E). Oxeas smooth, straight, thin, hastate: 525–*674*–779 × 3–*5*–6 µm, n = 15 (Fig. 7F). **Microscleres.** None.

Distribution and ecology. Currently only known from the Amathole region (Eastern Cape, South Africa). The material examined had bryozoan (TS 4018) and hydroid (TS 4039) epifauna. Depth: 204 m.

Provisional etymology. *Longus* (L.) = long, referring to the length of the oxea megascleres.

Remarks. The above material is assigned to *Lithoplocamia* as diagnosed by its massive to semi-encrusting form and skeletal structure (Hooper 2002b). There are four species known from the Indian Ocean (van Soest *et al.* 2020a), with the above most similar to *Lithoplocamia lithistoides* Dendy, 1922 (acanthostrongyles: 170 × 20 µm; styles: 350 × 18 µm; oxeas: 400 × 4 µm) described from the Seychelles and Mauritius, re-described by Hooper in 2002, and further recorded from the Red Sea and Western Arabian Sea by Burton (1959). However, the material examined differs from this species in having longer spicules, and lacking a nodular, hispid surface.

Of the remaining congeners in the Indian Ocean, all of which were described by Pulitzer-Finali in 1993, *L. indica* and *L. tuberculata* from the North Kenya Banks have exclusively acanthostrongyles, while *L. minor* from Mombasa has smaller spicules (acanthostrongyles: 115–165 × 7–9 µm; styles: 210–250 × 7–8 µm) and lacks oxeas.

Thus, the present material likely constitutes a new species, and the first record of *Lithoplocamia* from South Africa.

Key diagnostic characters:

- massive form;
- smooth and slippery surface, covered in sticky to slimy exudate;
- brittle;
- dark brown in life;
- choanosome a dense sub-isodictyal reticulation, with no axial compression;
- megascleres include acanthostrongyles, styles and long oxeas (>500 µm);
- no microscleres.

Subfamily Thrinacophorinae Hooper, 2002b

Genus *Ceratopsion* Strand, 1928

Type species: *Ceratopsis expansa* Thiele, 1898 (by original designation).

Diagnosis. Raspailiidae lacking echinating spicules, having an axially compressed choanosomal skeleton with reticulate fibres cored by sinuous styles or anisoxeas and a well differentiated radial extra-axial skeleton cored by longer megascleres (from Hooper 2002b).

Ceratopsion microxephora (Kirkpatrick, 1903)

(Fig. 8A–I, Table 7)

Synonymy.

Phakellia microxephora Kirkpatrick, 1903b: 242.

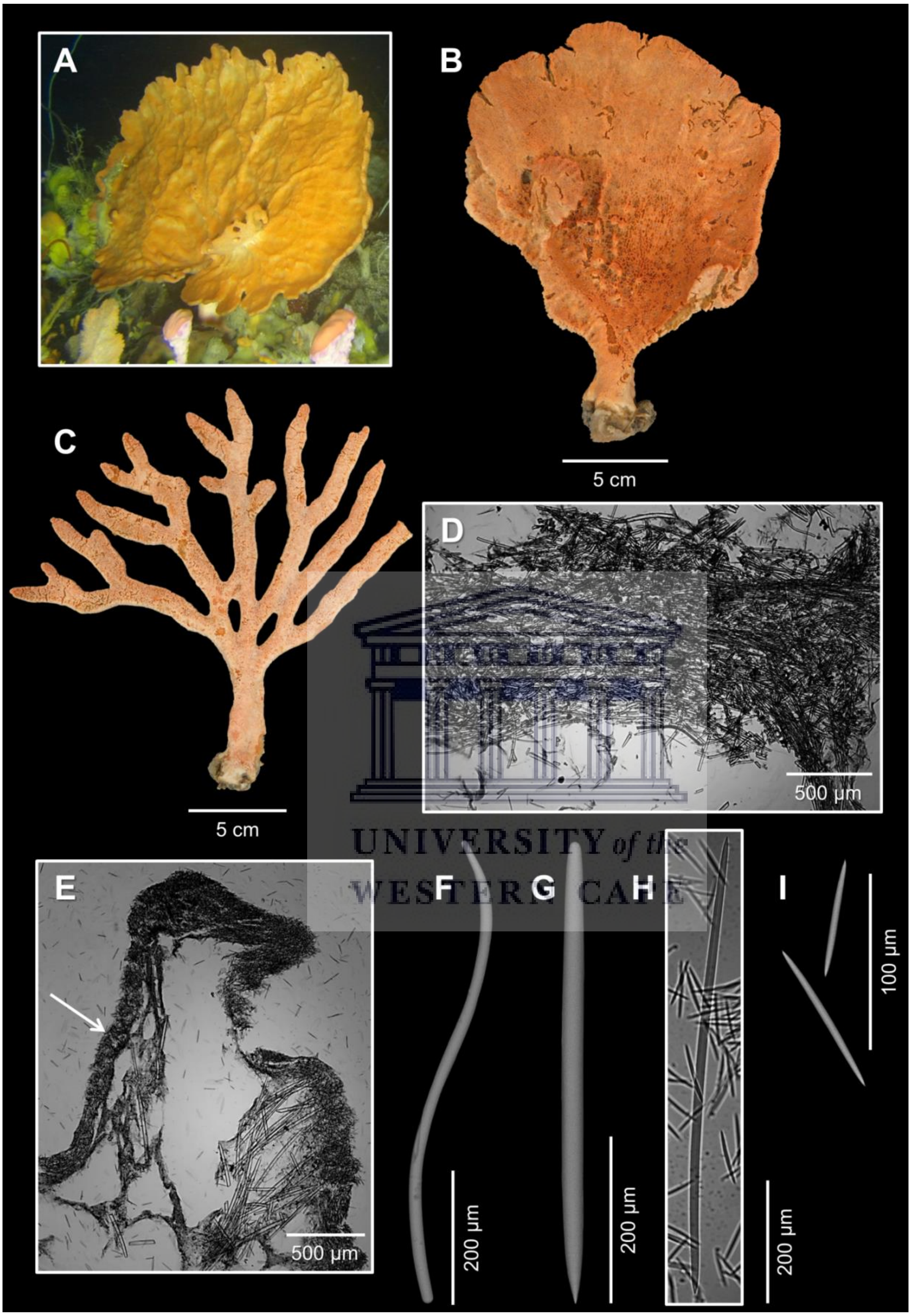

Figure 8: *Ceratopsion microxephora* (Kirkpatrick, 1903). A, species *in situ* (R43). B, specimen TS 4653. C, specimen TS 4644. D, choanosomal skeleton comprising a compressed axial reticulation. E, subectosomal skeleton and ectosome comprising a dermal membrane (arrow). F, strongyle. G, style. H, oxea. I, smooth microxeas.

Table 7: Comparative spicule dimensions and known location, form and depth for the accepted species of *Ceratopsion* Strand, 1928 occurring in Tristan da Cunha and South Africa according to van Soest *et al.* (2020a). Spicule dimensions expressed in µm, with specimens from this study (TS) given as minimum–*mean*–maximum length × width, n = 15.

	Megascleres			Microscleres	
Species	**Strongyles**	**Styles**	**Oxeas**	**Microxeas**	**Location/Form/Depth (m)**
1. *Ceratopsion incrustans* (Burton, 1932) (Orig. Descrip. as *Ceratopsis incrustans*)	-	I) 480 × 15 II) 300 × 6	-	100 × 4	Tristan da Cunha/encrusting/80–140
2. *Ceratopsion microxephora* (Kirkpatrick, 1903) (Orig. Descrip. as *Phakellia microxephora*)	670–1250 × 12–16	560 × 20	620 × 18	70 × 3	South Africa/stalked, flabellate/155
TS 3432	413–*733*–1135 × 8–*14*–23	409–*501*–579 × 13–*20*–26	408–*494*–571 × 12–*19*–24	59–*75*–83 × 3–*3*–4	Amathole region (Eastern Cape, South Africa)/erect, stalked, flabellate with lobes, orange/39
TS 3433	385–*754*–1127 × 8–*14*–20	373–*479*–591 × 9–*16*–22	357–*467*–575 × 11–*15*–22	50–*66*–73 × 3–*3*–4	Amathole region (Eastern Cape, South Africa)/erect, stalked, arborescent, light orange/39
TS 4447	460–*847*–1273 × 10–*15*–22	473–*551*–635 × 11–*17*–26	550–*612*–671 × 17–*20*–27	52–*64*–74 × 3–*3*–5	Amathole region (Eastern Cape, South Africa)/erect, stalked, flabellate with lobes, dirty light orange/90
TS 4449	527–*828*–1247 × 11–*16*–22	500–*621*–712 × 15–*20*–25	542–*660*–863 × 14–*18*–22	63–*76*–87 × 3–*4*–5	Amathole region (Eastern Cape, South Africa)/erect, stalked, flabellate with lobes, light dirty pink to off-white/90

Species	Megascleres			Microscleres	Location/Form/Depth (m)
	Strongyles	Styles	Oxeas	Microxeas	
TS 4653	430–*827*–1209 × 9–*14*–17	362–*477*–547 × 13–*17*–23	366–*438*–548 × 11–*19*–26	63–*72*–84 × 3–*4*–5	Amathole region (Eastern Cape, South Africa)/erect, stalked, flabellate with lobes, orange/36

Material examined. **TS 4653 (AI2-Spg421)**: ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–81, Station 3893 (33.1632º S, 27.7746º E–33.1625º S, 27.7753º E, Eastern Cape, South Africa), 36 m depth, amongst shell hash, SST 18 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 3 min, 03 September 2016. TS 3432 (BD26-Spg8), TS 3433 (BD26-Spg10), TS 3949 (BD26-Spg1(3)), TS 3958 (BD26-Spg1(12)), TS 3980 (BD26-Spg1(34)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–102, Station 3808 (33.1597º S, 27.7777º E–33.1616º S, 27.7778º E, Eastern Cape, South Africa), 39 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 20 min, 02 March 2016. TS 4103 (BD1-Spg28): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–10, Station 3716 (32.7531º S, 28.5177º E–32.7547º S, 28.5207º E, Eastern Cape, South Africa), 78 m depth, amongst cobbles and shell hash, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 24 min, 21 February 2016. TS 4269 (AI2-Spg37): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–1, Station 3813 (32.6816º S, 28.4585º E–32.6869º S, 28.4617º E, Eastern Cape, South Africa), 55–52 m depth, amongst rock, coquina/shell hash and pebbles, SST 21 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 10 min, 26 August 2016. TS 4366 (AI2-Spg134), TS 4367 (AI2-Spg135): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–21, Station 3833 (32.7580º S, 28.4589º E–32.7577º S, 28.4554º E, Eastern Cape, South Africa), 62–58 m depth, amongst rock and coquina/shell hash, SST 19 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 9 min, 28 August 2016. TS 4385 (AI2-Spg153): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–22, Station 3834 (32.7541º S, 28.4553º E–32.7531º S, 28.4533º E, Eastern Cape, South Africa), 54–52 m depth, amongst rock, SST 19 ºC, coll. R. Payne & I. Malick on R/V

Ellen Khuzwayo (Voyage 159), benthic dredge, duration 4 min, 28 August 2016. TS 4447 (AI2-Spg215), TS 4449 (AI2-Spg217): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–49, Station 3861 (32.9395º S, 28.2685º E–32.9363º S, 28.2757º E, Eastern Cape, South Africa), 90 m depth, amongst a shipwreck, shell hash and coarse sand with shell fragments, SST 21 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 12 min, 30 August 2016. TS 4644 (AI2-Spg412): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–81, Station 3893 (33.1632º S, 27.7746º E–33.1625º S, 27.7753º E, Eastern Cape, South Africa), 36 m depth, amongst shell hash, SST 18 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 3 min, 03 September 2016. TS 4718 (AI2-Spg486): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–97, Station 3909 (33.2020º S, 27.8586º E–33.1949º S, 27.8610º E, Eastern Cape, South Africa), 76–65 m depth, amongst cobbles, rock, shell hash and pebbles, SST 18 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 12 min, 05 September 2016.

Description. Erect, stalked, flabellate form with random flat lobes and irregular margin (Fig. 8A & B). Some specimens arborescent (e.g. TS 3433, TS 4644) (Fig. 8C). Length 17 cm, width 14 cm and thickness 3 cm. Thin dermal membrane present (<1 mm), worn away in places revealing beige, somewhat fibrous-looking, interior. Surface rugose, pitted and granular. Raised subcircular to irregular oscules (1–2 mm) throughout, but concentrated on one side of sponge and the apex. Texture spongy and dense, compressible, resilient but easily torn. Colour *in situ* orange, in preservative beige. Distinct, almost medicinal smell present.

Skeleton. Choanosomal skeleton comprises a compressed axial reticulation of fibres cored by flexuous strongyles, ~700–1000 µm across (Fig. 8D). Extra-axial skeleton consists of radially arranged subectosomal style and oxea tracts (~120–260 µm across), embedded in and perpendicular/oblique to axial core. Ectosomal skeleton comprises a dermal membrane (~160–760 µm thick) (Fig. 8E), consisting of a dense mass of confused microxeas.

Spiculation. Megascleres. Strongyles smooth, flexuous, with rounded apices, in a large size range with overlap: 430–*827*–1209 × 9–*14*–17 µm, n = 15 (Fig. 8F). Styles smooth, straight to slightly curved, with somewhat reduced rounded heads, acerate: 362–*477*–547 × 13–*17*–23 µm, n = 15 (Fig. 8G). Oxeas smooth, straight to slightly curved, acerate, variable: 366–*438*–548 × 11–*19*–26 µm, n = 15 (Fig. 8H). **Microscleres.** Microxeas smooth, straight to slightly curved medially, acerate: 63–*72*–84 × 3–*4*–5 µm, n = 15 (Fig. 8I).

Distribution and ecology. Known only from East London, South Africa. Occurs on or amongst various substrates in the Amathole region (Eastern Cape), including a shipwreck, cobbles, rock, coquina/shell hash, pebbles and coarse sand with shell fragments. Specimen TS 3432 had hydroid epifauna. Depth range: 36–155 m (previously 155 m).

Remarks. Assignment of the above material to *Ceratopsion* is supported by the erect/arborescent form, granular surface, and well differentiated axial and extra-axial skeletons without echinating spicules (Hooper 2002b).

The specimens conform closely to *Ceratopsion microxephora* from South Africa (strongyles: 670–1250 × 12–16 µm; styles: 560 × 20 µm; oxeas: 620 × 18 µm; microxeas: 70 × 3 µm), which has not been recorded in the taxonomic literature since the description in 1903. Kirkpatrick (1903b) noted that both the style and oxea megascleres were rare. In the above material examined, styles were uniform and abundant, but oxeas were variable, both in form and abundance per specimen (ranging from absent to rarely abundant and somewhat replacing styles). Thus, the oxeas are either style mutations, or both spicules types should be considered one spicule type that varies between the two depending on specimen.

Only one other congener occurs near South Africa, *Ceratopsion incrustans* (Burton, 1932). This encrusting species was described from Tristan da Cunha, and has only style megascleres.

Key diagnostic characters:

- erect, stalked, flabellate to arborescent form;
- dermal membrane often worn away, revealing beige fibrous-looking interior;
- rugose, pitted and granular surface;
- resilient;
- orange in life;
- skeleton comprises axial and extra-axial regions;
- megascleres include flexuous strongyles, styles and oxeas;
- microscleres exclusively smooth microxeas, <100 µm.

Order Biemnida Morrow, 2013

Family Biemnidae Hentschel, 1923

Genus *Biemna* Gray, 1867

Type species: *Halichondria varianti*a Bowerbank, 1858 (by original designation).

Diagnosis. [Biemnidae] with stylote or exceptionally oxeote megascleres arranged in plumoreticulate fashion; ectosomal skeleton consists of the brushed endings of choanosomal tracts; microscleres include sigmas, microxeas, commata and raphides (from Hajdu & van Soest 2002).

Biemna sigmodragma **Lévi, 1963**

(Fig. 9A–J, Table 8)

Synonymy.

Biemna megalosigma subsp. *sigmodragma* Lévi, 1963: 18.

Not: *Biemna megalosigma* Hentschel, 1912: 351; Uriz 1988: 61.

Material examined. **TS 3723 (BD25-Spg3)**: ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–101, Station 3807 (33.1347º S, 27.7689º E–33.1604º S, 27.7762º E, Eastern Cape, South Africa), 33 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 23 min, 02 March 2016. TS 2778: Amathole region, Station 491 (32.9350º S, 28.0933º E, Eastern Cape, South Africa), 55 m depth, coll. T. Samaai & S. Kerwath on R/V *Ellen Khuzwayo* (Voyage 131), benthic dredge, 24 February 2015. TS 2785: Amathole region, Station 492 (32.9250º S, 28.1000º E, Eastern Cape, South Africa), 39 m depth, coll. T. Samaai & S. Kerwath on R/V *Ellen Khuzwayo* (Voyage 131), benthic dredge, 27 February 2015. TS 3830 (BD25-Spg1(2)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–101, Station 3807 (33.1347º S, 27.7689º E–33.1604º S, 27.7762º E, Eastern Cape, South Africa), 33 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 23 min, 02 March 2016. TS 3955 (BD26-Spg1(9)), TS 3982 (BD26-Spg1(36)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–102, Station 3808 (33.1597º S, 27.7777º E–33.1616º S, 27.7778º E, Eastern Cape, South Africa), 39 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 20 min, 02 March 2016.

Description. Massive, basal mass that extends into erect outgrowths (up to 1 cm) (Fig. 9A). Length 7 cm, width 5 cm and thickness 2 cm. Thin detachable dermal membrane present (<1 mm), surface conulose, microhispid and rough, with no discernible oscules.

Texture dense and spongy, very compressible, soft and friable. Colour *in situ* light yellow-orange with dark red and green patches near apex, in preservative beige.

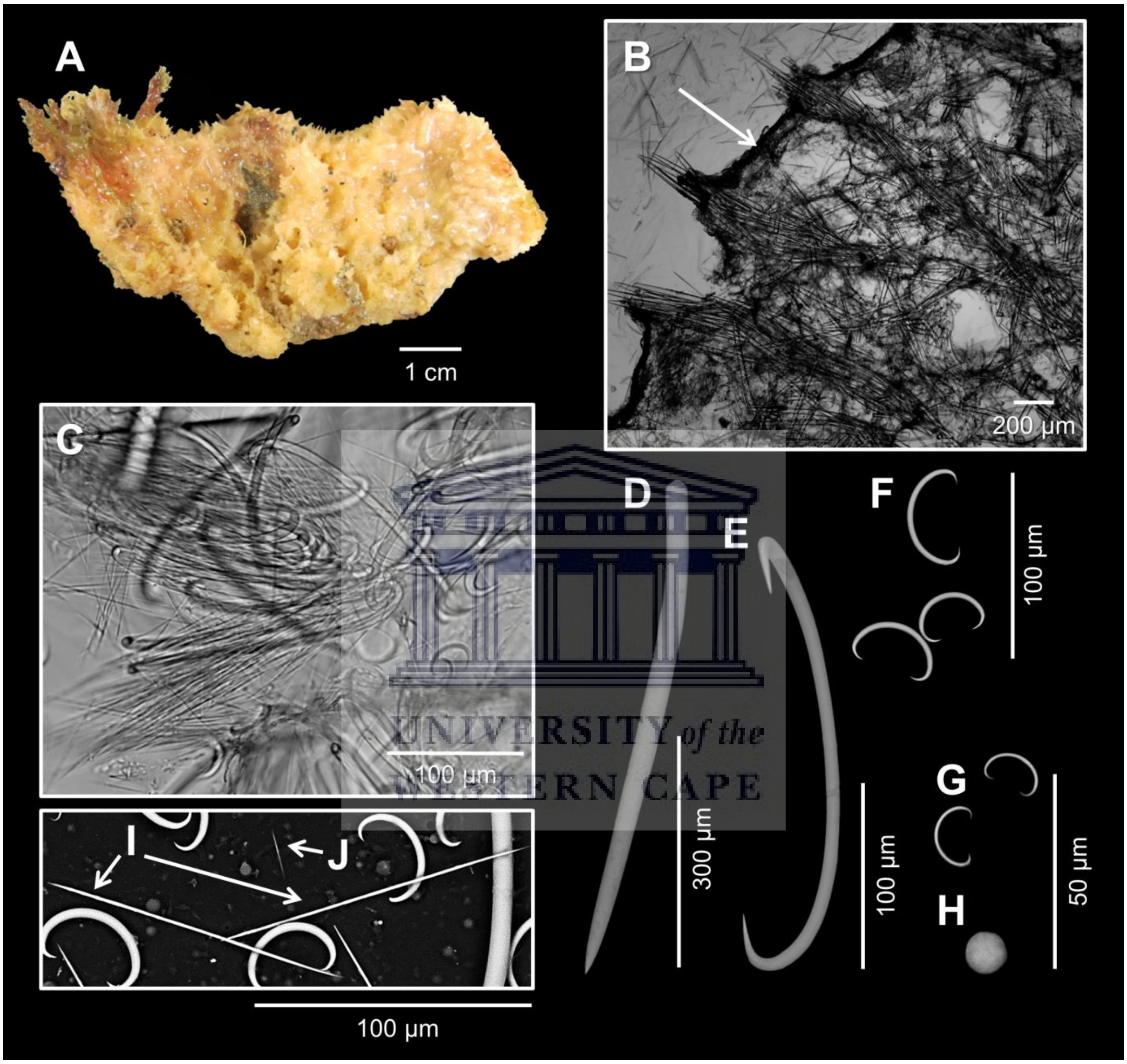

Figure 9: *Biemna sigmodragma* Lévi, 1963. A, specimen TS 3723. B, choanosomal skeleton, with ectosome comprising a detachable dermal membrane (arrow). C, sigmodragmata and trichodragmata. D, style. E, C-shaped sigma I. F, C-shaped sigmata II. G, C-shaped sigmata III. H, sphere. I, raphides. J, microxea.

Table 8: Comparative spicule dimensions and known location, form and depth for all records of *Biemna megalosigma* Hentschel, 1912 in southern Africa. Spicule dimensions expressed in µm, with specimens from this study (TS) given as minimum–*mean*–maximum length × width, n = 15.

	Megascleres	**Microscleres**					
Records	**Styles**	**Sigmata**	**Raphides**	**Microxeas**	**Spheres**	**Location/Form/Depth (m)**
1. *Biemna megalosigma* Hentschel, 1912 (Orig. Descrip.)	576–704 × 15–29	I) 72–216 II) 27–32 III) 15–18	136–208	40–112 × 2	9	Arafura Sea (Indonesia)/erect, massive, light white to brownish/8–10
2. *Biemna sigmodragma* Lévi, 1963 (Orig. Descrip. as *Biemna megalosigma* subsp. *sigmodragma*)	650–800 × 15–30	I) 200–210 × 8 II) 30–85 × 2–5 III) 10–11	110–120	30 × 1	-	South Africa/massive, yellowish/28
TS 2778	670–*761*–911 × 8–*22*–29	I) 256–*278*–306 × 10–*13*–16 II) 34–*55*–80 × 4–*4*–6 III) 16–*19*–23 × 1–*1*–1	111–*120*–130 × 1–*1*–2	28–*30*–33 × 1–*1*–1	3–*5*–7	Amathole region (Eastern Cape, South Africa)/massive with erect outgrowths, light dirty yellow/55
TS 2785	629–*717*–769 × 17–*20*–23	I) 182–*203*–222 × 6–*8*–9 II) 24–*48*–71 × 3–*3*–4 III) 9–*11*–13 × 1–*1*–1	72–*86*–97 × 1–*1*–2	18–*26*–32 × 1–*1*–1	4–*6*–8	Amathole region (Eastern Cape, South Africa)/massive with erect outgrowths, light dirty yellow/39
TS 3723	569–*657*–708 × 19–*26*–31	I) 193–*217*–230 × 6–*8*–10 II) 24–*46*–82 × 2–*3*–4 III) 10–*12*–14 × 1–*1*–1	93–*104*–114 × 1–*1*–2	23–*33*–44 × 1–*1*–2	5–*6*–8	Amathole region (Eastern Cape, South Africa)/massive, basal mass with erect outgrowths, light yellow-orange with dark red and green patches/33

	Megascleres	Microscleres				
Records	**Styles**	**Sigmata**	**Raphides**	**Microxeas**	**Spheres**	**Location/Form/Depth (m)**
TS 3830	610–*769*–914 × 15–*24*–28	I) 259–*292*–318 × 11–*12*–15 II) 27–*52*–71 × 3–*4*–5 III) 16–*18*–22 × 1–*1*–2	114–*128*–141 × 1–*1*–2	26–*30*–36 × 1–*1*–2	3–*4*–8	Amathole region (Eastern Cape, South Africa)/massive with erect outgrowths, light dirty yellow/33
TS 3955	553–*641*–703 × 15–*22*–28	I) 212–*227*–244 × 7–*9*–10 II) 26–*43*–73 × 3–*3*–5 III) 11–*12*–14 × 1–*1*–1	91–*106*–115 × 1–*1*–2	14–*23*–45 × 1–*1*–1	2–*4*–6	Amathole region (Eastern Cape, South Africa)/massive with erect outgrowths, beige/39
TS 3982	583–*758*–850 × 15–*21*–25	I) 265–*301*–320 × 5–*12*–17 II) 35–*53*–82 × 2–*4*–5 III) 17–*20*–24 × 1–*1*–1	114–*125*–138 × 1–*1*–2	26–*32*–34 × 1–*1*–2	2–*4*–5	Amathole region (Eastern Cape, South Africa)/massive with erect outgrowths, light dirty yellow/39
3. Undescribed *Biemna* sp. Uriz (1988) (As *Biemna megalosigma*)	880–1250 × 19–25	I) 270–312 × 10–14 II) 90–160 × 6–8 III) 40–65 × 3–4 IV) 20–29 × 2–5	140–170 × 3	40–63 × 2	-	Namibia/encrusting base with erect, flattened branch, conulose, yellow-ochre/183

Skeleton. Choanosomal skeleton consists of multispicular plumoreticulate style tracts (~110–530 µm across) which ascend vertically to surface and penetrate ectosome (extending to ~210–420 µm), which comprises a detachable dermal membrane (~30–150 µm) (Fig. 9B). Microscleres abundant throughout, with sigmata and raphides often forming sigmodragmata and loose trichodragmata respectively (Fig. 9C).

Spiculation. Megascleres. Styles smooth, straight to slightly curved, acerate to hastate: 569–*657*–708 × 19–*26*–31 µm, n = 15 (Fig. 9D). **Microscleres.** Sigmata smooth, C- to S-shaped, in three size classes: I) 193–*217*–230 × 6–*8*–10 µm, n = 15 (Fig. 9E); II) 24–*46*–82 × 2–*3*–4 µm, n = 15 (Fig. 9F); III) 10–*12*–14 × 1–*1*–1 µm, n = 15 (Fig. 9G). Spheres smooth, round: 5–*6*–8 µm, n = 15 (Fig. 9H). Raphides: 93–*104*–114 × 1–*1*–2 µm, n = 15 (Fig. 9I). Microxeas: 23–*33*–44 × 1–*1*–2 µm, n = 15 (Fig. 9J).

Distribution and ecology. Known only from South Africa, occurring amongst rock and shell (Lévi 1963). Specimen TS 3723 had worm casing epifauna. Depth range: 28–55 m (previously 28 m).

Remarks. Assignment of the above material to *Biemna* is based on its massive form with an uneven surface, due to a plumoreticulate choanosomal skeleton comprising styles of a single size class in tracts which penetrate the ectosomal skeleton, as well as the presence of sigmata, raphides, microxeas and spheres as microscleres (Hajdu & van Soest 2002).

The specimens conform closely to *Biemna megalosigma* var. *sigmodragma*, which was described from South Africa by Lévi in 1963 (styles: 650–800 × 15–30 µm; sigmata: I) 200–210 × 8 µm, II) 30–85 × 2–5 µm, III) 10–11 µm; raphides: 110–120 µm; microxeas: 30 × 1 µm). However, the parent *Biemna megalosigma* Hentschel, 1912 was described from the Arafura Sea (Indonesia), and has longer raphide (136–208 µm) and microxea (40–112 µm) microscleres. Thus, the elevation of this variety to species status is justified, hereafter referred to as *Biemna sigmodragma* Lévi, 1963. This species is easily distinguished from other South African congeners by the presence of large (>200 µm), robust sigmata.

Uriz (1988) later recorded *B. megalosigma* from Namibia, with an additional size class of sigmata, and longer styles (880–1250 × 19–25 µm) than reported for both the holotype and *B. sigmodragma*. Consequently, these specimens require further investigation, and likely description as a new species.

Key diagnostic characters:

- massive, basal mass that extends into erect outgrowths (up to 1 cm);
- conulose, microhispid and rough surface;
- no discernible oscules;
- light yellow-orange in life, with dark red and green patches near apex;
- sigmodragmata and loose trichodragmata present;
- megascleres exclusively one size class of styles, <1000 µm;
- microscleres include three size classes of sigmata, the largest often >200 µm;
- raphide (<150 µm), microxea (<50 µm), and sphere microscleres also present.

Family Rhabderemiidae Topsent, 1928

Genus *Rhabderemia* Topsent, 1890

Type species: *Microciona pusilla* Carter, 1876 (by subsequent designation).

Diagnosis. With rhabdostyles frequently bearing an extra basal spiral twist, in one or two size categories as the only megascleres. Microscleres, if present, include spirosigmas, micro(sub)(tylo)styles, thraustosigmas, thraustoxeas and toxas (from Hajdu & Desqueyroux-Faúndez 2008).

***Rhabderemia indica* Dendy, 1905**

(Fig. 10A–F, Table 9)

Synonymy.

Rhabderemia indica Dendy, 1905: 180; Hallmann 1917: 399; Topsent 1928: 65, 310; Burton 1959: 254; Thomas 1985: 270; Hooper 1990: 77; van Soest & Hooper 1993: 331.

Rhabderemia (Rhabderemia) indica; Hajdu & Desqueyroux-Faúndez 2008: 384, 385.

Material examined. **<u>TS 4472</u> (AI2-Spg240)**: ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–49, Station 3861 (32.9395º S, 28.2685º E–32.9363º S, 28.2757º E, Eastern Cape, South Africa), 90 m depth, amongst a shipwreck, shell hash and coarse sand with shell fragments, SST 21 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 12 min, 30 August 2016.

Description. Erect, columnar form (Fig. 10A). Length 11 cm, width 3 cm and thickness 3 cm. Surface velvety, with subcircular oscules (<1 mm) arranged in random, roughly stellate groups (1–2 mm). Texture spongy and dense, very compressible, tough and resilient. Colour *in situ*, and in preservative, light orange-beige.

Skeleton. Choanosomal skeleton plumoreticulate (Fig. 10B). Primary multispicular megasclere tracts (~50–260 µm across) perpendicular to surface, arranged around subdermal spaces, and interconnected by secondary multispicular megasclere tracts (~40–130 µm across). The former pierce somewhat indistinguishable dermal membrane lacking specialisation, and extend up to ~140 µm beyond surface (Fig. 10C). Microscleres abundant, scattered throughout.

Spiculation. Megascleres. Styles to rhabdostyles, smooth, acerate: 212–*245*–274 × 14–*24*–33 µm, n = 15 (Fig. 10D). **Microscleres.** Microstyles finely spined, straight to slightly curved, hastate: 35–*42*–45 × 2–*2*–3 µm, n = 15 (Fig. 10E). Spirosigmata, finely spined: 9–*12*–15 µm, n = 15 (Fig. 10F).

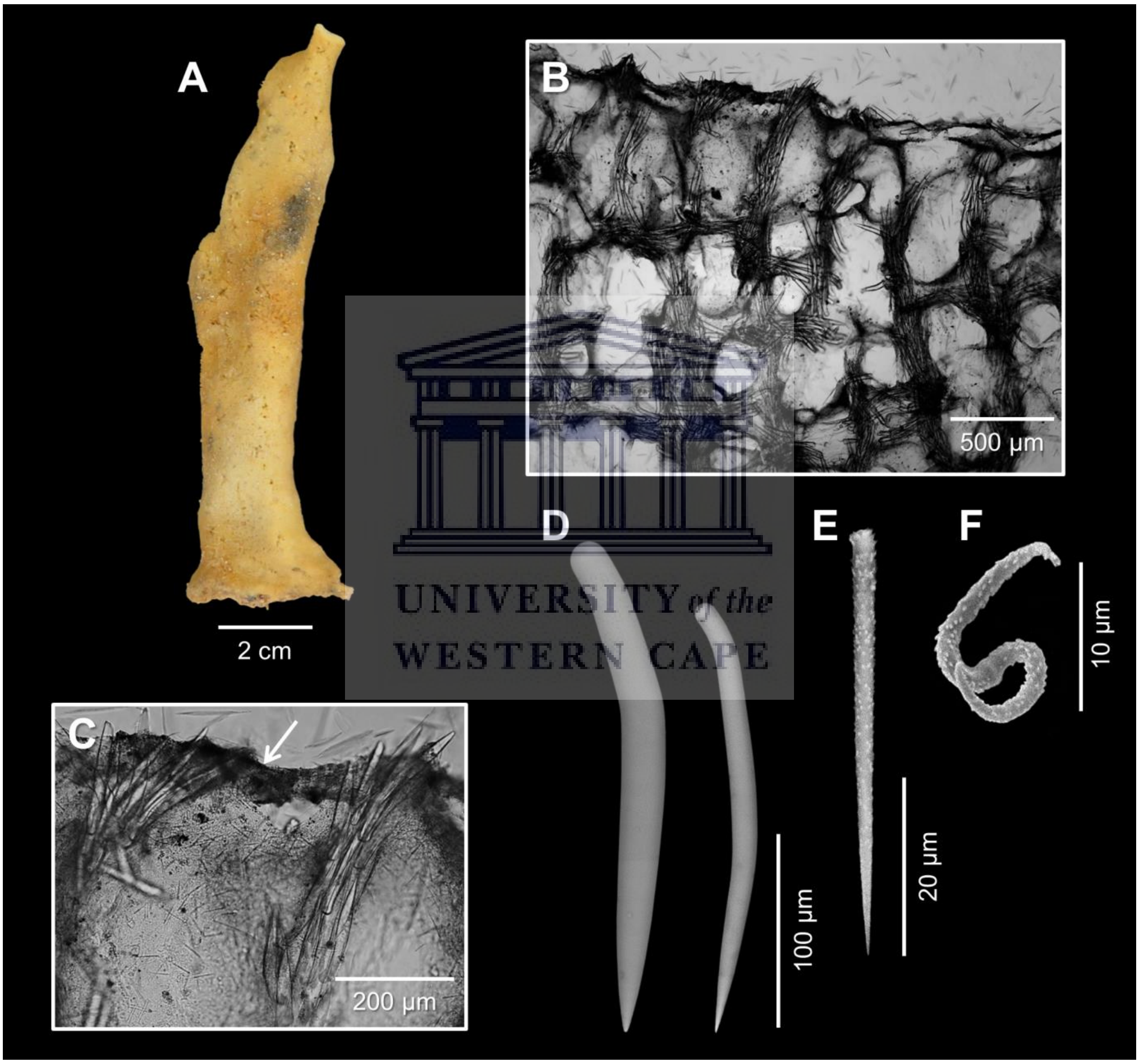

Figure 10: *Rhabderemia indica* Dendy, 1905. A, specimen TS 4472. B, choanosomal skeleton. C, primary multispicular megasclere tracts piercing somewhat indistinguishable dermal membrane (arrow). D, rhabdostyles. E, finely spined microstyle. F, finely spined spirosigma.

Table 9: Comparative spicule dimensions and known location, form and depth for the accepted species of *Rhabderemia* Topsent, 1890 occurring in South Africa and the Indian Ocean according to van Soest *et al.* (2020a). Spicule dimensions expressed in µm, with specimens from this study (TS) given as minimum–*mean*–maximum length × width, n = 15.

Species	Megascleres	Microscleres		Location/Form/Depth (m)
	Rhabdostyles ac: acanthose sm: smooth	**Microstyles** ac: acanthose sm: smooth	**Spirosigmata (S)/ Thraustosigmata (T)**	
1. *Rhabderemia acanthostyla* Thomas, 1968 (Orig. Descrip.)	ac: I) 109–*196*–315 × 6–*9*–12 sm: II) 84–*158*–258 × 2–*3*–4	-	(S) 12–*16*–25	South India and Sri Lanka/encrusting, dark brown/2
Thomas (1985)	ac: I) 109–315 × 6–12 sm: II) 84–258 × 2–4	-	(S) 12–23	South India and Sri Lanka/encrusting, dark brown
van Soest & Hooper (1993)	ac: I) 183–*233*–255 × 5–*9*–13 ac: II) 98–*122*–141 × 4–*5*–7	ac: 20–*29*–39 × <1	(S) I) 13–*15*–18 (S) II) 6–*7*–8	Indonesia and Vietnam/encrusting to column-like to short column-like branches that anastomose into loose mass, brown/0–36
2. *Rhabderemia batatas* Ilan, Gugel & van Soest, 2004 (Orig. Descrip.)	sm: 165–*218*–275 × 3–*4*–5	ac: 17–*24*–35	(S) 5–*7*–9	Red Sea/irregular with conical protuberances, exterior ochre to yellow, interior yellow/2

Species	Megascleres Rhabdostyles ac: acanthose sm: smooth	Microscleres Microstyles ac: acanthose sm: smooth	Spirosigmata (S)/ Thraustosigmata (T)	Location/Form/Depth (m)
3. *Rhabderemia bistylifera* Lévi, 1961 (Orig. Descrip.)	sm: 150–250 × 3–6	I) 110–130 × 1 II) 30–40 × <1	(S) 6–7	Seychelles/encrusting/2
van Soest & Hooper (1993) (Re-description of MNHN DCL 358)	sm: I) 258–305 × 5–6 sm: II) 131–220 × 4	ac: I) 110–*127*–141 × 1 ac: II) 30–*36*–43 × <1	(S) 6–*8*–10	Seychelles/thinly encrusting/2
4. *Rhabderemia burtoni* van Soest & Hooper, 1993 (Orig. Descrip.) (Re-description of NHMUK RN CXVI.A)	ac: I) 188–*246*–290 × 11–*12*–14 ac: II) 110–*135*–155 × 4–*6*–6	ac: 112–*136*–162 × 1	(T) 16	Salomon Islands (Chagos Archipelago)/fragment/108–216
Dendy (1922) (As *Rhabderemia pusilla*) (NHMUK RN CXVI.A)	sm: 200 × 11	ac: 164 × 1	16	Salomon Islands (Chagos Archipelago)/fragment/110–219
5. *Rhabderemia indica* Dendy, 1905 (Orig. Descrip.)	sm: 240 × 6	ac: 44 × 2	(S) 12	South India and Sri Lanka/encrusting to massive and irregular
Thomas (1985)	sm: 221–311 × 4–12	ac: 53–75 × 2	(S) 8–13	South India and Sri Lanka/encrusting to finger-shaped, dull grey
van Soest & Hooper (1993)	sm: 211–*238*–263 × 5–*7*–9	ac: 42–*46*–48 × 1–*1*–2	(S) 12–*13*–15	Gulf of Thailand/thickly encrusting to massive/15–18

Species	Megascleres Rhabdostyles ac: acanthose sm: smooth	Microscleres Microstyles ac: acanthose sm: smooth	Spirosigmata (S)/ Thraustosigmata (T)	Location/Form/Depth (m)
TS 4472	sm: 212–*245*–274 × 14–*24*–33	ac: 35–*42*–45 × 2–*2*–3	(S) 9–*12*–15	Amathole region (Eastern Cape, South Africa)/erect and columnar, light orange-beige/90
6. *Rhabderemia prolifera* Annandale, 1915 (Orig. Descrip.)	sm: 90–209 × 6–8	sm: 147	12	Port Mouat (Andaman and Nicobar Islands)/thinly encrusting
Thomas (1979)	sm: 105–*162*–210 × 4–*7*–8	ac: 82–*112*–142 × 1–2	12	Inhaca Island (Mozambique)/thinly encrusting, irregular
Thomas (1985)	sm: 90–209 × 5–8	147 × 1	12	Gulf of Mannar and Palk Bay (South India and Sri Lanka)/encrusting, pale grey
van Soest & Hooper (1993) (No material examined)	sm: I) 90–99 × 4–*7*–8 sm: II) 176–209 × 4–*7*–8	ac: 82–*112*–147 × 1–2	(S) 12–13	-
7. *Rhabderemia spirophora* (Burton, 1931) (Orig. Descrip. as *Hallmannia spirophora*)	sm: 240 × 9	sm: 45 × 2	(S) 6	South Africa/massive
van Soest & Hooper (1993)	sm: 240–*263*–286 × 6–*8*–9	ac: 45–*53*–61 × 1–*1*–2	(S) 6–*8*–10	South Africa/massive
TS 4272	sm: 278–*368*–407 × 18–*27*–34	ac: 48–*53*–58 × 2–*3*–4	(S) 5–*7*–8	Amathole region (Eastern Cape, South Africa)/massive, yellow-beige base with dark red apex/52–55

Species	Megascleres	Microscleres		Location/Form/Depth (m)
	Rhabdostyles ac: acanthose sm: smooth	**Microstyles** ac: acanthose sm: smooth	**Spirosigmata (S)/ Thraustosigmata (T)**	
TS 4304	sm: 341–*387*–412 × 16–*21*–27	ac: 53–*60*–65 × 2–*3*–3	(S) 5–*8*–10	Amathole region (Eastern Cape, South Africa)/massive, yellow-beige base with orange-red apex/38–43

Distribution and ecology. Known from several locations within the Indian Ocean, including South India and Sri Lanka (type locality), the Gulf of Aden and the Red Sea. Also found in the Gulf of Thailand (Pacific Ocean). Occurs on or amongst various substrates, including a shipwreck (Amathole region), rock, shell hash, coarse sand with shell fragments, and mud. Depth range: 15–366 m.

Remarks. Assignment of the above specimen to *Rhabderemia* is based on its plumoreticulate skeletal structure comprising smooth rhabdostyles, and presence of finely spined microstyle and spirosigma microscleres (van Soest & Hooper 1993; Hooper 2002c; Hajdu & Desqueyroux-Faúndez 2008). The use of subgenera *Rhabderemia* Topsent, 1890 and *Stylospira* Laubenfels, 1934 as diagnosed by Hajdu & Desqueyroux-Faúndez (2008) is not currently recognised by van Soest *et al.* (2020a), and is thus not followed here.

The specimen conforms closely to *Rhabderemia indica*, which was described from South India and Sri Lanka by Dendy in 1905 (rhabdostyles: 240 × 6 µm; microstyles: 44 × 2 µm; spirosigmata: 12 µm), and differs only in having much thicker megascleres. This species was subsequently reported from the Gulf of Aden, Red Sea (Burton 1959) and the Gulf of Thailand (van Soest & Hooper 1993), with this the first record from South Africa.

Six congeners are found in the Indian Ocean (van Soest *et al.* 2020a). *Rhabderemia bistylifera* Lévi, 1961, *Rhabderemia burtoni* van Soest & Hooper, 1993 and *Rhabderemia prolifera* Annandale, 1915, described from the Seychelles, Salomon Islands, and Port Mouat respectively, have very long microstyle microscleres, more than double the size of those reported for *R. indica*. *Rhabderemia acanthostyla*, which was described from South India and Sri Lanka by Thomas (1968), has spined rhabdostyles, while *Rhabderemia batatas* Ilan, Gugel & van Soest, 2004, from the Red Sea, has smaller microstyle (17–*24*–35 µm) and spirosigma (5–*7*–9 µm) microscleres. Finally, *Rhabderemia spirophora* (Burton, 1931) from South Africa, which is likely the closest relative of *R. indica* (van Soest & Hooper 1993;

Hajdu & Desqueyroux-Faúndez 2008), is differentiated by its large proportion of straight 'rhabdostyles' (i.e. more style-like megascleres) and smaller spirosigmata (~6 µm).

Somewhat outdated but still useful taxonomic keys for this genus can be found in both van Soest & Hooper (1993) and Hajdu & Desqueyroux-Faúndez (2008).

Key diagnostic characters:

- erect, columnar form;
- velvety surface;
- subcircular oscules (<1 mm) in random, roughly stellate groups (1–2 mm);
- resilient;
- light orange-beige in life;
- megascleres exclusively one size class of smooth rhabdostyles;
- microstyle (35–75 µm) and spirosigma (8–15 µm) microscleres.

***Rhabderemia spirophora* (Burton, 1931)**

(Fig. 11A–F, Table 9)

Synonymy.

Hallmannia spirophora Burton, 1931: 352.

Nisibaris spirophora; de Laubenfels 1936: 144, 152.

Rhabderemia spirophora; Hooper 1990: 78; van Soest & Hooper 1993: 332; Hooper 2002c: 513.

Rhabderemia (Rhabderemia) spirophora; Hajdu & Desqueyroux-Faúndez 2008: 384, 385.

Material examined. **<u>TS 4272</u> (AI2-Spg40)**: ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–1, Station 3813 (32.6816º S, 28.4585º E–32.6869º S, 28.4617º E, Eastern Cape, South Africa), 55–52 m depth, amongst rock, coquina/shell hash and pebbles, SST 21 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 10 min, 26 August 2016. TS 4304 (AI2-Spg72): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–3, Station 3815 (32.6511º S, 28.4609º E–32.6581º S, 28.4653º E, Eastern Cape, South Africa), 38–43 m depth, amongst rock, coquina/shell hash, pebbles and coarse sand with shell fragments, SST 20 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 10 min, 26 August 2016.

Description. Massive form (Fig. 11A). Length 5 cm, width 3 cm and thickness 3 cm. Surface microhispid and rough, with no discernible oscules. Texture spongy, compressible, soft and friable. Colour *in situ* yellow-beige with dark red apex, in preservative beige.

Skeleton. Choanosomal skeleton comprises multispicular plumoreticulate megasclere tracts (~90–220 µm across), arranged around extensive subdermal spaces (Fig. 11B), which pierce somewhat indistinguishable dermal membrane lacking specialisation (Fig. 11C), extending to ~50–100 µm beyond surface. Microscleres abundant, scattered throughout.

Spiculation. Megascleres. Styles to rhabdostyles, smooth, acerate: 278–*368*–407 × 18–*27*–34 µm, n = 15 (Fig. 11D). **Microscleres.** Microstyles finely spined, straight to slightly curved, hastate: 48–*53*–58 × 2–*3*–4 µm, n = 15 (Fig. 11E). Spirosigmata, finely spined: 5–*7*–8 µm, n = 15 (Fig. 11F).

Distribution and ecology. Known only from South Africa, occurring amongst rock, coquina/shell hash, pebbles and coarse sand with shell fragments in the Amathole region (Eastern Cape). The material examined had red algae (TS 4272, TS 4304), hydroid (TS 4272), worm casing (TS 4272) and barnacle (TS 4304) epifauna. Depth range: 38–55 m (previously unknown).

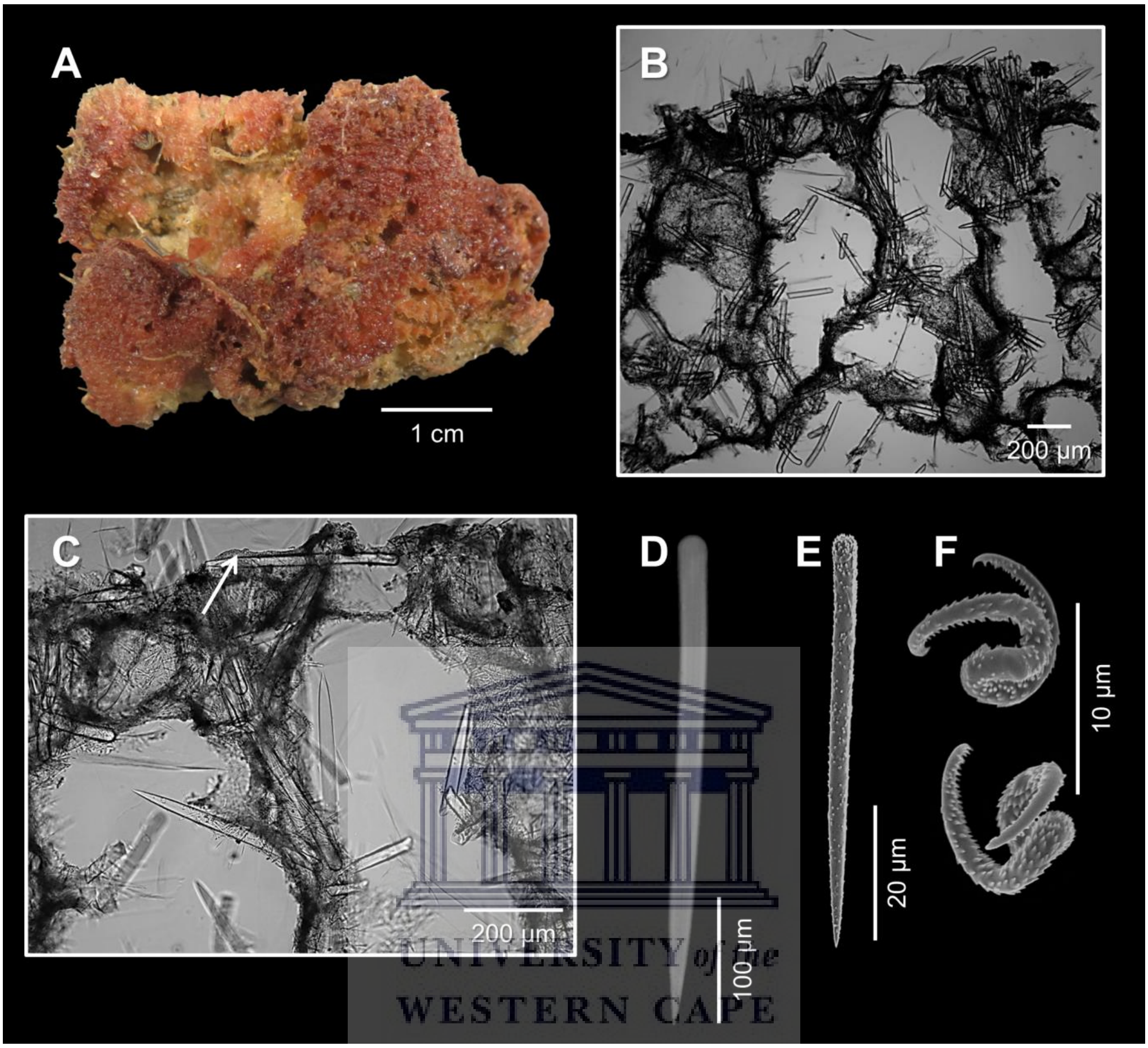

Figure 11: *Rhabderemia spirophora* (Burton, 1931). A, specimen TS 4272. B, choanosomal skeleton. C, multispicular megasclere tract piercing somewhat indistinguishable dermal membrane (arrow). D, style. E, finely spined microstyle. F, finely spined spirosigmata.

Remarks. The above material conforms closely to *Rhabderemia spirophora*, which was described by Burton (1931) from a dry beachcast fragment (‘rhabdostyles’: 240 × 9 µm; microstyles: 45 × 2 µm; spirosigmata: 6 µm), and re-described by van Soest & Hooper in 1993. The specimens differ only in having much longer and thicker megascleres, and slightly thicker microstyle microscleres, while also providing the first account of living colour and ecology.

This species differs from other Indian Ocean congeners in an almost identical way to that noted for *Rhabderemia indica* Dendy, 1905, as the two are very similar. However, *R. spirophora* is easily differentiated from the latter according to form (massive vs. erect), the large proportion of style-like megascleres (as opposed to true rhabdostyles), and smaller spirosigmata (van Soest & Hooper 1993).

Key diagnostic characters:

- massive form;
- microhispid and rough surface;
- no discernible oscules;
- soft and friable;
- yellow-beige in life, with dark red apex;
- one size class of smooth 'style' megascleres (no true rhabdostyles);
- microstyle (45–65 µm) and spirosigma (5–10 µm) microscleres.

Order Bubarida Morrow & Cárdenas, 2015

Family Bubaridae Topsent, 1894

Genus *Bubaris* Gray, 1867

Type species: *Hymeraphia vermiculata* Bowerbank, 1866 (by original designation).

Diagnosis. Bubaridae with basal skeleton formed by smooth sinuous or vermicular strongyles or strongyloxeas (from Alvarez & van Soest 2002).

***Bubaris amatholensis* sp. nov. ▲**

(Fig. 12A–E, Table 10)

Material examined. **TS 4143** **(BD27-Spg1)**: ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–105, Station 3811 (33.1959º S, 27.8636º E–33.1962º S, 27.8622º E, Eastern Cape, South Africa), 74 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 9 min, 02 March 2016. TS 3925 (BD16-INV01(Spg10)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–38, Station 3744 (32.9883º S, 28.3285º E–32.9932º S, 28.3229º E, Eastern Cape, South Africa), 151 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 7 min, 24 February 2016.

Description. Thinly encrusting on rock (Fig. 12A). Length 6 cm, width 6 cm and thickness ~1 mm. Surface hispid due to projecting styles <1 mm from substrate (Fig. 12B), fuzzy to the touch. Texture firm, barely compressible and tough. Colour *in situ* dark orange, in preservative beige.

Skeleton. Choanosomal skeleton comprised of individual styles projecting perpendicularly to substrate with heads embedded in a basal layer (~870–1220 µm) of vermiform strongyles to strongyloxeas (Fig. 12C). Specialised ectosomal skeleton absent.

Spiculation. Megascleres. Styles smooth, slightly curved, hastate, in a large size range with overlap: 198–*462*–1145 × 6–*17*–37 µm, n = 15 (Fig. 12D). Strongyles to strongyloxeas, smooth and vermiform, rounded to somewhat blunt pointed: 206–*344*–517 × 14–*19*–31 µm, n = 15 (Fig. 12E). **Microscleres.** None.

Distribution and ecology. Currently only known from the Amathole region (Eastern Cape, South Africa). Depth range: 74–151 m.

Provisional etymology. The species name is derived from the collection locality, which will become the type locality in the future formal description.

Remarks. The present material is assigned to *Bubaris* as diagnosed by its encrusting form and skeletal architecture which comprises a basal layer of smooth vermiform strongyles to strongyloxeas, with embedded styles projecting perpendicularly to the substrate, producing a hispid surface (Alvarez & van Soest 2002).

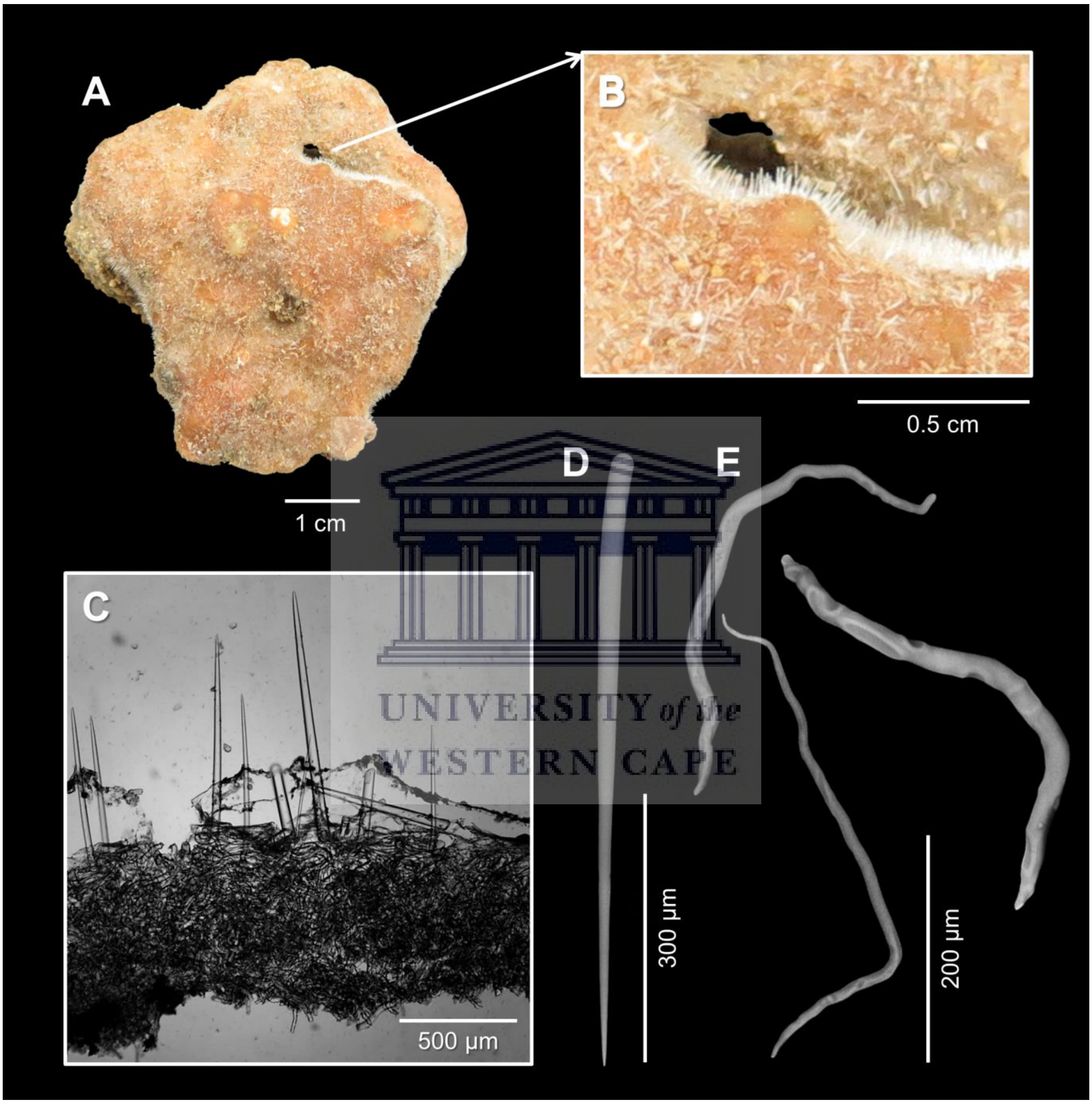

Figure 12: *Bubaris amatholensis* **sp. nov. ▲**. A, B, specimen TS 4143. C, choanosomal skeleton. D, style. E, vermiform strongyles to strongyloxeas.

Table 10: Comparative spicule dimensions and known location, form and depth for the accepted species of *Bubaris* Gray, 1867 occurring in the Indian and South Atlantic oceans according to van Soest *et al.* (2020a). Spicule dimensions expressed in µm, with specimens from this study (TS) given as minimum–*mean*–maximum length × width, n = 15.

Species	Oxeas	Styles	Strongyles (S)/ Strongyloxeas (SO)/ Oxeas (O)[2]	Raphides	Location/Form/Depth (m)
1. *Bubaris conulosa* Vacelet & Vasseur, 1971 (Orig. Descrip. as *Bubaris conulosus*)	-	380–740 × 12–13	(S) 650–920 × 8–10	-	Madagascar/erect, extended blade, conulose, red/50
Pulitzer-Finali (1993) (R.N. MBA.193 & R.N. MBA.468)	-	460–650 × 9–14	(S) 500–950 × 5–9	-	Mombasa/bright orange/7–30
Pulitzer-Finali (1993) (R.N. KEN.82)	-	490–950 × 14–21	(S) 1000 × 14	-	North Kenya Banks
2. *Bubaris durissima* Burton, 1928 (Orig. Descrip. as *Bubaris durissimma*)	240–372 × 11–16	180–480 × 12–16	(S) 600 × 13	-	Mergui Archipelago (Andaman Sea)/erect, branching/113
3. *Bubaris murrayi* Topsent, 1913 (Orig. Descrip.)	-	500–1000 × 25	(O) 700 × 14–25	-	Gough Island/massive, lobed/183
4. *Bubaris salomonensis* Dendy, 1922 (Orig. Descrip.)	-	1600 × 38	(S) 300 × 26	60	Salomon Islands (Chagos Archipelago)/thinly encrusting/137

[2]Oxeas are flexuous or vermiform as opposed to 'true' oxeas of column two.

Species	Oxeas	Styles	Strongyles (S)/ Strongyloxeas (SO)/ Oxeas (O)[2]	Raphides	Location/Form/Depth (m)
Lévi & Lévi (1989)	-	I) 2200–2800 × 22–35 II) 260–850 × 15–40	(S) 100–180 × 10–20	-	Eastern Philippines/thinly encrusting/85–90
5. *Bubaris amatholensis* sp. nov. ▲ (TS 4143)	-	198–*462*–1145 × 6–*17*–37	(S+SO) 206–*344*–517 × 14–*19*–31	-	Amathole region (Eastern Cape, South Africa)/thinly encrusting, dark orange/74
TS 3925	-	230–*630*–1078 × 11–*28*–43	(S+SO) 203–*332*–418 × 9–*27*–41	-	Amathole region (Eastern Cape, South Africa)/thinly encrusting, off-white/151

There are currently ten accepted species worldwide (van Soest *et al.* 2020a), none of which have been described or recorded from South Africa. *Bubaris conulosa* Vacelet & Vasseur, 1971, which was described from Madagascar, and later recorded from East Africa (Pulitzer-Finali 1993), is a bright orange to red species that has an erect, conulose form. It also has flexuous strongyles that are almost double the length of the present material (650–920 × 8–10 µm), and somewhat smaller styles (380–740 × 12–13 µm). Also described from the Indian Ocean, *Bubaris salomonensis* Dendy, 1922 is a thinly encrusting species found in the Salomon Islands (Chagos Archipelago), and later recorded from the Eastern Philippines by Lévi & Lévi (1989). Although having strongyles of a similar size to the present material (300 × 26 µm) these are flexuous as opposed to vermiform, the styles are larger (1600 × 38 µm) and Dendy (1922) notes the presence of raphides. *Bubaris durissima* Burton, 1928 from the Mergui Archipelago (Andaman Sea) has an erect, branching form and oxeas (240–372 × 11–16 µm). According to Burton (1928), strongyles (600 × 13 µm) are also present in the material, but these were not recorded by Morrow *et al.* (2019). In the South Atlantic Gough Island, *Bubaris murrayi* Topsent, 1913 is a massive, lobed species with larger flexuous oxeas (700 × 14–25 µm). Finally, inaccurate records (van Soest *et al.* 2020a) of the North Atlantic *Bubaris vermiculata* (Bowerbank, 1866) from the Kerguelen Islands by Boury-Esnault & van Beveren (1982) depict encrusting to arborescent sponges with both larger vermiform oxeas (583–*642*–1069 × 19–*28*–38 µm) and styles (I) 1361–*1803*–2503 × 14–*22*–29 µm; II) 535–*796*–972 × 19–*25*–32 µm). Thus, the present material likely constitutes a new species, and the first record of *Bubaris* from South Africa.

Key diagnostic characters:

- thinly encrusting form;
- hispid surface;
- dark orange in life;

- specialised ectosomal skeleton absent;
- megascleres exclusively styles and vermiform strongyles to strongyloxeas (<600 µm);
- no microscleres.

Order Merliida Vacelet, 1979

Family Hamacanthidae Gray, 1872

Genus *Hamacantha* Gray, 1867

Type species: *Hymedesmia johnsoni* Bowerbank, 1864 (by original designation).

Diagnosis. Hamacanthidae with diancistras (from Hajdu 2002).

Subgenus *Hamacantha (Vomerula)* Schmidt, 1880

Type species: *Vomerula tenda* Schmidt, 1880 (by monotypy).

Diagnosis. *Hamacantha* with monactinal megascleres (from Hajdu 2002).

***Hamacantha (Vomerula) esperioides* (Ridley & Dendy, 1886)**

(Fig. 13A–G, Table 11)

Synonymy.

Vomerula esperioides Ridley & Dendy, 1886: 337; Ridley & Dendy 1887: 60.

Hamacantha esperioides; Kirkpatrick 1903b: 253; Lévi 1963: 16; Uriz 1987: 60; Uriz 1988: 60; Hajdu 2002: 667.

Hamacantha (Vomerula) esperioides; Maduray 2013: iii; Samaai *et al.* 2018: 43.

Material examined. **<u>TS 4022</u> (BD15-Spg1(25))**: ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–36, Station 3742 (33.0137º S, 28.3142º E–33.0172º S, 28.3063º E, Eastern Cape, South Africa), 204 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 12 min, 24 February 2016.

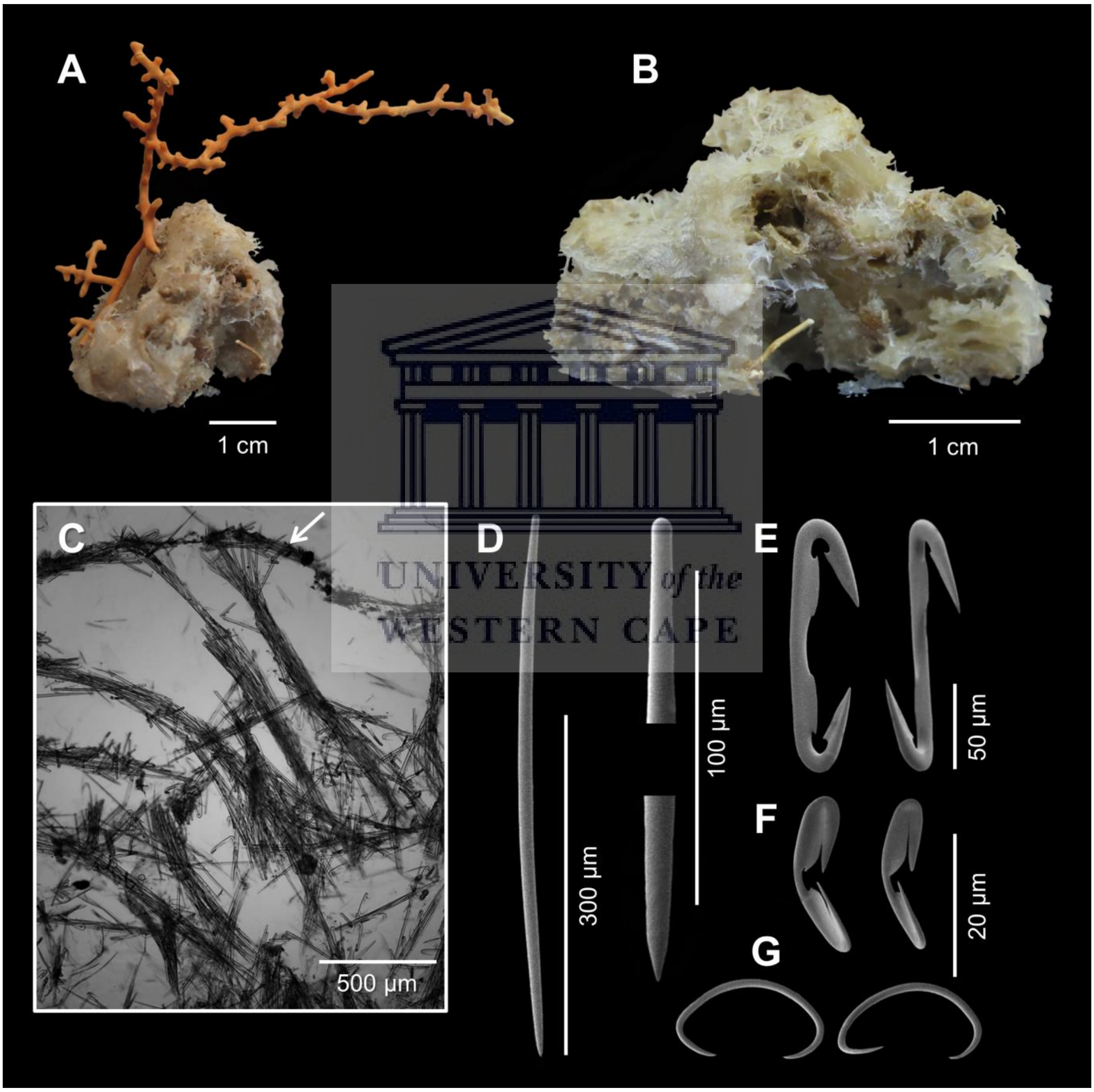

Figure 13: *Hamacantha (Vomerula) esperioides* (Ridley & Dendy, 1886). A, B, specimen TS 4022. C, cavernous choanosome with thin dermal membrane (arrow). D, style with close-up of apices. E, diancistras I. F, diancistras II. G, C-shaped sigmata.

Table 11: Comparative spicule dimensions and known location, form and depth for the accepted species of *Hamacantha (Vomerula)* Schmidt, 1880 occurring in South Africa and the south-west Atlantic according to van Soest *et al.* (2020a). Spicule dimensions expressed in µm, with specimen from this study (TS) given as minimum–*mean*–maximum length × width, n = 15.

	Megascleres	**Microscleres**		
Species	**Styles (Sty)/ Strongyles (Str)**	**Diancistras**	**Sigmata**	**Location/Form/Depth (m)**
1. *Hamacantha (Vomerula) esperioides* (Ridley & Dendy, 1886) (Orig. Descrip. as *Vomerula esperioides*)	(Sty) 700 × 19	177 × 19	38	South Africa & Uruguay-Buenos Aires Shelf/erect, leaf-like expansions, pale yellow/274–1097
Ridley & Dendy (1887) (Orig. Descrip. as *Vomerula esperioides*)	(Sty) 700 × 19	I) 177 × 19 II) 38	38	South Africa & Uruguay-Buenos Aires Shelf/erect, leaf-like expansions/274–1097
Lévi (1963) (As *Hamacantha esperioides*)	(Sty) 600–775 × 12	I) 150–165 × 12 II) 27–28	25–28	South Africa/massive fragment/201
Uriz (1987) (As *Hamacantha esperioides*)	(Sty) 580–630 × 12–17	I) 160–173 × 10–12 II) 28–32	22–33 × 2	South African-Namibian border/thickly encrusting to massive, lobate or tubular, with frequent anastomoses/260–269
Uriz (1988) (As *Hamacantha esperioides*)	(Sty) 520–610 × 12–18	I) 115–150 × 11–17 II) 20–30 × 2–3	20–28 × 2	South African-Namibian border/massive, lobed/209
TS 4022	(Sty) 395–*456*–518 × 8–*10*–12	I) 131–*139*–147 × 8–*10*–11 II) 18–*20*–23 × 4–*5*–6	16–*18*–23 × 1–*1*–1	Amathole region (Eastern Cape, South Africa)/massive fragment, growing around sea fan, beige/204

Species	Megascleres Styles (Sty)/ Strongyles (Str)	Microscleres Diancistras	Sigmata	Location/Form/Depth (m)
2. *Hamacantha (Vomerula) jeanvaceleti* Castello-Branco & Hajdu, 2018 (Orig. Descrip.)	(Sty) 398–*454*–524 × 10–*11*–12	I) 194–*236*–281 II) 29–*48*–62	-	Rio Grande Rise (south-west Atlantic)/thinly encrusting/1165–2200
3. *Hamacantha (Vomerula) klausruetzleri* Castello-Branco & Hajdu, 2018 (Orig. Descrip.)	(Sty) 398–*452*–514 × 7–*10*–12 (Str) 291–*326*–349 × 10–*12*–14	I) 175–*224*–262 II) 36–*44*–50	I) 74–*92*–115 II) 29–*39*–50	Rio Grande Rise (south-west Atlantic)/thin crust/1165–1245

Description. Massive fragment, growing around sea fan (Fig. 13A & B). Length 5 cm, width 4 cm and thickness 2 cm. Thin dermal membrane present (<1 mm), easily detachable, transparent but conspicuous, with skeletal reticulation readily visible to the naked eye. Surface rough, with random, irregular oscules (up to 3 mm). Texture fibrous, compressible, soft and friable. Colour *in situ* beige, in preservative off-white.

Skeleton. Choanosome cavernous, comprising a reticulation of thick multispicular megasclere tracts (~40–200 µm across), arranged around large and irregular subdermal spaces (Fig. 13C), possibly echinated by diancistras (size class I). Ectosomal skeleton comprises a dermal membrane (~50–170 µm thick), consisting of a dense tangential megasclere layer. Microscleres abundant, scattered throughout.

Spiculation. Megascleres. Styles smooth, straight to slightly curved, with reduced heads, somewhat blunt acerate, occasionally modified to strongyles: 395–*456*–518 × 8–*10*–12 µm, n = 15 (Fig. 13D). **Microscleres.** Diancistras, in two size classes: I) with straight shaft, 131–*139*–147 × 8–*10*–11 µm, n = 15 (Fig. 13E); II) with curved shaft, 18–*20*–23 × 4–*5*–6 µm, n = 15 (Fig. 13F). Sigmata smooth, C- to S-shaped: 16–*18*–23 × 1–*1*–1 µm, n = 15 (Fig. 13G).

Distribution and ecology. Known from South Africa (likely extending into Namibia), and the Uruguay-Buenos Aires Shelf (off Río de la Plata mouth). Occurs amongst loose rock, shell hash, coral rubble, sand and mud. The only specimen collected (TS 4022) was growing around a sea fan. Depth range: 86–1097 m.

Remarks. The single specimen examined above is assigned to *Hamacantha* and *Hamacantha (Vomerula)*, due to the presence of diancistras and monactinal megascleres (styles) respectively (Hajdu 2002).

Only one species is found in South Africa, *Hamacantha (Vomerula) esperioides* (Ridley & Dendy, 1886), which was described from abundant material collected off the

Agulhas Bank (with large specimens reaching up to 25 cm), and a single small fragment from the Uruguay-Buenos Aires Shelf. Further records have all been from South Africa (Kirkpatrick 1903b; Lévi 1963; Maduray 2013; Samaai *et al.* 2018), and the South African-Namibian border (Uriz 1987; Uriz 1988; Samaai *et al.* 2018). The above specimen conforms to the type material (styles: 700 × 19 µm; diancistras: I) 177 × 19 µm, II) 38 µm; sigmata: 38 µm), but has much smaller spicules, which may be due to its small, fragmentary nature.

Nearby congeners include *H. (V.) jeanvaceleti* and *H. (V.) klausruetzleri*, described by Castello-Branco & Hajdu (2018) from the Rio Grande Rise (south-west Atlantic). Both are deep-water, thinly encrusting species with larger diancistras, of which the second smaller size class are cyrtancistra-like in shape. The former species also lacks sigmata, while the latter species has two size classes of sigmata and additional strongyle megascleres.

Key diagnostic characters:

- massive form;
- conspicuous dermal membrane, with skeletal reticulation visible to naked eye;
- cavernous choanosome;
- diancistra I microscleres <200 µm, neither size class cyrtancistra-like in shape;
- one size class of sigma microscleres.

Order Poecilosclerida Topsent, 1928

Family Acarnidae Dendy, 1922

Genus *Iophon* Gray, 1867

Type species: *Halichondria scandens* Bowerbank, 1866 (by original designation).

Diagnosis. Non-fistular Acarnidae with a regular, uni- or pauci-spicular isodictyal choanosomal reticulation of smooth or spined styles, with or without echinating acanthostyles (from Hooper 2002a).

***Iophon regium* sp. nov. ▲**

(Fig. 14A–I, Table 12)

Material examined. **TS 3473 (BD4-Spg10)**, TS 3503 (BD4-Spg31): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–16, Station 3722 (32.8300º S, 28.4593º E–32.8327º S, 28.4573º E, Eastern Cape, South Africa), 87 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 9 min, 22 February 2016.

Description. Thickly encrusting on sea fan (Fig. 14A & B), with erect somewhat columnar outgrowths (Fig. 14C). Appears arborescent overall. Length 30 cm, width 35 cm and thickness 4 mm. Surface microhispid and velvety, with no discernible oscules. Texture spongy, very compressible, soft and friable. Colour *in situ* bright yellow, after freezing golden brown, in preservative light brown.

Skeleton. Choanosomal skeleton comprises an irregular isodictyal reticulation of acanthostyles, forming largely square meshes (Fig. 14D). Multispicular ascending tracts (~30–140 µm across), much thicker than uni- to pauci-spicular transverse connecting tracts (~10–50 µm across), producing a plumoreticulate appearance. The former pierce the surface, extending up to ~280 µm. Echinating acanthostyles present. Ectosome composed of irregular tangential to paratangential acanthotylote bundles (~10–50 µm across), sometimes forming erect brushes. Microscleres abundant, concentrated at surface, but found throughout. Mesohyl contains numerous brown granular cells (up to 17 µm).

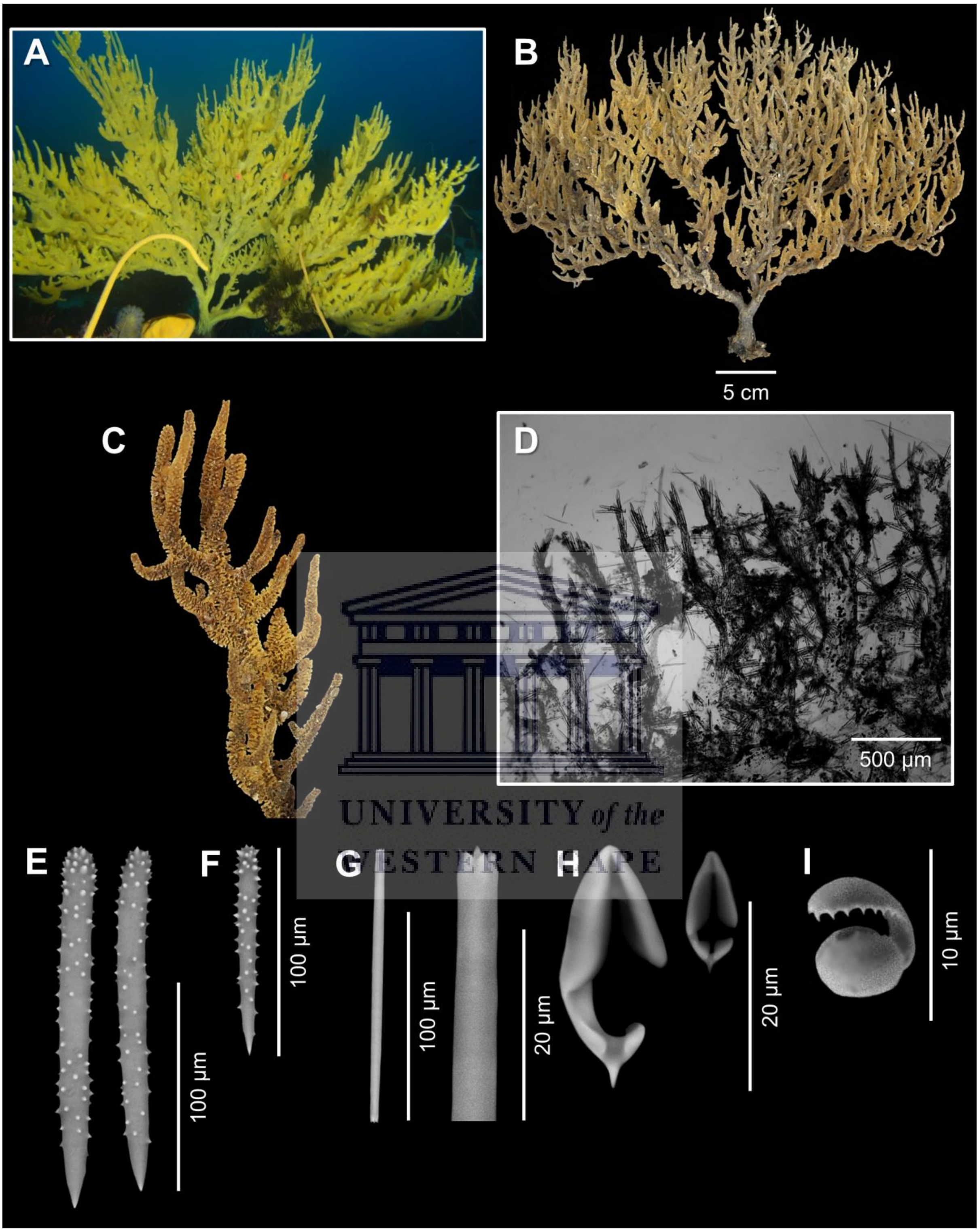

Figure 14: *Iophon regium* **sp. nov.** ▲. A, species *in situ* (R49). B, specimen TS 3473. C, close-up of erect somewhat columnar outgrowths. D, choanosomal skeleton. E, acanthostyles I. F, acanthostyle II. G, acanthotylote with close-up of much reduced spined apex and smooth shaft. H, palmate anisochelae with spurs, I and II. I, bipocilla.

Table 12: Comparative spicule dimensions and known location, form and depth for the accepted species of *Iophon* Gray, 1867 occurring in South Africa, as well as the Prince Edward and Kerguelen Islands, according to van Soest *et al.* (2020a). Spicule dimensions expressed in µm, with specimens from this study (TS) given as minimum–*mean*–maximum length × width, n = 15.

	Megascleres		**Microscleres**		
Species	**Styles** ac: acanthose sm: smooth	**Acanthotylotes**	**Anisochelae**	**Bipocilli**	**Location/Form/Depth (m)**
1. *Iophon abnormalis* Ridley & Dendy, 1886 (Orig. Descrip.)	ac: 350 × 13	280 × 8	I) 38 II) ~19	-	Marion Island/cylindrical, branched, black/91–137
2. *Iophon cheliferum* Ridley & Dendy, 1886 (Orig. Descrip. as *Iophon chelifer*)	ac: 400 × 20	300 × 10	19–30	19	South Africa, Prince Edward Island and between Prince Edward and Kerguelen Islands/massive, honeycombed, light brown to black/274–1006
Ridley & Dendy (1887) (As *Iophon chelifer*)	ac: 360–420 × 16–20	250–320 × 10	19–30	19	South Africa, Prince Edward Island and between Prince Edward and Kerguelen Islands/massive, honeycombed, light brown to black/274–1006
Boury-Esnault & van Beveren (1982) (As *Iophon chelifer*)	ac: 286–*313*–331 × 13–*17*–20	234–*266*–279 × 7–*7*–10	I) 25–*32*–34 II) 15–*19*–22	I) 19–*21*–22 II) 7–*6*–10	Kerguelen Islands/massive to blade-like, orange/207
Uriz (1987) (As *Iophon chelifer*)	ac: 260–320 × 15–20	205–270 × 6–8	I) 24–33 II) 11–15	I) 14–18 II) 10–12	South African-Namibian border/crust, brown/260–269

Species	Megascleres		Microscleres		Location/Form/Depth (m)
	Styles ac: acanthose sm: smooth	**Acanthotylotes**	**Anisochelae**	**Bipocilli**	
Uriz (1988) (As *Iophon chelifer*)	ac: 260–320 × 15–20	205–270 × 6–8	I) 24–33 II) 11–15	I) 14–18 II) 10–12	South African-Namibian border/encrusting, tan/260–269
3. *Iophon laminale* Ridley & Dendy, 1886 (Orig. Descrip. as *Iophon laminalis*)	sm: 630 × 22	340 × 1	25	13	Prince Edward Island/irregular, flat to slightly curved cake-like expansions, dark reddish brown/567
4. *Iophon proximum* (Ridley, 1881) (Orig. Descrip. as *Alebion proximum*)	ac: 158 × 10	158 × 8	25	11	Straits of Magellan/encrusting on a *Pecten*, dark brown/13–18
Boury-Esnault & van Beveren (1982)	ac: 125–*140*–154 × 6–*10*–12	144–*159*–173 × 6–*7*–10	18–*22*–25	7–9	Kerguelen Islands/spherical, brown/67
5. *Iophon proximum* var. *reticulare* Hentschel, 1914 (Orig. Descrip. as *Jophon proximus* var. *reticularis*)	ac: 104–152	120–160	18–24	-	Kerguelen Islands/massive (encrusting?), grey-brown to dark brown
6. *Iophon radiatum* Topsent, 1901 (Orig. Descrip. as *Iophon radiatus*) (No. 306)	ac: 550 × 16	300–350 × 5–6	I) 60 II) 17	8–12	West Antarctica/encrusting (?), massive, blackish brown/450
Topsent (1901) (No. 421)	ac/sm: 570–580 × 20	390 × 8–9	I) 53–70 II) 17	8–16	West Antarctica/irregular, plate-like, black/450
Boury-Esnault & van Beveren (1982) (As *Iophon radiatus*)	ac: 383–*457*–576 × 10–*14*–17	266–*323*–403 × 6–*9*–13	I) 26–*32*–39 II) 13–*18*–23	7–*8*–9	Kerguelen Islands/massive to spherical, brown/89–245

Species	Megascleres		Microscleres		Location/Form/Depth (m)
	Styles ac: acanthose sm: smooth	**Acanthotylotes**	**Anisochelae**	**Bipocilli**	
7. *Iophon unicorne* Topsent, 1907 (Orig. Descrip. as *Iophon unicornis*)	sm[3]: 435–470 × 11–15	240 × 8–10	18–20	-	Anvers Island (Antarctica)/erect, massive, irregular, brown/25
Boury-Esnault & van Beveren (1982) (As *Iophon unicornis*)	sm[3]: 326–*366*–406 × 12–*13*–13	234–*252*–266 × 6–*10*–12	16–*17*–18	8–*11*–13	Kerguelen Islands/caliculate, pink ochre/130
8. *Iophon regium* sp. nov. ▲ (TS 3473)	ac: I) 146–*160*–174 × 12–*15*–17 ac: II) 95–*108*–129 × 8–*10*–11	113–*127*–139 × 4–*4*–5	I) 23–*25*–27 × 6–*9*–10 II) 10–*11*–14 × 4–*4*–5	6–*7*–8	Amathole region (Eastern Cape, South Africa)/thickly encrusting on sea fan, with erect somewhat columnar outgrowths, bright yellow/87
TS 3503	ac: I) 153–*177*–189 × 10–*12*–15 ac: II) 99–*111*–123 × 6–*8*–10	118–*138*–150 × 3–*4*–5	I) 21–*24*–27 × 7–*8*–9 II) 11–*13*–14 × 4–*5*–5	6–*7*–9	Amathole region (Eastern Cape, South Africa)/thickly encrusting on sea fan, with erect somewhat columnar outgrowths, bright yellow/87
9. *Iophon ferrugineum* sp. nov. ▲ (TS 4041)	ac: 244–*264*–284 × 12–*17*–22	206–*227*–245 × 5–*6*–7	I) 16–*20*–22 × 5–*5*–6 II) 9–*10*–12 × 4–*4*–5	5–*6*–8	Amathole region (Eastern Cape, South Africa)/flat fragment, dark brown/204

[3] Styles are mucronate.

Species	Megascleres		Microscleres		Location/Form/Depth (m)
	Styles ac: acanthose sm: smooth	Acanthotylotes	Anisochelae	Bipocilli	
TS 4079	ac: 230–*254*–276 × 13–*15*–18	179–*217*–241 × 5–*7*–9	I) 16–*17*–18 × 5–*5*–7 II) 9–*12*–14 × 3–*4*–6	6–*7*–10	Amathole region (Eastern Cape, South Africa)/fragment, dark brown/87

Spiculation. Megascleres. Acanthostyles with reduced heads, spined throughout with largely smooth acerate tips, straight to slightly curved, in two size classes: I) 146–*160*–174 × 12–*15*–17 µm, n = 15 (Fig. 14E); II) 95–*108*–129 × 8–*10*–11 µm, n = 15 (Fig. 14F). Acanthotylotes strongylote, with smooth shaft and much reduced spined apices, straight: 113–*127*–139 × 4–*4*–5 µm, n = 15 (Fig. 14G). **Microscleres.** Palmate anisochelae with spurs, in two size classes (Fig. 14H): I) 23–*25*–27 × 6–*9*–10 µm, n = 15; II) 10–*11*–14 × 4–*4*–5 µm, n = 15. Bipocilli, inequiended: 6–*7*–8 µm, n = 15 (Fig. 14I).

Distribution and ecology. Currently only known from the Amathole region (Eastern Cape, South Africa). Both specimens are thickly encrusting on sea fans. Depth: 87 m.

Provisional etymology. *Regius* (L.) = kingly/royal, referring to the regal, golden yellow, form.

Remarks. The above material is assigned to *Iophon* as diagnosed by its non-fistulose, encrusting form, skeletal structure and microscleres comprising inequiended bipocilli and palmate anisochelae with spurs (Hooper 2002a).

Members of this genus are often found in cold and temperate waters (Hooper 2002a), with only one species described and/or recorded from mainland South Africa: *Iophon cheliferum* Ridley & Dendy, 1886. This species is easily differentiated by its larger megascleres (acanthostyles: 400 × 20 µm; acanthotylotes: 300 × 10 µm), and distinct clover-shaped bipocilli (19 µm).

The material examined is most similar to *Iophon proximum* (Ridley, 1881) (acanthostyles: 158 × 10 µm; acanthotylotes: 158 × 8 µm; anisochelae: 25 µm; bipocilli: 11 µm), which was described from the Straits of Magellan. This species was thought to have a somewhat cosmopolitan distribution, comprising specimens of great form and spicule variability (Burton 1932; Desqueyroux-Faúndez & van Soest 1996). Consequently, it was recorded from South Africa by Lévi (1963), Uriz (1987), Uriz (1988) and Samaai & Gibbons

(2005). These records are inconsistent and currently regarded as inaccurate (van Soest *et al.* 2020a), thus requiring further investigation. In addition, *Iophon regium* **sp. nov.** differs from the description provided by Ridley (1881) in having two size classes of acanthostyles and palmate anisochelae, as well as slightly smaller acanthotylotes without rounded apices. A doubtful variety, *Iophon proximum* var. *reticulare* Hentschel, 1914 from the Kerguelen Islands, has spicule sizes similar to *I. proximum* (and thus the above material), but lacks bipocilli.

All other congeners found around mainland South Africa (i.e. described and/or recorded from the Prince Edward and Kerguelen Islands) differ from *Iophon regium* **sp. nov.** in having much larger megascleres (>200 µm). Thus, the present material likely constitutes a new species, generally characterised in South Africa by its small megascleres and conspicuous form. Nevertheless, this genus requires extensive revision to determine specific limits in terms of spicule variability (Boury-Esnault & van Beveren 1982), while taxonomic work may also be hampered by its soft and friable nature, which often leads to fragmentation during collection.

Key diagnostic characters:

- thickly encrusting form, with erect somewhat columnar outgrowths;
- no discernible oscules;
- bright yellow in life;
- skeleton includes echinating acanthostyles;
- mesohyl contains numerous brown granular cells (up to 17 µm);
- megascleres small, <200 µm;
- megascleres include two size classes of acanthostyles, and acanthotylotes with smooth shafts;

- microscleres include two size classes of palmate anisochelae, and inequiended bipocilli.

***Iophon ferrugineum* sp. nov. ▲**

(Fig. 15A–H, Table 12)

Material examined. TS 4041 (BD15-Spg1(44)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–36, Station 3742 (33.0137º S, 28.3142º E–33.0172º S, 28.3063º E, Eastern Cape, South Africa), 204 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 12 min, 24 February 2016. TS 4079 (BD4-Spg1(11)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–16, Station 3722 (32.8300º S, 28.4593º E–32.8327º S, 28.4573º E, Eastern Cape, South Africa), 87 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 9 min, 22 February 2016.

Description. Flat fragment (Fig. 15A & B). Length 6 cm, width 4 cm and thickness 5 mm. Surface microhispid, velvety to rough, with regular subcircular oscules (~2 mm) throughout one side (Fig. 15A), and subcircular ostia (up to 1 mm) throughout the other (Fig. 15B). Texture dense but soft, somewhat compressible, very fragile. Colour *in situ,* and in preservative, dark brown.

Skeleton. Choanosomal skeleton comprises a regular isodictyal reticulation of acanthostyles, uni- to pauci-spicular (rarely more than three spicules per side), forming largely triangular or square meshes, occasionally round (Fig. 15C). Echinating acanthostyles absent. Ectosome composed of irregular tangential to paratangential acanthotylote bundles (~20–100 µm across) (Fig. 15D), sometimes forming erect brushes. Microscleres scarce, scattered throughout. Rare palmate anisochelae I rosettes observed in specimen TS 4079. Mesohyl contains numerous brown granular cells (up to 10 µm).

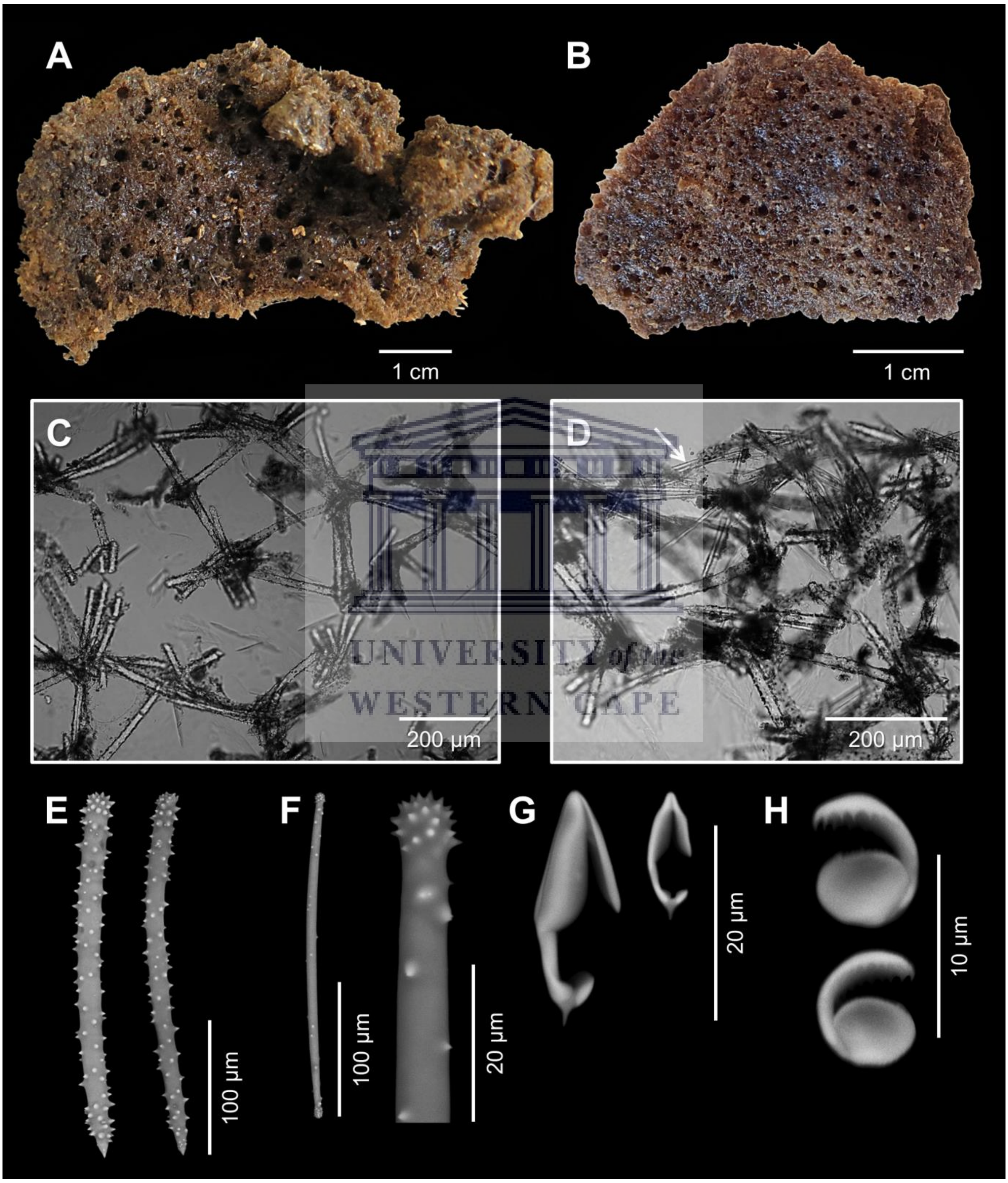

Figure 15: *Iophon ferrugineum* **sp. nov.** ▲. A, B, specimen TS 4041. C, choanosomal skeleton. D, ectosomal skeleton (arrow). E, acanthostyles. F, acanthotylote with close-up of spined apex and shaft. G, palmate anisochelae with spurs, I and II. H, bipocilli.

Spiculation. Megascleres. Acanthostyles spined throughout with short acerate tips, straight to slightly curved: 244–*264*–284 × 12–*17*–22 µm, n = 15 (Fig. 15E). Acanthotylotes with few random spines on shaft, and somewhat reduced rounded apices covered in spines, straight to slightly curved: 206–*227*–245 × 5–*6*–7 µm, n = 15 (Fig. 15F). **Microscleres.** Palmate anisochelae with spurs, in two size classes (Fig. 15G): I) 16–*20*–22 × 5–*5*–6 µm, n = 15; II) 9–*10*–12 × 4–*4*–5 µm, n = 15. Bipocilli, inequiended: 5–*6*–8 µm, n = 15 (Fig. 15H).

Distribution and ecology. Currently only known from the Amathole region (Eastern Cape, South Africa). Depth range: 87–204 m.

Provisional etymology. *Ferrugineus* (L.) = rusty, referring to the dark brown colouration and fragmented form.

Remarks. Although comprising similar microscleres to *Iophon regium* **sp. nov.**, the above material is easily differentiated by its form (flat fragment vs. encrusting), skeletal structure and slightly larger megascleres, of which the acanthostyles are only in one size class, and the acanthotylotes have rounded apices and spined shafts. *Iophon ferrugineum* **sp. nov.** also has larger megascleres and an additional size class of palmate anisochelae when compared to *Iophon proximum* (Ridley, 1881) and *Iophon proximum* var. *reticulare* Hentschel, 1914, the latter of which lacks bipocilli. All other congeners found in and around South Africa have larger styles (often >300 µm). Thus, the present material likely constitutes a new species.

Key diagnostic characters:

- flat fragmentary form;
- regular subcircular oscules (~2 mm) on one side, and ostia (up to 1 mm) on the other;
- dark brown in life;
- echinating acanthostyles absent;

- rare palmate anisochelae I rosettes;
- mesohyl contains numerous brown granular cells (up to 10 µm);
- megascleres >200 µm;
- megascleres include one size class of acanthostyles, and acanthotylotes with spined shafts;
- microscleres include two size classes of palmate anisochelae, and inequiended bipocilli.

Family Coelosphaeridae Dendy, 1922

Genus *Forcepia* Carter, 1874

Type species: *Forcepia colonensis* Carter, 1874 (by monotypy).

Diagnosis. Coelosphaeridae with forceps microscleres (from van Soest 2002a).

Subgenus *Forcepia (Forcepia)* Carter, 1874

Type species: *Forcepia colonensis* Carter, 1874 (by monotypy).

Diagnosis. *Forcepia* with reticulate skeleton and lacking echinating acanthostyles (from van Soest 2002a).

***Forcepia (Forcepia) mucosa* sp. nov. ▲**

(Fig. 16A–F, Table 13)

Material examined. **TS 4284** **(AI2-Spg52)**: ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–2, Station 3814 (32.6663º S, 28.4412º E–32.6714º S, 28.4397º E, Eastern Cape, South Africa), 29–35 m depth, amongst boulders, shell hash and pebbles, SST 20 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 10 min, 26 August 2016. TS 3495 (BD4-Spg34), TS 3509 (BD4-Spg40): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–16, Station 3722 (32.8300º S, 28.4593º E–32.8327º S, 28.4573º E, Eastern Cape, South Africa), 87 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 9 min, 22 February 2016. TS 3685 (BD1-Spg3(17)), TS 3745 (BD1-Spg59), TS 3753 (BD1-Spg29): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–10, Station 3716 (32.7531º S, 28.5177º E–32.7547º S, 28.5207º E, Eastern Cape, South Africa), 78 m depth, amongst cobbles and shell hash, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 24 min, 21 February 2016. TS 3761 (BD6-Spg16): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–18, Station 3724 (32.8345º S, 28.4682º E–32.8361º S, 28.4635º E, Eastern Cape, South Africa), 76 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 11 min, 22 February 2016. TS 4137 (BD10-Spg1(11)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–30, Station 3736 (32.7543º S, 28.4188º E–32.7568º S, 28.4152º E, Eastern Cape, South Africa), 45 m depth, amongst rhodoliths, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 6 min, 23 February 2016. TS 4334 (AI2-Spg102): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–20, Station 3832 (32.7597º S, 28.4110º E–32.7587º S, 28.4119º E, Eastern Cape, South Africa), 45 m depth, amongst rock, SST 20 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 5 min, 27 August 2016. TS 4373 (AI2-Spg141): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–21, Station 3833 (32.7580º S, 28.4589º E–32.7577º S, 28.4554º E, Eastern Cape, South Africa), 62–58 m depth, amongst rock and coquina/shell hash, SST 19 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 9 min, 28 August 2016. TS 4466 (AI2-Spg234): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–49, Station 3861 (32.9395º S, 28.2685º E–32.9363º S, 28.2757º E, Eastern Cape, South Africa), 90 m depth, amongst a shipwreck, shell hash and coarse sand with shell fragments, SST 21 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 12 min, 30 August 2016. TS 4648 (AI2-Spg416): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–81, Station 3893 (33.1632º S, 27.7746º E–33.1625º S, 27.7753º E, Eastern Cape, South Africa), 36 m depth, amongst shell hash, SST 18 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 3 min, 03 September 2016.

Description. Massive form, with fistules (up to 7 mm) (Fig. 16A). Length 6 cm, width 4 cm and thickness 2 cm. Thin dermal membrane present (<1 mm), surface undulating but smooth and slippery with a few, random, subcircular oscules (~2 mm). Texture dense and rubbery, somewhat compressible, breaks so-so. Colour *in situ* orange, in preservative beige. Slimy mucus and distinct smell present in life.

Skeleton. Choanosomal skeleton comprises an irregular reticulation of vague tylote tracts (~50–180 µm across) ascending obliquely to surface, and single megascleres arranged in a confused manner around large subdermal spaces (Fig. 16B). Ectosomal skeleton composed of tangential choanosomal tylotes, supporting thin dermal membrane (~90–230 µm across) (Fig. 16C). Microscleres and incorporated surrounding debris scattered throughout.

Spiculation. Megascleres. Tylotes smooth, slightly curved to flexuous, with well-developed oval apices: 508–*557*–608 × 7–*15*–19 µm, n = 15 (Fig. 16D). **Microscleres.** Forceps, robust and heavily spined, in two size classes (Fig. 16E): I) 133–*149*–160 × 6–*8*–

10 µm, n = 15; II) 66–*81*–97 × 4–*5*–6 µm, n = 15. Arcuate isochelae: 19–*21*–23 × 6–*7*–8 µm, n = 15 (Fig. 16F).

Distribution and ecology. Currently only known from the Amathole region (Eastern Cape, South Africa). Occurs on or amongst various substrates, including a shipwreck, boulders, cobbles, rock, rhodoliths, coquina/shell hash, pebbles and coarse sand with shell fragments. Often associated with sea fans and algae. Some material examined had algae (TS 3685, TS 3753, TS 4137, TS 4284, TS 4334, TS 4373), ascidian (TS 4648), bryozoan (TS 3753, TS 4137, TS 4648), and hydroid (TS 3495, TS 4648) epifauna, as well as worm (TS 4284) endofauna. Depth range: 29–90 m.

Provisional etymology. *Mucosus* (L.) = slimy, referring to the production of mucus observed in this species.

Remarks. The above material is assigned to *Forcepia (Forcepia)* as diagnosed by its massive form, reticulate choanosomal skeletal structure comprising smooth tylotes, which also lie tangentially to form the ectosomal skeleton, the absence of basal and/or echinating acanthostyles, and presence of spined forceps and arcuate isochelae microscleres (van Soest 2002a).

Only two species of *Forcepia (Forcepia)* have been recorded from the Indian Ocean, *Forcepia (Forcepia) agglutinans* Burton, 1933 from South Africa, and *Forcepia (Forcepia) stephensi* Dendy, 1922 from Cargados Carajos (Mauritius). Both species are thinly encrusting, have much smaller tylotes (280 µm), and only one size class of forceps. In addition, Dendy (1922) notes the presence of tylostyles and sigmata in *F. (F.) stephensi*. Thus, the present material likely constitutes a new species, generally characterised by a massive form, large tylotes (~560 µm) and two distinct size classes of robust forceps.

Key diagnostic characters:

- massive, fistulose form;

- surface undulating but smooth and slippery, covered in slimy mucus;
- orange in life;
- megascleres exclusively large (~560 µm) tylotes;
- microscleres include two size classes of robust forceps, sigmata absent.

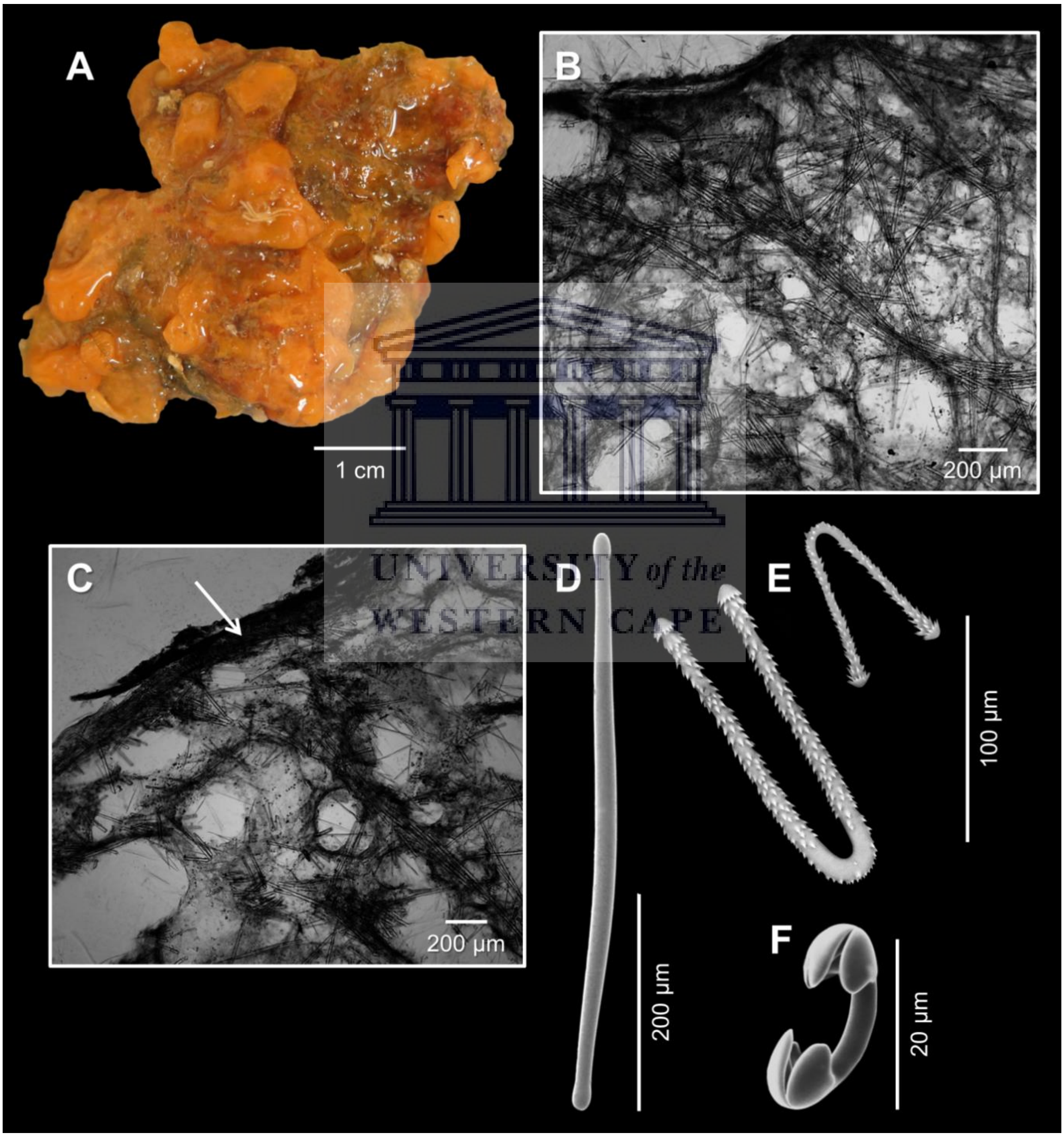

Figure 16: *Forcepia (Forcepia) mucosa* **sp. nov. ▲**. A, specimen TS 4284. B, choanosomal skeleton. C, ectosomal skeleton comprising thin dermal membrane (arrow). D, tylote. E, forceps. F, arcuate isochela.

Table 13: Comparative spicule dimensions and known location, form and depth for the accepted species of *Forcepia (Forcepia)* Carter, 1874 occurring in South Africa and Mauritius, according to van Soest *et al.* (2020a). Spicule dimensions expressed in µm, with specimens from this study (TS) given as minimum–*mean*–maximum length × width, n = 15.

Species	Megascleres		Microscleres			Location/Form/Depth (m)
	Tylostyles	**Tylotes**	**Forceps**	**Isochelae**	**Sigmata**	
1. *Forcepia (Forcepia) agglutinans* Burton, 1933 (Orig. Descrip. as *Forcepia agglutinans*)	-	280 × 6	100	28	-	South Africa/thinly encrusting
2. *Forcepia (Forcepia) stephensi* Dendy, 1922 (Orig. Descrip. as *Forcepia stephensi*)	200 × 2	280 × 4	57	15 × 7–10	14	Cargados Carajos (Mauritius)/thinly encrusting/51
3. *Forcepia (Forcepia) mucosa* sp. nov. ▲ (TS 4284)	-	508–*557*–608 × 7–*15*–19	I) 133–*149*–160 × 6–*8*–10 II) 66–*81*–97 × 4–*5*–6	19–*21*–23 × 6–*7*–8	-	Amathole region (Eastern Cape, South Africa)/massive, fistulose, orange/29–35
TS 3509	-	555–*592*–626 × 16–*18*–21	I) 106–*114*–126 × 6–*7*–8 II) 47–*62*–73 × 3–*4*–5	19–*21*–23 × 5–*6*–8	-	Amathole region (Eastern Cape, South Africa)/massive, fistulose, brown/87
TS 3685	-	485–*557*–628 × 14–*17*–21	I) 120–*138*–159 × 7–*8*–9 II) 43–*65*–74 × 3–*4*–5	19–*21*–23 × 6–*8*–9	-	Amathole region (Eastern Cape, South Africa)/massive, fistulose, reddish-brown/78

Species	Megascleres		Microscleres			Location/Form/Depth (m)
	Tylostyles	Tylotes	Forceps	Isochelae	Sigmata	
TS 3753	-	509–*570*–648 × 10–*17*–22	I) 125–*134*–155 × 6–*7*–9 II) 56–*61*–75 × 2–*4*–5	19–*21*–23 × 7–*8*–8	-	Amathole region (Eastern Cape, South Africa)/massive, fistulose, brown/78
TS 4334	-	506–*555*–600 × 10–*15*–18	I) 110–*126*–134 × 7–*8*–10 II) 49–*70*–85 × 2–*5*–6	18–*21*–24 × 5–*7*–8	-	Amathole region (Eastern Cape, South Africa)/massive, fistulose, orange/45
TS 4466	-	493–*566*–631 × 12–*16*–22	I) 111–*131*–147 × 6–*8*–11 II) 58–*67*–86 × 4–*5*–6	20–*22*–25 × 7–*8*–9	-	Amathole region (Eastern Cape, South Africa)/massive, fistulose, reddish-brown/90

Family Crellidae Dendy, 1922

Genus *Crella* Gray, 1867

Type species: *Cribrella elegans* Schmidt, 1862 (by original designation).

Diagnosis. Crellidae with ectosomal acanthoxeas or acanthostyles, oxeote, strongylote or stylote tornotes; basal acanthostyles may be present; microscleres arcuate isochelae (may be absent) (from van Soest 2002b).

Subgenus *Crella (Grayella)* Carter, 1869

Type species: *Grayella cyathophora* Carter, 1869 (by original designation).

Diagnosis. No chelae, no basal or echinating acanthostyles (from van Soest 2002b).

Crella (Grayella) erecta (Lévi, 1963)

(Fig. 17A–G, Table 14)

Synonymy.

Grayella erecta Lévi, 1963: 31.

Material examined. **<u>TS 4330</u> (AI2-Spg98)**: ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–20, Station 3832 (32.7597º S, 28.4110º E–32.7587º S, 28.4119º E, Eastern Cape, South Africa), 45 m depth, amongst rock, SST 20 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 5 min, 27 August 2016. NIWA 110804 (0CDN6305-N): Lighthouse Reef, NIWA Station Z17506 (33.0425º S, 27.9210º E, Eastern Cape, South Africa), 23 m depth, on rock, amongst rocky reef comprising of boulders and sand, coll. P. L. Colin, CRRF, via SCUBA, 08 February 1999, field identification by L. J. Bell Colin, CRRF, Palau. TS 4271 (AI2-Spg39): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–1, Station 3813 (32.6816º S, 28.4585º E–32.6869º S, 28.4617º E, Eastern Cape, South Africa), 55–52 m depth, amongst rock, coquina/shell hash and pebbles, SST 21 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 10 min, 26 August 2016.

Description. Erect pedunculate form (Fig. 17A & B). Length 5 cm, width 3 cm and thickness 1 cm. Thin dermal membrane present (<1 mm), fragile surface smooth and shiny, covered throughout in often perforated subcircular elevated areolae (~2 mm in diameter), with small oval oscules (<1 mm) on sponge apex. Interior cavernous, spongy and fibrous, very compressible but tough. Exterior colour *in situ* light orange, areolae light yellow and interior dark orange. Colour in preservative beige.

Skeleton. Choanosomal skeleton comprises tornotes in thick multispicular dendritic tracts (~60–230 µm across), arranged around large subdermal spaces, and surrounded by numerous confused interstitial acanthoxeas (Fig. 17C). Ectosomal skeleton comprises a dermal membrane (~70–370 µm thick), consisting of a dense tangential layer of intercrossing acanthoxeas (Fig. 17D).

Spiculation. Megascleres. Tornotes smooth, straight, conical: 285–*307*–333 × 4–*9*–12 µm, n = 15 (Fig. 17E) (specimens NIWA 110804 and TS 4271 have styles instead; see Fig. 17G and Table 14). Acanthoxeas with small straight spines, straight to slightly curved, frequently faintly centrotylote, acerate to hastate, in a large size range with overlap: 54–150 × 5–7 µm, n = 15 (Fig. 17F). **Microscleres.** None.

Distribution and ecology. Known only from South Africa. Occurs on rocky substrate amongst boulders, coquina/shell hash, pebbles and sand in the Amathole region (Eastern Cape). Depth range: 23–55 m (previously 36–46 m).

Remarks. Assignment of the above material to *Crella (Grayella)* is supported by the pedunculate form, presence of ectosomal acanthoxeas and smooth choanosomal styles/tornotes, as well as the absence of chelae and basal/echinating acanthostyles (van Soest 2002b).

Carter (1869) described *Crella (Grayella) cyathophora* from the Red Sea, with this species now recorded from several locations within the Western Indian Ocean region (van Soest *et al.* 2020a). In a later paper, this author noted that the British Museum (now the Natural History Museum, London) had purchased a dry specimen of this species, collected from Port Elizabeth in South Africa (Carter 1881). Dendy (1922), on examining Carter's material, found that the dry specimen differed from the type in having thicker and more distinctly hastate styles (occasionally becoming tornote), and regarded it as a variety. Based on this suggestion, Lévi (1963) described similar fresh material from South Africa as *Crella (Grayella) erecta*, largely characterised by a pedunculate form, the presence of tornotes (derived from styles), and slightly longer acanthoxeas with a larger size range. The above material conforms closely to this species (styles: 280–330 × 10 µm; acanthoxeas: 70–140 × 4–5 µm or tornotes: 300–340 µm; acanthoxeas: 60–130 µm), which has not been recorded in the taxonomic literature since the description.

Also described from the Red Sea, *Crella (Grayella) papillata* (Lévi, 1958) is an encrusting, papillate, red species that has thinner styles (250 × 1–3 µm) and acanthoxeas (80–100 × 1–3 µm), the latter with a narrow size range.

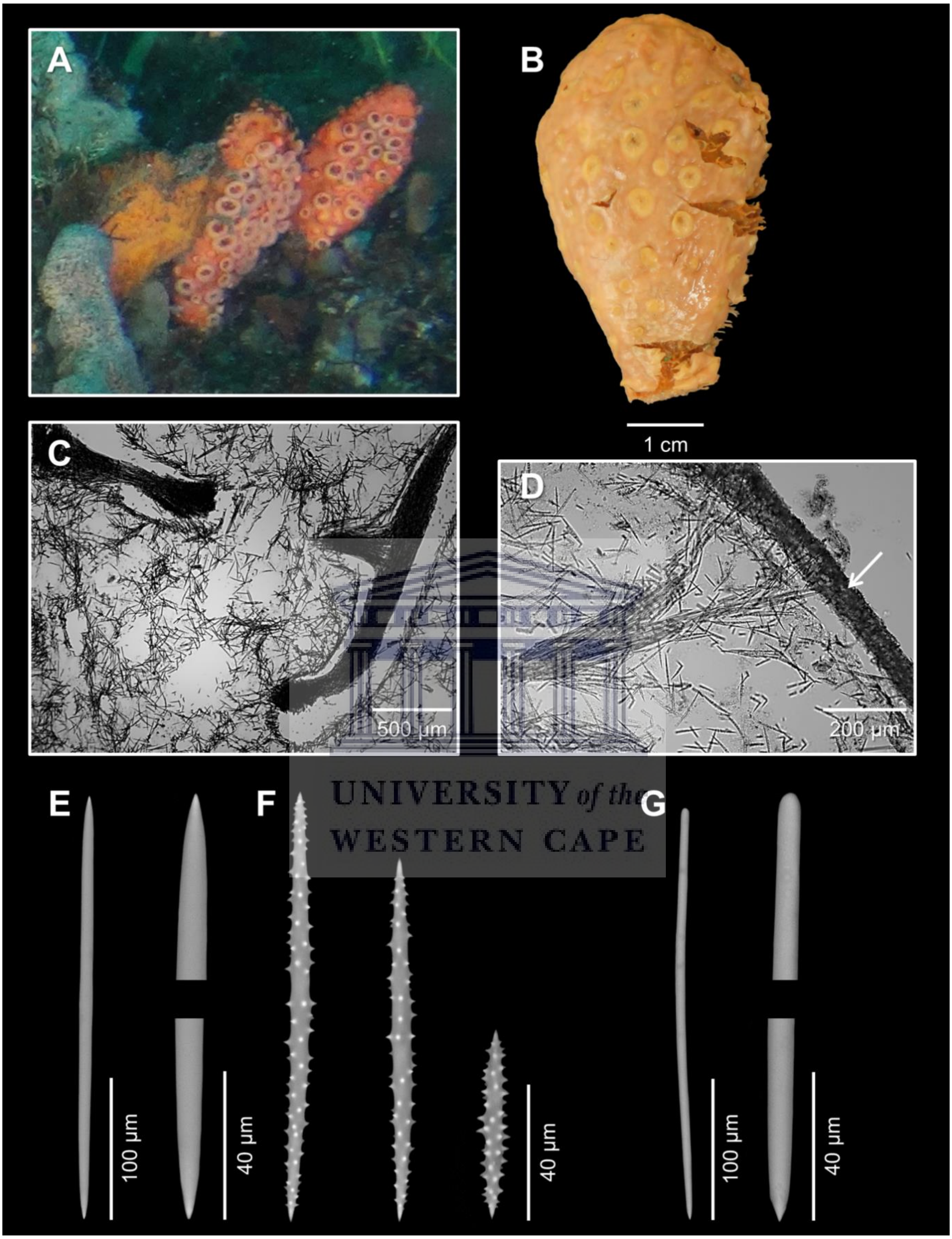

Figure 17: *Crella (Grayella) erecta* (Lévi, 1963). A, species *in situ* (R2). B, specimen TS 4330. C, choanosomal skeleton. D, ectosomal skeleton comprising dermal membrane (arrow). E, tornote with close-up of apices. F, acanthoxeas. G, style of specimen TS 4271 with close-up of apices.

Table 14: Comparative spicule dimensions and known location, form and depth for the accepted species of *Crella (Grayella)* Carter, 1869 occurring in South Africa and the Indian Ocean according to van Soest *et al.* (2020a). Spicule dimensions expressed in µm, with specimens from this study (NIWA/TS) given as minimum–*mean*–maximum length × width, n = 15.

Species	**Styles (S)/Tornotes (T)**	**Acanthoxeas**	**Location/Form/Depth (m)**
1. *Crella (Grayella) cyathophora* (Carter, 1869) (Orig. Descrip. as *Grayella cyathophora*)	(S?) ~282 × 4	~99 × 3	Gulf of Suez (Red Sea)/massive, spreading, areolate
Dendy (1922) (Orig. Descrip. as *Crella cyathophora* var. *acuata)*	(S) 300 × 5	120 × 5	Egmont (Chagos Archipelago)/irregular, lobed, areolate
Lévi (1958) (As *Grayella cyatophora)*	(S) 275 × 5	90–120 × 4	Red Sea/encrusting, areolate, red
Lévi (1961) (As *Grayella cyathophora*)	(S) 300–330 × 3–4	120 × 3	Aldabra/fragment, light beige/28
Pulitzer-Finali (1993) (As *Grayella cyatophora)* (R.N. KEN.139)	(S) 270–310 × 5–7	110–140 × 5–7	North Kenya Banks/pedunculate, fan-shaped, white/90
van Soest (2002b) (Re-description of NHMUK 1869.6.25.48)	(T) 279–*292*–306 × 3–*4*–5	96–*105*–117 × 2–*3*–3	Gulf of Suez (Red Sea)/massively encrusting, areolate
2. *Crella (Grayella) erecta* (Lévi, 1963) (Orig. Descrip. as *Grayella erecta*)	(S) 280–330 × 10	70–140 × 4–5	South Africa/erect, stalked, massive, areolate, light cream/46
Lévi (1963) (NAD 13T)	(T) 300–340	60–130	South Africa/erect, pedunculate, areolate, light cream/36

Species	Styles (S)/Tornotes (T)	Acanthoxeas	Location/Form/Depth (m)
NIWA 110804	(S) 267–*287*–307 × 5–*7*–9	47–140 × 4–6	Amathole region (Eastern Cape, South Africa)/erect, flat, branching to lobed, areolate, exterior orange, interior golden yellow/23
TS 4271	(S) 296–*315*–355 × 7–*8*–9	57–166 × 3–7	Amathole region (Eastern Cape, South Africa)/fragment, areolate, exterior orange, interior golden yellow/52–55
TS 4330	(T) 285–*307*–333 × 4–*9*–12	54–150 × 5–7	Amathole region (Eastern Cape, South Africa)/erect, pedunculate, areolate, exterior light orange, areolae light yellow, interior dark orange/45
3. *Crella (Grayella) papillata* (Lévi, 1958) (Orig. Descrip. as *Grayella papillata*)	(S) 250 × 1–3	80 × 1–3	Red Sea/encrusting, papillate, red/intertidal
Lévi (1998) (As *Crella papillata*)	(S) 270–290 × 1–5	100 × 1–3	New Caledonia/thickly encrusting to massive, papillate, bright red/8–25

Key diagnostic characters:

- erect, pedunculate form;
- smooth and shiny surface fragile, with subcircular elevated areolae (~2 mm);
- interior cavernous, fibrous and tough;
- exterior light orange in life, areolae light yellow and interior dark orange;
- megascleres are either styles or tornotes, and acanthoxeas (47–166 µm);
- no microscleres.

Family Esperiopsidae Hentschel, 1923

Genus *Amphilectus* Vosmaer, 1880

Type species: *Isodictya gracilis* Bowerbank, 1866 (by subsequent designation).

Diagnosis. Esperiopsidae with ladder-like skeleton of ascending and interconnecting spicule tracts; microscleres only small palmate isochelae (occasionally slightly anisochelate), usually no sigmas (from van Soest & Hajdu 2002).

Amphilectus informis (Stephens, 1915)

(Fig. 18A–E, Table 15)

Synonymy.

Esperiopsis informis Stephens, 1915: 450; Lévi 1963: 20; Samaai & Gibbons 2005: 74.

Amphilectus informis; Maduray 2013: 111.

Material examined. **<u>TS 4532</u> (AI2-Spg300)**: ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–58, Station 3870 (32.9485º S, 28.0577º E–32.9478º S, 28.0588º E, Eastern Cape, South Africa), 29 m depth, amongst boulders, shell hash and pebbles, SST 18 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 3 min, 31 August 2016.

Description. Thickly encrusting on sea fan (Fig. 18A & B). Length 3 cm, width 1 cm and thickness 2 mm. Surface hispid, velvety, with subcircular oscules (1 mm) on margin and circular ostia (<1 mm) throughout. Texture soft and spongy, very compressible, easily torn. Colour *in situ* light dirty yellow, in preservative beige. Sticky exudate present in life.

Skeleton. Choanosomal skeleton consists of a ladder-like anisotropic reticulation of ascending and interconnecting spicule tracts (Fig. 18C). Primary vertical fibres comprise multiserially arranged styles, which pierce dermal membrane, projecting slightly beyond surface as spicule tufts (~150–410 µm). These fibres are ~180–340 µm apart, connected by roughly horizontal single styles or multispicular secondary fibres. Spongin sparse, best developed at points where fibres transverse. Isochelae scattered throughout. Specialised ectosomal skeleton absent.

Spiculation. Megascleres. Styles smooth, slightly curved, acerate: 184–*201*–216 × 7–*12*–16 µm, n = 15 (Fig. 18D). **Microscleres.** Palmate isochelae: 26–*28*–30 × 5–*6*–7 µm, n = 15 (Fig. 18E).

Distribution and ecology. Known only from South Africa, common along the west coast (Samaai & Gibbons 2005). Occurs amongst boulders, rock, shell hash, pebbles and sand. Associated with foliose and encrusting algae (Samaai & Gibbons 2005). Often found encrusting on various benthic invertebrates, including hydroid colonies (Stephens 1915), barnacles (Lévi 1963), other sponges (e.g. *Stelletta trisclera* Lévi, 1967; Samaai & Gibbons 2005), and sea fans (this study). Depth range: 5–46 m.

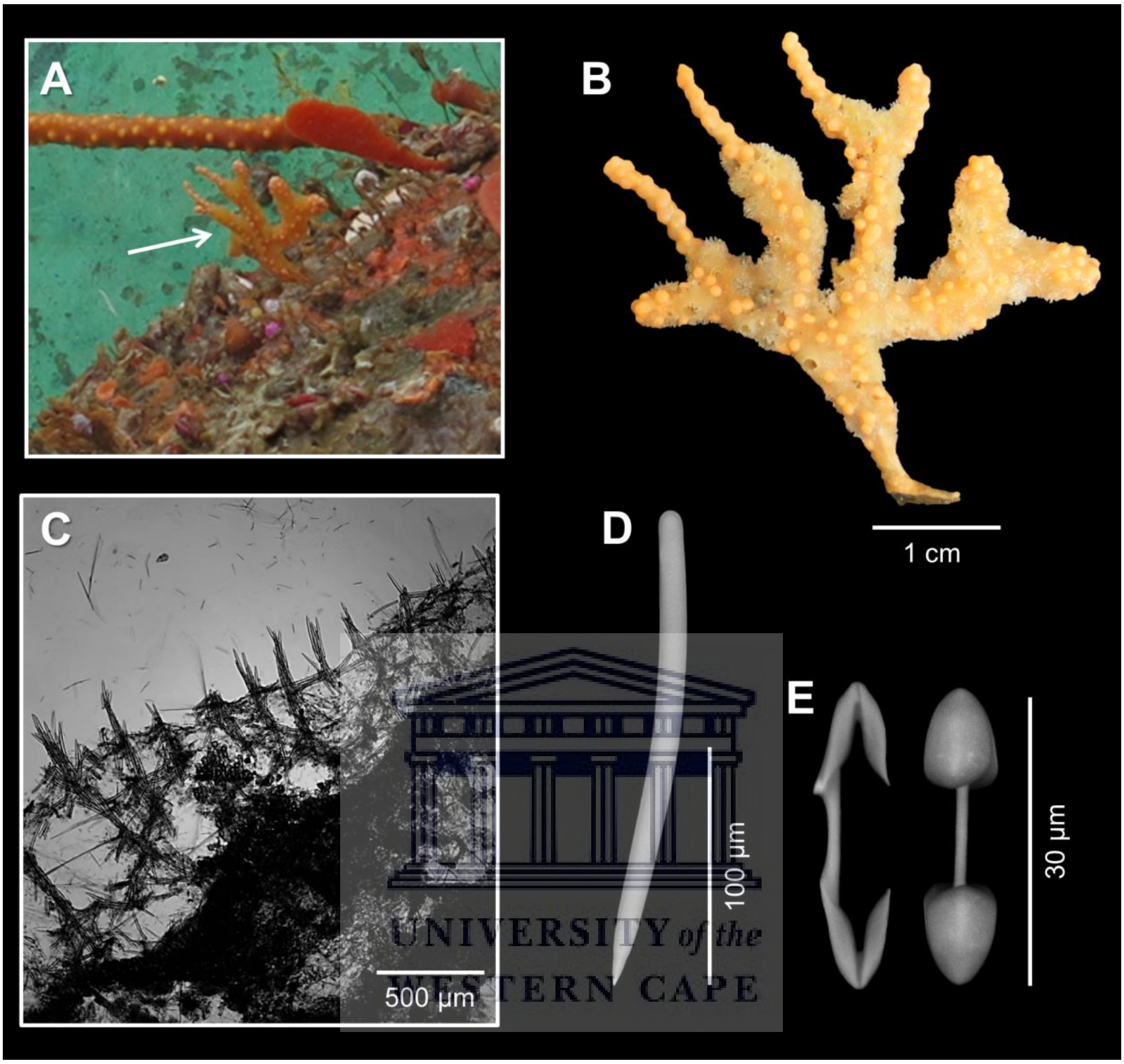

Figure 18: *Amphilectus informis* (Stephens, 1915). A, B, specimen TS 4532. C, choanosomal skeleton. D, style. E, palmate isochelae.

Table 15: Comparative spicule dimensions and known location, form and depth for the accepted species of *Amphilectus* Vosmaer, 1880 occurring in South Africa, Namibia and the Kerguelen Islands according to van Soest *et al.* (2020a). Spicule dimensions expressed in µm, with specimen from this study (TS) given as minimum–*mean*–maximum length × width, n = 15.

	Megascleres		**Microscleres**	
Species	**Strongyles**	**Styles**	**Isochelae**	**Location/Form/Depth (m)**
1. *Amphilectus informis* (Stephens, 1915) (Orig. Descrip. as *Esperiopsis informis*)	-	200–260 × 8–10	24–27 × 8	South Africa/encrusting/46
Lévi (1963) (As *Esperiopsis informis*)	-	220 × 9	22–24	South Africa/massive, globose, irregular, encrusting, ochre to grey/17–30
Samaai & Gibbons (2005) (As *Esperiopsis informis*)	-	137–*205*–207 × 9	26–*27*–30	South Africa/flat, encrusting, exterior black, interior brown/5–10
TS 4532	-	184–*201*–216 × 7–*12*–16	26–*28*–30 × 5–*6*–7	Amathole region (Eastern Cape, South Africa)/encrusting, light dirty yellow/29
2. *Amphilectus lesliei* (Uriz, 1988) (Orig. Descrip. as *Esperiopsis lesliei*)	270–330 × 10–16	220–280 × 5–7	34–53 × 2–3	Namibia/erect, stalked, flattened tubular branches/322
3. *Amphilectus rugosus* (Thiele, 1905) (Orig. Descrip. as *Esperiopsis rugosa*)	-	430 × 15	36	Calbuco (Chile)
Boury-Esnault & van Beveren (1982) (As *Esperiopsis rugosa*)	-	278–*429*–493 × 11–*13*–13	26–*31*–35	Kerguelen Islands/massive to blade-like, or encrusting/130–250
Uriz (1988) (As *Esperiopsis rugosa*)	-	210–526 × 7–18	21–25	Namibia/encrusting/322

Remarks. The single specimen examined above is assigned to *Amphilectus* as diagnosed by its encrusting form, velvety to finely hispid surface, the presence of only small palmate isochelae microscleres and a ladder-like skeleton comprising an anisotropic reticulation of short styles (van Soest & Hajdu 2002).

The specimen conforms closely to *Amphilectus informis*, which was described from the west coast of South Africa by Stephens in 1915 (styles: 200–260 × 8–10 µm; isochelae: 24–27 × 8 µm), and subsequently recorded by Lévi (1963), Samaai & Gibbons (2005), and Maduray (2013). *Amphilectus lesliei* (Uriz, 1988), described from Namibia, differs from this species due to its erect, stalked form, the presence of strongyles, as well as larger (but thinner) isochelae (34–53 × 2–3 µm). Another species from Namibia, *Amphilectus rugosus* (Thiele, 1905), which was originally described from Calbuco (Chile), and subsequently recorded from several Antarctic and Subantarctic locations, has styles almost double the size (430 × 15 µm) of those found in *A. informis*.

Key diagnostic characters:

- thickly encrusting on various benthic invertebrates;
- sticky exudate present;
- found in shallow water, 5–46 m;
- megascleres exclusively styles, <300 µm.

Family Guitarridae Dendy, 1924

Genus *Guitarra* Carter, 1874

Type species: *Guitarra fimbriata* Carter, 1874 (by monotypy).

Diagnosis. Guitarridae with placochelae, and palmate acanthoisochelae or bipocilla-like isochelae (from Hajdu & Lerner 2002).

***Guitarra flamenca* Carballo & Uriz, 1998**

(Figs. 19A–G & 20A–C, Table 16)

Synonymy.

Guitarra flamenca Carballo & Uriz, 1998: 809; Uriz & Carballo 2001: 417; Samaai & Gibbons 2005: 81.

Guitarra fimbriata var. *indica* Lévi, 1963: 25.

Material examined. TS 4749 (AI2-Spg517): ACEP *Imida* Frontiers Project (Cruise 2), Algoa Bay, Grid Ellen 159–108, Station 3920 (33.9948º S, 25.8891º E–33.9930º S, 25.8917º E, Eastern Cape, South Africa), 22–24 m depth, amongst rock and coquina/shell hash, SST 17 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 5 min, 08 September 2016. NIWA 110818 (0CDN6368-H): Orient Pier, East London Harbour, NIWA Station Z17504 (33.0278º S, 27.9175º E, Eastern Cape, South Africa), 5 m depth, on rock near cement wall, coll. P. L. Colin, CRRF, via SCUBA, 14 February 1999, field identification by L. J. Bell Colin, CRRF, Palau. TS 4293 (AI2-Spg61), TS 4300 (AI2-Spg68): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–3, Station 3815 (32.6511º S, 28.4609º E–32.6581º S, 28.4653º E, Eastern Cape, South Africa), 38–43 m depth, amongst rock, coquina/shell hash, pebbles and coarse sand with shell fragments, SST 20 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 10 min, 26 August 2016. TS 4439 (AI2-Spg207): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–44, Station 3856 (32.7035º S, 28.4311º E–32.6998º S, 28.4358º E, Eastern Cape, South Africa), 45–53 m depth, amongst rock and rhodoliths, SST 19 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 10 min, 30 August 2016.

Description. Thickly encrusting to subglobular form (Fig. 19B). Length 3 cm, width 2 cm and thickness 9 mm. Thin dermal membrane present (<1 mm), surface appears smooth, velvety to touch. Single, irregular oscule (4 mm) on apex, likely contracted in observed specimen; *in situ* image of specimen NIWA 110818 depicts oscules on apex of short fistules, multi-chambered (Fig. 19A). Texture spongy and dense, very compressible, soft and friable. Colour *in situ*, and in preservative, light orange. For subtidal specimens, colour *in situ* jet black with bright orange-yellow interior, in preservative black with brown-yellow interior (Samaai & Gibbons 2005, see also specimen NIWA 110818). Samaai & Gibbons (2005) report exudation of slimy mucus upon collection.

Skeleton. Choanosomal skeleton comprises an irregular isotropic reticulation of thick multispicular megasclere tracts (~50–150 µm across), arranged around subdermal spaces, and surrounded by numerous confused interstitial megascleres (Fig. 19C). These tracts ascend obliquely to surface where they form well-defined brushes, which pierce somewhat indistinguishable dermal membrane, extending up to ~50 µm. Microscleres abundant, scattered throughout, with placochelae also somewhat lining certain deeper subdermal spaces.

Spiculation. Megascleres. Tornostrongyles smooth, straight to flexuous, style-like with somewhat bulging rounded to lanceolate heads, acerate, occasionally with central swelling on shaft: 232–*264*–293 × 7–*9*–12 µm, n = 15 (Fig. 19D). **Microscleres.** Placochelae with very marked central constriction, hexagonal central pellucid area, and discontinuous fringed border, in two size classes: I) with circular plate end, 49–*53*–58 × 20–*24*–29 µm (alae) and/or 7–*9*–10 µm (shaft), n = 15 (Fig. 19E); II) with oval plate end, 28–*30*–32 × 8–*10*–10 µm (alae) and/or 2–*3*–5 µm (shaft), n = 15 (Fig. 19F). Bipocilla-like acanthoisochelae with straight, long, thin shaft, cup-shaped fused alae, and regular clusters of straight slender spines covering exterior: 11–*13*–15 × 3–*4*–5 µm, n = 15 (Fig. 19G, Fig. 20A & B).

Distribution and ecology. Known from Namibia and South Africa. Occurs amongst rock, coquina/shell hash, rhodoliths, pebbles and coarse sand with shell fragments. Associated with algae (e.g. *Laminaria* J.V. Lamouroux, 1813) and other invertebrates (Lévi 1963; Carballo & Uriz 1998; Uriz & Carballo 2001; Samaai & Gibbons 2005), with specimens TS 4439 and TS 4749 having worm casing and barnacle epifauna respectively. Material collected during the austral spring by Carballo & Uriz (1998) possessed embryos. Depth range: intertidal–53 m (previously intertidal–20 m).

Remarks. The above material is assigned to *Guitarra* as diagnosed by its fistulose form, skeletal structure comprising tornostrongyles of a single size class, and presence of placochela and bipocilla-like acanthoisochela microscleres (Uriz & Carballo 2001; Hajdu & Lerner 2002). Scanning electron microscopy (SEM) of the microscleres is essential to accurately identify species in this genus (e.g. Fig. 20, Carballo & Uriz 1998).

The specimens conform closely to *Guitarra flamenca*, which was described from Namibia by Carballo & Uriz in 1998 (tornostrongyles: 252–*312*–380 × 6–*12*–18 µm; placochelae: I) 74–95 × 17–23 µm, II) 31–50 × 4–9 µm; bipocilla-like acanthoisochelae: 11–19 µm), and differ only in having smaller spicules. They are most comparable to the material reported by Lévi (1963), which was the first record of this species from South Africa, albeit as a variety of *Guitarra fimbriata* Carter, 1874, which was thought to be cosmopolitan at the time (Burton 1929b). On reviewing several species of *Guitarra* with acanthoisochelae, via SEM of the microscleres, Carballo & Uriz (1998) found this variety to be conspecific with their new species, *G. flamenca*. The larger spicule sizes reported for the type specimen, as well as those later recorded by Samaai & Gibbons (2005), are likely due to the higher silica content and favourable trophic conditions (e.g. high productivity) found in Namibia and along the west coast of South Africa. This could also explain the absence of rounded silica formations in the material examined, which have thus far only been found in the holotype

(Carballo & Uriz 1998). Colouration of this species is variable (Samaai & Gibbons 2005), and seems to be depth-dependent, with shallow (light-exposed) specimens having a darker exterior.

Key diagnostic characters:

- thickly encrusting to subglobular/globular form;
- oscules on apex of short fistules, multi-chambered;
- depth-dependent colouration; shallow specimens have darker exterior;
- slimy mucus present;
- embryos present during austral spring;
- two size classes of placochela microscleres, I with circular plate end, II with oval plate end;
- bipocilla-like acanthoisochela microscleres.

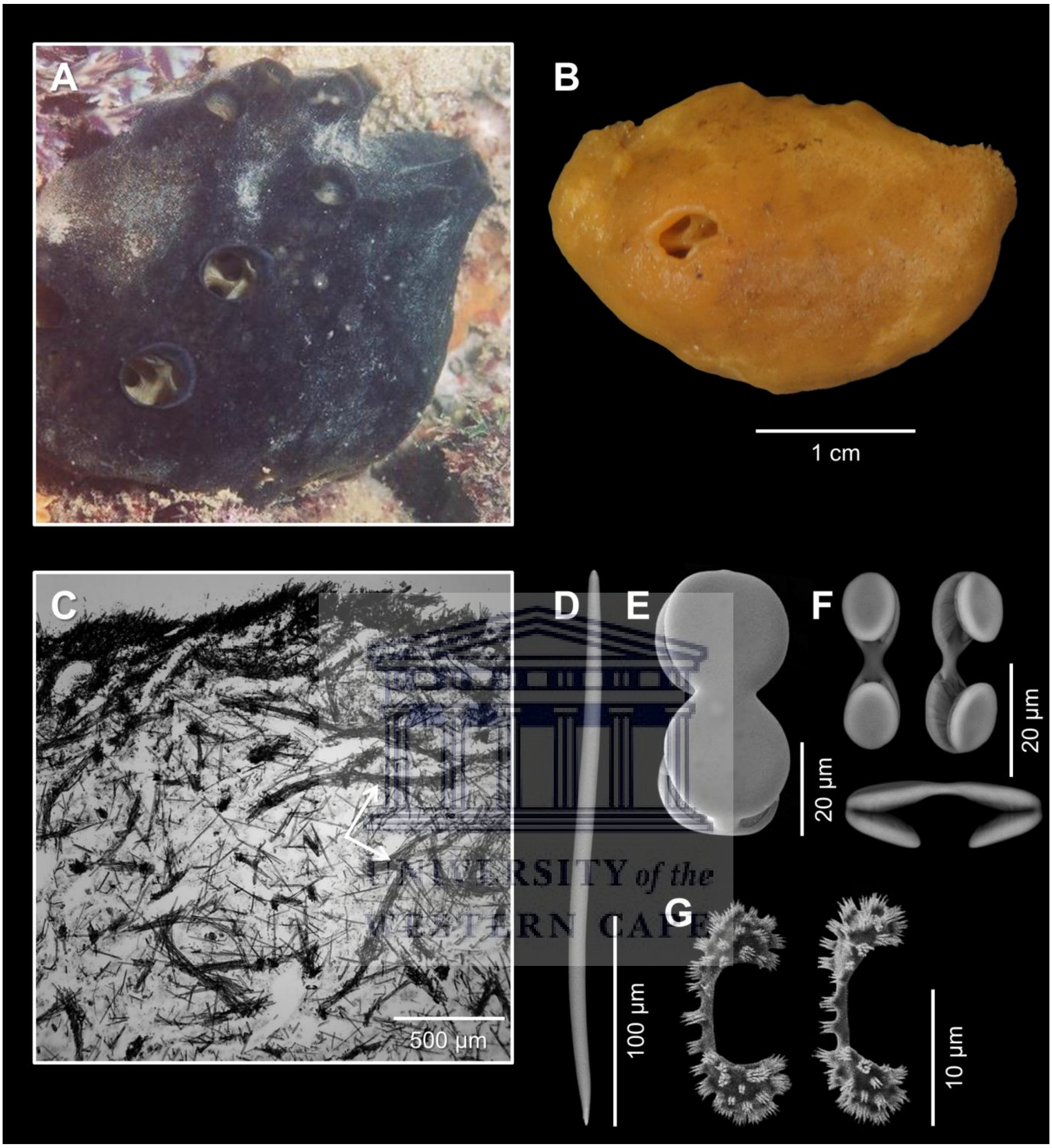

Figure 19: *Guitarra flamenca* Carballo & Uriz, 1998. A, species *in situ* (specimen NIWA 110818, reproduced with permission from the CRRF). B, specimen TS 4749. C, skeleton with thick multispicular megasclere tracts (arrows). D, style-like tornostrongyle. E, placochela I. F, placochelae II. G, bipocilla-like acanthoisochelae.

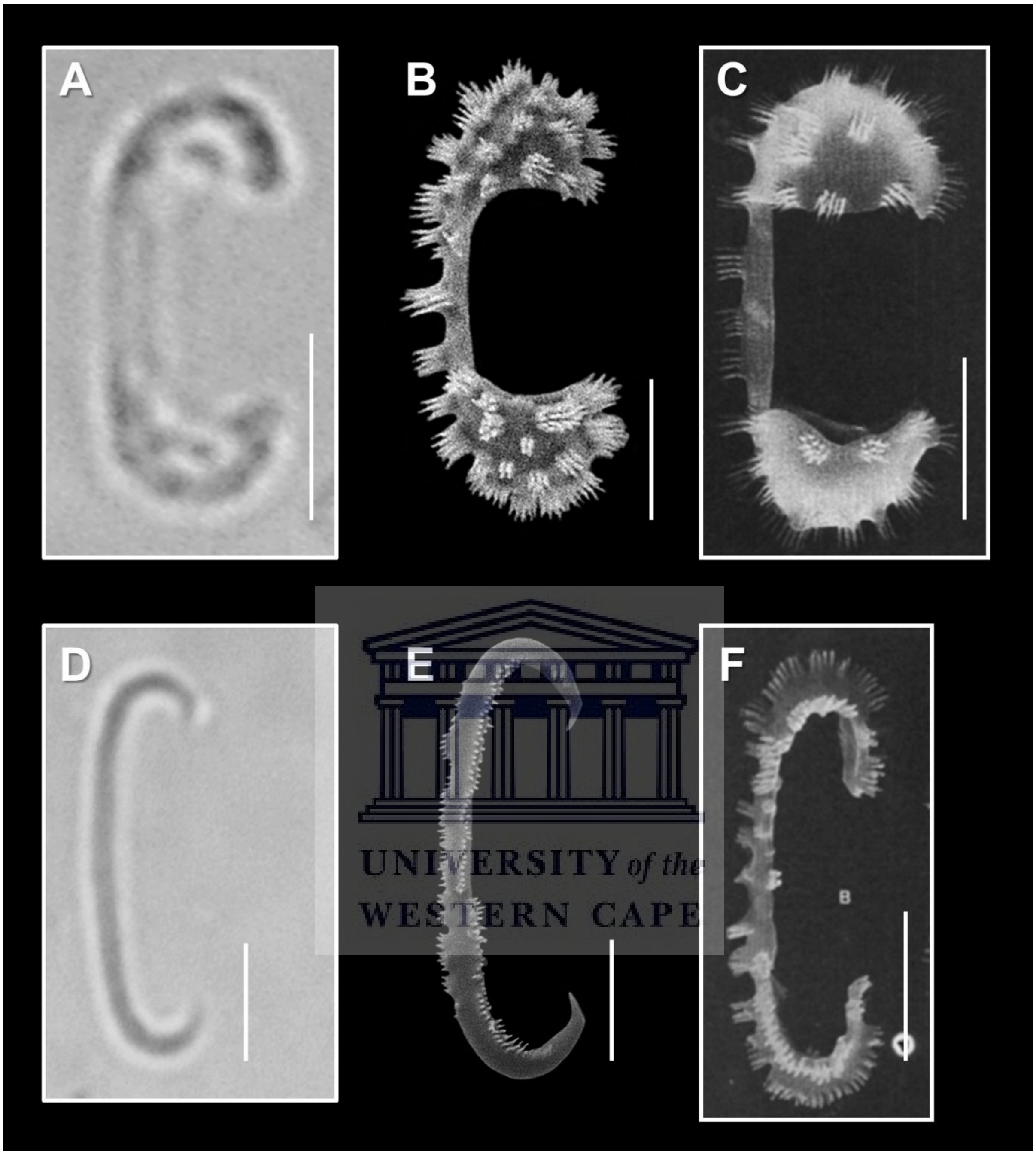

Figure 20: Comparative *Guitarra* Carter, 1874 acanthoisochela microscleres from this study. A–C, bipocilla-like acanthoisochelae of *Guitarra flamenca* Carballo & Uriz, 1998: A, B, from specimen TS 4749. C, from holotype by Carballo & Uriz (1998). D–F, sigmoid acanthoisochelae of *Guitarra indica* Dendy, 1916: D, E, from specimen TS 3903. F, from holotype by Carballo & Uriz (1998). Scale bars = 5 µm.

Table 16: Comparative spicule dimensions and known location, form and depth for the accepted species of *Guitarra* Carter, 1874 occurring in Namibia, South Africa and the Indian Ocean according to van Soest *et al.* (2020a). Spicule dimensions expressed in µm, with specimens from this study (NIWA/TS) given as minimum–*mean*–maximum length × width, n = 15.

	Megascleres	Microscleres		
Species	**Tornostrongyles**	**Placochelae** Alae (A)/Shaft (S)	**Acanthoisochelae**	**Location/Form/Depth (m)**
1. *Guitarra flamenca* Carballo & Uriz, 1998 (Orig. Descrip.)	252–*312*–380 × 6–*12*–18	I) 74–95 × 17–23 (S) II) 31–50 × 4–9 (S)	11–19	Shark Island, Lüderitz (Namibia)/encrusting, exterior dark brown, interior light brown/5
Lévi (1963) (As *Guitarra fimbriata* var. *indica*)	200–250 × 2–8	I) 40–50 × 12–25 II) 30 × 7–12	10–15	South Africa/massive to encrusting, ovoid or globular, exterior dark brown, interior reddish to orange-ochre/intertidal–15
Uriz & Carballo (2001) (Re-description of MNCN 1.01/177 & MNHN, LBIM-CL440)	252–*312*–380 × 6–*12*–18	I) 74–95 × 17–23 (S) II) 31–50 × 4–9 (S)	11–19	-
Samaai & Gibbons (2005)	273–*284*–338 × 12	I) 69–*72*–90 II) 55–*56*–69	18	South Africa/thickly encrusting, exterior jet black, interior bright orange-yellow/10–20
NIWA 110818	219–*241*–266 × 6–*7*–9	I) 44–*48*–52 × 19–*22*–24 (A)/7–*9*–10 (S) II) 29–*32*–35 × 9–*11*–13 (A)/3–*5*–7 (S)	9–*11*–12 × 4–*4*–5	Orient Pier, East London Harbour (Eastern Cape, South Africa)/globular, fistulose, exterior black, interior yellow/5

	Megascleres	Microscleres		
Species	**Tornostrongyles**	**Placochelae** Alae (A)/Shaft (S)	**Acanthoisochelae**	**Location/Form/Depth (m)**
TS 4293	278–*296*–318 × 7–*7*–9	I) 50–*52*–55 × 20–*22*–25 (A)/5–*8*–10 (S) II) 30–*33*–35 × 10–*11*–12 (A)/3–*4*–6 (S)	10–*11*–12 × 4–*4*–5	Amathole region (Eastern Cape, South Africa)/thickly encrusting, contracted, mustard yellow/38–43
TS 4300	246–*277*–303 × 7–*8*–9	I) 47–*52*–54 × 20–*22*–23 (A)/7–*8*–10 (S) II) 32–*34*–37 × 10–*11*–13 (A)/3–*4*–5 (S)	10–*11*–13 × 3–*4*–5	Amathole region (Eastern Cape, South Africa)/thickly encrusting, mustard yellow/38–43
TS 4439	277–*292*–303 × 9–*10*–12	I) 54–*60*–66 × 21–*25*–28 (A)/8–*9*–10 (S) II) 41–*45*–50 × 11–*13*–15 (A)/3–*4*–6 (S)	11–*12*–14 × 3–*4*–5	Amathole region (Eastern Cape, South Africa)/thickly encrusting, mustard yellow/45–53
TS 4749	232–*264*–293 × 7–*9*–12	I) 49–*53*–58 × 20–*24*–29 (A)/7–*9*–10 (S) II) 28–*30*–32 × 8–*10*–10 (A)/2–*3*–5 (S)	11–*13*–15 × 3–*4*–5	Algoa Bay (Eastern Cape, South Africa)/thickly encrusting to subglobular, light orange/22–24
2. ***Guitarra indica*** **Dendy, 1916** (Orig. Descrip.)	266 × 7	41 × 14 (A)	10[4]	Off Poshetra (Western India)/irregularly cushion-shaped, encrusting, slate grey to pale yellow/shallow water (likely <5 m)

[4]Measurement from Lévi (1963).

Species	Megascleres	Microscleres		Location/Form/Depth (m)
	Tornostrongyles	**Placochelae** Alae (A)/Shaft (S)	**Acanthoisochelae**	
Uriz & Carballo (2001) (Re-description of NHMUK 1920.12.9.35)	233–*261*–300 × 4–*6*–8	I) 37–46 × 5–8 II) 28–35 × 4–5	?	Western India/infralittoral
NIWA 110816	241–*295*–317 × 7–*8*–9	31–*48*–68 × 7–*13*–18 (A)/2–*6*–8 (S)	13–*15*–17 × 4–*4*–5	Cintsa (Eastern Cape, South Africa)/globular, fistulose, light orange/17
TS 3903	306–*332*–353 × 8–*10*–11	35–*48*–66 × 10–*13*–16 (A)/3–*5*–8 (S)	14–*15*–18 × 4–*5*–6	Amathole region (Eastern Cape, South Africa)/subglobular, contracted, light brown/76

Guitarra indica **Dendy, 1916**

(Figs. 20D–F & 21A–F, Table 16)

Synonymy.

Guitarra indica Dendy, 1916: 124; Lévi 1963: 25 (Not: *Guitarra fimbriata* var. *indica*); Carballo & Uriz 1998: 807; Uriz & Carballo 2001: 417; Hajdu & Lerner 2002: 654.

Material examined. **TS 3903** **(BD6-Spg1(12))**: ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–18, Station 3724 (32.8345º S, 28.4682º E–32.8361º S, 28.4635º E, Eastern Cape, South Africa), 76 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 11 min, 22 February 2016. NIWA 110816 (0CDN6352-O): Cintsa, NIWA Station Z17499 (32.8500º S, 28.1417º E, Eastern Cape, South Africa), 17 m depth, on rock, amongst reef comprising of rounded rock and sand, coll. P. L. Colin, CRRF, via SCUBA, 12 February 1999, field identification by M. Kelly, NIWA, Auckland..

Description. Subglobular, contracted form (Fig. 21B). Length 2 cm, width 2 cm and thickness 1 cm. Thin dermal membrane present (<1 mm), surface undulating but smooth. No oscules seen, likely contracted in observed specimen; *in situ* image of specimen NIWA 110816 depicts oscules on apex of fistules (Fig. 21A). Texture dense, very compressible, soft and friable. Colour *in situ*, and in preservative, light brown.

Skeleton. Choanosomal skeleton comprises an irregular isotropic reticulation of thick multispicular megasclere tracts (~30–150 µm across), arranged around subdermal spaces, and surrounded by numerous confused interstitial megascleres (Fig. 21C). These tracts ascend obliquely to surface where they form well-defined brushes, which pierce somewhat indistinguishable dermal membrane, extending up to ~70 µm. Microscleres abundant, scattered throughout, with placochelae also lining most subdermal spaces.

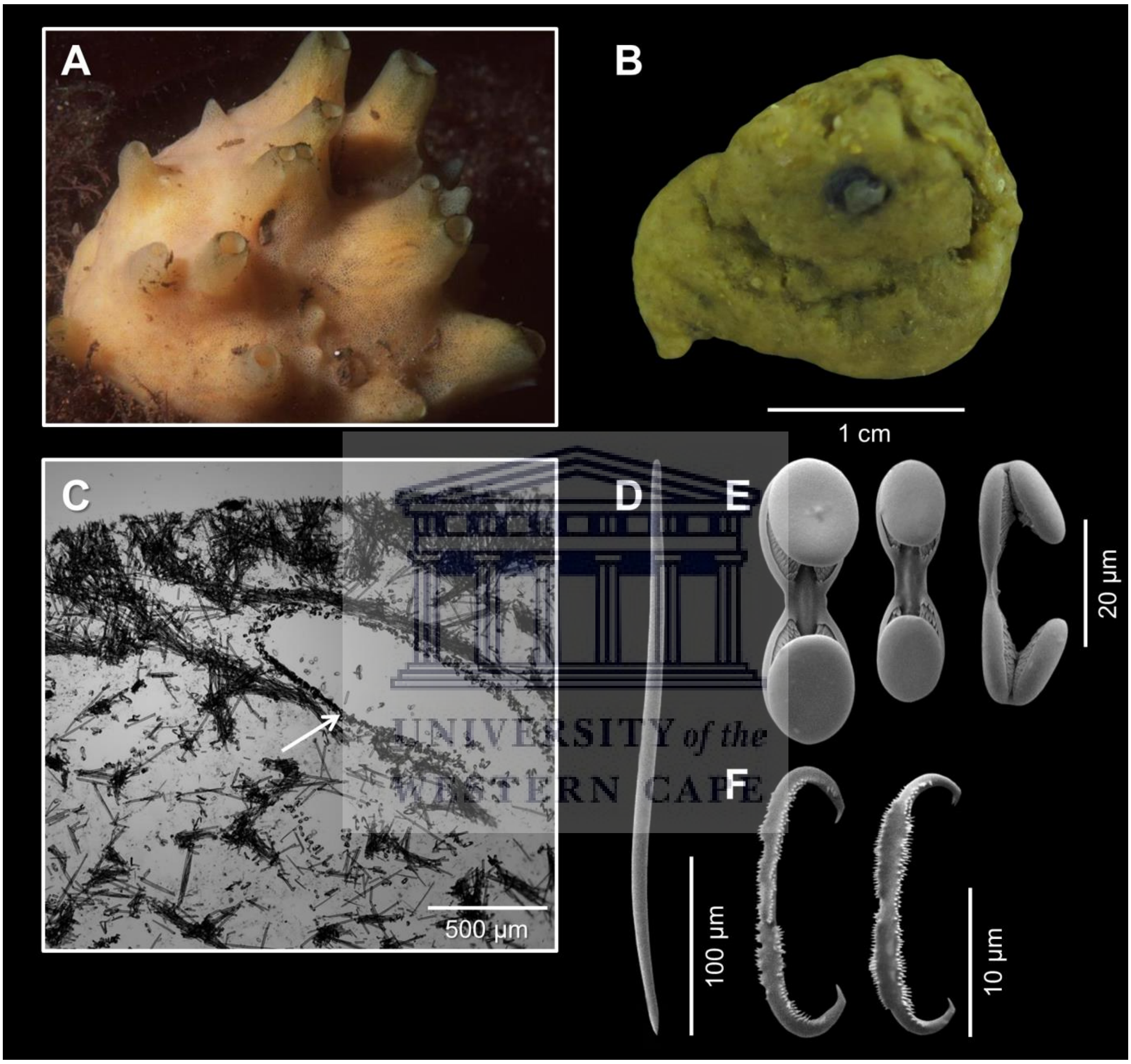

Figure 21: *Guitarra indica* Dendy, 1916. A, species *in situ* (specimen NIWA 110816, reproduced with permission from the CRRF). B, specimen TS 3903. C, skeleton with placochelae lining subdermal space (arrow). D, style-like tornostrongyle. E, placochelae. F, sigmoid acanthoisochelae.

Spiculation. Megascleres. Tornostrongyles smooth, straight to flexuous, style-like with rounded heads, somewhat bulging acerate to conical: 306–*332*–353 × 8–*10*–11 µm, n = 15 (Fig. 21D). **Microscleres.** Placochelae with marked central constriction, hexagonal central pellucid area, discontinuous fringed border, and oval plate end: 35–*48*–66 × 10–*13*–16 µm (alae) and/or 3–*5*–8 µm (shaft), n = 15 (Fig. 21E). Sigmoid acanthoisochelae with straight shaft, reduced lateral alae, and irregularly clustered straight slender spines: 14–*15*–18 × 4–*5*–6 µm, n = 15 (Fig. 20D & E, Fig. 21F).

Distribution and ecology. Previously known from Western India, likely extending into Indonesia and the Seychelles (Hajdu & Lerner 2002). Occurs amongst rocky reef and sand in the Amathole region (Eastern Cape, South Africa). Type material was attached to a polychaete worm casing, along with other sponges (Dendy 1916). Depth range: infralittoral–76 m (previously infralittoral, likely <5 m).

Remarks. The above material conforms to *Guitarra indica*, which was described from Western India by Dendy in 1916 (tornostrongyles: 266 × 7 µm; placochelae: 41 × 14 µm; sigmoid acanthoisochelae: 10 µm), and differs only in having slightly larger spicules. The acanthoisochelae of the type material (which Dendy incorrectly regarded as immature placochelae) also appear to be more heavily spined (Fig. 20D–F, see also Uriz & Carballo (2001)). Nevertheless, the intraspecific variation of *G. indica* is not well documented, with the Amathole specimens representing the first new material that has been investigated in detail since the original description, and the first record of this species from South Africa. Additional specimens have been collected from Indonesia and the Seychelles (Hajdu & Lerner 2002), but these are likely undescribed, with no sources provided by the World Porifera Database (van Soest *et al.* 2020a).

This species seems to display depth-dependent colouration, with shallower specimens exposed to light having a darker exterior (Dendy 1916). This characteristic is shared with the only congener previously recorded from South Africa (and the Indian Ocean), *Guitarra flamenca* Carballo & Uriz, 1998. In addition, both species have a similar form, megasclere type and size, as well as placochelae morphology. However, *G. flamenca* is easily differentiated by the presence of two size classes of placochelae, the larger with a circular plate end, and bipocilla-like acanthoisochelae.

Key diagnostic characters:

- thickly encrusting to subglobular/globular form;
- oscules on apex of fistules;
- depth-dependent colouration; shallow specimens have darker exterior;
- one size class of placochela microscleres, with oval plate end;
- sigmoid acanthoisochela microscleres.

Family Isodictyidae Dendy, 1924

Genus *Isodictya* Bowerbank, 1864

Type species: *Spongia palmata* Ellis & Solander, 1786 (by subsequent designation).

Diagnosis. Isodictyidae of flabellate/digitate growth forms; choanosomal skeleton reticulate or plumoreticulate (niphatid-like); megascleres are mostly diactinal, usually oxeas; microscleres, palmate isochelae, frequently with plate-like inner extensions of the falxes (from Hajdu & Lôbo-Hajdu 2002).

***Isodictya compressa* (Esper, 1797)**

(Fig. 22A–F, Table 17)

Synonymy.

Spongia compressa Esper, 1797: 200.

Spongia pannea Lamarck, 1814: 381; Topsent 1931: 41.

Desmacidon compressum; Ehlers 1870: 20, 31.

Desmacidon compressa; Vosmaer 1880: 159.

Chalina compressa; Carter 1882b: 112.

Homoeodictya compressa; Stephens 1915: 451; Lévi 1963: 20.

Isodictya compressa; Topsent 1931: 41; Samaai & Gibbons 2005: 68; van Soest *et al.* 2020b: 18.

Material examined. **TS 3928** **(BD21-Spg2)**: ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–74, Station 3780 (32.6674º S, 28.4269º E–32.6640º S, 28.4309º E, Eastern Cape, South Africa), 28 m depth, amongst boulders, rock and shell hash, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 9 min, 28 February 2016. NIWA 110812 (0CDN6340-Z): Cintsa, NIWA Station Z17499 (32.8500º S, 28.1417º E, Eastern Cape, South Africa), 16–17 m depth, on rock, amongst reef comprising of rounded rock and sand, coll. P. L. Colin, CRRF, via SCUBA, 12 February 1999, field identification by L. J. Bell Colin, CRRF, Palau.

Description. Erect, stalked, flabellate form (Fig. 22A). Upper area compressed, comprising a cluster of fused tubes. Length 15 cm, width 5 cm and thickness 3 cm. Surface ridged and microhispid, with conspicuous spicule tufts (up to 1 cm) throughout, and fringing large oscules (up to 1 cm) at apices of fused tubes (Fig. 22B). Subcircular to irregular ostia (<1 mm) throughout. Texture spongy and dense, very compressible, resilient but easily torn. Colour *in situ*, and in preservative, beige. Distinct, strong smell present.

Skeleton. Choanosomal skeleton plumoreticulate (Fig. 22C). Primary multispicular megasclere tracts (~80–200 µm across), without a distinct spongin sheath, run longitudinally through stalk, around subdermal spaces, and diverge towards surface to form plumose brushes. These tracts pierce indistinguishable dermal membrane lacking specialisation, projecting beyond surface as individual oxeas (~60–240 µm), or tufts (up to 1 cm) (Fig. 22D). Primary tracts are connected irregularly by perpendicular to oblique single oxeas or secondary multispicular megasclere tracts (~50–130 µm across). Isochelae scattered throughout.

Spiculation. Megascleres. Oxeas smooth, straight to slightly curved medially, acerate: 225–*373*–446 × 4–*21*–33 µm, n = 15 (Fig. 22E). **Microscleres.** Palmate isochelae: 20–*23*–26 × 5–*5*–6 µm, n = 15 (Fig. 22F).

Distribution and ecology. Type locality unknown. Esper (1797) provided an unlikely, vast geographic distribution (Norway, Greenland and North America to East India). Topsent (1931) suggested the Antilles. First recorded from South Africa by Carter (1882b). Occurs amongst boulders, rock, shell hash and sand in South Africa. Associated with foliose and encrusting algae, soft corals and sponges (e.g. *Amphilectus informis* (Stephens, 1915) and *Myxilla (Myxilla) simplex* (Baer, 1906)) (Stephens 1915; Samaai & Gibbons 2005). Depth range: 12–46 m.

Remarks. Assignment of the above material to *Isodictya* is supported by the flabellate form, plumoreticulate choanosomal skeleton, and presence of oxea megascleres and palmate isochelae microscleres (Hajdu & Lôbo-Hajdu 2002). Thirteen species have been described and/or recorded in and around South Africa (van Soest *et al.* 2020a). Of these, *Isodictya alata* (Stephens, 1915) and *Isodictya ectofibrosa* (Lévi, 1963), both South African endemics, possess arcuate isochelae and thus require further investigation and possible reassignment.

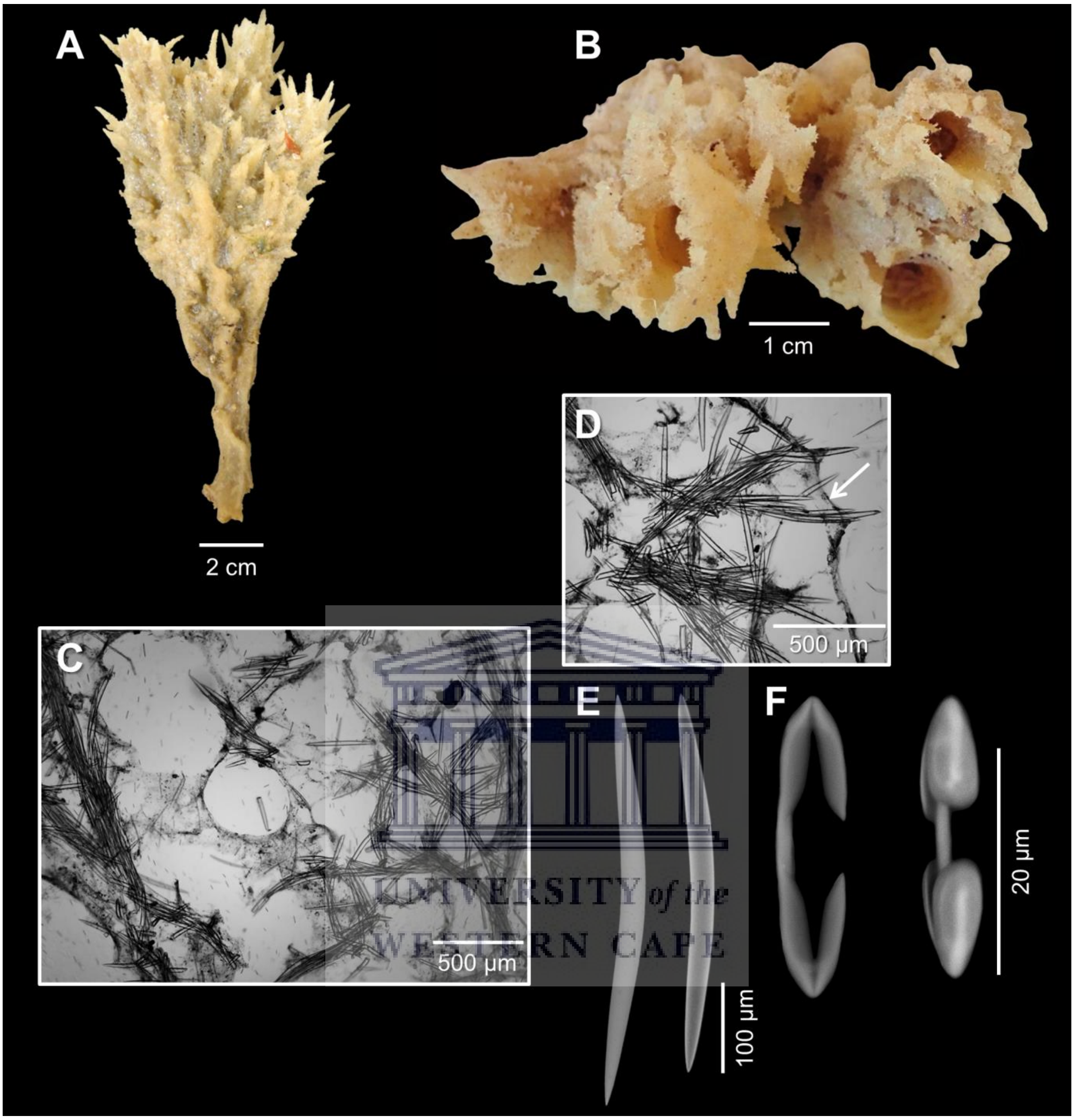

Figure 22: *Isodictya compressa* (Esper, 1797). A, specimen TS 3928. B, sponge apex with oscules fringed by spicule tufts. C, choanosomal skeleton. D, primary megasclere tracts piercing indistinguishable dermal membrane (arrow). E, oxeas. F, palmate isochelae.

Table 17: Comparative spicule dimensions and known location, form and depth for the accepted species of *Isodictya* Bowerbank, 1864 occurring in South Africa, Namibia and the Kerguelen Islands according to van Soest *et al.* (2020a). Spicule dimensions expressed in µm, with specimens from this study (NIWA/TS) given as minimum–*mean*–maximum length × width, n = 15.

Species	Megascleres	Microscleres	Location/Form/Depth (m)
	Oxeas	**Isochelae** ar: arcuate pa: palmate	
1. *Isodictya alata* (Stephens, 1915) (Orig. Descrip. as *Homoeodictya alata*)	300–425 × 10–15	ar: 16	South Africa/irregularly oval mass, flattened anastomosing branches/46
2. *Isodictya chichatouzae* Uriz, 1984 (Orig. Descrip. as *Isodictya chicha-touzae*)	I) 520–630 × 18–28 II) 215–260 × 8–9	pa: 30–33	Namibia/erect, stalked, vasiform branches/260–269
Uriz (1988)	I) 390–530 × 15–20 II) 160–210 × 20–26	pa: 20–26	Namibia/erect, stalked, cup-like, cream-yellow/245
3. *Isodictya compressa* (Esper, 1797) Ehlers (1870) (Re-description as *Desmacidon compressum*)	440	36	Norway, Greenland, North America to East India (?)/stalked, laterally compressed upper part
Carter (1882b) (As *Chalina compressa*)	~377 × 23	~25	South Africa (?)/stalked, battledore-shaped, compressed, light yellowish grey
Stephens (1915) (As *Homoeodictya compressa*)	400–500 × 20–24	pa: 27–32	South Africa/stalked, with broad compressed lobe/46
Topsent (1931) (As *Spongia pannea* & *Isodictya compressa*)	220–*490*–560 × 6–*27*–30	pa: 30 × 6–7	Antilles (?)/stalked with expanded blade

Species	Megascleres Oxeas	Microscleres **Isochelae** ar: arcuate pa: palmate	Location/Form/Depth (m)
Lévi (1963) (As *Homoeodictya compressa*)	400	pa: 23–*26*–31	South Africa/erect, pedunculate, massive, clavate, flabellate or branched/15
Samaai & Gibbons (2005)	364–*430*–501 × 14–32	pa: 28–*34*–36	South Africa/stalked, massive, flabellate, beige/12–20
NIWA 110812	332–*376*–433 × 17–*23*–30	pa: 20–*22*–25 × 5–*5*–6	Amathole region (Eastern Cape, South Africa)/stalked, flabellate, brown/16–17
TS 3928	225–*373*–446 × 4–*21*–33	pa: 20–*23*–26 × 5–*5*–6	Amathole region (Eastern Cape, South Africa)/erect, stalked, flabellate, with upper area compressed, comprising a cluster of fused tubes, beige/28
4. *Isodictya conulosa* (Ridley & Dendy, 1886) (Orig. Descrip. as *Desmacidon conulosa*)	700 × 57	pa: 32	South Africa/pedunculate, lobed, greyish yellow/18–37
Ridley & Dendy (1887) (Orig. Descrip. as *Desmacidon conulosa*)	700 × 57	pa: 32	South Africa/pedunculate, lobed/18–37
Lévi (1963) (As *Homoeodictya conulosa*)	650–750	pa: 26	South Africa/erect, pedunculate, lobed/49–57
5. *Isodictya dufresni* Boury-Esnault & van Beveren, 1982 (Orig. Descrip.)	218–*326*–416 × 5–*12*–20	pa: 19–*24*–33	Kerguelen Islands/thickly encrusting to cup-like, ochre/100–130

Species	Megascleres Oxeas	Microscleres Isochelae ar: arcuate pa: palmate	Location/Form/Depth (m)
6. *Isodictya ectofibrosa* (Lévi, 1963) (Orig. Descrip. as *Desmacidon ectofibrosa*) (PP 1E)	300–375 × 10–12	ar: 16	South Africa/massive, light yellow-grey
Lévi (1963) (SB 9)	225–325 × 10–13	-	South Africa/massive, branched, red/7
Lévi (1963) (MB 60A)	300–375	ar: 13–14	South Africa/massive, irregular, cream/17–20
Samaai & Gibbons (2005) (As *Fibula ectyofibrosa*)	318–*353*–382 × 14	ar: 18	South Africa/thickly encrusting, massive to erect and vase-like, bright orange-red/1–20
7. *Isodictya elastica* (Vosmaer, 1880)[5] (Orig. Descrip. as *Desmacidon elastica*)	130–160 × 13	pa: 24–30	South Africa
Stephens (1915) (As *Homoeodictya elastica*)	130–160 × 9–11	pa: 19–24	South Africa/upright, branched/46
Lévi (1963) (As *Homoeodictya elastica*)	190	pa: 26	South Africa/massive with fleshy, pedunculate or digitate blades, brownish/23
Samaai & Gibbons (2005)	155–*163*–172 × 14	pa: 25–*32*–35	South Africa & Namibia/erect, dendritic, branched, beige/1–25

[5]Measurements from Stephens (1915).

Species	Megascleres Oxeas	Microscleres Isochelae ar: arcuate pa: palmate	Location/Form/Depth (m)
Samaai & Gibbons (2005) (TS 294)	173–209 × 14	pa: 32–39	South Africa/12–15
Samaai & Gibbons (2005) (SAM-H4922/TS 297)	147–182 × 14	pa: 25–35	South Africa/3–5
Samaai & Gibbons (2005) (TS 388)	154–191 × 7	pa: 32–37	South Africa/3–5
Samaai & Gibbons (2005) (TS 415)	182–200 × 7–14	pa: 32	Namibia/25–29
TS 2789	101–*137*–153 × 6–*13*–16	pa: 19–*21*–26 × 4–*5*–6	Amathole region (Eastern Cape, South Africa)/erect, stalked, foliaceous, beige/<55
TS 3836	101–*139*–155 × 5–*13*–16	pa: 23–*25*–29 × 4–*5*–6	Amathole region (Eastern Cape, South Africa)/erect, stalked, foliaceous with flagelliform projections, beige/33
TS 3956	112–*141*–153 × 6–*12*–16	pa: 25–*27*–30 × 5–*5*–7	Amathole region (Eastern Cape, South Africa)/erect, stalked, flabellate with flagelliform projections, beige/39
TS 4326	117–*147*–171 × 5–*12*–15	pa: 24–*26*–28 × 5–*6*–7	Amathole region (Eastern Cape, South Africa)/erect, stalked, foliaceous, beige/45
TS 4539	113–*139*–155 × 6–*12*–15	pa: 23–*25*–28 × 5–*5*–6	Amathole region (Eastern Cape, South Africa)/erect, stalked, foliaceous, light orange/29

Species	Megascleres Oxeas	Microscleres Isochelae ar: arcuate pa: palmate	Location/Form/Depth (m)
TS 4661	104–*142*–168 × 6–*13*–17	pa: 25–*27*–29 × 6–*6*–7	Amathole region (Eastern Cape, South Africa)/erect, stalked, foliaceous with flagelliform projections, orange-red to beige/36
8. *Isodictya foliata* (Carter, 1885) (Orig. Descrip. as *Textiliforma foliata*)	~119 × 11	~25	South Africa/stalked, frondose, purple
Hajdu & Lôbo-Hajdu (2002)	120 × 10	pa: 25	South Africa/flabellate
9. *Isodictya frondosa* (Lévi, 1963) (Orig. Descrip. as *Homoeodictya frondosa*)	500	pa: 24	South Africa/erect, stalked, blade-like, dark ochre/70–77
10. *Isodictya grandis* (Ridley & Dendy, 1886) (Orig. Descrip. as *Homoeodictya grandis*)	450 × 40	pa: 63	South Africa/erect, lamelliform, branched, greyish yellow/18–37
Ridley & Dendy (1887) (Orig. Descrip. as *Desmacidon (Homoeodictya) grandis*)	450 × 40	pa: 63	South Africa/erect, lamelliform, branched/18–37
Lévi (1963) (As *Homoeodictya grandis*)	300	pa: 38	South Africa/erect, stalked, blade-like, ochre/44–52
Samaai & Gibbons (2005)	255–*273*–300 × 23	pa: 41–*43*–46	South Africa/erect, massive, compressed to lamelliform, orange-red/15–37
Maduray (2013)	298–*312*–331 × 24–*27*–31	pa: 43–*50*–58	South Africa/erect, compressed flabellate to massive fragment, orange/50–149

Species	Megascleres Oxeas	Microscleres Isochelae ar: arcuate pa: palmate	Location/Form/Depth (m)
TS 2776	279–*360*–412 × 8–*20*–28	pa: 38–*44*–49 × 12–*14*–18	Amathole region (Eastern Cape, South Africa)/finger-like fragment, yellow/55
TS 4538	304–*383*–416 × 7–*20*–24	pa: 36–*40*–45 × 12–*13*–15	Amathole region (Eastern Cape, South Africa)/fragments, beige/29
TS 4559	245–*377*–421 × 9–*26*–34	pa: 43–*48*–53 × 12–*14*–16	Amathole region (Eastern Cape, South Africa)/blade-like fragment, yellow/42–44
TS 4667	290–*373*–420 × 14–*25*–33	pa: 41–*46*–51 × 12–*14*–16	Amathole region (Eastern Cape, South Africa)/erect fragment with protruding blades, light yellow/36
11. *Isodictya kerguelenensis* (Ridley & Dendy, 1886) (Orig. Descrip. as *Homoeodictya kerguelenensis*)	350 × 19	pa: 28	Kerguelen Islands/lobate or digitate, light brownish yellow/46
Ridley & Dendy (1887) (Orig. Descrip. as *Desmacidon (Homoeodictya) kerguelenensis*)	350 × 19	pa: 28	Kerguelen Islands/stalked, lobate or digitate/46
Lévi (1956)	125–275 × 8	pa: 30 × 10	Kerguelen Islands/stalked, massive, cylindroconical/intertidal
Boury-Esnault & van Beveren (1982)	320–*421*–659 × 9–*15*–19	pa: 20–*23*–27	Kerguelen, Heard and Macdonald Islands/pedunculate, blade-like/6–260
12. *Isodictya multiformis* (Stephens, 1915) (Orig. Descrip. as *Homoeodictya multiformis*)	175–255 × 10–13	pa: 32–40 × 10	South Africa/thickly encrusting to erect, stalked, with coalescent rounded tubes to flattened branches or fan-like lobes/9–46

Species	Megascleres Oxeas	Microscleres Isochelae ar: arcuate pa: palmate	Location/Form/Depth (m)
Lévi (1963) (As *Homoeodictya multiformis*) (SCD 52B)	220–225	pa: 32–33	South Africa/attached to sea fan, branched/46
Lévi (1963) (FAL 230A)	270–290	pa: 32–35	South Africa/stalked, branched, greyish yellow/49
Samaai & Gibbons (2005)	I) 133–197 × 9–11 II) 105–151 × 2	pa: 29–35	South Africa/encrusting, epiphytic and massive to erect and fan-like, lobed, beige to purple with brown patches/1–27
TS 2803	178–*233*–253 × 4–*12*–14	pa: 26–*29*–31 × 7–*7*–8	Amathole region (Eastern Cape, South Africa)/thickly encrusting on sea fan and hydroids, dirty cream with pinkish tinge/<55
TS 3504	191–*237*–256 × 5–*12*–16	pa: 26–*30*–33 × 6–*7*–8	Amathole region (Eastern Cape, South Africa)/thickly encrusting on sea fan, light brown/87
TS 3725	181–*242*–259 × 4–*14*–16	pa: 27–*29*–31 × 6–*7*–8	Amathole region (Eastern Cape, South Africa)/thickly encrusting on sea fan, beige/78
TS 3995	187–*208*–223 × 8–*10*–12	pa: 26–*28*–31 × 6–*6*–7	Amathole region (Eastern Cape, South Africa)/thickly encrusting on hydroid, beige/28

Species	Megascleres Oxeas	Microscleres Isochelae ar: arcuate pa: palmate	Location/Form/Depth (m)
TS 4322	164–*207*–221 × 4–*12*–15	pa: 28–*30*–34 × 6–*6*–7	Amathole region (Eastern Cape, South Africa)/thickly encrusting on sea fan, light yellow/45
TS 4714	167–*232*–249 × 4–*14*–16	pa: 28–*31*–34 × 6–*7*–8	Amathole region (Eastern Cape, South Africa)/thickly encrusting on sea fan, dark beige/65–76
13. *Isodictya verrucosa* (Topsent, 1913) (Orig. Descrip. as *Homoeodictya verrucosa*)	520 × 17	pa: 27–37 × 6	Burdwood Bank (Malvinas, Falklands)/ cylindroconical column/102
Boury-Esnault & van Beveren (1982)	212–*288*–358 × 6–*11*–13	pa: 22–*27*–32	Kerguelen Islands/erect, stalked, cup-like, pink-ochre to grey/4–123

The specimens conform closely to *Isodictya compressa*, which was described as *Spongia compressa* by Esper in 1797, who suggested an extensive geographic distribution (Norway, Greenland and North America to East India). Ehlers (1870) re-described Esper's material (oxeas: 440 µm; isochelae: 36 µm), reassigned it to the genus *Desmacidon* Bowerbank, 1861, and noted that Esper had likely confused several species of a similar form, and that the type locality was unknown. On examining Bowerbank's collection in the Natural History Museum, London, Carter (1882) assigned a few South African specimens to this species, with reassignment to the genus *Chalina* Grant, 1861. Stephens (1915) recorded a further two specimens of this species from South Africa, supported by the examination of a fragment of the type specimen, and reassigned it to the genus *Homoeodictya* Ehlers, 1870. Subsequently, this species was synonymised with *Spongia pannea* Lamarck, 1814 by Topsent (1931), who suggested the Antilles as a possible type locality, and reassigned it to the genus *Isodictya*. Lévi (1963) and Samaai & Gibbons (2005) provide additional records of this species from South Africa. Finally, van Soest *et al.* (2020b) noted that *Spongia compressa* Esper, 1797 was a junior primary homonym of *Spongia compressa* Fabricius, 1780. However, the latter species was nominated as the type species of *Grantia* Fleming, 1828. As the former species was not considered congeneric with *Grantia compressa* after 1899, the homonymy was removed and the use of *Isodictya compressa* (Esper, 1797) maintained.

Ten other congeners occur in and around South Africa. *Isodictya chichatouzae* Uriz, 1984, described from the South African/Namibian border has two size classes of oxeas (I) 520–630 × 18–28 µm; II) 215–260 × 8–9 µm) and comprises vasiform branches to a cup-like form. *Isodictya conulosa* and *Isodictya grandis*, both described from South Africa by Ridley & Dendy (1886), comprise very large oxeas (700 × 57 µm) and characteristic large isochelae (63 µm) respectively. Also described from South Africa, *Isodictya elastica* (Vosmaer, 1880) and *Isodictya foliata* (Carter, 1885) have smaller oxeas (130–160 × 13 µm and ~119 × 11 µm respectively), often below 200 µm. Similarly, *Isodictya multiformis* (Stephens, 1915) also has smaller oxeas (175–255 × 10–13 µm), but often below 300 µm. In addition, this South African species is consistently found to be thickly encrusting on sea fans and/or hydroids in the Amathole region. The remaining four species are largely differentiated from *I. compressa* according to growth form. Moreover, *Isodictya kerguelenensis* (Ridley & Dendy, 1886) and *Isodictya verrucosa* (Topsent, 1913) have slightly narrower oxeas (350 × 19 µm and 520 × 17 µm respectively).

Overall, *Isodictya compressa* is generally identifiable by its conspicuous and consistent form, though the characteristic spicule tufts may be worn away in beach-cast specimens (Carter 1882b). Interestingly, specimens from this study and those noted in Carter (1882b), which were all collected from the south-east coast of South Africa, have smaller spicule sizes than those collected from the west coast and detailed in Stephens (1915), Lévi (1963) and Samaai & Gibbons (2005).

This genus is diverse in South Africa, with seven out of the ten species described and/or recorded from this country currently considered endemic (Appendix A). With relatively low spicule diversity, intraspecific spicule variation according to collection location, and often similar growth forms, extensive revision is required.

Key diagnostic characters:

- erect, stalked, flabellate form;
- upper area compressed, comprising a cluster of fused tubes with oscules (~1 cm) at apices;
- ridged surface, with conspicuous spicule tufts (up to 1 cm) throughout;
- resilient;
- beige in life;
- megascleres exclusively one size class of oxeas, 220–560 µm;

- microscleres exclusively one size class of palmate isochelae, 20–36 µm.

***Isodictya elastica* (Vosmaer, 1880)**

(Fig. 23A–G, Table 17)

Synonymy.

Desmacidon elastica Vosmaer, 1880: 132.

Homoeodictya elastica; Stephens 1915: 453; Burton 1936: 143; Lévi 1963: 22.

Isodictya elastica; Samaai & Gibbons 2005: 69.

Material examined. TS 4661 (AI2-Spg429): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–81, Station 3893 (33.1632º S, 27.7746º E–33.1625º S, 27.7753º E, Eastern Cape, South Africa), 36 m depth, amongst shell hash, SST 18 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 3 min, 03 September 2016. NIWA 110811 (0CDN6338-X): Orient Pier, East London Harbour, NIWA Station Z17503 (33.0278º S, 27.9175º E, Eastern Cape, South Africa), 3 m depth, on rock near cement wall, coll. P. L. Colin, CRRF, via SCUBA, 11 February 1999, field identification by M. Kelly, NIWA, Auckland. TS 2789: Amathole region, Station unknown (32.9333º S, 28.0800º E, Eastern Cape, South Africa), <55 m depth, coll. T. Samaai & S. Kerwath on R/V *Ellen Khuzwayo* (Voyage 131), benthic dredge, 27 February 2015. TS 3836 (BD25-Spg1(8)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–101, Station 3807 (33.1347º S, 27.7689º E–33.1604º S, 27.7762º E, Eastern Cape, South Africa), 33 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 23 min, 02 March 2016. TS 3947 (BD26-Spg1(1)), TS 3956 (BD26-

Spg1(10)), TS 3968 (BD26-Spg1(22)), TS 3969 (BD26-Spg1(23)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–102, Station 3808 (33.1597º S, 27.7777º E–33.1616º S, 27.7778º E, Eastern Cape, South Africa), 39 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 20 min, 02 March 2016. TS 4282 (AI2-Spg50): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–2, Station 3814 (32.6663º S, 28.4412º E–32.6714º S, 28.4397º E, Eastern Cape, South Africa), 29–35 m depth, amongst boulders, shell hash and pebbles, SST 20 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 10 min, 26 August 2016. TS 4308 (AI2-Spg76): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–3, Station 3815 (32.6511º S, 28.4609º E–32.6581º S, 28.4653º E, Eastern Cape, South Africa), 38–43 m depth, amongst rock, coquina/shell hash, pebbles and coarse sand with shell fragments, SST 20 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 10 min, 26 August 2016. TS 4326 (AI2-Spg94), TS 4335 (AI2-Spg103), TS 4340 (AI2-Spg108), TS 4346 (AI2-Spg114), TS 4347 (AI2-Spg115): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–20, Station 3832 (32.7597º S, 28.4110º E–32.7587º S, 28.4119º E, Eastern Cape, South Africa), 45 m depth, amongst rock, SST 20 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 5 min, 27 August 2016. TS 4536 (AI2-Spg304), TS 4539 (AI2-Spg307): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–58, Station 3870 (32.9485º S, 28.0577º E–32.9478º S, 28.0588º E, Eastern Cape, South Africa), 29 m depth, amongst boulders, shell hash and pebbles, SST 18 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 3 min, 31 August 2016.

Description. Erect, stalked, foliaceous form with flagelliform projections along margin (Fig. 23A & B). Length 11 cm, width 13 cm and thickness 3 mm. Surface velvety, with oscules arranged in numerous stellate groups (1–2 mm) (Fig. 23C), at regular intervals from one another (2–3 mm), on both sides of sponge. Texture spongy and dense, very compressible, resilient but easily torn. Colour *in situ* orange-red to beige, in preservative beige. Distinct, sweet smell present.

Skeleton. Choanosomal skeleton plumoreticulate, with incorporated sand grains (Fig. 23D). Primary multispicular megasclere tracts (~20–80 µm across), without a distinct spongin sheath, run longitudinally through sponge, around subdermal spaces, and diverge to form plumose brushes at surface. These tracts pierce indistinguishable dermal membrane lacking specialisation, projecting beyond surface as spicule tufts (up to ~150 µm) (Fig. 23E). Primary tracts are connected irregularly by perpendicular to oblique single oxeas or secondary multispicular megasclere tracts (~30–50 µm across), with somewhat distinct spongin sheath. Isochelae scarce, scattered throughout.

Spiculation. Megascleres. Oxeas smooth, straight to slightly curved medially, acerate: 104–*142*–168 × 6–*13*–17 µm, n = 15 (Fig. 23F). **Microscleres.** Palmate isochelae: 25–*27*–29 × 6–*6*–7 µm, n = 15 (Fig. 23G).

Distribution and ecology. Known only from South Africa and Namibia. Occurs amongst boulders, rock, coquina/shell hash, pebbles and coarse sand with shell fragments. Associated with red algae, while some material had coralline algae (NIWA 110811) and tube worm (TS 3956) epifauna. Four specimens (TS 4326, TS 4346, TS 4347, TS 4661) collected late August/early September possessed bright orange eggs (up to 3 mm) throughout (Fig. 23B). Depth range: 1–46 m.

Remarks. Of the 13 *Isodictya* species that have been described and/or recorded in and around South Africa (van Soest *et al.* 2020a), only two comprise small oxeas (<200 µm): *Isodictya elastica* (Vosmaer, 1880) and *Isodictya foliata* (Carter, 1885).

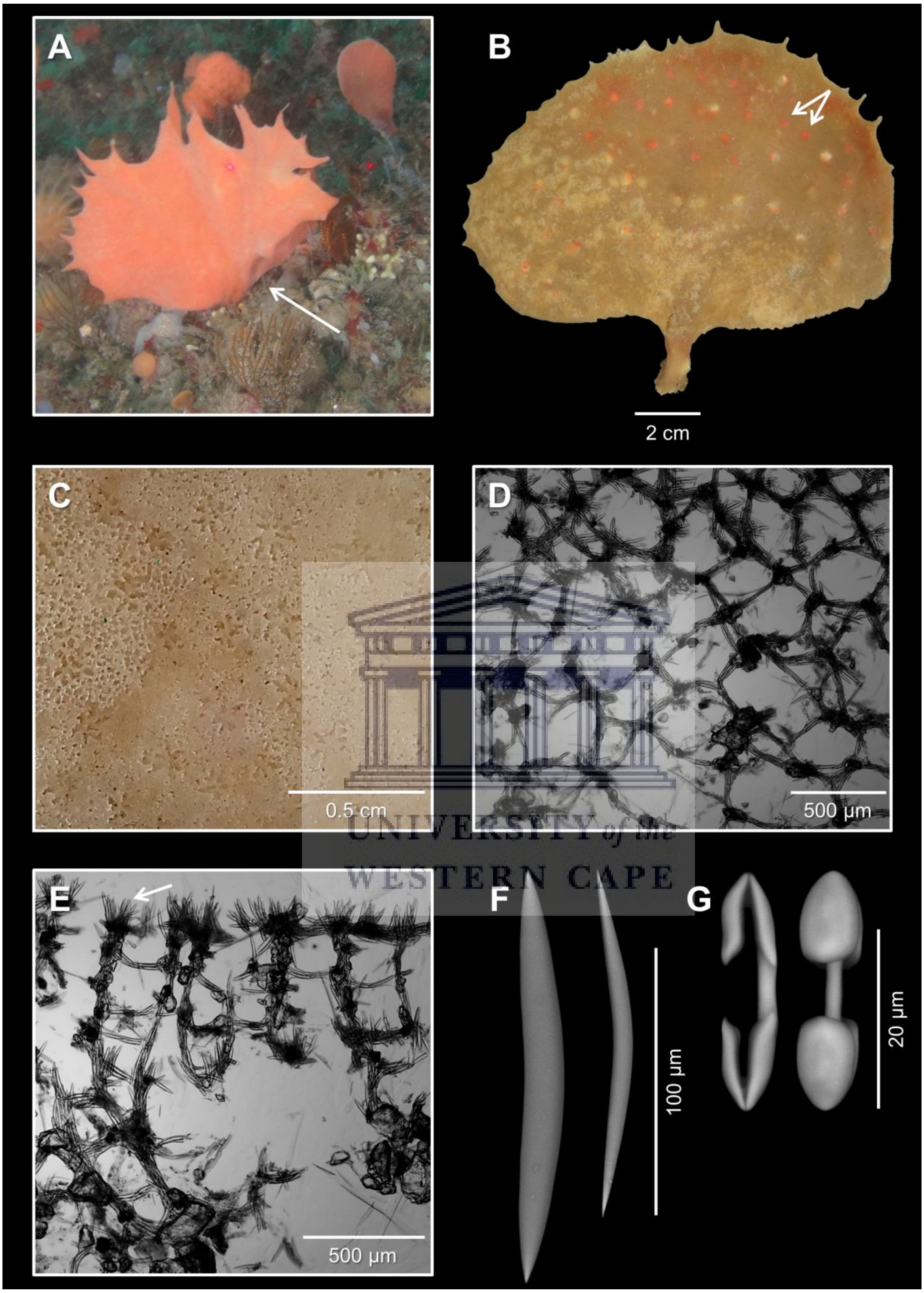

Figure 23: *Isodictya elastica* (Vosmaer, 1880). A, species *in situ* (R2). B, specimen TS 4661 with eggs (arrows). C, stellate groups of oscules. D, E, choanosomal skeleton with primary megasclere tracts piercing indistinguishable dermal membrane to form spicule tufts (arrow). F, oxeas. G, palmate isochelae.

Vosmaer (1880) described *Isodictya elastica* from South African specimens in the Leyden Museum (now the Naturalis Biodiversity Center, Leiden). Stephens (1915) assigned a single specimen from Saldanha Bay to this species, supported by the examination of the type material, for which she supplied the first spicule measurements (oxeas: 130–160 × 13 µm; isochelae: 24–30 µm). Lévi (1963) and Samaai & Gibbons (2005) provide additional records of this species from South Africa.

In 1885, Carter described *Isodictya foliata* from dry South African specimens in the British Museum (now the Natural History Museum, London). This species is very similar to both the material examined, and *I. elastica*, according to the form, the presence of stellate groups of oscules, and spicule measurements (oxeas: ~119 × 11 µm; isochelae: ~25 µm). Subsequently, this species was briefly mentioned by Hajdu & Lôbo-Hajdu (2002), but the type series was not examined.

Further research is required to determine whether these two species are conspecific, which seems likely. Until then, the material examined is assigned to *I. elastica*, as it was described first and has more comparative material, as opposed to *I. foliata*, which has not been recorded in the taxonomic literature since its description.

Key diagnostic characters:

- erect, stalked, foliaceous form with flagelliform projections along margin;
- velvety surface;
- oscules in stellate groups (1–2 mm), at regular intervals (2–3 mm), on both sides;
- resilient;
- orange-red to beige in life;
- skeleton with incorporated sand grains;
- bright orange eggs (up to 3 mm) present during late August/early September;

- megascleres exclusively one size class of small oxeas, <200 µm.

***Isodictya grandis* (Ridley & Dendy, 1886)**

(Fig. 24A–E, Table 17)

Synonymy.

Homoeodictya grandis Ridley & Dendy, 1886: 347; Lévi 1963: 23.

Desmacidon (Homoeodictya) grandis; Ridley & Dendy 1887: 111.

Desmacidon grande; Kirkpatrick 1903b: 252.

Isodictya grandis; Samaai & Gibbons 2005: 70; Maduray 2013: 45.

Material examined. **TS 4667 (AI2-Spg435)**: ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–81, Station 3893 (33.1632º S, 27.7746º E–33.1625º S, 27.7753º E, Eastern Cape, South Africa), 36 m depth, amongst shell hash, SST 18 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 3 min, 03 September 2016. TS 2776: Amathole region, Station 491 (32.9350º S, 28.0933º E, Eastern Cape, South Africa), 55 m depth, coll. T. Samaai & S. Kerwath on R/V *Ellen Khuzwayo* (Voyage 131), benthic dredge, 24 February 2015. TS 4538 (AI2-Spg306): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–58, Station 3870 (32.9485º S, 28.0577º E–32.9478º S, 28.0588º E, Eastern Cape, South Africa), 29 m depth, amongst boulders, shell hash and pebbles, SST 18 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 3 min, 31 August 2016. TS 4559 (AI2-Spg327): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–61, Station 3873 (32.9476º S, 28.0699º E–32.9458º S, 28.0731º E, Eastern Cape, South Africa), 42–44 m depth, amongst shell hash and coarse sand with shell fragments, SST 19 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 6 min, 31 August 2016.

Description. Erect fragment, with protruding blades (Fig. 24A & B). Length 5 cm, width 6 cm and thickness 5 mm. Surface microhispid and microconulose, prickly and rough. Oscules arranged in numerous stellate groups (~2 mm), at regular intervals from one another (~4 mm), on one side of sponge only (Fig. 24B). Texture spongy and dense, compressible, tears easily and breaks so-so. Colour *in situ* light yellow, in preservative beige.

Skeleton. Choanosomal skeleton plumoreticulate (Fig. 24C). Primary multispicular megasclere tracts (~130–270 µm across), without a distinct spongin sheath, run longitudinally through sponge, around subdermal spaces, and diverge to form plumose brushes at surface. These tracts pierce indistinguishable dermal membrane lacking specialisation, projecting up to ~350 µm beyond surface. Primary tracts are connected irregularly by perpendicular to oblique single oxeas or secondary multispicular megasclere tracts (~60–180 µm across). Isochelae scattered throughout.

Spiculation. Megascleres. Oxeas smooth, straight to slightly curved medially, acerate: 290–*373*–420 × 14–*25*–33 µm, n = 15 (Fig. 24D). **Microscleres.** Palmate isochelae with frontal ala possessing a stout backward projection, and slight irregular swelling in the middle of the shaft: 41–*46*–51 × 12–*14*–16 µm, n = 15 (Fig. 24E).

Distribution and ecology. Known only from South Africa. Occurs amongst boulders, rock, shell hash, pebbles and coarse sand with shell fragments. Associated with foliose and encrusting algae, sponges, soft corals (Samaai & Gibbons 2005) and *Phyllochaetopterus* Grube, 1863 (Lévi 1963). Depth range: 15–155 m.

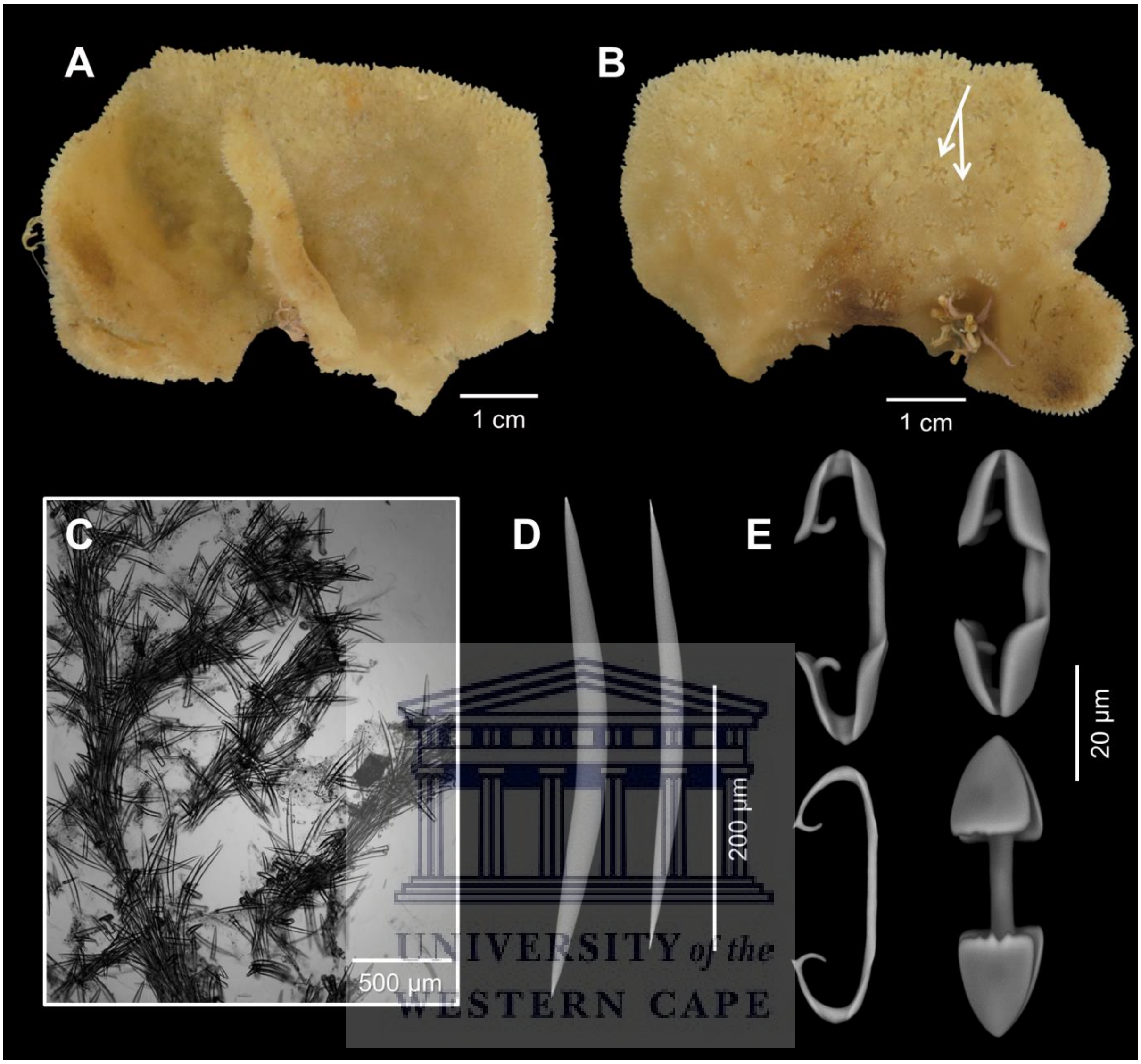

Figure 24: *Isodictya grandis* (Ridley & Dendy, 1886). A, B, specimen TS 4667 with stellate groups of oscules on one side only (arrows). C, choanosomal skeleton. D, oxeas. E, palmate isochelae.

Remarks. *Isodictya grandis* was described by Ridley & Dendy (1886) from a single specimen collected in False Bay (oxeas: 450 × 40 µm; isochelae: 63 µm), and was subsequently recorded by Kirkpatrick (1903b), who provided no measurements. The material examined conforms to this species, but has smaller spicules more comparable to those detailed by Lévi (1963) (oxeas: 300 µm; isochelae: 38 µm), Samaai & Gibbons (2005) (oxeas: 255–*273*–300 × 23 µm; isochelae: 41–*43*–46 µm), and Maduray (2013) (oxeas: 298–

312–331 × 24–*27*–31; isochelae: 43–*50*–58). This species has stellate groups of oscules on only one side, and is easily differentiated from local congeners due to the very large isochelae (~36–63 µm) of distinct form.

In 1977, Collette & Rützler reported this species from off the Amazon River mouth, but provided no description. Consequently, Muricy *et al.* (2011) included *I. grandis* in their 'Catalogue of Brazilian Porifera'. However, van Soest *et al.* (2020a) currently regard these records as inaccurate.

Key diagnostic characters:

- erect form, with protruding blades;
- microhispid and microconulose surface;
- oscules in stellate groups (~2 mm), at regular intervals (~4 mm), on one side;
- somewhat resilient;
- light yellow in life;
- microscleres exclusively large palmate isochelae (36–63 µm), of distinct form.

***Isodictya multiformis* (Stephens, 1915)**

(Fig. 25A–G, Table 17)

Synonymy.

Homoeodictya multiformis Stephens, 1915: 454; Lévi 1963: 24.

Platychalina multiformis; Burton 1936: 141.

Isodictya multiformis; Samaai *et al.* 1999: 518; Samaai & Gibbons 2005: 71; Maduray 2013: 67.

Material examined. **<u>TS 4322</u> (AI2-Spg90)**: ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–20, Station 3832 (32.7597º S, 28.4110º E–32.7587º S, 28.4119º E, Eastern Cape, South Africa), 45 m depth, amongst rock, SST 20 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 5 min, 27 August 2016. <u>TS 2803</u>: Amathole region, Station unknown (32.9333º S, 28.0800º E, Eastern Cape, South Africa), <55 m depth, coll. T. Samaai & S. Kerwath on R/V *Ellen Khuzwayo* (Voyage 131), benthic dredge, 27 February 2015. <u>TS 3504</u> (BD4-Spg32): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–16, Station 3722 (32.8300º S, 28.4593º E–32.8327º S, 28.4573º E, Eastern Cape, South Africa), 87 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 9 min, 22 February 2016. <u>TS 3725</u> (BD1-Spg37): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–10, Station 3716 (32.7531º S, 28.5177º E–32.7547º S, 28.5207º E, Eastern Cape, South Africa), 78 m depth, amongst cobbles and shell hash, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 24 min, 21 February 2016. <u>TS 3995</u> (BD21-Spg1(4)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–74, Station 3780 (32.6674º S, 28.4269º E–32.6640º S, 28.4309º E, Eastern Cape, South Africa), 28 m depth, amongst boulders, rock and shell hash, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 9 min, 28 February 2016. <u>TS 4714</u> (AI2-Spg482): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–97, Station 3909 (33.2020º S, 27.8586º E–33.1949º S, 27.8610º E, Eastern Cape, South Africa), 76–65 m depth, amongst cobbles, rock, shell hash and pebbles, SST 18 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 12 min, 05 September 2016.

Description. Thickly encrusting on sea fan (Fig. 25A–C). Length 12 cm, width 13 cm and thickness 4 mm. Surface velvety, with slightly raised subcircular oscules (up to 2 mm) on margin, and uniform subcircular ostia (<1 mm) evenly distributed throughout. Texture spongy, very compressible, soft and friable. Colour *in situ* white, after freezing light yellow, in preservative dark yellow.

Skeleton. Choanosomal skeleton plumoreticulate (Fig. 25D). Primary multispicular megasclere tracts (~30–120 µm across), without a distinct spongin sheath, run vertically to surface, around subdermal spaces, and diverge to form plumose brushes. These tracts pierce indistinguishable dermal membrane lacking specialisation, projecting up to ~380 µm beyond surface (Fig. 25E). Primary tracts are connected irregularly by perpendicular to oblique single oxeas or secondary paucispicular megasclere tracts (~20–50 µm across). Isochelae scattered throughout.

Spiculation. Megascleres. Oxeas smooth, straight to slightly curved, often medially, acerate: 164–*207*–221 × 4–*12*–15 µm, n = 15 (Fig. 25F). **Microscleres.** Palmate isochelae: 28–*30*–34 × 6–*6*–7 µm, n = 15 (Fig. 25G).

Distribution and ecology. Known only from South Africa. Occurs amongst boulders, cobbles, rock, shell hash, pebbles and coarse sand with shell fragments. Associated with foliose and encrusting algae, hydroids (e.g. *Sertularella* Gray, 1848), soft coral, and sponges (e.g. *Myxilla (Myxilla) simplex* (Baer, 1906)) (Stephens 1915; Lévi 1963; Samaai & Gibbons 2005). All material examined was thickly encrusting on sea fans (TS 2803, TS 3504, TS 3725, TS 4322, TS 4714) and/or hydroids (TS 2803, TS 3995). A large specimen examined by Stephens (1915), collected in late May, possessed many embryos. Depth range: 1–87 m (previously 1–77 m).

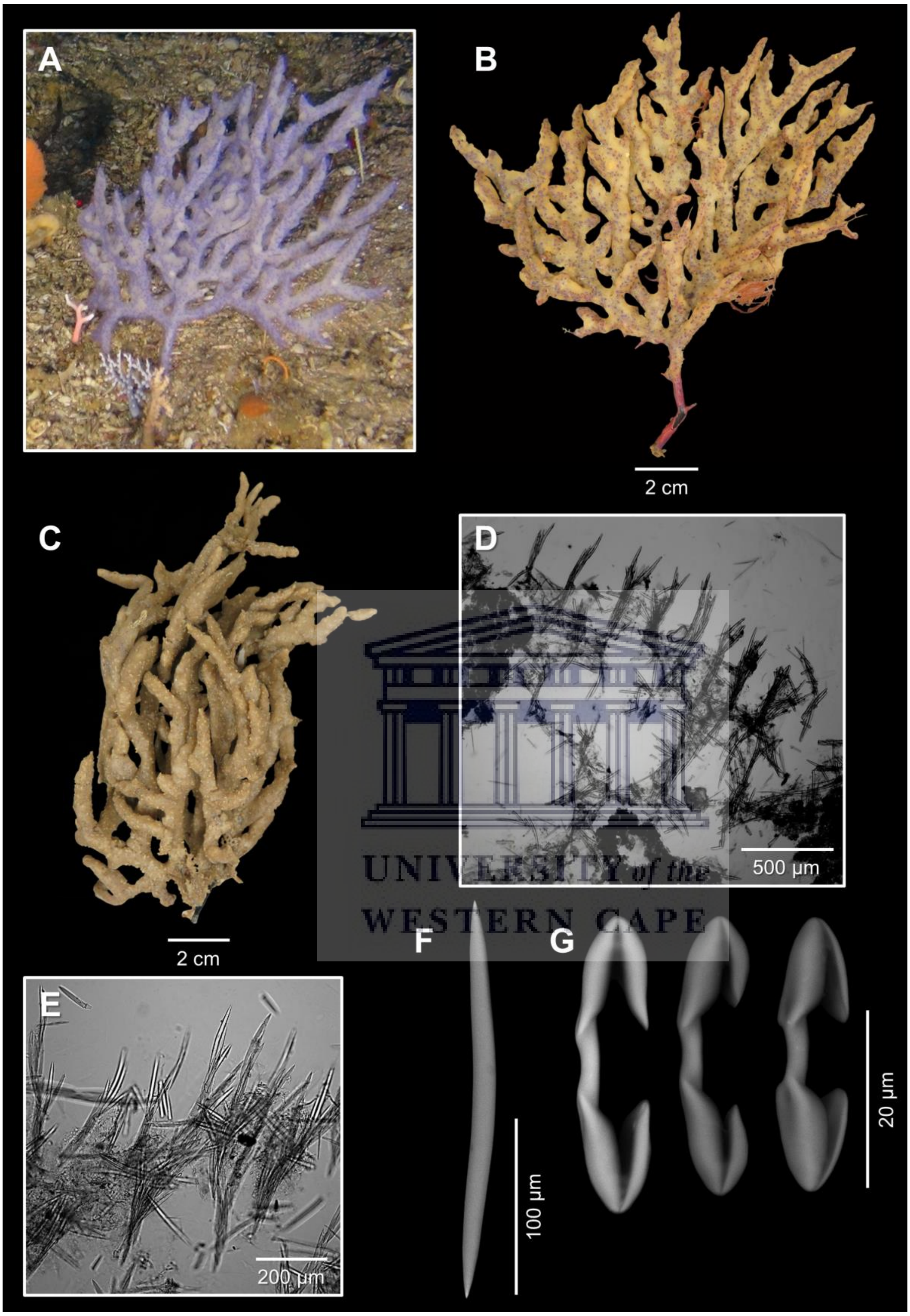

Figure 25: *Isodictya multiformis* (Stephens, 1915). A, species *in situ* (R88). B, specimen TS 4322. C, specimen TS 4714. D, choanosomal skeleton. E, primary multispicular megasclere tracts piercing indistinguishable dermal membrane. F, oxea. G, palmate isochelae.

Remarks. *Isodictya multiformis* was described by Stephens (1915) from over 60 specimens comprising various forms, collected in Saldanha Bay. The above material is assigned to this species, and easily differentiated from congeners in and around South Africa, based on its thickly encrusting/epiphytic form and relatively small megascleres. These are slightly larger than the oxeas reported for *Isodictya elastica* (Vosmaer, 1880) and *Isodictya foliata* (Carter, 1885), but are consistently less than 300 µm.

Key diagnostic characters:

- polymorphic, thickly encrusting/epiphytic in the Amathole region;
- velvety surface;
- slightly raised subcircular oscules (up to 2 mm) on margin;
- soft and friable;
- white, light yellow to beige in life;
- embryos present in late May;
- megascleres exclusively one size class of oxeas, <300 µm.

Family Myxillidae Dendy, 1922

Genus *Ectyonopsis* Carter, 1883

Type species: *Ectyonopsis ramosa* Carter, 1883 (by monotypy).

Diagnosis. Myxillidae with ectosomal diactinal spicules. Choanosomal di- or monactinal spicules: acanthostrongyles, and acanthostyles. Microscleres anchorate or unguiferate isochelae and sigmas. Choanosome with an isotropic reticulum (from Aguilar-Camacho & Carballo 2012).

***Ectyonopsis flabellata* (Lévi, 1963)**

(Fig. 26A–H, Table 18)

Synonymy.

Ectyonancora flabellata Lévi, 1963: 37.

Ectyonopsis flabellata; van Soest 2002c: 604; Samaai & Gibbons 2005: 59.

Material examined. TS 3482 (BD4-Spg38): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–16, Station 3722 (32.8300º S, 28.4593º E–32.8327º S, 28.4573º E, Eastern Cape, South Africa), 87 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 9 min, 22 February 2016.

Description. Erect fragment (Fig. 26A). Length 4 cm, width 2 cm and thickness 1 cm. Surface rough with regular, circular, oscules (<1 mm) throughout. Texture firm and dense, barely compressible, but brittle. Colour *in situ*, and in preservative, dark brown.

Skeleton. Choanosomal skeleton comprises an isotropic (somewhat isodictyal) reticulation of acanthostyles and acanthostrongyles (Fig. 26B), cemented at spongin nodes (Fig. 26C). Loose tornotes and isochelae scattered throughout choanosome, but concentrated in ectosome which comprises a detachable surface membrane (~120–450 µm), pierced by acanthostyle tips.

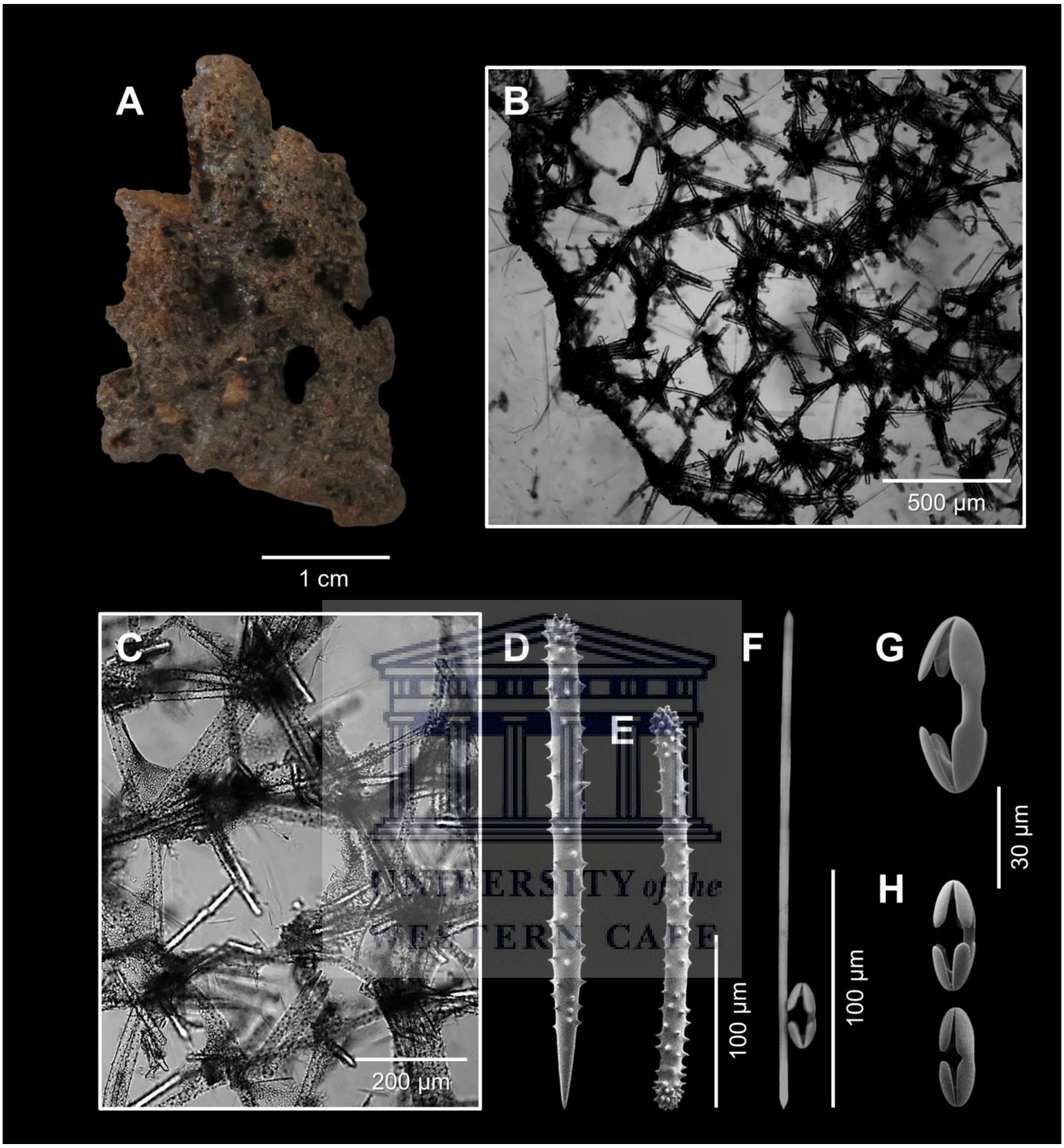

Figure 26: *Ectyonopsis flabellata* (Lévi, 1963). A, specimen TS 3482. B, choanosomal skeleton. C, spongin nodes. D, acanthostyle. E, acanthostrongyle. F, tornote. G, anchorate isochela I. H, anchorate isochelae II.

Table 18: Comparative spicule dimensions and known location, form and depth for the accepted species of *Ectyonopsis* Carter, 1883 occurring in South Africa and the Kerguelen Islands according to van Soest *et al.* (2020a). Spicule dimensions expressed in µm, with specimen from this study (TS) given as minimum–*mean*–maximum length × width, n = 15.

Species	Megascleres			Microscleres	Location/Form/Depth (m)
	Acanthostyles	**Acanthostrongyles**	**Tornotes**	**Isochelae**	
1. *Ectyonopsis flabellata* (Lévi, 1963)[6] (Orig. Descrip. as *Ectyonancora flabellata*)	225–300 × 20–25	220–250 × 22–25	145–180 × 7	I) 40–57 II) 27–32	South Africa/erect, flabellate, brown/14–51
Samaai & Gibbons (2005)	188–*207*–233	174–*189*–202	144–*174*–184	33–*36*–42	South Africa/encrusting, bulbous, dark red/15
TS 3482	293–*316*–345 × 16–*19*–22	227–*239*–251 × 13–*16*–19	178–*219*–246 × 3–*4*–5	I) 43–*47*–50 × 16–*17*–18 II) 23–*28*–30 × 9–*11*–13	Amathole region (Eastern Cape, South Africa)/erect, fragment, dark brown/87
2. *Ectyonopsis panis* (Boury-Esnault & van Beveren, 1982) (Orig. Descrip. as *Ectyonancora panis*)	256–*355*–512 × 13–*21*–26	211–*263*–314 × 13–*14*–19	272–*330*–365 × 6–*11*–13	25–*29*–33	Kerguelen Islands/massive/ 100–130
3. *Ectyonopsis pluridentata* (Lévi, 1963) (Orig. Descrip. as *Ectyonancora pluridentata*)	430–470 × 22–27	325–375 × 22–26	260–320 × 4	I) 85 II) 35–37	South Africa/massive, ochre/79–201

[6] Van Soest (2002c) gave same measurements in re-description of MNHN LBIM DCL. 548 & 549.

Spiculation. Megascleres. Acanthostyles heavily spined, with knob-like spines on the head and straight to hook-like spines on the shaft, straight to slightly curved, largely smooth hastate tips: 293–*316*–345 × 16–*19*–22 µm, n = 15 (Fig. 26D). Acanthostrongyles heavily spined, with knob-like spines on both apices and straight to hook-like spines on the shaft, straight to slightly curved: 227–*239*–251 × 13–*16*–19 µm, n = 15 (Fig. 26E). Tornotes smooth, straight, mucronate: 178–*219*–246 × 3–*4*–5 µm, n = 15 (Fig. 26F). **Microscleres.** Anchorate isochelae, spatuliferous and robust, tridentate, in two size classes: I) 43–*47*–50 × 16–*17*–18 µm, n = 15 (Fig. 26G); II) 23–*28*–30 × 9–*11*–13 µm, n = 15 (Fig. 26H).

Distribution and ecology. Known only from South Africa, occurring amongst rock, shell, gravel and sand. Associated with foliose and encrusting algae, as well as other sponges (Samaai & Gibbons 2005). Depth range: 14–87 m (previously 14–51 m).

Remarks. The single specimen examined above is assigned to *Ectyonopsis* as diagnosed by the presence of anchorate isochelae microscleres, diactinal ectosomal spicules (tornotes) and choanosomal di- and/or monactinal spicules (acanthostrongyles and acanthostyles), forming an isotropic reticulation (Aguilar-Camacho & Carballo 2012).

The specimen conforms closely to *Ectyonopsis flabellata*, which was described from South Africa by Lévi in 1963 (acanthostyles: 225–300 × 20–25 µm; acanthostrongyles: 220–250 × 22–25 µm; tornotes: 145–180 × 7 µm; isochelae: I) 40–57 µm, II) 27–32 µm), re-described by van Soest (2002c), and later recorded by Samaai & Gibbons (2005). Also from South Africa, *Ectyonopsis pluridentata* (Lévi, 1963) differs in its consistently larger megasclere sizes (acanthostyles: 430–470 × 22–27 µm; acanthostrongyles: 325–375 × 22–26 µm; tornotes: 260–320 × 4 µm), and larger pluridentate isochelae (85 µm). Finally, *Ectyonopsis panis* (Boury-Esnault & van Beveren, 1982) from the Kerguelen Islands has only one size class of isochelae (25–*29*–33 µm), as opposed to the two found in *E. flabellata*.

Key diagnostic characters:

- encrusting to erect, flabellate form;
- regular, circular, oscules (<1 mm) throughout;
- brittle;
- dark brown in life;
- acanthostyles <400 µm, acanthostrongyles and tornotes <300 µm;
- two size classes of tridentate anchorate isochelae, the larger <60 µm.

Genus *Myxilla* Schmidt, 1862

Type species: *Halichondria rosacea* Lieberkühn, 1859 (by subsequent designation).

Diagnosis. Myxillidae with ectosomal tylote tornotes with spined apices and a choanosomal reticulation of spined or smooth styles; microscleres include anchorate chelae with only three teeth (from van Soest 2002c).

Subgenus *Myxilla (Myxilla)* Schmidt, 1862

Type species: *Halichondria incrustans* Johnston, 1842 (by subsequent designation)

Diagnosis. *Myxilla* with isotropic skeleton made up of acanthostyles in a single size category (from van Soest 2002c).

Myxilla (Myxilla) lissotylota sp. nov. ▲

(Fig. 27A–H, Table 19)

Material examined. **TS 3674** **(BD1-Spg3(6))**: ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–10, Station 3716 (32.7531º S, 28.5177º E–32.7547º S, 28.5207º E, Eastern Cape, South Africa), 78 m depth, amongst cobbles and shell hash, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 24 min, 21 February 2016. TS 3481 (BD4-Spg41), TS 3500 (BD4-Spg35): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–16, Station 3722 (32.8300º S, 28.4593º E–32.8327º S, 28.4573º E, Eastern Cape, South Africa), 87 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 9 min, 22 February 2016. TS 3914 (BD6-Spg1(23)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–18, Station 3724 (32.8345º S, 28.4682º E–32.8361º S, 28.4635º E, Eastern Cape, South Africa), 76 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 11 min, 22 February 2016.

Description. Thickly encrusting on rock (Fig. 27A). Length 4 cm, width 5 cm and thickness 1 cm. Surface microhispid, rough, with uniform subcircular ostia (<1 mm) throughout (Fig. 27B). Texture soft and spongy, very compressible, fragile. Colour *in situ* light yellow, in preservative beige.

Skeleton. Choanosomal skeleton comprises a tight-meshed isotropic reticulation of acanthostyles cemented via spongin, without echinating spicules (Fig. 27C). Ectosomal skeleton presumably comprises tylotes arranged tangentially and/or in vertical brushes at surface (not seen). Microscleres scattered throughout.

Spiculation. Megascleres. Acanthostyles heavily spined, with straight to knob-like spines on the rounded head and straight to hook-like spines on the shaft, straight to slightly curved, acerate, rarely rounded to become aniso-acanthostrongyles: 283–*311*–327 × 17–*19*–21 µm, n = 15 (Fig. 27D). Tylotes smooth, straight, with reduced elongate apices: 169–*181*–198 × 2–*3*–4 µm, n = 15 (Fig. 27E). **Microscleres.** Sigmata smooth, C-shaped, with endings suddenly bent 90º: 70–*76*–85 × 2–*3*–4 µm, n = 15 (Fig. 27F). Anchorate isochelae, spatuliferous and robust, tridentate, in two size classes: I) 58–*70*–78 × 17–*20*–27 µm, n = 15 (Fig. 27G); II) 22–*28*–32 × 8–*11*–13 µm, n = 15 (Fig. 27H).

Distribution and ecology. Currently only known from the Amathole region (Eastern Cape, South Africa), occurring amongst cobbles and shell hash. Some material examined had hydroid and barnacle epifauna (TS 3674), as well as sponge (*Pachastrella caliculata* Kirkpatrick, 1902) endofauna (TS 3914). Depth range: 76–87 m.

Provisional etymology. *Lissos* (Gr.) = smooth, referring to the smooth tylote megascleres.

Remarks. Assignment of the above material to *Myxilla (Myxilla)* is based on the presence of a tight-meshed isotropic skeleton comprised of choanosomal acanthostyles in a single size class, ectosomal tylotes that presumably form a tangential skeleton and/or vertical brushes, as well as spatuliferous tridentate anchorate isochelae and sigmata microscleres (van Soest 2002c).

Of the 50 species of *Myxilla (Myxilla)* recorded worldwide (van Soest *et al.* 2020a), only *Myxilla (Myxilla) simplex* (Baer, 1906) was described from South Africa, and later recorded from the Gulf of Aden (Burton 1959) and Vema Seamount (Lévi 1969). This species, which has since been recorded in several works on South African sponges (see Table 19), differs from the above material in having shorter and thinner styles (166–218 × 4–11 µm), tornotes (159–166 × 4–8 µm), smaller sigmata (22–33 µm) and a single size class of smaller anchorate isochelae (14–18 µm). From the Indian Ocean, both *Myxilla (Myxilla) dendyi* Burton, 1959 and *Myxilla (Myxilla) seychellensis* Thomas, 1981, have tornotes, smaller sigmata (35 µm and 26–48 µm respectively), and a single size class of smaller isochelae (20 µm and 16 µm respectively). Thomas (1981) notes two size classes of acanthostyles and the presence of arcuate isochelae in his description of the latter species, and thus further investigation is required to determine whether it does indeed belong to this genus. Finally, *Myxilla (Myxilla) basimucronata* Burton, 1932 and *Myxilla (Myxilla) mollis* Ridley & Dendy, 1886, both recorded from the Kerguelen Islands (Boury-Esnault & van Beveren 1982), have longer styles (470 × 17 µm and 421–*457*–486 × 8 µm respectively), two size classes of smaller sigmata (I) 42 µm, II) 25 µm and I) 40–*45*–49 µm, II) 16–*22*–28 µm respectively) and two size classes of smaller anchorate isochelae (I) 42 µm, II) 21 µm and I) 32–*34*–40 µm, II) 24–*26*–28 µm respectively). *Myxilla (M.) mollis* is the only congener near the Amathole region to have tylotes, but Desqueyroux-Faúndez & van Soest (1996) note these as acanthose in their re-description of the holotype (NHMUK 1887.5.2.112).

Thus, the present material likely constitutes a new species, generally characterised by smooth tylotes, large sigmata in a single size class (~70 × 3 µm), and two size classes of anchorate isochelae (I) ~70 × 20 µm, II) ~27 × 11 µm).

Key diagnostic characters:

- thickly encrusting form;
- uniform subcircular ostia (<1 mm) throughout;
- fragile;
- megascleres include smooth tylotes;
- one size class of large sigma microscleres, ~70 µm;
- two size classes of tridentate anchorate isochela microscleres, I ~70 µm and II ~27 µm.

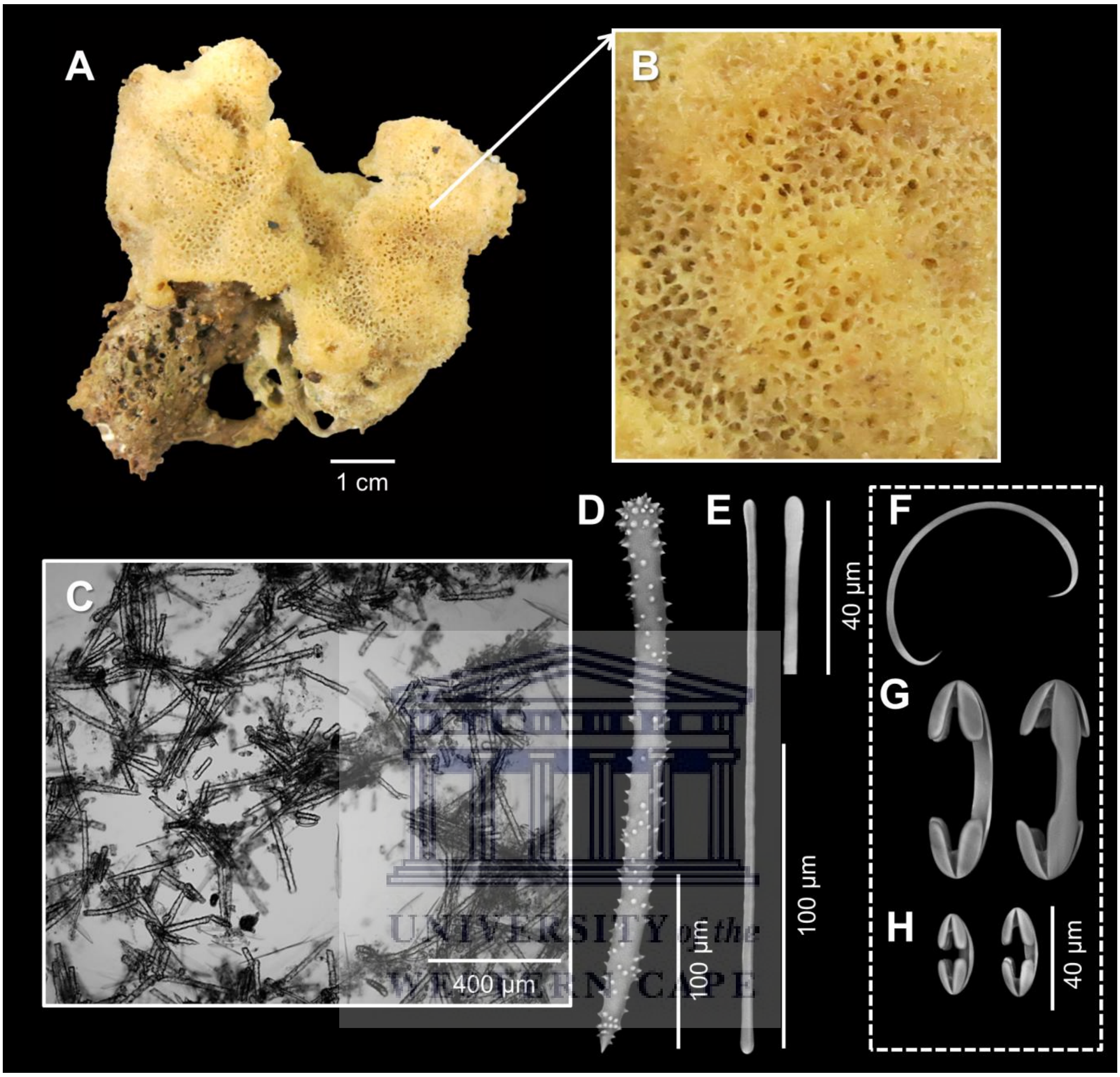

Figure 27: *Myxilla (Myxilla) lissotylota* **sp. nov.** ▲. A, specimen TS 3674. B, surface with uniform subcircular ostia. C, choanosomal skeleton. D, acanthostyle. E, tylote with close-up of smooth apex. F, C-shaped sigma. G, anchorate isochelae I. H, anchorate isochelae II.

Table 19: Comparative spicule dimensions and known location, form and depth for the accepted species of *Myxilla (Myxilla)* Schmidt, 1862 occurring in the Indian Ocean, the Kerguelen Islands and Vema Seamount according to van Soest *et al.* (2020a). Spicule dimensions expressed in µm, with specimens from this study (TS) given as minimum–*mean*–maximum length × width, n = 15.

Species	Megascleres		Microscleres		Location/Form/Depth (m)
	Styles ac: acanthose sm: smooth	**Tornotes (TO)/Tylotes (TY)** ac: acanthose sm: smooth	**Sigmata**	**Isochelae** an: anchorate ar: arcuate	
1. *Myxilla (Myxilla) basimucronata* Burton, 1932 (Orig. Descrip. as *Myxilla basimucronata*)	sm: 470 × 17	(TO) ac: 250 × 8	I) 42 II) 25	I) an: 42 II) an: 21	South Georgia/sub-ramose with cylindrical branches to dorso-ventrally flattened lobes/106–204
Boury-Esnault & van Beveren (1982) (As *Myxilla basimucronata*)	ac: 429–*490*–578 × 13–*19*–26	(TO) ac: 240–*268*–296 × 7–*8*–10	I) 48–*62*–83 × 2–*4*–7 II) 22–*28*–35 × 1–*2*–2	I) an: 32–*46*–54 × 3–*5*–7 II) an: 19–*21*–25	Kerguelen Islands/massive, lobed, orange/140–260
2. *Myxilla (Myxilla) dendyi* Burton, 1959 (Orig. Descrip. as *Myxilla dendyi*)	ac: 160 × 8	(TO) sm: 160 × 3	35	an: 20	Gulf of Aden & Western Arabian Sea/massive to encrusting, agglutinating/ 37–38
Thomas (1973) (As *Myxilla dendyi*)	ac: 121–*130*–151 × 4–*6*–8	(TO) sm: 142–*154*–160 × 1–*2*–2	12–*25*–33 × 1	an: 20	Seychelles/massively encrusting, light yellow, dermal region white

Species	Megascleres		Microscleres		Location/Form/Depth (m)
	Styles ac: acanthose sm: smooth	Tornotes (TO)/Tylotes (TY) ac: acanthose sm: smooth	Sigmata	Isochelae an: anchorate ar: arcuate	
3. *Myxilla (Myxilla) mollis* Ridley & Dendy, 1886 (Orig. Descrip. as *Myxilla mollis*)	sm: 420 × 10	(TY) sm: 220 × 6	63	an: 40	Southern Chile/massive, amorphous, light creamy yellow/448
Boury-Esnault & van Beveren (1982) (As *Myxilla mollis*)	sm: 493–*558*–614 × 16–*19*–22	(TY) ac: 253–*308*–339 × 6–*7*–10	I) 38–*52*–58 II) 26–*28*–32	I) an: 42–*49*–51 II) an: 19–*20*–24	Kerguelen Islands/blade-like, grey/365
Desqueyroux-Faúndez & van Soest (1996) (Re-description of NHMUK 1887.5.2.112)	ac: 421–*457*–486 × 8	(TY) ac: 227–*259*–283 × 4–*6*–8	I) 40–*45*–49 II) 16–*22*–28	I) an: 32–*34*–40 II) an: 24–*26*–28	Southern Chile/massive, amorphous, light creamy yellow/448
4. *Myxilla (Myxilla) seychellensis* Thomas, 1981 (Orig. Descrip. as *Myxilla seychellensis*)	I) ac: 180–*310*–330 × 2–*10*–12 II) ac: 75–*121*–168 × 4–*8*–13	(TO) ac/sm: 211–*235*–253 × 4	26–48	ar: 16	Seychelles/thickly encrusting, dark brown
5. *Myxilla (Myxilla) simplex* (Baer, 1906) (Orig. Descrip. as *Dendoryx simplex*)	ac/sm: 166–218 × 4–11	(TO) sm: 159–166 × 4–8	22–33	14–18	South Africa/lump-like, brown
Stephens (1915) (As *Myxilla simplex*)	ac/sm: 160–300 × 12–13	(TO) 160–200 × 8	35–55	an: 24–35	South Africa/rounded to oval, some encrusting/46
Lévi (1963) (As *Myxilla simplex*)	ac: 180–200 × 7–10	(TO) sm: 145–175 × 4–5	I) 30–32 × 1–2 II) 20–25 × 1–2 III) 10	I) 18–21 II) 15–16	South Africa/massive, pinkish-ochre/4–23

Species	Megascleres		Microscleres		Location/Form/Depth (m)
	Styles ac: acanthose sm: smooth	**Tornotes (TO)/Tylotes (TY)** ac: acanthose sm: smooth	**Sigmata**	**Isochelae** an: anchorate ar: arcuate	
Lévi (1969) (As *Myxilla simplex*)	ac: 130–150 × 4–6	(TO) sm: 140–170 × 4	I) 33–38 × 1 II) 20–25 × 1	15–17	Vema Seamount/massive, lobed, reddish-brown to reddish-beige
Uriz (1987) (As *Myxilla simplex*)	ac: 100–225 × 7–12	(TO) sm: 145–170 × 6–7	I) 32–40 × 2–3 II) 8–12 × 2	an: 25–32	South Africa/crust/260–269
Uriz (1988) (As *Myxilla simplex*)	ac: 190–230 × 10–16	(TO) sm: 150–180 × 5–19	I) 35–40 × 3 II) 10–13 × 1	an: 24–32	South Africa/thickly encrusting/232
Samaai & Gibbons (2005)	ac: 163–*191*–214 × 11	(TO) sm: 160–*170*–188 × 5	I) 34–*44*–51 II) 18–*21*–24	an: 18–*24*–30	South Africa/encrusting, yellow-orange/1–8
6. *Myxilla (Myxilla) lissotylota* sp. nov. ▲ (TS 3674)	ac: 283–*311*–327 × 17–*19*–21	(TY) sm: 169–*181*–198 × 2–*3*–4	70–*76*–85 × 2–*3*–4	I) an: 58–*70*–78 × 17–*20*–27 II) an: 22–*28*–32 × 8–*11*–13	Amathole region (Eastern Cape, South Africa)/thickly encrusting, light yellow/78
TS 3481	ac: 314–*331*–352 × 18–*22*–26	(TY) sm: 173–*192*–208 × 2–*3*–4	65–*72*–81 × 2–*3*–4	I) an: 51–*80*–87 × 18–*24*–28 II) an: 25–*29*–35 × 10–*12*–15	Amathole region (Eastern Cape, South Africa)/thickly encrusting, beige/87

Species	Megascleres		Microscleres		Location/Form/Depth (m)
	Styles ac: acanthose sm: smooth	**Tornotes (TO)/Tylotes (TY)** ac: acanthose sm: smooth	**Sigmata**	**Isochelae** an: anchorate ar: arcuate	
TS 3500	ac: 266–*305*–333 × 15–*19*–22	(TY) sm: 172–*184*–197 × 2–*3*–3	63–*72*–89 × 2–*3*–4	I) an: 53–*68*–79 × 15–*19*–23 II) an: 25–*28*–33 × 9–*11*–13	Amathole region (Eastern Cape, South Africa)/thickly encrusting, beige/87
TS 3914	ac: 280–*315*–345 ×16–*21*–26	(TY) sm: 177–*202*–221 × 2–*3*–4	68–*77*–85 × 2–*3*–4	I) an: 50–*72*–92 × 17–*24*–32 II) an: 22–*25*–30 × 9–*10*–13	Amathole region (Eastern Cape, South Africa)/thickly encrusting, light yellow/76

Order Suberitida Chombard & Boury-Esnault, 1999

Family Suberitidae Schmidt, 1870

Genus *Homaxinella* Topsent, 1916

Type species: *Axinella supratumescens* Topsent, 1907 (by original designation).

Diagnosis. Suberitidae with ramose habit and axial choanosomal skeleton; extra-axial skeleton of brushes of spicules and spicules in confusion. Megascleres exclusively styles in a large size variation; no microscleres (from van Soest 2002d).

***Homaxinella abnorma* sp. nov.** ▲

(Fig. 28A–E, Table 20)

Material examined. **TS 4663** **(AI2-Spg431)**: ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–81, Station 3893 (33.1632º S, 27.7746º E–33.1625º S, 27.7753º E, Eastern Cape, South Africa), 36 m depth, amongst shell hash, SST 18 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 3 min, 03 September 2016. TS 3422 (BD26-Spg17), TS 3951 (BD26-Spg1(5)), TS 3960 (BD26-Spg1(14)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–102, Station 3808 (33.1597º S, 27.7777º E–33.1616º S, 27.7778º E, Eastern Cape, South Africa), 39 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 20 min, 02 March 2016. TS 3496 (BD4-Spg20): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–16, Station 3722 (32.8300º S, 28.4593º E–32.8327º S, 28.4573º E, Eastern Cape, South Africa), 87 m depth, coll. R. Payne

& I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 9 min, 22 February 2016. TS 3848 (BD25-Spg1(20)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–101, Station 3807 (33.1347º S, 27.7689º E–33.1604º S, 27.7762º E, Eastern Cape, South Africa), 33 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 23 min, 02 March 2016. TS 4285 (AI2-Spg53): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–2, Station 3814 (32.6663º S, 28.4412º E–32.6714º S, 28.4397º E, Eastern Cape, South Africa), 29–35 m depth, amongst boulders, shell hash and pebbles, SST 20 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 10 min, 26 August 2016. TS 4338 (AI2-Spg106): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–20, Station 3832 (32.7597º S, 28.4110º E–32.7587º S, 28.4119º E, Eastern Cape, South Africa), 45 m depth, amongst rock, SST 20 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 5 min, 27 August 2016. TS 4436 (AI2-Spg204): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–44, Station 3856 (32.7035º S, 28.4311º E–32.6998º S, 28.4358º E, Eastern Cape, South Africa), 45–53 m depth, amongst rock and rhodoliths, SST 19 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 10 min, 30 August 2016. TS 4563 (AI2-Spg331), TS 4601 (AI2-Spg369): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–64, Station 3876 (33.2856º S, 27.9099º E–33.2826º S, 27.9134º E, Eastern Cape, South Africa), 103 m depth, amongst rock, coquina/shell hash and coral rubble, SST 21 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 10 min, 02 September 2016.

Description. Erect, semi-stalked, flabellate form (Fig. 28A & B). Length 8 cm, width 8 cm and thickness 5 mm. Surface rough, with few random subcircular oscules (<1 mm).

Texture firm and dense, barely compressible, brittle. Colour *in situ* dark yellow, in preservative beige.

Skeleton. Axial region consists of larger styles, forming a mass of tracts (~100–300 µm across) ascending both vertically and obliquely to surface, separated by less densely spiculated areas or spicules strewn in confusion (Fig. 28C). Extra-axial region comprises bouquets (~220–570 µm) and/or a confused arrangement of smaller styles surrounding tracts, and protruding slightly through surface (up to ~150 µm).

Spiculation. Megascleres. Axial styles smooth, straight to slightly curved, with reduced rounded heads, acerate: 411–*478*–552 × 16–*23*–33 µm, n = 15 (Fig. 28D). Extra-axial styles smooth, straight to slightly curved, with reduced heads, acerate to hastate: 181–*245*–377 × 5–*8*–12 µm, n = 15 (Fig. 28E). **Microscleres.** None.

Distribution and ecology. Currently only known from the Amathole region (Eastern Cape, South Africa). Occurs on or amongst various substrates, including boulders, rock, rhodoliths, coquina/shell hash, coral rubble and pebbles. Associated with red algae, sea fans and coral. Some material (TS 4285, TS 4436) had hydroid epifauna. Depth range: 29–103 m.

Provisional etymology. *Abnormis* (L.) = deviating from the rule/abnormal, referring to the flabellate form, as opposed to the ramose form characteristic of the genus *Homaxinella*.

Remarks. Although lacking the ramose form characteristic of *Homaxinella*, the above material is assigned to this genus based on the presence of exclusively styles in a large size range, and division of the skeleton into axial and extra-axial regions (van Soest 2002d).

Ridley & Dendy (1886) described two local congeners, *Homaxinella flagelliformis* from South Africa (later recorded from the Kerguelen Islands by Koltun in 1964), and *Homaxinella balfourensis* from the Kergeulen Islands (but found throughout Antarctica). Although both species have styles of a similar length to those found in the above material, they are much thinner (styles: I) 450 × 9 µm, II) 300 × 3 µm; styles: I) 420 × 8 µm,

II) ~210 µm respectively). They also differ in form, having finger-like branches and creeping root-like structures. Thus, the present material likely constitutes a new species.

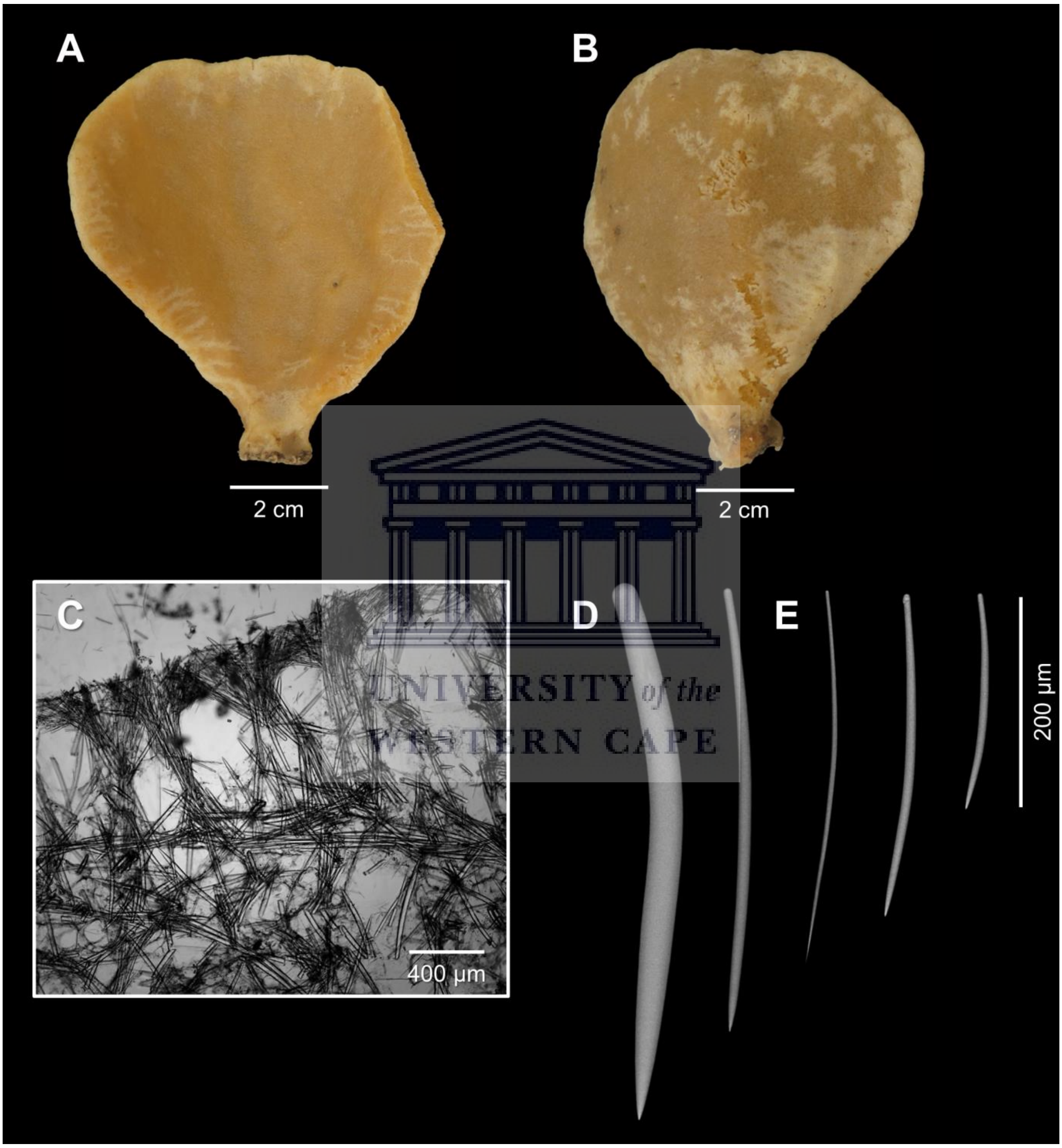

Figure 28: *Homaxinella abnorma* **sp. nov.** ▲. A, B, specimen TS 4663. C, skeletal architecture with axial and extra-axial regions. D, axial styles. E, extra-axial styles.

Table 20: Comparative spicule dimensions and known location, form and depth for the accepted species of *Homaxinella* Topsent, 1916 occurring in South Africa and the Kerguelen Islands according to van Soest *et al.* (2020a). Spicule dimensions expressed in µm, with specimens from this study (TS) given as minimum–*mean*–maximum length × width, n = 15.

Species	Styles	Location/Form/Depth (m)
1. *Homaxinella balfourensis* (Ridley & Dendy, 1886) (Orig. Descrip. as *Axinella balfourensis*)	I) 420 × 8 II) ~210	Kerguelen Islands/erect, stipitate with spreading roots and finger-like branches, yellowish-grey/37–110
Boury-Esnault & van Beveren (1982)	166–*343*–557 × 3–*6*–12	Kerguelen Islands/erect, stalked, ramified, branched, with rhizoids, yellow/120–245
van Soest (2002d) (Re-description of NHMUK 1887.5.2.18 & MNHN 760)	100–350 × 1–8	Antarctica & Subantarctic/erect, stalked, ramose, with roots to creeping stolons, yellow/35–200
2. *Homaxinella flagelliformis* (Ridley & Dendy, 1886) (Orig. Descrip. as *Raspailia flagelliformis*)	I) 450 × 9 II) 300 × 3	South Africa/erect, stipitate with long cylindrical whip-like branches, yellowish/18–37
Koltun (1964) (As *Raspailia flagelliformis*)	I) 440–500 × 9–12 II) 250–315 × 3–6	Kerguelen Islands/erect, stalked, elongate, rod-like, branched, greyish-yellow to grey/64
3. *Homaxinella abnorma* sp. nov. ▲ (TS 4663)	I) 411–*478*–552 × 16–*23*–33 II) 181–*245*–377 × 5–*8*–12	Amathole region (Eastern Cape, South Africa)/erect, semi-stalked, flabellate, dark yellow/36
TS 3422	I) 423–*490*–560 × 14–*22*–30 II) 156–*220*–323 × 6–*9*–12	Amathole region (Eastern Cape, South Africa)/erect, semi-stalked, flabellate, dark yellow/39
TS 3496	I) 462–*649*–803 × 13–*25*–34 II) 247–*297*–379 × 8–*10*–12	Amathole region (Eastern Cape, South Africa)/erect, stalked, flabellate, dark yellow/87

Species	Styles	Location/Form/Depth (m)
TS 4285	I) 416–*487*–566 × 15–*23*–36 II) 173–*229*–314 × 6–*8*–11	Amathole region (Eastern Cape, South Africa)/erect, semi-stalked, caliculate, dark yellow/29–35
TS 4563	I) 592–*676*–745 × 20–*30*–38 II) 250–*298*–355 × 9–*10*–12	Amathole region (Eastern Cape, South Africa)/erect, stalked, flabellate, light yellow/103
TS 4601	I) 646–*710*–800 × 13–*32*–39 II) 274–*326*–362 × 9–*11*–13	Amathole region (Eastern Cape, South Africa)/erect, semi-stalked, flabellate, dark yellow/103

Key diagnostic characters:

- erect, semi-stalked, flabellate form;
- brittle;
- dark yellow in life;
- skeleton comprises axial and extra-axial regions;
- megascleres two size classes of styles, thick: on average I >20 µm, II >8 µm;
- no microscleres.

Order Tetractinellida Marshall, 1876

Suborder Astrophorina Sollas, 1887

Family Ancorinidae Schmidt, 1870

Genus *Holoxea* Topsent, 1892

Type species: *Holoxea furtiva* Topsent, 1892 (by monotypy).

Diagnosis. Ancorinidae with oxeas, spiny (sanidaster-like) microrhabds and trichodragmata (from Uriz 2002).

***Holoxea massa* sp. nov. ▲**

(Fig. 29A–I, Table 21)

Material examined. **TS 3598** **(BD13-Spg10)**: ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–34, Station 3740 (32.9831º S, 28.3197º E–32.9846º S, 28.3176º E, Eastern Cape, South Africa), 104 m depth, amongst shell hash, coll. R. Payne &

I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 6 min, 24 February 2016. TS 3463 (BD17-Spg1(24)), TS 3789 (BD17-Spg1(48)), TS 3790 (BD17-Spg1(49)), TS 3807 (BD17-Spg1(66)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–39, Station 3745 (33.0229º S, 28.2883º E–33.0316º S, 28.2797º E, Eastern Cape, South Africa), 122 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 10 min, 24 February 2016. TS 3616 (BD13-Spg1(13)), TS 3617 (BD13-Spg1(14)), TS 3618 (BD13-Spg1(15)), TS 3619 (BD13-Spg1(16)), TS 3632 (BD13-Spg1(29)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–34, Station 3740 (32.9831º S, 28.3197º E–32.9846º S, 28.3176º E, Eastern Cape, South Africa), 104 m depth, amongst shell hash, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 6 min, 24 February 2016. TS 4458 (AI2-Spg226): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–49, Station 3861 (32.9395º S, 28.2685º E–32.9363º S, 28.2757º E, Eastern Cape, South Africa), 90 m depth, amongst a shipwreck, shell hash and coarse sand with shell fragments, SST 21 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 12 min, 30 August 2016.

Description. Massive, elongate form (Fig. 29A). Length 27 cm, width 12 cm and thickness 8 cm. Surface hispid and prickly, with subcircular oscules (2–4 mm) clustered in irregular patches on apex (Fig. 29B). Texture firm and tough. Colour *in situ* dark olive green to cream, in preservative cream.

Skeleton. Choanosomal skeleton comprises disorganized larger oxeas (Fig. 29C), forming loose tracts and protruding through surface (often >1 mm), joined by smaller erect oxeas that comprise ectosomal skeleton. Microscleres throughout, but trichodragmata abundant in choanosome and acanthomicrorhabds concentrated at surface, forming a layer of ~130–720 µm (Fig. 29D).

Spiculation. Megascleres. Oxeas smooth, straight to slightly curved medially, acerate to blunt, in two size classes: I) 1488–*2391*–2839 × 56–*92*–114 µm, n = 15 (Fig. 29E & G); II) 439–*594*–773 × 16–*25*–36 µm, n = 15 (Fig. 29F). **Microscleres.** Acanthomicrorhabds straight to slightly curved, with regular reduced tubercles and fine spination, not sanidaster-like: 13–*17*–22 × 3–*4*–5 µm, n = 15 (Fig. 29H). Trichodragmata: 22–*26*–34 × 8–*10*–12 µm, n = 15 (Fig. 29I).

Distribution and ecology. Currently only known from the Amathole region (Eastern Cape, South Africa), occurring amongst a shipwreck, shell hash and coarse sand with shell fragments. Often encrusted by various invertebrates, including barnacles, bryozoans, hard and soft coral, hydroids, sponges and worms. Accumulates sand and debris. Depth range: 90–122 m.

Provisional etymology. *Massa* (L.) = mass/lump, referring to the massive form.

Remarks. Assignment of the above material to *Holoxea* is supported by the massive form, presence of oxea megascleres in two size classes, as well as acanthomicrorhabds and trichodragmata as microscleres (Uriz 2002).

There are five species found worldwide, none of which have been described and/or recorded from the Indian Ocean (van Soest *et al.* 2020a). Both *Holoxea excavans* Calcinai, Bavestrello, Cerrano & Sarà, 2001 and *Holoxea valida* Thiele, 1900, from Taiwan and Ternate (Indonesia) respectively, are excavating/encrusting and lack trichodragmata. *Holoxea collectrix* Thiele, 1900, also from Ternate, and *Holoxea furtiva* Topsent, 1892 from the Mediterranean, are encrusting species that have smaller trichodragmata (15 × 6 µm and 8–10 × 6–8 µm respectively). Finally, from Brazil, *Holoxea violacea* Boury-Esnault, 1973 is a digitate, dark purple sponge that has smaller acanthomicrorhabds (6–11 µm) and only one size class of oxeas (1230–1510 × 14–28 µm).

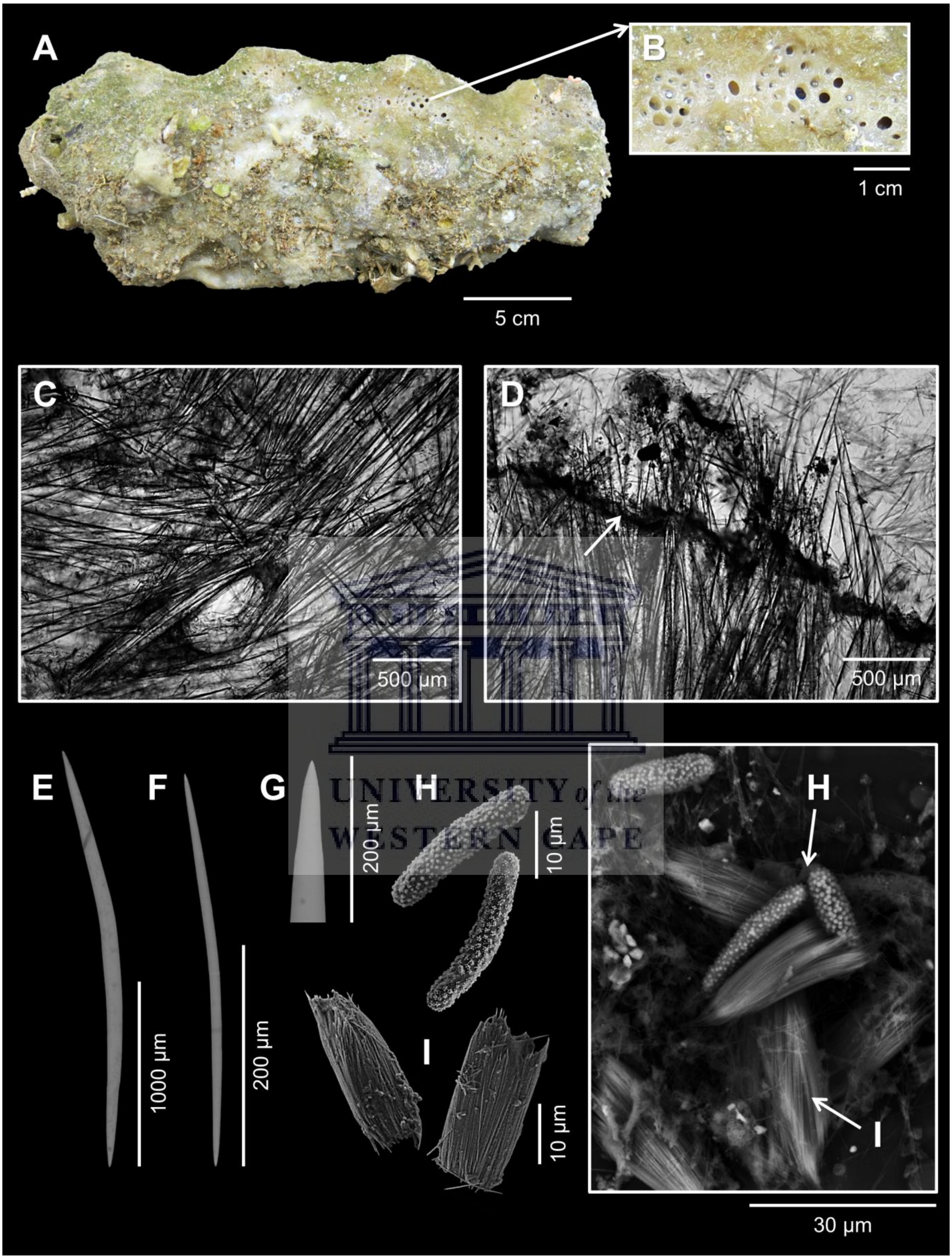

Figure 29: *Holoxea massa* **sp. nov. ▲**. A, specimen TS 3598. B, irregular oscule clusters. C, choanosomal skeleton. D, ectosomal skeleton, with acanthomicrorhabd layer (arrow). E, oxea I. F, oxea II. G, oxea I apex. H, acanthomicrorhabds. I, trichodragmata.

Table 21: Comparative spicule dimensions and known location, form and depth for the accepted species of *Holoxea* Topsent, 1892 occurring worldwide according to van Soest *et al.* (2020a). Spicule dimensions expressed in µm, with specimens from this study (TS) given as minimum–*mean*–maximum length × width, n = 15.

	Megascleres	Microscleres		
Species	**Oxeas**	**Acanthomicrorhabds**[7]	**Trichodragmata**	**Location/Form/Depth (m)**
1. *Holoxea collectrix* Thiele, 1900 (Orig. Descrip.)	1000 × 25	17–19 × 2	15 × 6	Ternate (Indonesia)/encrusting, black
2. *Holoxea excavans* Calcinai, Bavestrello, Cerrano & Sarà, 2001 (Orig. Descrip.)	I) 809–1055 × 37–40 II) 103–122 × 3–4	7–11 × 2	-	Taiwan/excavating, white/150–400
3. *Holoxea furtiva* Topsent, 1892 (Orig. Descrip.)	I) 1500 × 50 II) 700 × 12	20–22 × 1–2	8–10 × 6–8	Bandol, Banyuls (Western Mediterranean)/encrusting, endolithic, white
Uriz (2002) (Re-description of MNHN LBIM DT2414)	I) 1155–1660 × 25–55 II) 450–785 × 8–13	18–26 × 1–2	8–12 × 5–8	Bandol, Banyuls (Western Mediterranean)/encrusting, endolithic, white
4. *Holoxea valida* Thiele, 1900 (Orig. Descrip.)	2250 × 60	16 × 1	-	Ternate (Indonesia)/encrusting with thin extensions, grey-brown
5. *Holoxea violacea* Boury-Esnault, 1973 (Orig. Descrip.)	1230–1510 × 14–28	6–11	19–28 × 6–15	Fernando de Noronha and Atoll das Rocas (Brazil)/digitate, dark purple/27

[7]Often sanidaster-like.

Species	Megascleres	Microscleres		Location/Form/Depth (m)
	Oxeas	Acanthomicrorhabds[7]	Trichodragmata	
6. *Holoxea massa* sp. nov. ▲ (TS 3598)	I) 1488–*2391*–2839 × 56–*92*–114 II) 439–*594*–773 × 16–*25*–36	13–*17*–22 × 3–*4*–5	22–*26*–34 × 8–*10*–12	Amathole region (Eastern Cape, South Africa)/massive, elongate, dark olive green to cream/104
TS 3463	I) 1936–*2183*–2671 × 59–*81*–99 II) 423–*598*–895 × 15–*24*–34	13–*16*–22 × 3–*4*–6	21–*26*–41 × 4–*8*–14	Amathole region (Eastern Cape, South Africa)/massive, off-white to light brown/122
TS 3616	I) 1853–*2462*–3062 × 69–*92*–109 II) 194–*462*–689 × 13–*21*–32	14–*18*–21 × 4–*4*–5	21–*27*–50 × 6–*11*–17	Amathole region (Eastern Cape, South Africa)/massive, beige to light brown/104
TS 3619	I) 1599–*2179*–3039 × 61–*82*–112 II) 393–*627*–962 × 15–*24*–40	15–*18*–23 × 3–*4*–5	22–*24*–33 × 5–*9*–12	Amathole region (Eastern Cape, South Africa)/massive, light brown to grey/104
TS 3790	I) 1346–*2162*–2951 × 47–*79*–110 II) 181–*486*–672 × 8–*21*–29	12–*16*–21 × 4–*5*–6	22–*27*–38 × 4–*9*–12	Amathole region (Eastern Cape, South Africa)/massive, light brown to cream/122
TS 4458	I) 1409–*2190*–2753 × 44–*64*–82 II) 399–*540*–859 × 14–*20*–30	15–*18*–22 × 4–*5*–7	21–*25*–32 × 5–*11*–23	Amathole region (Eastern Cape, South Africa)/massive, light brown to cream/90

In addition, many of these species have sanidaster-like acanthomicrorhabds, while those present in the material above have regular reduced tubercles and fine spination. Thus, this South African species is easily differentiated from congeners with regards to its massive form, two size classes of oxea megascleres (the larger being very thick), non sanidaster-like acanthomicrorhabds and the presence of trichodragmata.

Of interest is *Ecionemia baculifera*, described by Kirkpatrick (1903b) from a depth of 165 m in South Africa. This massive, irregular species is hard with a rough surface. It comprises a confused mass of curved oxeas (360–1550 × 9–62 µm), and thin dermal layer formed by acanthose microstrongyles (no measurements provided). Further investigation of the holotype is required to confirm whether this species should be reassigned to *Holoxea*, which is likely, and to determine the level of potential similarity with the Amathole specimens. Until then, the material above is preliminarily considered a new species, and the first record of this genus in both South Africa and the Indian Ocean.

Key diagnostic characters:

- massive, elongate form;
- hispid surface;
- subcircular oscules (2–4 mm), clustered in irregular patches on apex;
- encrusted by various invertebrates;
- accumulates sand and debris;
- two size classes of oxea megascleres, the larger often >2000 µm;
- microscleres are non sanidaster-like acanthomicrorhabds and trichodragmata (~20–50 µm).

Genus *Stryphnus* Sollas, 1886

Type species: *Stryphnus niger* Sollas, 1886 (by subsequent designation).

Diagnosis. Thickly encrusting, massive, lobate, or cup-shaped Ancorinidae, typically purplish brown, brownish black, brown, or grey in life, frequently with differential colouration of the choanosome. Surface typically rough with projecting megascleres, and simple oscules are usually grouped. Ectosome is not detachable, but well-differentiated and translucent, with a diaphanous, gauzy, almost gelatinous cellular structure with pigmented and granular cells. Triaenes and oxeas lie obliquely or paratangentially to the surface. The deep ectosomal boundary is highly granular. Choanosome moderately heavily pigmented, moderately packed with oxeas and triaenes in some species, without strict radial orientation, cladomes of triaenes lie at the choanosome/ectosome boundary when they occur here. Megascleres are large oxeas and short-shafted dichotriaenes and/or plagiotriaenes, rarely, anatriaenes and protriaenes. Microscleres are large acanthose oxyasters usually confined to the choanosome, sanidasters, and/or amphisanidasters that form a crust at the sponge surface (from Kelly & Sim-Smith 2012).

***Stryphnus progressus* (Lendenfeld, 1907)**

(Fig. 30A–G, Table 22)

Synonymy.

Ancorina progressa Lendenfeld, 1907: 259; Samaai 2006: 4.

?*Stryphnus progressus*; Lévi 1969: 955.

Material examined. TS 3570 (BD7-Spg6): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–19, Station 3725 (32.8236º S, 28.5211º E–32.8198º S, 28.5158º E, Eastern Cape, South Africa), 199 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 14 min, 22 February 2016. TS 3418 (BD17-Spg3), TS 3440 (BD17-Spg1(1)): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–39, Station 3745 (33.0229º S, 28.2883º E–33.0316º S, 28.2797º E, Eastern Cape, South Africa), 122 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 10 min, 24 February 2016. TS 3540 (BD7-Spg14): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–19, Station 3725 (32.8236º S, 28.5211º E–32.8198º S, 28.5158º E, Eastern Cape, South Africa), 199 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 14 min, 22 February 2016. TS 4065 (BD4-Spg6): ACEP *Imida* Frontiers Project (Cruise 1), Amathole region, Grid Ellen 151–16, Station 3722 (32.8300º S, 28.4593º E–32.8327º S, 28.4573º E, Eastern Cape, South Africa), 87 m depth, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 151), benthic dredge, duration 9 min, 22 February 2016. TS 4486 (AI2-Spg254): ACEP *Imida* Frontiers Project (Cruise 2), Amathole region, Grid Ellen 159–49, Station 3861 (32.9395º S, 28.2685º E–32.9363º S, 28.2757º E, Eastern Cape, South Africa), 90 m depth, amongst a shipwreck, shell hash and coarse sand with shell fragments, SST 21 ºC, coll. R. Payne & I. Malick on R/V *Ellen Khuzwayo* (Voyage 159), benthic dredge, duration 12 min, 30 August 2016.

Description. Massive, lobed form (Fig. 30A). Length 8 cm, width 4 cm and thickness 3 cm. Surface hispid and prickly, with no discernible oscules. Texture firm and tough. Colour *in situ* dark purple-grey, in preservative dark brown.

Skeleton. Choanosome comprises a dense arrangement of confused oxea bundles around subdermal spaces (Fig. 30B), tangential, oblique or perpendicular to surface, and scattered microscleres. Amphisanidasters/sanidasters are concentrated in the collenchymatous cortex (~4 mm thick), which comprises dichotriaenes, arranged with cladome at surface and rhabdome inwards (Fig. 30C). Conspicuous granular cells and symbiotic algae present (first noted by Lendenfeld (1907)).

Spiculation. Megascleres. Oxeas smooth and thick, straight to slightly curved, blunt to slightly mucronate: 1298–*2476*–3128 × 46–*78*–100 µm, n = 15 (Fig. 30D). Dichotriaenes smooth, short-shafted, slightly mucronate: rhabdome 305–*469*–639 × 26–*48*–66 µm, cladome 269–*413*–517 µm, protoclads projecting outwards 38–*47*–61 × 24–*40*–57 µm, horizontal deuteroclads 80–*141*–208 × 12–*31*–44 µm, n = 15 (Fig. 30E). **Microscleres.** Acanthoxyasters with 4–9 pointed actines and hooked spines: actines 19–*25*–39 × 2–*2*–3 µm, diameter 32–*50*–69 µm, n = 15 (Fig. 30F). Amphisanidasters/sanidasters with straight axis and rounded conical actines, spined: 10–*12*–14 × 5–*7*–9 µm, n = 15 (Fig. 30G).

Distribution and ecology. Known from South Africa and possibly Vema Seamount. Occurs amongst a shipwreck, shell hash and coarse sand with shell fragments in the Amathole region (Eastern Cape, South Africa). Specimen TS 3440 had hydroid epifauna. Depth range: 84–199 m (previously 84 m).

Remarks. The above material is assigned to *Stryphnus* as diagnosed by the presence of large choanosomal oxeas in dense bundles tangential, oblique or perpendicular to the surface, a collenchymatous cortex comprising dichotriaenes, and both acanthose oxyaster and amphisanidaster/sanidaster microscleres (Kelly & Sim-Smith 2012).

The specimens conform closely to *Stryphnus progressus* described from South Africa by Lendenfeld in 1907 (oxeas: 2500–3000 × 65–115 µm; dichotriaenes: rhabdome 260–500 × 35–45 µm, cladome 250–400 µm, protoclads 80–100 µm, deuteroclads 80–120 µm; acanthoxyasters: 3–9 actines, actines 16–34 × 3 µm, diameter 33–67 µm; amphisanidasters/sanidasters: 12–14 × 8–10 µm).

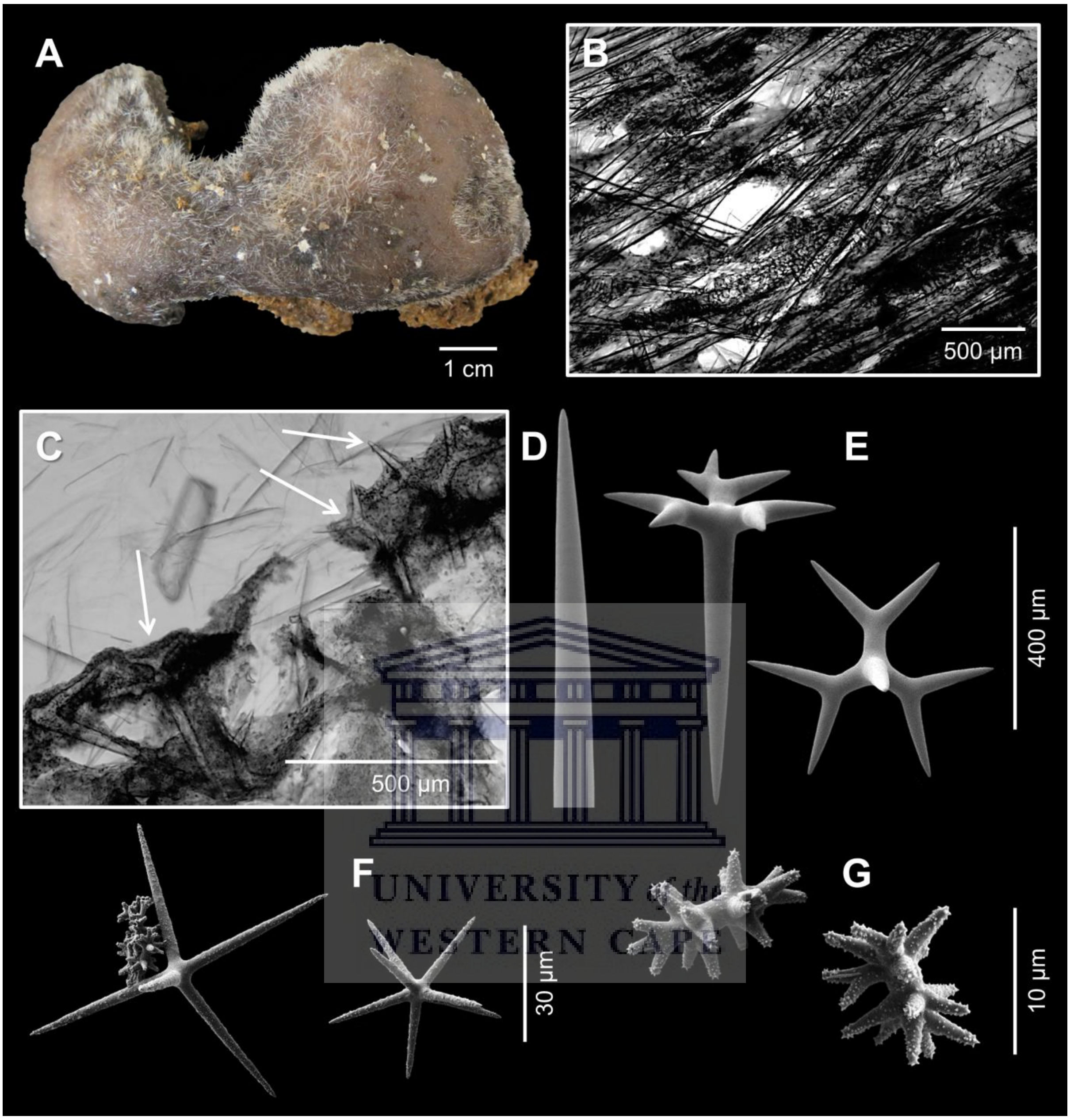

Figure 30: *Stryphnus progressus* (Lendenfeld, 1907). A, specimen TS 3570. B, choanosomal skeleton. C, collenchymatous cortex surface, with dichotriaenes (arrows). D, oxea apex. E, dichotriaenes. F, acanthoxyasters. G, amphisanidasters/sanidasters.

Table 22: Comparative spicule dimensions and known location, form and depth for the accepted species of *Stryphnus* Sollas, 1886 occurring in South Africa and on Vema Seamount according to van Soest *et al.* (2020a). Spicule dimensions expressed in µm, with specimens from this study (TS) given as minimum–*mean*–maximum length × width, n = 15.

Species	Megascleres		Microscleres		Location/Form/Depth (m)
	Oxeas	**Dichotriaenes** rh: rhabdome cl: cladome pr: protoclads de: deuteroclads	**Oxyasters** ac: acanthose sm: smooth a: actines (rays) d: diameter	**Amphisanidasters/ Sanidasters**	
1. ***Stryphnus progressus*** **(Lendenfeld, 1907)** (Orig. Descrip. as *Ancorina progressa*)	2500–3000 × 65–115	rh: 260–500 × 35–45 cl: 250–400 pr: 80–100 de: 80–120	ac 3–9 actines a: 16–34 × 3 d: 33–67	12–14 × 8–10	South Africa/compressed, lobed, exterior dark violet-brown to reddish, interior light dirty brown/84
?Lévi (1969)	1300–1800 × 15–40	rh: 220–275 × 11–17 pr: 30–45 de: 20–45	sm 7–9 actines a: 13–17 d: 20–30	9–13	Vema Seamount/massive, voluminous, lobed, exterior brownish grey, interior pinkish grey
TS 3418	1698–*2360*–3120 × 32–*63*–103	rh: 275–*380*–486 × 25–*35*–41 cl: 277–*360*–472 pr: 43–*60*–86 × 23–*32*–42 de: 68–*108*–159 × 17–*22*–30	ac 5–10 actines a: 14–*24*–34 × 1–*2*–3 d: 33–*49*–70	9–*11*–13 × 5–*6*–7	Amathole region (Eastern Cape, South Africa)/massive, lobed, exterior dark grey-brown, interior beige/122

Species	Megascleres: Oxeas	Megascleres: Dichotriaenes rh: rhabdome cl: cladome pr: protoclads de: deuteroclads	Microscleres: Oxyasters ac: acanthose sm: smooth a: actines (rays) d: diameter	Microscleres: Amphisanidasters/ Sanidasters	Location/Form/Depth (m)
TS 3440	1323–*2257*–2917 × 25–*73*–103	rh: 236–*378*–489 × 24–*40*–52 cl: 238–*413*–525 pr: 54–*72*–96 × 21–*37*–51 de: 71–*116*–165 × 18–*27*–36	ac 4–8 actines a: 13–*19*–33 × 2–*2*–3 d: 28–*39*–56	12–*14*–16 × 5–*7*–8	Amathole region (Eastern Cape, South Africa)/massive, exterior dark grey-brown, interior light grey-brown/122
TS 3540	1860–*2662*–3270 × 40–*80*–99	rh: 374–*485*–592 × 35–*51*–63 cl: 362–*432*–509 pr: 38–*61*–84 × 32–*42*–52 de: 108–*146*–191 × 21–*32*–46	ac 5–9 actines a: 21–*27*–38 × 2–*2*–3 d: 38–*55*–78	9–*13*–16 × 5–*7*–8	Amathole region (Eastern Cape, South Africa)/massive, exterior dark grey-brown, interior light grey/199
TS 3570	1298–*2476*–3128 × 46–*78*–100	rh: 305–*469*–639 × 26–*48*–66 cl: 269–*413*–517 pr: 38–*47*–61 × 24–*40*–57 de: 80–*141*–208 × 12–*31*–44	ac 4–9 actines a: 19–*25*–39 × 2–*2*–3 d: 32–*50*–69	10–*12*–14 × 5–*7*–9	Amathole region (Eastern Cape, South Africa)/massive, lobed, dark purple-grey/199
TS 4065	1527–*2023*–2374 × 44–*64*–72	rh: 269–*444*–638 × 34–*51*–70 cl: 294–*415*–621 pr: 26–*66*–105 × 26–*40*–59 de: 78–*129*–242 × 20–*30*–47	ac 6–10 actines a: 8–*11*–14 × 1–*2*–2 d: 18–*23*–33	10–*15*–19 × 5–*6*–7	Amathole region (Eastern Cape, South Africa)/massive, lobed, exterior dark grey-brown, interior dark grey-brown/87
TS 4486	1678–*2038*–2451 × 46–*66*–80	rh: 286–*361*–462 × 27–*37*–47 cl: 227–*289*–352 pr: 31–*51*–72 × 28–*34*–39 de: 65–*78*–102 × 18–*24*–28	ac 5–9 actines a: 13–*16*–21 × 2–*2*–3 d: 27–*34*–42	10–*11*–12 × 5–*6*–7	Amathole region (Eastern Cape, South Africa)/thickly encrusting to massive, dark grey/90

Species	Megascleres		Microscleres		Location/Form/Depth (m)
	Oxeas	**Dichotriaenes** rh: rhabdome cl: cladome pr: protoclads de: deuteroclads	**Oxyasters** ac: acanthose sm: smooth a: actines (rays) d: diameter	**Amphisanidasters/ Sanidasters**	
2. ***Stryphnus unguiculus*** **Sollas, 1886** (Orig. Descrip. as *Stryhnus unguicula*)	-	rh: 508 × 32 pr: 28 de: 40	-	-	South Africa
Sollas (1888)	I) 5712 × 87 II) 2680 × 95	rh: 508 × 32 pr: 28 de: 40 × 24	ac or sm a: 20	?	South Africa/compound, massive, lobed to mound-like, exterior deep brown, interior dark grey

This species was subsequently recorded from Vema Seamount by Lévi (1969) (oxeas: 1300–1800 × 15–40 µm; dichotriaenes: rhabdome 220–275 × 11–17 µm, protoclads 30–45 µm, deuteroclads 20–45 µm; oxyasters: 7–9 actines, actines 13–17 µm, diameter 20–30 µm; amphisanidasters/sanidasters: 9–13 µm). However, with smaller spicules and smooth oxyasters, this record requires further investigation.

Only one other congener occurs in South Africa (and the Western Indian Ocean), *Stryphnus unguiculus* Sollas, 1886, which differs largely due to the presence of an additional size class of large oxeas (5712 × 87 µm) and dichotriaenes with 'claw-like' clads.

Key diagnostic characters:

- massive, lobed form;
- hispid surface;
- no discernible oscules;
- dark purple-grey in life;
- collenchymatous cortex, ~4 mm thick;
- conspicuous granular cells and symbiotic algae present;
- one size class of oxea megascleres, <3500 µm;
- dichotriaene megascleres with straight clads, not 'claw-like'.

3.3 Depth Distribution

Seven, 36, and five sites were located in the shallow (1–30 m), mesophotic (31–150 m) and sub-mesophotic (>150 m) depth zones respectively. The majority of specimens (399, 84.2%) were collected from the mesophotic zone, which consequently had the highest number of species present at 66, of which 21 were apparent endemics to South Africa, and 25 were considered new to science. Seventeen of these new species were exclusive to this depth zone. The shallow and sub-mesophotic depth zones comprised 26 and 49 specimens respectively.

Both had a similar number of species (and new species) present, with 18 found in the shallow depth zone (four new), and 14 found in the sub-mesophotic depth zone (six new). Seven and four of the known species in the shallow and sub-mesophotic depth zones respectively were apparent endemics to South Africa, while no new species were exclusive to the former, and only two new species were exclusive to the latter depth zone (Appendix C). Expectedly, the mesophotic zone also comprised the majority of genera (48), families (31) and orders (10) (Appendices D, E, F). Of these, 28 genera, 12 families and one order were exclusive to this depth zone. The shallow depth zone comprised 12 genera (*Acarnus* and *Amphilectus* exclusive), 12 families (Esperiopsidae exclusive) and five orders. Similarly, 13 genera (*Hamacantha*, *Lithoplocamia* and *Macandrewia* exclusive), 12 families (Hamacanthidae and Macandrewiidae exclusive) and eight orders (Merliida exclusive), were documented from the sub-mesophotic zone.

The Michaelis-Menton species accumulation curve of the pooled dataset suggests that the sampling effort was sufficient to document the majority (78%) of heteroscleromorph demosponge species in the Amathole region (Fig. 31). This was also true for the mesophotic depth zone, with a predicted 77% of the species collected. However, further sampling was required in the shallow and sub-mesophotic depth zones, neither of which reached an asymptote.

Heteroscleromorph demosponge assemblages were significantly different according to depth zone (ANOSIM, $R = 0.263$, $p = 0.004$: Fig. 32). Pairwise tests indicate a significant difference between the shallow and mesophotic ($R = 0.32$, $p = 0.002$), as well as the shallow and sub-mesophotic ($R = 0.226$, $p = 0.01$), but not the mesophotic and sub-mesophotic ($R = 0.146$, $p = 0.135$) depth zones. The SIMPER results indicate that the shallow, mesophotic and sub-mesophotic assemblages had an average similarity of 4.1%, 13.8% and 10.8%

respectively, with the species that contributed at least 90% to the similarity within each depth zone detailed in Appendix G (Fig. 33).

The percentage contributions of higher taxonomic levels per depth zone are provided in Appendix H, which show that the shallow assemblage was dominated by four genera (*Isodictya*, *Guitarra*, *Mycale*, *Penares*), four families (Isodictyidae, Geodiidae, Guitarridae, Mycalidae) and two orders (Poecilosclerida, Tetractinellida). The demosponge fauna of the mesophotic depth zone was dominated by five genera (*Isodictya*, *Mycale*, *Penares*, *Phorbas*, *Tsitsikamma*), two families (Geodiidae, Latrunculiidae) and two orders (Poecilosclerida, Tetractinellida). Lastly, the sub-mesophotic assemblage was dominated by one genus (*Erylus*), two families (Geodiidae, Pachastrellidae) and one order (Tetractinellida).

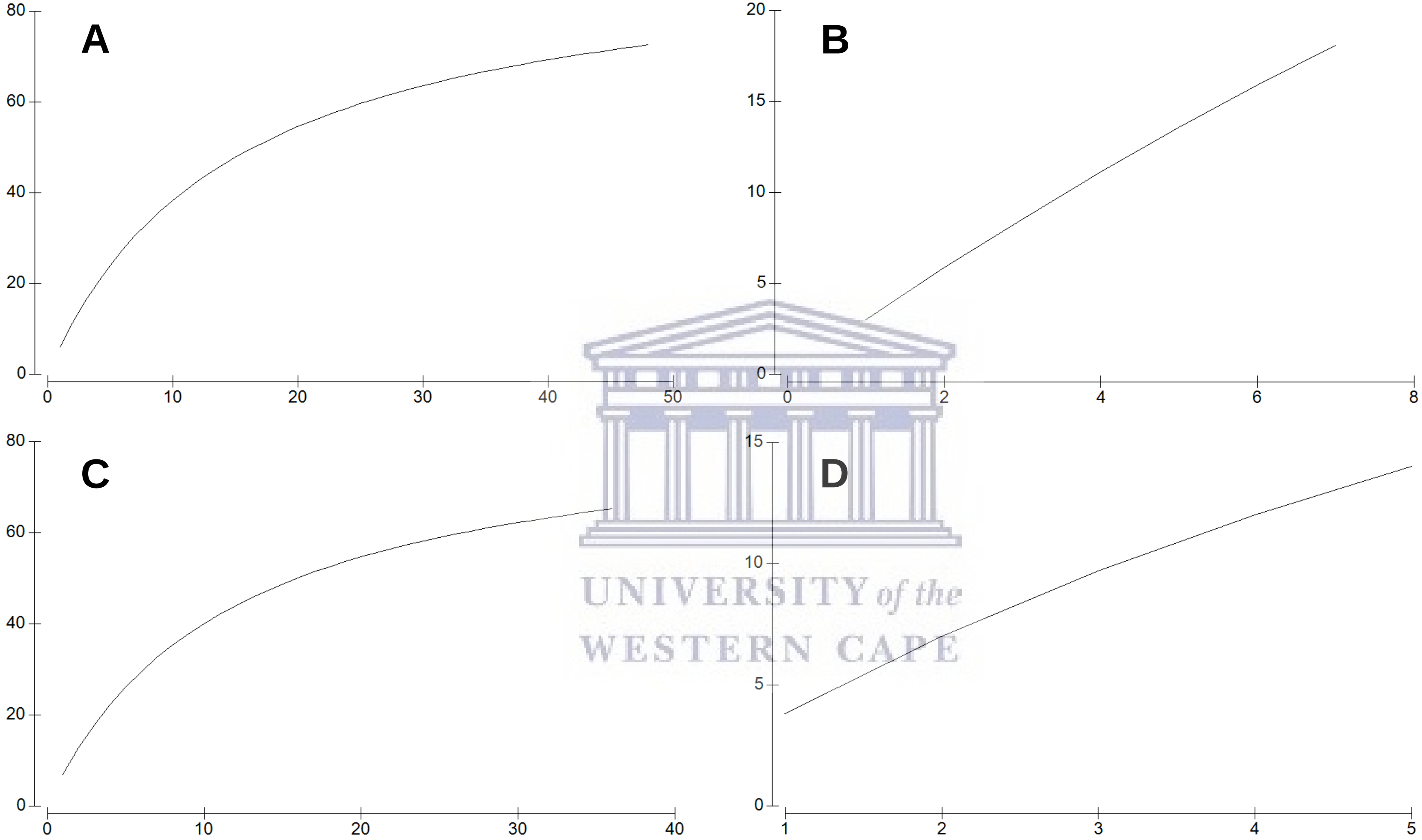

Figure 31: Michaelis-Menton species accumulation curves based on the pooled dataset (**A**, S_{max} = 95), and samples collected in the shallow (**B**, S_{max} = 111), mesophotic (**C**, S_{max} = 86) and sub-mesophotic (**D**, S_{max} = 43) depth zones of the Amathole region. The x-axes represent the collection effort (number of sites), and the y-axes represent the number of species.

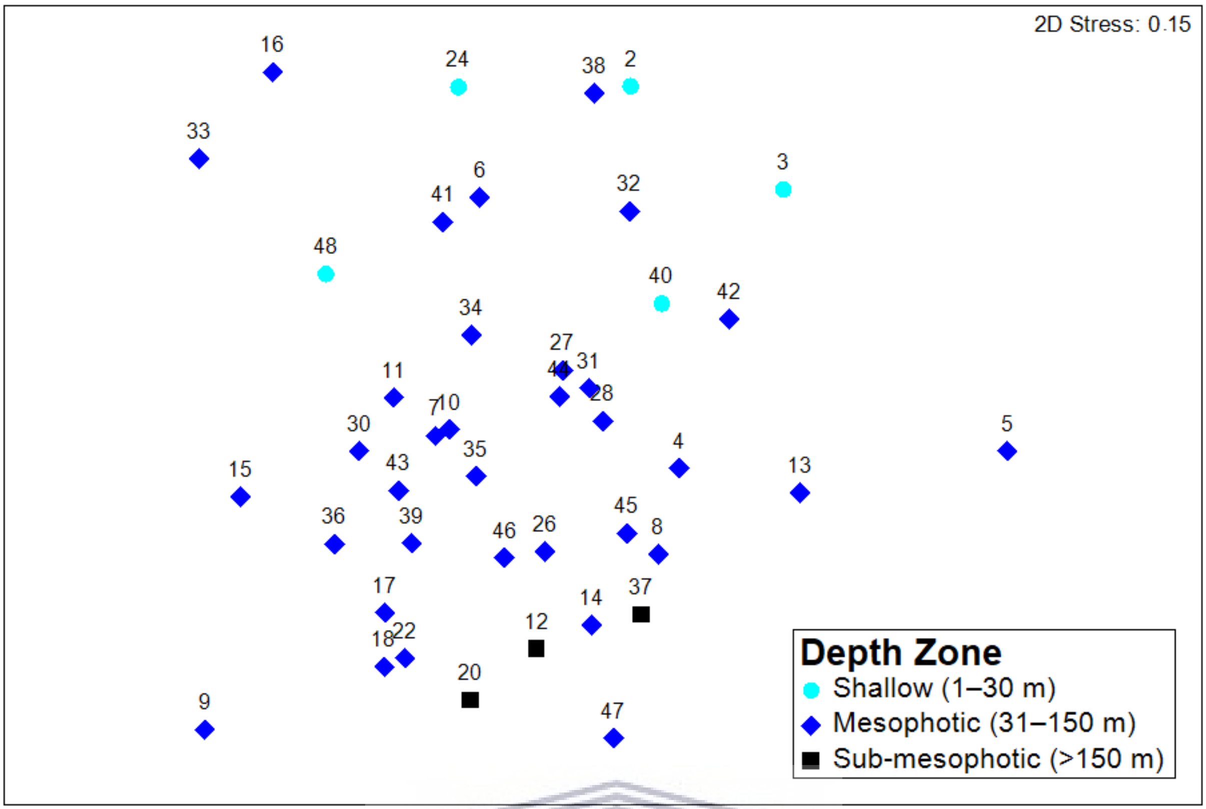

Figure 32: Non-metric multidimensional scaling (nMDS) ordination depicting the similarity between collection sites (detailed in Table 2), according to heteroscleromorph demosponge composition. Sites 1, 19, 21, 23, 25 and 29 were here removed as outliers, i.e. they comprised only a single species each and were located far from the other data points, thus distorting the figure.

Further SIMPER results indicate that the mesophotic and sub-mesophotic assemblages had the lowest average dissimilarity (89.5%), followed by the shallow and mesophotic (94.7%), and shallow and sub-mesophotic assemblages (100%). The species that contributed at least 50% to the difference between depth zones are detailed in Appendix I (Fig. 34). Overall, the mesophotic zone acts as a transition between the shallow and sub-mesophotic zones. Thirteen species, 10 genera, 11 families and five orders were shared between the shallow and mesophotic depth zones. Similarly, eight species, 10 genera, 10 families and seven orders were shared between the mesophotic and sub-mesophotic depth zones. In contrast, only two families and three orders were shared between the shallow and sub-mesophotic zones.

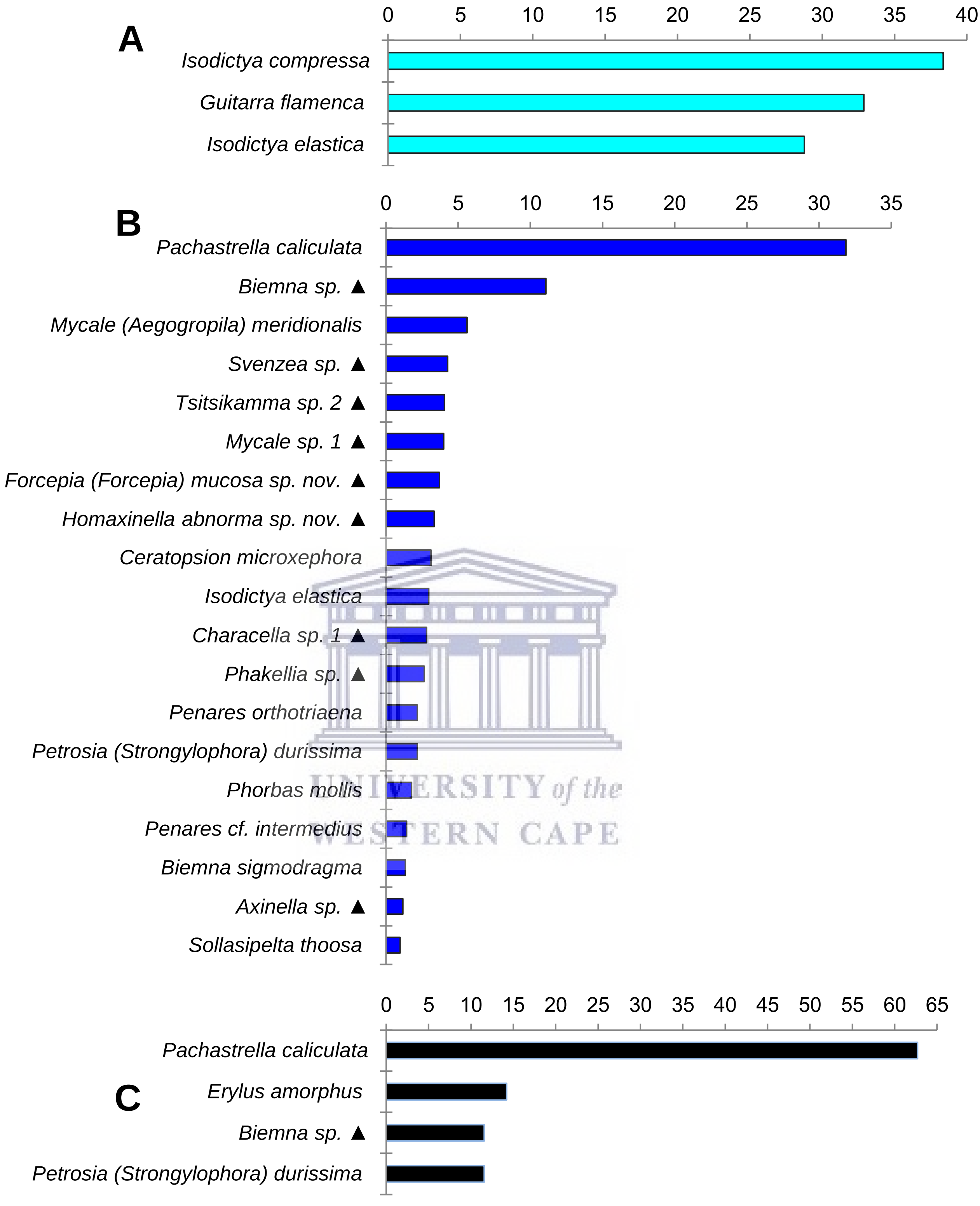

Figure 33: Results of SIMPER analysis indicating the percentage contribution (x-axes) of each species that overall contributed at least 90% to the similarity within the shallow (**A**), mesophotic (**B**), and sub-mesophotic (**C**) depth zones. The symbol (▲) denotes new species.

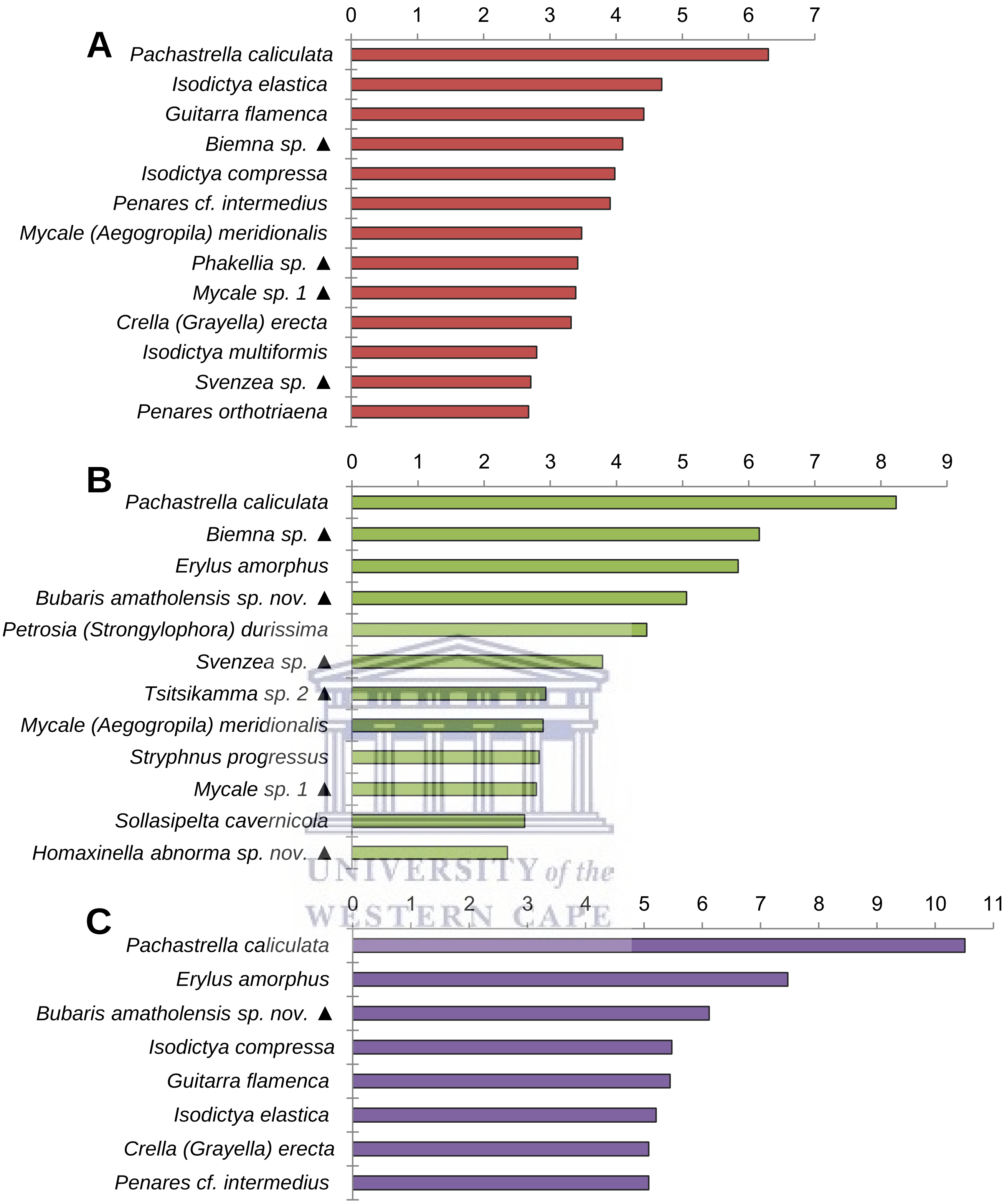

Figure 34: Results of SIMPER analysis indicating the percentage contribution (x-axes) of each species that overall contributed at least 50% to the difference between the shallow and mesophotic (**A**), mesophotic and sub-mesophotic (**B**), and shallow and sub-mesophotic (**C**) depth zones. The symbol (▲) denotes new species.

3.4 Biogeographic Affinities

Seventy-four heteroscleromorph demosponge species were collected from the Amathole region, with 27 likely new to science and 47 previously known. Of the latter, *Isodictya compressa* (Esper, 1797) was excluded due to the unknown type locality. The majority (55 species, 75.3%) have a restricted distribution around temperate southern Africa, here comprising southern Namibia up to and including the Natal ecoregion on the east coast of South Africa (Spalding *et al.* 2007) (Table 23). Six species (8.2%) are found within the Western Indian Ocean, with this study representing the southernmost distribution record for them. Finally, four species each (5.5%) are distributed across the Indo-Pacific, Indian and South Atlantic oceans.

Of the 47 previously known species, the majority were shared with the temperate southern African (37 species, 80.4%), Western Indo-Pacific (13, 28.3%), and Central Indo-Pacific (four, 8.7%) realms (Table 24). Two species each were shared with Vema Seamount and the temperate South American realm, while only one species each was shared with the Southern Ocean and temperate Australasian realms.

At the province level, the majority were shared with the Agulhas (29 species, 63.0%), Benguela (19, 41.3%), Western Indian Ocean (10, 21.7%), and West and South Indian Shelf (four, 8.7%). Within these provinces, the Amathole demosponge fauna was most similar to that found in the Agulhas (21 shared species, 45.7%), southern Benguela (19, 41.3%), Natal (13, 28.3%) and Western and Northern Madagascar (six, 13.0%) ecoregions. The Southeast Atlantic Deep Ocean, Delagoa, and South India and Sri Lanka ecoregions additionally shared three species each (6.5%) with the Amathole region.

Table 23: General biogeographic affinities of the 74 heteroscleromorph demosponge species from the Amathole region, with *Isodictya compressa* (Esper, 1797) excluded due to unknown type locality. Compiled using the World Porifera Database (van Soest *et al.* 2020a). The symbol (▲) denotes new species from this study, while (X) indicates presence, and (-) indicates absence.

Species	**Affinity**				
	Indo-Pacific	**Indian Ocean**	**Western Indian Ocean**	**Temperate Southern Africa**	**South Atlantic Ocean**
Acarnus claudei van Soest, Hooper & Hiemstra, 1991	-	-	-	X	-
Aciculites spinosa Vacelet & Vasseur, 1971	-	-	X	-	-
Amphilectus informis (Stephens, 1915)	-	-	-	X	-
Axinella sp. ▲	-	-	-	X	-
Biemna sp. ▲	-	-	-	X	-
Biemna sigmodragma Lévi, 1963	-	-	-	X	-
Bubaris amatholensis **sp. nov. ▲**	-	-	-	X	-
Ceratopsion microxephora (Kirkpatrick, 1903)	-	-	-	X	-
Characella sp. 1 ▲	-	-	-	X	-
Characella sp. 2 ▲	-	-	-	X	-
Coelodischela cf. *diatomorpha* Vacelet, Vasseur & Lévi, 1976	X	-	-	-	-
Crambe acuata (Lévi, 1958)	-	X	-	-	-
Crella (Grayella) erecta (Lévi, 1963)	-	-	-	X	-
Cyclacanthia sp. ▲	-	-	-	X	-
Didiscus cf. *placospongioides* Dendy, 1922	-	-	X	-	-
Ectyonopsis flabellata (Lévi, 1963)	-	-	-	X	-
Erylus amorphus Burton, 1926	-	-	-	X	-
Erylus gilchristi Burton, 1926	-	-	-	X	-
Erylus polyaster Lendenfeld, 1907	-	-	-	X	-
Fibulia ramosa (Ridley & Dendy, 1886)	-	-	-	-	X

Species	Affinity				
	Indo-Pacific	Indian Ocean	Western Indian Ocean	Temperate Southern Africa	South Atlantic Ocean
Forcepia (Forcepia) mucosa **sp. nov.** ▲	-	-	-	X	-
Geodia labyrinthica (Kirkpatrick, 1903)	-	-	-	X	-
Geodia libera Stephens, 1915	-	-	-	-	X
Guitarra flamenca Carballo & Uriz, 1998	-	-	-	X	-
Guitarra indica Dendy, 1916	-	X	-	-	-
Hamacantha (Vomerula) esperioides (Ridley & Dendy, 1886)	-	-	-	-	X
Hemiasterella vasiformis (Kirkpatrick, 1903)	-	-	X	-	-
Hemitedania sp. ▲	-	-	-	X	-
Histodermella natalensis (Kirkpatrick, 1903)	-	-	-	X	-
Holoxea massa **sp. nov.** ▲	-	-	-	X	-
Homaxinella abnorma **sp. nov.** ▲	-	-	-	X	-
Iophon regium **sp. nov.** ▲	-	-	-	X	-
Iophon ferrugineum **sp. nov.** ▲	-	-	-	X	-
Isodictya elastica (Vosmaer, 1880)	-	-	-	X	-
Isodictya grandis (Ridley & Dendy, 1886)	-	-	-	X	-
Isodictya multiformis (Stephens, 1915)	-	-	-	X	-
Lithochela conica Burton, 1929	-	-	-	X	-
Lithoplocamia longioxea **sp. nov.** ▲	-	-	-	X	-
Macandrewia cf. *auris* Lendenfeld, 1907	-	-	-	X	-
Microscleroderma hirsutum Kirkpatrick, 1903	-	X	-	-	-
Mycale sp. 1 ▲	-	-	-	X	-
Mycale sp. 2 ▲	-	-	-	X	-
Mycale (Aegogropila) meridionalis Lévi, 1963	-	-	-	X	-
Myxilla (Burtonanchora) sigmatifera (Lévi, 1963)	-	-	-	X	-
Myxilla (Myxilla) lissotylota **sp. nov.** ▲	-	-	-	X	-
Pachastrella caliculata Kirkpatrick, 1902	-	-	-	X	-
Pachymatisma sp. ▲	-	-	-	X	-

Species	Affinity				
	Indo-Pacific	Indian Ocean	Western Indian Ocean	Temperate Southern Africa	South Atlantic Ocean
Paradesmanthus macphersoni (Uriz, 1988)	-	-	-	X	-
Penares alatus (Lendenfeld, 1907)	-	-	-	X	-
Penares cf. *intermedius* (Dendy, 1905)	-	X	-	-	-
Penares orthotriaena Burton, 1931	-	-	X	-	-
Petromica (Petromica) tubulata (Kirkpatrick, 1903)	-	-	-	X	-
Petrosia (Strongylophora) durissima (Dendy, 1905)	X	-	-	-	-
Phakellia sp. ▲	-	-	-	X	-
Phorbas sp. ▲	-	-	-	X	-
Phorbas clathratus (Lévi, 1963)	-	-	-	X	-
Phorbas mollis (Kirkpatrick, 1903)	-	-	-	X	-
Placospongia sp. ▲	-	-	-	X	-
Poecillastra sp. ▲	-	-	-	X	-
Rhabderemia indica Dendy, 1905	X	-	-	-	-
Rhabderemia spirophora (Burton, 1931)	-	-	-	X	-
Sigmaxinella sp. ▲	-	-	-	X	-
Sollasipelta cavernicola (Vacelet & Vasseur, 1965)	-	-	X	-	-
Sollasipelta thoosa (Lévi, 1964)	-	-	X	-	-
Stelletta capensis Lévi, 1967	-	-	-	X	-
Stryphnus progressus (Lendenfeld, 1907)	-	-	-	-	X
Svenzea sp. ▲	-	-	-	X	-
Tedania (Tedania) tubulifera Lévi, 1963	-	-	-	X	-
Tethya magna Kirkpatrick, 1903	X	-	-	-	-
Theonella sp. ▲	-	-	-	X	-
Tsitsikamma sp. 1 ▲	-	-	-	X	-
Tsitsikamma sp. 2 ▲	-	-	-	X	-
Tsitsikamma sp. 3 ▲	-	-	-	X	-

Species	Affinity				
	Indo-Pacific	Indian Ocean	Western Indian Ocean	Temperate Southern Africa	South Atlantic Ocean
# Species	**4**	**4**	**6**	**55**	**4**
Percentage (%)	**5.5**	**5.5**	**8.2**	**75.3**	**5.5**

Table 24: Biogeographic affinities of the Amathole region sponge fauna based on the 47 known heteroscleromorph demosponge species from this study, with *Isodictya compressa* (Esper, 1797) excluded due to unknown type locality. Values indicate the number of species shared between the region, and each realm, province and/or ecoregion as defined in the global marine biogeographic classification system devised by Spalding *et al.* (2007). Within the temperate southern African realm, the ecoregions have been updated to reflect the comprehensive national classification system detailed in Sink *et al.* (2019b). Vema Seamount, which is featured in neither, is also included.

Realm		**Province**		**Ecoregion**	
Temperate Southern Africa	**37 (80.4%)**	Agulhas	**29 (63.0%)**	Agulhas (previously Agulhas Bank)	**21 (45.7%)**
				Natal	**13 (28.3%)**
				Southwest Indian Deep Ocean (new)	**1 (2.2%)**
		Benguela	**19 (41.3%)**	Southern Benguela (previously Namaqua)	**19 (41.3%)**
				Southeast Atlantic Deep Ocean (new)	**3 (6.5%)**
Western Indo-Pacific	**13 (28.3%)**	Western Indian Ocean	**10 (21.7%)**	Western and Northern Madagascar	**6 (13.0%)**
				Delagoa	**3 (6.5%)**
				East African Coral Coast	**2 (4.3%)**
				Seychelles	**2 (4.3%)**
				Cargados Carajos/Tromelin Island	**1 (2.2%)**
				Northern Monsoon Current Coast	**1 (2.2%)**
		West and South Indian Shelf	**4 (8.7%)**	South India and Sri Lanka	**3 (6.5%)**
				Western India	**1 (2.2%)**
		Red Sea and Gulf of Aden	**2 (4.3%)**	Southern Red Sea	**2 (4.3%)**
				Gulf of Aden	**1 (2.2%)**
		Bay of Bengal	**1 (2.2%)**	Eastern India	**1 (2.2%)**
		Somali/Arabian	**1 (2.2%)**	Western Arabian Sea	**1 (2.2%)**
Central Indo-Pacific	**4 (8.7%)**	Western Coral Triangle	**2 (4.3%)**	Eastern Philippines	**2 (4.3%)**

Realm		Province		Ecoregion	
		Eastern Coral Triangle	**1 (2.2%)**	Bismarck Sea	**1 (2.2%)**
		Northwest Australian Shelf	**1 (2.2%)**	Exmouth to Broome	**1 (2.2%)**
		Sunda Shelf	**1 (2.2%)**	Gulf of Thailand	**1 (2.2%)**
Temperate South America	**2 (4.3%)**	Warm Temperate Southwestern Atlantic	**2 (4.3%)**	Uruguay-Buenos Aires Shelf	**2 (4.3%)**
Vema Seamount	**2 (4.3%)**	Vema Seamount	**2 (4.3%)**	Vema Seamount	**2 (4.3%)**
Southern Ocean	**1 (2.2%)**	Subantarctic Islands	**1 (2.2%)**	Prince Edward Islands	**1 (2.2%)**
Temperate Australasia	**1 (2.2%)**	East Central Australian Shelf	**1 (2.2%)**	Manning-Hawkesbury	**1 (2.2%)**
		West Central Australian Shelf	**1 (2.2%)**	Houtman	**1 (2.2%)**

Chapter 4 – Discussion

The *Imida* Frontiers Project was initiated in 2015, under the auspices of the African Coelacanth Ecosystem Programme (ACEP, phase IV). As a component of this larger project, this study constitutes the first extensive investigation into the diversity, depth distribution and biogeographic affinities of the heteroscleromorph demosponge fauna from the historically unexplored Amathole region, where the first living coelacanth was discovered in 1938. The findings further augment our current knowledge of the South African sponge fauna.

4.1 Diversity

A total of 474 heteroscleromorph demosponges were collected during four expeditions comprising 48 sites across depths of 3–229 m. Seventy-four species were recorded, with representatives of 11 orders, two suborders, 34 families, four subfamilies, 53 genera and nine subgenera. Thus, the region supports a relatively high diversity of heteroscleromorph demosponges, despite its small extent (<200 km of coastline length). This is especially evident when compared to the 374 sponge species and seven varieties/forms documented from South Africa as a whole (Appendix A), which has a coastline of roughly 3 650 km (Griffiths *et al.* 2010). The elevated diversity could possibly be attributed to the position of the region within the transitional Agulhas-Natal ecoregion boundary zone (Sink *et al.* 2019b), as such regions are known to be sites of range-restricted species and relatively high richness (Awad *et al.* 2002; Acuña & Griffiths 2004; Scott *et al.* 2012). For example, Samaai (2006) found highest levels of endemism and richness among demosponges around Cape Town, which includes the Cape Point biogeographic boundary. However, these previous findings are likely artificial, as these sites often also correspond to areas of enhanced sampling activity (Awad *et al.* 2002; Acuña & Griffiths 2004; Scott *et al.* 2012; Griffiths & Robinson 2016).

The study region forms part of the Algoa to Amathole Ecologically or Biologically Significant Marine Area (EBSA) (Massie *et al.* 2019; online EBSA Portal). This EBSA site supports a high diversity of habitats and ecosystems(Sink *et al.* 2019b; Sink *et al.* 2019c; Sink *et al.* 2019d) that also serve to increase species richness (Schlacher *et al.* 2007; Hewitt *et al.* 2008; Sanciangco *et al.* 2013). Recorded habitat types include unconsolidated sediment, mesophotic reefs, rhodolith beds, fluvial fans, submarine canyons and an undocumented shipwreck (Dingle & Robson 1985; de Wet 2013; Dlamini 2017; Parker *et al.* 2017; Button 2018; Adams *et al.* 2020). The fluvial input from several prominent rivers in the area (e.g. Great Fish, Great Kei, Mbashe) likely benefits the sponge community through nutrient discharge, as found in Jew Shoal (Australia, Hooper & Kennedy 2002), the Derawan Islands (Indonesia, de Voogd *et al.* 2009), and off the Amazon River mouth (Moura *et al.* 2016; Francini-Filho *et al.* 2018). Likewise, inshore upwelling which extends southwards from Mbashe to the eastern edge of Algoa Bay (Schumann *et al.* 1988; Lutjeharms *et al.* 2000; Goschen & Schumann 2011; Russo *et al.* 2019) may also supply nutrient-rich water, and possibly enable the establishment of cold-temperate taxa. Finally, the elevated diversity could reflect the biogeographic influence of the Western Indian Ocean region (see Section 4.3 below).

It should be stressed that although the sampling effort was sufficient to document the majority (78%) of heteroscleromorph demosponges in the region, overall sponge diversity is underestimated. This reflects the fact that aspiculate demosponges have been excluded here, as too have specimens of Calcarea, Hexactinellida and Homoscleromorpha[8].

Of the heteroscleromorph demosponges, the orders Poecilosclerida (32 species) and Tetractinellida (22 species) were most speciose, together accounting for 72.9% of the

[8]At least 40 specimens of Homoscleromorpha were noted amongst the collection, but they were not examined. It is noteworthy that only one species is known from South Africa (Samaai *et al.* 2019).

recorded species. This is consistent with the dominance of these taxa in South Africa (Appendix A), where over a third of the sponge species are poecilosclerids. At the family level, the fauna was dominated by Geodiidae (order Tetractinellida; nine species), followed by Isodictyidae and Latrunculiidae (order Poecilosclerida; four species each). The latter is likely the most studied family in South Africa, largely because of their secondary metabolites (Davies-Coleman *et al.* 2019), with taxonomic work prolific and ongoing (Samaai *et al.* 2003, 2004a, 2004b, 2006, 2009a, 2012; Parker-Nance *et al.* 2019; Samaai *et al.* 2020a). Indeed, the country is a diversity hotspot for this family (Samaai *et al.* 2004a), which includes two endemic genera *Cyclacanthia* and *Tsitsikamma*, both of which were represented by new species in this study.

Of the 74 species obtained, 47 (63.5%) have been previously described, while 27 (36.5%) are likely new to science. Thirty-nine of the known species have been described and/or previously documented from South Africa. Twenty-five of these are currently considered endemic, while six species represent the first records since their original description(s) (e.g. *Ceratopsion microxephora* and *Crella (Grayella) erecta*). The remaining eight—*Guitarra indica*, *Penares* cf. *intermedius*, *Rhabderemia indica*, *Aciculites spinosa*, *Coelodischela* cf. *diatomorpha*, *Didiscus* cf. *placospongioides*, *Sollasipelta cavernicola* and *Sollasipelta thoosa*—represent new species records, while the last five also represent the first records of these genera in South Africa.

Of the 27 new species recorded here, eight were designated to *Bubaris*, *Hemitedania*, *Lithoplocamia*, *Placospongia*, *Characella*, *Holoxea* and *Svenzea*, representing the first records of these genera in South Africa, while the latter three also represent the first records of these genera in the Indian Ocean. Thus, this study has documented an additional 35 species and 11 genera for South Africa, and three genera for the Indian Ocean. These data will bring the total number of marine sponges from the South African Exclusive Economic Zone (EEZ) to 410, with six varieties/forms (*Biemna megalosigma* var. *sigmodragma* Lévi, 1963 here elevated to species status as *Biemna sigmodragma* Lévi, 1963).

The discovery of new species and records, as well as range extensions, was expected due to the poor state of marine sponge diversity knowledge in South Africa (Gibbons *et al.* 1999; Samaai 2006; Griffiths *et al.* 2010), with an estimated 900 species still undescribed (Griffiths *et al.* 2010). Presently, any relatively intensive collection effort leads to such findings (e.g. Samaai & Gibbons 2005; Maduray 2013; Samaai *et al.* 2019). This is further demonstrated in that many of the new species include some of the most abundant (e.g. *Biemna* sp.) and conspicuous (e.g. *Iophon regium* **sp. nov.**) specimens collected.

Although no sites were located in the coastal Amathole Marine Protected Area (MPA), 29 (60%) were situated in the Amathole Offshore MPA, which was declared as an extension of the former in 2019 (Sink *et al.* 2019d). Thus, 63 (85%) of the heteroscleromorph demosponge species recorded in this study receive some level of protection.

4.2 Depth Distribution

The heteroscleromorph demosponge assemblages of the Amathole region varied with depth, here defined as shallow (1–30 m), mesophotic (31–150 m) and sub-mesophotic (>150 m). This is consistent with previous findings, both in South Africa (Samaai *et al.* 2010; Maduray 2013), and elsewhere (Wilkinson & Cheshire 1989; Fromont *et al.* 2006; van Soest *et al.* 2007; Przeslawski *et al.* 2015; Howell *et al.* 2016; Alvarez *et al.* 2017; Longo *et al.* 2018; Pereira & Raghunathan 2018; Fortunato *et al.* 2020). Depth acts as a proxy for several environmental variables that correlate with it such as light, temperature and nutrients, which drive the distribution of sponge communities (Huang *et al.* 2011; Howell *et al.* 2016; Alvarez *et al.* 2017; Longo *et al.* 2018). The results of the pairwise tests indicate, however, that the mesophotic and sub-mesophotic assemblages were not significantly different (average dissimilarity = 89.5%, p = 0.135), likely due to the shared presence of two common species: *Pachastrella caliculata* and *Biemna* sp. This is consistent with a previous finding that deeper-living species occur across greater depth ranges than their shallow-water counterparts (Samaai *et al.* 2010).

Although depth was found to significantly structure sponge assemblages, the ANOSIM *R* value was relatively low (0.263). This could possibly be ascribed to the exclusion of aspiculate demosponges, and specimens from the other classes, with some taxa restricted to certain depth ranges. Globally, Homoscleromorpha are frequently found in shallow and dark/semi-dark ecosystems (van Soest *et al.* 2012), while hexactinellids are often located in deep, silica-rich environments (Alvarez *et al.* 2017). Depth restrictions were also documented in this study, with certain taxa exclusive to each zone. There tended to be a shift in dominance from Poecilosclerida at shallow depths, to Tetractinellida in the sub-mesophotic depth zone, as found in previous studies (Maldonado & Young 1996; Samaai *et al.* 2010; Pomponi *et al.* 2019). The presence of 'lithistids', and the genus *Lithoplocamia*, in the sub-mesophotic zone suggests that this assemblage may be primarily derived from the bathyal fauna (Lévi & Lévi 1983; Schlacher *et al.* 2007; Samaai *et al.* 2010). 'Lithistids' are also known to be diverse and common in the mesophotic zone (Pomponi *et al.* 2019), as documented here.

Alternatively, another factor could also be responsible for driving sponge assemblage structure, such as habitat type. This is evidenced in the low average similarities (<14%), and relatively high number of unique species (28%) that have only been recorded from a single site (de Voogd & Cleary 2008), which is suggestive of heterogeneity in species composition within each depth zone. Similar findings are commonly reported in sponge studies worldwide (van Soest 1993; Hooper *et al.* 2002; Hooper & Kennedy 2002; van Soest & Lavaleye 2005; Fromont *et al.* 2006; Schlacher *et al.* 2007; van Soest *et al.* 2007; Sorokin *et al.* 2007;

de Voogd & Cleary 2008; de Voogd *et al.* 2009; Pereira & Raghunathan 2018; Carballo *et al.* 2019). Unfortunately, habitat type could not be included in the analyses, as substrate collection and accurate classification was sporadic, with dredge samples likely representing a combination of substrate types found within the region (Rees 2009).

Finally, under-sampling could also contribute to the relatively low *R* value. This is supported by the high number of unique species (Fromont *et al.* 2006; de Voogd & Cleary 2008), and the species accumulation curves, which indicated that 77% of the heteroscleromorph demosponge species were collected from the mesophotic depth zone, but further sampling was required in the shallow and sub-mesophotic depth zones, the latter of which both contained new species.

The mesophotic assemblage comprised the highest number of species (66), and new species (25), which is likely due to the greater number of collection sites within this zone. The larger area and depth range included probably also played a role, with the mesophotic zone incorporating all specimens from 31–150 m, while the shallow and sub-mesophotic zones only incorporated those from 3–30 m and 150–229 m respectively. This finding is inconsistent with Samaai *et al.* (2010) who documented a decrease in sponge species richness with depth. Nevertheless, although understudied globally, the sponge fauna of the mesophotic zone is thought to comprise high diversity and numerous new species (Idan *et al.* 2018; Pomponi *et al.* 2019). This zone also acts as a transition between the shallow and sub-mesophotic zones, sharing taxa with both, and can serve as a refuge for stressed shallow-water species (Idan *et al.* 2018; Pomponi *et al.* 2019).

4.3 Biogeographic Affinities

If the 27 new species documented in this study are considered apparent endemics, and *Isodictya compressa* (Esper, 1797) is excluded due to the unknown type locality, the majority

(55 species, 75.3%) of the heteroscleromorph demosponges from the Amathole region have a restricted distribution around temperate southern Africa, here comprising southern Namibia up to and including the Natal ecoregion on the east coast of South Africa (Spalding *et al.* 2007). A further six species are found within the Western Indian Ocean, with this study representing the southernmost distribution record for them. Finally, four species each are distributed across the Indo-Pacific, Indian and South Atlantic oceans. This is in accordance with Scott *et al.* (2012) who found that oceanographic conditions impede 'average' range sizes in marine invertebrate taxa, with most species having a restricted range within southern Africa, or a wider Atlantic or Indo-Pacific distribution.

Due to their sessile nature and limited larval dispersal (Maldonado 2006), most sponges occur in local areas of endemism (van Soest *et al.* 2012; Bell *et al.* 2015), which is evidenced by the elevated level of apparent endemism in South Africa. For example, of the 374 species and seven varieties/forms in the country, 220 (58.8%) and six (85.7%) are apparent endemics respectively. Together, 59.3% are apparent endemics, which is consistent with the 57% previously reported by Samaai (2006), and is comparable to anemones (46%, Laird 2013) and bryozoans (57%, Boonzaaier 2017). However, this level of endemism is likely to be exaggerated due to the lack of taxonomic knowledge and sampling effort, both locally, and in adjacent areas (Gibbons *et al.* 1999; Griffiths & Robinson 2016). For example, the global community of sponge scientists comprises roughly 300 members (less than 150 specialists) from 72 counties, with the least located in Africa (1.5%) (Schönberg 2017).

Of the 47 known species recorded from the Amathole region, the majority are shared with the temperate southern African (37), Western Indo-Pacific (13), and Central Indo-Pacific (four) realms. Within these realms, most species were shared with the Agulhas (29), Benguela (19), Western Indian Ocean (10), and West and South Indian Shelf (four) provinces. Thus, the faunal affinities of the region are primarily with southern Africa, with additional influence from the Western Indian Ocean region. Similar findings have been documented for the east coast of South Africa, which has subtropical affinities with supplementary recruitment from the Indo-Pacific (Samaai 2006; Samaai *et al.* 2019). This result is not unexpected given the geographic location of the region on the south-east coast, the oceanographic regime of which is dominated by the Agulhas Current system (Lutjeharms 2007; Goschen *et al.* 2012). The heteroscleromorph demosponge fauna of the Amathole region shares only two species each with Vema Seamount and the temperate South American realm, while only one species each was shared with the Southern Ocean and temperate Australasian realms. This supports previous research that has shown little to no faunal links between the South African and Antarctic sponge fauna (Downey *et al.* 2012).

The Amathole region shares species with every ecoregion in South Africa. This is consistent with a previous finding that species can be distributed across neighbouring provinces/ecoregions (Maduray 2013), with boundaries passable (Burton 1932), due to the complex oceanographic regime. The heteroscleromorph demosponge fauna was most similar to that found in the Agulhas (21 shared species), southern Benguela (19), Natal (13) and Western and Northern Madagascar (six) ecoregions. Additionally, three species each were shared with the Southeast Atlantic Deep Ocean, Delagoa, and South India and Sri Lanka ecoregions.

Although most species were shared with the Agulhas ecoregion as would be expected, due to the location of the region within the transitional Agulhas-Natal ecoregion boundary zone (Sink *et al.* 2019b), more species were shared with the southern Benguela than with the Natal ecoregion. Speculating, this could be attributed to the historically under-sampled nature of the east coast (Samaai 2006; Samaai *et al.* 2019). That said, inshore upwelling which extends southwards from Mbashe (Schumann *et al.* 1988; Lutjeharms *et al.* 2000; Goschen & Schumann 2011; Russo *et al.* 2019), and freshwater discharge from the Mbashe River, may both act as barriers to dispersal (Ridgway *et al.* 1998; Teske *et al.* 2011). The former could also possibly facilitate the establishment of cold-temperate taxa. Furthermore, Indian Ocean biota could gain access to the South Atlantic Ocean via Agulhas rings (Primo & Vázquez 2004; Lutjeharms 2006), with inter-ocean exchange enhanced during interglacial stages (Peeters *et al.* 2004).

By contrast, the region has little connectivity with the Southeast Atlantic Deep Ocean and Southwest Indian Deep Ocean ecoregions, and only one species is shared with the latter. This may be indicative of poor sampling in the deeper regions off South Africa (Gibbons *et al.* 1999; Griffiths *et al.* 2010), but could also reflect taxa-specific depth restrictions (as detailed in Section 4.2).

The influence of the Western Indian Ocean region is evidenced by the species shared with the Delagoa and Western and Northern Madagascar ecoregions, likely driven by the Agulhas Current as discussed previously. Finally, the three species shared with the South India and Sri Lanka ecoregion require further genetic investigation, as widely distributed or cosmopolitan sponges have been increasingly found to comprise complexes of genetically distinct, but morphologically similar, sibling species (Klautau *et al.* 1999; Hooper *et al.* 2002; Boury-Esnault & Solé-Cava 2004; Plotkin & Boury-Esnault 2004; Nichols & Barnes 2005; Wörheide *et al.* 2005; Wörheide & Erpenbeck 2007).

4.4 Limitations

Estimates of overall sponge diversity in the Amathole region were limited in this study by the exclusion of aspiculate demosponges, and specimens from the other classes, as well as by poor sampling in both the shallow and sub-mesophotic depth zones. Specimens were largely collected using an epibenthic dredge, which can result in fragmentation and uneven catchability (Schlacher *et al.* 2007; Przeslawski *et al.* 2015). Moreover, substrate samples likely represent a combination of habitat types found within the heterogeneous region (Rees 2009). Thus, this study could have benefited from a more comprehensive array of sampling techniques, including intertidal work and more SCUBA dives, as well as specimen collection with a Remotely Operated Vehicle (ROV; used here exclusively for *in situ* sponge images). Finally, the biogeographic component should be considered with caution, due to the lack of taxonomic knowledge and sampling effort, both locally, and in adjacent areas.

In South Africa, taxonomic work is hampered by inaccessible, outdated and/or non-English literature, in addition to the historical deposition of South African sponge type material in European museums. Furthermore, although sponges are included in field guides (Branch *et al.* 2010; Samaai *et al.* 2018), identifying characteristics are perforce based mostly on gross morphology, with spicules and skeletal structures excluded. This, in combination with the need for a microscope for accurate identification, makes sponges inaccessible to non-specialists, including ecologists and community scientists, and often leads to misidentifications. South Africa has not been immune to the global, progressive loss of taxonomic expertise (Gibbons *et al.* 1999), and the country has few experts (Costello *et al.* 2010). Indeed, the majority of work is carried out by part-time/retired taxonomists or postgraduate students (Gibbons *et al.* 1999; Griffiths *et al.* 2010; Sink *et al.* 2019e). Sponges are a difficult group to study from a taxonomic perspective (Fromont *et al.* 2006; Schlacher *et al.* 2007; van Soest *et al.* 2007; Wörheide & Erpenbeck 2007; de Voogd *et al.* 2009; van Soest *et al.* 2012). Coupled with the lack of expertise, this means that the identification and description of species collected in biodiversity surveys and housed in museum collections is time-consuming and prolonged (Wörheide & Erpenbeck 2007).

4.5 Conclusion

Apart from providing an updated working list of the marine sponge species from South Africa, and contributing to the small body of work on mesophotic sponge assemblages worldwide, this study constitutes the first extensive investigation into the diversity, depth distribution and biogeographic affinities of the heteroscleromorph demosponge fauna from the Amathole region. The main findings were:

I) The region supports elevated heteroscleromorph demosponge diversity. This can be attributed to its position within the transitional Agulhas-Natal ecoregion boundary zone, the high habitat and ecosystem diversity and/or biogeographic influence of the Western Indian Ocean region. The fauna appears to be dominated by two orders (Poecilosclerida, Tetractinellida), and three families (Geodiidae, Isodictyidae, Latrunculiidae). Sixty-three (85%) of the species fall within the Amathole Offshore Marine Protected Area (MPA), and thus receive some level of protection.

II) New species and records, as well as range extensions, were discovered. Of the 74 species obtained, 47 were known, while 27 are likely new to science. The taxonomic descriptions of 23 species were provided here, eight as new. Overall, an additional 35 species and 11 genera were documented for South Africa, and an additional three genera were documented for the Indian Ocean. Consequently, after publication, the number of marine sponge species from the South African Exclusive Economic Zone (EEZ) will increase from 374 to 410 with six varieties/forms.

III) The heteroscleromorph demosponge assemblages changed with depth. Taxa-specific depth restrictions were evident, and there was a shift in dominance from Poecilosclerida to Tetractinellida with increasing depth. The low average similarities, and relatively high number of unique species, indicate heterogeneity in species composition within each depth zone, possibly driven by habitat type, though the latter could not be tested here. The mesophotic assemblage comprised the highest number of species, and new species, likely due to the greater number of collection sites within that zone.

IV) The majority of the heteroscleromorph demosponges have a restricted distribution around temperate southern Africa, with the remaining species having a wider Atlantic or Indo-Pacific distribution. Of the 47 known species recorded from the Amathole region, the faunal affinities were primarily with southern Africa, with additional influence from the Western Indian Ocean region, likely driven by the Agulhas Current. The region shares species with every ecoregion in South Africa, possibly due to the complex oceanographic regime, and comprises fauna most similar to that found in the Agulhas and southern Benguela ecoregions. Due to their sessile nature and limited larval dispersal, most sponges occur in local areas of endemism, which is evidenced by the elevated level of apparent endemism in South Africa (59.3%). Thus, widely distributed or cosmopolitan sponges require further investigation, as they probably comprise complexes of genetically distinct, but morphologically similar, sibling species.

Future work on the Amathole collection could include the description of the remaining new species and records, as well as further use of the ROV data to determine habitat types and associated sponge assemblages.

This study is only one component of the multidisciplinary *Imida* Frontiers Project. When combined with the bathymetric and geophysical surveys of benthic habitat, the ecological surveys, and predictive modelling, the spatial distribution of ecologically sensitive areas and their associated species will be determined. Presently, the high habitat, ecosystem and heteroscleromorph demosponge diversity, in addition to the presence of rare and endangered fish species, supports the position of the region within the Algoa to Amathole

Ecologically or Biologically Significant Marine Area (EBSA), and formation of the Amathole Offshore MPA in 2019.

Finally, given that an estimated 900 sponge species are thought to be undescribed around South Africa (Griffiths *et al.* 2010), there is a need to update and expand our knowledge of the South African sponge fauna, in order to make accurate specimen identification faster, and more accessible. Such species and distribution data is essential, as it feeds into the National Biodiversity Assessment and informs spatial planning initiatives and MPA development. Hence, the following recommendations are proposed:

I) **Revision.** All South African sponge type specimens should be located and re-described if necessary, using modern taxonomic protocols (e.g. SEM - scanning electron microscopy). This is essential, as most species have not been recorded since their initial description, and in some cases the latter are outdated, inadequate and inaccessible. The six varieties/forms also need further study, as too do the questionable species, as marked on the South African marine sponge species list. Many of the latter are widely-distributed or cosmopolitan, and likely comprise species complexes. Finally, extensive revision is required for speciose genera that occur in South Africa and the Western Indian Ocean region (e.g. *Geodia*, *Higginsia*). Many of the congeners are poorly described which precludes accurate comparison and identification. Widespread collaboration will be necessary to complete much of this work.

II) **Future Focus.** The sponge collection at the Iziko South African Museum needs attention, as it contains approximately 1 000 unaccesioned lots (Boonzaaier 2017). The increased use of genetic techniques could complement the traditional morphology-based taxonomy and would facilitate the quick identification of material, ease the workload of taxonomists and identify species complexes. More research should be conducted on aspiculate demosponges, and specimens from the other classes, while the understudied east coast and deeper environments off South Africa require further sampling. Finally, much work is needed on sponge ecology (e.g. symbiotic relationships). To the best of my knowledge, no explicit studies of sponge ecology have ever been conducted in the waters around South Africa.

III) **Accessibility.** Updated type specimen data, including both light and SEM images of spicules, *in situ* and deck pictures, as well as histological sections, should be uploaded or linked to the World Porifera Database and the relevant museum site. Furthermore, a field guide to South African sponges, including spicules and skeletal structures, should be produced. Lastly, the general public and community scientists could be engaged via the development of interactive keys and sponge-related projects on platforms like iNaturalist and Zooniverse.

Acuña, F.H. & Griffiths, C.L. (2004) Species richness, endemicity and distribution patterns of South African sea anemones (Cnidaria: Actiniaria & Corallimorpharia). *African Zoology*, 39 (2), 193–200.

Adams, L.A., Maneveldt, G.W., Green, A., Karenyi, N., Parker, D., Samaai, T. & Kerwath, S. (2020) Rhodolith bed discovered off the South African coast. *Diversity*, 12 (4), 125.

Adamson, R.S. & Stephenson, T.A. (1939) Marine biology in South Africa. *Nature*, 143 (3621), 503–504.

Aguilar-Camacho, J.M. & Carballo, J.L. (2012) New and little-known poecilosclerid sponges from the Mexican Pacific Ocean. *Zoological Studies*, 51 (7), 1139–1153.

Althaus, F., Hill, N., Ferrari, R., Edwards, L., Przeslawski, R., Schönberg, C.H.L., Stuart-Smith, R., Barrett, N., Edgar, G., Colquhoun, J., Tran, M., Jordan, A., Rees, T. & Gowlett-Holmes, K. (2015) A standardised vocabulary for identifying benthic biota and substrata from underwater imagery: the CATAMI classification scheme. *PLoS ONE*, 10 (10), e0141039.

Alvarez, B., Frings, P.J., Clymans, W., Fontorbe, G. & Conley, D.J. (2017) Assessing the potential of sponges (Porifera) as indicators of ocean dissolved Si concentrations. *Frontiers in Marine Science*, 4, 373.

Alvarez, B. & van Soest, R.W.M. (2002) Family Bubaridae Topsent, 1894. *In*: Hooper, J.N.A. & van Soest, R.W.M. (Eds.), *Systema Porifera. A Guide to the Classification of Sponges. Vol. 1*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 748–754.

Anđus, S., Tubić, B., Ilić, M., Đuknić, J., Gačić, Z. & Paunović, M. (2016) Freshwater sponges–skeletal structure analysis using light microscopy and scanning electron microscopy. *Water Research and Management*, 6 (2), 15–17.

Annandale, N. (1915) Some sponges parasitic on Clionidae with further notes on that family. *Records of the Indian Museum*, 11 (6), 457–478.

Appeltans, W., Ahyong, S.T., Anderson, G., Angel, M.V., Artois, T., Bailly, N., Bamber, R., Barber, A., Bartsch, I., Berta, A., Błażewicz-Paszkowycz, M., Bock, P., Boxshall, G., Boyko, C.B., Brandão, S.N., Bray, R.A., Bruce, N.L., Cairns, S.D., Chan, T., Cheng, L., Collins, A.G., Cribb, T., Curini-Galletti, M., Dahdouh-Guebas, F., Davie, P.J.F., Dawson, M.N., de Clerck, O., Decock, W., de Grave, S., de Voogd, N.J., Domning, D.P., Emig, C.C., Erséus, C., Eschmeyer, W., Fauchald, K., Fautin, D.G., Feist, S.W., Fransen, C.H.J.M., Furuya, H., Garcia-Alvarez, O., Gerken, S., Gibson, D., Gittenberger, A., Gofas, S., Gómez-Daglio, L., Gordon, D.P., Guiry, M.D., Hernandez, F., Hoeksema, B.W., Hopcroft, R.R., Jaume, D., Kirk, P., Koedam, N., Koenemann, S., Kolb, J.B., Kristensen, R.M., Kroh, A., Lambert, G., Lazarus, D.B., Lemaitre, R., Longshaw, M., Lowry, J., Macpherson, E., Madin, L.P., Mah, C., Mapstone, G., McLaughlin, P.A., Mees, J., Meland, K., Messing, C.G., Mills, C.E., Molodtsova, T.N., Mooi, R., Neuhaus, B., Ng, P.K.L., Nielsen, C., Norenburg, J., Opresko, D.M., Osawa, M., Paulay, G., Perrin, W., Pilger, J.F., Poore, G.C.B., Pugh, P., Read, G.B., Reimer, J.D., Rius, M., Rocha, R.M., Saiz-Salinas, J.I., Scarabino, V., Schierwater, B., Schmidt-Rhaesa, A., Schnabel, K.E., Schotte, M., Schuchert, P., Schwabe, E., Segers, H., Self-Sullivan, C., Shenkar, N., Siegel, V., Sterrer, W., Stöhr, S., Swalla, B., Tasker, M.L., Thuesen, E.V., Timm, T., Todaro, M.A., Turon, X., Tyler, S., Uetz, P., van der Land, J., Vanhoorne, B., van Ofwegen, L.P., van Soest, R.W.M., Vanaverbeke, J., Walker-Smith, G., Walter, T.C., Warren, A., Williams, G.C., Wilson, S.P. & Costello, M.J. (2012) The magnitude of global marine species diversity. *Current Biology*, 22 (23), 2189–2202.

Awad, A.A., Griffiths, C.L. & Turpie, J.K. (2002) Distribution of South African marine benthic invertebrates applied to the selection of priority conservation areas. *Diversity* *and Distributions*, 8 (3), 129–145.

Baer, L. (1906) Silicispongien von Sansibar, Kapstadt und Papeete. (Inaugural Dissertation: Berlin). *Archiv für Naturgeschichte*, 72 (1,1), 1–32.

van der Bank, M.G., Adams, R., Raimondo, D.C., Sink, K.J., van der Colff, D., Makhado, A., Kock, A., Porter, S., Seakamela, S.M., Louw, S., Mann, B.Q. & Bürgener, M. (2019) Chapter 9: The state of indigenous species. *In*: Sink, K.J., van der Bank, M.G., Majiedt, P.A., Harris, L.R., Atkinson, L.J., Kirkman, S.P. & Karenyi, N. (Eds.), *South African National Biodiversity Assessment 2018 Technical Report. Vol. 4. Marine Realm*. South African National Biodiversity Institute, Pretoria, South Africa, pp. 326–395.

Becking, L.E. (2013) Revision of the genus *Placospongia* (Porifera, Demospongiae, Hadromerida, Placospongiidae) in the Indo-West Pacific. *ZooKeys*, 298, 39–76.

Beckley, L.E. & van Ballegooyen, R.C. (1992) Oceanographic conditions during three ichthyoplankton surveys of the Agulhas Current in 1990/91. *South African Journal of Marine Science*, 12 (1), 83–93.

Bell, J.J. (2008) The functional roles of marine sponges. *Estuarine, Coastal and Shelf Science*, 79 (3), 341–353.

Bell, J.J., Bennett, H.M., Rovellini, A. & Webster, N.S. (2018) Sponges to be winners under near-future climate scenarios. *BioScience*, 68 (12), 955–968.

Bell, J.J., Davy, S.K., Jones, T., Taylor, M.W. & Webster, N.S. (2013) Could some coral reefs become sponge reefs as our climate changes? *Global Change Biology*, 19 (9), 2613–2624.

Bell, J.J., McGrath, E., Biggerstaff, A., Bates, T., Cárdenas, C.A. & Bennett, H. (2015) Global conservation status of sponges. *Conservation Biology*, 29 (1), 42–53.

Bergquist, P.R. & Hogg, J.J. (1969) Free amino acid patterns in Demospongiae: a biochemical approach to sponge classification. *Cahiers de Biologie Marine*, 10 (2), 205–

220.

Boonzaaier, M.K. (2017) *Diversity and zoogeography of South African Bryozoa*. PhD Thesis, University of the Western Cape, South Africa, 315 pp.

Borojević, R. (1967) Spongiaires d'Afrique du Sud. (2) Calcarea. *Transactions of the Royal Society of South Africa*, 37 (3), 183–226.

Boury-Esnault, N. (1973) Résultats Scientifiques des Campagnes de la "Calypso": Campagne de la "Calypso" au large des côtes atlantiques de l'Amérique du Sud (1961–1962). I. 29. Spongiaires. *Annales de l'Institut océanographique*, 49 (Supplément 10), 263–295.

Boury-Esnault, N. (1987) The *Polymastia* species (Demosponges, Hadromerida) of the Atlantic area. *In*: Vacelet, J. & Boury-Esnault, N. (Eds.), *Taxonomy of Porifera from the N.E. Atlantic and Mediterranean Sea. NATO ASI Series G, Ecological Sciences. Vol. 13*. Springer-Verlag, Berlin, Heidelberg, pp. 29–66.

Boury-Esnault, N. & van Beveren, M. (1982) Les démosponges du plateau continental de Kerguelen-Heard. *Comité national français des recherches antarctiques*, 52, 1–175.

Boury-Esnault, N. & Rützler, K. (1997) Thesaurus of sponge morphology. *Smithsonian Contributions to Zoology*, 596, 1–55.

Boury-Esnault, N. & Solé-Cava, A.M. (2004) Recent contribution of genetics to the study of sponge systematics and biology. *Bollettino dei Musei e degli Istituti Biologici dell'Università di Genova*, 68, 3–18.

Bowerbank, J.S. (1845) Description of a new genus of calcareous Sponge. *Annals and Magazine of Natural History*, 1, 15 (99), 297–300.

Bowerbank, J.S. (1858) On the anatomy and physiology of the Spongiadae. Part I. On the spicula. *Philosophical Transactions of the Royal Society*, 148 (2), 279–332.

Bowerbank, J.S. (1861) List of British sponges. *In*: McAndrew, R. (Ed.), *List of the British marine invertebrate fauna. Report of the British Association for the Advancement of*

Science. Vol. 30. Taylor & Francis, London, pp. 235–236.

Bowerbank, J.S. (1864) *A Monograph of the British Spongiadae. Vol. 1*. Ray Society, London, 290 pp.

Bowerbank, J.S. (1866) *A Monograph of the British Spongiadae. Vol. 2*. Ray Society, London, 388 pp.

Bowerbank, J.S. (1873) Contributions to a general history of the Spongiadae. Part IV. *Proceedings of the Zoological Society of London*, 3–25.

Branch, G.M., Griffiths, C.L., Branch, M.L. & Beckley, L.E. (2010) *Two Oceans: a guide to the marine life of southern Africa*. Random House Struik, Cape Town, South Africa, 456 pp.

Brøndsted, H.V. (1931) Die Kalkschwämme der Deutschen Südpolar Expedition 1901–1903. *Deutsche Südpolar-Expedition, 1901–1903*, 20, 1–47.

Brown, A.C. (2003) Centennial history of the Zoology Department, University of Cape Town, 1903–2003: a personal memoir. *Transactions of the Royal Society of South Africa*, 58 (1), 11–34.

Burton, M. (1926) Descriptions of South African sponges collected in the South African Marine Survey. Part I. Myxospongia and Astrotetraxonida. *Fisheries Bulletin. Fisheries and Marine Biological Survey Division, Union of South Africa*, Report 4 (Special Report 9), 1–29.

Burton, M. (1928) Report on some deep-sea sponges from the Indian Museum collected by R.I.M.S. "Investigator". Part II. Tetraxonida (concluded) and Euceratosa. *Records of the Indian Museum*, 30 (1), 109–138.

Burton, M. (1929a) Descriptions of South African sponges collected in the South African Marine Survey. Part II. The "Lithistidae", with critical survey of the desma-forming sponges. *Fisheries and Marine Biological Survey Division, Union of South Africa*, Report 7 (Special Report 1), 1–12.

Burton, M. (1929b) Porifera. Part II. Antarctic sponges. *In*: *British Antarctic ("Terra Nova") Expedition, 1910. Natural History Report. Zoology. 6 (4)*. British Museum (Natural History), London, pp. 393–458.

Burton, M. (1931) On a collection of marine sponges mostly from the Natal coast. *Annals of the Natal Museum*, 6 (3), 337–358.

Burton, M. (1932) Sponges. *Discovery Reports*, 6, 237–392.

Burton, M. (1933a) Four new marine sponges from Natal. *Annals of the Natal Museum*, 7 (2), 249–254.

Burton, M. (1933b) Report on a small collection of sponges from Stil Bay, S. Africa. *Annals and Magazine of Natural History*, 10, 11 (62), 235–244.

Burton, M. (1936) Notes on sponges from South Africa, with descriptions of new species. *Annals and Magazine of Natural History*, 10, 17 (97), 141–147.

Burton, M. (1959) Sponges. *In*: *Scientific Reports. John Murray Expedition 1933–34. 10 (5)*. British Museum (Natural History), London, pp. 151–281.

Button, R.E. (2018) *Remotely Operated Vehicle exploring ichthyofauna association with habitat from shore-shelf, in an endemism hotspot in South Africa*. MSc Thesis, University of Cape Town, South Africa, 62 pp.

Calcinai, B., Bavestrello, G., Cerrano, C. & Sarà, M. (2001) Boring sponges living into precious corals from the Pacific Ocean. *Italian Journal of Zoology*, 68 (2), 153–160.

Carballo, J.L. & Bell, J.J. (2017) Climate change and sponges: an introduction. *In*: Carballo, J.L. & Bell, J.J. (Eds.), *Climate Change, Ocean Acidification and Sponges*. Springer International Publishing, pp. 1–11.

Carballo, J.L., Cruz-Barraza, J.A., Vega, C., Nava, H. & del Carmen Chávez-Fuentes, M. (2019) Sponge diversity in Eastern Tropical Pacific coral reefs: an interoceanic comparison. *Scientific Reports*, 9, 9409.

Carballo, J.L. & Uriz, M.J. (1998) *Guitarra flamenca* sp. nov. (Porifera: Poecilosclerida) with a SEM revision of the spiny isochelae and placochelae in the genus. *Journal of the Marine Biological Association of the United Kingdom*, 78 (3), 807–819.

Cárdenas, P., Pérez, T. & Boury-Esnault, N. (2012) Sponge systematics facing new challenges. *Advances in Marine Biology*, 61, 79–209.

Cárdenas, P., Xavier, J.R., Reveillaud, J., Schander, C. & Rapp, H.T. (2011) Molecular phylogeny of the Astrophorida (Porifera, *Demospongiae*[p]) reveals an unexpected high level of spicule homoplasy. *PLoS ONE*, 6 (4), e18318.

Carter, H.J. (1869) On *Grayella cyathophora*, a new genus and species of sponges. *Annals and Magazine of Natural History*, 4, 4 (21), 189–197.

Carter, H.J. (1871) Description and illustrations of a new species of *Tethya*, with observations on the nomenclature of the Tethyadae. *Annals and Magazine of Natural History*, 4, 8 (44), 99–105.

Carter, H.J. (1874) Descriptions and figures of deep-sea sponges and their spicules from the Atlantic Ocean, dredged up on board H.M.S."Porcupine", chiefly in 1869; with figures and descriptions of some remarkable spicules from the Agulhas Shoal and Colon, Panama. *Annals and Magazine of Natural History*, 4, 14 (79), 207–221, 245–257.

Carter, H.J. (1875a) Notes introductory to the study and classification of the Spongida. Part II. Proposed classification of the Spongida. *Annals and Magazine of Natural History*, 4, 16 (92), 126–145.

Carter, H.J. (1875b) Notes introductory to the study and classification of the Spongida. *Annals and Magazine of Natural History*, 4, 16 (93), 177–200.

Carter, H.J. (1876) Descriptions and figures of deep-sea sponges and their spicules from the Atlantic Ocean, dredged up on board H.M.S."Porcupine", chiefly in 1869 (concluded).

Annals and Magazine of Natural History, 4, 18 (105, 106, 107, 108), 226–240, 307–324, 388–410, 458–479.

Carter, H.J. (1879) Contributions to our knowledge of the Spongida. *Annals and Magazine of Natural History*, 5, 3, 284–304, 343–360.

Carter, H.J. (1881) Contributions to our knowledge of the Spongida. *Annals and Magazine of Natural History*, 5, 8, 101–112, 118–120, 241–259.

Carter, H.J. (1882a) Contributions to our knowledge of the Spongida. Order II. Ceratina. *Annals and Magazine of Natural History*, 5, 8, 101–120.

Carter, H.J. (1882b) New sponges, observations on old ones, and a proposed new group. *Annals and Magazine of Natural History*, 5, 10 (55), 106–125.

Carter, H.J. (1882c) Some sponges from the West Indies and Acapulco in the Liverpool Free Museum described, with general and classificatory remarks. *Annals and Magazine of Natural History*, 5, 9 (52), 266–301, 346–368.

Carter, H.J. (1883) Contributions to our knowledge of the Spongida. *Annals and Magazine of Natural History*, 5, 12 (71), 308–329.

Carter, H.J. (1885) Descriptions of sponges from the neighbourhood of Port Phillip Heads, South Australia. *Annals and Magazine of Natural History*, 5, 16 (94), 277–294, 347–368.

Castello-Branco, C. & Hajdu, E. (2018) Two new *Hamacantha (Vomerula)* from the Rio Grande Rise (SW Atlantic) (Hamacanthidae, Porifera). *Zootaxa*, 4466 (1), 69–77.

Castelnau, F.L. (1861) *Mémoire sur les poissons de l'Afrique australe*. J.-B. Baillière et fils, Paris, 78 pp.

Chombard, C. & Boury-Esnault, N. (1999) Good congruence between morphology and molecular phylogeny of Hadromerida, or how to bother sponge taxonomists. *Memoirs of the Queensland Museum*, 44, 100.

Clarke, K.R. & Gorley, R.N. (2006) *PRIMER v6: User Manual/Tutorial*. PRIMER-E Ltd, Plymouth, United Kingdom, 190 pp.

Colgren, J. & Nichols, S.A. (2019) The significance of sponges for comparative studies of developmental evolution. *Wiley Interdisciplinary Reviews: Developmental Biology*, 9 (2), e359.

Collette, B.B. & Rützler, K. (1977) Reef fishes over sponge bottoms off the mouth of the Amazon River. *In*: *Proceedings of the Third International Coral Reef Symposium*. Miami, pp. 305–310.

Costello, M.J., Coll, M., Danovaro, R., Halpin, P., Ojaveer, H. & Miloslavich, P. (2010) A census of marine biodiversity knowledge, resources, and future challenges. *PLoS ONE*, 5 (8), e12110.

Cuvier, G. & Valenciennes, A. (1830) *Histoire naturelle des poissons. Tome Sixième. Livre Sixième. Partie I. Des Sparoïdes; Partie II. Des Ménides*. Chez F.G. Levrault, Paris, 559 pp.

Davies-Coleman, M.T., Antunes, E.M., Beukes, D.R. & Samaai, T. (2019) Colourful chemistry of South African latrunculid sponges. *South African Journal of Science*, 115 (5–6), 1–7.

Day, J.A. (2000) Marine and estuarine studies in South Africa: an historical perspective. *Transactions of the Royal Society of South Africa*, 55 (2), 101–105.

Dendy, A. (1905) Report on the sponges collected by Professor Herdman, at Ceylon, in 1902. *In*: Herdman, W.A. (Ed.), *Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar. Part III, Supplementary Reports 18*. Royal Society, London, pp. 57–246.

Dendy, A. (1916) Report on the non-calcareous sponges collected by Mr. James Hornell at Okhamandal in Kattiawar in 1905–6. *Report to the Government of Baroda on the*

Marine Zoology of Okhamandal in Kattiawar, 2, 93–146.

Dendy, A. (1922) Report on the Sigmatotetraxonida collected by H.M.S. "Sealark" in the Indian Ocean. *In*: *Reports of the Percy Sladen Trust Expedition to the Indian Ocean in 1905. Vol. 7*. Transactions of the Linnean Society of London, London, 18 (1), pp. 1–164.

Dendy, A. (1924) Porifera. Part I. Non-Antarctic sponges. *Natural History Report. British Antarctic ("Terra Nova") Expedition, 1910, Zoology*, 6 (3), 269–392.

Dendy, A. & Ridley, S.O. (1886) On *Proteleia sollasi*, a new genus and species of Monaxonid sponges allied to *Polymastia*. *Annals and Magazine of Natural History*, 5, 18 (104), 152–159.

Desqueyroux-Faúndez, R. & van Soest, R.W.M. (1996) A review of Iophonidae, Myxillidae and Tedaniidae occurring in the South East Pacific (Porifera: Poecilosclerida). *Revue suisse de Zoologie*, 103 (1), 3–79.

Dingle, R.V. & Robson, S. (1985) Slumps, canyons and related features on the continental margin off East London, SE Africa (SW Indian Ocean). *Marine Geology*, 67 (1–2), 37–54.

Dlamini, N. (2017) *Marine geology of the East London continental shelf*. MSc Thesis, University of KwaZulu-Natal, South Africa, 102 pp.

Downey, R.V., Griffiths, H.J., Linse, K. & Janussen, D. (2012) Diversity and distribution patterns in high southern latitude sponges. *PLoS ONE*, 7 (7), e41672.

Ehlers, E. (1870) *Die Esper'schen Spongien in der zoologischen Sammlung der K. Universität Erlangen*. E.Th. Jacob, Erlangen, 36 pp.

Ellis, J. & Solander, D. (1786) *The Natural History of many curious and uncommon Zoophytes, collected from various parts of the Globe. Systematically arranged and described by the late Daniel Solander. 4*. Benjamin White & Son, London, 206 pp.

Esper, E.J.C. (1797) *Fortsetzungen der Pflanzenthiere in Abbildungen nach der Natur mit*

Farben erleuchtet nebst Beschreibungen. Erster Theil. Raspe, Nürnberg, 230 pp.

Fabricius, O. (1780) *Fauna Groenlandica, systematice sistens animalia groenlandiae occidentalis hactenus indagata, quoad nomen specificium, triviale, vernaculumque, synonyma auctorum plurimum, descriptionem, locum, victum, generationem, mores, usum capturamque singuli, pro ut detegendi occasio fuit, maximaque parte secundum proprias observationes*. J.G. Rothe, Hafniae [= Copenhagen] & Lipsiae [= Leipzig], 452 pp.

Feuda, R., Dohrmann, M., Pett, W., Philippe, H., Rota-Stabelli, O., Lartillot, N., Wörheide, G. & Pisani, D. (2017) Improved modeling of compositional heterogeneity supports sponges as sister to all other animals. *Current Biology*, 27 (24), 3864–3870.

Fitt, W. (2020) Florida manatees *Trichechus manatus latirostris* actively consume the sponge *Chondrilla caribensis*. *PeerJ*, 8, e8443.

Fleming, J. (1828) *A history of British animals, exhibiting the descriptive characters and systematical arrangement of the genera and species of quadrupeds, birds, reptiles, fishes, Mollusca, and Radiata of the United Kingdom; including the indigenous, extirpated and extinct kinds; together with periodical and occasional visitants*. Bell & Bradfute, Edinburgh/James Duncan, London, 565 pp.

Folkers, M. & Rombouts, T. (2020) Sponges revealed: a synthesis of their overlooked ecological functions within aquatic ecosystems. *In*: Jungblut, S., Liebich, V. & Bode-Dalby, M. (Eds.), *YOUMARES 9 - The Oceans: Our Research, Our Future*. Springer, Cham, pp. 181–193.

Fortunato, H.F.M., de Paula, T.S., Esteves, E.L., Muricy, G. & Lôbo-Hajdu, G. (2020) Biodiversity and structure of marine sponge assemblages around a subtropical island. *Hydrobiologia*, 847 (5), 1281–1299.

Francini-Filho, R.B., Asp, N.E., Siegle, E., Hocevar, J., Lowyck, K., D'Avila, N., Vasconcelos, A.A., Baitelo, R., Rezende, C.E., Omachi, C.Y., Thompson, C.C. & Thompson, F.L. (2018) Perspectives on the Great Amazon Reef: extension, biodiversity, and threats. *Frontiers in Marine Science*, 5, 142.

Fromont, J., Vanderklift, M.A. & Kendrick, G.A. (2006) Marine sponges of the Dampier Archipelago, Western Australia: patterns of species distributions, abundance and diversity. *Biodiversity and Conservation*, 15, 3731–3750.

Gaino, E., Manconi, R. & Pronzato, R. (1995) Organizational plasticity as a successful conservative tactic in sponges. *Animal Biology*, 4, 31–43.

Gibbons, M.J. (1995) Marine biological diversity around South Africa. *In*: *100 Years of Marine Science in South Africa*. Chief Directorate Sea Fisheries, Cape Town, pp. 28–31.

Gibbons, M.J., Abiahy, B.B., Angel, M., Assuncao, C.M.L., Bartsch, I., Best, P., Biseswar, R., Bouillon, J., Bradford-Grieve, J.M., Branch, W., Burreson, E., Cannon, L., Casanova, J.-P., Channing, A., Child, C.A., Compagno, L., Cornelius, P.F.S., Dadon, J.R., David, J.H.M., Day, J., Della Croce, N., Emschermann, P., Erseus, C., Esnal, G., Gibson, R., Griffiths, C.L., Hayward, P.J., Heard, R., Heemstra, P., Herbert, D., Hessler, R., Higgins, R., Hiller, N., Hirano, Y.M., Kensley, B., Kilburn, R., Kornicker, L., Lambshead, J., Manning, R., Marshall, D., Mianzan, H., Monniot, C. & F., Newman, W., Nielsen, C., Patterson, G., Pugh, P., Roeleveld, M., Ross, A., Ryan, P., Ryland, J.S., Samaai, T., Schleyer, M., Schockaert, E., Seapy, R., Shiel, R., Sluys, R., Southward, E.C., Sulaiman, A., Thandar, A., van der Spoel, S., van Soest, R., van der Land, J., Vetter, E., Vinogradov, G., Williams, G. & Wooldridge, T. (1999) The taxonomic richness of South Africa's marine fauna: a crisis at hand. *South African Journal of Science*, 95 (1), 8–12.

Glynn, P.W. & Manzello, D.P. (2015) Bioerosion and coral reef growth: a dynamic balance. *In*: Birkeland, C. (Ed.), *Coral Reefs in the Anthropocene*. Springer, Netherlands, pp. 67–

97.

de Goeij, J.M., Lesser, M.P. & Pawlik, J.R. (2017) Nutrient fluxes and ecological functions of coral reef sponges in a changing ocean. *In*: Carballo, J.L. & Bell, J.J. (Eds.), *Climate Change, Ocean Acidification and Sponges*. Springer International Publishing, pp. 373–410.

de Goeij, J.M., van Oevelen, D., Vermeij, M.J.A., Osinga, R., Middelburg, J.J., de Goeij, A.F.P.M. & Admiraal, W. (2013) Surviving in a marine desert: the sponge loop retains resources within coral reefs. *Science*, 342 (6154), 108–110.

Goschen, W.S. & Schumann, E.H. (2011) *The physical oceanographic processes of Algoa Bay, with emphasis on the western coastal region*. South African Environmental Observation Network (SAEON) & Institute for Maritime Technology (IMT), South Africa, 82 pp.

Goschen, W.S., Schumann, E.H., Bernard, K.S., Bailey, S.E. & Deyzel, S.H.P. (2012) Upwelling and ocean structures off Algoa Bay and the south-east coast of South Africa. *African Journal of Marine Science*, 34 (4), 525–536.

Grant, R.E. (1836) Animal Kingdom. *In*: Todd, R.B. (Ed.), *The Cyclopaedia of Anatomy and Physiology. Vol. 1*. Sherwood, Gilbert, and Piper, London, pp. 107–118.

Grant, R.E. (1861) *Tabular view of the primary divisions of the animal kingdom, intended to serve as an outline of an elementary course of recent zoology (Cainozoology), or the natural history of existing animals*. Walton & Maberly, London, 91 pp.

Gray, J.E. (1848) *List of the specimens of British animals in the collection of the British Museum. Part 1. Centroniae or radiated animals*. British Museum, London, 173 pp.

Gray, J.E. (1867) Notes on the arrangement of sponges, with the descriptions of some new genera. *Proceedings of the Zoological Society of London*, 1867 (2), 492–558.

Gray, J.E. (1872) Notes on the classification of the sponges. *Annals and Magazine of Natural*

History, 4, 9 (54), 442–461.

Gray, J.E. (1873) Natal sponges. *Annals and Magazine of Natural History*, 4, 12 (69), 264.

Griffiths, C.L. (2005) Coastal marine biodiversity in East Africa. *Indian Journal of Marine Sciences*, 34 (1), 35–41.

Griffiths, C.L. & Robinson, T.B. (2016) Use and usefulness of measures of marine endemicity in South Africa. *South African Journal of Science*, 112 (3/4), 1–7.

Griffiths, C.L., Robinson, T.B., Lange, L. & Mead, A. (2010) Marine biodiversity in South Africa: an evaluation of current states of knowledge. *PLoS ONE*, 5 (8), e12008.

Grube, A.E. (1863) Beschreibung neuer oder wenig bekannter Anneliden. Sechster Beitrag. *Archiv für Naturgeschichte*, *Berlin*, 29, 37–69.

Haeckel, E. (1870) Prodromus of a system of the calcareous sponges. *Annals and Magazine of Natural History*, 4, 5 (27), 176–191.

Haeckel, E. (1872) *Die Kalkschwämme. Eine Monographie in zwei Bänden Text und einem Atlas mit 60 Tafeln Abbildungen. Vol. 1–3*. G. Reimer, Berlin, 484, 418 & 60 pp.

Hajdu, E. (1995) *Macroevolutionary patterns within the demosponge order Poecilosclerida. Phylogeny of the marine cosmopolitan genus Mycale, and an integrated approach to biogeography of the seas*. PhD Thesis, University of Amsterdam, Netherlands, 173 pp.

Hajdu, E. (2002) Family Hamacanthidae Gray, 1872. *In*: Hooper, J.N.A. & van Soest, R.W.M. (Eds.), *Systema Porifera. A Guide to the Classification of Sponges. Vol. 1*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 665–668.

Hajdu, E. & Desqueyroux-Faúndez, R. (2008) A reassessment of the phylogeny and biogeography of *Rhabderemia* Topsent, 1890 (Rhabderemiidae, Poecilosclerida, Demospongiae). *Revue Suisse de Zoologie*, 115 (2), 377–395.

Hajdu, E. & Lerner, C. (2002) Family Guitarridae Dendy, 1924. *In*: Hooper, J.N.A. & van

Soest, R.W.M. (Eds.), *Systema Porifera. A Guide to the Classification of Sponges. Vol. 1*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 651–655.

Hajdu, E. & Lôbo-Hajdu, G. (2002) Family Isodictyidae Dendy, 1924. *In*: Hooper, J.N.A. & van Soest, R.W.M. (Eds.), *Systema Porifera. A Guide to the Classification of Sponges. Vol. 1*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 703–706.

Hajdu, E. & van Soest, R.W.M. (2002) Family Desmacellidae Ridley & Dendy, 1886. *In*: Hooper, J.N.A. & van Soest, R.W.M. (Eds.), *Systema Porifera. A Guide to the Classification of Sponges. Vol. 1*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 642–650.

Hallmann, E.F. (1917) On the genera *Echinaxia* and *Rhabdosigma* (Porifera). *Proceedings of the Linnean Society of New South Wales*, 42 (2), 391–405.

Hentschel, E. (1912) Kiesel- und Hornschwämme der Aru- und Kei-Inseln. *Abhandlungen herausgegeben von der Senckenbergischen naturforschenden Gesellschaft*, 34 (3), 293–448.

Hentschel, E. (1914) Monaxone Kieselschwämme und Hornschwämme der Deutschen Südpolar Expedition 1901–1903. *Deutsche Südpolar-Expedition*, 15 (1), 35–141.

Hentschel, E. (1923) Erste Unterabteilung der Metazoa: Parazoa, Porifera-Schwämme. *In*: Kükenthal, W. & Krumbach, T. (Eds.), *Handbuch der Zoologie. Eine Naturgeschichteder Stämme des Tierreiches. Vol. 1. Protozoa, Porifera, Coelenterata, Mesozoa*. Walter de Gruyter & Co., Berlin, Leipzig, pp. 307–418.

Hewitt, J.E., Thrush, S.F. & Dayton, P.D. (2008) Habitat variation, species diversity and ecological functioning in a marine system. *Journal of Experimental Marine Biology and Ecology*, 366 (1–2), 116–122.

Heydrich, F. (1897) Melobesiae. *Berichte der Deutschen Botanischen Gesellschaft*, 15, 403–420.

Hogg, M.M., Tendal, O.S., Conway, K.W., Pomponi, S.A., van Soest, R.W.M., Gutt, J., Krautter, M. & Roberts, J.M. (2010) *Deep-sea Sponge Grounds: Reservoirs of Biodiversity*. UNEP-WCMC Biodiversity Series No. 32., UNEP-WCMC, Cambridge, United Kingdom, 84 pp.

Hooper, J.N.A. (1990) A new species of *Rhabderemia* Topsent (Porifera: Demospongiae) from the Great Barrier Reef. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences*, 7 (1), 65–78.

Hooper, J.N.A. (1996) Revision of Microcionidae (Porifera: Poecilosclerida: Demospongiae), with description of Australian species. *Memoirs of the Queensland Museum*, 40, 1–626.

Hooper, J.N.A. (2002a) Family Acarnidae Dendy, 1922. *In*: Hooper, J.N.A. & van Soest, R.W.M. (Eds.), *Systema Porifera. A Guide to the Classification of Sponges. Vol. 1*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 412–431.

Hooper, J.N.A. (2002b) Family Raspailiidae Hentschel, 1923. *In*: Hooper, J.N.A. & van Soest, R.W.M. (Eds.), *Systema Porifera. A Guide to the Classification of Sponges. Vol. 1*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 469–510.

Hooper, J.N.A. (2002c) Family Rhabderemiidae Topsent, 1928. *In*: Hooper, J.N.A. & van Soest, R.W.M. (Eds.), *Systema Porifera. A Guide to the Classification of Sponges. Vol. 1*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 511–513.

Hooper, J.N.A., Kelly, M. & Kennedy, J.A. (2000) A new *Clathria* (Porifera: Demospongiae: Microcionidae) from the Western Indian Ocean. *Memoirs of the Queensland Museum*, 45 (2), 427–444.

Hooper, J.N.A. & Kennedy, J.A. (2002) Small-scale patterns of sponge biodiversity (Porifera) from the Sunshine Coast reefs, eastern Australia. *Invertebrate Systematics*, 16 (4), 637–653.

Hooper, J.N.A., Kennedy, J.A. & Quinn, R.J. (2002) Biodiversity "hotspots", patterns of richness and endemism, and taxonomic affinities of tropical Australian sponges (Porifera). *Biodiversity and Conservation*, 11 (5), 851–885.

Hooper, J.N.A. & van Soest, R.W.M. (2002) *Systema Porifera. A Guide to the Classification of Sponges. Vol. 1 & 2*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, 1708 pp.

Howell, K.-L., Piechaud, N., Downie, A.-L. & Kenny, A. (2016) The distribution of deep-sea sponge aggregations in the North Atlantic and implications for their effective spatial management. *Deep Sea Research Part I: Oceanographic Research Papers*, 115, 309–320.

Huang, Z., Brooke, B. & Li, J. (2011) Performance of predictive models in marine benthic environments based on predictions of sponge distribution on the Australian continental shelf. *Ecological Informatics*, 6 (3–4), 205–216.

Idan, T., Shefer, S., Feldstein, T., Yahel, R., Huchon, D. & Ilan, M. (2018) Shedding light on an East-Mediterranean mesophotic sponge ground community and the regional sponge fauna. *Mediterranean Marine Science*, 19 (1), 84–106.

Ilan, M., Gugel, J. & van Soest, R.W.M. (2004) Taxonomy, reproduction and ecology of new and known Red Sea sponges. *Sarsia*, 89, 388–410.

Jesionowski, T., Norman, M., Żółtowska-Aksamitowska, S., Petrenko, I., Joseph, Y. & Ehrlich, H. (2018) Marine spongin: naturally prefabricated 3D scaffold-based biomaterial. *Marine Drugs*, 16 (3), 88.

Johnston, G. (1842) *A history of British sponges and lithophytes*. W.H. Lizars, Edinburgh, 264 pp.

Kelly, M. (2011) Phylum Porifera. Sponges. *In*: Richmond, M.D. (Ed.), *A Field Guide to the Seashores of Eastern Africa and the Western Indian Ocean Islands*. Sida/WIOMSA, pp. 116–127.

Kelly, M. & Sim-Smith, C. (2012) A review of *Ancorina*, *Stryphnus*, and *Ecionemia* (Demospongiae, Astrophorida, Ancorinidae), with descriptions of new species from New Zealand waters. *Zootaxa*, 3480 (1), 1–47.

Kirkpatrick, R. (1901) Description of a new hexactinellid sponge from South Africa. *Annals and Magazine of Natural History*, 7, 7 (41), 457–460.

Kirkpatrick, R. (1902) Descriptions of South African sponges. Part I. *Marine Investigations in South Africa*, 1, 219–232.

Kirkpatrick, R. (1903a) Descriptions of South African sponges. Part II. *Marine Investigations in South Africa*, 2 (14), 171–180.

Kirkpatrick, R. (1903b) Descriptions of South African sponges. Part III. *Marine Investigations in South Africa*, 2 (14), 233–264.

Kirkpatrick, R. (1913) Note on the occurrence of the euplectellid sponge *Regadrella phoenix* O. Schmidt, off the South African coast. *Annals of the South African Museum*, 13, 63–64.

Klautau, M., Russo, C.A.M., Lazoski, C., Boury-Esnault, N., Thorpe, J.P. & Solé-Cava, A.M. (1999) Does cosmopolitanism result from overconservative systematics? A case study using the marine sponge *Chondrilla nucula*. *Evolution*, 53 (5), 1414–1422.

Klautau, M. & Valentine, C. (2003) Revision of the genus *Clathrina* (Porifera, Calcarea). *Zoological Journal of the Linnean Society*, 139 (1), 1–62.

Koltun, V.M. (1964) Sponges of the Antarctic. Part 1. Tetraxonida and Cornacuspongida. *In*:

Pavlovskii, E.P., Andriyashev, A.P. & Ushakov, P.V. (Eds.), *Biological Reports of the Soviet Antarctic Expedition (1955–1958). Vol. 2(10)*. Academy of Sciences of the USSR, Nauka, Moscow-Leningrad, pp. 6–133, 443–448.

Laird, M.C. (2013) *Taxonomy, systematics and biogeography of South African Actiniaria and Corallimorpharia*. PhD Thesis, University of Cape Town, South Africa, 334 pp.

Lamarck, J.B.P.d.M. (1813–1814) Sur les polypiers empâtés. Suite du mémoire intitulé: Sur les Polypiers empâtés. Suite des éponges. *Annales du Muséum National d'Histoire Naturelle, Paris*, 20 (6), 294–312 (published 1813), 370–386, 432–458 (published 1814).

Lamouroux, J.V.F. (1813) Essai sur les genres de la famille des thalassiophytes non articulées. *Annales du Muséum National d'Histoire Naturelle, Paris*, 20, 21–47, 115–139, 267–293.

de Laubenfels, M.W. (1934) New sponges from the Puerto Rican deep. *Smithsonian Miscellaneous Collections*, 91 (17), 1–28.

de Laubenfels, M.W. (1936) A discussion of the sponge fauna of the Dry Tortugas in particular and the West Indies in general, with material for a revision of the families and orders of the Porifera. *Carnegie Institute of Washington Publication*, 467 (Tortugas Laboratory Paper 30), 1–225.

Lendenfeld, R. Von (1889a) *A Monograph of the Horny Sponges*. Trübner and Co., London, 936 pp.

Lendenfeld, R. Von (1889b) Das system der Spongien. *Biologisches Zentralblatt*, 9 (4), 113–127.

Lendenfeld, R. Von (1903) Porifera. Tetraxonia. *In*: Schulze, F.E. (Ed.), *Das Tierreich. Vol. 19*. Friedländer, Berlin, pp. 1–168.

Lendenfeld, R. Von (1907) Die Tetraxonia. *Wissenschaftliche Ergebnisse der Deutschen*

Tiefsee-Expedition auf der Dampfer Valdivia 1898–1899, 11 (1–2), i–iv, 59–374.

Lesser, M.P., Slattery, M. & Mobley, C.D. (2018) Biodiversity and functional ecology of mesophotic coral reefs. *Annual Review of Ecology, Evolution, and Systematics*, 49 (1), 49–71.

Lévi, C. (1953) Sur une nouvelle classification des démosponges. *Comptes rendus hebdomadaires des séances de l'Académie des Sciences*, 236 (8), 853–855.

Lévi, C. (1956) Éponges littorales des Îles Kerguelen récoltées par M. Angot. *Mémoires de l'Institut Scientifique de Madagascar*, A, 10, 25–34.

Lévi, C. (1958) Résultats scientifiques des Campagnes de la "Calypso". Campagne 1951–1952 en Mer Rouge (suite). 11. Spongiaires de Mer Rouge recueillis par la "Calypso" (1951–1952). *Annales de l'Institut océanographique*, 34 (3), 3–46.

Lévi, C. (1960) Les spongiaires à desmes astéroïdes. *Bulletin de l'Institut océanographique de Monaco*, 1179, 1–8.

Lévi, C. (1961) Résultats scientifiques des Campagnes de la "Calypso". Campagne 1954 dans l'Océan Indien (suite). 2. Les spongiaires de l'Ile Aldabra. *Annales de l'Institut océanographique*, 39 (1), 1–32.

Lévi, C. (1963) Spongiaires d'Afrique du Sud. (1) Poecilosclérides. *Transactions of the Royal Society of South Africa*, 37 (1), 1–72.

Lévi, C. (1964a) Spongiaires des zones bathyale, abyssale et hadale. *Galathea Report. Scientific Results of The Danish Deep-Sea Expedition Round the World, 1950–52*, 7, 63–112.

Lévi, C. (1964b) Spongiaires du canal de Mozambique. *Bulletin du Muséum National d'Histoire Naturelle*, *Paris*, 2, 36 (3), 384–395.

Lévi, C. (1967) Spongiaires d'Afrique du Sud. (3) Tétractinellides. *Transactions of the Royal Society of South Africa*, 37, 227–256.

Lévi, C. (1969) Spongiaires du Vema Seamount (Atlantique Sud). *Bulletin du Muséum National d'Histoire Naturelle*, 2, 41 (4), 952–973.

Lévi, C. (Ed.) (1998) *Sponges of the New Caledonian Lagoon*. Collection Faune et flore tropicales, No. 33, Éditions de l'Orstom, Paris, 214 pp.

Lévi, C. & Lévi, P. (1983) Eponges Tétractinellides et Lithistides bathyales de Nouvelle-Calédonie. *Bulletin du Muséum National d'Histoire Naturelle*, 4, 5 (1), 101–168.

Lévi, C. & Lévi, P. (1989) Spongiaires (MUSORSTOM 1 & 2). *In*: Forest, J. (Ed.), *Résultats des Campagnes MUSORSTOM 4*. Mémoires du Muséum National d'Histoire Naturelle, A (Zoologie), 143, pp. 25–103.

Li, L., Guo, C., Chen, Y. & Chen, Y. (2020) Optimization design of lightweight structure inspired by glass sponges (Porifera, Hexactinellida) and its mechanical properties. *Bioinspiration & Biomimetics*, 15 (3), 036006.

Lieberkühn, N. (1859) Neue Beiträge zur Anatomie der Spongien. *Archiv für Anatomie und Physiologie*, 30 (3), 353–382, 515–529.

List-Armitage, S.E. & Hooper, J.N.A. (2002) Discovery of *Petromica* Topsent in the Pacific Ocean: a revision of the genus with a new subgenus (*Chaladesma*, subgen. nov.) and a new species (*P.(C.) pacifica*, sp. nov.) (Porifera: Demospongiae: Halichondrida: Halichondriidae). *Invertebrate Systematics*, 16 (5), 813–835.

Longo, C., Cardone, F., Pierri, C., Mercurio, M., Mucciolo, S., Nonnis Marzano, C. & Corriero, G. (2018) Sponges associated with coralligenous formations along the Apulian coasts. *Marine Biodiversity*, 48 (4), 2151–2163.

Lundbeck, W. (1905) Porifera. (Part II.) Desmacidonidae (pars.). *In*: *The Danish Ingolf-Expedition*. Bianco Luno, Copenhagen, 6 (2), pp. 1–219.

Lutjeharms, J.R.E. (2006) The ocean environment off southeastern Africa: a review. *South African Journal of Science*, 102 (9), 419–426.

Lutjeharms, J.R.E. (2007) Three decades of research on the greater Agulhas Current. *Ocean Science*, 3 (1), 129–147.

Lutjeharms, J.R.E., Cooper, J. & Roberts, M. (2000) Upwelling at the inshore edge of the Agulhas Current. *Continental Shelf Research*, 20 (7), 737–761.

Maduray, S. (2013) *Studies on the diversity and spatial distribution of deep-water sponges along the west and south coasts of South Africa*. MSc Thesis, University of the Western Cape, South Africa, 132 pp.

Maldonado, M. (2006) The ecology of the sponge larva. *Canadian Journal of Zoology*, 84 (2), 175–194.

Maldonado, M., Aguilar, R., Bannister, R.J., Bell, J.J., Conway, K.W., Dayton, P.K., Díaz, C., Gutt, J., Kelly, M., Kenchington, E.L.R., Leys, S.P., Pomponi, S.A., Rapp, H.T., Rützler, K., Tendal, O.S., Vacelet, J. & Young, C.M. (2015) Sponge grounds as key marine habitats: a synthetic review of types, structure, functional roles, and conservation concerns. *In*: Rossi, S., Bramanti, L., Gori, A. & Orejas, C. (Eds.), *Marine Animal Forests*. Springer, Cham, pp. 1–39.

Maldonado, M. & Young, C.M. (1996) Bathymetric patterns of sponge distribution on the Bahamian slope. *Deep Sea Research Part I: Oceanographic Research Papers*, 43 (6), 897–915.

Mann, J., Sargeant, B.L., Watson-Capps, J.J., Gibson, Q.A., Heithaus, M.R., Connor, R.C. & Patterson, E. (2008) Why do dolphins carry sponges? *PLoS ONE*, 3 (12), e3868.

Marshall, W. (1876) Ideen über die Verwandtschaftsverhältnisse der Hexactinelliden. *Zeitschrift für wissenschaftliche Zoologie*, 27 (1), 113–136.

Maschette, D., Fromont, J., Platell, M.E., Coulson, P.G., Tweedley, J.R. & Potter, I.C. (2020) Characteristics and implications of spongivory in the Knifejaw *Oplegnathus woodwardi* (Waite) in temperate mesophotic waters. *Journal of Sea Research*, 157, 101847.

Massie, V., Clark, B., Hutchings, K., Dawson, J., Brown, E., Wright, A. & Laird, M. (2019) *Proposed Sea-based Aquaculture Development Zone in Algoa Bay, Eastern Cape – Draft Basic Assessment Report in Terms of the National Environmental Management Act (107 of 1998)*. Report prepared for the Department of Agriculture, Forestry and Fisheries by Anchor Research and Monitoring (Pty) Ltd, Cape Town, Souh Africa, 196 pp.

Matobole, R.M., van Zyl, L.J., Parker-Nance, S., Davies-Coleman, M.T. & Trindade, M. (2017) Antibacterial activities of bacteria isolated from the marine sponges *Isodictya compressa* and *Higginsia bidentifera* collected from Algoa Bay, South Africa. *Marine Drugs*, 15 (2), 47.

McQuaid, C.D. (2010) Balancing science and politics in South African marine biology. *South African Journal of Science*, 106 (11/12), 1–6.

Mehbub, M.F., Lei, J., Franco, C. & Zhang, W. (2014) Marine sponge derived natural products between 2001 and 2010: trends and opportunities for discovery of bioactives. *Marine Drugs*, 12 (8), 4539–4577.

Meyer, I., Reinecke, J., Roberts, M. & van Niekerk, J.L. (2013) *Assessment of the Ocean Energy Resources off the South African Coast*. Centre for Renewable and Sustainable Energy Studies, Faculty of Engineering, Stellenbosch University, South Africa, 65 pp.

Meyer, N., Wisshak, M. & Schönberg, C.H.L. (2019) Sponge bioerosion versus aqueous pCO_2: morphometric assessment of chips and etching fissures. *Facies*, 65, 27.

Morrow, C.C. & Cárdenas, P. (2015) Proposal for a revised classification of the Demospongiae (Porifera). *Frontiers in Zoology,* 12 (7), 1–27.

Morrow, C.C., Cárdenas, P., Boury-Esnault, N., Picton, B., McCormack, G., van Soest, R.W.M., Collins, A., Redmond, N., Maggs, C., Sigwart, J. & Allcock, L.A. (2019) Integrating morphological and molecular taxonomy with the revised concept of

Stelligeridae (Porifera: Demospongiae). *Zoological Journal of the Linnean Society*, 187 (1), 31–81.

Morrow, C.C., Picton, B.E., Erpenbeck, D., Boury-Esnault, N., Maggs, C.A. & Allcock, A.L. (2012) Congruence between nuclear and mitochondrial genes in Demospongiae: a new hypothesis for relationships within the G4 clade (Porifera: Demospongiae). *Molecular Phylogenetics and Evolution*, 62 (1), 174–190.

Morrow, C.C., Redmond, N.E., Picton, B.E., Thacker, R.W., Collins, A.G., Maggs, C.A., Sigwart, J.D. & Allcock, A.L. (2013) Molecular phylogenies support homoplasy of multiple morphological characters used in the taxonomy of Heteroscleromorpha (Porifera: Demospongiae). *Integrative and Comparative Biology*, 53 (3), 428–446.

Moura, R.L., Amado-Filho, G.M., Moraes, F.C., Brasileiro, P.S., Salomon, P.S., Mahiques, M.M., Bastos, A.C., Almeida, M.G., Silva, J.M.Jr., Araujo, B.F., Brito, F.P., Rangel, T.P., Oliveira, B.C.V., Bahia, R.G., Paranhos, R.P., Dias, R.J.S., Siegle, E., Figueiredo, A.G.Jr., Pereira, R.C., Leal, C.V., Hajdu, E., Asp, N.E., Gregoracci, G.B., Neumann-Leitão, S., Yager, P.L., Francini-Filho, R.B., Fróes, A., Campeão, M., Silva, B.S., Moreira, A.P.B., Oliveira, L., Soares, A.C., Araujo, L., Oliveira, N.L., Teixeira, J.B., Valle, R.A.B., Thompson, C.C., Rezende, C.E. & Thompson, F.L. (2016) An extensive reef system at the Amazon River mouth. *Science Advances*, 2 (4), e1501252.

Muricy, G., Hajdu, E., Minervino, J.V., Madeira, A.V. & Peixinho, S. (2001) Systematic revision of the genus *Petromica* Topsent (Demospongiae: Halichondrida), with a new species from the southwestern Atlantic. *Hydrobiologia*, 443 (1–3), 103–128.

Muricy, G., Lopes, D.A., Hajdu, E., Carvalho, M.S., Moraes, F.C., Klautau, M., Menegola, C. & Pinheiro, U. (2011) *Catalogue of Brazilian Porifera*. Série Livros 46, Museu Nacional, Rio de Janeiro, 300 pp.

Nardo, G.D. (1833) Auszug aus einem neuen System der Spongiarien, wonach bereits die

Aufstellung in der Universitäts-Sammlung zu Padua gemacht ist. *In*: *Isis, oder Encyclopädische Zeitung Coll*. Oken, Jena, pp. 519–523.

Ngwakum, B.B. (2019) *DNA barcoding of sponges (Phylum Porifera) in South Africa*. MSc Thesis, University of Johannesburg, South Africa, 119 pp.

Nichols, S.A. & Barnes, P.A.G. (2005) A molecular phylogeny and historical biogeography of the marine sponge genus *Placospongia* (Phylum Porifera) indicate low dispersal capabilities and widespread crypsis. *Journal of Experimental Marine Biology and Ecology*, 323 (1), 1–15.

Nielsen, C. (2019) Early animal evolution: a morphologist's view. *Royal Society Open Science*, 6 (7), 190638.

Orani, A.M., Barats, A., Zitte, W., Morrow, C. & Thomas, O.P. (2018) Comparative study on the bioaccumulation and biotransformation of arsenic by some northeastern Atlantic and northwestern Mediterranean sponges. *Chemosphere*, 201, 826–839.

Papatheodoulou, M., Jimenez, C., Petrou, A. & Thasitis, I. (2019) Endobiotic communities of marine sponges in Cyprus (Levantine Sea). *Heliyon*, 5 (3), e01392.

Parker-Nance, S., Hilliar, S., Waterworth, S., Walmsley, T. & Dorrington, R. (2019) New species in the sponge genus *Tsitsikamma* (Poecilosclerida, Latrunculiidae) from South Africa. *ZooKeys*, 874, 101–126.

Parker, D., Sink, K. & Kerwath, S. (2017) Dredging the depths of the Amathole to find sponges, corals and shipwrecks. *Maritime Review Africa*, 6–7.

Pawlik, J.R., Loh, T. & McMurray, S.E. (2018) A review of bottom-up vs. top-down control of sponges on Caribbean fore-reefs: what's old, what's new, and future directions. *PeerJ*, 6, e4343.

Pawlik, J.R. & McMurray, S.E. (2020) The emerging ecological and biogeochemical importance of sponges on coral reefs. *Annual Review of Marine Science*, 12, 315–337.

Peeters, F.J.C., Acheson, R., Brummer, G.-J.A., de Ruijter, W.P.M., Schneider, R.R., Ganssen, G.M., Ufkes, E. & Kroon, D. (2004) Vigorous exchange between the Indian and Atlantic oceans at the end of the past five glacial periods. *Nature*, 430 (7000), 661–665.

Pereira, P. & Raghunathan, C. (2018) Diversity of sponges in Marine Protected Areas of North Andaman, India. *Thalassas: An International Journal of Marine Sciences*, 34 (2), 361–372.

Pita, L., Rix, L., Slaby, B.M., Franke, A. & Hentschel, U. (2018) The sponge holobiont in a changing ocean: from microbes to ecosystems. *Microbiome*, 6, 46.

Plotkin, A. & Boury-Esnault, N. (2004) Alleged cosmopolitanism in sponges: the example of a common Arctic *Polymastia* (Porifera, Demospongiae, Hadromerida). *Zoosystema*, 26 (1), 13–20.

Plotkin, A., Morrow, C., Gerasimova, E. & Rapp, H.T. (2017) Polymastiidae (Demospongiae: Hadromerida) with ornamented exotyles: a review of morphological affinities and description of a new genus and three new species. *Journal of the Marine Biological Association of the United Kingdom*, 97 (6), 1351–1406.

Pomponi, S.A., Diaz, M.C., van Soest, R.W.M., Bell, L.J., Busutil, L., Gochfeld, D.J., Kelly, M. & Slattery, M. (2019) Sponges. *In*: Loya, Y., Puglise, K.A. & Bridge, T.C.L. (Eds.), *Mesophotic Coral Ecosystems. Coral Reefs of the World. Vol. 12*. Springer, Cham, pp. 563–588.

Powell, A., Clarke, M.E., Fruh, E., Chaytor, J.D., Reiswig, H.M. & Whitmire, C.E. (2018) Characterizing the sponge grounds of Grays Canyon, Washington, USA. *Deep Sea Research Part II: Topical Studies in Oceanography*, 150, 146–155.

Primo, C. & Vázquez, E. (2004) Zoogeography of the southern African ascidian fauna. *Journal of Biogeography*, 31 (12), 1987–2009.

Procheş, Ş. & Marshall, D.J. (2002) Diversity and biogeography of southern African intertidal Acari. *Journal of Biogeography*, 29 (9), 1201–1215.

Pronzato, R. & Manconi, R. (2008) Mediterranean commercial sponges: over 5000 years of natural history and cultural heritage. *Marine Ecology*, 29 (2), 146–166.

Przeslawski, R., Alvarez, B., Kool, J., Bridge, T., Caley, M.J. & Nichol, S. (2015) Implications of sponge biodiversity patterns for the management of a marine reserve in Northern Australia. *PLoS ONE*, 10 (11), e0141813.

Pulitzer-Finali, G. (1993) A collection of marine sponges from East Africa. *Annali del Museo Civico di Storia Naturale Giacomo Doria*, 89, 247–350.

QGIS Development Team (2020) QGIS Geographic Information System. Open Source Geospatial Foundation Project. Available from: http://qgis.osgeo.org (accessed 10 November 2020)

Rasser, M.W. & Riegl, B. (2002) Holocene coral reef rubble and its binding agents. *Coral Reefs*, 21, 57–72.

Rees, H.L. (Ed.) (2009) *Guidelines for the study of the epibenthos of subtidal environments*. ICES Techniques in Marine Environmental Sciences No. 42, ICES, Copenhagen, Denmark, 88 pp.

Regan, C.T. (1908) A collection of fishes from the coasts of Natal, Zululand, and Cape Colony. *Annals of the Natal Museum*, 1 (3), 241–255.

Renard, E., Leys, S.P., Wörheide, G. & Borchiellini, C. (2018) Understanding animal evolution: the added value of sponge transcriptomics and genomics. *BioEssays*, 40 (9), e1700237.

Ribeiro, S.M. & Muricy, G. (2011) Taxonomic revision of Brazilian *Tethya* (Porifera: Hadromerida) with description of four new species. *Journal of the Marine Biological Association of the United Kingdom*, 91 (7), 1511–1528.

Ridgway, T.M., Stewart, B.A., Branch, G.M. & Hodgson, A.N. (1998) Morphological and genetic differentiation of *Patella granularis* (Gastropoda: Patellidae): recognition of two sibling species along the coast of southern Africa. *Journal of Zoology*, 245 (3), 317–333.

Ridley, S.O. (1881) XI. Spongida. Horny and siliceous sponges of Magellan Straits, S.W. Chili, and Atlantic off S.W. Brazil. *In*: Gunther, A. (Ed.), *Account of the Zoological Collections made during the Survey of H.M.S. "Alert" in the Straits of Magellan and on the Coast of Patagonia*. Zoological Society, London, pp. 107–137, 140–141.

Ridley, S.O. & Dendy, A. (1886) Preliminary report on the Monaxonida collected by H.M.S. "Challenger". *Annals and Magazine of Natural History*, 5, 18 (107), 325–351, 470–493.

Ridley, S.O. & Dendy, A. (1887) Report on the Monaxonida collected by H.M.S. "Challenger" during the years 1873–1876. *Report on the Scientific Results of the Voyage of H.M.S. "Challenger", 1873–1876. Zoology*, 20 (59), 1–275.

Robinson, T.B., Peters, K. & Brooker, B. (2020) Chapter 9. Coastal invasions: the South African context. *In*: van Wilgen, B., Measey, J., Richardson, D.M., Wilson, J.R. & Zengeya, T.A. (Eds.), *Biological Invasions in South Africa*. Invading Nature - Springer Series in Invasion Ecology, Vol. 14, Springer, Cham, pp. 229–247.

Russo, C.S., Lamont, T., Tutt, G.C.O., van den Berg, M.A. & Barlow, R.G. (2019) Hydrography of a shelf ecosystem inshore of a major western boundary current. *Estuarine, Coastal and Shelf Science*, 228, 106363.

Samaai, T. (1998) *Systematics, phylogeny, and biogeography of a selection of poecilosclerid sponges from Ouderkraal, on the west coast of South Africa*. MSc Thesis, Imperial College & Natural History Museum, London.

Samaai, T. (2002) *Systematics of the family Latrunculiidae Topsent (Porifera: Demospongiae) and consideration of the diversity and biogeography of shallow-water sponges of western South Africa*. PhD Thesis, University of the Western Cape, South

Africa.

Samaai, T. (2006) Biodiversity “hotspots”, patterns of richness and endemism, and distribution of marine sponges in South Africa based on actual and interpolation data: a comparative approach. *Zootaxa*, 1358 (1), 1–37.

Samaai, T. & Gibbons, M.J. (2005) Demospongiae taxonomy and biodiversity of the Benguela region on the west coast of South Africa. *African Natural History*, 1 (1), 1–96.

Samaai, T., Gibbons, M.J. & Kelly, M. (1999) Morphological phylogenetic considerations on the relationships of *Isodictya* Bowerbank,1865. *Memoirs of the Queensland Museum*, 44, 517–523.

Samaai, T., Gibbons, M.J. & Kelly, M. (2006) Revision of the genus *Latrunculia* du Bocage, 1869 (Porifera: Demospongiae: Latrunculiidae) with descriptions of new species from New Caledonia and the northeastern Pacific. *Zootaxa*, 1127 (1), 1–71.

Samaai, T., Gibbons, M.J. & Kelly, M. (2009a) A revision of the genus *Strongylodesma* Lévi (Porifera: Demospongiae: Latrunculiidae) with descriptions of four new species. *Journal of the Marine Biological Association of the United Kingdom*, 89 (8), 1689–1702.

Samaai, T., Gibbons, M.J., Kelly, M. & Davies-Coleman, M. (2003) South African Latrunculiidae (Porifera: Demospongiae: Poecilosclerida): descriptions of new species of *Latrunculia* du Bocage, *Strongylodesma* Lévi, and *Tsitsikamma* Samaai & Kelly. *Zootaxa*, 371 (1), 1–26.

Samaai, T., Gibbons, M.J., Kerwath, S., Yemane, D. & Sink, K. (2010) Sponge richness along a bathymetric gradient within the iSimangaliso Wetland Park, South Africa. *Marine Biodiversity*, 40 (3), 205–217.

Samaai, T., Gibbons, M.J. & Muricy, G. (2017a) Validation of *Tethya samaaii* Ribeiro & Muricy, 2011, replacement name for the sponge *Tethya rubra* Samaai & Gibbons, 2005 (Demospongiae, Tethyida, Tethyidae). *Zootaxa*, 4347 (3), 592–594.

Samaai, T., Govender, V. & Kelly, M. (2004a) *Cyclacanthia* n.g. (Demospongiae: Poecilosclerida: Latrunculiidae *incertea sedis*), a new genus of marine sponges from South African waters, and description of two new species. *Zootaxa*, 725 (1), 1–18.

Samaai, T., Janson, L. & Kelly, M. (2012) New species of *Latrunculia* from the Agulhas shelf, South Africa, with designation of a type species for subgenus *Biannulata* (Demospongiae, Poecilosclerida, Latrunculiidae). *Zootaxa*, 3395 (1), 33–45.

Samaai, T. & Kelly, M. (2002) Family Latrunculiidae Topsent, 1922. *In*: Hooper, J.N.A. & van Soest, R.W.M. (Eds.), *Systema Porifera. A Guide to the Classification of Sponges. Vol. 1*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 708–719.

Samaai, T., Kelly, M., Ngwakum, B., Payne, R., Teske, P.R., Janson, L., Kerwath, S., Parker, D. & Gibbons, M.J. (2020a) New Latrunculiidae (Demospongiae, Poecilosclerida) from the Agulhas ecoregion of temperate southern Africa. *Zootaxa*, 4896 (3), 409–442.

Samaai, T., Keyzers, R. & Davies-Coleman, M. (2004b) A new species of *Strongylodesma* Lévi, 1969 (Porifera; Demospongiae; Poecilosclerida; Latrunculiidae) from Aliwal Shoal on the east coast of South Africa. *Zootaxa*, 584 (1), 1–11.

Samaai, T., Maduray, S., Janson, L., Gibbons, M.J., Ngwakum, B. & Teske, P.R. (2017b) A new species of habitat–forming *Suberites* (Porifera, Demospongiae, Suberitida) in the Benguela upwelling region (South Africa). *Zootaxa*, 4254 (1), 49–81.

Samaai, T., Payne, R.P., Maduray, S. & Janson, L. (2018) Phylum Porifera. *In*: Atkinson, L.J. & Sink, K.J. (Eds.), *Field Guide to the Offshore Marine Invertebrates of South Africa*. Malachite Marketing and Media, Pretoria, South Africa, pp. 37–64.

Samaai, T., Pillay, R. & Janson, L. (2019) Shallow-water Demospongiae (Porifera) from Sodwana Bay, iSimangaliso Wetland Park, South Africa. *Zootaxa*, 4587 (1), 1–85.

Samaai, T., Pillay, R. & Janson, L. (2020b) Suggestion of *Spongia (Heterofibria) peddemorsi* as replacement name for *Spongia (Heterofibria) cooki* Samaai, Pillay & Janson, 2019. *Zootaxa*, 4728 (1), 149–149.

Samaai, T., Pillay, R. & Kelly, M. (2009b) *Cymbastela sodwaniensis* sp. nov. (Halichondrida: Axinellidae): a first record of this sponge genus in South Africa. *Journal of the Marine Biological Association of the United Kingdom*, 89 (8), 1679–1687.

Sanciangco, J.C., Carpenter, K.E., Etnoyer, P.J. & Moretzsohn, F. (2013) Habitat availability and heterogeneity and the Indo-Pacific Warm Pool as predictors of marine species richness in the tropical Indo-Pacific. *PLoS ONE*, 8 (2), e56245.

Schlacher, T.A., Schlacher-Hoenlinger, M.A., Williams, A., Althaus, F., Hooper, J.N.A. & Kloser, R. (2007) Richness and distribution of sponge megabenthos in continental margin canyons off southeastern Australia. *Marine Ecology Progress Series*, 340, 73–88.

Schleyer, M.H. & Celliers, L. (2005) Modelling reef zonation in the Greater St Lucia Wetland Park, South Africa. *Estuarine, Coastal and Shelf Science*, 63 (3), 373–384.

Schleyer, M.H., Heikoop, J.M. & Risk, M.J. (2006) A benthic survey of Aliwal Shoal and assessment of the effects of a wood pulp effluent on the reef. *Marine Pollution Bulletin*, 52 (5), 503–514.

Schmidt, O. (1862) *Die Spongien des Adriatischen Meeres*. Wilhelm Engelmann, Leipzig, 88 pp.

Schmidt, O. (1870) *Grundzüge einer Spongien-Fauna des Atlantischen Gebietes*. Wilhelm Engelmann, Leipzig, 88 pp.

Schmidt, O. (1880) Die Spongien des Meerbusen von Mexico (Und des caraibischen Meeres). Heft II. Abtheilung II. Hexactinelliden. Abtheilung III. Tetractinelliden. Monactinelliden und Anhang. Nachträge zu Abtheilung I (Lithistiden). *In*: *Reports on* *the dredging under the supervision of Alexander Agassiz, in the Gulf of Mexico, by the USCSS "Blake"*. Gustav Fischer, Jena, pp. 33–90.

Schönberg, C.H.L. (2017) Culture, demography and biogeography of sponge science: from past conferences to strategic research? *Marine Ecology*, 38 (2), e12416.

Schönberg, C.H.L., Fang, J.K. & Carballo, J.L. (2017) Bioeroding sponges and the future of coral reefs. *In*: Carballo, J.L. & Bell, J.J. (Eds.), *Climate Change, Ocean Acidification and Sponges*. Springer International Publishing, pp. 179–372.

Schrammen, A. (1924) Die Kieselspongien der oberen Kreide von Nordwestdeutschland. III. und letzter teil. Mit beiträgen zur stammesgeschichte. *Monographien zur Geologie und Paläontologie*, 1 (2), 1–159.

Schulze, F.E. (1904) Hexactinellida. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf der Dampfer "Valdivia" 1898–1899*, 4, 1–266.

Schumann, E.H., Ross, G.J.B. & Goschen, W.S. (1988) Cold water events in Algoa Bay and along the Cape south coast, South Africa, in March/April 1987. *South African Journal of Science*, 84 (7), 579–584.

Scott, R.J., Griffiths, C.L. & Robinson, T.B. (2012) Patterns of endemicity and range restriction among southern African coastal marine invertebrates. *African Journal of Marine Science*, 34 (3), 341–347.

Sim-Smith, C. & Kelly, M. (2019) Review of the sponge genus *Penares* (Demospongiae, Tetractinellida, Astrophorina) in the New Zealand EEZ, with descriptions of new species. *Zootaxa*, 4638 (1), 1–56.

Simion, P., Philippe, H., Baurain, D., Jager, M., Richter, D.J., Di Franco, A., Roure, B., Satoh, N., Quéinnec, É., Ereskovsky, A., Lapébie, P., Corre, E., Delsuc, F., King, N., Wörheide, G. & Manuel, M. (2017) A large and consistent phylogenomic dataset supports sponges as the sister group to all other animals. *Current Biology*, 27 (7), 958–

967.

Sink, K.J., Harris, L.R., van der Bank, M.G., Franken, M., Skowno, A., Driver, A., Atkinson, L.J., Fairweather, T.P., Kerwath, S., Majiedt, P.A., Robinson, T., Pfaff, M., Rikhotso, W., Smith, C. & van Niekerk, L. (2019a) Chapter 11: Key findings, priority actions and knowledge gaps. *In*: Sink, K.J., van der Bank, M.G., Majiedt, P.A., Harris, L.R., Atkinson, L.J., Kirkman, S.P. & Karenyi, N. (Eds.), *South African National Biodiversity Assessment 2018 Technical Report. Vol. 4. Marine Realm*. South African National Biodiversity Institute, Pretoria, South Africa, pp. 407–455.

Sink, K.J., Harris, L.R., Skowno, A.L., Livingstone, T., Franken, M., Porter, S., Atkinson, L.J., Bernard, A., Cawthra, H., Currie, J., Dayaram, A., de Wet, W., Dunga, L. V, Filander, Z., Green, A., Herbert, D., Karenyi, N., Palmer, R., Pfaff, M., Makwela, M., Mackay, F., van Niekerk, L., van Zyl, W., Bessinger, M., Holness, S., Kirkman, S.P., Lamberth, S. & Lück-Vogel, M. (2019b) Chapter 3: Marine ecosystem classification and mapping. *In*: Sink, K.J., van der Bank, M.G., Majiedt, P.A., Harris, L.R., Atkinson, L.J., Kirkman, S.P. & Karenyi, N. (Eds.), *South African National Biodiversity Assessment 2018 Technical Report. Vol. 4. Marine Realm*. South African National Biodiversity Institute, Pretoria, South Africa, pp. 49–109.

Sink, K.J., Holness, S., Skowno, A.L., Franken, M., Majiedt, P.A., Atkinson, L.J., Bernard, A., Dunga, L.V., Harris, L.R., Kirkman, S.P., Oosthuizen, A., Porter, S., Smit, K. & Shannon, L. (2019c) Chapter 7: Ecosystem threat status. *In*: Sink, K.J., van der Bank, M.G., Majiedt, P.A., Harris, L.R., Atkinson, L.J., Kirkman, S.P. & Karenyi, N. (Eds.), *South African National Biodiversity Assessment 2018 Technical Report. Vol. 4. Marine Realm*. South African National Biodiversity Institute, Pretoria, South Africa, pp. 249–282.

Sink, K.J., Sibanda, S.M., Fielding, P., Skowno, A.L., Franken, M., Harris, L.R., Adams, R.

& Baleta, T. (2019d) Chapter 8: Ecosystem protection level. *In*: Sink, K.J., van der Bank, M.G., Majiedt, P.A., Harris, L.R., Atkinson, L.J., Kirkman, S.P. & Karenyi, N. (Eds.), *South African National Biodiversity Assessment 2018 Technical Report. Vol. 4. Marine Realm*. South African National Biodiversity Institute, Pretoria, South Africa, pp. 283–325.

Sink, K.J., Skowno, A.L., Green, A., Landschoff, J., Lamont, T. & Franken, M. (2019e) Chapter 1: Introduction and approach. *In*: Sink, K.J., van der Bank, M.G., Majiedt, P.A., Harris, L.R., Atkinson, L.J., Kirkman, S.P. & Karenyi, N. (Eds.), *South African National Biodiversity Assessment 2018 Technical Report. Vol. 4. Marine Realm*. South African National Biodiversity Institute, Pretoria, South Africa, pp. 1–25.

Smith, J.L.B. (1939) A living fish of Mesozoic type. *Nature*, 143 (3620), 455–456.

van Soest, R.W.M. (1980) Marine sponges from Curaçao and other Caribbean localities. Part II. Haplosclerida. *Studies on the Fauna of Curaçao and other Caribbean Islands*, 62 (191), 1–173.

van Soest, R.W.M. (1993) Distribution of sponges on the Mauritanian continental shelf. *Hydrobiologia*, 258 (1–3), 95–106.

van Soest, R.W.M. (2002a) Family Coelosphaeridae Dendy, 1922. *In*: Hooper, J.N.A. & van Soest, R.W.M. (Eds.), *Systema Porifera. A Guide to the Classification of Sponges. Vol. 1*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 528–546.

van Soest, R.W.M. (2002b) Family Crellidae Dendy, 1922. *In*: Hooper, J.N.A. & van Soest, R.W.M. (Eds.), *Systema Porifera. A Guide to the Classification of Sponges. Vol. 1*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 556–566.

van Soest, R.W.M. (2002c) Family Myxillidae Dendy, 1922. *In*: Hooper, J.N.A. & van Soest, R.W.M. (Eds.), *Systema Porifera. A Guide to the Classification of Sponges. Vol. 1*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 602–620.

van Soest, R.W.M. (2002d) Family Suberitidae Schmidt, 1870. *In*: Hooper, J.N.A. & van Soest, R.W.M. (Eds.), *Systema Porifera. A Guide to the Classification of Sponges. Vol. 1*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 227–244.

van Soest, R.W.M., Boury-Esnault, N., Hooper, J.N.A., Rützler, K., de Voogd, N.J., Alvarez, B., Hajdu, E., Pisera, A.B., Manconi, R., Schönberg, C., Klautau, M., Kelly, M., Vacelet, J., Dohrmann, M., Díaz, M.-C., Cárdenas, P., Carballo, J.L., Ríos, P., Downey, R. & Morrow, C.C. (2020a) World Porifera Database. Available from: http://www.marinespecies.org/porifera (accessed 09 November 2020)

van Soest, R.W.M., Boury-Esnault, N., Vacelet, J., Dohrmann, M., Erpenbeck, D., de Voogd, N.J., Santodomingo, N., Vanhoorne, B., Kelly, M. & Hooper, J.N.A. (2012) Global diversity of sponges (Porifera). *PLoS ONE*, 7 (4), e35105.

van Soest, R.W.M., Cleary, D.F.R., de Kluijver, M.J., Lavaleye, M.S.S., Maier, C. & van Duyl, F.C. (2007) Sponge diversity and community composition in Irish bathyal coral reefs. *Contributions to Zoology*, 76 (2), 121–142.

van Soest, R.W.M. & Hajdu, E. (2002) Family Esperiopsidae Hentschel, 1923. *In*: Hooper, J.N.A. & van Soest, R.W.M. (Eds.), *Systema Porifera. A Guide to the Classification of Sponges. Vol. 1*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 656–664.

van Soest, R.W.M. & Hooper, J.N.A. (1993) Taxonomy, phylogeny and biogeography of the marine sponge genus *Rhabderemia* Topsent, 1890 (Demospongiae, Poecilosclerida). *Scientia Marina*, 57 (4), 319–351.

van Soest, R.W.M., Hooper, J.N.A. & Butler, P.J. (2020b) Every sponge its own name: removing Porifera homonyms. *Zootaxa*, 4745 (1), 1–93.

van Soest, R.W.M., Hooper, J.N.A. & Hiemstra, F. (1991) Taxonomy, phylogeny and biogeography of the marine sponge genus *Acarnus* (Porifera: Poecilosclerida). *Beaufortia*, 42 (3), 49–88.

van Soest, R.W.M. & Lavaleye, M.S.S. (2005) Diversity and abundance of sponges in bathyal coral reefs of Rockall Bank, NE Atlantic, from boxcore samples. *Marine Biology Research*, 1 (5), 338–349.

van Soest, R.W.M. & de Voogd, N.J. (2018) Calcareous sponges of the Western Indian Ocean and Red Sea. *Zootaxa*, 4426 (1), 1–160.

Sollas, W.J. (1885) A classification of the sponges. *Annals and Magazine of Natural History*, 5, 16 (95), 395.

Sollas, W.J. (1886) Preliminary account of the tetractinellid sponges dredged by H.M.S. "Challenger'' 1872–76. Part I. The Choristida. *Scientific Proceedings of the Royal Dublin Society (new series)*, 5, 177–199.

Sollas, W.J. (1887) Sponges. *In*: Black, A. & Black, C. (Eds.), *Encyclopaedia Britannica. Vol. 22*. Edinburgh, pp. 412–429.

Sollas, W.J. (1888) Report on the Tetractinellida collected by H.M.S. "Challenger" during the years 1873–1876. *Report on the Scientific Results of the Voyage of H.M.S. "Challenger", 1873–1876. Zoology*, 25 (63), 1–458.

Sorokin, S., Fromont, J. & Currie, D. (2007) Demosponge biodiversity in the Benthic Protection Zone of the Great Australian Bight. *Transactions of the Royal Society of South Australia*, 131 (2), 192–204.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A. & Robertson, J. (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience*, 57 (7), 573–583.

Stephens, J. (1915) Atlantic sponges collected by the Scottish National Antarctic Expedition. *Transactions of The Royal Society of Edinburgh*, 50 (2), 423–467.

Strand, E. (1928) Miscellaniea nomen-clatorica zoologica et palaeontologica. *Archiv für Naturgeschichte*, 92 (8), 30–75.

Tabachnick, K.R. & Lévi, C. (1999) Revision of *Lophophysema* (Porifera: Hexactinellida: Hyalonematidae). *Invertebrate Taxonomy*, 13 (3), 495–509.

Teske, P.R., von der Heyden, S., McQuaid, C.D. & Barker, N.P. (2011) A review of marine phylogeography in southern Africa. *South African Journal of Science*, 107 (5/6), 514.

Thiele, J. (1898) Studien über pazifische Spongien. I. Japanische Demospongien. *Zoologica. Original — Abhandlungen aus dem Gesamtgebiete der Zoologie. Stuttgart*, 24 (1), 1–72.

Thiele, J. (1900) Kieselschwämme von Ternate. I. *Abhandlungen herausgegeben von der Senckenbergischen Naturforschenden Gesellschaft. Frankfurt*, 25, 19–80.

Thiele, J. (1905) Die Kiesel- und Hornschwämme der Sammlung Plate. *Zoologische Jahrbücher*, Supplement 6 (Fauna Chilensis III), 407–496.

Thomas, P.A. (1968) Studies on Indian sponges - I. Two new species of silicious sponges belonging to the genera *Echinodictyum* Ridley and *Rhadberemia* Topsent (Class: Demospongiae Sollas, Order: Poecilosclerida Topsent). *Journal of the Marine Biological Association of India*, 10 (2), 245–249.

Thomas, P.A. (1973) Marine Demospongiae of Mahe Island in the Seychelles Bank (Indian Ocean). *Annales du Musée royal de l'Afrique centrale. Sciences zoologiques*, 203, 1–96.

Thomas, P.A. (1979) Studies on sponges of the Mozambique Channel. I. Sponges of the Inhaca Island. II. Sponges of Mambone and Paradise Islands. *Annales du Musée royal de l'Afrique centrale, Tervuren. Sciences zoologiques*, 8, 227, 1–73.

Thomas, P.A. (1981) A second collection of marine Demospongiae from Mahe Island in the Seychelles Bank (Indian Ocean). *Annales du Musée royal de l'Afrique centrale, Tervuren. Sciences zoologiques*, 233, 1–63.

Thomas, P.A. (1985) Demospongiae of the Gulf of Mannar and Palk Bay. *In*: James, P.S.B.R. (Ed.), *Recent Advances in Marine Biology*. Today & Tomorrow's Printers and Publishers, New Delhi, pp. 205–365.

Topsent, E. (1890) Notice préliminaire sur les spongiaires recueillis durant les campagnes de l'Hirondelle. *Bulletin de la Société zoologique de France*, 15, 26–32, 65–71.

Topsent, E. (1892) Diagnoses d'éponges nouvelles de la Méditerranée et plus particulièrement de Banyuls. *Archives de Zoologie expérimentale et générale*, 2, 10 (Notes et Revue 6), xvii–xxviii.

Topsent, E. (1893) Nouvelle série de diagnoses d'éponges de Roscoff et de Banyuls. *Archives de Zoologie expérimentale et générale*, 3, 1 (Notes et Revue 10), xxxiii–xliii.

Topsent, E. (1894) Une réforme dans la classification des Halichondrina. *Mémoires de la Société zoologique de France*, 7, 5–26.

Topsent, E. (1901) Spongiaires. Résultats du voyage du S.Y. "Belgica'' en 1897–99 sous le commandement de A. de Gerlache de Gomery. *Expédition antarctique belge*. *Zoologie*, 4, 1–54.

Topsent, E. (1905) Étude sur les Dendroceratida. *Archives de Zoologie expérimentale et générale*, 4, 3 (8), 171–192.

Topsent, E. (1907) Poecilosclérides nouvelles recueillies par le Français dans l'Antarctique. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 13, 69–76.

Topsent, E. (1913) Spongiaires de l'Expédition Antarctique Nationale Ecossaise. *Transactions of the Royal Society of Edinburgh*, 49 (3), 579–643.

Topsent, E. (1916) Diagnoses d'éponges recueillies dans l'Antarctique par le Pourquoi-Pas?

Bulletin du Muséum National d'Histoire Naturelle, Paris, 1, 22 (3), 163–172.

Topsent, E. (1922) Les mégasclères polytylotes des Monaxonides et la parenté des Latrunculiines. *Bulletin de l'Institut océanographique de Monaco*, 415, 1–8.

Topsent, E. (1928) Spongiaires de l'Atlantique et de la Méditerranée provenant des croisières du Prince Albert ler de Monaco. *Résultats des campagnes scientifiques accomplies par le Prince Albert I. Monaco*, 74, 1–376.

Topsent, E. (1931 [1930]) Éponges de Lamarck conservées au Muséum de Paris. *Archives du Muséum National d'Histoire Naturelle, Paris*, 6, 5, 1–56.

Turon, X., Codina, M., Tarjuelo, I., Uriz, M.J. & Becerro, M.A. (2000) Mass recruitment of *Ophiothrix fragilis* (Ophiuroidea) on sponges: settlement patterns and post-settlement dynamics. *Marine Ecology Progress Series*, 200, 201–212.

Urban, F. (1908) Die Kalkschwämme der Deutschen Tiefsee-Expedition. *Zoologischer Anzeiger*, 33, 247–252.

Urban, F. (1909) Die Calcarea. *In*: Fisher, G. (Ed.), *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899. Vol. 19.* Jena, pp. 1–40.

Uriz, M.J. (1984) Descripción de nuevas esponjas del litoral de Namibia (sudoeste de África). *Resultados Expediciones Científicas*, 12, 107–116.

Uriz, M.J. (1985) First contribution to the knowledge of the sponge-fauna of the Namibian shelf. Demospongia collected by the Benguela V and the Valdivia I Spanish expeditions. *In*: Bas, C., Margalef, R. & Rubies, P. (Eds.), *International Symposium on the Most Important Upwelling Areas off Western Africa (Cape Blanco and Benguela). Vol. 2*. Instituto de Investigaciones Pesqueras, Barcelona, pp. 639–649.

Uriz, M.J. (1987) Sponges from the south-west of Africa: description of species. *In*: Jones, W.C. (Ed.), *European Contributions to the Taxonomy of Sponges*. Sherkin Island Marine

Station, Sherkin Island, County Cork, pp. 54–73.

Uriz, M.J. (1988) Deep-water sponges from the continental shelf and slope off Namibia (Southwest Africa): classes Hexactinellida and Demospongia. *Monografías de Zoología Marina*, 3, 9–157.

Uriz, M.J. (1990) Possible influence of trawl fishery on recent expansion in the range of *Suberites tylobtusa* in the southeast Atlantic. *In*: Rützler, K. (Ed.), *New Perspectives in Sponge Biology*. Smithsonian Institution Press, Washington, D.C., pp. 309–315.

Uriz, M.J. (2002) Family Ancorinidae Schmidt, 1870. *In*: Hooper, J.N.A. & van Soest, R.W.M. (Eds.), *Systema Porifera. A Guide to the Classification of Sponges. Vol. 1*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 108–126.

Uriz, M.J. & Carballo, J.L. (2001) Phylogenetic relationships of sponges with placochelae or related spicules (Poecilosclerida, Guitarridae) with a systematic revision. *Zoological Journal of the Linnean Society*, 132, 411–428.

Vacelet, J. (1979) Descriptions et affinités d'une éponge sphinctozoaire actuelle. *In*: Lévi, C. & Boury-Esnault, N. (Eds.), *Biologie des Spongiaires. Sponge Biology*. Colloques Internationaux du Centre National de la Recherché Scientifique, Paris, 291, pp. 483–493.

Vacelet, J. & Vasseur, P. (1965) Spongiaires des grottes et surplombs des récifs de Tuléar (Madagascar). *Recueil des travaux de la Station marine d'Endoume*, 2–4, 71–123.

Vacelet, J. & Vasseur, P. (1971) Éponges des récifs coralliens de Tuléar (Madagascar). *Téthys*, Supplément 1, 51–126.

Vacelet, J., Vasseur, P. & Lévi, C. (1976) Spongiaires de la pente externe des récifs coralliens de Tuléar (Sud-Ouest de Madagascar). *Mémoires du Muséum National d'Histoire Naturelle*, A (Zoologie), 49, 1–116.

de Voogd, N.J., Becking, L.E. & Cleary, D.F.R. (2009) Sponge community composition in the Derawan Islands, NE Kalimantan, Indonesia. *Marine Ecology Progress Series*, 396, 169–180.

de Voogd, N.J., Becking, L.E., Hoeksema, B.W., Noor, A. & van Soest, R.W.M. (2004) Sponge interactions with spatial competitors in the Spermonde Archipelago. *Bollettino dei Musei e degli Istituti Biologici dell'Università di Genova*, 68, 253–261.

de Voogd, N.J. & Cleary, D.F.R. (2008) An analysis of sponge diversity and distribution at three taxonomic levels in the Thousand Islands/Jakarta Bay reef complex, West-Java, Indonesia. *Marine Ecology*, 29 (2), 205–215.

Vosmaer, G.C.J. (1880) The sponges of the Leyden Museum. 1. The family of the Desmacidinae. *Notes from the Leyden Museum*, 2, 99–164.

Voultsiadou, E. (2007) Sponges: an historical survey of their knowledge in Greek antiquity. *Journal of the Marine Biological Association of the United Kingdom*, 87 (6), 1757–1763.

Voultsiadou, E. (2010) Therapeutic properties and uses of marine invertebrates in the ancient Greek world and early Byzantium. *Journal of Ethnopharmacology*, 130 (2), 237–247.

Waterworth, S.C., Jiwaji, M., Kalinski, J.J., Parker-Nance, S. & Dorrington, R.A. (2017) A place to call home: an analysis of the bacterial communities in two *Tethya rubra* Samaai and Gibbons 2005 populations in Algoa Bay, South Africa. *Marine Drugs*, 15 (4), 95.

Webster, N.S. & Taylor, M.W. (2012) Marine sponges and their microbial symbionts: love and other relationships. *Environmental Microbiology*, 14 (2), 335–346.

Webster, N.S. & Thomas, T. (2016) The sponge hologenome. *mBio*, 7 (2), e00135-16.

de Wet, W.M. (2013) *Bathymetry of the South African continental shelf*. MSc Thesis, University of Cape Town, South Africa, 306 pp.

Wild, S., Allen, S.J., Krützen, M., King, S.L., Gerber, L. & Hoppitt, W.J.E. (2019) Multinetwork-based diffusion analysis reveals vertical cultural transmission of sponge tool use within dolphin matrilines. *Biology Letters,* 15 (7), 20190227.

Wilkinson, C.R. & Cheshire, A.C. (1989) Patterns in the distribution of sponge populations across the central Great Barrier Reef. *Coral Reefs*, 8 (3), 127–134.

Wörheide, G. & Erpenbeck, D. (2007) DNA taxonomy of sponges—progress and perspectives. *Journal of the Marine Biological Association of the United Kingdom*, 87 (6), 1629–1633.

Wörheide, G., Solé-Cava, A.M. & Hooper, J.N.A. (2005) Biodiversity, molecular ecology and phylogeography of marine sponges: patterns, implications and outlooks. *Integrative and Comparative Biology*, 45 (2), 377–385.

Wulff, J.L. (2001) Assessing and monitoring coral reef sponges: why and how? *Bulletin of Marine Science*, 69 (2), 831–846.

Wulff, J.L. (2006) Ecological interactions of marine sponges. *Canadian Journal of Zoology*, 84 (2), 146–166.

Wyllia, K., Nabila, B., Kheiredine, O. & Farid, D. (2018) Sponges (Porifera) as bioindicator species of environmental stress from de Gulf of Annaba (Algeria). *Biodiversity Journal*, 9 (4), 319–324.

Xavier, J. & van Soest, R.W.M. (2007) Demosponge fauna of Ormonde and Gettysburg Seamounts (Gorringe Bank, north-east Atlantic): diversity and zoogeographical affinities. *Journal of the Marine Biological Association of the United Kingdom*, 87 (6), 1643–1653.

Appendix A: List of marine sponges from the South African Exclusive Economic Zone (EEZ), excluding the Prince Edward Islands. Compiled using the World Porifera Database (WPD, van Soest *et al.* 2020a), and available taxonomic literature. Taxa are presented in alphabetical order and largely follow the classification proposed in the *Systema Porifera* (Hooper & van Soest 2002), with revision by Morrow & Cárdenas (2015), currently considered accurate by the WPD. The symbols (Q) and (*) denote questionable species and endemic species/varieties/forms respectively, while endemic genera are underlined. New species and records from this study will only be added after publication. Last updated February 2020.

Phylum Porifera Grant, 1836
Class Calcarea Bowerbank, 1862
Subclass Calcaronea Bidder, 1898

Order Leucosolenida Hartman, 1958
Family Amphoriscidae Dendy, 1893
1. *Amphoriscus kryptoraphis* Urban, 1908*
2. *Leucilla australiensis* (Carter, 1886) (Q)
3. *Leucilla capsula* (Haeckel, 1870)*
4. *Leucilla uter* Poléjaeff, 1883 (Q)

Family Grantiidae Dendy, 1893
5. *Amphiute lepadiformis* Borojevic, 1967*
6. *Grantia socialis* Borojevic, 1967*
7. *Leucandra algoaensis* (Bowerbank, 1864)*
8. *Leucandra armata* (Urban, 1908)
9. *Leucandra bathybia* (Haeckel, 1869)
10. *Leucandra bleeki* (Haeckel, 1872)*
11. *Leucandra hentschelii* Brøndsted, 1931
12. *Leucandra minor* (Urban, 1908)
13. *Leucandra spissa* (Urban, 1909)*
14. *Sycodorus hystrix* Haeckel, 1870

Family Heteropiidae Dendy, 1893
15. *Grantessa ramosa* (Haeckel, 1872)*
16. *Grantessa rarispinosa* Borojevic, 1967*
17. *Heteropia glomerosa* (Bowerbank, 1873)
18. *Sycettusa hastifera* (Row, 1909)

Family Lelapiidae Dendy & Row, 1913
19. *Kebira tetractinifera* van Soest & de Voogd, 2018*

Family Leucosoleniidae Minchin, 1900
20. *Leucosolenia arachnoides* (Haeckel, 1872) (Q)
21. *Leucosolenia eustephana* Haeckel, 1872*

Family Sycettidae Dendy, 1893

22. *Sycon defendens* Borojevic, 1967*
23. *Sycon dunstervillia* (Haeckel, 1872)*
24. *Sycon elegans* (Bowerbank, 1845)
25. *Sycon gelatinosum* (Blainville, 1834)
26. *Sycon kerguelense* Urban, 1908
27. *Sycon lunulatum* (Haeckel, 1872)*
28. *Sycon munitum* Jenkin, 1908
29. *Sycon natalense* Borojevic, 1967*

Subclass Calcinea Bidder, 1898

Order Clathrinida Hartman, 1958

Family Clathrinidae Minchin, 1900

30. *Arturia africana* (Klautau & Valentine, 2003)*
31. *Arturia hirsuta* (Klautau & Valentine, 2003)
32. *Clathrina pulcherrima* (Dendy, 1891)
33. *Clathrina rotunda* Klautau & Valentine, 2003*
34. *Ernstia cordata* (Haeckel, 1872)*

Family Leucascidae Dendy, 1893

35. *Leucascus schleyeri* van Soest & de Voogd, 2018*

Family Leucettidae Laubenfels, 1936

36. *Leucetta homoraphis* (Poléjaeff, 1883) (Q)
37. *Leucetta trigona* Haeckel, 1872*

Class Demospongiae Sollas, 1885
Subclass Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012

Order Agelasida Hartman, 1980

Family Agelasidae Verrill, 1907

38. *Agelas oxeata* Lévi, 1961

Order Axinellida Lévi, 1953

Family Axinellidae Carter, 1875

39. *Axinella natalensis* (Kirkpatrick, 1903)*
40. *Axinella weltnerii* (Lendenfeld, 1897)
41. *Cymbastela sodwaniensis* Samaai, Pillay & Kelly, 2009*
42. *Dragmacidon sanguineum* (Burton, 1933)*
43. *Phakellia rubra* Samaai, Pillay & Janson, 2019*

Family Raspailiidae Nardo, 1833

Subfamily Cyamoninae Hooper, 2002

44. <u>*Waltherarndtia*</u> *caliculatum* (Kirkpatrick, 1903)*

Subfamily Echinodictyinae Hooper, 2002

45. *Echinodictyum jousseaumi* Topsent, 1892
46. *Echinodictyum marleyi* Burton, 1931*

Subfamily Raspailiinae Nardo, 1833

47. *Aulospongus involutus* (Kirkpatrick, 1903)
48. *Endectyon gorgonioides* (Kirkpatrick, 1903)*
49. *Raspailia (Raspailia) urizae* Hooper, 2012
50. *Raspailia rigida* Ridley & Dendy, 1886*

Subfamily Thrinacophorinae Hooper, 2002

51. *Ceratopsion microxephora* (Kirkpatrick, 1903)*

Family Stelligeridae Lendenfeld, 1898

52. *Higginsia bidentifera* (Ridley & Dendy, 1886)*
53. *Higginsia natalensis* Carter, 1885*

Order Biemnida Morrow, 2013

Family Biemnidae Hentschel, 1923

54. *Biemna anisotoxa* Lévi, 1963
55. *Biemna megalosigma* var. *sigmodragma* Lévi, 1963
56. *Biemna pedonculata* Lévi, 1963*
57. *Biemna polyphylla* Lévi, 1963*
58. *Biemna rhabdostyla* Uriz, 1988
59. *Sigmaxinella arborea* Kirkpatrick, 1903*
60. *Sigmaxinella incrustans* Kirkpatrick, 1903*

Family Rhabderemiidae Topsent, 1928

61. *Rhabderemia spirophora* (Burton, 1931)*

Order Bubarida Morrow & Cárdenas, 2015

Family Desmanthidae Topsent, 1893

62. *Paradesmanthus macphersoni* (Uriz, 1988)
63. *Petromica (Petromica) digitata* (Burton, 1929)*
64. *Petromica (Petromica) plumosa* Kirkpatrick, 1903*
65. *Petromica (Petromica) tubulata* (Kirkpatrick, 1903)*

Order Clionaida Morrow & Cárdenas, 2015

Family Clionaidae d'Orbigny, 1851

66. *Cliona celata* Grant, 1826 (Q)
67. *Cliona grandis* Samaai, Pillay & Janson, 2019*
68. *Cliona lobata* Hancock, 1849 (Q)
69. *Cliona orientalis* Thiele, 1900
70. *Spheciospongia capensis* (Carter, 1882)*
71. *Spheciospongia excentrica* (Burton, 1931)
72. *Spheciospongia globularis* (Dendy, 1922)
73. *Spheciospongia ndabazithe* Samaai, Pillay & Janson, 2019*
74. *Spheciospongia purpurea* (Lamarck, 1815) (Q)
75. *Spheciospongia vagabunda* (Ridley, 1884)

Order Haplosclerida Topsent, 1928

Family Callyspongiidae Laubenfels, 1936

76. *Callyspongia (Callyspongia) fadwae* Samaai, Pillay & Janson, 2019*
77. *Callyspongia (Callyspongia) tubulosa* (Linnaeus, 1759)
78. *Callyspongia (Cladochalina) diffusa* (Ridley, 1884)
79. *Callyspongia (Cladochalina) foliacea* (Esper, 1797)*
80. *Callyspongia (Toxochalina) dendyi* (Burton, 1931)
81. *Callyspongia (Toxochalina) ridleyi* (Dendy, 1905)
82. *Callyspongia (Toxochalina) robusta* (Ridley, 1884)
83. *Callyspongia confoederata* (sensu Ridley, 1884)
84. *Callyspongia hospitalis* (Stephens, 1915)*
85. *Callyspongia mammillata* (Burton, 1933)*

Family Chalinidae Gray, 1867

86. *Haliclona (Gellius) glacialis* (Ridley & Dendy, 1886)
87. *Haliclona (Gellius) jorii* (Uriz, 1984)
88. *Haliclona (Haliclona) anonyma* (Stephens, 1915)*
89. *Haliclona (Haliclona) stilensis* Burton, 1933
90. *Haliclona (Reniera) ciocalyptoides* Burton, 1933*
91. *Haliclona saldanhae* (Stephens, 1915)*
92. *Haliclona simplicissima* (Burton, 1933)*
93. *Haliclona stephensi* Burton, 1932*
94. *Haliclona submonilifera* Uriz, 1988
95. *Haliclona tulearensis* Vacelet, Vasseur & Lévi, 1976

Family Niphatidae van Soest, 1980
96. *Haliclonissa sacciformis* Burton, 1932
Family Petrosiidae van Soest, 1980
97. *Neopetrosia similis* (Ridley & Dendy, 1886)
98. *Petrosia (Strongylophora) vulcaniensis* Samaai & Gibbons, 2005*
99. *Xestospongia hispida* (Ridley & Dendy, 1886)
100. *Xestospongia viridenigra* (Vacelet, Vasseur & Lévi, 1976)
Family Phloeodictyidae Carter, 1882
101. *Oceanapia eumita* (Kirkpatrick, 1903)*
102. *Oceanapia ramsayi* (Lendenfeld, 1888) (Q)

Order Merliida Vacelet, 1979
Family Hamacanthidae Gray, 1872
103. *Hamacantha (Vomerula) esperioides* (Ridley & Dendy, 1886)

Order Poecilosclerida Topsent, 1928
Family Acarnidae Dendy, 1922
104. *Acarnus claudei* van Soest, Hooper & Hiemstra, 1991*
105. *Iophon cheliferum* Ridley & Dendy, 1886
106. *Paracornulum coherens* Lévi, 1963*
Family Chondropsidae Carter, 1886
107. *Chondropsis isimangaliso* Samaai, Pillay & Janson, 2019*
108. *Chondropsis lamella* (Lendenfeld, 1888)
109. *Psammoclema inordinatum* (Kirkpatrick, 1903)*
Family Cladorhizidae Dendy, 1922
110. *Cladorhiza ephyrula* Lévi, 1964*
Family Coelosphaeridae Dendy, 1922
111. *Coelosphaera (Coelosphaera) navicelligera* (Ridley, 1885)
112. *Forcepia (Forcepia) agglutinans* Burton, 1933*
113. *Forcepia (Leptolabis) australis* (Lévi, 1963)*
114. *Histodermella natalensis* (Kirkpatrick, 1903)*
115. *Inflatella belli* (Kirkpatrick, 1907)
116. *Lissodendoryx (Anomodoryx) coralgardeniensis* Samaai & Gibbons, 2005*
117. *Lissodendoryx (Ectyodoryx) arenaria* Burton, 1936
118. *Lissodendoryx (Lissodendoryx) areolata* Lévi, 1963*
119. *Lissodendoryx (Lissodendoryx) digitata* (Ridley & Dendy, 1886)*
120. *Lissodendoryx (Lissodendoryx) pygmaea* (Burton, 1931)*
121. *Lissodendoryx (Lissodendoryx) stephensoni* Burton, 1936*
122. *Lissodendoryx (Lissodendoryx) ternatensis* (Thiele, 1903)
Family Crambeidae Lévi, 1963
123. *Crambe acuata* (Lévi, 1958)
124. *Lithochela conica* Burton, 1929*
Family Crellidae Dendy, 1922
125. *Crella (Grayella) erecta* (Lévi, 1963)*
126. *Crella caespes* (Ehlers, 1870)
Family Dendoricellidae Hentschel, 1923
127. *Fibulia ramosa* (Ridley & Dendy, 1886)
Family Esperiopsidae Hentschel, 1923
128. *Amphilectus informis* (Stephens, 1915)*
129. *Esperiopsis papillata* (Vosmaer, 1880)*
Family Guitarridae Dendy, 1924
130. *Guitarra flamenca* Carballo & Uriz, 1998
131. *Tetrapocillon novaezealandiae* Brøndsted, 1924 (Q)
Family Hymedesmiidae Topsent, 1928
132. *Hymedesmia (Hymedesmia) aurantiaca* Lévi, 1963

133. *Hymedesmia (Hymedesmia) parva* Stephens, 1915*
134. *Phorbas bardajii* (Uriz, 1988)
135. *Phorbas benguelensis* (Uriz, 1984)
136. *Phorbas clathratus* (Lévi, 1963)*
137. *Phorbas clathrodes* (Dendy, 1922)
138. *Phorbas dayi* (Lévi, 1963)*
139. *Phorbas fibrosus* (Lévi, 1963)*
140. *Phorbas lamellatus* (Lévi, 1963)*
141. *Phorbas mollis* (Kirkpatrick, 1903)*
142. *Phorbas pustulosus* (Carter, 1882) (Q)

Family Iotrochotidae Dendy, 1922

143. *Iotrochota nigra* (Baer, 1906)
144. *Iotrochota sinki* Samaai, Pillay & Janson, 2019*

Family Isodictyidae Dendy, 1924

145. *Isodictya alata* (Stephens, 1915)*
146. *Isodictya chichatouzae* Uriz, 1984
147. *Isodictya compressa* (Esper, 1797)
148. *Isodictya conulosa* (Ridley & Dendy, 1886)*
149. *Isodictya ectofibrosa* (Lévi, 1963)*
150. *Isodictya elastica* (Vosmaer, 1880)
151. *Isodictya foliata* (Carter, 1885)*
152. *Isodictya frondosa* (Lévi, 1963)*
153. *Isodictya grandis* (Ridley & Dendy, 1886)*
154. *Isodictya multiformis* (Stephens, 1915)*

Family Latrunculiidae Topsent, 1922

155. *Cyclacanthia bellae* (Samaai, Gibbons, Kelly & Davies-Coleman, 2003)*
156. *Cyclacanthia cloverlyae* Samaai, Govender & Kelly, 2004*
157. *Cyclacanthia mzimayiensis* Samaai, Govender & Kelly, 2004*
158. *Latrunculia (Biannulata) algoaensis* Samaai, Janson & Kelly, 2012*
159. *Latrunculia (Biannulata) gotzi* Samaai, Janson & Kelly, 2012*
160. *Latrunculia (Biannulata) kerwathi* Samaai, Janson & Kelly, 2012*
161. *Latrunculia (Biannulata) lunaviridis* Samaai, Gibbons, Kelly & Davies-Coleman, 2003*
162. *Latrunculia (Biannulata) microacanthoxea* Samaai, Gibbons, Kelly & Davies-Coleman, 2003*
163. *Latrunculia (Latrunculia) biformis* Kirkpatrick, 1908
164. *Strongylodesma algoaensis* Samaai, Gibbons, Kelly & Davies-Coleman, 2003*
165. *Strongylodesma aliwaliensis* Samaai, Keyzers & Davies-Coleman, 2004*
166. *Strongylodesma tsitsikammaensis* Samaai, Gibbons, Kelly & Davies-Coleman, 2003*
167. *Tsitsikamma favus* Samaai & Kelly, 2002*
168. *Tsitsikamma michaeli* Parker-Nance, 2019*
169. *Tsitsikamma nguni* Parker-Nance, 2019*
170. *Tsitsikamma pedunculata* Samaai, Gibbons, Kelly & Davies-Coleman, 2003*
171. *Tsitsikamma scurra* Samaai, Gibbons, Kelly & Davies-Coleman, 2003*

Family Microcionidae Carter, 1875

Subfamily Microcioninae Carter, 1875

172. *Clathria (Axosuberites) benguelaensis* Samaai & Gibbons, 2005*
173. *Clathria (Clathria) axociona* Lévi, 1963
174. *Clathria (Clathria) conica* Lévi, 1963*
175. *Clathria (Clathria) dayi* Lévi, 1963*
176. *Clathria (Clathria) elastica* Lévi, 1963*
177. *Clathria (Clathria) hexagonopora* Lévi, 1963*
178. *Clathria (Clathria) indica* Dendy, 1889
179. *Clathria (Clathria) irregularis* (Burton, 1931)*
180. *Clathria (Clathria) juncea* Burton, 1931*
181. *Clathria (Clathria) lobata* Vosmaer, 1880*
182. *Clathria (Clathria) multiformis* Samaai, Pillay & Janson, 2019*

183. *Clathria (Clathria) oculata* Burton, 1933*
184. *Clathria (Clathria) omegiensis* Samaai & Gibbons, 2005*
185. *Clathria (Clathria) pachystyla* Lévi, 1963*
186. *Clathria (Clathria) parva* Lévi, 1963
187. *Clathria (Clathria) ramsayiensis* Samaai, Pillay & Janson, 2019*
188. *Clathria (Clathria) rhaphidotoxa* Stephens, 1915
189. *Clathria (Clathria) typica* sensu Kirkpatrick, 1903
190. *Clathria (Clathria) whiteleggii* Dendy, 1922
191. *Clathria (Clathria) zoanthifera* Lévi, 1963*
192. *Clathria (Isociella) oudekraalensis* Samaai & Gibbons, 2005*
193. *Clathria (Microciona) namibiensis* (Uriz, 1984)
194. *Clathria (Microciona) stephensae* Hooper, 1996*
195. *Clathria (Microciona) tenuis* (Stephens, 1915)*
196. *Clathria (Thalysias) anomala* (Burton, 1933)*
197. *Clathria (Thalysias) cullingworthi* Burton, 1931*
198. *Clathria (Thalysias) delaubenfelsi* (Lévi, 1963)*
199. *Clathria (Thalysias) hooperi* Samaai & Gibbons, 2005*
200. *Clathria (Thalysias) lissoclada* (Burton, 1934) (Q)
201. *Clathria (Thalysias) mauriceburtoni* van Soest & Hooper, 2020*
202. *Clathria (Thalysias) nervosa* (Lévi, 1963)*
203. *Clathria (Thalysias) oxitoxa* Lévi, 1963*
204. *Clathria (Thalysias) procera* (Ridley, 1884)
205. *Echinochalina (Echinochalina) isochelifera* (Uriz, 1988)

Subfamily Ophlitaspongiinae Laubenfels, 1936

206. *Antho (Acarnia) kellyae* Samaai & Gibbons, 2005*
207. *Antho (Acarnia) prima* (Brøndsted, 1924) (Q)
208. *Artemisina vulcani* Lévi, 1963*
209. *Echinoclathria dichotoma* (Lévi, 1963)*

Family Mycalidae Lundbeck, 1905

210. *Mycale (Aegogropila) crassissima* (Dendy, 1905)
211. *Mycale (Aegogropila) meridionalis* Lévi, 1963*
212. *Mycale (Aegogropila) simonis* (Ridley & Dendy, 1886)*
213. *Mycale (Aegogropila) tapetum* Samaai & Gibbons, 2005*
214. *Mycale (Carmia) phyllophila* Hentschel, 1911 (Q)
215. *Mycale (Carmia) pulvinus* Samaai & Gibbons, 2005*
216. *Mycale (Carmia) samaaii* van Soest & Hooper, 2020*
217. *Mycale (Carmia) toxifera* (Dendy, 1896) (Q)
218. *Mycale (Grapelia) burtoni* Hajdu, 1995*
219. *Mycale (Mycale) anisochela* Lévi, 1963
220. *Mycale (Mycale) massa* (Schmidt, 1862) (Q)
221. *Mycale (Mycale) sulcata* Hentschel, 1911
222. *Mycale (Mycale) trichela* Lévi, 1963*
223. *Mycale (Oxymycale) stephensae* Samaai & Gibbons, 2005*
224. *Mycale (Paresperella) atlantica* Stephens, 1917 (Q)
225. *Mycale (Paresperella) claudei* van Soest & Hooper, 2020*
226. *Mycale (Paresperella) levii* (Uriz, 1987)
227. *Mycale (Zygomycale) parishii* (Bowerbank, 1875)

Family Myxillidae Dendy, 1922

228. *Ectyonopsis flabellata* (Lévi, 1963)*
229. *Ectyonopsis pluridentata* (Lévi, 1963)*
230. *Hymenancora tenuissima* (Thiele, 1905)
231. *Myxilla (Burtonanchora) sigmatifera* (Lévi, 1963)
232. *Myxilla (Ectyomyxilla) chilensis* Thiele, 1905
233. *Myxilla (Ectyomyxilla) kerguelensis* (Hentschel, 1914)
234. *Myxilla (Myxilla) simplex* (Baer, 1906)

235. *Plocamiancora denticulata* Topsent, 1927 (Q)
236. *Plocamiancora walvisensis* (Uriz, 1988)

Family Podospongiidae Laubenfels, 1936

237. *Podospongia natalensis* (Kirkpatrick, 1903)*

Family Tedaniidae Ridley & Dendy, 1886

238. *Tedania (Tedania) brondstedi* Burton, 1936*
239. *Tedania (Tedania) scotiae* Stephens, 1915
240. *Tedania (Tedania) stylonychaeta* Lévi, 1963*
241. *Tedania (Tedania) tubulifera* Lévi, 1963*

Order Polymastiida Morrow & Cárdenas, 2015

Family Polymastiidae Gray, 1867

242. *Polymastia atlantica* Samaai & Gibbons, 2005
243. *Polymastia littoralis* Stephens, 1915*
244. *Proteleia sollasi* Dendy & Ridley, 1886*
245. *Sphaerotylus strobilis* Plotkin, Morrow, Gerasimova & Rapp, 2017*
246. *Sphaerotylus vanhoeffeni* Hentschel, 1914

Order Scopalinida Morrow & Cárdenas, 2015

Family Scopalinidae Morrow, Picton, Erpenbeck, Boury-Esnault, Maggs & Allcock, 2012

247. *Stylissa carteri* (Dendy, 1889)

Order Suberitida Chombard & Boury-Esnault, 1999

Family Halichondriidae Gray, 1867

248. *Amorphinopsis fenestrata* (Ridley, 1884)
249. *Axinyssa tenuispiculata* (Burton, 1931)
250. *Axinyssa tethyoides* Kirkpatrick, 1903*
251. *Ciocalypta penicillus* Bowerbank, 1862 (Q)
252. *Ciocalypta tyleri* Bowerbank, 1873
253. *Halichondria (Halichondria) capensis* Samaai & Gibbons, 2005*
254. *Halichondria (Halichondria) gilvus* Samaai & Gibbons, 2005*
255. *Hymeniacidon kerguelensis* var. *capensis* Hentschel, 1914*
256. *Hymeniacidon stylifera* (Stephens, 1915)
257. *Hymeniacidon sublittoralis* Samaai & Gibbons, 2005*

Family Suberitidae Schmidt, 1870

258. *Aaptos alphiensis* Samaai & Gibbons, 2005*
259. *Aaptos durissima* (Carter, 1882)*
260. *Aaptos nuda* (Kirkpatrick, 1903)*
261. *Homaxinella flagelliformis* (Ridley & Dendy, 1886)
262. *Protosuberites hendricksi* Samaai & Gibbons, 2005*
263. *Protosuberites reptans* (Kirkpatrick, 1903)*
264. *Suberites dandelenae* Samaai & Maduray, 2017
265. *Suberites kelleri* Burton, 1930
266. *Suberites stilensis* Burton, 1933

Order Tethyida Morrow & Cárdenas, 2015

Family Hemiasterellidae Lendenfeld, 1889

267. *Hemiasterella magna* Pulitzer-Finali, 1993
268. *Hemiasterella vasiformis* (Kirkpatrick, 1903)*
269. *Hemiasterella vasiformis* var. *minor* (Kirkpatrick, 1903)*

Family Tethyidae Gray, 1848

270. *Halicometes pediculata* (Lévi, 1964)*
271. *Stellitethya incrustans* Samaai, Pillay & Janson, 2019*
272. *Tethya magna* Kirkpatrick, 1903
273. *Tethya samaaii* Ribeiro & Muricy, 2011*

Order Tetractinellida Marshall, 1876
Suborder Astrophorina Sollas, 1887
Family Ancorinidae Schmidt, 1870
274. *Ancorina corticata* Lévi, 1964
275. *Ancorina nanosclera* Lévi, 1967
276. *Chelotropella sphaerica* Lendenfeld, 1907
277. *Dercitus natalensis* (Burton, 1926)*
278. *Ecionemia baculifera* (Kirkpatrick, 1903)*
279. *Ecionemia obtusum* Lendenfeld, 1907*
280. *Jaspis digonoxea* (de Laubenfels, 1950) (Q)
281. *Rhabdastrella actinosa* (Lévi, 1964)
282. *Rhabdastrella primitiva* (Burton, 1926)*
283. *Rhabdastrella spinosa* (Lévi, 1967)*
284. *Stelletta agulhana* Lendenfeld, 1907*
285. *Stelletta agulhana* var. *paucistella* Burton, 1926*
286. *Stelletta capensis* Lévi, 1967*
287. *Stelletta cyathioides* Burton, 1926*
288. *Stelletta farcimen* Lendenfeld, 1907*
289. *Stelletta grubioides* Burton, 1926*
290. *Stelletta herdmani* Dendy, 1905
291. *Stelletta horrens* Kirkpatrick, 1902*
292. *Stelletta horrens* var. *subcylindrica* Burton, 1926*
293. *Stelletta obtusus* (Lendenfeld, 1907)*
294. *Stelletta purpurea* Ridley, 1884
295. *Stelletta retroclada* (Lévi, 1967)*
296. *Stelletta rugosa* Burton, 1926*
297. *Stelletta sphaerica* Burton, 1926*
298. *Stelletta trisclera* Lévi, 1967*
299. *Stryphnus progressus* (Lendenfeld, 1907)
300. *Stryphnus unguiculus* Sollas, 1886*
Family Geodiidae Gray, 1867
Subfamily Erylinae Sollas, 1888
301. *Erylus amorphus* Burton, 1926*
302. *Erylus gilchristi* Burton, 1926*
303. *Erylus polyaster* Lendenfeld, 1907*
304. *Pachymatisma areolata* Bowerbank, 1872
305. *Pachymatisma monaena* Lendenfeld, 1907*
306. *Penares alatus* (Lendenfeld, 1907)*
307. *Penares orthotriaena* Burton, 1931
308. *Penares sphaera* (Lendenfeld, 1907)
Subfamily Geodiinae Gray, 1867
309. *Geodia basilea* Lévi, 1964*
310. *Geodia dendyi* Burton, 1926*
311. *Geodia gallica* (Lendenfeld, 1907)*
312. *Geodia globosa* (Baer, 1906)*
313. *Geodia labyrinthica* (Kirkpatrick, 1903)*
314. *Geodia libera* Stephens, 1915
315. *Geodia littoralis* Stephens, 1915
316. *Geodia megaster* Burton, 1926*
317. *Geodia ovifractus* Burton, 1926*
318. *Geodia ovifractus* var. *cyathioides* Burton, 1926*
319. *Geodia perarmata* Bowerbank, 1873
320. *Geodia robusta* Lendenfeld, 1907*
321. *Geodia stellata* Lendenfeld, 1907*
Family Macandrewiidae Schrammen, 1924

322. *Macandrewia auris* Lendenfeld, 1907*
Family Pachastrellidae Carter, 1875
323. *Pachastrella caliculata* Kirkpatrick, 1902*
324. *Pachastrella isorrhopa* Kirkpatrick, 1902*
325. *Triptolemma incertum* (Kirkpatrick, 1903)*
Family Theonellidae Lendenfeld, 1903
326. *Discodermia natalensis* Kirkpatrick, 1903
327. *Theonella swinhoei* Gray, 1868
328. *Theonella timmi* Samaai, Pillay & Janson, 2019*
Family Vulcanellidae Cárdenas, Xavier, Reveillaud, Schander & Rapp, 2011
329. *Poecillastra tenuirhabda* (Lendenfeld, 1907)
330. *Poecillastra tuberosa* (Lévi, 1964)*
Suborder Spirophorina Bergquist & Hogg, 1969
Family Scleritodermidae Sollas, 1888
331. *Microscleroderma hirsutum* Kirkpatrick, 1903
Family Siphonidiidae Lendenfeld, 1903
332. *Gastrophanella mammilliformis* Burton, 1929*
333. *Lithobactrum forte* Kirkpatrick, 1903*
Family Tetillidae Sollas, 1886
334. *Cinachyrella hamata* (Lendenfeld, 1907)*
335. *Craniella atropurpurea* (Carter, 1870)*
336. *Craniella australis* Samaai & Gibbons, 2005
337. *Craniella cranium* (Müller, 1776) (Q)
338. *Craniella cranium* f. *microspira* Lévi, 1967*
339. *Craniella metaclada* (Lendenfeld, 1907)
340. *Fangophilina gilchristi* (Kirkpatrick, 1902)*
341. *Tetilla bonaventura* Kirkpatrick, 1902*
342. *Tetilla capillosa* Lévi, 1967*
343. *Tetilla casula* (Carter, 1871)*
344. *Tetilla pedonculata* Lévi, 1967*
Suborder Thoosina Carballo, Bautista-Guerrero, Cárdenas, Cruz-Barraza & Aguilar-Camacho, 2018
Family Thoosidae Cockerell, 1925
345. *Alectona wallichii* (Carter, 1874)

Order Trachycladida Morrow & Cárdenas, 2015
Family Trachycladidae Hallmann, 1917
346. *Trachycladus spinispirulifer* (Carter, 1879)

Subclass Keratosa Grant, 1861

Order Dendroceratida Minchin, 1900
Family Darwinellidae Merejkowsky, 1879
347. *Aplysilla lacunosa* Keller, 1889
348. *Darwinella warreni* Topsent, 1905*
Family Dictyodendrillidae Bergquist, 1980
349. *Dictyodendrilla caespitosa* (Carter, 1886) (Q)

Order Dictyoceratida Minchin, 1900
Family Dysideidae Gray, 1867
350. *Dysidea chalinoides* (Burton, 1931)*
351. *Dysidea cinerea* Keller, 1889
352. *Euryspongia coerulea* Samaai, Pillay & Janson, 2019*
353. *Lamellodysidea herbacea* (Keller, 1889)
Family Irciniidae Gray, 1867
354. *Ircinia aruensis* (Hentschel, 1912) (Q)

355. *Ircinia echinata* (Keller, 1889) (Q)
356. *Ircinia livida* Samaai, Pillay & Janson, 2019*
357. *Psammocinia alba* Samaai, Pillay & Janson, 2019*
358. *Psammocinia arenosa* (Lendenfeld, 1888)
359. *Sarcotragus australis* (Lendenfeld, 1888)

Family Spongiidae Gray, 1867

360. *Coscinoderma nardorus* (Lendenfeld, 1886) (Q)
361. *Leiosella caliculata* Lendenfeld, 1889 (Q)
362. *Spongia (Heterofibria) peddemorsi* Samaai, Pillay & Janson, 2020*
363. *Spongia (Heterofibria) smaragdus* Samaai, Pillay & Janson, 2019*

Family Thorectidae Bergquist, 1978

Subfamily Phyllospongiinae Keller, 1889

364. *Phyllospongia papyracea* (Esper, 1806)
365. *Phyllospongia schulzei* Lendenfeld, 1889*

Subfamily Thorectinae Bergquist, 1978

366. *Fasciospongia costifera* (Lamarck, 1814) (Q)
367. *Fasciospongia operculum* (Lendenfeld, 1897)

Subclass Verongimorpha Erpenbeck, Sutcliffe, De Cook, Dietzel, Maldonado, van Soest, Hooper & Wörheide, 2012

Order Chondrillida Redmond, Morrow, Thacker, Diaz, Boury-Esnault, Cardenas, Hajdu, Lobo-Hajdu, Picton, Pomponi, Kayal & Collins, 2013

Family Chondrillidae Gray, 1872

368. *Chondrilla australiensis* Carter, 1873

Order Verongiida Bergquist, 1978

Family Aplysinidae Carter, 1875

369. *Aplysina capensis* Carter, 1875*
370. *Aplysina minuta* Lendenfeld, 1889

Family Ianthellidae Hyatt, 1875

371. *Hexadella kirkpatricki* Burton, 1926

Class Hexactinellida Schmidt, 1870
Subclass Amphidiscophora Schulze, 1886

Order Amphidiscosida Schrammen, 1924

Family Hyalonematidae Gray, 1857

372. *Hyalonema (Cyliconema) curvisclera* (Lévi, 1964)*
373. *Hyalonema (Cyliconema) eupinnulum* (Lévi, 1964)*
374. *Lophophysema gilchristi* Tabachnick & Lévi, 1999*

Subclass Hexasterophora Schulze, 1886

Order Lyssacinosida Zittel, 1877

Family Euplectellidae Gray, 1867

Subfamily Corbitellinae Gray, 1872

375. *Regadrella phoenix* Schmidt, 1880 (Q)

Family Rossellidae Schulze, 1885

Subfamily Acanthascinae Schulze, 1897

376. *Rhabdocalyptus baculifer* Schulze, 1904*
377. *Rhabdocalyptus plumodigitatus* Kirkpatrick, 1901*

Subfamily Lanuginellinae Gray, 1872

378. *Caulophacus (Caulophacus) basispinosus* Lévi, 1964

Subfamily Rossellinae Schulze, 1885

379. *Crateromorpha (Crateromorpha) lankesteri* Kirkpatrick, 1902*
380. *Rossella antarctica* Carter, 1872

Class Homoscleromorpha Bergquist, 1978

Order Homosclerophorida Dendy, 1905
Family Plakinidae Schulze, 1880
381. *Plakortis pulvillus* Samaai, Pillay & Janson, 2019*

Total # of species: 374 (220 or 58.8% endemic)
Total # of questionable species: 27
Total # of varieties and forms: 7 (6 or 85.7% endemic)

Appendix B: Heteroscleromorph demosponges from the Amathole region (Eastern Cape, South Africa), per collection site. The symbols (▲) and (*) denote new and South African endemic species respectively, while South African endemic genera are underlined. The depth zone is denoted by the symbols S (shallow: 1–30 m), M (mesophotic: 31–150 m) and SM (sub-mesophotic: >150 m) following Lesser *et al*. (2018).

Site/Station	**Depth (m)** **Zone**	**Species**
1) ELondon 1 (Lighthouse Reef)	23 S	*Crella (Grayella) erecta* (Lévi, 1963)*
2) EL Harb 1 (Orient Pier)	3–5 S	*Guitarra flamenca* Carballo & Uriz, 1998 *Isodictya elastica* (Vosmaer, 1880)
3) Cintsa 1	16–17 S	*Guitarra indica* Dendy, 1916 *Isodictya compressa* (Esper, 1797) *Phakellia* sp. ▲
4) 491	55 M	*Biemna sigmodragma* Lévi, 1963* *Isodictya grandis* (Ridley & Dendy, 1886)* *Pachastrella caliculata* Kirkpatrick, 1902* *Phakellia* sp. ▲
5) 492	39 M	*Biemna sigmodragma* Lévi, 1963*
6) Unknown	<55 M	*Isodictya elastica* (Vosmaer, 1880) *Isodictya multiformis* (Stephens, 1915)* *Mycale (Aegogropila) meridionalis* Lévi, 1963* *Placospongia* sp. ▲ <u>*Tsitsikamma*</u> sp. 2 ▲

Site/Station	Depth (m) Zone	Species	
7) 3716	78 M	*Axinella* sp. ▲ *Biemna* sp. ▲ *Ceratopsion microxephora* (Kirkpatrick, 1903)* *Characella* sp. 1 ▲ *Erylus polyaster* Lendenfeld, 1907* *Forcepia (Forcepia) mucosa* **sp. nov.** ▲ *Geodia labyrinthica* (Kirkpatrick, 1903)* *Hemiasterella vasiformis* (Kirkpatrick, 1903)* *Hemitedania* sp. ▲ *Isodictya multiformis* (Stephens, 1915)* *Lithochela conica* Burton, 1929*	*Mycale* sp. 1 ▲ *Mycale (Aegogropila) meridionalis* Lévi, 1963* *Myxilla (Myxilla) lissotylota* **sp. nov.** ▲ *Pachastrella caliculata* Kirkpatrick, 1902* *Pachymatisma* sp. ▲ *Paradesmanthus macphersoni* (Uriz, 1988) *Phorbas mollis* (Kirkpatrick, 1903)* *Poecillastra* sp. ▲ *Sollasipelta thoosa* (Lévi, 1964) *Theonella* sp. ▲
8) 3717	87 M	*Mycale* sp. 1 ▲ *Pachastrella caliculata* Kirkpatrick, 1902* *Tethya magna* Kirkpatrick, 1903	
9) 3721	90 M	*Svenzea* sp. ▲	
10) 3722	87 M	*Axinella* sp. ▲ *Biemna* sp. ▲ *Characella* sp. 1 ▲ *Ectyonopsis flabellata* (Lévi, 1963)* *Forcepia (Forcepia) mucosa* **sp. nov.** ▲ *Hemitedania* sp. ▲ *Homaxinella abnorma* **sp. nov.** ▲ *Iophon regium* **sp. nov.** ▲ *Iophon ferrugineum* **sp. nov.** ▲ *Isodictya multiformis* (Stephens, 1915)* *Mycale* sp. 1 ▲	*Mycale* sp. 2 ▲ *Mycale (Aegogropila) meridionalis* Lévi, 1963* *Myxilla (Myxilla) lissotylota* **sp. nov.** ▲ *Pachastrella caliculata* Kirkpatrick, 1902* *Pachymatisma* sp. ▲ *Phorbas* sp. ▲ *Phorbas clathratus* (Lévi, 1963)* *Sigmaxinella* sp. ▲ *Stryphnus progressus* (Lendenfeld, 1907) *Svenzea* sp. ▲ *Tedania (Tedania) tubulifera* Lévi, 1963*

Site/Station	Depth (m) Zone	Species
11) 3724	76 M	*Axinella* sp. ▲ *Characella* sp. 1 ▲ *Forcepia (Forcepia) mucosa* **sp. nov.** ▲ *Guitarra indica* Dendy, 1916 *Hemitedania* sp. ▲ *Myxilla (Myxilla) lissotylota* **sp. nov.** ▲ *Pachastrella caliculata* Kirkpatrick, 1902* *Phorbas mollis* (Kirkpatrick, 1903)* *Sollasipelta cavernicola* (Vacelet & Vasseur, 1965) *Sollasipelta thoosa* (Lévi, 1964) *Theonella* sp. ▲
12) 3725	199 SM	*Biemna* sp. ▲ *Pachastrella caliculata* Kirkpatrick, 1902* *Petrosia (Strongylophora) durissima* (Dendy, 1905) *Stryphnus progressus* (Lendenfeld, 1907)
13) 3732	56 M	*Mycale* sp. 1 ▲ *Mycale* sp. 2 ▲
14) 3734	68 M	*Biemna* sp. ▲ *Pachastrella caliculata* Kirkpatrick, 1902*
15) 3736	45 M	*Characella* sp. 1 ▲ *Crambe acuata* (Lévi, 1958) *Forcepia (Forcepia) mucosa* **sp. nov.** ▲ *Penares orthotriaena* Burton, 1931 *Petrosia (Strongylophora) durissima* (Dendy, 1905) *Svenzea* sp. ▲
16) 3737	31 M	*Cyclacanthia* sp. ▲ *Tsitsikamma* sp. 2 ▲

Site/Station	Depth (m) Zone	Species
17) 3739	94 M	*Axinella* sp. ▲ *Biemna* sp. ▲ *Pachastrella caliculata* Kirkpatrick, 1902* *Penares alatus* (Lendenfeld, 1907)* *Penares* cf. *intermedius* (Dendy, 1905) *Penares orthotriaena* Burton, 1931 *Petrosia (Strongylophora) durissima* (Dendy, 1905) *Poecillastra* sp. ▲ *Sollasipelta cavernicola* (Vacelet & Vasseur, 1965) *Sollasipelta thoosa* (Lévi, 1964) *Theonella* sp. ▲
18) 3740	104 M	*Holoxea massa* **sp. nov.** ▲ *Myxilla (Burtonanchora) sigmatifera* (Lévi, 1963) *Pachastrella caliculata* Kirkpatrick, 1902* *Penares* cf. *intermedius* (Dendy, 1905) *Petrosia (Strongylophora) durissima* (Dendy, 1905) *Sollasipelta thoosa* (Lévi, 1964) *Theonella* sp. ▲
19) 3741	194 SM	*Erylus amorphus* Burton, 1926*
20) 3742	204 SM	*Biemna* sp. ▲ *Characella* sp. 2 ▲ *Erylus amorphus* Burton, 1926* *Erylus gilchristi* Burton, 1926* *Hamacantha (Vomerula) esperioides* (Ridley & Dendy, 1886) *Iophon ferrugineum* **sp. nov.** ▲ *Lithoplocamia longioxea* **sp. nov.** ▲ *Macandrewia* cf. *auris* Lendenfeld, 1907* *Pachastrella caliculata* Kirkpatrick, 1902* *Petrosia (Strongylophora) durissima* (Dendy, 1905) *Sollasipelta cavernicola* (Vacelet & Vasseur, 1965) *Svenzea* sp. ▲

Site/Station	Depth (m) Zone	Species
21) 3744	151 SM	*Bubaris amatholensis* **sp. nov.** ▲
22) 3745	122 M	*Aciculites spinosa* Vacelet & Vasseur, 1971 *Biemna* sp. ▲ *Coelodischela* cf. *diatomorpha* Vacelet, Vasseur & Lévi, 1976 *Erylus gilchristi* Burton, 1926* *Erylus polyaster* Lendenfeld, 1907* *Holoxea massa* **sp. nov.** ▲ *Pachastrella caliculata* Kirkpatrick, 1902* *Penares* cf. *intermedius* (Dendy, 1905) *Penares orthotriaena* Burton, 1931 *Petrosia (Strongylophora) durissima* (Dendy, 1905) *Sollasipelta thoosa* (Lévi, 1964) *Stryphnus progressus* (Lendenfeld, 1907)
23) 3770	25 S	*Penares* cf. *intermedius* (Dendy, 1905)
24) 3780	28 S	*Isodictya compressa* (Esper, 1797) *Isodictya multiformis* (Stephens, 1915)* *Placospongia* sp. ▲
25) 3789	83 M	*Sollasipelta cavernicola* (Vacelet & Vasseur, 1965)
26) 3790	85 M	*Biemna* sp. ▲ *Mycale* sp. 1 ▲ *Mycale (Aegogropila) meridionalis* Lévi, 1963* *Pachastrella caliculata* Kirkpatrick, 1902* *Svenzea* sp. ▲

Site/Station	Depth (m) Zone	Species
27) 3807	33 M	*Biemna* sp. ▲ *Biemna sigmodragma* Lévi, 1963* *Homaxinella abnorma* **sp. nov.** ▲ *Isodictya elastica* (Vosmaer, 1880) *Mycale (Aegogropila) meridionalis* Lévi, 1963* *Pachastrella caliculata* Kirkpatrick, 1902* *Phakellia* sp. ▲ *Placospongia* sp. ▲ *Tsitsikamma* sp. 2 ▲
28) 3808	39 M	*Biemna* sp. ▲ *Biemna sigmodragma* Lévi, 1963* *Ceratopsion microxephora* (Kirkpatrick, 1903)* *Hemiasterella vasiformis* (Kirkpatrick, 1903)* *Homaxinella abnorma* **sp. nov.** ▲ *Isodictya elastica* (Vosmaer, 1880) *Mycale (Aegogropila) meridionalis* Lévi, 1963* *Pachastrella caliculata* Kirkpatrick, 1902* *Phakellia* sp. ▲ *Phorbas mollis* (Kirkpatrick, 1903)* *Tedania (Tedania) tubulifera* Lévi, 1963*
29) 3811	74 M	*Bubaris amatholensis* **sp. nov.** ▲
30) 3813	52–55 M	*Axinella* sp. ▲ *Biemna* sp. ▲ *Ceratopsion microxephora* (Kirkpatrick, 1903)* *Characella* sp. 1 ▲ *Crella (Grayella) erecta* (Lévi, 1963)* *Fibulia ramosa* (Ridley & Dendy, 1886) *Pachastrella caliculata* Kirkpatrick, 1902* *Paradesmanthus macphersoni* (Uriz, 1988) *Penares* cf. *intermedius* (Dendy, 1905) *Rhabderemia spirophora* (Burton, 1931)* *Theonella* sp. ▲ *Tsitsikamma* sp. 1 ▲ *Tsitsikamma* sp. 2 ▲ *Tsitsikamma* sp. 3 ▲

Site/Station	Depth (m) Zone	Species
31) 3814	29–35 M	*Forcepia (Forcepia) mucosa* **sp. nov.** ▲ *Homaxinella abnorma* **sp. nov.** ▲ *Isodictya elastica* (Vosmaer, 1880) *Pachastrella caliculata* Kirkpatrick, 1902* *Phakellia* sp. ▲ *Phorbas mollis* (Kirkpatrick, 1903)*
32) 3815	38–43 M	*Guitarra flamenca* Carballo & Uriz, 1998 *Isodictya elastica* (Vosmaer, 1880) *Mycale* sp. 1 ▲ *Rhabderemia spirophora* (Burton, 1931)* *Stelletta capensis* Lévi, 1967*
33) 3831	47 M	*Crambe acuata* (Lévi, 1958) *Tsitsikamma* sp. 2 ▲
34) 3832	45 M	*Crambe acuata* (Lévi, 1958) *Crella (Grayella) erecta* (Lévi, 1963)* *Cyclacanthia* sp. ▲ *Forcepia (Forcepia) mucosa* **sp. nov.** ▲ *Homaxinella abnorma* **sp. nov.** ▲ *Isodictya elastica* (Vosmaer, 1880) *Isodictya multiformis* (Stephens, 1915)* *Microscleroderma hirsutum* Kirkpatrick, 1903 *Mycale (Aegogropila) meridionalis* Lévi, 1963* *Pachastrella caliculata* Kirkpatrick, 1902* *Penares orthotriaena* Burton, 1931 *Petrosia (Strongylophora) durissima* (Dendy, 1905) *Phorbas mollis* (Kirkpatrick, 1903)* *Tsitsikamma* sp. 1 ▲ *Tsitsikamma* sp. 2 ▲
35) 3833	58–62 M	*Ceratopsion microxephora* (Kirkpatrick, 1903)* *Characella* sp. 1 ▲ *Forcepia (Forcepia) mucosa* **sp. nov.** ▲ *Pachastrella caliculata* Kirkpatrick, 1902* *Pachymatisma* sp. ▲

Site/Station	Depth (m) Zone	Species
36) 3834	52–54 M	*Ceratopsion microxephora* (Kirkpatrick, 1903)* *Characella* sp. 1 ▲ *Pachastrella caliculata* Kirkpatrick, 1902* *Penares alatus* (Lendenfeld, 1907)* *Penares orthotriaena* Burton, 1931 *Phorbas clathratus* (Lévi, 1963)* *Svenzea* sp. ▲
37) 3845	222–229 SM	*Pachastrella caliculata* Kirkpatrick, 1902*
38) 3856	45–53 M	*Guitarra flamenca* Carballo & Uriz, 1998 *Homaxinella abnorma* **sp. nov.** ▲
39) 3861	90 M	*Biemna* sp. ▲ *Ceratopsion microxephora* (Kirkpatrick, 1903)* *Characella* sp. 1 ▲ *Forcepia (Forcepia) mucosa* **sp. nov.** ▲ *Hemiasterella vasiformis* (Kirkpatrick, 1903)* *Hemitedania* sp. ▲ *Holoxea massa* **sp. nov.** ▲ *Mycale* sp. 1 ▲ *Mycale* sp. 2 ▲ *Pachastrella caliculata* Kirkpatrick, 1902* *Penares alatus* (Lendenfeld, 1907)* *Penares* cf. *intermedius* (Dendy, 1905) *Penares orthotriaena* Burton, 1931 *Petromica (Petromica) tubulata* (Kirkpatrick, 1903)* *Petrosia (Strongylophora) durissima* (Dendy, 1905) *Rhabderemia indica* Dendy, 1905 *Stryphnus progressus* (Lendenfeld, 1907) *Svenzea* sp. ▲
40) 3870	29 S	*Amphilectus informis* (Stephens, 1915)* *Isodictya elastica* (Vosmaer, 1880) *Isodictya grandis* (Ridley & Dendy, 1886)* *Mycale* sp. 1 ▲ *Mycale (Aegogropila) meridionalis* Lévi, 1963* *Phorbas mollis* (Kirkpatrick, 1903)*

Site/Station	Depth (m) Zone	Species
41) 3872	41 M	*Cyclacanthia* sp. ▲ *Hemitedania* sp. ▲ *Mycale (Aegogropila) meridionalis* Lévi, 1963* *Phakellia* sp. ▲ *Tsitsikamma* sp. 1 ▲ *Tsitsikamma* sp. 2 ▲
42) 3873	42–44 M	*Isodictya grandis* (Ridley & Dendy, 1886)* *Mycale (Aegogropila) meridionalis* Lévi, 1963* *Phorbas mollis* (Kirkpatrick, 1903)*
43) 3876	103 M	*Axinella* sp. ▲ *Histodermella natalensis* (Kirkpatrick, 1903)* *Homaxinella abnorma* **sp. nov.** ▲ *Mycale* sp. 1 ▲ *Mycale (Aegogropila) meridionalis* Lévi, 1963* *Pachastrella caliculata* Kirkpatrick, 1902* *Paradesmanthus macphersoni* (Uriz, 1988) *Penares alatus* (Lendenfeld, 1907)* *Penares* cf. *intermedius* (Dendy, 1905) *Penares orthotriaena* Burton, 1931 *Petrosia (Strongylophora) durissima* (Dendy, 1905) *Svenzea* sp. ▲ *Tsitsikamma* sp. 3 ▲
44) 3893	36 M	*Ceratopsion microxephora* (Kirkpatrick, 1903)* *Didiscus* cf. *placospongioides* Dendy, 1922 *Forcepia (Forcepia) mucosa* **sp. nov.** ▲ *Homaxinella abnorma* **sp. nov.** ▲ *Isodictya elastica* (Vosmaer, 1880) *Isodictya grandis* (Ridley & Dendy, 1886)* *Lithochela conica* Burton, 1929* *Pachastrella caliculata* Kirkpatrick, 1902* *Tethya magna* Kirkpatrick, 1903 *Tsitsikamma* sp. 1 ▲

Site/Station	**Depth (m)** **Zone**	**Species**
45) 3897	78 M	*Biemna* sp. ▲ *Geodia libera* Stephens, 1915 *Pachastrella caliculata* Kirkpatrick, 1902* *Phakellia* sp. ▲ *Tethya magna* Kirkpatrick, 1903
46) 3909	65–76 M	*Biemna* sp. ▲ *Ceratopsion microxephora* (Kirkpatrick, 1903)* *Isodictya multiformis* (Stephens, 1915)* *Pachastrella caliculata* Kirkpatrick, 1902* *Petromica (Petromica) tubulata* (Kirkpatrick, 1903)* *Svenzea* sp. ▲
47) 3913	82 M	*Biemna* sp. ▲
48) 3920	22–24 S	*Acarnus claudei* van Soest, Hooper & Hiemstra, 1991* *Guitarra flamenca* Carballo & Uriz, 1998 *Hemitedania* sp. ▲ *Penares orthotriaena* Burton, 1931 *Tethya magna* Kirkpatrick, 1903

Appendix C: Heteroscleromorph demosponges from the Amathole region, per depth zone. The symbols (▲) and (*) denote new and South African endemic species respectively, while South African endemic genera are underlined. The symbol (▲) denotes new species found exclusively in that respective depth zone (DZ).

Shallow (1–30 m)	**Mesophotic (31–150 m)**	**Sub-mesophotic (>150 m)**
*Acarnus claudei**	*Aciculites spinosa*	*Biemna* sp. ▲
*Amphilectus informis**	*Axinella* sp. ▲	*Bubaris amatholensis* **sp. nov.** ▲
*Crella (Grayella) erecta**	*Biemna* sp. ▲	*Characella* sp. 2 ▲
Guitarra flamenca	*Biemna sigmodragma**	*Erylus amorphus**
Guitarra indica	*Bubaris amatholensis* **sp. nov.** ▲	*Erylus gilchristi**
Hemitedania sp. ▲	*Ceratopsion microxephora**	*Hamacantha (Vomerula) esperioides*
Isodictya compressa	*Characella* sp. 1 ▲	*Iophon ferrugineum* **sp. nov.** ▲
Isodictya elastica	*Coelodischela* cf. *diatomorpha*	*Lithoplocamia longioxea* **sp. nov.** ▲
*Isodictya grandis**	*Crambe acuata*	*Macandrewia* cf. *auris**
*Isodictya multiformis**	*Crella (Grayella) erecta**	*Pachastrella caliculata**
Mycale sp. 1 ▲	*<u>Cyclacanthia</u>* sp. ▲	*Petrosia (Strongylophora) durissima*
*Mycale (Aegogropila) meridionalis**	*Didiscus* cf. *placospongioides*	*Sollasipelta cavernicola*
Penares cf. *intermedius*	*Ectyonopsis flabellata**	*Stryphnus progressus*
Penares orthotriaena	*Erylus gilchristi**	*Svenzea* sp. ▲
Phakellia sp. ▲	*Erylus polyaster**	
*Phorbas mollis**	*Fibulia ramosa*	
Placospongia sp. ▲	*Forcepia (F.) mucosa* **sp. nov.** ▲	
Tethya magna	*Geodia labyrinthica**	
	Geodia libera	
	Guitarra flamenca	
	Guitarra indica	
	*Hemiasterella vasiformis**	
	Hemitedania sp. ▲	
	*Histodermella natalensis**	
	Holoxea massa **sp. nov.** ▲	
	Homaxinella abnorma **sp. nov.** ▲	
	Iophon regium **sp. nov.** ▲	
	Iophon ferrugineum **sp. nov.** ▲	
	Isodictya elastica	
	*Isodictya grandis**	
	*Isodictya multiformis**	
	*<u>Lithochela</u> conica**	
	Microscleroderma hirsutum	
	Mycale sp. 1 ▲	
	Mycale sp. 2 ▲	
	*Mycale (Aegogropila) meridionalis**	
	Myxilla (Burtonanchora) sigmatifera	

Shallow (1–30 m)	Mesophotic (31–150 m)	Sub-mesophotic (>150 m)
	Myxilla (M.) lissotylota **sp. nov.** ▲	
	*Pachastrella caliculata**	
	Pachymatisma sp. ▲	
	Paradesmanthus macphersoni	
	*Penares alatus**	
	Penares cf. *intermedius*	
	Penares orthotriaena	
	*Petromica (Petromica) tubulata**	
	Petrosia (Strongylophora) durissima	
	Phakellia sp. ▲	
	Phorbas sp. ▲	
	*Phorbas clathratus**	
	*Phorbas mollis**	
	Placospongia sp. ▲	
	Poecillastra sp. ▲	
	Rhabderemia indica	
	*Rhabderemia spirophora**	
	Sigmaxinella sp. ▲	
	Sollasipelta cavernicola	
	Sollasipelta thoosa	
	*Stelletta capensis**	
	Stryphnus progressus	
	Svenzea sp. ▲	
	*Tedania (Tedania) tubulifera**	
	Tethya magna	
	Theonella sp. ▲	
	Tsitsikamma sp. 1 ▲	
	Tsitsikamma sp. 2 ▲	
	Tsitsikamma sp. 3 ▲	
# sites: 7	# sites: 36	# sites: 5
# specimens: 26	# specimens: 399	# specimens: 49
# species: 18	# species: 66	# species: 14
# new species: 4	# new species: 25	# new species: 6
# new species exclusive to DZ: 0	# new species exclusive to DZ: 17	# new species exclusive to DZ: 2
# South African endemic species: 7	# South African endemic species: 21	# South African endemic species: 4

Appendix D: Sponge genera from the Amathole region per depth zone, where (X) indicates presence and (-) absence.

Genus	Shallow (1–30 m)	Mesophotic (31–150 m)	Sub-mesophotic (>150 m)
Acarnus	X	-	-
Aciculites	-	X	-
Amphilectus	X	-	-
Axinella	-	X	-
Biemna	-	X	X
Bubaris	-	X	X
Ceratopsion	-	X	-
Characella	-	X	X
Coelodischela	-	X	-
Crambe	-	X	-
Crella	X	X	-
Cyclacanthia	-	X	-
Didiscus	-	X	-
Ectyonopsis	-	X	-
Erylus	-	X	X
Fibulia	-	X	-
Forcepia	-	X	-
Geodia	-	X	-
Guitarra	X	X	-
Hamacantha	-	-	X
Hemiasterella	-	X	-
Hemitedania	X	X	-
Histodermella	-	X	-
Holoxea	-	X	-
Homaxinella	-	X	-
Iophon	-	X	X
Isodictya	X	X	-
Lithochela	-	X	-
Lithoplocamia	-	-	X
Macandrewia	-	-	X
Microscleroderma	-	X	-
Mycale	X	X	-
Myxilla	-	X	-
Pachastrella	-	X	X
Pachymatisma	-	X	-
Paradesmanthus	-	X	-
Penares	X	X	-
Petromica	-	X	-
Petrosia	-	X	X
Phakellia	X	X	-
Phorbas	X	X	-

Genus	Shallow (1–30 m)	Mesophotic (31–150 m)	Sub-mesophotic (>150 m)
Placospongia	X	X	-
Poecillastra	-	X	-
Rhabderemia	-	X	-
Sigmaxinella	-	X	-
Sollasipelta	-	X	X
Stelletta	-	X	-
Stryphnus	-	X	X
Svenzea	-	X	X
Tedania	-	X	-
Tethya	X	X	-
Theonella	-	X	-
Tsitsikamma	-	X	-

Appendix E: Sponge families from the Amathole region per depth zone, where (X) indicates presence and (-) absence.

Family	Shallow (1–30 m)	Mesophotic (31–150 m)	Sub-mesophotic (>150 m)
Acarnidae	X	X	X
Ancorinidae	-	X	X
Axinellidae	X	X	-
Biemnidae	-	X	X
Bubaridae	-	X	X
Coelosphaeridae	-	X	-
Crambeidae	-	X	-
Crellidae	X	X	-
Dendoricellidae	-	X	-
Desmanthidae	-	X	-
Esperiopsidae	X	-	-
Geodiidae	X	X	X
Guitarridae	X	X	-
Hamacanthidae	-	-	X
Hemiasterellidae	-	X	-
Hymedesmiidae	X	X	-
Isodictyidae	X	X	-
Latrunculiidae	-	X	-
Macandrewiidae	-	-	X
Mycalidae	X	X	-
Myxillidae	-	X	-
Neopeltidae	-	X	X
Pachastrellidae	-	X	X
Petrosiidae	-	X	X
Placospongiidae	X	X	-
Raspailiidae	-	X	X
Rhabderemiidae	-	X	-
Scleritodermidae	-	X	-
Scopalinidae	-	X	X
Suberitidae	-	X	-
Tedaniidae	X	X	-
Tethyidae	X	X	-
Theonellidae	-	X	-
Vulcanellidae	-	X	-

Appendix F: Sponge orders from the Amathole region per depth zone, where (X) indicates presence and (-) absence.

Order	**Shallow (1–30 m)**	**Mesophotic (31–150 m)**	**Sub-mesophotic (>150 m)**
Axinellida	X	X	X
Biemnida	-	X	X
Bubarida	-	X	X
Clionaida	X	X	-
Haplosclerida	-	X	X
Merliida	-	-	X
Poecilosclerida	X	X	X
Scopalinida	-	X	X
Suberitida	-	X	-
Tethyida	X	X	-
Tetractinellida	X	X	X

Appendix G: Results of SIMPER analysis indicating the percentage contribution (bold) of each species that overall contributed at least 90% to the similarity within depth zones. Average similarities within depth zones given in parentheses. The symbol (▲) denotes new species.

Shallow (4.1%)		Mesophotic (13.8%)		Sub-mesophotic (10.8%)	
Isodictya compressa	**38.36**	*Pachastrella caliculata*	**31.87**	*Pachastrella caliculata*	**62.7**
Guitarra flamenca	**32.88**	*Biemna* sp. ▲	**11.07**	*Erylus amorphus*	**14.21**
Isodictya elastica	**28.77**	*Mycale (Aegogropila) meridionalis*	**5.61**	*Biemna* sp. ▲	**11.55**
		Svenzea sp. ▲	**4.26**	*Petrosia (Strongylophora) durissima*	**11.55**
		Tsitsikamma sp. 2 ▲	**4.04**		
		Mycale sp. 1 ▲	**4**		
		Forcepia (Forcepia) mucosa **sp. nov.** ▲	**3.7**		
		Homaxinella abnorma **sp. nov.** ▲	**3.34**		
		Ceratopsion microxephora	**3.11**		
		Isodictya elastica	**2.96**		
		Characella sp. 1 ▲	**2.8**		
		Phakellia sp. ▲	**2.65**		
		Penares orthotriaena	**2.17**		
		Petrosia (Strongylophora) durissima	**2.17**		
		Phorbas mollis	**1.76**		
		Penares cf. *intermedius*	**1.42**		
		Biemna sigmodragma	**1.33**		
		Axinella sp. ▲	**1.16**		
		Sollasipelta thoosa	**0.98**		

Appendix H: Percentage contribution (bold) of higher taxonomic levels per depth zone.

Depth Zone	Order		Family		Genus	
Shallow (1–30 m)	Poecilosclerida	**72.2**	Isodictyidae	**22.2**	*Isodictya*	**22.2**
	Tetractinellida	**11.1**	Geodiidae	**11.1**	*Guitarra*	**11.1**
	Axinellida	**5.6**	Guitarridae	**11.1**	*Mycale*	**11.1**
	Clionaida	**5.6**	Mycalidae	**11.1**	*Penares*	**11.1**
	Tethyida	**5.6**	Acarnidae	**5.6**	*Acarnus*	**5.6**
			Axinellidae	**5.6**	*Amphilectus*	**5.6**
			Crellidae	**5.6**	*Crella*	**5.6**
			Esperiopsidae	**5.6**	*Hemitedania*	**5.6**
			Hymedesmiidae	**5.6**	*Phakellia*	**5.6**
			Placospongiidae	**5.6**	*Phorbas*	**5.6**
			Tedaniidae	**5.6**	*Placospongia*	**5.6**
			Tethyidae	**5.6**	*Tethya*	**5.6**
Mesophotic (31–150 m)	Poecilosclerida	**43.9**	Geodiidae	**12.1**	*Isodictya*	**4.5**
	Tetractinellida	**28.8**	Latrunculiidae	**6.1**	*Mycale*	**4.5**
	Biemnida	**7.6**	Ancorinidae	**4.5**	*Penares*	**4.5**
	Axinellida	**6.1**	Biemnidae	**4.5**	*Phorbas*	**4.5**
	Bubarida	**4.5**	Guitarridae	**4.5**	*Tsitsikamma*	**4.5**
	Tethyida	**3.0**	Hymedesmiidae	**4.5**	*Biemna*	**3.0**
	Clionaida	**1.5**	Isodictyidae	**4.5**	*Erylus*	**3.0**
	Haplosclerida	**1.5**	Mycalidae	**4.5**	*Geodia*	**3.0**
	Scopalinida	**1.5**	Myxillidae	**4.5**	*Guitarra*	**3.0**
	Suberitida	**1.5**	Acarnidae	**3.0**	*Iophon*	**3.0**
			Axinellidae	**3.0**	*Myxilla*	**3.0**
			Coelosphaeridae	**3.0**	*Rhabderemia*	**3.0**
			Crambeidae	**3.0**	*Sollasipelta*	**3.0**
			Desmanthidae	**3.0**	*Aciculites*	**1.5**
			Neopeltidae	**3.0**	*Axinella*	**1.5**
			Pachastrellidae	**3.0**	*Bubaris*	**1.5**
			Raspailiidae	**3.0**	*Ceratopsion*	**1.5**
			Rhabderemiidae	**3.0**	*Characella*	**1.5**
			Scleritodermidae	**3.0**	*Coelodischela*	**1.5**
			Tedaniidae	**3.0**	*Crambe*	**1.5**
			Bubaridae	**1.5**	*Crella*	**1.5**
			Crellidae	**1.5**	*Cyclacanthia*	**1.5**
			Dendoricellidae	**1.5**	*Didiscus*	**1.5**
			Hemiasterellidae	**1.5**	*Ectyonopsis*	**1.5**
			Petrosiidae	**1.5**	*Fibulia*	**1.5**
			Placospongiidae	**1.5**	*Forcepia*	**1.5**
			Scopalinidae	**1.5**	*Hemiasterella*	**1.5**
			Suberitidae	**1.5**	*Hemitedania*	**1.5**
			Tethyidae	**1.5**	*Histodermella*	**1.5**
			Theonellidae	**1.5**	*Holoxea*	**1.5**

Depth Zone	Order		Family		Genus	
Mesophotic (31–150 m)			Vulcanellidae	**1.5**	*Homaxinella*	**1.5**
					Lithochela	**1.5**
					Microscleroderma	**1.5**
					Pachastrella	**1.5**
					Pachymatisma	**1.5**
					Paradesmanthus	**1.5**
					Petromica	**1.5**
					Petrosia	**1.5**
					Phakellia	**1.5**
					Placospongia	**1.5**
					Poecillastra	**1.5**
					Sigmaxinella	**1.5**
					Stelletta	**1.5**
					Stryphnus	**1.5**
					Svenzea	**1.5**
					Tedania	**1.5**
					Tethya	**1.5**
					Theonella	**1.5**
Sub-mesophotic (>150 m)	Tetractinellida	**50.0**	Geodiidae	**14.3**	*Erylus*	**14.3**
	Axinellida	**7.1**	Pachastrellidae	**14.3**	*Biemna*	**7.1**
	Biemnida	**7.1**	Acarnidae	**7.1**	*Bubaris*	**7.1**
	Bubarida	**7.1**	Ancorinidae	**7.1**	*Characella*	**7.1**
	Haplosclerida	**7.1**	Biemnidae	**7.1**	*Hamacantha*	**7.1**
	Merliida	**7.1**	Bubaridae	**7.1**	*Iophon*	**7.1**
	Poecilosclerida	**7.1**	Hamacanthidae	**7.1**	*Lithoplocamia*	**7.1**
	Scopalinida	**7.1**	Macandrewiidae	**7.1**	*Macandrewia*	**7.1**
			Neopeltidae	**7.1**	*Pachastrella*	**7.1**
			Petrosiidae	**7.1**	*Petrosia*	**7.1**
			Raspailiidae	**7.1**	*Sollasipelta*	**7.1**
			Scopalinidae	**7.1**	*Stryphnus*	**7.1**
					Svenzea	**7.1**

Appendix I: Results of SIMPER analysis indicating the percentage contribution (bold) of each species that overall contributed at least 50% to the difference between depth zones. Average dissimilarities between depth zones given in parentheses. The symbol (▲) denotes new species.

Shallow & Mesophotic (94.7%)		Mesophotic & Sub-mesophotic (89.5%)		Shallow & Sub-mesophotic (100%)	
Pachastrella caliculata	**6.3**	*Pachastrella caliculata*	**8.23**	*Pachastrella caliculata*	**10.51**
Isodictya elastica	**4.69**	*Biemna* sp. ▲	**6.16**	*Erylus amorphus*	**7.47**
Guitarra flamenca	**4.42**	*Erylus amorphus*	**5.84**	*Bubaris amatholensis* **sp. nov.** ▲	**6.12**
Biemna sp. ▲	**4.1**	*Bubaris amatholensis* **sp. nov.** ▲	**5.06**	*Isodictya compressa*	**5.48**
Isodictya compressa	**3.98**	*Petrosia (Strongylophora) durissima*	**4.46**	*Guitarra flamenca*	**5.45**
Penares cf. *intermedius*	**3.91**	*Svenzea* sp. ▲	**3.79**	*Isodictya elastica*	**5.21**
Mycale (Aegogropila) meridionalis	**3.48**	*Tsitsikamma* sp. 2 ▲	**2.93**	*Crella (Grayella) erecta*	**5.08**
Phakellia sp. ▲	**3.42**	*Mycale (Aegogropila) meridionalis*	**2.89**	*Penares* cf. *intermedius*	**5.08**
Mycale sp. 1 ▲	**3.39**	*Stryphnus progressus*	**2.83**		
Crella (Grayella) erecta	**3.32**	*Mycale* sp. 1 ▲	**2.79**		
Isodictya multiformis	**2.8**	*Sollasipelta cavernicola*	**2.61**		
Svenzea sp. ▲	**2.71**	*Homaxinella abnorma* **sp. nov.** ▲	**2.35**		
Penares orthotriaena	**2.68**				