Distribution and diversity of octocorals from longline by-catch around South Georgia, UK

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Declaration of Originality

I, Michelle Lisa Taylor, declare that this thesis and the work presented, whilst acknowledging the contributions of colleagues, are my own. Acknowledgements list the specific support I have received from others. If I have consulted published works they are referenced, as are quotes. And, this document should not be considered the original description of the new species of Thouarella (in Chapter 2).
Abstract

In recent decades man’s forays into the deep sea have been increasingly frequent and wide-reaching; the most immediately intense and widespread activity being fisheries. United Nations (UN) General Assembly Resolutions on Sustainable Fishing on the High Seas call for assessment of fishing impacts with the aim of helping fisheries to avoid damaging vulnerable marine ecosystems.

Octocorals form the majority of by-catch in the bottom-longline fishery for Patagonian toothfish, *Dissostichus eleginoides* Smitt, 1898, around South Georgia. I employed several methods to investigate octocoral extent, location and diversity using by-catch from this fishery. Preliminary video analysis from camera arrays attached to bottom-longlines found whip corals interacted with longlines less than bushy, fan-shaped corals or *Stylasteridae*. Stylasteridae were however very fragile with 42% of interactions likely resulting in mortality through dislodgement.

Deep-sea octocorals are relatively understudied with many families and genera requiring revision and, as such, morphologically identifying octocorals is a difficult task; I thus investigated by-catch diversity by embedding octocorals caught from this South Georgia fishery into a wider Octocorallia phylogenetic tree. Three polyphyletic groups were resolved. Putative species numbers were estimated from morphological and phylogenetic analysis. Morphological identifications of one family of octocorals, Primnoidae, were compared to phylogenetic trees and the probability species were monophyletic tested using the statistical programme, Species Delimitation for Geneious. Six families, at least 21 genera (including three new discoveries) composing of a minimum of 34 species were caught as by-catch. *Thouarella* Gray, 1870, was the most common genus caught and a revision of this genus is presented.

Using recently created fine scale (150 m by 150 m) bathymetry of South Georgia, a depth-derived megahabitat map was created and octocoral occurrence data used to predict octocoral habitat suitability. Shelf troughs, crest and slope areas were highlighted as highly suitable octocoral habitat which substantially overlaps fishing areas. Current management protection regulations were found to protect highly suitable octocoral habitat.
Acknowledgements

“There is one kind of robber whom the law does not strike at, and who steals what is most precious to men: time.”

Napoleon I, Maxims, 1815.

Time is the most precious thing any of us has and the people I acknowledge here gave some of theirs to me; I am truly grateful (and lucky).

Firstly, I would like to thank my parents and step-mum for being so encouraging and giving me the opportunity and freedom to follow my career goals, against all odds. Family and friends have been an endless source of enthusiasm throughout, more so in recent months than I could hope for, and I thank you all from the bottom of my heart.

Academically, I have been very fortunate to have the support of two excellent supervisors: Prof Alex Rogers (University of Oxford) and Dr David Agnew (Marine Resources Assessment Group, formerly of Imperial College, London), whose sage advice has kept me on the scientific straight and narrow and whose guiding hand can be seen throughout these pages.

From within my CASE partner organisation, the Marine Resources Assessment Group, I am indebted to Dr Rebecca Mitchell most of all; couldn’t have done it without you. Dr Mitchell, James Clark, John Pearce and Tom Peatman spent many hours collating data and troubleshooting queries; the devil is in the detail and they made sure the details were right. Within the British Antarctic Survey Dr Mark Belchier has been crucial in getting specimens into my eager hands and the Government of South Georgia and the South Sandwich Islands has lent its support to this research from the beginning.

The octocoral realm has been abundantly welcoming and I have been fortunate enough to work with some of the best. I’d specifically like to thank Dr Stephen Cairns (Smithsonian Institution) for his hospitality and introduction to octocoral taxonomy; his mentoring was priceless and I cherish his continued support and friendship. To Dr Manfred Grasshoff (Senckenberg Forschungsinstitut und Museum in Frankfurt) and his wife, Monika, I would like to extend my thanks for their warmth in hosting my flying visit. To Dr Phil Alderslade who has offered advice on taxonomic writing technique, the high standard of which I hope I can uphold.

I would like to acknowledge The Institute of Zoology, where the majority of this work was completed. Dada Gottelli, Dr Ruth Brown and Dr Kate Ciborowski are goddesses of the genetics lab and saved me more than once. Dr Chris Yesson’s advice and GIS expertise has also been crucial. And in recent months the University of Oxford has given me space and support; especially their Supercomputing team.

Last, and far from least, to the jocular, crazed, pedantic, statistically-gifted, animal-obsessed, coffee-drinking, toast-eating tribe of friends I have had the privilege of sharing offices with; I am indebted to each and every one of you. For my sanity I thank you. Hopefully I repaid the favour.
“If CO₂ emissions continue on current trends, ocean acidification will threaten the existence of cold-water corals before we have even started to understand and appreciate their biological richness and importance for the marine ecosystem.”
Raven et al., 2005, pp.27

The ocean is a mighty harmonist.
William Wordsworth

“From these remarks it will be seen that I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms. The term variety, again, in comparison with mere individual differences, is also applied arbitrarily, and for mere convenience sake.”
Darwin, 1859, pp. 52

“The oceans are the planet's last great living wilderness, man's only remaining frontier on earth, and perhaps his last chance to produce himself a rational species.”
John L. Cullney, Wilderness Conservation, September-October 1990

“How inappropriate to call this planet Earth when it is quite clearly Ocean.”
Arthur C. Clarke
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- Description
- Distribution
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- Octocorallia phylogenetics
- Octocoral MOTU diversity and 'integrative taxonomy'

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---

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- Laboratory protocols
- Alignment
- Species delimitation

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- Phylogenetic analysis
- PTP test
- Signal saturation
- ILD (Incongruence length difference) Test

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- Phylogenetic trees
- Species Delimitation results

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- Primnoidae: By-catch species richness

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---

#### 3.9 Acknowledgements

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---

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---

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CHAPTER ONE

1 Introduction

1.1 Deep-sea ecosystems and cold-water corals

With waters over 1000 m deep covering 62% of the planet the deep sea is the largest environment on Earth (Roberts, 2002). It is also, proportionally, the least well known, sampled and studied (Ramirez-Llodra et al., 2010). Research is expensive and methods are inhibited because instruments and viewing platforms need to withstand several hundred atmospheres of pressure beneath the ocean’s surface. Historically the deep sea was thought to be a featureless zone, barren and lacking biodiversity. This stance has changed dramatically with exploration revealing novel habitats such as cold seeps (reviewed in Sibuet and Olu, 1998), hydrothermal vents (Van Dover, 2000), hydrocarbon seeps (Paull et al., 1984) and whale falls (Smith et al., 1989); And research into deep-sea ecosystems such as sediments (Wolff, 1977; Gage and Tyler, 1991) and coral gardens (Roberts et al., 2006) have also found them to be unexpectedly diverse.

Abyssal plains dominate the deep sea (Snelgrove et al., 1997). Within this huge area there are rare zones of hard substrata found on slopes of continents and oceanic islands, mid-ocean ridges (reviewed in Ramirez-Llodra et al., 2010), and particularly on seamounts (Rogers, 1994), and parts of trenches and canyons (De Leo et al., 2010). On a smaller scale, hard substrata include bedrock, boulders and drop stones (from icebergs and retreating glaciers; Oschmann, 1990). It is on and around these features that distinct suspension-feeding communities of sessile megafauna, such as sponges (Porifera), stony corals (Scleractinia), octocorals (Octocorallia), and black corals (Antipatharia) become attached, creating habitat for other species (e.g. associates of sponges, Klitgaard, 1995; coral, Stone, 2006; Roberts et al., 2006; black coral, Grange, 1991; and octocorals, Metaxas and Davis, 2005).

The existence of cold-water coral has been known to science since the 18th century, first recorded by the Right Reverend Erich Pontoppidan, Bishop of Bergen, in the 1755 book *The Natural History of Norway*, and probably much earlier to fishermen. The dedicated observation and study of deep-water coral habitats in situ, however, has only begun in the last 25 years as advances in acoustic survey technology and research submersibles have allowed exploration of deeper environments. Cold-water
corals are found in all the world’s oceans and seas (Freiwald et al., 2004; Rogers et al., 2007), on terrains ranging from fjords to continental shelves to submarine banks and seamounts. Although best known from North Atlantic and south western Pacific temperate waters, there are records from tropical waters off the African coast (Le Guilloux et al., 2009), Caribbean Antilles, the Indo-Pacific and the polar regions (Rogers, 1999; Freiwald et al., 2004; Roberts and Hirshfield, 2004; Rogers et al., 2007). Their distribution is, however, strongly biased by research effort (Roberts et al., 2006; Rogers et al., 2007).

The descriptive term “cold-water corals” encompasses many cnidarians including stony corals (Scleractinia), soft corals (Octocorallia – including bamboo corals, sea fans and gorgonians), precious black corals (Antipatharia, Figure 1.1b) and hydrocorals/ lace corals (Stylasteridae). Cold-water corals can grow individually, in beds, and in reefs. Out of an estimated total of 5160, 3356 (65%) of coral species occur in the deep sea (see Table 1; Roberts et al., 2009). The proportion of deep-water coral species is greater for stylasterids (90%), black corals (Antipatharia, 75%) and octocorals (74%) (modified from Roberts et al., 2009). There is a wide-held belief that deep-sea Scleractinia are ‘solitary’, however 26% are colonial (Cairns, 2007); of these, 17 species are reef-forming with just 6 species being wide-spread (Roberts et al., 2009). These three-dimensionally complex structures create many niches for a wide variety of life to exist in the deep sea, providing habitat for fish (adult and juvenile), crustaceans, molluscs, echinoderms, anemones, bryozoans, foraminiferans, sponges and many other taxa.

Unlike shallow-water corals, deep cold-water corals exist without light and feed on zooplankton (Freiwald, 2003; Duinevald et al., 2004; Sherwood et al., 2005), such as copepods (Kiriakoulakis et al., 2005), suspended organic matter, and dissolved organic matter (Mortensen, 2001; Duinevald et al., 2004). Arborescent morphology in many cold-water corals elevates polyps above the benthic boundary layer, where water movement is sluggish, into faster flowing currents (Wainwright and Koehl, 1976). Faster currents maximize exposure to food particles and remove fine scale detritus. On a larger scale, deep-water corals are often found in areas of current acceleration caused by steep topography (Genin et al., 1992) associated with features such as seamounts (Genin et al., 1986; Rogers et al., 2007; Waller et al., 2011), or
where water flows through narrow passages and over hard substrata e.g. straits, canyons (reviewed in Ramirez-Llodra et al., 2010; De Leo et al., 2010).

1.2 Octocorals

Deep-sea corals are a diverse group (see Table 1.1) the most speciose of which are octocorals. Octocorallia are a well-defined morphological, monophyletic, subclass (France et al., 1996; Bernston et al., 2001) of over 2000 species (Williams and Cairns, 2006). Octocorallia (Figure 1.1a,c) and Antipatharia (Figure 1.1b), though not reef-forming, can develop into dense ‘coral gardens’ which are important structural habitats (Krieger and Wing, 2002; Metaxas and Davis, 2005; Stone, 2006; Sánchez, 2005).

The subclass Octocorallia includes soft corals, sea whips and sea fans, sea pens and blue coral. This ecologically diverse group exist in a variety of marine habitats, from shallow-water tropical reefs through to the deep sea. They are identified by the eight pinnate tentacles surrounding each polyp mouth, and eight corresponding complete unpaired mesenteries. The vast majority of octocorals are colonial, with forms ranging from simple sheets to complex tree-like structures (Bayer, 1973). Most octocorals have small, calcitic sclerites within their tissue and along their branches which occur in a wide variety of shapes and sizes (Bayer et al., 1983). These sclerites serve different functions, such as limiting adjacent sclerite movement, providing rigidity, giving support, as well as enabling flexibility (Lewis and von Wallis, 1991).

Unfortunately, plasticity in morphological characteristics makes octocorals particularly difficult to identify to species level. To compound the already tasking endeavour of species identification, often only ancient literature (with either limited or no illustrations) is available, and there have been several within-group phylogenetic reconstructions (Kükenthal, 1919; Bayer, 1956; Bayer, 1981; Bernston et al., 1999; Grasshoff, 1999).
Table 1.1. Classification of seven coral groups including total number of species (as of March 2007 with recent octocoral descriptions included; Cairns 2007) and number of deep-water (>50m) species. Modified from Roberts et al. 2009.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Common names or some or all taxa</th>
<th>Number of species</th>
<th>Number of species found &gt;50m deep</th>
<th>% found &gt;50m</th>
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<td>622</td>
<td>41</td>
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<tr>
<td>Order Zoanthidea (in part)</td>
<td>Zoanthids, gold coral (<em>Gerardia</em> spp.)</td>
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<td>100</td>
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<tr>
<td>Order Antipatharia</td>
<td>Black, whip, wire and thorny corals</td>
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<td>182*</td>
<td>75</td>
</tr>
<tr>
<td>Subclass Octocorallia (=Alcyonaria)</td>
<td>Soft corals, gorgonians, sea fans, sea whips, sea feathers, precious, pink, red, golden, bamboo, leather and horny corals, sea pens</td>
<td>3169*</td>
<td>2335*</td>
<td>74</td>
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<td>Class Hydrozoa</td>
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<td>Suborder Capitata</td>
<td>Hydrocorals, fire corals, millepores</td>
<td>17</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>5170*</td>
<td>3366*</td>
<td>65</td>
</tr>
</tbody>
</table>
Gorgonian octocorals are differentiated from alcyonacean octocorals by their semi-rigid scleroproteinaceous skeleton. The order Gorgonacea, which contained all gorgonian octocorals, was abolished (Bayer, 1981) and all its taxa placed within Alcyonacea. Unfortunately the designation Gorgonacea is still widely used (UNEP-WCMC Species database, Genbank, WORMS), and this can cause confusion. Alcyonacea are now nominally placed in six suborders: Holaxonia, Scleraxonia, Stolonifera, Alcyoniina, Protoalcyonaria (Bayer, 1981) and Calcaxonia (Grasshoff, 1999); these represent two major phylogenetic clades (Holaxonia-Alcyoniina - soft corals - and Calcaxonia-Pennatulacea) and a third minor clade (*Anthomastus-Corallium*) whose relationship with the major clades remains unresolved (McFadden et al., 2006). The surety of many families is debated with authors quoting between 38-46 families of extant octocorals.

![Figure 1.1](image)

**Figure 1.1** a) Unknown Alcyonacea, (b) Unknown Antipatharia, (c) Close-up of bamboo coral polyp, *Keratoisis* sp. Approximate size of polyp is 3mm across. (a) and (b) care of MRAG, (c) taken by author.

Octocoral systematics relies on a combination of characters such as axial composition (if any), presence or absence of spicules, colony symmetry and form, branching arrangement, polyp arrangement and clustering, and sclerite morphology (Bayer, 1981). As Valenciennes, (1855) wrote, sclerites are found across genera so cannot be used to differentiate at this level, but they can be used in species diagnosis and are in fact usually essential for species identification (Bayer et al., 1983; see Chapter 2). There are around a dozen deep-sea octocoral taxonomists globally; a tragic symptom of the decline in taxonomic training seen across all fauna (Wheeler, 2004; Wheeler, 2010). Given this paucity of expertise and the increasing interest, exploration, and exploitation of the deep sea, I investigated molecular techniques to estimate octocoral diversity, primarily in Primnoidae (Chapter 3), embedded in a background of morphological knowledge (Chapter 2).
1.3 Study area: South Georgia Island, sub-Antarctic

“There are very few places on our planet at which we can overlay such strong geographical, physical, oceanographic, historical human pressure and biodiversity data”

Barnes et al., in press

The Scotia Sea (Figure 1.2) formed in the last ca 50 Myr (Barker, 2001), as the continental link from South America to the Antarctic Peninsula began to erode. The detailed history of this separation is still not certain (Thomson, 2004) but the formation of the Drake Passage undoubtedly provided an important pathway for circumpolar water movement and a direct link between organisms of the Pacific and Atlantic oceans. The opening likely began as a shallow gateway around 50 Myr ago with deep water flow commencing 34-40 Myr ago (Livermore et al., 2007).

Figure 1.2. Map of Scotia Sea showing major features with bathymetry (reproduced from Thomson 2004). 1000 m, 2000 m and 3000 m submarine contours are shown.

In the late Oligocene, there were believed to be major ice sheets across Antarctica suggesting that present-day sea surface temperatures of +2°C to -2°C were then established (Briggs, 2003). This cold climate meant many early Tertiary warm/temperate species became extinct. The subsequent opening of the Drake Passage (causing geographical isolation), in combination with invasions of cold/temperate species from the northern hemisphere, has been hypothesised to be
significant in contributing to the highly distinctive fauna now found in Antarctica (Briggs, 2003).

Between approximately 50° South and 65° South, a circumpolar eastward circulation, named the Antarctic Circumpolar Current (ACC), dominates (Orsi et al., 1995). ACC flow is topographically constrained in many places around its circulation, the greatest restriction occurring in the Drake Passage, between South America and the Antarctic Peninsula (Figure 1.3). From here the ACC emerges into the Scotia Sea, and encounters one of the biggest topographic barriers in the Southern Ocean, the island system known as the Scotia Arc.

The northern most island in the Scotia Arc chain is South Georgia (Figure 1.2). South Georgia is believed to have migrated to its current position from an original location adjacent to Tierra del Fuego (Mukasa and Dalziel, 1996). This position means South Georgia divides the ACC, with the Polar Front (PF) flowing to the north and the Southern ACC front (SACCF) to the south (see Figure 1.3). Both these fronts are temporally and spatially variable (PF: Trathan et al., 1997; SACCF: Boehme et al., 2008). In addition, the South Georgia shelf is the warmest area (~4°C) and has the highest seasonal range in the Southern Ocean (Barnes et al., 2006). This physical and biological variability contributes to the high productivity (Atkinson et al., 2001) and diversity (Barnes, 2008) found around South Georgia. The strong flowing current and numerous areas of hard substrata make this island ideal for coral growth yet the systematics, ecology and genetic structure of deep-water corals has been little studied.
Figure 1.3. The Scotia Sea and surrounding areas showing the general position of the major frontal systems in relation to bottom topography. SAF, sub-Antarctic Front; PF, Polar Front; SACCF, Southern Antarctic Circumpolar Front; SB, Southern ACC Boundary; WF, Weddell Front; MEB, Maurice Ewing Bank; NWGR, North West Georgia Rise (depth contours shown for 1000 and 2000 m). Reproduced from Murphy et al., 2007.

1.4 Threats to deep-water habitats

Technological advances in recent decades have opened up the deep sea to an increasing number of human activities (reviewed in Glover and Smith, 2003 and Davies et al., 2007) that may result in loss of biodiversity, changes in ecosystem function and decreased resilience, which consequentially mean losses to the goods and services the deep sea provides. Whether activities are for the advancement of science and our understanding of the deep sea, or for gas and oil exploration, altering deep-sea habitats may have very long term (Danovaro et al., 2001; reviewed in Davies et al., 2007), potentially permanent, impacts (in the case of nodule growth post-mining, millions of years; Ghosh and Mukhopadhyay, 2000; McMurtry, 2001 in Glover and Smith, 2003). The three threats with the widest, most immediate global impacts are climate change, ocean acidification and fisheries.

1.4.1 Climate change and ocean acidification

The deep sea was long thought to be impervious to, or at least well buffered against, activities on the surface (Menzies, 1965, referenced in Davies et al., 2007). Research
into historical changes in deep-sea communities has shown that in the past deep-sea ecosystems have been impacted by rapid climate change (over centuries or less; Yasuhara et al., 2008) and current research confirms that cycles in deep-sea fauna distribution and abundances are in fact linked to, and impacted by, surface activities (e.g. organic matter flux to the deep sea, Gooday, 2002; epibenthic megafaunal changes at 4100 m in relation to El Niño/El Niña events, Ruhl and Smith, 2004; reviewed in Glover et al., 2010). This raises the question of climate change impacts in the deep sea and around South Georgia, my study location.

The northern and southern limits of many species geographical ranges coincide at South Georgia (Barnes et al., 2009), making this a potential hotspot to detect climate impacts. Although some of the most substantial long-term warming recorded from circum-Polar areas is found around South Georgia (Whitehouse et al., 2008), marine areas studied at 200 m were unchanged however there was some indication of slight warming below 200 m although the author believed the data were insufficient for further analysis. More research into the effects of climatic temperature increases in deeper waters is essential.

It is predicted that as atmospheric CO$_2$ increases, it will continue to be absorbed by the oceans. Absorbed CO$_2$ reacts with water molecules in seawater to create carbonic acid, making oceans more acidic (Raven et al., 2005). Cold-water Scleractinia species are in essence calcium carbonate or aragonitic (the metastable form of calcium carbonate) structures. There has been a mixed response across tested calcifying organisms with reductions in calcium carbonate saturation resulting in both reduced and increased net calcification, and even no response at all (Ries et al., 2009). Cold-water corals already exist in areas less favourable to calcification, meaning increases in pH could affect these ecosystems earlier than others and with greater effects (Raven et al., 2005). That said, one of the few physiological experiments on deep-water corals that studied effects of pH reduction found, even with an aragonite saturation level below 1, calcification still occurs, albeit at a slower rate (Maier et al., 2009). It is predicted that 70% of coral areas with aragonite saturation in pre-industrial times, will be unsaturated by 2099 (Guinotte et al., 2006); although, being in shallower water, seamount summits appear to be potential refuges (Tittensor et al., 2010). Under several relatively modest “business as usual” IPCC scenarios, the
Southern Ocean is predicted to be more severely influenced by ocean acidification than other regions, with the exception of the Arctic Ocean which will also be badly affected; the aragonite saturation horizon (which gets closer to the ocean surface as acidification intensifies) is predicted to reach the surface leaving the Southern Ocean under-saturated by 2050 (Orr et al., 2005).

Within octocorals the effects of ocean acidification are more difficult to understand because some octocorals have proteinaceous gorgonian axes whilst others are solidly calcitic or aragonite calcium carbonate (Bayer and Macintyre, 2001). As calcite is less soluble, perhaps octocorals will be modestly buffered against ocean acidification, more so than Scleractinia. However, as skeletal mineral composition has been verified in just 58 octocoral species (which varied between calcite, aragonite, amorphous carbonate hydroxylapatite and gorgonin; Bayer and Macintyre, 2001), the impacts remain very much understudied and poorly understood. It has been speculated that corals with tissue protecting their carbonate skeletons (many octocorals) may fare better in the immediate future should their habitat become corrosive (Hofmann et al., 2010).

In essence more needs to be known about not just the effects of ocean acidification on calcification but the synergistic effects of other climate-related stressors (warming, hypoxia, etc) on physiology, reproduction, and metabolic processes and their potentially cascading consequences in the deep sea (Fabry et al., 2008; Hofmann et al., 2010); this could prevent the statement below becoming true:

“If CO2 emissions continue on current trends, ocean acidification will threaten the existence of cold-water corals before we have even started to understand and appreciate their biological richness and importance for the marine ecosystem.”

Raven et al. 2005, p.27

1.4.2 Fisheries

Fisheries are widely considered to have the most far-reaching and serious impacts on deep-sea habitats globally. Deep-water fisheries began in the 1950s to 60s as a result of continuing decline of shallow-water fisheries, the establishment of exclusive economic zones (Pauly et al., 2005; Figure 1.4) and improved gear and tool
technology, enabling effective fishing in deeper waters (Koslow et al., 2000; Roberts, 2002).

In some regions, effects on fish populations have been severe. After huge initial deep-water harvests in species such as pelagic armourhead (*Pseudopentaceros wheeleri* Hardy 1983) in the North Pacific, redfish (*Sebastes* sp.) in the northeast and northwest Atlantic, scorpaenids (*Sebastolobus* sp.) and *Coryphaenoides* sp. in the North Pacific, and orange roughy (*Hoplostethus atlanticus*, Collett 1889) around southeast Australia and New Zealand, catches rapidly declined (Koslow et al., 2000). This caused exploitation to expand into wider geographic locations and even greater depths in an effort to maintain catches (Clark, 1999; Koslow et al., 2000). In the northwest Atlantic 5 deep-water fish species, ranging from rare to common species, and those targeted commercially and as by-catch, were categorised as endangered under IUCN criteria; the relative abundance over a 17-year period had declined by 87-99% and declines estimated over three generations (the IUCN benchmark) were 99-100% (Devine et al., 2006).

![Figure 1.4. Mean depth of global fisheries landings by latitude from 1950 to 2000. Reproduced from Pauly et al., 2005.](image)

There is also some evidence from the northeast Atlantic that commercial fishing within the shallower areas of fish species ranges reduces abundance in deeper areas, beyond the maximum depths commercial fisheries are allowed. Effects within these deeper areas were not previously considered, have not been monitored, and are not covered by management regimes (Bailey et al., 2009). Additionally, compared to coastal fisheries, a higher percentage of deep-water fishing is illegal, unreported and/or unregulated (IUU; UNEP, 2007; Rogers and Gianni, 2010).
The slow-growing, late maturation, low fecundity, and long-lived existence of fish in the deep-sea, makes populations vulnerable to overfishing (Froese and Sampang, 2004; Morato et al., 2006), and means the effects of fishing could be long-lasting and have uncertain recovery consequences. Longevity is also often associated with late maturity. Orange roughy, *Hoplostethus atlanticus*, can live for 150 years and do not mature until 25-35 years old (Horn et al., 1998). These life history characteristics make deep-sea fish particularly vulnerable to exploitation.

Many commercial fishery species seem to be associated with deep-water coral habitat (Costello et al., 2005; Stone, 2006); for instance, more and larger commercial and non-commercial fish were found on *Lophelia pertusa* reefs than in non-coral habitats in the North Atlantic (Husebø et al., 2002). High densities of commercial fish have also been found on North Pacific gorgonian reefs (Stone, 2006). That said, the functional role of deep-water corals in fish population processes, if any, requires further investigation (Auster, 2005).

![Figure 1.5. Schematic of trawl with rockhoppers](image-url) Schematic of trawl with rockhoppers (large circular discs that ride over obstructions on the seabed). Image redrawn from NOAA Explorer website.

Trawling is the principal gear used in deep-water fisheries providing 80% of deep-sea harvest in 2001 (Gianni, 2004). Bottom-trawling is often compared to forest clear-cutting (Watling and Norse, 1998; Roberts, 2002) and is associated with high levels of marine disturbance and by-catch of benthic fauna, including cold-water corals.
(Koslow et al., 2001; Hall-Spencer et al., 2002). An estimated 40% of all trawled areas are now deeper than the continental shelf (McAllister et al., 1999). Trawl doors, which can weigh 2 to 5 tonnes each, keep open the net and are required to be larger in deeper and rougher seabed conditions (see Figure 1.5). Trawls increasingly now include a line of large rubber discs or steel discs called rockhoppers (see Figure 1.5), that ride over obstructions such as boulders or coral that could snag the net (Watling and Norse, 1998). Where intensive trawling is focused on small areas, such as seamount summits (O’Driscoll and Clark, 2005), most framework-building coral is removed (Koslow et al., 2001; Clark and Rowden, 2009). Examples of such damage have raised concern amongst the international community with regards to fishing impacts on vulnerable marine ecosystems (VMEs) such as coral reefs, sponge fields and coral gardens (UNGA, 2003; UNGA, 2005).

Globally there is increasing focus on VME fishing impacts. The United Nations (UN) General Assembly Resolution on Sustainable Fishing on the High Seas (61-105 and 64-72, UNGA, 2007; UNGA, 2009) includes actions such as assessing the impacts of bottom fishing, identifying areas with vulnerable habitats, and closing these areas to damaging activities. Implementation of these resolutions by Regional Fisheries Management Organisations (RFMOs) commenced at the end of 2008.

Although trawling is very common globally it is not allowed around South Georgia. The primary fishing gear is bottom longlines. All bottom-contact gear is damaging to deep-water corals (Edinger et al., 2007), however, bottom-longline fisheries are believed to have less impact on benthic habitats and have lower benthic by-catch than trawls (Connolly and Kelly, 1996). Longlines (see Figure 1.6) are, however, deployed in “rough” (un-trawlable) areas that are a good habitat for corals (Edinger et al., 2007), so could be causing comparatively more widespread damage if overall the fishing is concentrated on a smaller area. Impacts of any damage, in both the short and long term, in respect to regeneration, species composition changes and resilience is largely unstudied (Hilborn, 2007).
The significance of deep-water coral by-catch in bottom-longline fisheries in the Antarctic and sub-Antarctic has never before been investigated beyond reports that cold-water corals were present in some areas exploited by the bottom-longline Patagonian toothfish, *Dissostichus eleginoides*, fishery (Rice et al., 2007). Management of this fishery has taken into account high density and high diversity coral areas and areas of high macrourid and ray by-catch (Agnew et al., 2007) to create three restricted impact areas (RIAs). The RIAs have been in place since 2007 and exclude all fishing. One area has been expanded in 2010 to protect Patagonian toothfish spawning and juvenile areas. It is from this Patagonian toothfish fishery that by-catch studied here originates (see Chapters 4 and 5).

### 1.5 South Georgia Patagonian toothfish fishery

The South Georgia Patagonian toothfish, *Dissostichus eleginoides* Smitt, 1898, fishery uses bottom-longline gear between 500 – 2000m in depth. A condition of the 2005 Marine Stewardship Council certification of this fishery (MSC, 2005) was to locate and possibly manage areas with species rich benthic habitats. As such, the Marine Resources Assessment Group (MRAG, Ph.D. CASE partner and organiser of South Georgia fisheries observers) initiated by-catch studies that included benthic
fauna (Agnew et al., 2007). One thousand nine-hundred and thirty-five samples from fisheries observers and research vessels were collected (90 samples of which were procured through a collaboration with British Antarctic Survey), a taxonomic breakdown of which is presented in Chapter 5.

Around South Georgia, octocorals were believed to be concentrated on the upper shelf slope, at 500-1200m, although greatest by-catch in recent years were between 1000-1400m, where fishing effort and thus sampling, had been high (Agnew et al., 2007). Agnew et al., (2007) reported, when compared to well-studied regions such as the northeast Atlantic, relatively high octocoral diversity around South Georgia. Specifically, 17 primnoid genera were sampled, 15 of which were endemic to this region (about 50% of known primnoid genera globally; López-González et al., 2002), and a number of which were undescribed (a typical situation with octocoral taxonomy; Parrish and Baco, 2007). This emphasises the importance of octocoral diversity around South Georgia.

Figure 1.7 Patagonian toothfish, *Dissostichus eleginoides*. Photo credit: MRAG
1.6 Aims and objectives – the data chapter breakdown

This thesis is broken down into four data chapters that are written as manuscripts for submission. Submission status of papers is written on chapter title pages.

As Primnoidae were found in by-catch more than any other octocoral family this is where morphological identifications were focused. Within Primnoidae, the common bottlebrush genera of *Thouarella* were most prevalent and, as this genus had not been studied holistically since 1924, a taxonomic revision was completed (Chapter 2).

In order to estimate the species richness of octocoral by-catch being caught by the longline fishing industry around South Georgia, a phylogenetic analysis was undertaken and by-catch sequences embedded within a wider phylogeny of Octocorallia (Chapter 3).

This new knowledge of South Georgia octocoral species richness was spatially rooted into mega-habitat maps. An octocoral habitat suitability analysis was also seen as an important step in informing fisheries management about the types of areas current fishing regulations and the newly created Restricted Impact Areas protect (Chapter 4).

Given the increased international importance placed on vulnerable marine ecosystems in recent years (Auster et al., 2011; UNGA, 2007; UNGA, 2009), I was keen to understand the actual impact of a longline on benthic habitats. By-catch research is always undertaken knowing that gear has an inherent selectivity bias on the diversity and abundance of organisms retrieved and I also wanted to investigate this. As such I examined camera footage from three longline sets. As identifications from camera footage are not possible beyond family level (and sometimes not even suborder) longline selectivity investigations focused on colony morphologies (whip, bushy, fan) and the octocoral diversity this encompasses (Chapter 5).

The final chapter (Chapter 6) offers an overview of discoveries, conclusions and suggestions of areas for future research.
CHAPTER TWO
2 A revision of the genus Thouarella Gray, 1870 (Octocorallia: Primnoidae) including illustrated artificial key and a new species description

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2.1 Abstract

This research comprises a comprehensive revision of the entire Thouarella genus. Thirty-five holotypes of the initial 38 Thouarella species, two varieties and one form were examined. The number of original Thouarella species has been reduced to 25, mostly through synonymisation or new genus combinations. In the process several new species have also been identified, one of which is described here, Thouarella nov. sp. The genus is split into two groups based on polyp arrangement: Group 1 with isolated polyps and Group 2 with polyps in pairs or whorls. An illustrated dichotomous key and detailed character table of 24 Thouarella species are presented alongside an up-to-date account of all species described in the 19th and 20th centuries and summaries of the few described from 2000 onwards.

It is proposed that Thouarella longispinosa is synonymised with Dasystenella acanthina, T. versluysi with T. brucei, and T. tenuisquamis, T. flabellata and T. carinata with T. laxa. Lastly, that T. diadema T. undulata, T. alternata, T. recta, T. superba, and T. bayeri are transferred to Plumarella.

Keywords: Octocorallia, Cnidaria, Primnoidae, Thouarella, taxonomic revision, sub-Antarctic.
CHAPTER TWO

2.2 Introduction

*Thouarella* Gray, 1870 are primnoid octocorals within the subclass Anthozoa. Octocorals usually have small calcium carbonate sclerites over or within their tissue (with a few notable exceptions discussed in Alderslade and McFadden, 2007). There are a wide variety of sclerite shapes and sizes (Bayer et al., 1983) serving different functions such as limiting adjacent sclerite movement, giving rigidity and support, as well as flexibility (Lewis and Wallis, 1991). Primnoids, with the exception of one species of *Mirostenella* which has a jointed axis, have solid continuous, gorgonin axes (Cairns and Bayer, 2009). They are found worldwide but are especially common in the Antarctic region (*Thouarella* is no exception) and occur predominantly deeper than 400 m, the deepest from 5850 m (although primnoids have been recorded from 8m; Cairns and Bayer, 2009).

*Thouarella* is an architecturally delicate genus in which the majority of species have flower-like, open operculate polyps covered with thin sclerites. Species of *Thouarella* are locally abundant in many areas of the deep sea, especially in the sub-Antarctic, and play an important ecological role, providing habitat for many creatures. Although relatively common, little research has focused on species identifications beyond the original type descriptions, many of which are from the turn of the last century. Often considered the “bottlebrush” genus, *Thouarella* in fact has a range of branching forms, similar to several other genera, resulting in specimens being frequently misidentified.

*Thouarella* is a group of very closely-related species; their morphology and many characters historically used to separate species and subgenera are quite variable and the genus has been in need of revision given the number of species described and time since last revision. Having reviewed all available holotypes I present the most thorough review of this common genus to date and I have made some significant changes to the understanding of some species within this genus and the key characters involved in species identification.
2.2.1.1 Abbreviations

NMNH – National Museum of Natural History, Smithsonian Institution, Washington DC, USA.
NHM – Natural History Museum, London, UK.
MNHUW – Museum of Natural History, Wroclaw University.
UMUT – University Museum, University of Tokyo.
ZMA - Zoological Museum, University of Amsterdam.
MNHWU - Museum of Natural History, Wroclaw University.
ZMH – Zoological Museum, University of Hamburg.
SMF – Senckenberg Forschungsinstitut und Museum Frankfurt.
MYA – million years ago
ZGR - Zapata-Guardiola, Rebeca
SJ - Schleyer, Jon

2.3 **History of Thouarella systematics**

The type species of *Thouarella* Gray, 1870 was originally described as *Primnoa* Lamouroux, 1812 by Valenciennes in the report from the 1836–1839 *Venus* expedition (1846). A brief mention of *P. antarctica* appears in Valenciennes (1855) although merely as a referenced example of one of the five gorgonian forms—“the fifth form consist[ing] of larger or smaller scales, more or less covered with small spines” (taken from the English translation of Valenciennes, Selby et al., 1855, pp.179). When the classification of gorgonians was reorganised by John Edward Gray in 1857, primnoids were placed under Lithophyta. Two species of *Primnoa* were described in Gray’s 1859 paper: *P. lepadifera* (now *P. resedaeformis*) and *P. antarctica*. These species were separated by their branching morphology with the former described as “tree-like” and the latter with “spreading branches” (pp. 483). *Primnoa antarctica* was then listed in Kölliker’s 1865 gorgonian descriptions under Primnoaceae but it wasn’t until 1870 that *Thouarella* was established by Gray, who named the genus after the captain of the *Venus* expeditions, Abel Du Petit-Thouars. At this point the description was of a bottlebrush morphology but the finer morphological specifics were unclear as “polyp-cells smooth, bell-shaped, scattered
on upper side of branches, covered with four or five series of imbricate scales” (Gray, 1870: 45) are listed as defining characters. Gray described and illustrated a new specimen of *Thouarella antarctica* in 1872 (catalogue number NHM1872.4.29.1). It is unclear if he ever sought out the holotype from Paris Museum because, as the author has studied Gray’s 1872 specimen, it appears to be *T. brucei* Thomson & Richie, 1906.

The next major work concerning *Thouarella* was Wright and Studer, (1889) whose descriptions of H.M.S. *Challenger* expedition samples included four new species (*T. moseleyi*, *T. affinis*, *T. koellikeri*, and *T. variabilis*, the latter including three varieties) and a reclassification of *Plumarella hilgendorfi* Studer, 1878 to *T. hilgendorfi*. They listed a specimen of *Thouarella antarctica*, however sclerites (pl. 11, Figure 6) of the specimen only loosely resemble those of *T. antarctica* (Figures 2.4, 2.5). Versluys, (1906: 36) expressed some doubt over Wright and Studer’s *T. antarctica* identification, however he still placed the sample within *T. antarctica* putting any physical differences down to depth variation.

Figure 2.1 First illustration of *Thouarella antarctica* (from Valenciennes 1846) (a.) full colony; (b.) close up of polyps.
Several *Thouarella* species were described from 1906 to 1912: Thomson and Richie (1906: 852–4) described *T. brucei*; Versluiys (1906: 30–2) described *T. laxa* and *T. tydemani* and split *Thouarella* into three groups (‘Hilgendorfi’, ‘isolated’ and ‘Antarctic’); Kinshita described *T. typica* in 1907 and in 1908 Roule, described *T. pendulina*; Kinoshita assessed Primnoidae (1908a) adding three new species (*T. coronata*, *T. parva*; 1908c,d) and a new subgenus, *Diplocalyptra*, as well as placing *Amphilaphis biserialis* within *Thouarella* (1908c). Kükenthal began work on *Thouarella* between 1907 and 1915, describing nine new species (see Table 2.1) and two new subgenera, *Epithouarella* and *Euthouarella* (Kükenthal, 1907; 1908; 1912; 1915). Thomson described *T. hicksoni* in 1911 (pp. 886–7) and finally, Nutting (1912) described *T. alternata*, *T. recta* and *T. superba*.

Thomson and Henderson (1906) published a comparison table for *Thouarella* species however it was Kükenthal (1915; 1919; 1924) who wrote the major diagnostic keys for this genus. The subgenera in 1915 stood as:

- **Amphilaphis** Studer, 1887—differentiated on dichotomous branching mode;
- **Euthouarella** Kükenthal, 1915—polyps in pairs or whorls of up to 4;
- **Parathouarella** Kükenthal, 1915—isolated polyps with spined, leaf-shaped marginals;
- **Epithouarella** Kükenthal, 1915—isolated polyps with marginals lacking a long spine.

Kükenthal did not discuss the subgenus *Diplocalyptra* (species with dichotomous branching), described by Kinoshita (1908a), presumably not knowing of its existence as most was written in Japanese. And, as *Parathouarella* included the type species *T. antarctica* it was thus redundant. From 1956 *Parathouarella* was simply called *Thouarella* (*Thouarella*) (Bayer 1956). *Amphilaphis* was removed from *Thouarella* by Kinoshita (1908b), however this removal was not mentioned or followed in later papers by Kükenthal (1912; 1915; 1924). In 1981 (pp. 1936) Bayer treated *Amphilaphis* as a valid genus on the basis that it has eight full rows of body-wall scales rather than the six rows of body-wall scales with two reduced adaxial rows, as found in *Thouarella* (Cairns & Bayer 2009. Brito, (1993) merged *Amphilaphis* with *Thouarella* based on Bayer’s exclusion of the genus in a purported 1988 paper that I cannot locate and is not listed in the references. Thus, although *Amphilaphis* is very similar to *Thouarella* in many respects (discussed in the *Thouarella* genus
description), in this study I just consider the so-called ‘original’ Thouarella species and those incorporated into Thouarella in peer-review journals (see Table 2.1). The genus Amphilaphis remains (as of Bayer, 1981) and requires revision.

Aurivillius, (1931) described T. hilgendorfi forma plumatilis after which there was a 60 years hiatus in Thouarella descriptions until Cairns (2006) provided a revised species list and described three new species. Additionally, in the last few years, five new species of Thouarella have been described from Antarctica (Zapata-Guardiola and Lopez-Gonzalez, 2010a,b). As exploitation of the deep sea and scientific exploration spreads to wider geographical locations and depths, there shall likely be many more Thouarella species described.

2.4 Biology and reproduction

Octocoral reproduction and environmental/biological cues and factors affecting reproduction have been studied extensively in shallow water tropical and temperate latitudes but little study has focused on octocoral reproduction in the deep ocean e.g. Bayer (1996), Brito et al. (1997), Cordes et al. (2001), Slattery and McClintock (1997), Orejas et al. (2002, 2007). Considering only Antarctica, generally reproductive patterns are mostly defined by characteristics such as prolonged gametogenesis, delayed maturation, low fecundity, large yolky eggs, and in many cases, predominance of non-pelagic or at least lecithotrophic development, brooding, brood protection, viviparity, slow embryonic development, advanced newly hatched juvenile stages, and slow growth (Pearse et al., 1991). A recent study of three prinnoid species suggested that morphology may play a role in reproductive output, with bottlebrush-shaped Dasystenella acanthina (Wright and Studer, 1889) and a Thouarella species having over-lapping generations of more than one a year, and fan-shaped Fannyella rossi Gray, 1872 and F. spinosa (Thomson and Rennet, 1931) having annual reproduction (Orejas et al., 2007). A relationship between morphology and reproductive output has also been suggested by studies on gorgonians at lower latitudes (Brazeau and Lasker, 1989). These studies, however, represent a very limited sample size and phylogenetic representation; much more research is required on reproduction, life histories and molecular ecology of octocorals to help understand patterns of population connectivity and factors effecting reproductive success.
## Thyarella

### Table 2.1 *Thyarella* species - Groups 1 and 2

<table>
<thead>
<tr>
<th>Species</th>
<th>Synonym(s)</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Group 1 – Isolated polyps</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. <em>T. antarctica</em> (Valenciennes, 1846)</td>
<td></td>
<td>Falkland Islands, SW Atlantic</td>
</tr>
<tr>
<td>2. <em>T. variabilis</em> Wright and Studer, 1889</td>
<td><em>T. variabilis gracilis</em> Wright and Studer, 1889</td>
<td>Circum-Antarctic</td>
</tr>
<tr>
<td>3. <em>T. brevispinosa</em> Wright and Studer, 1889</td>
<td></td>
<td>SW Atlan., S. Indian Ocean, SW to S. Atlantic</td>
</tr>
<tr>
<td>5. <em>T. koellikeri</em> Wright and Studer, 1889</td>
<td></td>
<td>Mid-S. Atlan., SE Pacific, Antarctic Peninsula</td>
</tr>
<tr>
<td>7. <em>T. striata</em> Kükenthal, 1907</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8. <em>T. crenelata</em> Kükenthal, 1907</td>
<td></td>
<td>Circum sub-Antarctic South Africa</td>
</tr>
<tr>
<td>9. <em>T. clavata</em> Kükenthal, 1907</td>
<td></td>
<td>Circum-Antarctic Chile, S/SW Atlantic, S. Indian Ocean, Antarctic Peninsula</td>
</tr>
<tr>
<td>10. <em>T. pendulina</em> (Roule, 1908)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>11. <em>T. chilensis</em> Kükenthal, 1908</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12. <em>T. hicksoni</em> Thomson, 1911</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15. <em>T. minuta</em> Zapata-Guardiola and López-González, 2010a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>17. <em>T. parachilensis</em> nov. sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Group 2 – Paired or whorled polyps</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>18. <em>T. hilgendorfi</em> (Studer, 1878)</td>
<td><em>T. typica</em> Kinoshita, 1907</td>
<td>Japan</td>
</tr>
<tr>
<td>19. <em>T. moseleyi</em> Wright and Studer, 1889</td>
<td><em>T. tenuissquamis</em> Kükenthal, 1908</td>
<td>Kermadec, New Zealand, Indonesia</td>
</tr>
<tr>
<td>22. <em>T. coronata</em> Kinoshita, 1908c</td>
<td></td>
<td></td>
</tr>
<tr>
<td>23. <em>T. parva</em> Kinoshita, 1908d</td>
<td></td>
<td></td>
</tr>
<tr>
<td>24. <em>T. biserialis</em> (Nutting, 1908)</td>
<td><em>Amphilaphis biserialis</em></td>
<td>Hawaii</td>
</tr>
<tr>
<td>25. <em>T. grasshoffi</em> Cairns, 2006</td>
<td></td>
<td>N. Atlantic</td>
</tr>
</tbody>
</table>
2.5 Materials and Methods

I examined all available type specimens (35 of the 38 holotypes were procured and examined) and hundreds of additional specimens, the majority of which were from the USNM and the SMF. The unseen holotypes are those of: *T. tydemani* Versluys, 1906, which was not seen first hand but detailed images of the remaining three slides of material (taken by ZGR) were examined; the colony *T. parva* Kinoshita, 1908d, is missing from the University of Tokyo museum and unsuccessful attempts were made to locate non-type material and thus the description relies entirely on original hand drawings of one polyp and sclerites (Kinoshita 1908d); the colony of *T. crenelata* Kükenthal, 1907, was not able to be sent from ZMB however this species has some distinct and recognisable characters (Kükenthal 1907) so scanning electron microscopy (SEM) images were procured from voucher specimens held within USNM collections.

2.5.1 Methods

When viewing primnoid polyps under a stereo dissecting light microscope it is useful to dye them using a permanent light-coloured marker pen that highlights sclerite texture and outline. Flattened art clay provides a tacky surface for rolling polyps across so it is possible to view all sides and count the number of scales. To view individual sclerites a polyp was first submerged in ethanol, held gently between tweezers, and a small, soft paintbrush swiped gently over surfaces to remove sand, tissue and other items that may obscure the viewing of sclerites. Polyps were then dissolved in a drop of sodium hypochlorite (bleach). Once free, sclerites were washed with distilled water several times to remove all remnants of bleach. Sclerites were then washed with 70% ethanol and several successions of stronger ethanol solutions, up to 95%, before being dried. These dried sclerites were placed on stubs for SEM. An eyelash or piece of hair embedded in a lump of art clay on the end of a pencil was useful in manoeuvring individual sclerites onto SEM stubs (similar to methods described in Alderslade, 1998). Similarly, a fine haired paint brush with all but two hairs removed was equally useful for this task.

Modern morphological studies of primnoids rely on SEM images. All images within this publication were taken from stubs coated in gold: palladium 60:40 alloy, to thickness between 30 and 40nm, at the Smithsonian Institution SEM Laboratory on an
Amray 1810 SEM with Lanthanumhexaboride electron source and at Cambridge University Department of Materials, on a JEOL GSM–6340F Field Emission SEM.

2.6 Results

2.6.1 Historical summary of the Thouarella species groups

Versluys (1906) first grouped Thouarella species into the “Hilgendorfi-Gruppe” (species with polyps in pairs and whorls), species with isolated polyps (without a group name) and the “Antarctica-Gruppe”, which also has isolated polyps.

Kükenthal (1912) again grouped Thouarella species (“Hilgendorfi-gruppe”, “Antarctica-gruppe” and “Köllikeri-gruppe”, with the latter having isolated polyps but being differentiated by having a longer marginal scale spine than those remaining in the “Antarctica-gruppe”) and later elevated these groups to subgenera (1919). With Amphilaphis removed (Kinoshita 1908a; Bayer 1981) and Diplocalyptra incorporated (Kinoshita 1908c), Thouarella had subgenera separated according to colony branching, polyp placement (whorled, paired, isolated), and the elongation of marginal scale distal edges (Cairns and Bayer, 2009).

2.6.1.1 Antarctica group

Within Group 1 (isolated polyps) there are a number of very closely related species separated by the smallest of variations. In particular the ‘Antarctica group’ (Versluys 1906) deserves mention because some of these species could be considered a single variable species. Versluys originally only listed T. antarctica (Valenciennes, 1846), T. affinis Wright and Studer, 1889 and T. variabilis Wright and Studer, 1889 of which I disregard T. variabilis as it has very long marginals making it distinct from the remaining species. Versluys (1906) grouped these species as they had isolated polyps and a bottlebrush colony arrangement. Kükenthal (1912) considered the ‘Antarctica group’ to include: T. antarctica, T. affinis, T. chilensis Kükenthal, 1908, and T. crenelata and he mentioned that isolated polyp arrangement was a stronger character than branching arrangement; something with which I agree.

2.6.1.2 Köllikeri–gruppe

This includes T. koellikeri (Wright & Studer, 1889), T. variabilis, T. versluysi Kükenthal, 1907, T. striata Kükenthal, 1907, T. clavata Kükenthal, 1908, T. brucei
(Thomson and Richie, 1906), and *T. hicksoni*, Thomson, 1911—species with isolated polyps and foliate, elongated marginals. In 1919, Kükenthal rearranged the entire genus, moving *T. antarctica* into the ‘Köllikeri group’, as it has relatively tall marginals, leaving *T. crenelata*, *T. chilensis* and *T. affinis* in the ‘Antarctica group’ with isolated polyps and shorter marginals. It is this latter group where there are now a number of very similar species.

*Thouarella crenelata* has distinctive serrate distal borders to marginal scales and a high number of scales in the longitudinal abaxial row and is thus quite different from the remaining ‘Antarctica’/‘Köllikeri’ group species. *Thouarella koellikeri*, *T. viridis*, Zapata-Guardiola and López-González, 2010a, *T. antarctica*, and *T. chilensis* are all very similar, having isolated polyps larger than 1.5 mm and low triangular marginals. All of these species have very small differences in the number of body-wall scales in the abaxial row and the complexity of the marginal keel. Although all species have a similar polyp size they vary in polyp density; the number of polyps per cm splits this group into two as *T. antarctica* and *T. chilensis* have very clustered polyps, more than 15 per cm (up to double this in fact), whereas the remaining two species have lower polyp densities. *Thouarella antarctica* and *T. chilensis* are considered distinct as the latter has operculars and marginals with a heavily ridged outer surface and a full opercular cone, all absent in *T. antarctica*, which has thinner opercular scales with a relatively smooth outer surface, as do the marginals of *T. antarctica*. *Thouarella chilensis* also tends to have more scales in the abaxial row than *T. antarctica*. Both *T. koellikeri* and *T. viridis* have tall opercular cones, however, as the latter has protruding toothed submarginals.

Given the relatively small, but apparently consistent, differences separating these species it will be interesting to investigate their genetic relatedness; work that is currently underway.

1.1.1.1 Hilgendorfi-gruppe

On a species level there are many changes within *Thouarella* in this paper. One deserving special mention is the *Hilgendorfi* complex of species (“hilgendorfi-gruppe” sensu, Kükenthal 1912).
In 1906, Versluys placed *T. hilgendorfi* (Studer, 1878), *T. laxa* Versluys, 1906, *T. moseleyi* Wright and Studer, 1889, and *T. tydemani* Versluys, 1906 into the *T. hilgendorfi* group. In 1912 *T. typica* Kinoshita, 1907, *T. longispinosa* Kükenthal, 1912, *T. carinata* Kükenthal, 1908, *T. tenuisquamis* Kükenthal, 1908 and *T. flabellata* Kükenthal, 1907 were added to this group by Kükenthal. Some 100 years later I find myself approaching a similar task in assessing these species whose identifying feature is their paired or whorled polyp arrangement.

Disregarding *T. longispinosa*, which is now considered to be *Dasystenella acanthina* (see species description), this group now looks quite different due to several synonymisations.

*Thouarella laxa* was described from Japan by Versluys (1906). The following year Kükenthal (1907) described *T. flabellata* from Somalia and *T. tenuisquamis* (originally described as *Thouarella regularis* Kükenthal, 1907) from Nicobar, northwest of Sumatra, briefly stating it could be similar to *T. laxa*. These species were not specifically compared to each other or *T. laxa* by Kükenthal, perhaps due to the large distance between their type locations. In 1908 Kükenthal described *T. carinata* from Okinawa and subsequently remarked that it differed from *T. laxa* in having denser branchlets and polyp whorls, as well as different sclerite shapes (Kükenthal 1919). The differences seen between these species in this study are very minor (as discussed in species descriptions) and for this reason I conclude that these species (*T. laxa*, *T. tenuisquamis*, *T. flabellata* and *T. carinata*) are conspecific and propose their synonymisation under the senior synonym *T. laxa*.

Kükenthal (1924) separated *T. tydemani* and *T. laxa* based on the number of whorls per cm (6 to 4), which, as already mentioned, is a variable character, but *Thouarella laxa* polyps (Figure 2.32c) look very similar to those of *T. tydemani* (see Zapata-Guardiola & López-González 2010a). A recent paper (Zapata-Guardiola & López-González 2010a) shows that *T. tydemani* polyps have toothed ridges on the inner surface of body-wall scales, perpendicular to the distal border; these are absent in *T. laxa*. *Thouarella moseleyi* has similar body-wall scale morphology, however, the reduced height of marginals and the clavate polyp shape make *T. moseleyi* distinct from both *T. tydemani* and *T. laxa*. *Thouarella laxa* is bottlebrush and *T. tydemani* is pinnate and the former has polyps that are more inclined to the branchlet than the
latter (which are almost perpendicular), longer, more flexible branchlets and less pairs/whorls per cm, making these distinct species.

The sclerites, number of whorls per cm and number of polyps per whorl of *T. hilgendorfi* and *T. typica* are nearly identical and as these character differences can vary widely within colonies and species I agree with Cairns (2010) that these two species should also be synonymised.

The “hilgendorfi” group thus includes:

– *T. hilgendorfi* (synonym: *T. typica*)

– *T. laxa* (synonyms: *T. tenuisquamis*, originally described as *T. regularis*, *T. flabellata*, *T. carinata*)

– *T. moseleyi*

– *T. tydemani*

In essence, the polyps and sclerites of all of “Hilgendorfi” species (with the exception of *T. moseleyi*, whose polyps are clavate) have nearly identical shapes and sizes. It is astounding that species looking so similar are found from Hawaii (*T. hilgendorfi*) to east Africa (*T. laxa*, formerly *T. flabellata*). I have kept these species separate based on branching structure but would be interested to see if genetic studies support this distinction; this research is currently underway.

### 2.6.2 Species groups

As already mentioned, before this revision *Thouarella* had subgenera separated according to colony branching (Diplocalyptra), polyp placement (whorled and paired—“Hilgendorfi group”, isolated—“Antarctica” and “Köllikeri” groups), and the elongation of marginal scale distal edges (with “Köllikeri” having longer marginals than “Antarctica” species; Cairns and Bayer, 2009). I query the reliability of two of these characters as colony branching can vary within a species (*Thouarella* seems particularly variable in this respect making this character unsuitable for subgeneric separation), and the entire spectrum of elongation of the distal edge of marginal scales, from rounded to spinose, can be found in *Thouarella* making this character also a poor choice for assigning species to subgenera. Polyp placement, however, is a more reliable character; species with isolated polyps being easily distinguished from
those with paired or whorled polyps and, although some species with paired polyps infrequently have whorls of 3 and even 4 polyps, this is very rare in species with isolated polyps. Consequently, given that Thouarella species are very closely related, I acknowledge this close relationship by splitting Thouarella into species groups rather than subgenera. Furthermore, as discussed above, the most reliable character available to group Thouarella species is polyp placement and it is on this character that I, as Versluys partially did (1906), base my species group delineations (Table 2.1): Group 1–species with isolated polyps and Group 2–species with polyps in pairs or whorls. Group 1 would thus include both “Antarctica” and “Köllikeri” groups. The “Hilgendorfi” group is now Group 2.

Within Group 1 the number of abaxial body-wall scales, polyp size, number of polyps per cm and polyp shape are equally important when determining species. Group 2 species are very similar at a polyp level and differentiation is based primarily on branching arrangement and branchlet rigidity. See Table 2.3 for more details.

2.7 Thouarella morphology and characters

2.7.1 Branching structure

The complex morphological structure of Thouarella makes it an ideal habitat for many species. Thouarella in this study were often found harbouring polychaetes along their axis between branchlet planes, brittlestars clinging to branchlet tips, amphipods wedged between polyps, and egg cases and ascidians attached to stems and branchlets (Figure 2.2).

The most common Thouarella branching structure is a bottlebrush form (see Figure 2.2a), with branchlets arranged on all sides of the main stem in at least three directions. Thouarella species are also pinnate (featherlike branching, branchlets on each side of branch, Figure 2.30a), pinnate to bipinnate (pinnate branching where branchlets are also pinnately branched), dichotomous (repeated bifurcation of branching; Bayer et al. 1983, see Figure 2.34a) and bilateral to bottlebrush (where branchlets occur in at least three directions, and are thus technically bottlebrush, however branchlets curve into one plane creating a bilateral appearance; see Figure 2.12a). In some instances, overall colony structure can be one shape and branching
structure different, for example T. hilgendorfi has a uniplanar, flabellate colony shape yet individual bottlebrush branches.

2.7.2 Polyp shape, arrangement, and distribution

Polyps of Thouarella are generally flared distally (this ranges from modest to widely flared) or clavate (having a tall operculum, visible from side view e.g. T. koellikeri, Figure 2.12c, or an operculum beneath encasing marginals and thus not visible e.g. T. parachilensis nov. sp, Figure 2.28c). Polyps open widely to take in food and this function, and the associated change in polyp shape, should be remembered when undertaking species identifications: polyps are not a fixed shape.

Thouarella polyps occur individually (isolated, e.g. T. crenelata, Figure 2.18b), in pairs (e.g. T. laxa, Figure 2.32c. T. laxa polyps also occur in whorls), or in whorls (e.g. T. coronata, Figure 2.34c) of up to 5.

The density of polyps (number of polyps per cm) is often related, in some degree, to polyp size. There will be more 1 mm long polyps per cm than those 2.5 mm long. This is an important point to consider and the reason why I did not use the number of polyps/pairs/whorls per cm in the dichotomous key. However, this is still sometimes a useful factor in species identifications and can be used as long as the polyp length in the species description is cross referenced. Polyp length is the length measured abaxially from polyp tip to base
2.7.3 Sclerites

The variation and differences of size, shape and arrangement of sclerites is used in species diagnosis. Reading through some original literature pertaining to *Thouarella* identification it became clear that the terms “opercular”, “circumopercular” and
“marginal” have been used in different ways at different times. To avoid confusion, all sclerite categories are defined below.

**Operculars** (Figure 2.3f–i) fulfil the functional role of covering the polyp head. There are eight operculars in *Thouarella* and they can be arrowhead-shaped (with a dented proximal edge, Figure 2.3h,i), acute isosceles triangles/lanceolate (Figure 2.3f) or tongue-shaped (rounded distal edge, Figure 2.3g).

**Accessory operculars** (Figure 2.3a–e) have been found in several *Thouarella* species. Originally noted by Kinoshita (1908b, pl. 5), they are smaller (250–500 µm) than operculars, often of a similar shape, and usually adhere to the inner surface of typical operculars (and against the polyp body/tentacle-base); they tend to be found in one ring, although two rings have been described in *Plumarella* (formerly *Thouarella*) *bayeri* (Zapata-Guardiola & López-González, 2010b), and are often less than eight in number. Similar small operculars are found in *Convexella* Bayer, 1996 and *Digitogorgia* Zapata-Guardiola & López-González, 2010c.

**Marginals** (Figure 2.3j–l), or circumoperculars, are the more proximal transverse circle of scales that tend to be the same size or larger than the operculars and usually fold over the operculars, forming a protective cone when the polyp contracts. There are eight marginals and the inner surface is keeled. These keels are diagnostic at the genus level; their presence is the only character that separates *Thouarella* from *Plumarella* (Cairns, 2010).

**Submarginals** (Figure 2.3m–o) are the next most proximal transverse circle of scales below the marginals. They are sometimes differentiated from body-wall scales in having a more pointed distal edge and occasionally a reduced keel on the inner surface and are thus often specifically included in species descriptions.

**Body-wall scales** (Figure 2.3p–s) generally form the majority of scales covering the polyp body in longitudinal rows beneath the submarginals to the polyp base. Abaxial body-wall scales are usually larger than those situated adaxially. Body-wall scales have tubercles covering the inner surface, as is common for the proximal third to two-thirds of most sclerites. From marginals to polyp base the number of scales in each transverse circle often decreases as the polyp attenuates.

**Coenenchymal** scales form one or two layers along branches. Most sclerites within a category are generally the same shape however coenenchymal scales are often a range of shapes: circular, oval and elliptical, possibly as all edges are free to develop.
Other commonly used terms and structures include:

**Keels** are an important characteristic in *Thouarella* species (*Plumarella* and *Thouarella* may look very similar but the presence of a keel distinguishes that a species is *Thouarella* not *Plumarella* (Cairns 2010). Within *Thouarella* there are simple keels (Figure 2.3k), complex keels (Figure 2.3l), channelled keels (Figure 2.3j), keels with lateral projections (visible from the outer surface e.g. Figure 2.5h) and unsurprisingly, with the high level of variability in *Thouarella*, there are specimens that can span two of these forms. The text below is provided to enable the reader to understand my descriptions of keeled marginals:

- *T. brucei* marginals have a complex keel (Figure 2.15f), the most common amongst *Thouarella* species often with small lateral projections visible from the outer surface, as with marginals of *T. antarctica* (Figure 2.5h).
- *T. affinis* has marginals with a simple keel (Figure 2.11h).
- *T. variabilis* has a channelled marginal keel (Figure 2.3j).
- *Plumarella diadema* (Cairns 2006) (formerly *Thouarella diadema*) does not have a keel but a spine with longitudinal parallel ridges (a bifurcate example of which is seen in Figure 2.36d).

The term **serrated** is usually applied to the distal edge of sclerites (see distal edges of *T. brucei*, Figure 2.15g). In *Thouarella* most sclerite edges are actually **finely serrate** (see Figures 2.3g,n,o).

**Coarsely or roughly lobate** (e.g. Figure 2.3j,p,r) has been used to describe the uneven, sometimes tuberculate proximal edges of most *Thouarella* sclerites.

**Pectinate** is truly comb-like and only found in *Thouarella crenelata* (Figure 2.19f,h,j), *Plumarella recta* (Nutting, 1912) and *P. alternata* (Nutting, 1912), the latter two both formerly placed in *Thouarella* (Figure 2.3i,k).

### 2.8 Species synonymisations and removals

I consider there to be 25 species within *Thouarella* (Table 2.1). In the dichotomous key, scale bars are included and are usually the same within each couplet (e.g. 6a and 6b). This was not possible with colony images as their size differed enormously, thus colony/branchlet lengths are listed.
Several species of *Thouarella* are proposed for synonymisation within this study. *Thouarella laxa* Versluys, 1906, *T. tenuisquamis* Kükenthal, 1908, *T. flabellata* Kükenthal, 1915 and *T. carinata* Kükenthal, 1915 are proposed as conspecific and thus synonymised with the senior synonym *T. laxa*. In addition, *Thouarella variabilis* var. typical Wright and Studer, 1889 and *T. variabilis* var. *gracilis* Wright and Studer, 1889 are proposed as synonymised under *T. variabilis*, and *T. variabilis* var. *brevispinosa* Wright and Studer, 1889 raised to species level (*T. brevispinosa*). I also propose that *Thouarella versluysi* Kükenthal, 1907 is synonymised with *T. brucei* Thomson and Ritchie, 1906.

*Plumarella sardana* (formerly *Thouarella sardana*) (Zapata-Guardiola & López-González, 2010b) and *P. diadema* (formerly *T. diadema*) (Cairns, 2006) are conspecific and thus synonymised as *P. diadema*.

Lastly, mostly due to clarification of the difference between *Plumarella* and *Thouarella* (Cairns, 2010), the species in Table 2.2 have been removed from *Thouarella*.

Table 2.2 Species removed from *Thouarella* genus

<table>
<thead>
<tr>
<th>Old designation</th>
<th>New combination</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>T. longispinosa</em> Kükenthal, 1912</td>
<td><em>Dasystenella acanthina</em></td>
</tr>
<tr>
<td><em>T. alternata</em> Nutting, 1912</td>
<td><em>Plumarella alternata</em> n. comb.</td>
</tr>
<tr>
<td><em>T. recta</em> Nutting, 1912</td>
<td><em>Plumarella recta</em> n. comb.</td>
</tr>
<tr>
<td><em>T. superba</em> Nutting, 1912</td>
<td><em>Plumarella superba</em> n. comb.</td>
</tr>
<tr>
<td><em>T. bayeri</em> Zapata-Guardiola and López-González, 2010b</td>
<td><em>Plumarella bayeri</em> n. comb.</td>
</tr>
</tbody>
</table>
Key to Thouarella species

Group 1 – species having isolated polyps

1a. Up to 5 scales in the abaxial row: 2
1b. Five scales or above in the abaxial row: 9

2a. Polyps less than 1.5mm long: 3
2b. Polyps larger than 1.5mm long: 5

3a. Polyps less than 1mm long. *T. minuta*
3b. Polyps 1–1.5mm long: 4

4a. Polyps appressed to branchlet, 0.9–1.2 mm long, pointed opercular, marginals with simple keel. *T. pendulina*, see figs. 22, 23
4b. Polyps inclined at 30° to appressed against branchlet, 1.0–1.25 mm long, opercular tongue-shaped, marginals with strong, complex keel. *T. hicksoni*, see figs. 26, 27

5a. Colony pinnate to bipinnate, polyps clavate and orientate toward one face of the colony. *T. bipinnata* (see Cairns, 2006)
5b. Colony bushy/ bilaterally bottlebrush or bottlebrush shaped, polyps distally flared and isolated: 6

6a. Marginals elongated, almost spinose. *T. variabilis*, see figs. 6, 7
6b. Marginals triangular, can have pointed distal edge: 7

7a. Marginals with heavily ridged inner surfaces. *T. striata*, see figs. 16, 17
7b. Marginals with relatively smooth inner surfaces, sometimes with small ridges adjacent to keel: 8

8a. Opercular scales triangular with wide distal edge, inner surface ridged (i), marginals with dense tubercles (ii). *T. andeep*
8b. Opercular scales wide triangular-shaped with pointed distal edge, inner surface with keel (i), marginals with sparse tubercles (ii and polyp in 6b). *T. brucei*, see figs. 14, 15
CHAPTER TWO

9a. Polyps clavate (and see 12a): 10
9b. Polyps distally flared: 13

10a. Polyps with tall operculum, visible from side view (see 9a, 11b): 11
10b. Polyps with operculum hidden in side view, lower than marginals (e.g. 12a,b): 12

11a. Heavily ridged inner distal edge of marginals and submarginals, 6–7 abaxial scales. T. viridis (see 9a and Zapata-Guardiola & López-González, 2009)
11b. Pointed marginals and submarginals with small keels on inner surface, 7–10 abaxial scales. T. koelikeri, figs. 12, 13

12a. 6–10 abaxial scales, polyps clavate, polyps evenly spaced along branchlets, operculum open. T. crenata, figs. 18, 19
12b. 7–11 abaxial scales, polyps globular, in dense clusters at branchlet tips, operculum encased by marginals. T. parachilensis, figs. 28, 29

13a. Most marginals tall triangular, some abaxial marginals widely triangular: 16
13b. Most marginals wide triangular to diamond shaped: 14

14a. Tongue-shaped opercular. T. affinis, figs. 10, 11
14b. Lanceolate opercular, heavily ridged: 15

15a. Thick, heavily ridged marginals and opercular scales, 7–9 abaxial scales. T. chilensis, figs. 24, 25
15b. Relatively smooth, delicate opercular and marginal scales (see 15b) with wide lateral projections off keel, 5–7 abaxial scales. T. antarctica, figs. 4, 5

16a. Polyps < 2mm long, 5-6 abaxial scales. T. clavata, figs. 20, 21
16b. Polyps > 2mm long, 6-8 abaxial scales. T. brevispinosa (also see 9b), figs. 8, 9
Revision of *Thouarella*

**Group 2 – polyps in pairs or whorls**

1a. Branchlets depart branch in two directions, uniplanar (*T. coronata*, colony 13 cm): 2

1b. Branchlets depart in at least three directions (*T. hilgendorfi*, branchlets 7 cm long): 6

2a. Branching dichotomous: 3
2b. Branching pinnate: 5

3a. Polyp head conical or rounded, polyps depart branchlet at 45° (see 4a): 4
3b. Polyps distally flared, depart branchlet at 90°. *T. coronata* (also see 1a and figs. 34, 35)

4a. No keel on inner surface of marginals, polyp head conical. *T. parva*, figs. 40a,b
4b. Keel on inner surface of marginals, rounded polyps. *T. biserialis*

5a. Branchlets alternately pinnate, paired distally flared polyps (rarely whorls of three), departing at 70–80°, elongated marginals. *T. tydemanii*
5b. Branching opposite pinnate, paired clavate polyps depart at 90°, modestly pointed marginals. *T. moseleyi*, figs. 30, 31

6a. Branchlets depart in 3 directions (see i), although can appear pinnate, long flexible branchlets, paired polyps depart at 90° (see below). *T. laxa*, figs. 32, 33
6b. True bottlebrush, branchlets departing in all directions, polyps in pairs’ whorls of 3, depart branchlet at 45–60°: 7

7a. Polyps clavate. *T. Grasshoffii*
7b. Polyps distally flared. *T. hilgendorfi*
Table 2.3 Tabular key for the species of *Thouarella*

<table>
<thead>
<tr>
<th>GROUP 1</th>
<th>Isolated polyps</th>
<th>Polyp arrangement &amp; distribution (polyps/cm)</th>
<th>Polyp angle from branchlet</th>
<th>Polyp shape</th>
<th>Polyp length</th>
<th>No. scales in LAB</th>
<th>Opercular keeled?</th>
<th>Opercular shape</th>
<th>Marginal keel</th>
<th>Marginal shape</th>
<th>Unique characters</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>T. bipinnata</strong></td>
<td>Uniplanar, pinnate to bipinnate</td>
<td>Isolated, 10–13</td>
<td>80–90°</td>
<td>Modestly clavate</td>
<td>2.4</td>
<td>3–5</td>
<td>Yes, multiple ridges</td>
<td>Lanceolate</td>
<td>Lateral extensions</td>
<td>Rounded base, pointed distally</td>
<td>Clavate, large polyps, with tall oper.</td>
</tr>
<tr>
<td><strong>T. clavata</strong></td>
<td>BB/ bilateral appearance</td>
<td>Isolated</td>
<td>45–60°</td>
<td>Distally flared</td>
<td>1.5–2</td>
<td>5–6</td>
<td>Yes, single, large</td>
<td>Lanceolate to triangular</td>
<td>Ridges lateral to keel</td>
<td>Modest distal point</td>
<td>Very similar to <em>T. brucei</em>, require more specimens</td>
</tr>
<tr>
<td><strong>T. koellikeri</strong></td>
<td>Bushy, BB/ bilateral appearance</td>
<td>Isolated, 12–15</td>
<td>45–60°</td>
<td>Clavate, tall, coned oper.</td>
<td>1.6–2.5</td>
<td>7–10</td>
<td>Yes, single, large</td>
<td>Arrow-headed</td>
<td>Strong with small lateral projections</td>
<td>Short triangle, wide keel</td>
<td>Rounded submarg. with teeth</td>
</tr>
<tr>
<td><strong>T. affinis</strong></td>
<td>BB/ bilateral appearance</td>
<td>Isolated, 7–9</td>
<td>45–60°</td>
<td>Clavate, rare modest distally flared polyp</td>
<td>1.1–2.1</td>
<td>6–7</td>
<td>Yes, ridged</td>
<td>Tongue-shaped</td>
<td>Keeled abaxial, rest with ridges</td>
<td>Widely triangular to diamond</td>
<td>Clavate/rare modest distally flared polyp, diamond marg., rounded operculars</td>
</tr>
<tr>
<td><strong>T. viridis</strong></td>
<td>Bushy, BB/ bilateral appearance</td>
<td>Isolated, 14–15</td>
<td>45–60°</td>
<td>Clavate, tall cone</td>
<td>2.1–2.5</td>
<td>6–7</td>
<td>Yes, single, large</td>
<td>Lanceolate</td>
<td>Multi-channel, adjacent ridges</td>
<td>Widely triangular, pointed</td>
<td>Often green when alive</td>
</tr>
<tr>
<td><strong>T. brucei</strong></td>
<td>Bushy, BB / bilateral</td>
<td>Isolated, 9–12</td>
<td>40–45°</td>
<td>Distally flared</td>
<td>1.5–2.3</td>
<td>4–5</td>
<td>Yes, single, large</td>
<td>Triangular</td>
<td>Channelled, smooth lateral to keel</td>
<td>Triangular</td>
<td>4–5 ab. scales, operculars keeled &amp; triangular</td>
</tr>
<tr>
<td><strong>T. andeep</strong></td>
<td>Bushy, BB/ bilateral appearance</td>
<td>Isolated, 10–11</td>
<td>80–90°</td>
<td>Distally flared, tall conical oper.</td>
<td>1.9–3.4</td>
<td>4–5</td>
<td>Yes, large operculars ridged</td>
<td>Tongue-shaped</td>
<td>Strong, channelled</td>
<td>Wide triangle</td>
<td>Large polyp, tall operculum</td>
</tr>
<tr>
<td><strong>T. brevispinosa</strong></td>
<td>BB, 3 directions</td>
<td>Isolated, 7–11</td>
<td>45°</td>
<td>Distally flared, operculum lower than marginals</td>
<td>2.5–3</td>
<td>6–8</td>
<td>Yes</td>
<td>Isosceles triangle</td>
<td>Channelled keel</td>
<td>Tall triangle</td>
<td>Similar to <em>T. brucei</em>, more scales in LAB</td>
</tr>
<tr>
<td><strong>T. striata</strong></td>
<td>BB, colony flabellate</td>
<td>Isolated, 14–16</td>
<td>60–80°</td>
<td>Distally flared</td>
<td>1.5–2</td>
<td>4–6</td>
<td>Yes</td>
<td>Isosceles triangle</td>
<td>Wide, flat, channelled</td>
<td>Tall triangle</td>
<td>Striated outer scale surface</td>
</tr>
<tr>
<td><strong>T. antarctica</strong></td>
<td>BB</td>
<td>Isolated, 25–60–80°</td>
<td></td>
<td>Modest</td>
<td>1.6–2</td>
<td>5–7</td>
<td>Yes –</td>
<td>Thin</td>
<td>Wide lateral</td>
<td>Tall triangle</td>
<td>Tight polyp</td>
</tr>
</tbody>
</table>
### Revision of *Thouarella*

<table>
<thead>
<tr>
<th>Species</th>
<th>Colony shape</th>
<th>Polyp arrangement &amp; distribution</th>
<th>Polyp angle from branchlet</th>
<th>Polyp shape</th>
<th>Polyp length</th>
<th>No. scales in LAB</th>
<th>Opercular keeled?</th>
<th>Opercular shape</th>
<th>Marginal keel</th>
<th>Unique character</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>T. chilensis</em></td>
<td>BB</td>
<td>Isolated, 11–23</td>
<td>45–85°</td>
<td>Distal flare, delicate scales</td>
<td>2.3</td>
<td>Single, large</td>
<td>Lanceolate projections, visible from outer surface view</td>
<td>Triangle to arrow-headed</td>
<td>Lateral projections,</td>
<td>Triangular</td>
</tr>
<tr>
<td><em>T. crenelata</em></td>
<td>BB</td>
<td>Isolated</td>
<td>60–90°</td>
<td>Modest distal flare, boxy Clavate</td>
<td>2</td>
<td>6–10</td>
<td>Multi-ridged, lateral ridges</td>
<td>lanceolate to arrow-headed</td>
<td>Triangular</td>
<td>Oval</td>
</tr>
<tr>
<td><em>T. parachilensis</em></td>
<td>BB</td>
<td>Isolated, 18–48 at tips</td>
<td>60–90°</td>
<td>Clavate, globular</td>
<td>2.4–2.8</td>
<td>8–15, 11</td>
<td>Simple with adjacent ridges</td>
<td>Simple with pointed distal edge</td>
<td>Oval to round</td>
<td>Spinose keeled marg.</td>
</tr>
<tr>
<td><em>T. variabilis</em></td>
<td>BB</td>
<td>Isolated, 5–10</td>
<td>60°</td>
<td>Distally flared</td>
<td>1.5–1.85</td>
<td>4–5</td>
<td>Isosceles triangles</td>
<td>Tongue, rounded tip</td>
<td>Spinose, channelled</td>
<td>Tall triangle, nearly spinose Tear-shaped</td>
</tr>
<tr>
<td><em>T. hicksoni</em></td>
<td>BB</td>
<td>Isolated, 16–22</td>
<td>30° to appressed</td>
<td>Operculum pointed, weakly flared</td>
<td>1–1.25</td>
<td>4–5</td>
<td>Yes</td>
<td>Mongrel tip</td>
<td>Triangle to arrow-shaped</td>
<td>Short triangle to tear-shaped</td>
</tr>
<tr>
<td><em>T. pendulina</em></td>
<td>BB</td>
<td>Isolated, 27–41</td>
<td>Appressed</td>
<td>Modestly clavate, pointed operculum Conical operculum</td>
<td>0.9–1</td>
<td>4–5</td>
<td>Yes</td>
<td>Simple keel</td>
<td>Tongue, rounded tip</td>
<td>Simple to single channelled</td>
</tr>
<tr>
<td><em>T. minuta</em></td>
<td>BB</td>
<td>Isolated, 11–18</td>
<td>Appressed</td>
<td>Conical operculum</td>
<td>0.7–1</td>
<td>3–4</td>
<td>Yes</td>
<td>Tongue, rounded tip</td>
<td>Simple to single channelled</td>
<td>Round to rhomboid Very small polyps</td>
</tr>
</tbody>
</table>

**GROUP 2**

<table>
<thead>
<tr>
<th>Species</th>
<th>Colony shape</th>
<th>Polyp arrangement &amp; distribution</th>
<th>Polyp angle from branchlet</th>
<th>Polyp shape</th>
<th>Polyp length</th>
<th>No. scales in LAB</th>
<th>Opercular keeled?</th>
<th>Opercular shape</th>
<th>Marginal keel</th>
<th>Unique character</th>
</tr>
</thead>
<tbody>
<tr>
<td>§ <em>T. hilgendorfi</em></td>
<td>Uniplanar flabellate colony, irregular dichotomous branching, BB branches</td>
<td>Pairs/whorls of 3,</td>
<td>45°</td>
<td>Distally flared</td>
<td>1–1.4</td>
<td>5–6</td>
<td>Yes</td>
<td>Lanceolate Simple Tall triangle, spinose Branches BB, shorter, sturdier branchlets</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>T. grasshoffi</em></td>
<td>Colony taller than</td>
<td>Paired/rare whorls of 3,</td>
<td>45–60°</td>
<td>Pointed conical</td>
<td>max. 1.3</td>
<td>5</td>
<td>Y</td>
<td>Lanceolate Simple, smooth adjacent to keels Broad base, pointed tear- True BB</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>Description</td>
<td>Polyp Form</td>
<td>Polyp Size</td>
<td>Ridges</td>
<td>Polyp Shape of Branchlet Tips</td>
<td>Branchlet Shape</td>
<td>Notes</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-----------------</td>
<td>------------------------------------------------------</td>
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<td></td>
</tr>
<tr>
<td><em>T. laxa</em></td>
<td>3 directions, appears uniplanar pinnate</td>
<td>Paired/ whorls of 3, 5–7</td>
<td>45°–60°</td>
<td>1.2–1.5</td>
<td>Distally flared</td>
<td>Triangular, appear tongue-shaped</td>
<td>Simple, single channelled</td>
<td>Branches BB, flexible, longer branchlets</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>T. moseleyi</em></td>
<td>Uniplanar pinnate</td>
<td>Paired</td>
<td>90°</td>
<td>1.5</td>
<td>Clavate with tall conical oper.</td>
<td>Thinn to wide lanceolate</td>
<td>Keeled abaxial marginal, remainder ridged</td>
<td>Polyps clavate, inclined 90°</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>T. tydemani</em></td>
<td>Uniplanar, alternately pinnate</td>
<td>Paired/, rare whorls of 3, 6/cm</td>
<td>70–80°</td>
<td>~1.5</td>
<td>Distally flared</td>
<td>Tall, almost spinose</td>
<td>Tall, almost spinose</td>
<td>Polyps clavate, inclined 90°</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>T. parva</em></td>
<td>Uniplanar, dichotomous</td>
<td>Paired, 6/cm</td>
<td>45°</td>
<td>~1</td>
<td>Conical</td>
<td>Thin to wide lanceolate</td>
<td>Yes?</td>
<td>Irregularly triangular?</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>T. coronata</em></td>
<td>Uniplanar, dichotomous</td>
<td>Paired/ rare whorls of 3, 5–7</td>
<td>90°</td>
<td>1.9–2.1</td>
<td>Distally flared</td>
<td>Triangular, with rounded distal edge</td>
<td>Small, simple</td>
<td>Polyps distally flared, inclined 90°</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>T. biserialis</em></td>
<td>Uniplanar, dichotomous</td>
<td>Paired/ rare whorls of 3</td>
<td>45°</td>
<td>1.2–1.5</td>
<td>Cylindrical conical</td>
<td>Lanceolate to widely-triangular</td>
<td>Triangular</td>
<td>Biserial polyp placement</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Type species of genus
§ Type species of Group
LAB – longitudinal abaxial row

Abbreviations: sm. – small, oper. – operculum, marg. – marginal, submarg. – submarginal, ab. – abaxial, BB – bottlebrush colony morphology (3 or more directions of branching). Tip refers to branchlet tips.
2.9 Discussion

2.9.1 Morphological characters

Kükenthal created his last key for *Thouarella* species in 1924. In it, the number of abaxial scales and whorls of polyps per cm is used to differentiate between the many species. I believe that these characters are far from fixed and can vary substantially within a colony making Kükenthal’s key unreliable as he did not allow for ranges within these characters. That said, the number of polyps per cm is still important in species identification with the consideration that this value can be modestly variable.

Colony formation can be altered by the presence of annelid commensals that induce branchlets to curve and form tube-like tunnels along axes (Brito 1993); this must be considered when looking at specimens. However, by examining where branchlets depart the branch, the arrangement can be recognised. Colonies of *Thouarella* are a range of forms (pinnate, dichotomous, bottlebrush, bottlebrush but appearing planar), which in octocorals is relatively unusual to have within one genera (Bayer, 1956; 1981). Polyp similarity (usually distally flared with 8 operculars and 8 keeled marginals) brings the species of *Thouarella* together.

The range in number of abaxial scales given in *Thouarella* species descriptions is necessary because as polyps enlarge as they brood and coenenchymal scales (at polyp base, colonial tissue between polyps) appear to become part of the polyp body. Without this consideration, brooding specimens could be regularly misconstrued as different or new species. I suggest that many polyps of a colony, from the tip to the base of branchlets and from the tip to the base of the colony, are examined in species identification as variability within a colony is common.

Generally, polyp placement (isolated, paired, whorled), the number of abaxial scales (which usually has a small range), the number of polyps per cm, and the colony form are the most important characters in identifying *Thouarella* species as they are relatively fixed and thus reliable. Beyond this, marginal scale shape, including the elongation of marginal distal edges, and average polyp size are all informative.
A character that is considered less important within this study is the outer surface texture of sclerites. Around commensal tubes, polyps tend to have thicker, calcified sclerites (Brito 1993), as is commonly noted in other primnoids (Bayer 1964; Eckelbarger et al. 2005), so making taxonomic use of this character alone is ill-advised.

2.9.2 Did Thouarella originate in the Antarctic?
Many authors have discussed primnoid character evolution (Kinoshita 1908a; Versluys 1906; Cairns & Bayer 2009). Both Versluys (1906) and Kinoshita (1908a) thought it advantageous for there to be fewer scales on polyps, that were of a larger size and this holds true in recent primnoid morphological studies where, for instance, Primnoeides, with its simple opercular and numerous small body-wall scales not arranged in rows, is considered basal to all other primnoid genera (see Cairns 2006; Cairns & Bayer 2009). Many genera compared to Thouarella in this revision are unsurprisingly from within the same grouping in the phylogenetic analysis of morphological characters undertaken in Cairns and Bayer (2009). Most genera within this grouping occur in Antarctica, where the earliest clade within the Primnoidae, according to morphological analysis, also occurs, suggesting Antarctica could be the origin of the family (Cairns & Bayer 2009). Antarctica cooled around c. 42 MYA in the Eocene with a permanent ice sheet established from around 34 MYA (Tripati et al., 2005). These low temperatures and the tectonic drift of the Australian continent created an isolation that has made Antarctica’s present-day marine biota the world’s most distinctive and one of three centres of species origin globally (Briggs, 2003). Prehistoric dispersals from Antarctica to other ocean basins and trenches have been proposed for other invertebrates e.g. holothurians (Gebruk, 1990, noted in Briggs 2003) and cephalopods (Strugnell et al., 2008). However, molecular phylogenetic analyses are required to confirm Primnoidae origins. It is noteworthy that population fragmentation and isolation in times of glacial maxima could have been important mechanisms for allopatric speciation in Antarctic fauna, increasing taxonomic diversity (Clarke and Crame, 1989; 2010; Rogers, 2007). Seventeen species of Thouarella are found in the Antarctic, sub-Antarctic and south Atlantic waters whereas just 9 are known from the rest of the world (3 from Japan, 1 from Asia to the Pacific, another from Asia to East Africa, one each from the North Atlantic, Indonesia, Hawai‘i and South Africa). With high numbers of species from high
latitudes of the southern hemisphere one could speculate that this region is the centre for radiation of *Thouarella*, however, as already mentioned, genetic studies are required to clarify this (see Chapter 3).

Interestingly, all non-sub-Antarctic/Antarctic/southern Atlantic species, with the exception of *T. hicksoni* (from South Africa), fall within Group 2 (species with polyps in pairs/whorls). Polyps of Group 2 species look very similar, with species differing mostly in branching morphology (this is a tentative comment on branching morphology as such small fragments of some holotypes remain). Group 2 species, as already mentioned, occur from East Africa to Hawaii, crossing the Indian and Pacific Oceans. It remains to be seen how important branching structure is in the evolution of *Thouarella*. Within primnoids it does not appear to be very informative in determining phylogeny (Cairns & Bayer 2009).

All species descriptions are based on the holotype unless otherwise stated. Species are ordered first by group and then according to chronological precedence. All images of sclerites are of the holotypes or syntypes unless otherwise noted.
CHAPTER TWO

2.10 Systematic Account

Subclass Octocorallia
Order Alcyonacea
Suborder Calcaxonia Grasshoff, 1999
Family Primnoidae Milne-Edwards, 1857
Thouarella Gray, 1870

*Primnoa* Valenciennes, 1846: pl.12, figs. 2, 2a (only images).— Milne-Edwards, 1857: 140.—Gray, 1857: 286; 1859: 483.—Kölliker, 1865: 135


*Rhopalonella* Roule, 1908: 2–3, pl.1, figs. 5–8

*Thouarella* (Diplocalyptra) Kinoshita, 1908b: 454, 457 (key to subgenus), pl.17, fig. 2 (in Japanese, English translation at USNM); 1908c: 517–519 (in Japanese, English translation at USNM); 1908d: 52 (key to subgenus, in German)

*Thouarella* (Epithouarella) Kükenthal, 1915: 150–151 (key to subgenus and species); 1919: 435 (key to subgenus and species); 1924: 299 (key to subgenus and species).—Bayer, 1956: F220


*Thouarella* (Parathouarella) Kükenthal, 1915: 150 (key to species); 1919: 425–426 (key to species); 1924: 296–297 (key to subgenus and species)


1 Calcaxonia are not monophyletic in recent phylogenetic studies (McFadden et al. 2006) however a taxonomic revision has not been completed.
2.10.1 Definition

Colony consists of a main stem, generally simple with rare divisions. Branching either pinnate, dichotomous, or in a bottlebrush manner where it is branched in at least three directions. Polyps isolated, paired, or in whorls, generally upwardly inclined at 45–90° from branchlet. Polyp heads wider than base and completely protected by 5–15 (generally 5–8) longitudinal rows of scales. Adaxial body-wall scales often reduced in size and number.

Well-developed, conical operculum consisting of eight operculars; on rare occasions accessory operculars found beneath operculum. Operculum surrounded by eight marginals, often in two alternating rings of four as operculum circumference is not large enough to accommodate eight adjacent marginals. Marginals keeled on inner surface; keels simple, ornate, channelled, or complex. Marginals often fold over operculum, with the keel fitting into the concave outer opercular surface. Opercular scales lanceolate, arrowhead-shaped or tongue-shaped, often with a keel.

2.10.2 Distribution

A wide global distribution: South Africa, Chile, western Atlantic from Burdwood Bank to northern Florida, Japan, Aleutian Islands, Australia, Tasman Sea, New Zealand, especially common around Antarctica/sub-Antarctic. Found from 60–2100 m depth.

2.10.3 Comparisons

*Thouarella* was placed close to three genera within the most recent phylogenetic morphologic analysis of Primnoidae (Cairns & Bayer 2009): *Pyrogorgia* Cairns and Bayer, 2009, *Amphilaphis* Studer and Wright, in Studer, 1887 and *Convexella* Bayer, 1996. The bottlebrush form of *Thouarella* can also be easily mistaken for several other genera with similar branching morphologies.

The only species of *Thouarella* that has the distinctive “radiating spinose ridges” (Cairns & Bayer 2009) of *Pyrogorgia* is *T. striata*, but the polyps of the latter are isolated and the colonies bushy. This is very unlike the uniplanar, dichotomous colony shape and polyp whorls of *Pyrogorgia*. 
According to Cairns and Bayer (2009) *Amphilaphis* differs from *Thouarella* in having eight ‘complete’ rows of body-wall scales, whereas *Thouarella* has 6 with two reduced rows adaxially. The reduction is a particularly difficult character to differentiate and a revision of *Amphilaphis* is required to confirm this character’s significance. *Amphilaphis* species are not considered within this revision.

Species of *Convexella* may be similar to some species of *Thouarella*, but the marginal scales of the former have a smooth, distal inner surface whereas those of the latter have a keel.

*Thouarella* is most closely related, in terms of polyp morphology, to *Plumarella* and *Amphilaphis*. *Plumarella* is uniplanar, often plumose; only six species of *Thouarella* are truly uniplanar, although some bottlebrush arrangements are compressed giving a uniplanar appearance (e.g. *T. brucei*). *Plumarella* polyps are usually alternately biserial (there are a few species with isolated polyps). Within *Thouarella* only *T. bipinnata* Cairns, 2006, *T. minuta* and *T. koellikeri* have polyps that are approximately biserial. *Plumarella* marginals are fixed i.e. do not fold over operculars (although this is a difficult character to explicate, especially in species with long-spined marginals e.g. *T. variabilis*) whereas *Thouarella* often have longitudinal indentations in operculars that marginal keels fit into, indicating marginal movement. *Plumarella* has 8 rows of body-wall scales; the number of scales in a row can be reduced adaxially, very similar to *Thouarella*. *Plumarella* polyps are often 90° to branchlet, whereas those of *Thouarella* are mostly 45–80°. All of these characters are not exclusive to either *Thouarella* or *Plumarella*. The only diagnostic character to separate the two genera is presence or absence of keeled marginals; a keeled marginal is considered to signify *Thouarella*, unkeeled *Plumarella* (Cairns, 2010).

As already mentioned, there are a number of genera with bottlebrush colonies that are often mistaken for *Thouarella*. The similarities and differences between these genera and *Thouarella* are listed here:

Colonies of *Dasystenella* Versluys, 1906 have a bottlebrush formation and are often misidentified as *Thouarella*. *Dasystenella* primarily differs from *Thouarella* in having just 5 marginals, compared to 8 in the latter. Only one species of *Dasystenella* has
be described (*D. acanthina*) yet much variation was observed between amongst specimens seen throughout this study. *Dasystenella* requires further investigation as there is likely more than one species (Cairns 2006).

Although it has a bottlebrush colony shape, the newly described genus *Tauroprimnoa* Zapata-Guadiola & López-González, 2010a differs from *Thouarella* in having only 4 marginals.

The recently described bottlebrush genera *Digitogorgia* Zapata-Guardiola & López-González, 2010c has marginals with a smooth inner surface and numerous irregular longitudinal rows of body-wall sclerites and is thus distinct from *Thouarella*.

*Fannyella (Scyphogorgia)* Cairns and Bayer, 2009 is also a bottlebrush form and separated from *Fannyella (Cyanthogorgia)* Cairns and Bayer, 2009 only by branching morphology (the latter being dichotomously branched, verging on pinnate). *Fannyella* Gray, 1872 has ascus-type body-wall scales that have a distinct boundary separating their exposed distal area from the covered proximal area, while *Thouarella* has an even, unsectioned, non-ascus outer sclerite surface. I have not followed the example of Cairns and Bayer (2009) by spilting *Thouarella* based on branching pattern.

Colonies of *Parastenella* Versluys, 1906 are mostly uniplanar, however, they can be bushy with isolated, paired or whorled polyps and could be easily mistaken for *Thouarella*. The most distinctive difference between these two genera is the morphology of the distal border of the marginal scales; *Parastenella* have a fluted hollow structure whereas those of *Thouarella* are unfluted.

### 2.11 Species Group 1 – isolated polyps

#### 2.12 Thouarella antarctica (Valenciennes, 1846)

**Thouarella antarctica** Gray, 1870: 69.—Wright & Studer, 1889: 65–66, pl. 21
  fig.1.—Thomson & Henderson, 1906: 38 (list).—Gravier, 1914: 48–56, pl. 7
  figs. 31–34, pl.10 figs. 52–55 (samples not seen).—Molander, 1929: 75
  (samples not seen)

Not **Thouarella antarctica**: Hickson, 1907: 9–10, pl.2, figs. 19, 24 (= unknown)

**Thouarella (Parathouarella) antarctica**: Kükenthal, 1915: 150 (key); 1919: 433–435;
  1924: 299

Not **Thouarella (Euthouarella) antarctica**: Broch, 1965: 24–26, pl. 2, figs. 5–7, (= **T. pendulina**)

Not **Thouarella (Thouarella) antarctica**: Cairns & Bayer, 2009: 27 (listed), 33–34, fig. 6, g–l (= **T. chilensis**)

**Material examined**: holotype, MNHN, Oct.0000–208, 1836–1839 Venus expedition, Malouine Islands, Falkland Islands, depth unknown; ZMH, R/V *W. Herwig*, sta. 270, south of Falkland Islands, SW Atlantic, 53°00′S, 60°00′W, 375 m, 9 Feb 1971; ZMH, R/V *W. Herwig*, sta. 256, Burdwood Bank, SW Atlantic, 53°56′S, 63°40′W, 400 m, 6 Feb 1971; ZMH, R/V *W. Herwig*, sta. 311, off Patagonia, SW Atlantic, 46°54′S, 60°28′W, 480 m, 18 Feb 1971; ZMH, R/V *W. Herwig*, sta. 361, west of Falkland Islands, SW Atlantic, 51°55′S, 61°50′W, 200 m, 12 Jul 1966; NHM89.5.27.43, H.M.S. *Challenger*, sta. 148A, off Crozet Island, 46°53′S, 51°52′E, 1005 m, 3 Jan 1874; USNM 97965, R/V *Hero*, cruise 715, sta. 870, 54°34′S, 64°W, 84 m, 24 Oct 1971.

**Thouarella antarctica** is the type species of **Thouarella**. Unfortunately, the holotype, held in MNHN, is in very poor condition. F.M. Bayer had studied the holotype and identified one NMNH catalogued specimen as **T. antarctica** (USNM 97966). Having studied the holotype I disagree with Cairns and Bayer (2009) that USNM 97966 is **T. antarctica**; this is in fact **T. chilensis** as it has more scales in the longitudinal row than is usual for **T. antarctica**, wider and thicker operculars and marginals that are not smooth edged. Some additional specimens of **T. antarctica** were found at SMF (belonging to ZMH), listed above. Description of sclerites and images herein are from three holotype polyps, no SEM images of whole polyps were taken as the specimen was too fragile and thus only a partial opercular view was possible (Figure 2.4e). Colony and polyp description from specimens listed above.
2.12.1 *Description*

Colonies rarely branched. Branchlets depart main stem in up to 5 directions from all sides of branches in a typical bottlebrush arrangement. Branchlets are generally simple, however some secondary branching occurs. Axis yellow, tough, horny, can be brittle towards apex. Holdfast calcareous.

Polyps isolated, 1.6–2.3 mm long (average 2 mm), modestly flared distally, projecting from all sides of the branchlet at 60–80°, tightly placed at 25–30 polyps per cm (such that, in lateral view, most polyps overlap), more clustered at branchlet tips, and some polyps occur on main stem. Five to seven scales in each abaxial row (Figure 2.4c), 5–6 scales laterally; eight longitudinal rows reducing to 5 at polyp base.

There are two circles of four operculars; one upper, one lower (Figure 2.4e), and they can join to form a full cone although sometimes there are gaps. Operculars are triangular to lanceolate (Figure 2.5a-f), 415–820 µm tall (average 650 µm), 200–480 µm wide (330 average µm), H:W of 1.7–2.1 (average 2) and have a longitudinally concave outer surface with granules radially arranged from a proximal centre, fading towards the distal edges. The inner opercular surface has a large complex multi-keel (with several lateral projections), and the distal half has dense, small tubercles in the centre and serrated ridges towards the distal edge). Lateral and distal edge finely serrate; proximal edge coarsely lobate.

Marginals triangular (Figure 2.5g–i), broader than operculars, 645–870 µm high (average 760 µm), 390–750 µm wide (average of 600 µm), with a lower average H:W than opercular, 1.3 (range from 1–1.7). Inner surface bears a complex multi-keel with lateral extensions (Figure 2.5j) which can project beyond the scale edges, and thus be visible from outer surface; tubercles cover inner surface proximally reaching keel base. Outer surface with granules radially arranged from central proximal area; tubercles rarely occur along basal sclerite edge. Distal area of keel and lateral edge of marginal are finely serrated; proximal edges coarsely lobate and covered with tubercles.

Submarginals circular to widely elliptical in shape (Figure 2.5k-n), 430–650 µm tall (average 760 µm), 370–750 µm wide (average 600 µm), H:W 1–1.7 (average 1.3) and
CHAPTER TWO

tend to have a pointed distal edge and a small median distal keel (Figure 2.5m) or teeth on the inner surface. The scales in the row beneath the submarginals is also sometimes modified in the same manner.

Body-wall scales (Figure 2.5o-v) circular to elliptical, 380–460 µm tall, 440–530 µm wide (average 420 and 500 µm respectively), wider than tall, average H:W of 0.85 (range from 0.7–1), with small and sometimes strong ridges on distal edge of inner surface (Figure 2.5o,t). Sometimes abaxial body-wall scale at polyp base is very wide (Figure 5o). Inner surface densely covered in tubercules, outer surface sparsely covered with granules sometimes arranged radially from central area.

Coenenchymal scales (Figure 2.5w) small, 160–330 µm tall, 190–380 µm wide (average of 220 and 300 µm respectively), H:W 0.4–1 (average 0.75), irregularly circular to oval with a regular distribution of peaked granules on the outer surface, and a dense arrangement of tubercules on the inner surface. All above sclerites have an irregularly coarse, lobate proximal edge and a finely serrate distal edge.

2.12.2 Distribution
Known from 500 km north of the Falkland Islands to the southern tip of South America, 200–480 m depth. An unseen sample has been described from Crozet Island (1005 m, Wright & Studer 1889), so range perhaps extends further east.

2.12.3 Remarks
The holotype is from the Falkland Islands and consists of one branch broken off mid-stem (Figure 2.4b). The original description of *T. antarctica* (as *Primnoa antarctica*) by Valenciennes had a beautiful illustration of the colony and polyps (see Figure 2.1). Through a microscope, operculars do appear elongated and the illustration reflects this, although exaggerated; the image is otherwise a good likeness. Descriptions thereafter rely heavily upon this drawing as well as Milne-Edwards’ (1857) original, short description. Kölliker (1865) did give further details of body-wall scale dimensions (still under the name *P. antarctica*) but Gray’s (1870, pp. 45) redescription as *T. antarctica* only gives a general description: “Coral simple, with long, simple filiform branches, spreading on all side of the stem. Bark formed in large imbricated scales. Polyp-cells smooth, bell-shaped, scattered on upperside of branches, covered with four or five series of imbricate scales.”
Revision of Thouarella

Wright and Studer’s (1889) description of Thouarella, alongside several new species, gives the first moderately detailed definition of the genus and more information about T. antarctica. Kükenthal (1915, 1919) correctly described T. antarctica as having marginal scales with lateral projections off the keel, and this remains one of this species defining characteristics. In 1924 Kükenthal listed T. antarctica as having 9 or 10 scales in the abaxial row but I believe this is a mistake. Kükenthal listed 4–6 abaxial scales in both his 1915 and 1919 keys.

Samples NHM1962.7.20.180 (dated 1913, Hickson) and NHM1962.7.20.179 (marked sample 2) are not T. antarctica.

The bottlebrush colony form, distally flared polyps and ornately keeled marginals make T. antarctica just as representative of Thouarella as any found within Group 1. Essentially, T. antarctica is the “type species of the group”.

2.12.4 Comparisons
Several species have a similar number of longitudinal abaxial row scales as T. antarctica and are thus compared here:

As previously mentioned the polyps of T. antarctica are very similar to those of T. koellikeri, T. chilensis and T. viridis, which are distally flared (although in T. antarctica the polyps could be said to be more splayed than the others) with outwardly curved body-wall scales and marginals with a complex keel.

Thouarella koellikeri generally has longer polyps than T. antarctica due to a greater number of body-wall scales in the abaxial row (7-10 as against 5-7). Branchlets of the former leave the stem in mainly two directions, whereas T. antarctica has a bottlebrush form, and the operculars have simple keels whereas the former have several small ridges/stripations adjacent to the keel.

The opercular cone of polyps of T. viridis is more closely fitted than that of T. antarctica; the former has shorter marginals that are less elongated with wide lateral extensions of the keel rarely visible when viewed from the abaxial side of the polyp,
something that is the norm in *T. antarctica*. Also operculars of *T. viridis* have a larger, pronounced keel than those of *T. antarctica*, which are complex and spread laterally.

The densely placed polyps of *T. chilensis*, the true bottlebrush morphology and modest marginals make it easily mistaken for *T. antarctica*. However, polyps of *T. chilensis* have on average more scales in the abaxial row and marginals with keels that are not as wide as *T. antarctica* (and thus not often visible from the abaxial side). Also, the polyps of *T. chilensis* are wider and tend to be longer. Nonetheless, these species are very similar and differences between them should be confirmed after viewing more specimens.

*Thouarella variabilis* differs from *T. antarctica* in having longer, near-spinose marginals, polyps that are more flared, and smaller, thinner, lanceolate operculars.

*Thouarella brevispinosa* polyps are generally longer than those of *T. antarctica*, have more scales in the abaxial row, with larger marginals that have a longer, simpler keel, lacking the lateral extensions common in *T. antarctica*.

*Thouarella brucei* and *T. antarctica* polyps are similarly shaped, but marginal keels of the former are simpler, inner and outer opercular surfaces tend to be smoother, the abaxial row has fewer scales, and colonies can appear bilateral rather than the bottlebrush form of *T. antarctica*.

*Thouarella striata* has distinctive striations on the marginal scale inner surface that are absent in *T. antarctica*. In addition, marginals have less complex keels (although not hugely), that aren’t visible from an abaxial side view, and generally fewer scales in the abaxial row.

*Thouarella clavata* and *T. bipinnata* have similarly sized polyps as *T. antarctica* (the polyps of *T. bipinnata* are only slightly larger), however, polyps of *T. bipinnata* are clavate (*T. antarctica* has more splayed polyps) and its colony uniplanar (whereas *T. antarctica* is bottlebrush). *Thouarella clavata* is bottlebrush (although branchlets sometimes bend creating a bilateral appearance) and has a similar number of abaxial
scales as *T. antarctica* but the polyps are less densely arranged and branchlets longer, thinner and less rigid than those of *T. antarctica*.

*Thouarella minuta* polyps are under 1 mm long making them much smaller than *T. antarctica* polyps.

### 2.13 Thouarella variabilis Wright and Studer, 1889

Figures 2.6, 2.7

*Thouarella variabilis* var. a typical Wright & Studer, 1889: 68–69, pl. 21, fig. 1 (incorrectly listed as pl. 14, figs. 1–2).—Thomson & Henderson, 1906: 40 (list)

*Thouarella variabilis* var. *c* gracilis Wright & Studer, 1889: 70.—Thomson & Henderson, 1906: 40 (list)

*Thouarella variabilis*: Menneking, 1905: 260–262, pl. 9, figs. 9, 10, 21, 22 (samples not seen).—Versluys, 1906: 37–38.—Gravier, 1914: 56–61, pl. 1 fig. 6, pl. 3 fig. 13–14 (samples not seen).—Kükenthal, 1915: 150 (key).—Molander, 1929: 74–5 (samples not seen).—Broch, 1965: 30–31, pl. 6, figs. 17–19.—Brito, Tyler & Clarke, 1997: 63–69

Not *Thouarella variabilis*: Thomson, 1927: 33, pl. 1 fig. 10, (=unknown)

*Thouarella (Parathouarella) variabilis*: Kükenthal, 1919: 428, fig. 202 (in text); 1924: 297 (key).—Thomson & Rennet, 1931: 27–30, pl. 7, fig. 3, pl. 9, figs. 4–5 (samples not seen)

*Thouarella aff. variabilis*: Kükenthal, 1912: 305–306, figs. 9–12 (in text), pl. 20, fig. 2

*Thouarella (Thouarella) variabilis typica*: Cairns & Bayer, 2009: 27 (listed)

*Material examined*: syntype of var. a typical, NHM 89.5.27.56, H.M.S. *Challenger*, sta. 145, SE of Prince Edward Island, 46°43′S, 38°43′30″E, 256 m, 27 Dec 1873, 3.5 cm fragment; *T. variabilis* var. *gracilis*, NHM 1889.5.27.55–56, sta. 145, SE of Prince Edward Island, 46°43′S, 38°4′30″E, 256 m, 27 Dec 1873, 3.5 cm fragment; USNM 76897, R/V *Eltanin*, Antipodes Island, New Zealand, 49°51′S, 178°35′E, 2010–2100 m, 26 Feb 1968, 1 colony; USNM 98226, R/V *Hero*, cruise 731, sta. 1842, west of Renaud Island, Biscoe Islands, Antarctic Peninsula, 65°30′S, 67°31′W, 180 m, 24 Feb
1973; USNM 1130283, R/V Glacier, cruise 1, sta. 5, 76˚00’S, 55˚00’W, 457 m, 9 Feb 1968, 2 colonies.

2.13.1 Description of var. a typical
Main stem simple. Wright and Studer (1889: pl. 21, fig. 1) recorded a specimen 300 mm tall. Axis brown-yellow, firm but brittle towards base, more flexible distally. Branchlets leave main stem in three to four directions, fourth branch often in line with first in spiral formation. Branchlets occur at intervals of 1.5–2 mm, at near right angle to main stem, 50–150 mm long, thin, flexible and frequently branched two or three times (usually dividing close to stem, in the proximal one third).

Wide, distally flared polyps (Figure 2.6b,d–f) isolated on branchlets and stem, upwardly inclined at 60˚, arranged in irregular short spirals of three or four with 5–10 polyps per cm (sometimes more closely spaced at branchlet base). Polyps 1.5–1.85 mm tall (average 1.7 mm) including the long marginal spines, with 4–5 scales in the abaxial row, 2–3 adaxially; number of longitudinal rows reduces quickly from 8 at marginals to 4 or 5 at base.

Polyps sheathed in four categories of scales: 8 operculars, 8 marginals, one or two circlets of pointed submarginals and a variable number of body-wall scales.

Operculars do not form an opercular cone so there are gaps into the opercular cavity (Figure 2.6e). Operculars shaped like an isosceles triangle (Figure 2.7a–c) ranging in size from 330–650 µm tall (average 470 µm), 150–370 µm wide (average 250 µm), H:W 1.1–2.4 (average 1.9); just over half the size of marginals. Proximal half of the inner surface is tuberculate; flat-surfaced keel on inner surface (Figure 2.7c). Outer scale surface is covered with granules that extend radially from central point in proximal half.

Marginals long (Figure 2.7e–g), 650–960 µm (average 800 µm), 430–580 µm wide (average 520 µm), average H:W of 1.6, usually splayed out and too long to be able to fold over the operculum neatly. Sometimes the abaxial two or three marginals are much longer than those adaxially (Figure 2.6e). Outer surface with two or three longitudinal furrows down the length of the spine; granules cover remaining scale
area (Figure 2.7e,g). Two or three shallow channels run the length of the keel which is elongated with a spinose distal end (Figure 2.7f); base of the keel is tuberculate.

Submarginals with pointed distal edge (Figure 2.7h–k). Submarginals are wider than the marginals, 440–610 µm wide (average 525 µm), 520–600 µm tall (average 560 µm), curving away from the polyp body (similar slant to marginals) and thus visible from an anterior view (see Figures 6e, marked 1 and 6f).

Body-wall scales round to elliptical (Figure 2.7l–n), larger and wider towards polyp head (average of 400 µm tall, 485 µm wide, H:W 0.9), smaller and round towards base (average of 325 µm tall, 455 µm wide, H:W 1.2). The distal edge of all sclerites is finely serrate; proximal edge is irregularly lobate.

Outer layer of coenenchymal scales elliptical (Figure 2.7o,s,p), 190–320 µm long (average 240 µm), 590–750 µm wide (average 680 µm) with an average H:W of 0.35. Inner layer of scales are smaller, thin and roughly circular (Figure 2.7q,r) with granules on the outer surface and a finely tuberculate inner surface. Coenenchymal scales generally have finely serrated proximal and distal edges.

2.13.2 Distribution
Circum-Antarctic, from 115 to 2100 m depth.

2.13.3 Remarks
Thouarella variabilis var. a typical (hereafter called T. variabilis typica) and T. variabilis var. gracilis Wright & Studer, 1889 have identical polyp shape and structure, and sclerite sizes and shapes. Thouarella variabilis var. gracilis is described as, what I interpret from Wright and Studer (1889), as having more secondary and tertiary ramification than T. variabilis typica. However, there are varying degrees of ramification within a single colony and given the identical nature of all sclerites these two varieties are thus proposed for synonymisation under T. variabilis.

Within the material examined, I found branching of T. variabilis occurred in up to four directions (rather than three directions as noted in Wright & Studer 1889). Some juvenile colonies can appear almost pinnate (e.g. SMF, EPOS 03, sta. 281) although
on closer inspection branchlets depart in three directions. Also, although there is some regularity with spiral branchlet placement, it is not consistent.

USNM 1130283 and SMF ‘Am Twist’ samples have smaller polyps than the holotype, maximum length of 1.5 mm rather than 1.5–1.85 mm, but are otherwise identical.

The complex bushy bottlebrush shape of *T. variabilis* specimens make them ideal habitat for associates; worms, brittlestars and ascidians were found within specimen branches.

True to its name, *T. variabilis* can have polyps that look dissimilar (Brito, 1993); polyps with elongated claw-like marginals are shown in Figure 2.6c (some of these polyps were brooding) and open flared polyps with elongated submarginals are also common (Figure 2.6b).

### 2.13.4 Comparisons

*Thouarella variabilis* is unusual within *Thouarella* in having long marginals that don’t fold over the operculum neatly and it is this long, keeled marginal that makes this species distinct from all others. *Thouarella variabilis* has a similar number of abaxial row scales as *T. pendulina, T. hicksoni, T. brucei,* and *T. striata* and comparisons to these species are made here:

Polyps of *Thouarella pendulina* are much smaller and are more clustered (up to 70 per cm) than those of *T. variabilis.*

Polyps of *Thouarella hicksoni* are a similar size and have a comparable number of abaxial scales to those of *T. variabilis,* however, isosceles triangle-shaped operculars on the latter differ from the blunt, rounded distal edge of operculars of the former (which subsequently form a tighter opercular cone). Also, *T. hicksoni* lacks spinose submarginals, although they can have a pointed distal edge.

Polyps of *T. brucei* are a similar size to *T. variabilis* but have wider triangular operculars.
Opercular, marginal and submarginal sclerites of *T. striata* have distinctive deep striations that could be confused with the sometimes dense granules on the outer surface of *T. variabilis* sclerites. However, inner marginal surfaces of *T. striata* have pointed ridges running perpendicular to distal edges, lateral to the keel; these are absent in *T. variabilis*.

Although now transferred to *Plumarella*, the former *Thouarella* species *T. diadema* has polyps with 3–5 body-wall scales in the abaxial row and polyps of a similar-size and shape to those of *T. variabilis*. The major difference between these two species is that marginals of the former lack a keel (the defining difference between *Plumarella* and *Thouarella*).

### 2.14 Thouarella brevispinosa Wright and Studer, 1889, new rank

Figures 2.8, 2.9


*Thouarella (Thouarella) var. brevispinosa*: Cairns & Bayer, 2009: 27 (listed)

**Material examined**: Holotype, NHM89.5.27.54, 12 cm, H.M.S. *Challenger*, sta. 145A, 46°41’S, 38°10’E, off Prince Edward Island, 566 m, 27 Dec 1873; ZMH, R/V *W. Herwig*, sta. 245, SW Atlantic, 36°49’S, 54°02’W, 550 m, 14 Jun 1966.

**2.14.1 Description**

Holotype consists of one broken, branch (Figure 2.8a). Branchlets mostly simple (some secondary, and even tertiary branching), longest is 25 mm, arranged around main stem in at least four directions in a bottlebrush formation.

Polyps large, 2.5–3 mm long, and isolated on stems and branchlets at wide intervals of 7–11 per cm. Polyps distally inclined at 60° and distally flared with splayed marginals (Figure 2.8b–d). Each polyp has 6–7 scales in abaxial row (Figure 2.8c) and 7 longitudinal rows reducing to 4 at polyp base. Four categories of scales cover each
Polyp: 8 operculars, 8 marginals, pointed submarginals and a variable number of body-wall scales.

Opercular tips meet in an apex to form a cone. They are shaped like isosceles triangles (Figure 2.9a–c; although sometimes they have a rounded distal edge, Figure 2.9f,g) with a squared proximal edge (Figure 2.9f,g), 270–770 µm tall (average 540 µm), 200–410 µm wide (average 310 µm), H:W 1.2–2.1 (average 1.7), with a single, large keel on inner surface, sometimes with small lateral ridges running parallel to the keel (Figure 2.9a). Proximal half to third of inner surface tuberculate; outer surface longitudinally concaved towards the distal edge; there are sparse granules and occasional fine ridges in a radial pattern from the proximal area.

Marginals are 510–830 µm long (average 730 µm), 490–600 µm wide (average 530 µm), with H:W 1.0–1.6 (average 1.4) and have a broad angular base (Figure 2.9i,j) and a central, sometimes almost spinose, distal projection (Figure 2.9h). The inner surface is keeled. The keel has a single channel running longitudinally from scale centre. There are 2–3 ridges parallel to the keel (more developed than in operculars) and tubercules cover the proximal area with a smooth band distally that has infrequent small ridges perpendicular to distal edge. The outer marginal surface has rows of granules radiating from the centre of the scale.

Generally there are two circlets of abaxial and lateral submarginals; the submarginals have a pointed distal edge (Figure 2.9l–n) and a reduced keel on the inner surface (Figure 2.9k,l). The adaxial submarginals have a more rounded distal edge, more typical of body-wall scales (Figure 2.9k). Submarginals wider than marginals, 550–690 µm (average 610 µm), 450–620 µm tall (average 540 µm), with H:W 0.8–1.0 (average 0.9). The inner surface is tuberculate and the outer surface has sparse granules sometimes spread radially towards distal edges (Figure 2.9m).

Body-wall scales elliptical to circular (Figure 2.9o–s); distal edge curves gently away from the polyp body. Inner surface covered in tubercles and outer surface with sparse granules; the proximal edge can also be covered in tubercles. The distal edge of all sclerites is finely serrate; proximal edge is irregularly lobate.
Revision of Thouarella

Coenenchymal scales oval to round or angular shape (Figure 2.9t), with very sparse, irregular, granules on outer surface; the inner surface is tuberculate.

2.14.2 Distribution
Known only from two locations: the type location off Prince Edward Island, and east of Buenos Aires, Argentina, approximately 7300 km away. Depth range is 550–566 m.

2.14.3 Comparisons
Thouarella brevispinosa has larger polyps with more scales in the abaxial row than T. variabilis. The former also has sparser branching and larger operculars with a more complete opercular cone than the latter. I thus propose this variety is elevated to species rank, namely Thouarella brevispinosa.

Polyps of Thouarella brevispinosa are distally flared and a similar size to polyps of T. antarctica, T. striata, and T. affinis and are thus compared here:

Thouarella affinis has a similar number of scales in the abaxial row as T. brevispinosa however the majority of polyps in the latter have taller marginals that are more acutely elongate, than the former (whose marginals are modestly pointed).

The size and shape of the marginals of T. brevispinosa and T. striata are very similar, however the inner surface of marginals of the latter have robust ridges flanking the keel while the former have fine ridges. Thouarella striata sclerites are thick; those of T. brevispinosa are more delicate. Tubercles on the scales of T. striata are also more densely arranged and the polyps tend to be smaller.

Thouarella brevispinosa has fewer scales in the abaxial row than T. koellikeri and abaxial marginals are taller and wider, creating a more flared polyp shape; polyps of the latter are smaller and clavate.

2.15 Thouarella affinis Wright and Studer, 1889
Figures 2.10, 2.11
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*Thouarella affinis* Wright & Studer, 1889: 66–68, pl.11, fig. 3.—Thomson & Henderson, 1906: 38 (list).—Kükenthal, 1912: 302 (listed)

*Thouarella (Epithouarella) affinis*: Kükenthal, 1915: 151 (key); 1919: 435–436; 1924: 300 (key)

*Thouarella (Thouarella) affinis*: Cairns & Bayer, 2009: 27 (listed)

**Material examined:** Holotype, 65 mm fragment, NHM1889.5.27.44, H.M.S. *Challenger*, sta. 135D, off Inaccessible Island, Tristan de Cunha, 37˚25’S, 12˚22’30”W, 91–128 m, 15 Jul 1874; ZMH, R/V *W. Herwig*, sta. 232, east of Isla de los Estados, Tierra del Fuego, Argentina, SW Atlantic, 54˚46’S, 62˚30’W, 800 m, 1971. As only a small fragment was available descriptions of axis and colony morphology were taken from type description.

2.15.1 **Description**

Colony bottlebrush. Branchlets emerge in all directions at almost right angles (Figure 2.10a). Axis yellow, stiff, and brittle; although stem apex is more flexible. Stem twists in a long 360˚ spiral from base to a quarter-length from apex whereupon the next twist commences.

Branchlets mostly simple, some forking (dividing usually in basal region of branchlet), upwardly inclined 60–90˚, up to 50 mm long, emanating in spirals from three sides of main stem; four branchlets form a spiral, but as stem twists the spiral is difficult to follow. Branching dense, 1.5–2 mm between branchlets; denser towards apex.

Polyps isolated, 1.1–2.1 mm long, 7–9 per cm, (denser placement at branchlet apex, which generally has a polyp at the tip), can be modestly flared but generally with a wide, rounded head extending from slender polyp body making them clavate (Figure 2.10b,c; H:W of 1.3–2.1, average 1.7). The polyps are arranged in short spirals of 3 to 4 and angled distally at 45–60˚. Each polyp has eight longitudinal rows, 6–7 scales in each abaxial row, 5 adaxially.

Tall rounded operculum rises above marginals. Operculars isosceles-triangle shaped (Figure 2.11a,b) or tongue-shaped (Figure 2.11c–g), 540–780 µm tall (average 610
µm), 220–350 µm wide (average 280 µm), average H:W of 2.2 (range from 1.8–2.5). Outer scale surface is longitudinally concave with granules across proximal area and occasional low ridges spreading radially from centre towards distal edge (Figure 2.11d–f). Inner surface with low, multiple-ridged keel (Figure 2.11a,b), or dense area of low ridges (Figure 2.11c); proximal half of scale is tuberculate.

Marginals diamond-shaped (Figure 2.11h–j), 460–610 µm tall (average 525 µm), 460–640 µm wide, average H:W of 1 (ranges from 0.8–1.3). The inner surface has a smooth band along the distal edge which is broken by a small, simple keel (Figure 2.11h) with two or three adjacent ridges; the remainder is tuberculate. Adaxial marginals frequently have no defined keel with just four or five short, sharp ridges perpendicular to distal edge (Figure 2.11i). Outer surface mostly smooth with some granules that often form radial ridges (Figure 2.11j).

Body-wall scales a range of shapes from circular, oval to elliptical (Figure 2.11k–q), generally broader than tall, 350–490 µm tall (average 430 µm), 380–780 µm wide (average 540 µm), average H:W of 0.8 (ranges from 0.6–1.1) and curved slightly away from polyp body. Tubercles cover the inner scale surface. Granules occur sparsely on the outer surface and sometimes tubercles occur along the proximal edge. The distal edge of all sclerites is finely serrate; the proximal edge is irregularly lobate.

There is a single layer of irregularly shaped coenenchymal scales that are circular (Figure 2.11r-u) or sometimes elongated (Figure 2.11v,w), 190–280 µm long (average 225 µm), 230–430 µm wide (average 300 µm), average H:W of 0.8 (range from 0.4–1.1). There are large prominent granules/ridges on the outer surface of coenenchymal scales and fine tubercles on the inner surface.

2.15.2 Distribution
Known only from type location, Tristan de Cunha, and Inaccessible Island, mid South Atlantic. Known from 91–800 m.

2.15.3 Remarks
The holotype material examined was damaged so the number of polyps per cm may be an underestimate.
2.15.4 Comparisons

Wright and Studer (1889) considered *T. affinis* very similar to *T. antarctica*; these species do have a similar number of scales in the abaxial row (6–7 *T. affinis*, 5–7 *T. antarctica*) but the latter has a more complex, structured keel with large lateral projections compared to the modest keels of the former.

The polyps of *Thouarella viridis* are a similar shape and size to *T. affinis* and they also have similar shaped marginals, although those of *T. viridis* are slightly taller. But the operculars of *Thouarella viridis* are pointed, while those of *T. affinis* are tongue-shaped and the body-wall scales of the former have more pronounced ridges perpendicular to the distal edge (that are visible in lateral polyp view) than the latter.

The polyps of *Thouarella affinis* are more rounded than those of *T. brucei*. The latter also has fewer scales in the abaxial row and marginals that are narrower with a higher H:W ratio.

Polyps of *Thouarella koellikeri* tend to be longer than those of *T. affinis*, with more scales in the abaxial row. The former has pointed triangular operculars whereas those of the latter are tongue-shaped.

2.16 *Thouarella koellikeri* Wright and Studer, 1889

Figures 2.12, 2.13

*Thouarella köllikeri* Wright & Studer, 1889: 64–65, pl.11 fig.5.—Thomson & Henderson, 1906: 38 (list).—Versluys, 1906: 35

*Thouarella (Parathouarella) köllikeri*: Kükenthal, 1915: 150 (key); 1919: 435; 1924: 299

*Thouarella (Thouarella) koellikeri*: Cairns & Bayer, 2009: 27 (list)

*Material examined:* syntype, NHM 1889.5.27.41 and USNM 1002247, fragment of syntype (whole holotype at NHM), H.M.S. Challenger, sta. 308, 50°08’30”S, 74°41’W, 320 m, 5 Jan 1876, 1 colony; USNM 1112997, sample 5, Puyuhapi, Chile, South Pacific Ocean, 30 m, 10 Jan 2000, 2 colonies, no location information; USNM 1002247, sample 174, Chile, South Pacific Ocean, no location information, 25 m, 12
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Mar 2006, 2 colonies; NHM (no catalogue number), H.M.S. *Challenger*, 51°27’30”S, 74°3’W, 730 m, 10 Jan 1856, fragment; SMF, R/V *W. Herwig*, sta. 245, SW Atlantic, 36°49’S, 54°02’W, 550 m, 14 Jun 1966; SMF, R/V *W. Herwig*, sta. 376, SW Atlantic, 43°23’S, 60°19’W, 100 m, 16 Jul 1966; SMF, R/V *W. Herwig*, sta. 311, Patagonian Shelf, SW Atlantic, 46°54’S, 60°28’W, 480 m, 18 Feb 1971; SMF, R/V *W. Herwig*, sta. 293, North Falkland Islands, 49°36’S, 59°25’W, 350 m, 13 Feb 1971; USNM 97997, R/V *Eltanin*, cruise 7, sta. 499, south of Coronation Island, South Orkney Islands, sub-Antarctic, 62°06’S 45°08’W to 62°06’S 45°10’W, 485 m, 20 Feb 1963, 7 colonies; USNM 98169, R/V *Eltanin*, cruise 6, sta. 339, west of Beauchene Island, Falkland Islands, sub-Antarctic, 53°06’S, 59°27’W, 512–586 m, 3 Dec 1962; USNM 98019, R/V *Eltanin*, cruise 12, sta. 1089, NE of Clarence Island, South Shetland Islands, Antarctic Ocean, 60°47’S, 53°30’W, 641 m, 14 Apr 1964; USNM 79475, R/V *Eltanin*, cruise 9, sta. 740, east of Cape Horn, Drake Passage, South Atlantic Ocean, 56°06’S, 66°19’W, 384–494 m, 18 Sep 1963; USNM 1130298, R/V *Hero*, cruise 721, sta. 1075, 64°47’24”S, 64°07’36”W, south of Anverse Island, Palmer Basin, Antarctica, 91–110 m, 23 Feb 1972.

2.16.1 Description

Colonies with two or three main stems (Figure 2.12a). Branchlets mostly undivided, leaving main axis primarily in two directions around 120° apart, roughly alternately pinnate; between these two rows of branchlets (at 60°) there is often another row of branchlets. These three planes/rows of branchlets depart on one side and there are occasional branchlets directly opposite (240°); these branchlets tend to be short/broken, especially towards colony base, potentially due to the reduced protection these branchlets receive. Branching arrangement can appear pinnate however branchlets are on all sides of main axis in four directions, and thus the colony is bottlebrush.

Polyps clavate with rounded opercular cone (Figure 2.12c,e), emanate from main stem and branchlets in roughly alternate arrangement (Figure 2.12b), 12–15 per cm (more clustered towards branchlet tips), upwardly inclined at 45–60°, 1.6–2.5 mm long (average 2.2). Sclerites in 8 longitudinal rows, 7–10 scales in abaxial row (Figure 2.12d) but reduced in number adaxially, just 5–7.
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Each polyp has four categories of scales: 8 operculars, 8 marginals, 8 submarginals and many body-wall scales.

Operculars are an isosceles triangle- (Figure 2.13a,d) to arrowhead-shaped (Figure 2.13b), 360–560 µm tall (average 480), 180–350 µm wide (average 250), average H:W 1.95, having a large single keel on their inner surface (side view of keel, Figure 2.13c) with corresponding deeply concave longitudinal outer surface (Figure 2.13b). Proximal half of the inner surface is covered with small densely placed tubercles; outer surface has ridges arranged radially from proximal third.

As the distal circumference of a polyp is not wide enough to accommodate 8 marginal scales they are arranged in two alternating circles of four with their lateral edges overlapping (Figure 2.12e). Marginals fold over operculars, fitting into the concave outer surface of operculars. Marginals triangular distally, pointed but not spinose (Figure 2.13e–g), 420–580 µm tall (average 480 µm), wider than operculars at 340–520 µm (average 430), average H:W 1.1. Abaxial marginals are more pointed than those adaxially. Marginals are rounded laterally and with a flat proximal edge. The inner surface bears a large keel usually with lateral projections (Figure 2.13e). Tubercles are more widely spaced than on operculars but still cover the basal portion of the inner surface. The outer surface has granules in radial rows from central proximal are that fade towards scale edges (Figure 2.13g).

Submarginals are shorter than marginals (Figure 2.13h–k), 320–590 µm tall (average 430 µm), 230–490 µm wide (average 430 µm), average H:W 1. Generally submarginals have a more rounded distal edge than marginals but are more pointed on the abaxial side of the polyp (Figure 2.13h,j) than the adaxial (Figure 2.13k). The row beneath submarginals also sometimes has scales with a modest distal point and a small keel on the inner surface. Submarginals differ from marginals as tubercles cover a larger proportion of inner surface.

Body-wall scales arch slightly away from the polyp body and are variously shaped; generally pentagonal with a rounded distal edge or circular (Figure 2.13l–p), 280–520 µm tall (average 390 µm), 220–600 µm wide (average 380 µm), average H:W 1. Inner surface tuberculate with a thin smooth band distally that can bear multiple small
ridges (Figure 2.13l,o); outer surface covered in granules. Distal edge of all sclerites are finely serrate; proximal edge irregularly lobate.

Coenenchymal scales small, circular (Figure 2.13q), 120–180 µm diameter (average 150 µm), average H:W 1, edges finely serrate. Outer surface has radial ridges from centre to the scale edge; inner surface tuberculate.

2.16.2 Distribution
Found from the southern coast of Chile, Argentinian coast, and off the Antarctic Peninsula at 91–1920 m depth.

2.16.3 Remarks
Contrary to Wright and Studer (1889), who described dorsal branchlets as simple and short (10–25 mm), some colonies have dorsal branchlets up to 51 mm with a similar polyp orientation and axis flexibility as ventral and lateral branchlets.

2.16.4 Comparisons
Versluys (1906) described *T. koellikeri* ramification as similar to *T. moseleyi* and the two species do have long, fine, flexible branchlets that could appear similar. However, the latter has pinnate, uniplanar colonies and the former colonies that are bottlebrush to bilateral in form. *Thouarella koellikei* has isolated polyps and polyps of *T. moseleyi* are in pairs.

*Thouarella koellikeri* most closely resembles *T. viridis*, as both have clavate polyps and a bushy, bottlebrush to bilateral appearance. However, *T. koellikeri* has longer marginals with a single keel, whereas marginals of *T. viridis* are shorter and have 2–4, sometimes 5, longitudinal ridges instead of a keel. Distal inner surface ridges are found on a few rows of *T. viridis* submarginals whereas *T. koellikeri* polyps tend to have a small, single keel on the first row of submarginals. *Thouarella koellikeri* polyps also have more scales in the abaxial row than *T. viridis*.

Although most are modestly flared, some polyps of *T. antarctica* have a similar clavate polyp shape as those of *T. koellikeri*. The latter has longer polyps (reflected in having 7–10 scales in the abaxial row, rather than 5–7). The marginals of *Thouarella antarctica* larger and bear a more complex keel than those of *T. koellikeri*; in fact, all
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sclerites are smaller on *T. koellikeri*. Also, *T. antarctica* has a true bottlebrush colony whereas *T. koellikeri* branchlets leave the main stem in two or three directions giving it a bushy to bilateral appearance.

The bushy appearance of *T. koellikeri* is similar to that of *T. bipinnata* however the former has polyps with a wider head and, when dried, the body-wall scales reflect away from the polyp body in *T. koellikeri* whereas the latter has longer, thinner polyps, taller operculars, and marginals with a higher H:W ratio.

*Thouarella koellikeri* has similar sclerite shapes as both *T. brevispinosa* and *T. brucei*. *Thouarella brucei*, however, has distally-flared polyps and fewer scales in the abaxial row, longer marginals bearing a more acute distal point, and flatter keels, whereas *T. brevispinosa*, although having a similar number of abaxial scales, has taller marginals and more flared, open polyps that *T. koellikeri* (see Table 2.3).

2.17 **Thouarella brucei** Thomson and Ritchie, 1906

Figures 2.14, 2.15

*Thouarella brucei* Thomson & Ritchie, 1906: 852–854, pl. 1 fig. 1, pl. 2 fig. 1.—Kükenthal, 1919: 439; 1924: 301

*Thouarella versluysi* Kükenthal, 1907: 202–203

*Thouarella (Thouarella) brucei*: Cairns & Bayer, 2009: 27 (listed)

Not *Thouarella brucei*: Broch, 1965: 27–28, pl. 4 (= Digitogorgia sp.)

*Material examined:* holotype, NHM 1933.3.13.130, Scotia (Scottish National Antarctic expedition of 1902–04), Burdwood Bank or Gough Island, 102–182 m, 1 Dec 1903 or 22 April 1904.; fragment of holotype, ZMA COEL03574; *Thouarella versluysi*, syntype, MNHWU, D.T.E. sta. 103, South Africa, 35°10’S, 23°2’W, 500 m, two 2.5 cm fragments; USNM 1130164, R/V *Eltanin*, cruise 22, sta. 1536, west tip of South Georgia, sub-Antarctic, 54°30’S, 39°20’W, 659–686 m, 8 Feb 1966, 6 colonies (4–7 cm long); USNM 98029, R/V *Eltanin*, cruise 22, sta. 1536, west tip of South Georgia, Antarctica, 54°29’S, 39°22’W, 659–686 m, 8 Feb 1966, 2 colonies (30 cm, 12 cm); USNM 98337, R/V *Eltanin*, cruise 21, sta. 290, west mouth of Strait of Magellan, Antarctica, 52°41’S 74°35’W to 52°45’S 74°28’W, 188–247 m, 6 Jan 1966,
3 colonies; USNM 98195, R/V Islas Orcadas, cruise 575, sta. 93, South Georgia Island, Antarctic Ocean, 54°38′48″S, 38°51′18″W, 261–270 m, 9 Jun 1975, 1 colony.

2.17.1 Description
Holotype rigid, sparsely branched (Figure 2.14b). Main axis robust and stiff although smaller branchlets are more flexible. Axis light yellow, side branchlets a lighter shade. Axis is circular in cross-section.

Branching is in up to 4 directions all around main axis at irregular intervals; rows of branchlets emanating at a 60° separation, upwardly inclined. Overall colony structure appears more bilateral than bottlebrush as the close set branchlets curve into one plane. Secondary and tertiary branchlet branching is common.

Polyps isolated, 1.5–2.3 mm long, some occurring on main axis, arising in all directions on branchlets, 9–12 per cm, modestly flared distally (Figure 2.14a,c) and upwardly inclined at 40–45°. Each polyp has 7 longitudinal rows, 4–5 scales in the abaxial row and 2-3 in the adaxial.

Two rings, one consisting of four smaller, lower scales, the other of four larger, upper operculars, form the operculum. Upper operculars align with the outer ring of marginals; lower operculars with the inner ring of marginals. Operculars range in size from 390–680 µm high (average of 510 µm), 170–330 µm wide (average of 250 µm), H:W 1.5–2 (average 2) in the holotypes. Operculars triangular with rounded tongue-shaped distal edge (Figure 2.15a–e). Outer surface longitudinally concave with sparse granules (Figure 2.15a,b) Simple keel on inner surface; tuberculate proximally.

Marginals also occur in two rings, upper and lower. Marginals rhomboid (Figure 2.15f–h), 490–760 µm high (average of 635 µm), 350–570 µm wide (average of 470 µm), H:W 1.1– 1.7 (average 1.4) in the holotype (smaller sizes in voucher specimens). The inner surface of marginals bear a longitudinally channelled multi-keel (Figure 2.15f); sometimes the keel has a flat central area. The inner marginal surface is tuberculate below the keel base; outer surface has granules at the centre and is smooth towards scale edges.
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Submarginals are square to oval-shaped, with an arched distal edge (Figure 2.15j), 230–670 µm high (average 440 µm), 230–615 µm wide (average 380 µm) with smaller H:W than marginals (average of 1.14). The inner surface is tuberculate with a thin, smooth band along the distal edge; outer surface with sparsely placed granules.

Body-wall scales large (Figure 2.15k–l), 160–560 µm high (average 320 µm), 160–590 µm wide (average 350 µm), generally circular to elliptical (average H:W 0.9). The outer surface has granules and small ridges at the distal edge; the inner surface is tuberculate. The proximal edge of all scales is coarsely lobate; the distal edge is finely serrate.

Coenenchymal scales are circular (Figure 2.15n) with a diameter of 50–150 µm. The outer surface is covered with sharp-peaked granules and small radial ridges; the inner surface is tuberculate.

2.17.2 Distribution
Mid to southwest Atlantic, off southern coast of Chile and the Antarctic Peninsula, Found from 100–686 m depth.

2.17.3 Remarks
Thouarella versluysi was described one year after T. brucei by Kükenthal (1907). Kükenthal mentioned that T. versluysi was very similar to T. brucei but without further explanation. Kükenthal also went as far as listing T. brucei as species dubiae atque incertae sedis in his 1924 key. Thouarella versluysi and T. brucei both have bottlebrush colony morphology (although T. brucei can appear bilateral it is technically bottlebrush). There was not enough material to determine the colony shape of the T. versluysi syntype, however the original description and colony picture are bottlebrush (Kükenthal 1907). Both species have isolated polyps upwardly inclined at between 40–60° and 4–6 scales in their abaxial rows. Thouarella versluysi has slightly smaller polyps than T. brucei, a slightly lower opercular scale H:W (average of 1.8 versus 2), a higher marginal scale H:W ratio (average of 1.7 versus 1.4), and the abaxial surface of T. brucei scales have more peaked granules. These are however very minor differences and not enough, in my opinion, to separate these specimens as individual species; Thouarella versluysi is thus synonymised with T. brucei.
Specimens examined in this study are morphologically identical to the holotype but have slightly smaller polyp lengths and, as a consequence, smaller sclerite sizes.

2.17.4 Comparisons

Thouarella brucei and T. brevispinosa have marginal and opercular scales of an almost identical shape. Thouarella brevispinosa has larger polyps with more scales in the abaxial row than T. brucei (6–8 rather than 4–5) and branchlets of the former are more tightly placed. More material is required of both species to confirm the differences and similarities listed here. Investigations should also look into the possibility that these two species are sexually dimorphic colonies of the same species as they are strikingly similar.

Thouarella brucei shares a similar bilateral–bottlebrush branching morphology with T. koellikeri, T. bipinnata and T. andeep. Thouarella brucei has polyps that are flared distally similar to T. andeep, whereas T. koellikeri and T. bipinnata have clavate polyps arranged in an irregular alternate manner. Thouarella brucei has fewer scales in the abaxial row than T. koellikeri. The operculars of T. andeep have a smooth inner surface whereas those of T. brucei, whose polyps are smaller, have a simple keel (see Table 2.3).

Polyps of T. brucei examined in this study have a similar size and number of abaxial scales as T. hicksoni (although T. brucei holotype polyps are larger than those of T. hicksoni). Thouarella brucei, however, has operculars that can form a full cone, whereas operculars of T. hicksoni are thinner and do not form an opercular cone. Polyps of the latter are also far more clustered.

2.18 Thouarella striata Kükenthal, 1907

Figures 2.16, 2.17

Thouarella striata Kükenthal, 1907: 204–205; 1915: 150 (key); 1919: 426–428, text figs. 197–201.—Broch, 1965: 31–32, pl. 7, figs. 20–21 (sample not seen)
Not Thouarella striata: Nutting, 1912: 69, pl. 10 figs. 2, 2a (sample not seen)
Thouarella stricta: Molander, 1929: 75 (spelled incorrectly)
Thouarella (Parathouarella) striata: Thomson & Rennet, 1931: 27
**Thouarella (Thouarella) striata**: Cairns & Bayer, 2009: 27 (listed)

*Material examined:* holotype, MNHWU, Nr. 57, Bouvet Island, 54°26′S, 3°24′E, 457 m; ZMH, R/V *W. Herwig*, sta. 285, Patagonian Shelf, SW Atlantic, 42°19′S, 58°01′W, 825 m, 21 Jun 1966, 2.5 cm fragment; ZMH, R/V *W. Herwig*, sta. 244, SW Atlantic, 36°51′S, 54°01′W, 800 m, 14 Jun 1966.

As only a 2.5 cm fragment was examined, general morphology is taken from the original description (Kükenthal 1907) and new specimen, above.

### 2.18.1 Description

Colony rarely branched in a bottlebrush form, with mostly simple (rare secondary branching) 25 mm length branchlets emerging from main stem at almost 90°, some branchlets arranged in one plane.

Polyps isolated, weakly inclined towards branchlet at 45–80° (Figure 2.16b); they are closely arranged, 14–20 per cm (more densely arranged at branchlet bases) and are variable in shape, some clavate, some modestly flared distally (holotype has distally flared polyps, Figure 2.16c,d), 1.5–2.2 mm long (average 1.85 mm). There are 4–6 scales in an abaxial row (Figure 2.16d), 3–4 in adaxial rows.

Operculars are isosceles triangle-shaped and acutely pointed (Figure 2.17a–c), 520–780 µm long (average 660 µm), 230–350 µm wide (average 295 µm), average H:W 2.3. The inner opercular surface is keeled; keel often with multiple adjacent perpendicular ridges (Figure 2.17b,c), and the proximal third of the inner surface is tuberculate. The outer surface is concave longitudinally with low ridged striations radiating from proximal centre (Figure 2.17a).

Marginals are arranged in 2 alternate circles of 4, one inner and one outer (Figure 2.16e); although this is not consistent. Marginals are wider than operculars, 530–680 µm (average 600 µm), and slightly shorter, 520–680 µm (average of 600 µm), average H:W 1, with a triangular distal area and are more squared proximally (Figure 2.17d–f) than operculars. Marginals have a strong, multi-ridged keel with lateral ridges running perpendicular to distal edge, the proximal half of the inner surface is heavily...
Revision of *Thouarella*

tuberculate; the outer surface is covered with dense granules and shallow meandering striations radiate from the scale centre to the distal edge (Figure 2.17d,f).

Submarginals are shorter than marginals, 530–540 µm tall, 520–700 µm (average 610 µm) wide, average H:W 0.88, with a modest distal point (Figure 2.17g,h). The inner surface is tuberculate across the basal four-fifths of the scale, with a band of ridges running perpendicular to the distal edge; the outer surface is covered with densely placed granules. All sclerites have finely a serrate distal edge and a coarsely lobate proximal edge.

Body-wall scales are generally rounded (average H:W 1; Figure 2.17 j–m) with a pointed arch along the distal edge (Figure 2.17k,m); some abaxial body-wall scales also have a sculpted distal edge (Figure 2.17i). Body-wall scales 270–580 µm tall (average 428 µm), 240–650 µm wide (average 448 µm), scales progressively reduce in size from polyp head to base. Body-wall scales have heavily tuberculate inner surface, a smooth band along the distal edge with a few ridges perpendicular to edge; the outer surface has deep radial ridges running from the central proximal area and individual granules along the proximal edge. The distal edge is irregular; the proximal edge is coarsely lobate.

Coenenchymal scales elliptical to circular-shaped (Figure 2.17n–q) with serrated edges. Outer surface covered in granules or is heavily sculpted (Figure 2.17q); inner surface densely tuberculate.

2.18.2 Distribution
From Bouvet Island, South Atlantic, to Burdwood Bank (Broch 1965) and the Patagonian Shelf, 457–800 m depth. Broch’s unconfirmed identification (1965) was from 110 m.

2.18.3 Remarks
*Thouarella striata* has a variable polyp form. The surfaces of holotypic scales, both inner and outer, are deeply ridged; other specimens have finer striations on the outer surface but similar deep ridges on the inner.

The specimen from station 244 from ZMH (June 1966) was brooding.
2.18.4 Comparisons

With the number of abaxial scales ranging from 4–6 *T. striata* is comparable to several species, namely *T. variabilis, T. brucei, T. pendulina, T. hicksoni, T. bipinnata* and *T. andeep* (see Table 2.3).

*Thouarella variabilis* generally has fewer scales in the abaxial row than *T. striata* and lacks wide triangular marginals and striations on the inner surface of the sclerites.

The bushy/bilateral to bottlebrush appearance of *T. brucei* colonies can look very similar to *T. striata* and polyps of the former are of a comparable size to the latter, however, the former has sclerites with a smoother outer surface whereas the latter has distinct striations. The inner surfaces of marginals of *T. brucei* are also relatively smooth lateral to the keel whereas those of *T. striata* have strong ridges.

Although slightly larger, the wide distally flared shape of polyps of *T. andeep* are similar to *T. striata*. The primary difference is that the operculars of *T. andeep* have a smooth inner surface and rounded distal edge whereas operculars of *T. striata* are triangular with a strong keel. Polyps of *Thouarella andeep* also have fewer scales in the abaxial row and accessory operculars, which have so far not been found in specimens of *T. striata*.

When compared to *T. striata*, polyps of *T. pendulina* are smaller and more tightly placed, without open, splayed marginals and the outer surface of sclerites lack ridges or striations in addition to which *T. pendulina* has a true bottlebrush colony shape.

Polyps of *T. hicksoni* are smaller and more densely arranged than those of *T. striata*, and although there are granules on the outer surface of sclerites in the former, striations are absent.

*Thouarella bipinnata* is uniplanar whereas *T. striata* has a bushy, bottlebrush colony shape. Polyps of the former are clavate, and again, the former lacks striations on the outer and inner surfaces of sclerites.
2.19 Thouarella crenelata Kükenthal, 1907

Figures 2.18, 2.19

Thouarella crenelata Kükenthal, 1907: 205; 1912: 302

Thouarella (Epithouarella) crenelata: Kükenthal, 1915: 151 (key); 1919: 436–438, text figs. 216–219, pl. 43, fig. 70; 1924: 300–301.—Cairns & Bayer, 2009: 28 (listed), fig. 7i–m

Material examined: Holotype material was too fragile to send from MNHWU. Type locality is eastern Bouvet Island, southern Atlantic Ocean, 457 m depth. Holotype held in ZMB, fragment in MNHWU. Although no material was located in the Smithsonian collection or elsewhere from this location, many specimens that match descriptions of T. crenelata were located, all from the sub-Antarctic region.

USNM 98086 (SEM stubs T53 & T68, stored at NMNH), R/V Hero, cruise 824, sta. 26–1, Lecointe Island, Brabant Island, Palmer Archipelago, Antarctic Peninsula, 64°14′03″S, 61°57′57″W, 238–285 m, 24 Mar 1982; USNM 99148, R/V Marion Dufresne, cruise 42, sta. 22, Mac Robertson Land, Lars Christensen Coast, north of Cape Darnley, Antarctica, 66°58′S, 72°52′E, 525 m, 26 Jan 1958; USNM 98160, R/V Hero, cruise 731, sta. 1947, Flandres Bay, Danco Coast, Antarctic Peninsula, 65°00′31″S, 63°28′06″W, 204–250 m, 11 Mar 1973; USNM 1128900, R/V Hero, cruise 731, sta. 1939, Wednesday Island, Butler Passage, Palmer Archipelago, Antarctic Peninsula, 64°58′39″S, 63°45′46″W, 75–120 m, 9 Mar 1973; USNM 1071563, R/V Hero, cruise 731, sta. 1812, Bismarck Strait, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°51′54″S, 63°39′45″W, 280–300 m, 19 Feb 1973; USNM 80154, R/V Professor Siedlecki, cruise 601, sta. 29, South Georgia Island, sub-Antarctic, 54°32′S, 39°05′W, 201–210 m, 3 Dec 1986; USNM 98028, R/V Eltanin, cruise 22, sta. 1536, west tip of South Georgia Island, sub-Antarctic, 54°29′S, 39°22′W, 659–686 m, 8 Feb 1966; USNM 97996, R/V Eltanin, cruise 7, sta. 499, south of Coronation Island, South Orkney Islands, sub-Antarctic, 62°06′S 45°08′W to 62°06′S 45°10′W, 485 m, 20 Feb 1963; USNM 58162, R/V Eastwind, sta. 006C, west of Brabant Island, South Shetland Islands, Antarctic Peninsula, 64°50′S, 63°12′W, 283.5 m, 29 Jan 1966; USNM 76900, R/V Edisto, Deep Freeze

2.19.1 Description
Colonies sparsely branched (see Figure 2.18a), longest specimen (USNM 98086) 35 cm. Branchlets bottlebrush in arrangement although some colonies appear uniplanar where branchlets curve in two directions. Branchlets mostly simple with some secondary branching, up to 30 mm long, emanating in all directions (although most are in 3–4 directions) at an angle of between 60–90°. Colonies tend to be dark to light yellow.

Polyps are isolated, clavate (Figure 2.18b,d), 2.3–3.0 mm long (average 2.1 mm), upwardly inclined at 60–90°, 5–11 per cm at branchlet bases, 8–19 at tips. Each polyp has 8 longitudinal rows, 6–10 (average 8) scales in abaxial row (Figure 2.18c) reducing to 6–7 per row adaxially. Sclerites get shorter and wider from polyp tip to base.

Operculars are lanceolate to arrow-head shaped (Figure 2.19a–d); 530–710 µm tall (average 610 µm), 270–380 µm wide (average 325 µm), H:W 1.7–2.4 (average 1.9). The inner surface has a single large keel (keel side view Figure 2.19e) and layers of
lateral projections adjacent; these multiple sharp ridges adjacent to the keel lead to an irregular distal edge. Lateral areas above the tuberculate base on the inner surface are relatively smooth with a finely serrate edge. The outer surface has many sharp radial ridges oriented perpendicular to the distal edge (similar to those adjacent to the keel); the centre of the scale is smooth with a deep longitudinal valley (Figure 2.19d); granules proximally and some tubercles showing at the proximal edge.

Marginals are oval-shaped with a curved to pointed, pectinate distal edge (Figure 2.19f,g); scales 380–510 µm tall (average 438 µm), 340–480 µm wide (average 420 µm), H:W 1 (average 0.9–1.2), bearing a large keel on the inner surface with multiple serrate projections (Figure 2.19f); there are smooth areas adjacent to the keel and sparse tubercules cover the proximal half. The outer surface has sparse, large granules, some stretching into radial ridges from the central distal area; tubercles area also visible at the proximal edge (Figure 2.19g). The marginal has a finely serrate lateral edge. Adaxial marginals have a reduced keel with tubercles covering the majority of the inner surface of the scale.

Submarginals elliptical in shape (Figure 2.19h–l), 410–450 µm tall (average 430 µm), 600–610 µm wide (average 600 µm), H:W 0.7–0.75 (average 0.7). The proximal two-thirds of the inner surface is tuberculate with a smooth band across the distal third; there are 3 or 4 small keels and ridges perpendicular to the distal edge (Figure 2.19j–l). From a side view the keel and ridges have large serrations. The outer surface is smooth with sparse granules centrally (Figure 2.19h,i) and rare radial ridges and tubercles proximally. The distal edge has wide serrations; submarginals have a coarsely lobate proximal edge.

Body-wall scales quite wide and elliptical (Figure 2.19m–o), 600–620 µm (average 610 µm) wide, and short, only 290–400 µm tall (average 345 µm), with a H:W 0.5–0.7 (average 0.6). The inner surface is tuberculate with a smooth band along the distal edge (Figure 2.19m). Radial ridges along the distal edge of the outer surface result in a serrated distal edge; lateral areas are relatively smooth. There are granules across the proximal area with some tubercles visible at the proximal edge (Figure 2.19n,o).
Coenenchymal scales are smaller than body-wall scales, disc-shaped (Figure 2.19p), 150 µm diameter, with an irregularly serrate distal edge. The outer surface has granules and radial markings, the inner surface is tuberculate.

2.19.2 Distribution
Circum sub-Antarctic, 75–686 m depth.

2.19.3 Remarks
Some branches appear uniplanar, as in the holotype, as branchlets curve in two directions; Kükenthal (1912) refers to this as ‘biradial’. It is likely a result of a commensal annelid moulding branchlets around its body.

2.19.4 Comparisons
*Thouarella crenelata*, *T. chilensis* and *T. parachilensis* are morphologically alike and probably closely related (see Table 2.3). The shape of their polyps and sclerites are similar, although *T. parachilensis* has a more bulbous head than the more modestly clavate polyps of *T. crenelata*, and *T. chilensis* polyps are more boxy. The number of abaxial scales was used to differentiate between *T. crenelata* and *T. chilensis* (Kükenthal 1915), however, the range of abaxial scale counts in all three species overlap making this a poor defining character: *T. crenelata* 6–11 (average 8), *T. parachilensis* 8–15 (average 11), *T. chilensis* 6–8. As well as varying sclerite shapes and sizes, the most prominent difference among these species is the intensity of polyp placement at branchlets tips: *T. crenelata* has 9–19 polyps per cm (average 11), *T. parachilensis* 18–48 (average 32) and *T. chilensis* 21–28. The clustered polyp arrangement at branchlet tips of *T. parachilensis* are double the number of polyps per cm at branchlet bases: 9–30 (average 16) for *T. parachilensis*, whereas *T. crenelata* has relatively regular polyp placement along branchlets with just a modest increase in number towards tips: 5–11 (average 8). Although there is moderate overlap in these ranges *T. parachilensis* branchlet tips are ‘barrel-shaped’ with tight polyp placement and thus distinguishable from *T. crenelata*. The marginals of *T. crenelata* also have a more pronounced serrate distal edge and a much more deeply and distinctly ridged outer opercular surface (and most other sclerite categories) than *T. chilensis* or *T. parachilensis*. 
Thouarella crenelata and T. viridis are very similar. They were described as different species based on the number of scales in the abaxial row (Zapata-Guardiola & Lopez Gonzalez 2010a). This study reports an expansion in the number of scales in the abaxial row of T. crenelata from 9–10 (Kükenthal 1915; 1924) to 6–11 (average of 8), which overlaps that of T. viridis (6–7). Marginals of Thouarella crenelata have a pectinate distal edge whereas those of T. viridis, although having a strong keel, lack this character. Additionally, marginals of T. crenelata have a more tightly placed multiple keel running into one structure (serrated in side view), rather than a multiple simple keel with clear, straight, separate prominences, as seen in T. viridis.

Thouarella crenelata branching was originally described as similar to T. koellikeri (Kükenthal 1907), which has nearly pinnate branching, leaving one side of the axis naked, (described as “biradial” by Kükenthal 1919). Specimens identified here as T. crenelata are bottlebrush but can have a bilateral appearance when branchlets curve in two directions. There is a similar number of scales in the abaxial row of T. koellikeri as T. crenelata and both have polyps that are clavate, however, T. koellikeri has a simpler opercular keel.

Thouarella crenelata has a comparable number of scales and a similar number of polyps per cm as T. clavata. The former has more densely placed, longer polyps at branchlet tips and marginals with larger serrations in comparison to the smooth to finely serrate edge of the latter.

2.20 Thouarella clavata Kükenthal, 1908

Figures 2.20, 2.21

Thouarella aff. antarctica: Kükenthal, 1907: 203–4
Thouarella clavata Kükenthal, 1908: 11
Thouarella (Parathouarella) clavata: Kükenthal, 1919: 430–433, text figs. 209–212, pl.43, fig. 69
Thouarella (Thouarella) clavata: Cairns & Bayer, 2009: 27 (listed)

Material examined: holotype, ZMB Cni 6080, D.T.E Agulhasstrom, sta. 103, SW of Port Elizabeth, South Africa, 35˚10.5’S, 23˚2.0’E, 500 m, and 2 cm dried syntype,
MNHWU. As so little material was available for study the colony description was based on Kükenthal’s 1908 study and his more detailed 1919 record of this species. There is some confusion surrounding this species as the name “clavata” would suggest a club-shaped polyp however Kükenthal’s colony photo (Figure 2.20a) and text figures both have polyps that are distally flared (1919). The specimen from ZMB had clavate polyps, very unlike those seen in Kükenthal (1919); they look similar to T. crenelata in fact. As the MNHWU specimen more closely resembles images within Kükenthal (1919) I have based descriptions on this specimen, the syntype (Figure 2.20b,c). However, it was not possible to take SEM images of sclerites as the specimen was in a very poor condition. A second specimen of T. clavata was found (USNM 1140264) whose polyps and sclerites (Figure 2.20d, 21) are identical to the few SEM images obtained from the syntype.

2.20.1 Description
Axis base slightly curved, straighter main stem (no holdfast), branching is dense and in all directions (Figure 2.20a), however, branchlets curve to create two planes: ventral and dorsal. Branchlets are mostly 30 mm long (some 35 mm), often forked at the branchlet base, and orientated at almost 90° to the main stem. Dorsal plane branchlets are greatly shortened and proximal branchlets are also reduced in length.

Generally polyps are sparsely placed on branchlets (Figure 2.20d), 7–8 per cm. Polyps are distally flared (Figure 2.20c, 2.21c) with a low conical operculum; polyps are 1.4–1.7 mm tall (average 1.5), isolated and mostly in a single plane, however, Kükenthal’s description (1919) mentions dense polyp clusters covering 10 mm of branchlet tips. No polyps are on the main stem. Each polyp has 8 longitudinal rows of scales, 6–7 scales in two abaxial rows (Figure 2.21a) and 4 scales in each adaxial row.

Some inner opercular are very small; they are a tall–triangle shape (Figure 2.21d,h), 350–390 μm tall (average 370 μm), 150–230 μm wide (average 180 μm), H:W of 1.6–2.5 (average 2.1). Most opercular are larger with a wider triangle shape (Figure 2.21e–g), 590–770 μm tall (average 680), 340–420 μm wide (average 390), H:W of 1.5–1.9 (average 1.7). Opercular have a simple smooth keel on the inner surface (Figure 2.21e), are tuberculate proximally; the outer surface is deeply concaved and smooth (Figure 2.21g). The proximal edge is coarsely lobate; the distal edge is serrate.
Revision of *Thouarella*

Marginals triangular with angular base and tuberculate across proximal inner surface, 790–900 µm tall (average 860 µm), 480–650 µm wide (average 600 µm), H:W of 1.4–1.6 (average 1.5), keel is simple and flat with lateral projections (Figure 2.21j); the outer surface is covered in granules (Figure 2.21i).

Submarginals rounded with peaked distal edge, 690–750 µm tall (average 720 µm), 650–730 µm wide (690 average µm), H:W of 1. There is a small keel on the inner surface corresponding to the peak on the distal edge (Figure 2.21k). The remainder of the inner surface is tuberculate; the outer surface is covered in granules (Figure 2.21l).

Body-wall scales with circular distal edge, often elliptical (Figure 2.21m,n), 220–340 µm tall (average 260 µm), 250–490 µm wide (average 330 µm), H:W of 0.4–1.5 (average 0.9), the proximal edge is coarsely lobate. The inner surface is tuberculate, with a thin smooth band along the distal margin; the outer surface is relatively smooth.

Coenenchymal scales are smaller than body-wall scales, 120–220 µm tall (average 160 µm), 140–250 µm wide (average 190 µm), H:W of 0.5–1.2 (average 0.9), a circular to widely elliptical shape (Figure 2.21o–s) with a very smooth outer surface and tuberculate inner surface.

2.20.2 Distribution
Only known from type location, southwest of Port Elizabeth, South Africa, 500 m depth.

2.20.3 Remarks
The hand-drawn images in Kükenthal (1919, text figs. 209 and 210) show a modestly flared polyp and polyps on the plate image (XLIII) also appear distally flared however Kükenthal described them as clavate. The syntype from UMHWU was in a bad condition; sclerites were brittle and partially dissolved when they were cleaned in SEM stub preparation. However, the polyps were distally flared, as in Kükenthal (1919) illustrations. The ZMA sample afforded clearer SEM images but polyps were clavate and not like those illustrated in Kükenthal (1919) and the opercular keel was strong whereas it was described by Kükenthal (1907) as weak. The illustration of *T.*
clavata (Kükenthal 1919) shows a distally flared polyp with pointed marginals and the holotype description mentions clustered polyps. The UMHWU sample most closely resembles this description and I am thus inclined to believe this is the true T. clavata, although this makes the name T. clavata a mystery.

More samples of this species are required from the type location to complete a full description and improve comparisons (below).

Two polyp morphs were illustrated in Kükenthal (1919, Fig. 210), one polyp may have been brooding.

2.20.4 Comparisons
The number of polyps per cm, number of abaxial scales (5–6), and flared polyp shape would make this species comparable to T. antarctica, T. brucei, and T. andeep (Table 2.3). Thouarella antarctica has a bottlebrush colony shape and shorter, more rigid branchlets than T. clavata. The remaining species have a bottlebrush to bilateral appearance similar to T. clavata, although T. andeep has shorter more rigid branchlets and marginals that are more acutely pointed than those of T. clavata.

The polyps of T. clavata and T. brucei look almost identical. The species have some differences, with T. brucei colonies appearing more thinly branched than those of T. clavata (Figure 2.20a) however these differences in growth form are very minor. Thouarella brucei was originally described from Burdwood Bank and is found around Antarctica whereas T. clavata is found just off the south coast of South Africa so there could be a separation in geographical distribution. More material of T. clavata is required to confirm these two species are distinct.

2.21 Thouarella pendulina (Roule, 1908)
Figures 2.22, 2.23

Rhopalonella pendulina Roule, 1908: 4, pl.1, fig. 5–8.—Gravier, 1914: 70–77, text figs. 86–98, pl. 5, figs. 21–15.— Kükenthal, 1912: 290
Thouarella pendulina: Kükenthal, 1915: 151; 1919: 440; 1924: 302
Revision of *Thouarella*

*Thouarella (Thouarella) pendulina*: Cairns & Bayer, 2009: 27 (listed).—Zapata-Guardiola & López-González, 2010a: 179

*Thouarella antarctica*: Broch, 1965: 24–26, pl.2, figs. 5–7

**Material examined**: 3 cm fragment of holotype/paratype branchlet, MNHN–Octo.0000–0211 Expedition *Antarctique Francaise* (1903–1905), no. 640 collected, Booth (Wandel) Island; USNM 98341, R/V *Islas Orcadas*, cruise 876, sta. 111, Coronation Island, South Orkney Islands, sub-Antarctic, 60°25′36″S, 46°25′18″W, 97–128 m, 16 Feb 1976, 2 colonies; USNM 98359, R/V *Hero*, cruise 721, sta. 1075, Arthur Harbour, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°47′24″S, 64°7′36″W, 91–104 m, 23 Feb 1972, 3 colonies; USNM 1130339, R/V *Eltanin*, cruise 27, sta. 1896, Franklin Island, Victoria Land, Antarctica, 76°10′S, 168°17′E, 70–81 m, 18 Jan 1967; USNM 1130348, south end of Balleny Islands, Buckle Island, Antarctica, 66°53′S, 163°19′E, 55–164 m, 10 Feb 1974, 15 colonies; USNM 1130344, R/V *Hero*, cruise 731, sta. 1756, Arthur Harbour, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°47′14″S, 64°06′43″W, 91 m, 17 Feb 1973; USNM 85314, R/V *Hero*, cruise 721, sta. 1073, Arthur Harbor, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°47′30″S, 64°07′36″W, 64–100 m, 23 Feb 1972; USNM 98149, R/V *Hero*, cruise 691, sta. 33, Arthur Harbor, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 63°46′30″S, 61°47′51″W, 73–91 m, 13 Feb 1969; USNM 98150, R/V *Hero*, cruise 702, sta. 507, Port Lockroy, Wiencke Island, Palmer Archipelago, Antarctic Peninsula, 64°49′18″S, 63°31′21″W, 64–128 m, 17 Mar 1970; USNM 98158, R/V *Hero*, cruise 731, sta. 1944, Neumayer Channel, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°46′40″S, 63°25′33″W, 100–150 m, 11 Mar 1973; USNM 98170, R/V *Eltanin*, cruise 6, sta. 435, Astrolabe Island, Bransfield Strait, Antarctic Peninsula, 63°14′S, 58°42′W, 73 m, 8 Jan 1963; USNM 98171, R/V *Eltanin*, cruise 6, sta. 436, Astrolabe Island, Bransfield Strait, Antarctic Peninsula, 63°13′S, 58°47′W, 73 m, 8 Jan 1963; USNM 98228, R/V *Islas Orcadas*, cruise 876, sta. 107, Coronation Island, South Orkney Islands, sub-Antarctic, 60°26′30″S, 46°22′48″W, 102–108 m, 16 Feb 1976; USNM 98335, off south end of Buckle Island, Balleny Islands, Antarctic, 66°53′S, 163°19′E, 55–164 m, 10 Feb 1974; USNM 98343, USAP, SOSC–L46, Antarctic, 63°17′S, 62°09′W, 12 Jan 1973; USNM 98360, R/V *Hero*, cruise 721, sta. 5438, Arthur Harbor, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°47′27″S, 64°07′W, 32–90 m, 27 Mar
1972; USNM 98363 and 98390 (same location), R/V Islas Orcadas, cruise 876, sta. 112, Coronation Island, South Orkney Islands, sub-Antarctic, 60°27′48″S, 46°23′06″W, 93–102 m, 16 Feb 1976; USNM 1120943, R/V Hero, cruise 691, sta. 28, south of Low Island, South Shetland Islands, sub-Antarctic, 63°25′30″S, 62°09′30″W, 91 m, 10 Feb 1969; USNM 1129159, R/V Eltanin, cruise 32, sta. 2059, south of Pennall Bank, Ross Sea, Antarctica, 77°58′30″S, 178°4′58″E, 655 m, 25 Jan 1968; USNM 1130330, R/V Hero, cruise 691, sta. 33, Hoseason Island, Bransfield Strait, Antarctic Peninsula, 63°36′30″S, 61°47′51″W, 73–91 m, 13 Feb 1969; USNM 1130342, R/V Eltanin, cruise 27, sta. 1896, Victoria Land, Franklin Island, Ross Sea, Antarctic, 76°10′01″S, 168°16′58″E, 70–81 m, 18 Jan 1967; USNM 1130344, R/V Hero, cruise 731, sta. 1756, Arthur Harbor, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°47′13″S, 64°6′42″W, 91 m, 17 Feb 1973; USNM 1130345, R/V Eltanin, cruise 51, sta. 5762, Moubray Pennell Bank, Victoria Land, Ross Sea, Antarctic, 76°2′6″S, 179°57′W, 347–358 m, 9 Feb 1972; USNM 1130347, R/V Hero, cruise 731, sta. 1915, west of Bonaparte Point, Arthur Harbor, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°47′S, 64°4′32″W, 35–60 m, 6 Mar 1973; USNM 1130349, R/V Hero, cruise 731, sta. 1823, Arthur Harbor, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°47′20″S, 64°6′58″W, 90–110 m, 20 Feb 1973; SMF, EPOS 03, sta. 212, GSN 2, Weddell Sea, 60°50′S, 55°38.9′W, 414 m, 15 Jan 1989; SMF, Terre Adélie, Antarctica, D114, Patrick Arnaud leg, no precise location or depth information; SMF, R/V Hero, sta. 90, South Janus Island, Palmer Archipelago, Antarctica, 73–100 m, 23 Mar 1972, no precise location information; SMF, R/V Hero, sta. 90, South Janus Island, Palmer Archipelago, Antarctica, 62–90 m, 23 Mar 1972, no precise location information.

2.21.1 Description
Holotype 34.5 cm long, 60 mm at widest point. Colony bottlebrush (Figure 2.22a,b), seemingly flagelliform but with occasional branching. Branchlets leave main axis in at least 4 directions, extend horizontally, then droop, most have secondary and tertiary branching which can appear simple as splitting is very close to the axis. Branchlets 1–3 mm apart, up to 40–42 mm long. Axis is woody with fine longitudinal striations, flexible, except at colony base which is thickened into a calcified holdfast; axis 5–6 mm diameter at base.
Polyps are crowded (Figure 2.22c,d), 27–41 per cm (average 34), 0.9–1.2 mm long (average of 1 mm), 2–3 times longer than their diameter, irregularly arranged on branchlets. There are fewer polyps at branchlet bases, and they are more clustered at the centre and tips of branchlets; there are no polyps on the main stem. Polyps are cylindrical at their base, thicker towards the operculum, with a slightly rounded polyp shape and pointed distal head. There are 4–5 scales in abaxial rows (Figure 22d), fewer in adaxial rows.

Eight operculars create a tall cone rising above marginals, the two adaxial operculars are reduced in size. Operculars are in two alternate circles, one inner, one outer, however adaxial operculars tend to be inside inner opercular circle. There are 6–7 isosceles triangle to arrowhead-shaped operculars, each having an acute pointed distal edge (Figure 2.23 b–e). Size ranges from 260–490 µm long (average 357 µm), 150–320 µm wide (average 240 µm), average H:W 1.5. There are one or two adaxially placed, smaller, diamond-shaped operculars (Figure 2.23a). The outer surface is moderately concave longitudinally and there are sparse granules originating from the proximal area, sometimes aligned radially. The inner surface has a simple keel, which may be half the opercular length (Figure 2.23c,d), sometimes channelled and flattened; the proximal half of the inner surface is tuberculate.

Marginals in two, inner and outer, alternate circles of four, although adaxial marginals are reduced and do not conform to this pattern (Figure 2.22e). Six of eight marginals are triangular (Fig. 2.23f–j), taller, wider, and rounder than operculars, 330–650 µm tall (average 460 µm), 250–430 µm wide (average 330 µm), average H:W 1.4. Generally inner lateral marginals have a pointed distal edge that can lean right or left (Fig. 2.23g,h). The remaining two adaxial marginals are reduced in size and more circular; reduction can be extreme such that marginals are sometimes not visible from anterior view. The outer surface has sparse granules proximally and some tubercles at the proximal margin; the inner surface has a modest keel and is tuberculate proximally with a thin smooth band at the distal edge. Some abaxial submarginals have a pointed distal edge (Fig. 2.23k).

Large angular, circular and elliptical body-wall scales of variable number cover the polyp (Fig. 2.23l–o) in rows; they are 210–600 µm long (average 350 µm), 230–510
μm wide (average 340 μm), average H:W 1, and larger towards the polyp anterior. The outer surface has granules, denser at the base dispersing towards the distal edge; the inner surface is tuberculate. All above sclerites have a finely serrate distal edges and roughly lobate proximal edge.

Coenenchymal scales are small, 150–280 μm tall (average 220 μm), 120–200 μm wide (average 165 μm), irregularly circular (Fig. 2.23p–t), average H:W 1.34. The inner surface is tuberculate with sparse granules on the outer surface.

2.21.2 Distribution
Circum-Antarctic, 32–655 m depth.

2.21.3 Remarks
Thouarella pendulina was originally described within Rhopalonella, a genus differentiated from Thouarella in having densely arranged polyps (Roule 1908). This tight clustering remains one of the distinguishing characteristics of this species although it is now considered to be within Thouarella.

Thouarella pendulina does have two alternating rings of marginals however adaxial marginals are usually not synchronised with the alternating pattern and are reduced and thus not visible from the anterior (Fig. 2.22e). Polyps of Thouarella pendulina can be compressed against the stem, reducing the number of adaxial body-wall scales per row to one or two. This is an oddity within Thouarella whose polyps generally depart the stem at 45–60° and have at least 3–4 adaxial body-wall scales per rows.

Thouarella pendulina has a variable gross morphology. Some colonies have tightly packed stems of simple branchlets, which themselves are densely covered in polyps; some have sparser branching (1–2 per cm) with fewer polyps per cm on branchlets. Others have branching between these extremes.

2.21.4 Comparisons
There are several species that have a similar number of abaxial scales (4–5) as T. pendulina and should thus be compared here (Table 2.3).
Thouarella pendulina could most easily be mistaken for *T. hicksoni*, whose colony is bottlebrush and polyps similar sized (with 4–5 scales in the abaxial row), shaped, and clustered (although *T. pendulina* more so). However, operculars of *T. hicksoni* are tongue-shaped, whereas those of *T. pendulina* are triangular/rhomboid with a pointed distal edge. Also, the inner surface of opercular of *T. hicksoni* do not have a well-defined keel, instead tending to have an area of longitudinal ridges.

Although having a similar number of abaxial body-wall scales as *T. pendulina*, *T. brucei* has an almost bilateral colony appearance (it is technically bottlebrush), polyps that are larger and more flared, and larger opercular than those of the former.

*Thouarella andeep* also has 4–5 scales in the abaxial row however polyps are flared and larger, making opercular and marginals larger than *T. pendulina* sclerites; polyps are also less clustered, and more splayed than those of *T. pendulina*. Additionally, the outer surface of scales of *T. andeep* are finely striated whereas those of *T. pendulina* are smooth with sparse granules.

The gross morphology of some ramified *T. pendulina* is very similar to that of *T. variabilis*. *Thouarella variabilis* has longer polyps that are less clustered and almost spinose marginals, absent in the former.

*Thouarella striata* has larger polyps than *T. pendulina* and distinctive striations on the inner surface of sclerites (lateral to the keel on marginals and perpendicular to the distal edge on other sclerites) that are absent in *T. pendulina*.

*Thouarella pendulina* has a similar shaped polyp to *T. longispinosa* (=*Dasystenella acanthina*) however the former has 8 marginals (not 5 as in *Dasystenella*) and its polyps do not occur in whorls.

2.22 *Thouarella chilensis* Kükenthal, 1908

Figures 2.24, 2.25

*Thouarella chilensis* Kükenthal, 1908: 11; 1912: 302–4 (incorrectly described as new), text figs. 4–8, pl.11, fig. 5; 1915: 150 (key)
Thouarella (Epithouarella) chilensis: Kükenthal, 1919:436, text fig. 215; 1924: 300.—Cairns & Bayer, 2009: 28 (listed)

Material examined: holotypes, C1780, ZMH, Iquique, Chile, no depth, 14 cm colony; NHM89.5.27.43, H.M.S. Challenger, sta. 148A, off Crozet Island, sub-Antarctic, 46°5’S, 51°52’E, 1005 m, 3 Jan 1874, 1 fragment; USNM 1129149, R/V Islas Orcadas, cruise 575, sta. 65, Candlemas Island, South Sandwich Islands, Scotia Sea, 56°44’17”S, 26°58’36”W, 302–375 m, 31 May 1975; USNM 97967, R/V Hero, cruise 715, sta. 873, Thetis Bay, Tierra del Fuego, Argentina, 54°34’S, 65°50’W, 118 m, 26 Oct 1971; USNM 97966, R/V Hero, cruise 715, sta. 873, Thetis Bay, Tierra del Fuego, Argentina, 54°34’S, 65°50’W, 119 m, 26 Oct 1971, 2 colonies (8.5 cm, 9 cm); USNM 1099387, R/V Lawrence M. Gould, cruise LMG06–05, sta. 2, off Isla Grande de Tierra del Fuego, Argentina, South Atlantic Ocean, 53°47’S, 64°53’W, 120 m, 15 May 2006, 3 small fragments; USNM 98283, R/V Eltanin, cruise 11, sta. 974, north of Cape San Diego, Tierra del Fuego, Argentina, South Atlantic Ocean, 53°33’S, 64°56’W, 119–124 m, 12 Feb 1964, 7 colonies; USNM 97965, R/V Hero, cruise 715, sta. 870, north of Islas de los Estados, Argentina, 54°34’S, 64°00’W, 84 m, 24 Oct 1971; MNHN, MD 42, sta. 5, CP 30, Williams Bank, SE Indian Ocean, 53°18’S, 73°19’E, 250 m, 15 Jan 1983; SMF, EPOS 3, sta. 290, AT 24, Cape Norvegia, Weddell Sea, Antarctica, 71°05.9’S, 12°34’W, 522–531 m, 19 Feb 1985; ZMH, R/V W. Herwig, sta. 278, Patagonian Shelf, SW Atlantic, 40°57’S, 56°52’W, 200 m, 21 Jun 1966; ZMH, R/V W. Herwig, sta. 142, Patagonian Shelf, SW Atlantic, 42°06’S, 57°55’W, 788–765 m, 04 Jan 1971; ZMH, R/V W. Herwig, sta. 590, Burdwood Bank, SW Atlantic, 54°39.1’S, 61°44.6’W, 940–960 m, 1978; MNHN, MD 24, sta. 42, CM 59, Léna Bank, sub-Antarctic, 52°59’S, 44°22.7’E, 295–325 m, 4 Sep 1980; SMF, R/V W. Herwig 1971, sta. 277, 52°S, 55°20’W, 1200 m; SMF, MD 42, sta. 22, 1968, no location information.

2.22.1 Description
Holotype is a single bottlebrush branch (Fig. 2.24a), although other colonies are sparsely branched, similar to T. parachilensis (Fig. 2.28a). Short, 15 mm, rigid branchlets depart the main axis in at least 4 directions. Colonies are generally a light yellow to white shade.
Polyps are isolated, upwardly inclined at 45–80°, 2.5–2.75 mm long, 11–23 per cm on branchlets, densely placed at branchlet tips, 21–28 per cm (Fig. 24b). Polyps have 8 longitudinal rows and 6–8 scales in each abaxial row (Fig. 2.24c).

Opercular scales triangular to arrow-head shaped (Fig. 2.25e–g), 415–510 µm tall (average 460 µm), 200–300 µm wide (average 250 µm), H:W 1.65–2.00 (average 1.8). The outer surface is smooth with granules arranged radially from the proximal central area (Fig. 2.25e,f); the inner surface bears a complex, multiple keel (Fig. 2.25g). Accessory operculars are occasionally present (Fig. 2.25a–d); approximately 225–150 µm tall, 100–115 µm wide, average H:W of 1.7 (1.5–1.95).

Marginals are a wide triangle shape (Fig. 2.25h–l), 520–565 µm tall (average 535 µm), 460–560 µm wide (average 510 µm), H:W 0.9–1.2 (average 1). The outer surface has granules arranged radially from the proximal central area (Fig. 2.25h,i,l). The inner surface has a strong multi-keel with rough edges (Fig. 2.25j,k); sometimes keel has lateral extensions that are visible from the outer surface. The proximal inner surface is covered with tubercles and areas lateral to the keel are often ridged.

Submarginals are more rounded, wider and shorter than marginals, having a modest distal point (Fig. 2.25m–o), H:W of 0.8, height around 350 µm, width around 400 µm. The inner surface is tuberculate, with occasional ridges perpendicular to distal edge. The outer surface has granules in a radial pattern, similar to marginals.

Body-wall scales are roughly elliptical (Fig. 2.25p–t), 290–400 µm tall (average 350 µm), 445–700 µm wide (average 560 µm), H:W 0.4–0.8 (average 0.6). The outer surface bears peaked granules towards the central proximal area that develop into ridges towards the distal edge; tubercles are visible at the proximal edge. The inner surface is tuberculate, with a relatively smooth band along the distal edge that often has small ridges. The proximal edge of all sclerites is coarsely lobate with a distal edge that is irregular to serrate (unless otherwise stated).

Coenenchymal scales are similar shapes to body-wall scales except more circular and slightly smaller; down to 250 µm diameter (Fig. 2.25u–w).
2.22.2 Distribution
Patagonian Shelf, southern Atlantic Ocean, Antarctic Peninsula and southern Indian Ocean, 84–960 m depth.

2.22.3 Remarks
The holotype of *T. chilensis* was located in the ZMH however it was not marked as a holotype. The location and date of inscription by Kükenthal (1908) match the original type description and I thus believe C1780 to be the holotype. This specimen was originally listed by the collector Schnehagen (possibly Capt. J. Schnehagen, although his collections were primarily from the South China Seas) as *T. antarctica* and redescribed by Kükenthal in 1908.

The dense cylindrical clusters of *T. chilensis* polyps were used by Kükenthal to distinguish this species from *T. affinis* and *T. crenelata* (Kükenthal 1915; 1924). As diagrams were not clear there have been several samples of *Thouarella* with denser clusters of polyps at branchlet tips than the holotype of *T. chilensis*; these are in fact a new species, *T. parachilensis* (described below). A sample of *T. chilensis* was also incorrectly considered to be a voucher of *T. antarctica* (USNM 97966; see Cairns & Bayer 2009).

2.22.4 Comparisons
The dense polyp arrangement of *T. chilensis* makes it easily mistaken for both *T. antarctica* and *T. parachilensis*. Sclerites of *T. chilensis* have an ornamented distal edge with several ridges adjacent to the keel. Marginals of *T. antarctica* have a smoother edge that are more acutely pointed than those of *T. chilensis*. The latter also has, on average, more scales in abaxial rows than the former. *Thouarella antarctica* opercular also tend to be thinner and more delicate than those of *T. chilensis*. Polyps of *T. parachilensis* are rounded and globular with 8–15 scales in the abaxial row; in contrast, polyps of *T. chilensis* are more squat and boxy with just 6–8 abaxial scales.

Polyps of *T. chilensis* are very similar to those of *T. crenelata*, both species having similar polyp and sclerite sizes and shapes. Polyps of *T. chilensis* are more clustered on branchlets than those of *T. crenelata*, whose polyps are more evenly spaced. Without the holotype of *T. crenelata* it is difficult to be certain, however, specimens
and literature seen within this study suggest that *T. crenelata* polyps are more rounded than those of *T. chilensis*.

*Thouarella chilensis* has 7–10 abaxial body-wall scales, more than *T. viridis* (6–7) and *T. affinis* (6–7) which both also have sparser polyp placement, taller body-wall scales with a higher H:W. *Thouarella affinis* also has flared rather than clavate polyps.

*Thouarella koellikeri* has a similar number of scales in the abaxial row as *T. chilensis*. Sclerites of the former are more delicate with thinner body-wall scales, marginals that curve away from polyp body and have a simple keel whereas sclerites of the latter are thicker with more ornamented marginals that have a wide, complex keel (the lateral extensions of which can be seen from an abaxial view).

### 2.23 Thouarella hicksoni Thomson, 1911

Figures 2.26, 2.27

*Thouarella hicksoni* Thomson, 1911: 886–887, pl.44, fig. 3, 3a, pl. 45, fig. 1.—Kükenthal, 1919: 439–40; 1924: 301–2.—Stiansy, 1940:32, text fig. G, pl. 4, fig. 21.—Williams, 1992: 277–280, fig. 1H, 66–68.—Cairns & Bayer, 2009: 27 (listed)

*Thouarella Hicksoni*: Tixier-Durivault, 1954:625

*Material examined:* 8.5 cm and 4.5 cm fragments of holotype, NHM 1962.7.20.36, off Cape St. Francis, South Africa, 135 m, rocky substratum, 19 Feb 1902; USNM 53911, south of Port Elizabeth, South Africa, 34˚15' S, 25˚05' E, 11 m, SCD 8–J, collected by J. Day, 1958, 2 colonies; USNM 53912 + USNM 53813 (same location), SCD 3–D, South Africa, 34˚30' S, 24˚40' E, collected by J. Day, 102 m, 18 Apr 1958.

As only a small fragment of the holotype was seen I could not comment on branching from the central stem and have relied on the original description and additional specimens (listed above) for the description.

#### 2.23.1 Description

Colony is bottlebrush in shape, tapering at the tip (Figure 2.26a). Branchlets emanate in 4 directions approximately perpendicular to main stem, and are tightly placed at 1
CHAPTER TWO

mm intervals (Figure 2.26b,e); secondary and tertiary ramification is common, occurring close to branchlet base. Axis is yellow, iridescent, and has fine longitudinal striations when bare.

Polyps rarely occur on stem; they are usually isolated and can be spiralled in three directions but this is inconsistent. Polyps modestly flared, 1–1.25 mm long, H:W 1.79–1.95, clustered (16–22 per cm, less towards branchlet bases). Each polyp has 7 longitudinal rows of body-wall scales reducing to 4 rows at base; 4–5 scales in the abaxial rows (Figure 2.26c), 3–4 in the outer and inner lateral rows, and 2–3 scales in the adaxial rows.

Eight opercular, 300–360 µm tall (average 330 µm), 170–210 µm wide (average 190 µm), average H:W 1.7. Two to three of the largest opercular have a pointed distal edge (Figure 2.27e); remainder are tongue-shaped (Figure 2.27d). Opercular have a longitudinally concave outer surface, which is smooth, with sparse tubercles at the proximal edge; the inner surface has longitudinal median ridges or a small simple keel, and the proximal third is tuberculate.

Beneath the eight opercular there are 2–4 (perhaps more in other colonies) accessory opercular (Figure 2.27a–c) that are 200–210 µm long (average 200 µm), 110 µm wide; a fraction the size of regular opercular, with a H:W 1.75–1.9 (average 1.8). They have a smooth inner and outer surface, although some have small median longitudinal ridges or a small keel (as with larger operculars; Figure 2.27a).

Marginals form two alternate circles of 4 inner and 4 outer scales, although the pattern is not strict. Marginals have a wide circular to oval base, and are pointed distally (Figure 2.27f–h), with a complex keel on the inner surface (lateral keel projections can sometimes be visible from an abaxial view), 350–480 µm tall (average 400 µm), 220–320 µm wide (average 280 µm), average H:W 1.4 (range of 1.1–2). Adaxial marginals are often shorter with a reduced or absent distal point (as compressed against polyp). The inner surface is tuberculate with smooth lateral areas adjacent to the keel; the outer surface is smooth with granules extending from the proximal central area, gradually diminishing in number towards the distal edge.
Revision of *Thouarella*

Submarginals elliptical with a smooth, rounded distal edge; abaxial submarginals often have a moderately pointed distal edge (Figure 2.27i,j). Submarginals are 250–270 µm tall (average 260 µm), 260–280 µm tall wide (average 270 µm), average H:W 0.9. The inner surface has small, simple single or double (and rarely treble) keels; the central area is tuberculate with a smooth band along the distal edge lateral to keels. The outer surface is identical to body-wall scales, as described below.

Body-wall scales semi-circular (Figure 2.27k), fan-shaped (Figure 2.27o) to circular (Figure 27l–n), with an irregularly lobate proximal edge, 190–270 µm tall (average 220 µm), 140–310 µm wide (average 240 µm), average H:W 0.9 (range of 0.7–1.4). The outer surface is covered with granules proximally, some tubercles at proximal edge; the inner surface is tuberculate with a smooth band along the distal edge. The proximal edge of all sclerites is roughly lobate; the distal edge is finely serrated.

Coenenchymal scales are circular (Figure 2.27p), 110–150 µm tall (average 130 µm), 100–180 µm wide (average 140 µm), average H:W 1, having a smooth outer surface and tuberculate inner surface.

2.23.2 Distribution
Only known from Port Elizabeth region, South Africa, 11–135 m depth.

2.23.3 Remarks
Contrary to Thomson’s description (1911), stems at the colony base tend to be shorter; likely due to wear.

A small, circular, pebble-encrusted casing (perhaps an egg case) was found within branchlets of the holotype.

2.23.4 Comparisons
*Thouarella hicksoni* and *T. pendulina* are very similar, sharing a comparable number of abaxial body-wall scales, polyp length, and clustered polyp arrangement. However, *T. hicksoni* has fewer polyps per cm and opercular that are tongue-shaped with a blunt, rounded distal edge (Table 2.3).
Thouarella striata, T. variabilis, and T. andeep have a similar number of scales in the abaxial rows as T. hicksoni however these species have large, distally flared polyps arranged less densely on branchlets than T. hicksoni.

Thouarella hicksoni has a similar number of scales in the abaxial rows, and marginal and opercular scale shapes similar to T. brucei, however, the former generally has smaller (noting that some additional specimens of T. brucei have smaller polyps than the holotype), more pointed polyps, more clustered, finer, flexible branchlets that are arranged in true bottlebrush form.

2.24 Thouarella bipinnata Cairns, 2006

Thouarella bipinnata Cairns, 2006: 176–181, figs. 8, 9.—Cairns & Bayer, 2009: 28 (listed)

Material examined holotype, USNM 53015, Gerda 177, Straits of Florida, off northwest corner of Little Bahamas Bank, 27˚17’N, 79˚34’W, 686 m depth, 30 Jun 1963. And, all from original description (Cairns 2006).

2.24.1 Description

Description modified from original (Cairns 2006).

Colonies uniplanar and delicate, irregularly pinnate to bipinnate (occasionally 2 branchlets occur contiguously on the same side of the stem). Largest specimen (holotype) is 9 cm tall and 10 cm wide with a basal axis diameter of 1.6 mm. Holotype has 4 larger diameter branchlets near the colony base, each with a series of smaller branchlets, up to 30 mm long, roughly alternate at intervals of 5–15 mm. Axis golden-yellow with a white calcareous discoidal holdfast.

Polyps occur on main stem and branchlets in a roughly alternating arrangement. Occasionally 2 polyps are arranged opposite each other but there is no consistent tendency towards pairing or whorls. Holotype polyps are orientated toward one face of the colony. Polyps are spaced 11–14 per cm, stand perpendicular to branchlet, are slightly clavate, up to 2.4 mm long with a H:W of 1.8–2.2. Each polyp has 6–8 longitudinal rows, the scales increasing in size proximally as polyp diameter.
decreases so that at the polyp base there are no adaxial scales and the inner-laterals are either reduced or absent.

Opercular scales are lanceolate-shaped, maximum 900 µm tall, H:W of 2.1–2.9 and form a well-defined operculum. The opercular outer surface has radial ridges from the proximal centre and has a deep concave, corresponding to a large simple keel on the inner surface which has many adjacent ridges; tubercules cover the proximal third.

Marginals are arranged in inner and outer ring of 4 scales each with edges overlapping. Marginal scales are the same size as opercular but more rounded in shape with a pointed distal edge and lower H:W of 1.3–2.1. The inner surface bears a complex keel with wide lateral projections; remaining inner surface is tuberculate with a thin smooth distal band along the lateral edge. The outer surface has modest radial ridges from the proximal centre.

Submarginals are oval with a short, pointed distal edge, 500–600 µm tall with a H:W of 0.9–0.95. The inner surface is tuberculate with a wide smooth edge distally and ridges perpendicular to the edge; the outer surface is mostly smooth with rare granules arranged radially from proximal centre.

Body-wall scales are roughly rectangular, sometimes rounded, usually broader than wide (H:W of 0.85–0.9); can be 800 µm wide towards the polyp base. The outer surface is covered in granules and sometimes ridged; inner surface is tuberculate, often with ridges perpendicular to the distal edge. As with all sclerites the distal edge is finely serrated and proximal edge coarsely lobate.

Coenenchymal scales are irregular shaped, up to 600 µm in diameter, and have a highly concave outer surface.

For images see Cairns (2006).

2.24.2 Distribution
Disjointed distribution: Blake Plateau, off northern Florida, and Straits of Florida, off Little Bahamas Bank, to Guyana, 507–1000 m depth.
2.24.3 Comparisons

*Thouarella bipinnata* is the only species within Group 1 that is truly uniplanar with bipinnate to pinnate branching.

There are several species that can appear bilateral e.g. *T. koellikeri*, which also has roughly alternating polyps of a similar size to *T. bipinnata*, however, *T. koellikeri* polyps are more clavate, there are double the number of scales in the abaxial row (7–10, rather than 3–5 in *T. bipinnata*) and *T. koellikeri* has a lower opercular cone than *T. bipinnata*. *Thouarella affinis* and *T. viridis* can both appear bilateral however the polyps of both have more scales in the abaxial row (6–7) than *T. bipinnata*. *Thouarella brucei* and *T. andeep* can have a bilateral colony shape and both have 4–5 scales in the abaxial row of polyps, comparable to *T. bipinnata*. However, *T. bipinnata* has slightly clavate polyps, very different from the distally flared polyps of *T. andeep* and *T. brucei*.

2.25 *Thouarella viridis* Zapata-Guardiola and López-González, 2010a

*Thouarella viridis* Zapata-Guardiola & López-González, 2010a: page numbers not available.

Holotype (not examined), ZMH C11744, ANT XIX/5, sta. PS61/164–01, west of South Georgia, Antarctica, 53°23.8’S, 42°42.03’W, 312.5–321.6 m, 9 Apr 2002.

*Material examined:* USNM 1128949, paratype, Antarktis XIX/5, R/V Polarstern, sta. PS61/167–01, west of South Georgia Island, sub-Antarctic, 53°23.68’S, 42°42.23’W, 306–342.7 m, 9 Apr 2002, 1 colony, 1 fragment; USNM 1130303 and USNM 98027 (same location), R/V *Eltanin*, cruise 22, sta. 1536, west tip of South Georgia Island, sub-Antarctic, 54°30’S, 39°20’W, 659–686 m, 8 Feb 1966; USNM 78401, R/V *W. Herwig*, sta. 217, Le Maire Strait, Tierra del Fuego, Argentina, 54°22’S, 64°42’W, 106–110 m, 23 Sep 1962; ZMH, R/V *W. Herwig*, sta. 328, Patagonian Shelf, SW Atlantic, 42°52’S, 58°38’W, 1200 m, 22 Feb 1971; ZMH, R/V *W. Herwig*, sta. 285, Patagonian Shelf, SW Atlantic, 42°19’S, 58°01’W, 825 m, 21 Jun 1966; ZMH, R/V *W. Herwig*, sta. 311, Patagonian Shelf, SW Atlantic, 46°54’S, 60°28’W, 480 m, 18 Feb 1971; ZMH, R/V *W. Herwig*, sta. 243, Burdwood Bank, SW Atlantic,
Revision of *Thouarella*

54°57’S, 56°54’W, 500 m, 04 Feb 1971; ZMH, R/V *W. Herwig*, sta. 271, south Falkland Islands, sub-Antarctic, 52°40’S, 60°39’W, 405 m, 09 Feb 1971.

2.25.1 Description

Description modified from Zapata-Guardiola and López-González (2010a).

Holotype consists of a fragment of one colony. The main stem has two lateral branches and there is a third row of branching that can be curved, giving the colony a bilateral appearance although it is bottlebrush. Branchlets up to 30 mm long, 7–8 per cm, usually simple with occasional secondary branching. Fresh specimens are a shade of green, fading to white after preservation. Axis ochre coloured, stiff and thick, basal axis diameter of 4 mm.

Polyps clavate, 1.5–2.1 mm long, with a conical operculum, isolated but emanating from branchlets in irregular spirals, more clustered towards branchlet tip and sparser at base, even occasionally opposite, average 14–15 per cm. Polyps have 8 longitudinal rows, 6–7 scales in each abaxial row.

Opercular scales lanceolate, some with a wide bilobed base, 620–780 µm long, 470–640 µm wide. The inner surface bears a prominent simple keel, often with lateral ridges and longitudinal ridges adjacent to keel; dense tubercles cover the proximal third of the scale. The outer surface is deeply longitudinally concave, corresponding to keel on the inner surface; proximal surface has radial ridges from proximal centre and granules distally.

Marginal scales are pentagonal to a wide triangle shape, 450–630 µm long, 470–640 µm wide. The inner surface has a multiple-keel with smooth areas adjacent although some have a longer keel area; tubercles cover the proximal two-thirds to three-quarters of the inner surface. The outer marginal surface is covered with low relief granules.

Body-wall scales and submarginals undifferentiated; both fan-shaped with a rounded distal edge, wider than tall, 270–510 µm tall, 340–740 µm wide, decreasing in size towards polyp base. The inner surface is tuberculate, with a smooth distal band.
broken by several ridges perpendicular to the distal edge; the occurrence of ridges decreases from polyp tip to base. The outer surface is similar to marginals. All sclerites have a coarsely lobate proximal edge.

Coenenchymal scales round to elliptical-shaped, up to 130–360 µm long. Inner surface tuberculate, outer surface with closely spaced granules that stretch into ridges. Edge is irregular with warts proximally; distal edge is finely serrate.

For images see the original description (Zapata-Guardiola and López-González 2010a).

2.25.2 Distribution
These specimens extend this species range from the Falkland Islands and South Georgia Island, west to the Patagonian Shelf. Found from 106–825 m depth.

2.25.3 Remarks
Unusual green shading makes this species easily recognisable.

2.25.4 Comparisons
Operculars of *T. viridis* are laterally thin with a deep longitudinal groove on the outer surface, a complex keel and many longitudinal adjacent ridges on the inner surface. Conversely, *T. antarctica* has a relatively shallow groove on the outer surface and the keel is more focused, with multiple ridges extending from a central point. *Thouarella antarctica* also has polyps that are more flared than *T. viridis*, which are clavate.

*Thouarella koellikeri* has more scales in the abaxial row than *T. viridis* (7–10 in the former, 6–7 the latter), so although polyps are a comparable size, scales of *T. koellikeri* are generally smaller. Marginal keels of the former are simple whereas the latter keels have adjacent ridges. *Thouarella koellikeri* abaxial body-wall scales also lack the distinctive teeth/ridges found on *T. viridis*.

*Thouarella parachilensis* has very clustered polyps at branchlet tips that are absent in *T. viridis*, and the flat operculum of the former differs markedly from the tall, rounded operculum of the latter.
Thouarella affinis has a similar number of scales in the abaxial row as T. viridis however marginals of the former have simpler keels than the latter. The latter also has multiple ridges on the inner distal edge of submarginals and some body-wall scales, absent in the former.

Polyps of T. crenelata are clavate, similar to those of T. viridis, however, the latter has a tall operculum whereas the former has an operculum not visible in lateral view. Thouarella crenelata also tends to have more scales in the abaxial row than T. viridis and the latter has multiple keels and deep ridges absent in the former.

2.26 Thouarella minuta Zapata-Guardiola and López-González, 2010a

Thouarella minuta Zapata-Guardiola & López-González, 2010a: page numbers not available

Holotype (not examined), ZIZMH C11742, ANT XXI–2, sta. PS65–166–01, Austasen, Antarctica, 70°56.83’S, 10°32.61’W, 253.2–338 m, 15 Dec 2003.

Material examined: paratype, USNM 1128948, ANT XXI/2, sta. PS65/166–01, Austanen, Cape Norvegia, Antarctica, 70°56.83’S, 10°32.61’W, 253.2–338 m, 15 Dec 2003; USNM 82873, Deep Freeze II, sta. 17, Staten Island, Tierra del Fuego, Argentina, 71°18’S, 13°32’W, 238 m, 27 Dec 1956; SMF, EPOS 3, sta. 257, AT19, Weddell Sea, Cape Norvegia, Antarctica, 71°39.5’S, 12°34.7’W, 301–330 m, 15 Feb 1989.

2.26.1 Description
Description modified from original (Zapata-Guardiola and López-González 2010a):

Holotype a single branch 66 cm long, 5.5 cm wide, branchlets emerge from all sides in a bottlebrush arrangement although the basal 9 cm of the main branch is without branchlets. Branchlets up to 45 mm long, simple at base then splitting into two sometimes three branchlets; terminal branchlets are up to 35 mm long. Axis woody, light brown in colour, diameter 3 mm; holotype fixed to a rock by a greyish discoidal holdfast, 13 mm diameter.
Polyps alternate or in loose spirals, 11–18 per cm, very small, 0.71–0.96 mm long, 0.3–0.44 mm wide, cone-shaped and appressed against branchlets and main stem. Polyps have 3–4 abaxial scales in 5 longitudinal abaxial rows, a quick reduction from 8 marginals at the polyp tip.

Tall, conical operculum made of isosceles triangle or spoon-shaped opercular scales 250–450 µm long, 70–160 µm wide, reduced in size on adaxial side of polyp. The inner opercular surface has a simple, sometimes flat surfaced keel and tubercules across the keel base with a smooth band along the distal edge of the scale. The outer opercular surface is smooth with very few, small granules towards proximal edge.

Marginals round to rhomboid-shaped, 210–280 µm long, 160–230 µm wide, reduced in size on adaxial side of polyp. The proximal two-thirds of the inner surface is tuberculate with a smooth band along the distal edge broken by a small, simple keel; the outer surface is smooth.

Submarginals indistinguishable from body-wall scales; both are circular to widely elliptical, 220–280 µm diameter, adaxial scales reduced in size. The inner surface is tuberculate; the outer surface is smooth. All sclerites have a finely serrate distal edge and coarsely lobate proximal edge.

Coenenchymal scales are round to elliptical, 120–220 µm maximum diameter. The inner surface is sparsely tuberculate; the outer surface is smooth to slightly sculpted with sparse ridges and granules sometimes arranged radially.

Images of colony and sclerites are in the original description (Zapata-Guardiola and López-González 2010a).

2.26.2 Distribution
These specimens extend the range of *T. minuta* from Austasen to circum-Antarctic, at depths of 226–610 m.

2.26.3 Remarks
*Thouarella minuta* has the smallest polyps of any described *Thouarella* species.
2.26.4 Comparisons
With three to four scales in the longitudinal abaxial row, *T. minuta* is comparable to *T. variabilis, T. striata, T. pendulina, T. hicksoni* and *T. andeep* (Table 2.3). However, all these species generally have polyps of 1 mm or above. The smallest polyps are found in *T. pendulina* and *T. hicksoni*, which sometimes have polyps of 1 mm. *Thouarella hicksoni* opercular are blunt-tipped and those of *T. pendulina* are more triangular than the tear-shaped opercular of *T. minuta.*

2.27 *Thouarella andeep* Zapata-Guardiola and López-González, 2010b

Figure 2.40c,d

*Thouarella andeep* Zapata-Guardiola & López-González, 2010b: 142–145, fig. 8c,d, 11–13

Holotype (not examined), ZMH C11744, R/V *Polarstern*, Antarktis XXIV/2, sample no. PS7/048–01, off Atka Bay, Antarctica, 70˚24’S, 8˚19’43”W, 601.8 m, 17 Jan 2008, 2 fragments.

*Material examined:* paratype, USNM 1123418, details same as holotype; USNM 98298, R/V *Eltanin*, sta. 1089, Clarence Island, NE of South Shetland Islands, sub-Antarctic, 60˚47’S, 53˚30’W, 641 m, 17 Apr 1964; USNM 1130294, R/V *Hero*, cruise 721, sta. 1144, Bismarck Strait, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64˚52’09”S, 63˚50’09”W, 440–480 m, 14 Mar 1972; USNM 1130291, R/V *Hero*, cruise 824, sta. 35–B, 64˚50’33”S, 63˚51’00”W, 312–330 m, 26 Mar 1982, 1 fragment; USNM 1130289, R/V *Eltanin*, cruise 12, sta. 1081, east of South Orkney Islands, Scotia Ridge, Antarctica, 60˚34’S, 40˚44’W, 345–350 m, 13 Apr 1964; USNM 98276, R/V *Eltanin*, cruise 27, sta. 1870, Cape Adare, Victoria Land, Ross Sea, Antarctica, 71˚16’S, 171˚31’E, 659–714 m, 14 Jan 1967; USNM 85296, R/V *Eltanin*, cruise 11, sta. 970, SW coast of Staten Island, Tierra del Fuego, Argentina, 54˚59’S, 64˚53’W, 586–641 m, 11 Feb 1964, 1 fragment; USNM 1130287, R/V *Eltanin*, cruise 12, sta. 1089, NE of Clarence Island, South Shetland Islands, Antarctic Ocean, 60˚47’S, 53˚30’W, 641 m, 14 Apr 1964; SMF, EPOS 3, sta. 293, GSN 15, 20 Feb 1989, 1 colony, no location information.
2.27.1 Description
Description modified from Zapata-Guardiola and López-González (2010b):

Colonies appear alternately pinnate although branching is in three directions: two pinnate rows creating a plane and one row of branching between these two rows. Colonies are light pink or white with a bronze axis. The largest colony is 8 cm long (USNM 98276); axis and branchlets are very rigid, 21–22 mm long.

Polyps isolated, 10–11 per cm (more clustered at branchlet tips), upwardly inclined 80–90° from branchlets and main stem, 1.9–3.4 mm long, very wide (0.7–0.95 mm) distally flared shape with a tall conical operculum. Polyps have 7 longitudinal rows, quickly reducing to 4 at base with 4–5 scales in each abaxial row.

Five to six tongue-shaped accessory opercular lie underneath opercular scales, 240–420 µm tall, 70–300 µm wide. The inner surface is tuberculate across the proximal half, smooth distally and has no keel; the outer surface is smooth sometimes with smooth ridges proximally.

Opercular scales are arranged in two alternate circles of four, tongue-shaped, sometimes constricted distally, 510–1100 µm tall, 340–520 µm wide. The outer circle of opercular are larger; the inner surface has large ridges perpendicular to the distal edge, no distinct keel, and dense tubercles proximally. Smaller opercular have a smooth inner surface and no ridges; the outer surface has small ridges radiating from central proximal area.

Marginals are a wide triangle-shape with pointed distal edge, 950–1320 µm tall, 740–990 µm wide. The inner surface can have a complex keel (Figure 2.40c,d) or an area of reduced ridges; area adjacent to keel area is smooth, dense tubercules proximally. The outer surface has dense granules.

Submarginals not differentiated from body-wall scales; both are irregularly fan-shaped, elliptical, and oval, 540–840 µm maximum length. The inner surface is densely tuberculate sometimes with a very thin smooth band along the distal margin;
the outer surface has dense granules. As with all sclerites, the distal edge is finely serrate and proximal edge coarsely lobate.

Coenenchymal scales have a diverse range of shapes from circular to oval to lobate, 60–93 µm maximum length. These scales have a densely tuberculate inner surface and outer surface with dense granules, often heavily ridged.

Images of this species are found in the original description (Zapata-Guardiola and López-González 2010b).

2.27.2 Distribution
Specimens described here extend the range of *T. andeep* to include the southwest Atlantic Ocean, off the tip of South America, and circum-Antarctic areas, 312–714 m.

2.27.3 Remarks
*Thouarella andeep* was originally described as having a bottlebrush colony. This is true in the strictest sense of the word, however, as in many *Thouarella* species, branching is not in all directions (usually just in three) the overall appearance of which can look alternately pinnate. I also add that marginals do have a keel (see Figure 2.40c,d, from paratype).

2.27.4 Comparisons
With 4–5 scales in the longitudinal abaxial row, a bottlebrush branching arrangement, and distally flared polyps, *T. andeep* is comparable to: *T. minuta*, *T. pendulina*, *T. hicksoni*, *T. variabilis*, *T. striata*, and *T. brucei* (Table 2.3). *Thouarella minuta*, *T. pendulina*, *T. hicksoni* and *T. variabilis* all have polyps smaller than those of *T. andeep*. Of the remainder, *T. striata* often has distinct deep striations on the outer surface of body-wall sclerites whereas *T. andeep* has fine granules and lacks the striations common on the inner surface of *T. striata* sclerites. Furthermore, *T. brucei* has a keel on its opercular that is lacking in *T. andeep*; *Thouarella brucei* also usually has smaller polyps than *T. andeep*.

2.28 *Thouarella parachilensis* sp. nov.
Figures 2.28, 2.29
CHAPTER TWO

Type and type locality: holotype, USNM 98338, R/V Islas Orcadas, cruise 575, sta. 90, South Georgia Island, sub-Antarctic, 54°50’36”S, 37°23’48”W, 223–227 m, 7 Jun 1975, 1 colony; paratypes, USNM 98190 (SEM images), R/V Professor Siedlecki, cruise 86–01, sta. 121, 53°57’S, 38°10’W, South Georgia Island, sub-Antarctic, 90–100 m, 6 Dec 1986, 1 colony; paratype, ZSL, SG09, Ev. 35, 53°44.07’S, 37°14.58’W, NW of South Georgia Island, sub-Antarctic, 125 m, 18 Jan 2009; USNM 84341, R/V Professor Siedlecki, cruise 86–01, sta. 122, 53°55’S, 38°03’W, South Georgia Island, sub-Antarctic, 119–130 m, 16 Dec 1986; USNM 97951, R/V Islas Orcadas, cruise 575, sta. 12, 53°38’12”S, 37°54’42”W, South Georgia Island, sub-Antarctic, 130–137 m, 13 May 1975; USNM 98087, R/V Professor Siedlecki, cruise 86–01, sta. 19, 54°02’S, 39°06’W, South Georgia Island, sub-Antarctic, 212–224 m, 2 Dec 1986; USNM 98387, R/V Hero, cruise 721, sta. 1144, Bismarck Strait, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°52’09”S, 63°50’09”W, 440–480 m, 14 Mar 1972; USNM 98361, R/V Hero, cruise 731, sta. 1884, Quintana Island, Wilhelm Archipelago, Antarctic Peninsula, 65°06’12”S, 64°59’51”W, 100–180 m, 3 Mar 1973; USNM 98104, R/V Professor Siedlecki, cruise 86–01, sta. 9AND10, Shag Rocks, South Georgia Island, sub-Antarctic, 53°3’S, 41°57’W, 133–165 m, 30 Nov 1986; USNM 98173, R/V Eltanin, cruise 22, sta. 1536, west tip South Georgia Island, sub-Antarctic, 54°30’S, 39°20’W, 659–686 m, 8 Feb 1966; USNM 98085, R/V Eltanin, cruise 12, sta. 993, west of Aspland Island, South Shetland Islands, Antarctic Ocean, 61°25’01”S, 56°31’01”W, 300 m, 13 March 1963; USNM 98159, R/V Hero, cruise 731, sta. 1944, Neumayer Channel, Anvers Island, Palmer Archipelago, Antarctic Peninsula, 64°46’40”S, 63°25’33”W, 100–150 m, 11 Mar 1973.

2.28.1 Etymology
Named after Thouarella chilensis, for which this species was often mistaken.

2.28.2 Description
Colonies flabellate (Figure 2.28a), sparsely branched, usually brown-red in coloration, largest specimen (holotype) 290 mm long, 200 mm wide. Branches are feather-shaped with shorter branches at apex and toward base. Branchlets sturdy, departing perpendicular to branch on all sides in a bottlebrush arrangement, 3–5 branchlets per cm, maximum of 30 mm long, shorter towards base, mostly simple with some secondary branching, ramification usually close to branchlet base.
Revision of *Thouarella*

Polyps globular (Figure 2.28b,c) with a flat operculum sometimes with a flat adaxial surface (as compressed against neighbouring inner polyps; Figure 2.28e). Polyps are 2.5–2.8 mm long, placed at an almost right-angle to branchlets at branchlet bases but upwardly inclined towards tips (up to 45°). Polyps are spaced at less than 1 mm intervals, 9–30 per cm at branchlet bases, in a dense cluster at branchlet tips that form an almost solid cylinder of polyps (‘barrel-shaped’, Figure 2.28c), 18–48 per cm at tips. Each polyp has 8 longitudinal rows of scales, 8–15 scales in the abaxial rows (average 11, Figure 28d), and a reduced number adaxially. Scales progressively wider and shorter from polyp head to base.

Operculum is flat. Opercular are arrow or lanceolate-shaped (Figure 2.29a–f), but can be wider and pentagonal, 420–510 µm tall (average 460 µm), 230–410 µm wide (average 340 µm), average H:W 1.4 (1.2–1.8). The inner surface has a large, multiple-ridged keel (Figure 2.29a,f) and many adjacent ridges resulting in a pectinate distal edge; proximal half is tuberculate. The outer surface has deep longitudinal indentations (Figure 2.29b–e), large granules extend into ridges that run perpendicular to the distal edge; tubercles placed along the proximal edge.

Marginals wider than opercular, 340–510 µm (average 440 µm), 380–470 µm tall (average 430 µm), average H:W of 1 (range from 0.7–1.2), oval-shaped with pointed distal edge (Figure 2.29g,h). The inner surface is keeled with smaller adjacent keels leading to a serrated distal edge, proximal two-thirds is tuberculate; distal third smooth lateral to keel and ridges. The outer surface has a longitudinal groove; sparse, large granules occur toward the proximal edge, where tubercles are visible.

Submarginals are clearly visible from an anterior polyp view (Figure 2.28e), distal edges slightly curved away from the polyp body. Submarginals are elliptical (Figure 29i–k), wider than marginals, 540–890 µm (average 700 µm) and about the same height, 350–550 µm (average 430 µm), average H:W of 0.6 (range from 0.4–0.9). Ridges infrequent on the inner surface perpendicular to distal edge, which is serrate; the remainder of the inner surface is tuberculate. The outer surface has sparse granules proximally, some tubercles visible.
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Body-wall scales elliptical, very broad (Figure 2.29l–q), curved around polyp circumference, average height 380 \( \mu \text{m} \) (270–520 \( \mu \text{m} \)), width 790 \( \mu \text{m} \) (620–1000 \( \mu \text{m} \)), average H:W 0.5 (range from 0.4–0.6). The inner surface is tuberculate with a thin smooth band along the distal edge; the outer surface has large, sparse, peaked granules concentrated in the centre of the scale and sporadic tubercles proximally with remainder smooth; the distal edge has large serrations. All above sclerites have a coarsely lobate proximal edge.

Coenenchymal scales are circular to elliptical (Figure 2.29r), 240–320 \( \mu \text{m} \) diameter, similar dimensions as smaller body-wall scales, but flatter, with less curvature, and a strongly jagged distal edge.

2.28.3 Distribution

*Thouarella parachilensis* has been found 1000 km west of, and around, the waters of South Georgia Island and south to the Antarctic Peninsula, 90–480 m.

2.28.4 Remarks

This species has long been incorrectly presumed to be *T. chilensis* because of the densely clustered polyps at branchlet tips that were mistaken for the densely arranged polyps of *T. chilensis* as described by Kükenthal (1908; 1915; 1924).

2.28.5 Comparisons

It is the cylindrical arrangement of clustered bulbous polyps at branchlet tips that make *T. parachilensis* noticeably different from other *Thouarella* species. *Thouarella parachilensis* has 8–15 abaxial row scales (average of 11); the only *Thouarella* species with a comparable number are *T. koellikeri*, *T. chilensis*, *T. crenelata* and *T. brevispinosa*.

*Thouarella koellikeri* has 7–10 scales in the longitudinal abaxial row and a tall operculum of large operculars with a simple keel, rather than a flat operculum with much smaller operculars bearing a complex keel, as in *T. parachilensis*. *Thouarella brevispinosa* has 6–8 scales in the abaxial row and distally flared, more evenly spaced polyps than the clavate, clustered polyp arrangement seen in *T. parachilensis* (Table 2.3).
Polyps of *T. parachilensis* are bulbous and more rounded usually with a higher number of scales in the abaxial rows than *T. crenelata* or *T. chilensis*. *Thouarella crenelata* has a more open opercular in anterior view than *T. parachilensis* and *T. chilensis* has more boxy polyps.

2.29 **Species Group 2 – polyps in pairs or whorls**

2.30 **Thouarella hilgendorfi (Studer, 1878)**

*Plumarella hilgendorfi* Studer, 1878: 648–649, pl. 2, figs. 15a–e

*Thouarella hilgendorfi*: Wright & Studer, 1889: 62, figs. 18–25.—Versluys, 1906: 24–29, pl. 2, fig. 7, text figs.—Thomson & Henderson, 1906: 38 (list).—Roule, 1908: 1.—Kinoshita, 1908a: 21–22, pl. 5, fig. 42.—Nutting, 1912: 66–67.—Aurivillius, 1931: 248–252, pl. 5, fig. 8, text fig. 48.—Chave & Malahoff, 1998: Table 1 (listed)

Not *Thouarella hilgendorfi*, Thomson, 1927: 33–34, pl. 1, fig. 23, pl. 4, fig. 4, 5.—Carpine & Grasshoff, 1985: 32 (=*T. grasshoffi*)

*Thouarella typica* Kinoshita, 1907: 230; 1908a: 23–24, pl. 2, fig. 9, pl. 5, fig. 43.—Nutting, 1912: 68

*Thouarella hilgendorfi* forma *plumatilis* Aurivillius, 1931: 252–256, pl. 5, fig. 9


*Material examined*: holotype, ZMB Cni 2070 (see Versluys, 1906). “Jeddabay” (=Tokyo Bay), Japan, 548 m, 60 mm fragment; USNM 56812, *Star II* (station unknown), Kaiwi Channel between Oahu and Molokai, 21°18’N, 157°32’W, 366 m, 1977, 1 large dried colony, SEM C1393-1397.

2.30.1 **Description**

Modified from description in Cairns (2010):
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Colonies flabellate, consisting of several main branches that are irregularly dichotomous. Each main branch covered by numerous closely-spaced, undivided, 20–25 mm length branchlets originating from all sides of main branches in a bottlebrush arrangement. Largest specimen (USNM 56812) 48 cm tall, 34 cm wide, with a broken basal stem, diameter of 9.5 mm. Axis pale yellow to bronze, covered by white coenenchyme and polyps.

Polyps 1–1.4 mm long, flared distally, slightly inclined upward, in whorls of 3 on branchlets and placed randomly on larger-diameter branches, 6–7 whorls per cm. Approximately 1 in 20 polyps are highly modified by a pair of parasitic copepods, each modified polyp being much larger (up to 1.6 mm long and 1.2 mm in diameter and thus 2–3 times volume of a typical polyp). Parasite-modified polyps lack opercular, and their body-wall scales flare outward, having a ridged inner face, and a coarse serrate distal margin. Generally polyps have 8 longitudinal rows of body-wall scales: usually 6 or 7 abaxial pairs, 5 or 6 outer-lateral pairs, 3 or 4 inner-lateral pairs, and only 1 or 2 adaxial pairs.

Opercular scales are triangular, often arranged in 2 quartets, alternating in size, the larger opercular are 350–450 µm long (H:W of 1.4–2.1), the smaller only 180–230 µm long (H:W of 1.6–2.2) are highly curved. Opercular outer surface is smooth, with a serrate distal edge; the longitudinally concave outer surface corresponds to a smooth, convex (not ridged or keeled) inner surface.

Marginals also occur in 2 quartets, as are submarginals, the innermost 4 aligned with inner marginals, and outer 4 submarginals with outer marginals.

Marginal scales with a broad elliptical base, prominently spinose distal projection, up 500–600 µm tall, 300–400 µm wide (H:W of 1.2–1.8), distal 60–65% of scale occupied by projecting spine. The outer distal surface is smooth, proximal area with granules; the inner surface bears 3–4 prominent spines, finely serrate ridges forming a complex keel that fits into the longitudinal furrow on corresponding opercular outer surface.
Submarginal scales similar to marginals but with a much shorter distal spine (35% length of scale) and correspondingly lower H:W of 1.2. Body-wall scales crescent-shaped with a finely serrate distal edge, smooth outer surface, and are usually wider than long (H:W of 0.6–0.8). The adaxial side of polyps are covered with particularly wide adaxial and inner lateral body-wall scales.

Coenenchymal scales similar to body-wall scales, most elliptical in shape with a smooth, flat outer surface and a finely serrate distal edge.

For images see Cairns (2010).

2.30.2 Distribution
Hawaii, Japan, Indonesia, and Indian Ocean (164–750 m depth).

2.30.3 Remarks
*Thouarella typica* is identical to *T. hilgendorfi* and were synonymised in Cairns (2010).

2.30.4 Comparisons
Within Group 2 only three species have bottlebrush branching arrangement: *T. grasshoffi* Cairns, 2006, *T. hilgendorfi* and *T. laxa*. *Thouarella grasshoffi* and *T. hilgendorfi* have true bottlebrush branches whereas *T. laxa* branchlets are mostly in one plane, although the length and flexibility of branchlets means the latter can appear bottlebrush. Colonies of *T. grasshoffi* tend to be taller than they are wide, with rare branching, whereas *T. hilgendorfi* is wider than tall, and flabellate. Polyps of *T. grasshoffi* and *T. hilgendorfi* are a very similar size, the former having slightly lower marginals and a pointed conical polyp rather than the distally flared polyps of the latter.

2.31 *Thouarella moseleyi* Wright and Studer, 1889

*Figures 2.30, 2.31*

*Thouarella moseleyi* Wright & Studer, 1889: 61–62, pl. 14, fig. 1, 1a, pl. 21, fig. 2.— Versluys, 1906: 29–30, figs. 26, 27 (in text)
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*Thouarella moseleyi* var. *spicata*: Thomson & Henderson, 1906: 38, 42–43, pl. 3, figs. 2, 4 (sample not seen)

*Material examined:* 6 cm colony, holotype, NHM 1889.5.27.39, H.M.S. *Challenger*, sta. 171, Kermadec Islands, NE of New Zealand, 28°33’S, 177°50’E, 1097 m, 15 Jul 1874.

2.31.1 Description

Holotype approximately 160 mm long (from Wright & Studer 1889: pl. 14, fig. 1). Branchlets pinnate, possibly alternately pinnate (Figure 2.30a,b), although colony can appear bottlebrush as branchlets are flexible and curve in all directions. Branchlets are mostly simple, some with secondary branching, 15–20 mm long. Axis thin, calcareous, flexible and “somewhat flattened” (Wright & Studer 1889).

Polyps are clavate with a tall, conical operculum (Figure 2.30c). Polyps 1.5 mm long, in a paired arrangement, standing perpendicular to branchlet, some on main stem. Each polyp has 6 longitudinal rows as the number of scales reduces rapidly adaxially from 8 marginals; 4–5 scales in the longitudinal abaxial row, 3–4 in adaxial rows.

Thin, lanceolate opercular (can be wider with rounded distal edge, Figure 2.31b), 450–640 µm tall (average 510 µm), 140–270 µm wide (average 200 µm), H:W 2.2–3.1 (average 2.6). The inner surface is smooth with a simple keel running longitudinally from the tip three-quarters the length of the opercular (Figure 2.31c); the proximal quarter is tuberculate. Wider opercular have a wider, ridged area on the inner surface rather than a distinct keel (Figure 2.31b). The outer surface is longitudinally concave and smooth, with granules arranged radially from proximal centre; tubercles visible at proximal edge. The opercular edge appears smooth, but may be worn and thus not representative.

Marginals are twice as wide as operculars, 400–410 µm (average 406 µm), 455–510 µm tall (average 480 µm), H:W 1.1–1.3 (average 1.2), and are a broad-base triangle to square-shape (Figure 2.31d–f). The inner surface has 4 or 5 tall, thin keels (Figure 31d,f) with smooth areas lateral to keel; remainder is tuberculate. The outer surface is longitudinally concave, smooth, with granules distributed radially from proximal
Revision of *Thouarella*

centre; some tubercles visible at proximal edge (Figure 2.31e). The distal edge is irregular, possibly worn; proximal edge is coarsely lobate.

Submarginals are almost circular, slightly elliptical (Figure 2.31g,h), 320–420 \( \mu \m \) tall (average 383 \( \mu \m \)), 470–480 \( \mu \m \) wide (average 475 \( \mu \m \)), H:W 0.7–0.9 (average 0.8). The inner surface is tuberculate, distal edge with a wide area of perpendicular ridges rather than a keel. The outer surface and scale edges as described for body-wall scales below.

Body-wall scales are circular (Figure 2.31i–l) with convex distal edge, 300–400 \( \mu \m \) tall (average 340 \( \mu \m \)), 300–475 \( \mu \m \) wide (average 370 \( \mu \m \)), H:W 0.7–1.2 (average 0.9). The inner surface is tuberculate with a thin smooth band along the distal edge and occasionally small teeth. The outer surface is smooth with sparse granules across the proximal area; the distal edge is smooth and the proximal edge is coarsely lobate.

There are two layers of coenenchymal scales (Figure 2.31m): the inside layer of sclerites are circular; the outside layer are elliptical. The inner surface of coenenchymal scales is tuberculate with a smooth band running along the distal edge; the outer surface is smooth, sometimes with sparse granules. The distal edge is smooth; proximal edge is coarsely lobate.

2.31.2 *Distribution*

Known from two locations (excluding var. *spicata*): northwest of the Kermadec Islands in the South Pacific and north of Sumbawa Island in Indonesia, 6600 km away. Found from 794–1097 m.

2.31.3 *Remarks*

The number of polyps per cm was impossible to tell from the small remnant holotype fragment. More material of this species from the type location is required to confirm the differences between it and *T. laxa*, which has very similar polyp morphology and pinnate branching.

A variation of *T. moseleyi* (var. *spicata*) was described in Thomson and Henderson (1906). The differences between the holotype and variant are mainly a taller conical operculum and marginals with a more elongated, pointed spine (which may be bifid)
on the variant. The tall conical operculum is similar to *T. grasshoffii*, however *T. grasshoffii* has a true bottlebrush branching arrangement.

2.31.4 Comparisons
Within Group 2 only two other species, *T. laxa* and *T. tydemani*, have pinnate colonies or colonies that appear pinnate.

The ridges running perpendicular to the distal edge of body-wall scales on *T. moseleyi* are similar to the recent description of *T. tydemani* body-wall scales by Zapata-Guardiola and López-González (2010a). *Thouarella tydemani* however has long spinose marginals and a distally-flared polyp whereas polyps of *T. moseleyi* are clavate with shorter marginals.

Polyps of *T. moseleyi* are more robust than *T. laxa*, with wider marginals that are not as spinose, a fitted opercular cone and several ridges running perpendicular to the distal edge of submarginals which are not present in *T. laxa*.

### 2.32 Thouarella laxa Versluys, 1906
Figures 2.32, 2.33

*Thouarella laxa* Versluys, 1906: 30–32, pl. 1, fig. 5; pl. 3, fig. 8; text figs. 28–33.—Aurivillius, 1931: 255–256

Not *Thouarella laxa*: Kükenthal & Grozawsky, 1908: 36–37, pl. 2, fig. 13


*Thouarella flabellata* Kükenthal, 1907: 207

*Thouarella (Euthouarella) flabellata*: Kükenthal, 1915: 150 (key); 1919: 408 (key), 418–420, pl. 42, fig. 64, figs. 182–186 in text; 1924: 294–295.—Cairns & Bayer, 2009: 28 (listed)

*Thouarella regularis* Kükenthal, 1907: 206–207

*Thouarella tenuisquamis*: Kükenthal, 1908: 11; 1915: 150 (key), 151

*Thouarella (Euthouarella) tenuisquamis*: Kükenthal, 1919: 408 (key), 421, pl.42, fig. 65, figs. 187–190 in text; 1924: 295.—Cairns & Bayer, 2009: 28 (listed)
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*Thouarella carinata* Kükenthal, 1908: 11–12; 1915: 150 (key)

*Thouarella (Euthouarella) carinata*: Kükenthal, 1915: 150 (key); 1919: 408 (key), 423–425, pl. 42, fig. 66; 1924:296.—Cairns & Bayer, 2009: 28 (listed)

**Material examined**: two branchlets (80 mm, 90 mm) of *T. laxa* holotypes, ZMA, COEL03576, Siboga expedition, sta. 88, Strait of Makassar, Sulawesi, Indonesia, 0°34′06″N, 119°08′05″E, 1301 m, 20 June 1899; *Thouarella tenuisquamis*, syntype, MNHWU, northwest of Sumatra, Malaysia, south of Nicobar, 4°53′01″N, 93°33′05″E, 752 m; *Thouarella carinata*, fragment of syntype (85 mm), USNM 50127, Golden Hind, sta. 38, Okinawa and “Urugakanal”, Japan, 731 m; *Thouarella flabellata*, three fragments of holotype (75 mm, 45 mm, 40 mm), sta. 257, east coast of Somalia, 1°48′02″N, 45°42′05″E, 1644 m.

### 2.32.1 Description

Colony sparsely branched (Figure 2.32a), main stem generally having alternate pinnate branchlets with infrequent branching between these two planes and sometimes on the dorsal face; this forms a rudimentary bottlebrush arrangement (Figure 2.32b). Branchlets flexible, upwardly inclined at 45°, easily bent, feather-shaped, generally simple, longest is approximately 40 mm.

Polyps distally-flared and wide (Figure 2.32c,d), upwardly inclined at 45–60°, 1.2–1.5 mm long, rarely on main stem, usually in pairs or whorls of three on branchlets, 5–7 pairs per cm. Each polyp has 7 longitudinal rows, 5–6 scales in the longitudinal abaxial row.

Operculars arranged roughly in two alternate rings of four (Figure 2.32e): scales are smaller in inner ring (Figure 2.33a–c), 280–300 µm tall (average 292 µm), 140–210 µm wide (average 166 µm), H:W 1.8 (range from 1.4–2.1); larger scales in outer ring, 370–630 µm tall (average 500 µm), 120–370 µm wide (average 292 µm), H:W 1.9 (ranges from 1.3–3.1). Larger opercular are triangular (Figure 2.33e) although, if broken, have a rounded, blunt apex, usually with slight tapering to a thinner distal edge (Figure 2.33f) making them tongue-shaped; jagged, semi-circle proximal edge. The outer opercular surface is smooth and concave longitudinally, having small granules proximally and tubercles at base; the inner surface has fine tubercles.
covering the proximal third, the remainder is smooth with longitudinal central ridges (no distinct keel). Smaller opercular are lanceolate with a smooth outer surface that has a small number of granules at the base and is slightly concave; the inner surface is smooth with fine tubercles over the proximal quarter to third.

Marginals are 570–800 µm tall (average 705 µm), broad (wider than largest opercular) 370–550 µm, average H:W 1.5 (range from 1.3–1.7) with a circular base and a triangular, acutely pointed distal edge (Figure 2.33f–h). The outer surface is smooth with low relief granules proximally; the inner surface has 2 or 3 ridges longitudinally along the keel (which is sometimes flattened) and tubercles covering the proximal half in a semi-circle leaving smooth wings lateral to the keel and along the distal edge.

Submarginals are as described below for body-wall scales but slightly wider, 410–490 µm (average 470 µm), and taller, 500–610 µm (average 570 µm), H:W: 1.2, with a pointed distal edge and small keel on the inner surface (Figure 2.33i,j) which has adjacent ridges perpendicular to distal edge.

Body-wall scales are mostly circular (Figure 2.33k–n), 250–590 µm tall (average 320 µm), 280–390 µm wide (average 310 µm), average H:W 1 (range from 0.6–1.7). The outer surface is mostly smooth with some granules proximally; the inner surface is tuberculate with a smooth band along the distal edge.

Coenenchymal scales are circular to elliptical (Figure 2.33o), 100–310 µm long (average 200 µm), 130–290 µm wide (average 200 µm), H:W 0.4–1.5 (average 1). All sclerites have a finely serrate distal and roughly lobate proximal edge.

2.32.2 Distribution
From east coast of Africa (Somalia) to east Asia (Sumatra, Philippines, Japan). Depth range of 400–1644 m.

2.32.3 Remarks
*Thouarella laxa* was recently redescribed by Zapata-Guardiola and López-González (2010a) however the polyp illustrated was incongruent with the holotype in that it showed the opercular head turning at an angle rather than a regular distally-flared shape (Figure 2.32c,d).
Although *T. laxa*, *T. carinata*, *T. flabellata* and *T. tenuisquamis* have been described from disparate locations such as Somalia and Japan, at a polyp and sclerite level these specimens are identical. *Thouarella flabellata* has fewer pairs or whorls of polyps per cm (5–6) than *T. tenuisquamis* (7–8), *T. laxa* (5–7) and *T. carinata* (7–8). *Thouarella carinata* is more likely to have three polyps in a whorl whereas the remainder tend towards pairs, however, the number of polyps per whorl may increase with colony age and is variable in other *Thouarella* species (e.g. *T. grasshoffi*), so this small discrepancy should not be considered species defining. The holotype of *T. carinata* and *T. tenuisquamis* were single branches and may well be one branch of a flabellate colony (see Figure 2.32a,b of *T. laxa*). *Thouarella carinata* also has a more extended distal edge on marginals. However, the holotype of the remaining species were in a relatively poor condition with few intact polyps; many polyps having marginals reduced in length through wear. The marginals that were intact looked identical to those of *T. laxa*. In all these specimens the inner surface of small opercular tended to be smooth and larger opercular had a longitudinally ridged area distally. The outer surface of all sclerites is smooth with sparse granules. *Thouarella tenuisquamis* has paired polyps whereas other specimens have polyps in pairs or whorls of three. However, this can be a colony-specific difference and is again not considered to be a species defining character. The differences described above are minor and despite the long distances between type localities, the minor differences in branching, polyp and sclerite shapes are not sufficient to delineate unique species. *Thouarella carinata*, *T. flabellata* and *T. tenuisquamis* are thus proposed for synonymisation with *T. laxa*, this name having priority.

2.32.4 Comparisons

*Thouarella laxa* has a similar distally-flared polyp shape to *T. hilgendorfi* and *T. tydemani* and sclerites of these species are all nearly identical. *Thouarella laxa* however has long, flexible branchlets emanating from the stem in at least three directions whilst *T. tydemani* branching is alternately pinnate. *Thouarella hilgendorfi* branchlets are bottlebrush but branching is denser, with sturdier, less flexible branchlets, and there are more whorls and pairs per cm than *T. laxa*. These could easily be characters that may be affected by environmental factors and, at a polyp level, these species are identical. Sampling of fresh material from type locations and
perhaps genetic studies could shed light on the relationship between these two species and *T. grasshoffi*, which also has a similar polyp structure.

*Thouarella moseleyi* has more rounded polyps than *T. laxa* and consequently shorter, thinner marginals. The opercular cone of the former is more fitted than the latter and the former has several ridges running perpendicular to the distal edge of submarginals which are not present in latter. A minute piece of *T. moseleyi* was examined but more is required to confirm the difference between these species as sclerite measurements, sclerite arrangement and polyp arrangement are very similar.

### 2.33 Thouarella tydemani Versluys, 1906

*Thouarella tydemani* Versluys, 1906: 34–35, pl. 1, fig. 2, figs. 34–37 (in text)  
*Thouarella tydemany*: Brito, 1993: 220–221  
?*Hookerella pulchella* Gray, 1870: 45  
*Thouarella (Euthouarella) tydemani*: Cairns & Bayer, 2009: 28 (listed)

**Holotype (not examined):** COEL09256, ZMA, Siboga expedition, sta. 297, Lesser Sunda Islands, Indonesia, 10°39'S, 123°40'E, 520 m, 27 Jan 1900, 200 mm colony. Only three mounted slides remain of this species, images of which were seen. They contain two branchlets, polyps and coenenchymal scales. The original colony is presumed lost as no holotype was present at ZMA (Zapata-Guardiola & López-González 2010a) or any of the other museums contacted within this study. As no material was available the type description was used for species comparisons.

#### 2.33.1 Description

Colony flat with infrequent uniplanar branching. Branchlets simple, 15–20 mm long, rarely 30 mm, alternately pinnate with few ventral branchlets.

Polyps distally flared, approximately 1.5 mm long, standing at 80–90° inclination from branchlets, paired, rarely in whorls of 3, 6 per cm; some polyps on main branch.

Opercular in a modest cone of 4 four larger, outer, longitudinally concave opercular and four smaller, inner, distally blunt opercular.
Marginals are 450–500 \( \mu m \) long, almost spinose with a keel visible on the inner surface. Body-wall scales appear circular, some bearing ridges perpendicular to the distal edge.


### 2.33.2 Distribution
Known only from the type location: Lesser Sunda Islands, Indonesia, 520 m.

### 2.33.3 Remarks
Versluys (1906) separated *Thouarella laxa* and *T. tydemani*, the latter having wider, larger polyps. Zapata-Guardiola and López-González (2010a) illustrated that variation in nearly all characters (size of polyps, number of whorls per cm, number of polyps per whorl etc) in *T. laxa* was broad enough to encompass the dimensions seen in *T. tydemani*. The only difference found between *T. laxa* and *T. tydemani* was body-wall scales of the latter had short ridges perpendicular to the distal edge, which were absent in *T. laxa*.

Versluys (1906) also considered *Hookerella pulchella* (Gray, 1870) very similar to *T. tydemani* in colony form but he did not mention number of polyps per cm or sclerite shape. Without a reliable illustration or accurate description from Gray (1870), Versluys introduced *T. tydemani*, ignoring *H. pulchella*, the holotype or a specimen of which can not be located.

### 2.33.4 Comparisons
*Thouarella tydemani* was compared to *T. laxa* by Versluys (1906) and rightly so as the polyps of these species are nearly identical in every respect. Body-wall scales of *T. tydemani* may bend away from the polyp body, have ridges perpendicular to their distal edge, and slightly shorter marginals than *T. laxa* (this is in contrast to Zapata-Guardiola & López-González, 2010a, who found marginals were on average 370 \( \mu m \) in *T. laxa* and thus shorter than *T. tydemani*), however it is the branching pattern that make these species truly distinct. *Thouarella laxa* has long, flexible branchlets departing the stem in at least three directions whereas *T. tydemani* colonies are mostly
pinnate with more rigid branchlets. Additionally, polyps of *T. laxa* have a flat operculum and branchlets inclined at a 45–60°, rather than 90° as in *T. tydemani*. More material of *T. tydemani* would help to assess further differences between these two species.

Polyps of *T. tydemani* are distally-flared and look very similar to those of *T. hilgendorfi* however the pinnate branching structure of *T. tydemani* makes this species very different from the bottlebrush branches of *T. hilgendorfi*.

### 2.34 Thouarella coronata Kinoshita, 1908

Figures 2.34, 2.35

*Thouarella (Diplocalyptra) coronata* Kinoshita, 1908c: 519–520, fig.2; 1908b: 56–59, figs.4–6 (in text).—Cairns & Bayer, 2009: 28 (list), 35, figs.7a–g

*Thouarella coronata*: Aurivillius, 1931: 255 (listed)

*Thouarella (Euthouarella) coronata*: Kükenthal, 1915: 150 (key); 1924: 296 (key)

*Material examined:* USNM 50118, UMIT (fragment of which is USNM 50118), 20 mm of holotype, Uji Island, Kyushu Island, 146 m, May 1908, 13 cm colony. A small fragment of the holotype was available for study however colony shape and branchlet arrangement narrative below relies heavily on original description.

#### 2.34.1 Description

Colony dichotomously branched (Figure 2.34a). Basal branchlets up to 50 mm, 5–12 mm apart, on rare occasions 20 mm. Axis brown with a yellowish metallic lustre.

Polyps distally flared with a slender polyp body (Figure 2.34d,e), 1.9–2.1 mm long, standing perpendicular to branchlet in pairs and sometimes whorls of three (Figure 2.34c), 5–7 pairs or whorls per cm. Eight marginals, but only 7 longitudinal rows of body-wall scales, 5–6 scales in the abaxial rows.

Opercular are tear-shaped (Figure 2.35d–h), 260–455 µm tall (average 290 µm), 120–240 µm wide (average 180 µm), average H:W 1.6 (range from 1.3–2). The outer
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surface is smooth; the inner surface has a small elliptical tubercle area proximally, a smooth distal area, and rarely, low longitudinal ridges.

Beneath opercular there are 3–4 (perhaps more in other samples) small accessory opercular (Figure 2.35a–c): 80–200 µm tall (average 150 µm), 70–140 µm wide (average 100 µm), average H:W 1.1. The outer surface is smooth, inner surface also smooth with a small patch of tubercles proximally; edges are relatively smooth (not serrated).

Marginals equilateral triangle-shaped (Figure 2.35i–k); 430–560 µm tall (average 490 µm), 270–330 µm wide (average 310 µm), average H:W 1.6 (range from 1.3–2.1). The outer surface is smooth with some granules proximally. The inner surface has a multi-ridged keel and smaller ridges adjacent to the keel; smooth areas lateral to ridges with tubercles covering the proximal half from the keel base. Marginal proximal edge is roughly lobate, and may be angular.

Some submarginals with small keels or ridges on the distal edge of the inner surface; submarginals pointed distally (Figure 2.35i,m). Submarginals have a tuberculate inner surface with a thin smooth band along the distal edge; the outer surface is smooth with some granules proximally.

Body-wall scales are circular (Figure 2.35n–p), 190–340 µm tall (average 250 µm), 200–310 µm wide (average 240 µm), average H:W 1.1 (range from 0.9–1.2). The outer surface is smooth, sometimes with granules proximally; inner surface tuberculate with smooth band along distal edge, infrequent small median ridges running perpendicular to distal edge. The distal edge of all sclerites is finely serrate; proximal edge is coarsely lobate.

Coenenchymal scales are circular (Figure 2.35q), around 130 µm diameter, much smaller than body-wall scales; the outer surface is smooth and slightly concave with edges raised from axis. The inner surface is tuberculate.

Several hundred cylindrical rodlets were found in each tentacle.
CHAPTER TWO

2.34.2 Distribution
Known only from type locality, Kyushu Island, Japan, 146 m depth.

2.34.3 Remarks
This is the only Thouarella species known to contain tentacular rodlets, a sclerite category often found in Plumarella.

2.34.4 Comparisons
Apart from T. coronata Kinoshita, 1908c only two other species within Group 2 have dichotomous, uniplanar branching: T. parva, also from Japan, and T. biserialis (Nutting, 1908), from Hawai‘i. Kinoshita’s drawings (1908d, figs. 1,2) indicate that T. parva differs from T. coronata in having shorter, more rounded marginals and polyps diverging from branchlets at approximately 45° rather than 90°.

Sclerites of T. biserialis and T. coronata are very similar. Marginals of T. biserialis appear to curve over the operculum creating a cylindrical, rounded polyp, whereas those of T. coronata are flared outward. Polyps of the former are inclined at 45° and the latter are perpendicular to branchlets. The importance of these characters remains unclear, but for now these species appear to be distinct.

2.35 Thouarella parva Kinoshita, 1908

Figure 2.40a,b

*Thouarella (Diplocalyptra) parva* Kinoshita, 1908d: 53–56, figs. 1–3.—Cairns & Bayer, 2009: 28 (list)

*Thouarella (Amphilaphis) parva*: Küenthal, 1915: 149 (key); 1919: 410; 1924: 290 (key)

_Type and type locality:_ Kodzu Island, Japan, depth unknown.
Unfortunately the holotype was not present within the University of Tokyo museum collection (Dr Ueshima, pers. comm.); Kinoshita’s original description of a 73 mm fragment (1908d) is thus summarised.

2.35.1 Description
Dichotomously branched colony. Branchlets diverge from main stem at around 50°, 5–13 mm between branchlets. Colony colour is white, axis light yellow.
Polyps are 1 mm long, inclined to branchlet at around 45°, widest point of the polyp is around the marginals; polyp slender towards base (Figure 2.40a). Polyps are arranged in pairs, 6 per cm. Each polyp has 8 longitudinal rows of body-wall scales, 5–6 scales in abaxial rows and 5 in outer and inner lateral rows, reducing to four adaxially.

From a lateral view operculars are completely concealed by marginals. Very small accessory opercular are present (Figure 2.40bI). Opercular are lanceolate (Figure 2.40bII), 160–360 µm tall, 90–160 µm wide. The distal half of outer opercular surface is slightly concave; both inner and outer surfaces having granules arranged radially in the proximal area. The inner surface is likely to be tuberculate proximally as all Thouarella sclerites are.

Marginals are an irregular triangle-shape (Figure 2.40bIII) and approximately the same size as largest opercular (400 µm), although wider proximally.

Body-wall scales not as tall as marginals (350–380 µm) and broader (Figure 2.40bV, bVI). The outer surface of body-wall scales has radially arranged granules from central proximal area; the inner surface is tuberculate with a smooth band along the distal edge, occasionally with several ridges perpendicular to the distal edge.

Coenenchymal scales are smaller than body-wall scales, circular to elliptical in shape. The outer surface is sculpted and folded with sparse tubercles on the inner surface. Distal and lateral edges of all sclerites are finely serrate with a coarsely lobate proximal edge.

2.35.2 Distribution
Kodzu Island and Sagami Bay, Japan; depth unknown.

2.35.3 Remarks
Kinoshita was the first to note accessory opercular in Thouarella (1908d, fig. 2, shown here in Figure 2.40b) and T. parva remains one of the few Thouarella species with this kind of sclerite.
Thouarella parva marginals (Figure 2.40bIII) appear to have a small ridge-like keel on the inner surface, and if so, this species is Thouarella. However, this is far from clear and the rounded distal edge on what appear to be marginals in Figure 2.40b, and lack of a clear keel could indicate that this is actually a species of Plumarella. More material is required to confirm the placement of T. parva within Thouarella.

2.35.4 Comparisons
Dichotomous branching precludes this species from being T. hilgendorfi, T. moseleyi, T. laxa, T. tydemani or T. grasshoffi from within Group 2. Additionally, these species all have tall, triangular marginals that are absent in T. parva.

Only two other Thouarella species have dichotomous branching: T. coronata and T. biserialis. Polyps of T. coronata diverge at 90° to the branch, whereas those of T. parvas depart at 45°. This seems to be a very small difference however without more material of T. parva it is impossible to verify character variation between these species. There is believed to be specimens of T. parva in Japan. Until this material is examined these species will be kept separate.

Polyps of both T. parva and T. biserialis depart from branchlets at approximately 45° and all their sclerites appear to be very similar shapes and sizes. Thouarella biserialis have distinct keels on marginals, which may be present on T. parva, but the polyps of T. biserialis are clavate whereas those of T. parva are modestly flared.

2.36 Thouarella biserialis (Nutting, 1912)

Amphilaphis biserialis Nutting, 1908: 573, pl. 43, fig. 4, pl. 47, fig. 4.—Cairns & Bayer, 2009: 28 (listed)

Thouarella biserialis: Kinoshita, 1908c: 519–520, 2 text figs.—Kükenthal, 1915: 151 (listed); 1919: 438–9; 1924: 301.—Parrish & Baco, 2007: 192 (listed)

Thouarella (Diplocalyptra) biserialis: Cairns, 2010: figs. 2–3

Material examined: holotypes, USNM 22583, two short branches, USFWS Albatross 398210, Mawiliwili, Kaua’i Island, Hawaii, North Pacific Ocean, 21°56’25″N, 159°21’40″W, 73–426 m, June 1902.
2.36.1 Description
Modified from description in Cairns (2010):

Holotype, in two fragments of 4 cm and 3 cm, appears to be from a dichotomously branched, uniplanar colony. Polyps cylindrical, 1.2–1.5 mm long, curved upward at 45°, in pairs standing on opposite sides of branchlets in plane of flabellum, rarely in whorls of 3. There are 6–7 scales in 8 longitudinal rows, 5–6 in outer lateral rows, 2–3 in inner lateral rows and 1–2 adaxially. Adaxial rows short (redundant), revealing a largely naked adaxial face.

Opercular scales are lanceolate to widely-triangular, small (up to 280 µm long), and bluntly tipped, with a H:W of 1.6–2.0. The outer opercular surface is flat and has granules proximally; the distal inner surface is smooth (unkeeled), bearing rounded longitudinal bulges.

Marginal scales triangular, up to 400 µm long, H:W of 1.5–1.8, wide multi-keel area on inner surface and rare granules on the outer surface. Marginal scales fold over smaller opercular, shielding them from view.

Body-wall scales often wider than tall (H:W of 0.67–1.1), up to 290 µm long; those in upper polyp have a series of longitudinal ridges on the distal inner surface, resulting in a serrated distal edge.

Coenenchymal scales are elliptical, up to 300 µm in diameter, outer surface concave and smooth with some granules.

For images see Cairns (2010).

2.36.2 Distribution
Known only from type locality southeast of Kaua‘i, Hawaii, 73–426 m.

2.36.3 Comparisons
Being dichotomously branched with polyps in pairs T. biserialis is comparable to T. parva and T. coronata. Thouarella parva is most similar to T. biserialis as both have polyps that depart branchlets at 45° and more rounded marginals than T. coronata,
however, *T. biserialis* has a distinct keel on the inner surface of its marginals, something not clearly illustrated for *T. parva*. Additionally, polyps of *T. biserialis* appear more clavate than those of *T. parva* and *T. coronata*. Polyps of *T. coronata* are a similar size to those of *T. biserialis* however they diverge from branchlets at 90° rather than 45°. Additionally, polyps of *T. biserialis* are clavate rather than distally-flared, as in *T. coronata*, which also has taller, more pointed marginals than *T. parva*.

### 2.37 Thouarella grasshoffi Cairns, 2006

*Thouarella (Euthouarella) grasshoffi* Cairns, 2006: 184–188, figs, 1a, 12, 13.—Cairns & Bayer, 2009: 28 (listed)

*Material examined:* holotype USNM 1078188, Manning Seamount, north Atlantic Ocean, 38°08.74’N, 61°05.473’W, 1458 m, 16 May 2004, and all lots from Cairns (2006).

#### 2.37.1 Description

Description modified from Cairns (2006).

Colony consists of 1–3 main branches from which numerous closely spaced (usually less than 2 mm apart) branchlets originate on all sides of the main branch in a bottlebrush arrangement. Branchlets are undivided, 4 cm long and flexible in tension. Holotype is a single main stem 35 cm tall and 8–9 cm wide that has been broken from its base. Axis is 2.4 mm in diameter and a brownish colour.

Polyps occur randomly on main stem and in regular pairs (10–20% of polyp projections are whorls of three) every 1.5–1.9 mm on branchlets. Polyps curve upward toward branch tip, rarely longer than 1.3 mm, 0.7 mm in diameter. Sclerites are in 6–8 longitudinal rows with 5–7 scales in a longitudinal abaxial row.

Opercular scales form a tall cone. Opercular are isosceles triangle-shaped with a pointed apex, 260–620 µm long but most are 450–550 µm, H:W of 2.1–3.2. The proximal quarter of the inner surface is tuberculately, distal half bears one to several
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finely serrate keels. The outer surface has granules in a radial pattern from the central proximal area.

Marginal scales are not arranged in two defined rings as in most but two sets of 3 of the marginals have both lateral edges overlapping those of the adjacent marginals; the two remaining marginals have one side above and the other below their adjacent marginal. Marginals have acute pointed tips with a broad base, H:W of 0.93–2.1, up to 540 µm long. The proximal half of the inner surface is tuberculate, distal half bears 1–3 modest longitudinal keels; the outer surface is covered in granules.

Submarginal scales rounded, almost elliptical, broader than tall (H:W of 0.65–0.89), up to 340 µm long; adaxial scales rarely larger than 220 µm. Some submarginals have a small point at the distal edge and corresponding small ridge perpendicular distal edge on the inner surface. Inner surface of rounded submarginal distal edge and body-wall scales flanked by a smooth distal band; tubercules occur across the proximal three-quarters of the scale. The outer surface of sclerites is smooth with a few granules proximally. The distal edge of all sclerites is finely serrate with a coarsely lobate proximal edge.

Coenenchymal scales are elliptical to elongate in shape, rarely more than 320 µm long, H:W of 1.3–1.8; tuberculate inner surface, slightly concave, smooth outer surface sometimes with rare granules.

For images see Cairns (2006).

2.37.2 Distribution
Western Atlantic, New England Seamount Chain; 814–1458 m. Eastern Atlantic, Cape Verde Archipelago, Great Meteor Seamount, Azores Archipelago, Celtic Sea; 720–1760 m.

2.37.3 Comparisons
*Thouarella grasshoffi* is unique within Group 2 in having a true bottlebrush colony shape (*T. hilgendorfi* does have bottlebrush branches but has a wider, flabellate colony shape, see Table 2.3). Branchlets of *T. laxa* are pinnate but can appear bottlebrush because its flexible branchlets can be curved. Polyps of *T. laxa* are a
similar size with similar spacing as *T. grasshoffi*, however, *T. laxa* has a low opercular cone and shorter opercular with a blunt distal edge, whereas *T. grasshoffi* has a tall opercular cone, reflected in tall, triangular opercular. There is also a geographical separation between the two species, *T. grasshoffi* being found in the North Atlantic and *T. laxa* in the west Pacific to Indian Ocean.

Most species within Group 2 have polyps that are distally flared; *Thouarella grasshoffi* and *T. moseleyi* have more rounded, clavate polyps. The latter differs from the former in having shorter marginals and pinnate branchlets (so the colony can appear bilateral), whereas *T. grasshoffi* has a bottlebrush colony form.

### 2.38 New species combinations

#### 2.39 Plumarella diadema (Cairns, 2006), new combination

*Figure 2.36*

*Thouarella (Thouarella) diadema* Cairns, 2006: 181–184, figs. 10–11.—Cairns & Bayer, 2009: 28 (listed)

*Thouarella sardana* Zapata-Guardiola & López-González, 2010b: 136–139, figs. 2c,d, 5, 7

*Material examined*: holotypes (not examined), USNM 1078187, R/V *Calypso*, sta. 1776, 241 km SE of Sao Paulo, Brazil, 24°54'04"S, 44°26'00"W, 1000 m; *Thouarella sardana* paratype (examined), USNM 1123420, Antarktis XIX/5, R/V *Polarstern*, sample no. PS61/164–01, west of South Georgia Island, sub-Antarctic, 53°23'48"S, 42°42'02"W, 312–321 m, 9 Apr 2002; paratype of *T. sardana*, USNM 1123420; USNM 1130273, USNM 1129185 and USNM 1130274 (from same location), R/V *Eltanin*, cruise 22, sta. 1536, west tip of South Georgia Island, sub-Antarctic, 54°30’S, 39°20’W, 659–686 m, 8 Feb 1966; USNM 98090, R/V *Eltanin*, cruise 6, sta. 339, west of Beauchene Island, south of Falkland Islands, sub-Antarctic, 53°06’S, 59°27’W, 512–586 m, 3 Dec 1962, 2 colonies; USNM 98095 and USNM 98094 (same location), R/V *Eltanin*, cruise 9, sta. 740, east of Cape Horn, Drake Passage, Tierra del Fuego, Argentina, 56°06’S, 66°24’W, 384–494 m, 18 Sep 1963; USNM 98098 and USNM 77396 (from same location), R/V *Eltanin*, cruise 22, sta. 1592, Burdwood Bank, Scotia Sea, 54°44’S, 55°33’W, 1647–2044 m, 14 Mar 1966; USNM
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2.39.1 Description
See original description (Cairns 2006) except the specimens above, including the holotype of *T. diadema*, usually have 2–8 small accessory opercular beneath opercular scales.

The original description of polyp arrangement was “roughly alternating” (Cairns 2006, pp.181), however, with the wider body of material examined here, I conclude that this is not strictly true as usually polyps originate from all sides of branchlets. Lastly, *P. diadema* can have a pinnate colony structure (USNM 98089, Figure 2.36b,c) and most colonies appear bilateral, although they have branching in three directions and are technically thus bottlebrush.

Some marginals of USNM 98030 have double spines and bifurcate operculars, likely variation in a single colony (Figure 2.36d,e).

2.39.2 Distribution
Additional specimens expand the range of *P. diadema* from São Paulo, Brazil, south to the tip of Argentina and east to South Georgia Island, sub-Antarctic. Depth range: 278–3693 m.

2.39.3 Remarks
*Thouarella sardana* was differentiated from *T. diadema* in having accessory opercular (Zapata-Guardiola & López-González 2010b). The holotype of *T. diadema* does have accessory opercular, although they were not mentioned specifically in the original description (Cairns 2006), and thus these species are conspecific (accessory opercular do not occur in every polyp). *Thouarella diadema* has no keel on the inner surface of its marginals and it is thus considered to be a *Plumarella*.
USNM 98098, a deep specimen of *P. diadema* (1647–2044 m), did not have accessory opercular in any of the polyps studied but was identical in every other respect to this species. The deepest specimen, USNM 98089 (3350–3693 m), is pinnate but polyps and sclerites are identical to *P. diadema*.

One specimen from SMF (WH 1971, sta. 191) has much smaller polyps, a maximum of 2 mm, half the size of other specimens, and a very bushy, ramified branching structure. Some marginal scales of this specimen have wider, winged bases and a smoother inner surface. However, in all other respects, this specimen was identical to *P. diadema* and is thus included here; perhaps this was a juvenile specimen.

### 2.39.4 Comparisons

*Plumarella diadema* differs from *P.* (formerly *Thouarella*) *bayeri* Zapata-Guardiola and Lopez-Gonzalez, 2010b in having more acutely triangular/arrowhead-shaped opercular, and bushy/bottlebrush colonies rather than dichotomous branching.

*Thouarella variabilis* is very similar to *P. diadema* except polyps are smaller and spines of *T. variabilis* marginals are keeled, with 2–3 longitudinal ridges, rather than a channelled circular spine, as in *P. diadema*. The difference between these two spines, one keeled, one channelled, are at the boundary of *Thouarella* and *Plumarella*. Additionally, operculars on *T. variabilis* tend to be thinner, leaving visible gaps into the polyp from an anterior view, whereas *P. diadema* operculars are wider, covering the operculum.

The long spines of *P. diadema* can be mistaken for those of *Dasystenella acanthina*. Polyps of *D. acanthina* occur in whorls and that genus is defined by having five, rather than eight, marginal scales.

#### 2.40 *Plumarella recta* (Nutting, 1912), new combination

Figures 2.37c,d, 2.38

*Thouarella recta* Nutting, 1912: 67–68, pl. 7, figs. 1, 1a, pl. 19, fig. 2.—Kükenthal, 1919: 440–1; 1924: 302.—Aurivillius, 1931: 255–256

*Thouarella (Thouarella) recta*: Cairns & Bayer, 2009: 28 (listed)
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*Material examined:* 5 cm fragment of holotype, USNM 30040, R/V *Albatross*, sta. 5079, south of Omae Zaki, Honshu Island, Japan, 34°15’N, 138°E, 475–505 m, 19 Oct 1906.

2.40.1 *Description*

Colony appears uniplanar however branchlets depart main stem in 3 directions (2 at 160° creating an almost flat surface, with a third row placed sporadically along the dorsal spine at 260°), thus technically bottlebrush (Figure 2.37c). Two ventral branchlet rows depart alternately from the stem. Branchlets usually simple, sometimes forked, upwardly inclined 60°, longest branchlet was 24 mm.

Polyps stand at 90° to branchlet (Figure 2.37d), 1.2–1.4 mm long, generally isolated in one plane along branchlet, 7–9 polyps per cm, modestly flared distally (Figure 2.38m).

Operculum a raised cone of eight acute triangle-shaped opercular (Figure 2.38n,c–e), 260–320 µm tall (average 290 µm), 120–230 µm wide (average 165 µm), H:W 1.4–2.3 (average 1.8). The distal and lateral edge is serrate although lateral edges of some are pectinate; proximal edges roughly lobate. The inner surface is smooth (unkeeled) with a small patch of tubercles in centre proximally; the outer surface is smooth with several small granules in central proximal area.

Between two and four accessory opercular are found underneath opercular (Figure 2.38a,b, images of *P. recta* sclerites which are identical to those of *P. alternata*), generally less than 200 µm tall and 100 µm wide, round-tipped, tongue-shaped with a small patch of tubercles at the base of the inner surface and a smooth outer surface.

Marginals have circular base with elongated smooth distal spine; circular base has a pectinate edge which can continue up edges of the scale (Figure 2.38f–h). Marginals are too long to fold over opercular, 320–840 µm (average 530 µm), 165–350 µm wide (average 220 µm), H:W 1.4–3.3 (average 2.5); adaxial marginals smaller than abaxial. The inner surface is smooth with a sparse tuberculate circle at the base; the outer surface is smooth with few small granules towards proximal area of basal circle.
Body-wall scales mostly elliptical to fan-shaped (Figure 2.38i–k) although shape obscured by large pectinate lateral and distal edges; some body-wall scales smaller and placed irregularly, disrupting row placement. Body-wall scales 190–290 µm tall (average 230 µm), 255–365 µm wide (average 290 µm), H:W 0.7–1 (average 0.8). The outer surface is smooth with few granules; the inner surface has sparse tubercules and a tuberculate proximal edge.

Coenenchymal scales are numerous, small, circular to elliptical (Figure 2.38l), 100–120 µm tall (average 110 µm), 80–160 µm wide (average 125 µm), H:W 0.7–1.4 (average 0.9), edges are serrate. The inner surface has only several sparse tubercles; the outer surface is smooth with just a few granules.

2.40.2 Distribution
Only known from the south coast of Honshu Island, Japan, 475–505 m.

2.40.3 Remarks
All species of *Thouarella* have keels on the inner surface of their marginals, but *T. recta* does not, and is thus transferred to *Plumarella*. A smooth unkeeled inner opercular and marginal surface, elongated marginals unable to fold over operculum, and smooth outer surface of body-wall scales are characters found in *P. recta* and common to *Plumarella*.

The holotype is mostly denuded of polyps making the estimation of polyps per cm tentative.

The longitudinal rows of scales along the polyp body are dotted with small circular body-wall scales (see Figure 2.38m), which makes counting the number of scales in the two abaxial rows difficult. Nutting (1912) counted 8–9 scales in a longitudinal row. Within this study I counted 4–6 large scales in the abaxial rows, discounting smaller proximal circular scales.

2.40.4 Comparisons
*Plumarella recta* is most similar to *P. alternata* (see below) except that its polyps stand at 90° to the branchlet whereas those of the latter are at 45°, and roughly

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alternating. Without being certain of the importance of this morphological feature, and despite the identical appearance of these polyps, these species are kept distinct.

### 2.41 Plumarella alternata (Nutting, 1912), new combination

Figure 2.37a,b

*Thouarella alternata* Nutting, 1912: 69–70, pl.9, figs 1, 1a, pl. 19, fig 3.—Aurivillius, 1931: 255–256

*Thouarella attenuata:* Kükenthal, 1919: 438 (spelled incorrectly); 1924: 301

*Thouarella (Thouarella)* alternata: Cairns & Bayer, 2009: 27 (listed)

**Material examined:** holotype; USNM 30053 R/V Albatross, Northwestern Pacific Expedition, sta. 5080, west of Izu Islands, Honshu Island, Japan, 34˚10'30"N, 138˚40'E, 924 m, 19 Oct 1906 and USNM 30054, R/V Albatross, Northwestern Pacific Expedition, sta. 5079, south of Omae Zaki, Honshu Island, Japan, 34˚15’N, 138˚E, 869–924 m, 19 Oct 1906.

**2.41.1 Diagnosis**

Identical to *P. recta* (identical sclerites to Figure 2.38), except polyps are upwardly facing at 45˚ and roughly alternating (Figure 37a,b).

**2.41.2 Distribution**

Currently only known from Honshu Island, Japan, 869–924 m.

**2.41.3 Remarks**

The lack of marginal keels and alternating polyps suggest that this species be placed within *Plumarella*.

**2.41.4 Comparisons**

The alternating and isolated polyp arrangements in both *P. alternata* and *P. recta* are not consistent and the differentiation between these polyp arrangements is minor. However, without further material or knowing of the importance of polyp orientation, I am hesitant to synonymise these species despite their identical sclerite and polyp sizes and shapes.

### 2.42 Plumarella superba (Nutting, 1912)
CHAPTER TWO

Primnodendron superbum Nutting, 1912: 71–72, pl. 9, fig. 2, 2a; pl. 19, fig. 4

Thouarella (Amphilaphis) superba: Kükenthal, 1919: 412; 1924: 291

Thouarella superba: Dautova, 2007: 299 (sample not seen)

Thouarella (Thouarella) superba: Cairns & Bayer, 2009: 28 (listed).—Heifetz et al., 2005: 133 (listed)

Plumarella superba: Cairns, in press

Material examined: holotype, USNM 50150, R/V Albatross, Northwestern Pacific Expedition, sta. 4778, Semisopochini Island, western Aleutian Islands, North Pacific, 78–133 m, 5 Jun 1906.

2.42.1 Description

See full description in Cairns (in press).

2.42.2 Distribution

Aleutian Islands, possibly to western Boreal Pacific, Sakhalin Island (Dautova 2007). Depth range of 29–133 m.

2.42.3 Remarks

Note that gross morphology of colony is dichotomously uniplanar, with clear dorsal and ventral faces. Branches have branchlets on all sides in a bottlebrush arrangement, however ventral and dorsal branchlets are much shorter than lateral branchlets.

The lack of a keel on the inner surface of marginals suggests that this species is a Plumarella, as the genus description of Plumarella has expanded to include bottlebrush colonies and specifically species with a smooth inner marginal surface, i.e. unkeeled (Cairns, 2010).

2.43 Plumarella bayeri (Zapata-Guardiola and López-González, 2010b), new combination

Thouarella bayeri Zapata-Guardiola & López-González, 2010b: 133–135, figs. 2a,b, 3,4.

Material examined: holotype, ZIZMH C11738 (not examined), paratype, USNM 1123419, details same as holotypes, R/V Polarstern, ANT XIX/5, sta. PS61/164–01,
Revision of *Thouarella*

west South Georgia Island, sub-Antarctic, 53°23.80′S, 42°42.03′W, 312.5–321.6 m, 9 Apr 2002.

2.43.1 Description
Recently and fully described in Zapata-Guardiola and López-González (2010b).

2.43.2 Distribution
Currently known only from the west coast of South Georgia Island, 306–342 m.

2.43.3 Remarks
The marginals of *T. bayeri* are unkeeled (the inner surface has a long circular spine with longitudinal ridges), which suggests that it should not be considered a *Thouarella* but a *Plumarella*. The description of *Plumarella* has expanded to include colonies with bottlebrush branches, such as *P. superba* (Cairns, 2010), making *T. bayeri* more suitably classified as *Plumarella*.

Apart from colony shape *P. bayeri* is identical to *P. diadema*, which is bottlebrush (although can appear bilateral).

2.44 *Plumarella undulata* (Zapata-Guardiola and López-González, 2010b), new combination

*Thouarella undulata* Zapata-Guardiola & López-González, 2010b: 133–135, figs. 2a,b, 3,4

*Type and type locality:* holotype: ZIZMH C11742, ANT XIX/5, sta. PS61/167–01, west of South Georgia, Antarctica, 53°23.68′S, 42°42.23′W, 306–342.7 m, 9 Apr 2002.

*Material examined:* *Thouarella undulata* paratype, USNM 1123421, sample PS61/167–01, Antarktis XIX/5, R/V Polarstern, west of South Georgia Island, sub-Antarctic, 53°23′41″S, 42°42′14″W, 306–342.7 m, 9 Apr 2002, 2 colonies (110 mm, 100 mm); USNM 98291, R/V *Eltanin*, sta. 305, west of Sars Bank, Drake Passage, Chile, Antarctic, 59°59′S/70°43′W to 59°58′S/70°32′W, 2782–2827 m, 1 Nov 1962, 2 colonies; USNM 99150, R/V *Polarstern*, EPOS3, sta. 295, AGT 26, Queen Maud Land, Coats Land, Off Cape Norvegia, Antarctic, 71°08′48″S, 13°48′06″W, 2037 m,
21 Feb 1989; USNM 1129186 and USNM 1130315 (same location), R/V Eltanin, cruise 22, sta. 1536, 54°30’S, 39°20′31″W, 659–686 m, 8 Feb 1966.

2.44.1 Description
Recently and fully described in Zapata-Guardiola and López-González (2010b).

I would like to highlight the radially arranged granules and striations on the outer surface of the operculars.

2.44.2 Distribution
Specimens from this study extend the known range of *P. undulata* across the southwest Atlantic Ocean and south to Cape Norvegia, Antarctica, 306–2827 m depth.

2.44.3 Remarks
Because the marginals are long, spinose, and unkeeled, this species should be placed in *Plumarella* (see Cairns, 2010).

The only character that differentiates *P. diadema* from *P. undulata* is the extreme longitudinal curving and outer surface striations of *P. undulata* operculars. *Plumarella diadema* operculars can be curved and the two largest tend to have some abaxial striations, however, less so than *P. undulata* and the majority are generally smooth.

### 2.45 *Dasystenella acanthina* (Wright and Studer, 1889)

*Figure 2.39*

*Stenella acanthina* Wright & Studer, 1889: 59, pl.14, fig. 3, pl. 20, fig. 10.

*Stenella (Dasystenella)* Versluys, 1906: 39,48

*Thouarella longispinosa* Kükenthal, 1912: 299, figs.1−3

*Thouarella (Euthouarella) longispinosa*: Kükenthal, 1915: 151 (in part); 1919: 441 (in part); 1924: 302 (in part).—Broch, 1965: 26–27, pl.3 figs. 8–10

*Thouarella longispinosa*: Gravier, 1914: 61–63, pl. 7, figs. 35–36, pl.10, figs. 52–55.—Thomson & Rennet, 1931: 24–26.—Utinomi, 1964: 11–12, fig. 6, pl. 2


Revision of *Thouarella*

*Material examined:* *Dasystenella acanthina*, syntype, NHM 89.5.27.48a, Deutsch Subpolar Expedition 1901–1903, Gauss–Station, off Argentina, 385 m, 12 Jan 1903; *Thouarella longispinosa* syntype, MNHWU and SMF; USNM 84325, R/V *Eltanin*, cruise 12, sta. 1083, east of South Orkney Islands, Scotia Ridge, Antarctic, 60°51’S, 42°57’W, 284 m, 14 Apr 1964.

The MNHWU syntype specimen of *T. longispinosa* is in poor condition with few intact polyps. The SMF sample is in a good condition. Examination of all polyps confirmed the below synonymisation. Colony description was taken from Kükenthal (1912).

### 2.45.1 Description of *Thouarella longispinosa* syntype (MNHWU)

*Colony bottlebrush. Branchlets 22 mm long.*

Polyps 1.5–2 mm long, distally flared (Figure 2.39c), upwardly inclined, in whorls of three or four, rarely in pairs, with 5 whorls per cm. Polyps covered with a small number of scales in 5 longitudinal rows, reducing to 4 at the polyp base. Each polyp has 4 scales in an abaxial row (Figure 2.39c), two lateral rows, each with three scales, and two reduced rows of three small scales adaxially.

Tall conical operculum of eight elongated isosceles triangle-shaped opercular, although not evenly spread around opercular circumference, with two reduced inner adaxial opercular being smaller (Figure 2.39h) than abaxial opercular (Figure 2.39k), both of which have proximally diagonal bases depending on their opercular position. The inner surface bears a single, flattened opercular keel. Opercular are 100–430 µm wide (average 260 µm), 555–970 µm long (average 770 µm). Tubercles cover the proximal half of the inner surface; smaller opercular have fewer tubercles. The outer surface has a slightly concave median longitudinal groove and is usually smooth; infrequent radial ridges from central proximal area.

Polyps have five marginals; three very long abaxial marginals (Figure 2.39n, similar in shape to large operculars) 530–1340 µm tall (average 840 µm), 300–570 µm wide (average 440 µm), H:W 1.3–2.6 (average 1.9), two that are outer laterals (Figure
2.39m). The remaining two small, square to circular-shaped marginals are placed adaxially (Figure 2.39b1) and are a similar size to smaller body-wall scales (Figure 2.39f,g). Large marginals do not fold over the operculum but are upwardly inclined and lean slightly adaxially giving the two laterals a diagonal proximal edge (Figure 2.39m,n). Proximal half of the inner surface is covered in tubercles to base of keel; the keel is channelled. The outer surface is smooth with sparse granules and a modest longitudinal groove.

Body-wall scales can be large (same size as largest operculars) and circular (Figure 2.39e), 220–500 μm tall (average 350 μm), 200–570 μm wide (average 420 μm), H:W 0.8–1.1 (average 0.9). Tubercles cover the inner surface; the outer surface is smooth with some granules across the central proximal area of larger scales. Body-wall scales have a finely serrated distal edge.

Coenenchymal scales are small and circular to elliptical in shape (Figure 2.39l), 150–200 μm wide and tall. All sclerites have a coarsely lobate proximal edge.

2.45.2 Distribution
Tierra del Fuego, South Shetland Islands and Scotia Ridge between South Orkney and South Sandwich Islands, 110–5087 m.

2.45.3 Remarks
When Kükenthal (1912) transferred Stenella acanthina to Thouarella he mentioned that it was very similar to T. longispinosa (Kükenthal 1915). Thomson and Rennet (1931) described T. longispinosa as having 4–5 marginals. Thouarella longispinosa does have 5 marginals and is thus Dasystenella. Brito (1993) does not explain clearly the inclusion of D. acanthina in Thouarella and I believe this is incorrect based on the lower number of marginals found in D. acanthina.

Thouarella longispinosa specimens from MNHWU and SMF differ from the holotype of D. acanthina in having operculars and marginals more similar in size to each other; although marginals are generally longer than D. acanthina with a higher H:W of 2.7, compared to 2.1 in D. acanthina (Cairns 2006). However, Cairns (2006) lists some D. acanthina from southerly latitudes with marginals that have a much higher H:W of 3.5, and smaller, more upwardly inclined polyps. Given this wide variation and
limited differences between *T. longispinosa* and the description of *D. acanthina*, I propose that *T. longispinosa* be synonymised with *D. acanthina*, noting that a revision of *Dasystenella* is required.
2.46 Figures
Figure 2.3 Examples of sclerite categories. Accessory opercular (a.) Thouarellia chilensis, (b,c.) T. hicksoni, (d,e.) T. coronata; Opercular (f.) T. clavata, (g.) T. affinis, (h.) T. koellikeri, (i.) T. antarctica; Marginals (j.) T. variabilis, (k.) T. affinis, (l.) T. crenelata; Submarginals (m.) T. coronata, (n.) T. koellikeri, (o.) T. hicksoni; Body-wall scales (p.) T. clavata, (q.) T. hicksoni, (r,s.) T. parachilensis; Coenenchymal scales (t.) T. laxa, (u.) T. crenelata, (v.) T. antarctica.
Figure 2.4 Thouarella antarctica; (a.) 21 cm colony SMF, R/V W. Hertwig 1971, sta. 256; (b.) holotype, MNHN, Oct.0000-208; (c.) abaxial polyp view of holotype; (d.) close up of branchlet from SMF sample; (e.) stereo opercular view of holotype polyp, some marginals missing; (f.) opercular view of holotype polyp with marginals.
Revision of *Thouarella*

Figure 2.5 *Thouarella antarctica*; (a,c.) outer and (b, d-f.) inner surface of opercular scales; (g,h.) outer and (i,j.) inner surface of marginal scales; (k,l.) inner and (m,n.) outer surface of submarginal scales; (o-q,s.t.) inner and (r,u,v.) outer surface of body-wall scales; (w.) coenenchymal scales – inner surface top row first and second left, bottom row second left, remainder are of the outer surface.
Figure 2.6 Thouarella variabilis; (a.) 22 cm long colony, syntype, NHM 89.5.27.56; (b.) Close up of several polyps; (c.) close up of brooding polyps; (d.) lateral view of two polyps; (e.) stereo opercular view, NB – 1 indicates submarginal scale; (f.) abaxial polyp view.
Figure 2.7 *Thouarella variabilis*; (a.) 22 cm long colony, syntype, NHM 89.5.27.56; (b.) Close up of several polyps; (c.) close up of brooding polyps; (d.) lateral view of two polyps; (e.) stereo opercular view, NB – 1 indicates submarginal scale; (f.) abaxial polyp view.
Figure 2.8 *Thouarella brevispinosa*; (a.) 12 cm colony NHM 89.5.27.54; (b.) lateral polyp view; (c.) abaxial polyp view; (d.) stereo opercular view.
Revision of *Thouarella*

Figure 2.9. *Thouarella brevispinosa*: (a,d–f.) inner and (b,c,g.) outer surface of opercular scales; (h.) inner and (i,j) outer surface of marginal scales – the lateral and distal edges of j are eroded; (k,l) inner and (m,n) outer surface of submarginal scales; (o–q) outer and (r,s) inner surface of body-wall scales; (t) coenenchymal scales – inner surface on top right and bottom three right scales, remainder show the outer surface.
Figure 2.10 Thouarella affinis; (a.) 13 cm long colony, holotype, NHM 1889.5.27.44, with polychaete along axis; (b.) lateral polyp view; (c.) close up of polyps; (d.) stereo opercular view.
Figure 2.11. *Thouarella affinis*; (a-c,g.) inner and (d–f.) outer surface of opercular scales; (h,i.) inner and (j.) outer surface of marginal scales; (k–n.) outer and (o–q.) inner surface of body-wall scales; (r,w.) outer and (s–v.) inner surface of coenenchymal scales. Some SEM images by ZGR.
Figure 2.12. *Thouarella koellikeri*; (a.) 19 cm long colony, syntype, NHM 1889.5.27.41; (b.) close up of branchlet; (c.) lateral polyp view; (d.) abaxial polyp view; (e.) stereo opercular view.
Figure 2.13. *Thouarella koellikeri*; (a,d.) inner and (b.) outer surface of opercular scales; (c.) side view of opercular keel; (e.) inner and (f,g.) outer surface of marginal scales; (h–j.) inner and (k.) outer surface of submarginal scales; (l,o.) inner and (m,n,p.) outer surface of body-wall scales; (q.) top left, fourth and fifth from left on top row and fifth on bottom row are of the inner surface of coenenchymal scales, the remainder are outer surface images. Some SEM by ZGR.
Figure 2.14. Thouarella brucei; (a.) abaxial view of polyp; (b.) 6.5 cm long fragment of holotype, ZMA. COEL03574; (c.) lateral view of polyp; (d.) stereo opercular view
Figure 2.15 *Thouarella brucei*; (a–b.) outer surface and (c–e.) inner surface of opercular scales; (f.) inner and (g–h.) outer surface of marginal scales; (i.) inner and (j.) outer surface of submarginal scales; (k,m.) inner and (l.) outer surface of body-wall scales; (n.) coenenchymal scales, top row outer surface, bottom row inner surface. Photo and some SEM by ZGR.
Figure 2.16 *Thouarella striata*; (a.) 14 cm long colony (SMF 1966, sta. 285); (b.) fragment of holotype (from MNHWU), 2.5 cm long; (c.) lateral polyp view; (d.) abaxial polyp view; (e.) stereo opercular view. Photo (b.) by ZGR.
Figure 2.17. *Thouarella striata* (all sclerites from MNHWU holotype); (a.) outer and (b,c.) inner surface of operculars; (d,f.) outer and (e.) inner surface of marginal scales; (g,h.) inner surface of submarginal scales; (i) abaxial body-wall scale with sculpted distal edge, (j,l.) inner surface of circular body-wall scales, (k.) inner and (m.) outer surface of body-wall scales; (n–p.) outer and (q.) inner surface of coenenchymal scales.
Figure 2.18 *Thouarella crenelata*; (a.) USNM 98086, colony 35 cm; (b.) polyps of USNM 98086; (c.) abaxial polyp view; (d.) close up of holotype polyps, ZMB; (e.) stereo opercular view of USNM 98086 polyp.
Figure 2.19. *Thouarella crenelata*; Images of USNM 98086 sclerites (a-c.) inner, (d.) outer and (e.) lateral view of operculars; (f.) inner and (g.) outer surface of marginal scales; (h,i.) outer and (j-l.) inner surface of submarginal scales; (m.) inner and (n,o.) outer surface of body-wall scales; (p.) outer surface of coenenchymal scale.
Figure 2.20. *Thouarella clavata*; (a.) image of holotype colony, 11 cm, fig. 69 from Kükenthal 1919; (b.) fragment of syntype branchlet, MNHWU; (c.) close up of two polyps, syntype MNHWU; (d) colony, USNM 1140264; (e.) close up of polyps of USNM 1140264. Photos by SJ.
Figure 2.21. *Thouarella clavata*, images of USNM 1140264; (a.) abaxial view of polyp; (b.) stereo opercular view of polyp; (c.) lateral polyp view; (d,e,f.) inner and (g,h.) outer surface of operculars; (i.) outer and (j.) inner surface of marginals; (k.) inner and (l.) outer surface of submarginals; (m.) inner and (n.) outer surface of body-wall scales; (o,p,q.) outer and (r,s.) inner surface of coenenchymal scales.
Figure 2.22. *Thouarella pendulina*; (a.) holotype from MNHN, Oct.0000-0211, broken; (b.) complete colony, 22 cm, USNM 98359; (c.) close up of polyps of USNM 98359; (d.) abaxial and lateral view of polyps on branchlet of holotype; (e.) stereo opercular view.
Revision of *Thouarella*

Figure 2.23. *Thouarella pendulina*; (a,c,d.) inner and (b,e.) outer surface of opercular scales; (f,g,h.) inner and (h.i.) outer surface of marginal scales; (k.) inner surface of submarginal; (l.) outer and (m–o.) inner surface of body-wall scales; (p–r.) outer and (s,t.) inner surface of coenenchymal scales.
Figure 2.24 Thouarella chilensis; (a.) holotype colony, 14 cm, ZMH C1780; (b.) close up of polyps; (c.) abaxial and lateral views of polyps; (d.) stereo opercular view of polyp.
Figure 2.25. *Thouarella chilensis*; (a–c.) inner and (d.) outer surface of accessory operculars; (e,f.) outer and (g.) inner surface of opercular scales; (h,i,l.) outer and (j,k.) inner surface of marginal scales; (m.) inner and (n,o.) outer surface of submarginal scales; (p,r,t.) outer and (q,s.) inner surface of body-wall scales; (u.) inner and (v,w.) outer surface of coenenchymal scales.
Figure 2.26. *Thouarella hicksoni*; (a.) 4.5 cm colony NHM 1962.7.20.36; (b.) close up of branchlet; (c.) abaxial polyp view; (d.) lateral polyp view; (e.) branchlet; (f.) stereo opercular view of polyp.
Figure 2.27. *Thouarella hicksoni*; (a.) inner and (b,c.) outer surface of accessory opercular scales; (d,e.) inner surface of opercular scales; (f,g.) inner and (h.) outer surface of marginal scales; (i,j.) inner surface of submarginal scales; (k,n.) inner and (l,m,o.) outer surface of body-wall scales; (p.) outer surface of a coenenchymal scales. Photos by JS.
Figure 2.28. *Thouarella parachilensis* sp. nov; (a.) holotype colony, 29 cm long, 20 cm wide, USNM 98338; (b,c.) close up of ‘barrel-shaped’ clusters of polyps; (d.) abaxial polyp view; (e.) stereo opercular view. Photo by SJ.
Revision of *Thouarella*

Figure 2.29. *Thouarella parachilensis* sp. nov; (a,f.) inner and (b-e.) outer surface of opercular sclerites; (g.) outer and (h.) inner surface of marginal scales; (i,k.) outer and (j.) inner surface of submarginal scales; (l,n,p,q.) outer and (m,o.) inner surface of body-wall scales; (r.) coenenchymal scales – top row right, middle row right, bottom row left show the outer surface, remainder inner surface.
Figure 2.30. *Thouarella moseleyi*; (a.) 6 cm colony, holotype, NHM 1889.5.27.39; (b.) close up of the few remaining polyps; (c.) lateral view of polyp; (d.) stereo opercular view.
Figure 2.31. *Thouarella moseleyi*; (a.) outer and (b,c.) inner surface of opercular scales; (d,f.) inner and (e.) outer surface of marginal scales; (g,h.) inner surface of submarginal scales; (i,l.) inner and (j,k.) outer surface of body-wall scales; (m.) coenenchymal scales – outer surface shown on top left and bottom right scales, remainder show the inner surface. Some SEM by ZGR.
Figure 2.32. _Thouarella laxa_; (a,b.) original images of _T. laxa_ holotype from Versluys, 1906, 20 cm colony and close up of small branch, ZMA COEL03576; (c.) pair of polyps; (d.) polyp of _T. carinata_, now synonymised with _T. laxa_; (e.) stereo opercular view of _T. laxa_. Photos by JS.
Figure 2.33. *Thouarella laxa*: (a,b,d.) inner and (c,e.) outer surface of opercular scales; (f.) outer and (g,h.) inner surface of marginal scales; (i,j.) inner surface of submarginal scales; (k,n.) inner and (l,m.) outer surface of body-wall scales; (o.) coenenchymal scales – outer surface bottom right, remainder are the inner surface.
Figure 2.34. Thouarella coronata; (a.) image of holotype UMUT, 13 cm colony; (b.) close up of holotype, UMUT; (c.) whorl of three polyps; (d.) abaxial polyp view; (e.) lateral polyp view; (f.) stereo opercular view. SEM by RZG.
Figure 2.35. Thouarella coronata; (a,b.) outer and (c.) inner surface of accessory operculars; (d,g,h.) outer and (e,f.) inner surface of opercular scales; (i,j.) outer and (k.) inner surface of marginal scales; (l,m.) inner surface of submarginal scales; (n.) inner and (o,p.) outer surface of body-wall scales; (q.) coenenchymal scales – inner surface top row left, bottom row right and middle; remainder are the outer surface. Some SEM by ZGR.
Figure 2.36. *Plumarella diadema*; (a.) 6 cm colony, holotype, USNM 1078187; (b.) close up of polyps of USNM 98089, pinnate colony form; (c.) 10 cm pinnate colony form, USNM 98089; (d.) inner and (e.) outer surface of bifurcate marginal of holotype specimen, USNM 1078187. Photos by SJ.
Figure 2.37. *Plumarella recta* and *P. alternata*; (a.) approx. 16 cm *P. alternata* colony, holotype, USNM 30097; (b.) close up of *P. alternata* polyps; (c.) 5.5 cm *P. recta* colony, holotype, USNM 30040; (d.) close up of *P. recta* polyps. Photos by RZG.
Figure 2.38. *Plumarella recta* sclerites, identical to those of *P. alternata*; (a.) inner and (b.) outer surface of accessory operculars; (c,d.) inner and (e.) outer surface of opercular scales; (f,g.) inner and (h.) outer surface of marginal scales; (i.) outer and (j,k.) inner surface of body-wall scales; (l.) coenenchymal scales – first column of scales show the inner surface, remainder are the outer surface; (m.) lateral view of *P. recta* polyp; (n.) stereo opercular view of *P. recta* polyp. SEM taken by ZGR.
Revision of *Thouarella*

Figure 2.39. *Dasystenella acanthina*, images from the MNHWU syntype of *Thouarella longispinosa* which is synonymised here with *D. acanthina*; (a.) 4.8 and 2 cm colony fragments; (b.) adaxial polyp view; (c.) abaxial polyp view; (d.) stereo opercular view; (e) outer and (f,g.) inner body-wall scales; (h–k.) inner surface opercular scales; (l.) coenenchymal scales, upper scale outer surface, lower scale inner surface; (m.) inner and (n.) outer surface of marginal scales. NB - some operculars are missing. ‘1’ indicates small adaxial marginal scale. Image (a.) by ZG
Figure 2.40. *Thouarella parva*. (d.) lateral polyp view, modified from Fig. 1 Kinoshita, 1908d; (e.) sclerites from Kinoshita, 1908d – I. accessory operculars, II. operculars, III. marginals, IV. submarginals, V,VI. body-wall scales (f,g.) inner surface of *Thouarella andeep* marginals, USNM 1123418.

2.47 Acknowledgements

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photos; James Soda for preparing stubs and taking some SEM images; Diane Wyse for sclerite measurements and species identifications; and Jon Schleyer for specimen photographs. I reserve special mention and thanks for the late, great Dr F. M. Bayer, whose beautiful SEM images also grace these pages. And, of course, I appreciate the very useful comments of three anonymous reviewers that ultimately improved the manuscript.
CHAPTER THREE
3 Molecular phylogenetics and species richness of octocorals from longline by-catch around South Georgia, UK

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In preparation for Molecular Phylogenetics and Evolution

3.1 Abstract

Managers of the longline Patagonian toothfish fishery around South Georgia were interested in knowing the species richness of octocorals that were being commonly caught as by-catch. As octocoral taxonomy is convoluted and time-consuming molecular techniques were pursued to investigate octocoral species richness. By-catch octocorals are here placed into a wider Octocorallia (excluding Helioporacea) phylogeny to investigate their species richness using a COI+igr1+msh1 gene combination (alongside analyses with igr1 removed). Phylogenetic trees of Octocorallia are presented comprising at least 108 genera and 142-156 species across 28 families.

Trees constructed using Bayesian inference (BI) was had more structure than maximum likelihood analyses and stronger node support. Across all analyses, deeper tree nodes manifested stronger support than the tips of clades. Analyses consistently resolved three clades within Octocorallia (Clade 1 – Scleraxonia/Alcyoniina/Holaxonias; Clade 2 – Pennatulacea/Calcaxonia; Clade 3 – majority Calcaxonia). Previous analyses, with a different spread of species, resolved three different clades. The inclusion of igr1 in BI analysis placed Pennatulacea towards the base of Octocorallia phylogeny, otherwise the three clades were in a polytomy. Few octocoral families were resolved as monophyletic; this confirms that taxonomic re-evaluations are required across this subclass.

Primnoidae are the octocoral family most frequently caught as by-catch around South Georgia. With 11 of the 37 described genera of Primnoidae represented (not including 2 new genera), this is the largest genetic study of this family so far. Considering just by-catch, 34 species in 21 genera of octocorals were identified and morphologically
verified. As such it was possible, using the recently created Species Delimitation plug-in to Geneious (Biomatters Ltd), to explore the phylogenetic evidence for monophyly of the Primnoidae in morphological species concepts in an integrative manner. Most species were confirmed as monophyletic; however, polyphyly within genera and some species of Primnoidae inhibited the use of some statistics within the programme.

This research shows that estimates of octocoral species richness are possible to gather from phylogenetic data (most successfully from Primnoidae, the family most commonly caught as by-catch around South Georgia). Such integrative taxonomic research feeds directly into management decisions and opens the prospect of similar work in other fisheries.

*Keywords*: Primnoidae, molecular operational taxonomic unit, MOTU, integrative taxonomy, Octocorallia.
In recent years there has been heightened international interest regarding vulnerable deep-water habitats (UNGA, 2003; 2005), especially in relation to fisheries impacts (UN General Assembly Resolutions on Sustainable Fishing on the High Seas 61-105 and 64-72, 2007; 2009). Octocorals are a prominent component of many deep-sea benthic communities (Metaxas and Davis, 2005; Stone, 2006) and were found to be the major component of by-catch in the Patagonian toothfish, Dissostichus eleginoides Smitt, 1898, fishery around South Georgia (see Chapter 5; Wakeford et al., 2006). Given the dwindling number of deep sea octocoral taxonomists globally, the increasing scale of human activities in the deep sea (Glover and Smith, 2003; Davies et al., 2007), and potential impacts from these activities (Danovaro et al., 2001; reviewed in Davies et al., 2007), new methods of quantifying octocoral species richness are required. This research aimed to quantify the species richness of octocorals in by-catch using phylogenetic analyses and molecular operational taxonomic unit (MOTU) diversity (Floyd et al., 2002).

3.2.1 Patagonian toothfish fishery of South Georgia

The South Georgia Patagonian toothfish fishery uses bottom longline gear between 700 – 2000 m (previously 550 – 2000 m) in depth. By-catch of a range of benthic marine life is commonly hooked and brought to the surface as by-catch. The 2004 Marine Stewardship Council certification of the toothfish fishery (MSC 2004) initiated more specific studies of benthic community location, extent and composition (Agnew et al., 2007; Wakeford et al., 2006). Octocorals were by far the most abundant benthic taxa in by-catch around South Georgia (Wakeford et al., 2006; see Chapter 5). These initial studies of benthic diversity resulted in three temporary Restricted Impact Areas being created where fishing is excluded, other than for research purposes. In the present study Cnidaria constituted 80% of by-catch samples, of which 72% were Octocorallia (see Chapter 5). Agnew et al. (2007) reported high octocoral diversity around South Georgia and here I wish to investigate this richness to a species level using phylogenetic and morphological analyses in an integrative taxonomic approach (Dayrat, 2005; Will et al., 2005).
3.2.2 Octocorallia phylogenetics

Cnidaria (of which Octocorallia comprise a subclass) exhibit very slow rates of mitochondrial evolution (Shearer et al., 2002) and, consequently, genetic markers have low levels of variation; often more so in octocorals than other anthozoans (France et al., 1996). Many octocoral genetic markers have been tested for variation (cytochrome oxidase I, COI, France and Hoover, 2002; ND3, ND4L; France and Hoover, 2001; ND2, ND6, McFadden et al., 2004; ITS2, Aguilar and Sanchez, 2007a; b). The nuclear gene ITS2 manifests the most variance, however, this marker is often a multi-copy gene, requiring denaturing gel electrophoresis (DGGE; Sánchez and Dorado, 2008) to ensure the acquisition of homologous copies from different specimens. The alignment of resultant sequences has been informed by looking at the secondary structure. However, these methodologies were unclear and were not replicated successfully in this study (Aguilar and Sanchez, 2007a; b). No other nuclear markers with useful phylogenetic signal have so far been found.

The most variant mitochondrial marker in octocorals is msh1 (France and Hoover, 2001; van der Ham et al., 2009). Unusually, msh1 (MutS homologue) is not known in any other metazoan (Culligan et al., 2000), providing a synapomorphy for octocorals, and is a reputed protein-coding DNA mismatch repair gene (Pont-Kingdon et al., 1998; Beagley et al., 1995). The presence of msh1 has been proposed as the reason for the slow rates of mtDNA evolution found in octocorals (France and Hoover, 2001). This is, however, disputed, as allele activity loss in yeast msh1 does not lead to an increase in mismatches during meiosis (Sia and Kirkpatrick, 2005). From this relatively depauperate group of markers a combination of COI with the COI-COII intergenic region (igr1) and msh1 appeared to offer the most variation (McFadden et al., 2010a; b), and were thus utilised here.

Octocorals are a well-defined morphological, monophyletic subclass (Bayer, 1981; France et al., 1996; Bernston et al., 2001). However, their ordinal and subordinal structure are divergent between morphological and molecular studies (see Figure 3.1 for summary; Bernston et al., 2001, Sanchez et al., 2003; McFadden et al., 2006). The most recent and detailed phylogenetic tree of Octocorallia was presented by McFadden et al. (2006; see Figure 3.1) using ND2 and msh1. This and previous phylogenetic octocoral studies support three clades within Octocorallia (reviewed in
Phylogenetics of octocorals

McFadden et al., 2010b); broadly, the three contain Holaxonia–Alcyoniina, Calcaxonia–Pennatulacea, and a smaller Anthomastus-Corallium clade (see Table 3.4). However, within Calcaxonia–Pennatulacea there was little resolution of subordinal or family-level relationships (McFadden et al., 2006).

The research presented here thus embeds South Georgia by-catch octocoral specimens into the order Alcyonacea (disregarding the order Helioporacea in the Octocorallia) using the COI+igr1+msh1 gene combination.

![Figure 3.1 Comparison of morphological and molecular octocoral taxonomy over time.*indicates suborder Calcaxonia, added by Grasshoff (1999)** indicates placement of Calcaxonia and Helioporacea by Bernston et al. (2001) that was not supported by McFadden et al. (2006). McFadden et al. (2006) unresolved suborders represent a few taxa near the phylogeny base that were unresolved. Figure reproduced from McFadden et al. (2010a).]

3.2.3 Octocoral MOTU diversity and ‘integrative taxonomy’

Few deep-sea octocorals have been sequenced, making barcoding techniques that refer to pre-existing databases (phylogenetic: Blaxter, 2004; coalescent: Abdo and Golding, 2007; likelihood ratio test: Matz and Nielsen, 2005; Bayesian: Munch et al., 2008) impossible. Morphological identifications were made (see Chapter 2) and as such, it was possible to investigate the probability of these putative species being monophyletic with the Species Delimitation plug-in (Masters et al., 2011) in Geneious (Biomatters Ltd) in an integrative taxonomic approach (Dayrat, 2005; Will et al.,
2005); a concept rapidly being adopted (Padial and De La Riva, 2010; Schlick-Steiner et al., 2010). In this way an investigation of by-catch species richness is undertaken.

### 3.3 Aims

The questions this research aimed to answer were (1) Does the COI+igr1+msh1 gene combination have sufficient variability to resolve phylogenetic relationships within Octocorallia? (2) Can COI+igr1+msh1 resolve species-level relationships within Octocorallia? (3) Are estimates of octocoral by-catch species richness best procured using phylogenetics or morphological studies, and does an integrative taxonomic approach provide additional information?

### 3.4 Methods

#### 3.4.1 Sample collection

Fisheries observers collected samples of by-catch from 16 bottom-longline vessels between 2005 and 2009. Fishing was concentrated between 500-2000 m. Pictures of by-catch were taken and small snippets of corals preserved in 70-90% ethanol and sent to the Zoological Society of London (ZSL) to be identified to the highest possible taxonomic level.

#### 3.4.2 Laboratory protocols

Total DNA was extracted using DNeasy Kits (Qiagen) from preserved material. PCR reactions were conducted using 8 µl of Multiplex PCR Master Mix with HotStarTaq (Qiagen), 2 µl of DNA, 0.8 µl of each primer (2 µM) and 0.4 µl of H₂O in 12 µl reactions. The primers for msh1 were ND42599F (France and Hoover 2002) and Mut3458R (Sánchez et al., 2003) and the PCR protocol followed was: 15 min initial extension at 95°C to activate the HotStarTaq, 35 cycles of 1 min at 94°C, 1 min at 52°C, 2 min at 72°C, with a final extension of 30 min at 60°C. For COI+igr1, COII8068F (McFadden et al., 2004) and COIOCTr (reverse of COIOCTf; France and Hoover, 2002) primers were used, as per McFadden et al. (2010ab). The PCR protocol was modified from McFadden et al., (2001): an initial hotstart extension of 15 min at 95°C was followed by 30 cycles of 30 sec at 94°C, 1.5 min at 58°C, 1 min at 72°C, with a final extension at 72°C for 5 min.
Table 3.1 Primers

<table>
<thead>
<tr>
<th>Gene</th>
<th>Primer name</th>
<th>Primer sequence and reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>msh1</td>
<td>ND42599F</td>
<td>5’-GCCATTATGGTTAACTATTAC-3’ (France and Hoover, 2002)</td>
</tr>
<tr>
<td></td>
<td>Mut3458</td>
<td>5’-TSGAGCAAAAGCCCACTCC-3’ (Sanchez et al. 2003)</td>
</tr>
<tr>
<td>COI+igr1</td>
<td>COII8068F</td>
<td>5’-CCATAACAGGACTAGGCAGCATC-3’ (McFadden et al 2004)</td>
</tr>
<tr>
<td></td>
<td>COIOCTr</td>
<td>5’-ATCATAAGCAGGAGCCATTAC-3’ (France and Hoover 2002)</td>
</tr>
</tbody>
</table>

Amplified products were either sent to the Natural Environment Research Council (NERC) Biomolecular Analysis Facility at the University of Edinburgh for sequencing or cleaned and sequenced at the Institute of Zoology, London. PCR reactions were purified using QIAquick PCR Purification centrifuge kits (Qiagen) following the manufacturer’s instructions. DNA was sequenced in both directions using the aforementioned primers. Sequencing reactions totalled 15 µl: 3 µl cleaned PCR product, 2 µl of ABI BigDye Terminator v 3.1 kit (Applied Biosystems), 4 µl Better Buffer (Gel Company), 3 µl 0.8 Mm primer and 3 µl dH₂O. Sequencing reaction thermal cycle parameters consisted of one cycle at 96°C, followed by 25 cycles of 10 sec at 96°C, 5 sec at 50°C, and 4 min at 60°C with no final extension. Sequencing reaction product was cleaned by adding 4 µl of 125 mM EDTA and 30 µl of 100% ethanol. After mixing, the solutions were centrifuged for 30 mins at 3000 x g (at 4°C). The plate was immediately inverted on tissue paper to remove supernatant, leaving the DNA pellet. 30 µl of 70% ethanol was added to each sample and centrifuged for 15 mins at 1650 x g (at 4°C). Again, supernatant was removed by inverting samples onto tissue paper. Any remaining ethanol was evaporated by incubation at 55°C for 2 mins. Purified sequencing product was resuspended in 10 µl formamide and heated to 95°C for 2 mins, snap-cooled and sequenced on an Applied Biosystems 3100 Prism automated DNA sequencer.

3.4.3 Alignment

Alignment and corrections by eye were completed in Geneious Pro 5.0.2 from Biomatters Ltd (http://www.biomatters.com), as were the amino acid translations; 379 were included in these analyses, representing 409 specimens as 30 identical sequences were found using pairwise genetic distances in MEGA 4.1 (Tamura et al., 2007) so one sequence of each identical set was selected to remain in the alignment. Of the 379 sequences, 273 were original sequences procured using the protocol above; the
remainder were from previous analyses downloaded from GenBank (GB) that are included to present the most detailed phylogenetic tree of Octocorallia possible. Initial stop codons (TGA) were reassigned to specify tryptophan in the invertebrate mitochondrial translation table, leaving no stop codons or misplaced reading frames within the alignment, indicating that no pseudogenes were amplified (Bensasson et al., 2001).

3.4.4 Species delimitation

Pairwise distance data are quick and easy to create. A wide analysis of species classification methods revealed that the distance approach (k-nearest neighbour) was consistently the most reliable, always being amongst the best performing (Austerlitz et al., 2009). A recent pairwise genetic distance study by Plaisance et al., (2009) used step-function analysis to separate species; however, this and all threshold methods (10x the mean intraspecific variation for the group, Hebert et al., 2004; minimising combined false-positive and false-negative error rates, Meyer and Paulay, 2005) have so far relied on some level on subjective visual assessment of either tree-structure, a minimum level of combined false-positives and false-negatives, or an inflexion point (as in Plaisiance et al., 2009) to separate species. Given the limited number of sequences available for each family (Isididae being the exception; however, there are few identifications to species level), all specimens of the most diverse and abundant family in by-catch, the Primnoidae, were morphologically identified to species level and, as such, a new Geneious plug-in that assigns probability of monophyly to putative species (Masters et al., 2011) was tested alongside inferred ‘species’ groups from phylogenetic analyses (Blaxter, 2004).

3.5 Analysis

3.5.1 Nucleotide model selection

The best-fit models of nucleotide substitution were selected using JModeltest v0.1.1 (Posada, 2008; Guindon and Gascuel, 2003) and are listed in Table 3.1. Using a best-fit model increases accuracy and power of phylogenetic analyses.
Table 3.2 Nucleotide models for genes and gene combinations selected by JModeltest.

<table>
<thead>
<tr>
<th>Genes tested</th>
<th>AIC</th>
<th>AICc</th>
<th>BIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>msh1</td>
<td>GTR+G</td>
<td>K80+G</td>
<td>TVM+G</td>
</tr>
<tr>
<td>COI</td>
<td>TIM2+I+G</td>
<td>K80+G</td>
<td>TIM2+I+G</td>
</tr>
<tr>
<td>igr1</td>
<td>TIM+G</td>
<td>TIM+G</td>
<td>K80</td>
</tr>
<tr>
<td>All-genes excluding igr1</td>
<td>TIM2+I+G</td>
<td>TIMI+G</td>
<td>TIM2 +I+G</td>
</tr>
<tr>
<td>All-genes</td>
<td>TIM2+I+G</td>
<td>TIMI+G</td>
<td>TIM2 +I+G</td>
</tr>
</tbody>
</table>

3.5.1.1 Gapcoding

Gaps can be very informative to phylogenetic analyses (Giribet and Wheeler, 1999; Simmons et al., 2001, 2008; Müller, 2006) and as such were coded in FastGap (Borchsenius, 2009) according to the simple indel-coding (SIC) method described by Simmons and Ochoterena, (2000). All analyses were completed without gaps coded for comparison (results not shown) however those with coded gaps were more highly resolved and with higher support.

3.5.2 Phylogenetic analysis

Tests for genetic structure, saturation of phylogenetic signal and gene incongruence were completed. Phylogenetic trees were constructed using maximum likelihood (ML) and Bayesian inference (BI) at the Oxford Supercomputing Centre, University of Oxford (UK). Briarium species were designated as outgroups following McFadden et al., (2006).

ML analyses were undertaken in GARLI 1.0 (Zwickl, 2006) with default settings and between 650-750 bootstrap replicates. Analyses were completed at least twice to ensure topology converged on the same tree. Consensus trees were created using SumTrees in DendroPy (Sukumaran and Holder, 2010).

BI analyses were conducted using MrBayes v.3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). JModelTest indicated TIM2+I+G provided the best-fit model for the combined dataset under BIC (Table 3.1). In MrBayes the general time reversible (GTR) model (six parameter nucleotide substitution-rate matrix) was thus chosen with \( \gamma \)-distributed rate variation across sites (G) for genes, run with no prior-parameter values as this constitutes the closest approximation of TIM and TVM models available in MrBayes. MrBayes was run with a partitioned model, generally with 4 partitions representing the 3 gene areas and gap-coded data. Models for each partition were: GTR for msh1 and COI, K80 for igr1 and a
Felsenstein-type (Felsenstein, 1981) mixed model, which allows for unequal character-state frequencies (with $\gamma$-distributed rate variation) to analyse gap data. MrBayes was run at least twice for between 7-10 million Monte Carlo Markov Chain (MCMC) generations (over 8 chains) for both ‘with’ and ‘excluding igr1’ alignments. Runs excluding igr1 did not independently converge, however, the highest posterior probabilities from two runs were at the same local optima and these runs were used in the ensuing analyses. Convergence was verified by checking for stationary posterior-distribution traces (generations vs. LnL) using TRACER v1.5 (Rambaut and Drummond, 2007); a “hairy straight caterpillar” indicated good mixing and convergence (Drummond et al., 2007). Topology convergence was examined using the web tool Are We There Yet (AWTY; Nylander et al., 2008; Wilgenbusch et al., 2004). Burn-in was set to 25% of runs. Analyses of this large data set were very computer intensive (e.g. individual BI analyses took ~450 hrs of supercomputer cluster time). In BI analysis there were step-changes in likelihood to new local optima up to 5 million generations, however, none were observed in any analysis after this point.

3.5.3 PTP test

A permutation tail probability (PTP) test (Archie, 1989; Faith and Cranston, 1991) was undertaken in PAUP* (Swofford, 2000). The PTP test indicated data showed significantly more structure than random data ($P = 0.02$).

3.5.4 Signal saturation

Saturation of phylogenetic signal was examined in DAMBE (Xia and Xie, 2001) using an information entropy-based index of substitution saturation (Xia et al., 2003). All genes combined and both individual genes showed no signs of saturation ($\text{ISS}<\text{ISS.c, } P=0$), validating the data for phylogenetic analyses.

3.5.5 ILD (Incongruence length difference) Test

Given the size of this dataset the parsimony based ILD test (Farris et al., 1994) was too computationally demanding to run beyond 50 repetitions. It is believed that a significance threshold of 0.05 may be too conservative for the ILD test (Sullivan, 1996; Cunningham, 1997); the result of $P = 0.02$ thus suggests rate homogeneity across msh1 and COI+igr1. There has been much criticism of ILD test accuracy (Cunningham, 1997; Dolphin et al., 2000; Barker and Lutzoni, 2002). In an effort to
assess the combinability of \textit{msh1} and COI+igr1 further, analyses of genes separately and combined were undertaken. No conflict was seen between \textit{msh1} and COI highly supported clades suggesting these genes share similar phylogenetic histories.

### 3.6 Results

#### 3.6.1 Genes

An aligned sequence of 864 bp of the COI coding region was obtained, 970 including \textit{igr1} and 895 bp of \textit{msh1} (Table 3.2), making all gene alignments 1865 bp long. Contrary to previous COI investigations (McFadden et al., 2010ab), we found length variation within the ‘Folmer region’ in a handful of the GB samples. These INDELS account for some of the length variation between McFadden et al. (2010b) and research presented here. Both the \textit{igr1} and \textit{msh1} regions manifested length variation. The latter maintained a correct amino acid reading frame. There was extreme variability in \textit{igr1} compared to the remainder of COI making the alignment irresolute. For this reason analyses were completed with and without its inclusion.

<table>
<thead>
<tr>
<th>Gene region</th>
<th>Nucleotide length (including gaps)</th>
</tr>
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<tbody>
<tr>
<td>COI coding</td>
<td>864</td>
</tr>
<tr>
<td>COI+igr1</td>
<td>971</td>
</tr>
<tr>
<td>msh1 coding</td>
<td>894</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Gene combination name</th>
<th>Gene combination</th>
<th>% pairwise identity</th>
<th>% identical sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>All-gene</td>
<td>msh1+COI+igr1</td>
<td>88.7</td>
<td>22.8</td>
</tr>
<tr>
<td>No igr1</td>
<td>msh1+COI</td>
<td>91.1</td>
<td>24.4</td>
</tr>
</tbody>
</table>

Genbank sequence FJ264908, listed as \textit{Anthothela nuttingi}, is from specimen USNM 94435 which, according to the NMNH website, is \textit{Pinnigorgia perroteti} (Stiasny). Genbank sequence GQ342434 listed as \textit{Leptophyton benayahui} is actually \textit{Protodendron brunnei} (C.S. McFadden, pers. comm.). \textit{Azoria bayeri} López-González and Gili, 2001 (GB GQ342407) is now called \textit{Azoriella bayeri} (López-González and Gili, 2008).

Samples of the Octocorallia order Heliporacea were not available for the phylogeny. Just two species of the order Pennatulacea (GQ342455 \textit{Renilla} sp. and GQ342414 \textit{Actinoptilum molle}) were included making this study heavily focused on Alcyonacea.
3.6.2 Phylogenetic trees

As igr1 was difficult to align analyses were performed with and without its inclusion (Table 3.3). There were minor differences in support between ML and BI analyses at the tree base but consistently, across analyses, three distinct, well-supported clades within Octocorallia were resolved (C1-3, see Table 3.4, Figures 3.2-3.4). However, ML analysis excluding igr1 (Figure 3.5) yielded a mixed clade of Alcyoniidae and other families separate from Clade 3 (C3). Additionally, analyses excluding igr1 had more structure within clades than all-gene analyses and BI had more structure than ML analyses (see Figures 3.2-3.5) and discussions thus concentrate on BI.

3.6.2.1 Overview of clades

Broadly, phylogenetic tree topology was similar across analyses: ML analysis excluding igr1 is the exception with a mixed clade of mostly Alcyoniidae and Chrysogorgiidae creating a fourth unresolved clade within a polytomy (Figure 3.5i). All analyses clustered Homophyton verrucosa, Titanideum frauenfeldii, Erythropodium caribaeorum (all from family: Anthothelidae, suborder: Scleraxonia), Ideogorgia capensis (family: Keroeididae, suborder: Holaxonia), and Telestula cf. spiculicola (family: Clavulariidae, suborder: Stononifera) at the base of the octocoral phylogenetic tree (Figures 3.2, 3.3), as in McFadden et al., (2006). For ease of cross-reference, clades from this research are listed next to those from the most recent octocoral phylogeny (McFadden et al., 2006) in Table 3.4. Within clades, again there were broad similarities between analyses but with some small variations between ML and BI as well as between all gene and excluding igr1 trees.

Clade one (C1; Table 3.4, see Figures 3.2-3.5) included all specimens of the suborder Scleraxonia, the majority of soft corals (suborder: Alcyoniina), a few specimens of Clavulariidae (Suborder: Stolonifera) and one specimen of Holaxonia (represented by Paramuricea sp., GB FJ264914). Both ML and BI analysis yielded higher resolution when igr1 was excluded from analyses. Within C1, BI analysis yielded more resolved nodes and structure, with ML (all-gene and no igr1) having polytomies although unresolved clades of ML match BI. In BI all-gene analysis, Alaskagorgia aleutiana (Plexauridae) was in a large polytomy within C1 (Figure 3.2i); in BI analysis excluding igr1 A. aleutiana falls basal to a group including all Acanthogorgiidae, most Gorgoniidae and some other Plexauridae (Figure 3.3i).
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Ellisellidae was recovered as a sister to Pennatulacea, separate from deep-water Calcaxonia, in McFadden et al. (2006), and this is supported here in Clade two (C2; Table 3.4). However, placement of Pennatulacea and Ellisellidae (Suborder: Calcaxonia) together differs from results in McFadden et al., (2006) as the clade is separated from the ‘majority Calcaxonia’ clade (C3, see Figures 3.2-3.5), this also occurs in Sanchez et al. (2003; using 18S). Ellisellidae are also polyphyletic. In all analyses, with the exception of all-gene BI analysis where C2 was basal to other major clades, C2 fell within a polytomy with the other two major clades. It should be noted that genera from Group 3 in McFadden et al. (2006; Anthomastus ritteri, Corallium ducale and a new genus of Alcyoniidae) were not represented within this analysis (as different genes were used, different specimens were available on GenBank) making their placement unknown; perhaps there is a fourth group within Octocorallia should these species be included. Within the study by Sanchez et al. (2003) Umbellula (Umbellulidae: Pennatulacea) and Anthomastus sp. fall basal to a mixed clade of Scleraxonia, Alcyoniina, and Calcaxonia.

Calcaxonia form the bulk of Clade 3 (C3, Table 3.4) with a few specimens of Holaxonias and Stolonifera embedded within a clade of Alcyoniidae of the suborder Alcyoniina. This mixed clade, alongside a member each of the Isididae and Primnoidae and two of the Chrysogorgiidae (although the placement of these specimens requires reanalysis), are found in a sister clade to the remaining C3 sequences. Ifalukella yanii (Family: Ifalukellidae) and Stephanogorgia faulkneri (Family: Chrysogorgidae), along with non-Antarctica Genbank Isididae sequences, fall basal to the remaining Chrysogorgiidae and Isididae in the BI analysis excluding igr1 (Figure 3.3), and are in a polytomy separate from the remaining Primnoidae in all other analyses. As already mentioned, a mixed clade of Alcyoniidae is found as a fourth clade in ML analysis excluding igr1 (Figure 3.5i). In remaining analyses, Acrossata was embedded within C3, indicating that pinnule-less polyps are not an ancestral character but represent a secondary loss of pinnules in this genus (Alderslade and McFadden, 2007). As discussed briefly in Cairns and Bayer (2009), it appears that jointed axes have evolved at least twice in Isididae and Mirostenella, which fall in separate clades.
Figure 3.2 Phylogenetic relationships among Octocorallia using all-genes BI analysis. Three to five letter and number combinations before taxonomic names represent ZSL catalogue numbers; two letters preceding 6 letters represent Genbank accession numbers. +1 – represents the named sequence and another identical sequence (e.g. +2, two other sequences etc). 1 – Scleraxonia/Alcyoniina/ Holaxonia; 2 – Pennatulacea/Calcaxonia; 3 – majority Calcaxonia

Figure 3.3 Phylogenetic relationships among Octocorallia using msh1 and COI (excluding igr1) in BI analysis. Three to five letter and number combinations before taxonomic names represent ZSL catalogue numbers; two letters preceding 6 letters represent Genbank accession numbers. +1 – represents the named sequence and another identical sequence (e.g. +2, two other sequences etc). 1 – Scleraxonia/Alcyoniina/ Holaxonia; 2 – Pennatulacea/Calcaxonia; 3 – majority Calcaxonia

**Colour legend for Figures 3.2-3.5**
Phylogenetics of octocorals
Phylogenetics of octocorals

Figure 3.4
Figure 3.4. Phylogenetic relationships among Octocorallia using all-genes ML analysis (601 bootstrap replicates). Three to five letter and number combinations before taxonomic names represent ZSL catalogue numbers; two letters preceding 6 letters represent Genbank accession numbers. +1 – represents the named sequence and another identical sequence (e.g. +2, two other sequences etc). 1 – Scleraxonia/Alcyoniina/ Holaxonia; 2 – Pennatulacea/Calcaxonia; 3 – majority Calcaxonia.

Figure 3.5 Phylogenetic relationships among Octocorallia using msh1 and COI (excluding igr1) in ML analysis (734 bootstrap replicates). Three to five letter and number combinations before taxonomic names represent ZSL catalogue numbers; two letters preceding 6 letters represent Genbank accession numbers. +1 – represents the named sequence and another identical sequence (e.g. +2, two other sequences etc). 1 – Scleraxonia/Alcyoniina/ Holaxonia; 2 – Pennatulacea/Calcaxonia; 3 – majority Calcaxonia.

Table 3.5 Breakdown of three subordinal groups octocoral families showing variation from the McFadden et al. (2006) phylogenetic tree. Group numbering matches that of McFadden et al. (2006). # Not represented in McFadden et al., 2006. § Not represented in this study.

<table>
<thead>
<tr>
<th>Family groupings</th>
<th>Suborder (Order: Alcyonacea unless * = Pennatulacea)</th>
<th>Family groupings in McFadden et al. 2006</th>
<th>Suborder (Order: Alcyonacea unless ¥ = Helioporacea, * = Pennatulacea)</th>
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<td>Acanthogorgiidae</td>
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<td>Holaxonia</td>
<td>Plexauridae</td>
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<tr>
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<td>Holaxonia</td>
<td>Gorgoniidae</td>
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<td>Neptheidae</td>
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<td>Nidaliidae</td>
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<td>Alcyoniidae</td>
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<td>Scleraxonia</td>
<td>Coelogorgiidae §</td>
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<td>Keroeidda §</td>
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<td>Echinoptilidae</td>
<td>Sessiliforae*</td>
<td>Protoptilidae §</td>
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<td>Renillidae</td>
<td>Sessiliforae*</td>
<td>Renillidae</td>
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<tr>
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<td>Virgulariidae</td>
<td>Sessiliforae*</td>
<td>Protoptilidae §</td>
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<td>Pennatulidae ¥</td>
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<td>Acrossotidae #</td>
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<td>Kophobelemnidae §</td>
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<td>Alcyoniina</td>
<td>Umbellulidae §</td>
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<td>Calcaxonia</td>
<td>Primnoidae</td>
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<td>Ifalukellidae</td>
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</table>

Table 3.5 Breakdown of three subordinal groups octocoral families showing variation from the McFadden et al. (2006) phylogenetic tree. Group numbering matches that of McFadden et al. (2006). # Not represented in McFadden et al., 2006. § Not represented in this study.

<table>
<thead>
<tr>
<th>Family groupings</th>
<th>Suborder (Order: Alcyonacea unless ¥ = Helioporacea, * = Pennatulacea)</th>
<th>Group 3 – Anthomastus / Corallium</th>
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<td>Alcyoniidae</td>
<td>Alcyoniina</td>
</tr>
<tr>
<td></td>
<td>Coralliidae</td>
<td>Scleraxonia</td>
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</tbody>
</table>

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The order Pennatulacea was recovered in a monophyletic group; Alcyonacea and its five suborders were not. This analysis does not support the previous incorporation of Ellisellidae as a sister taxon to Pennatulacea (McFadden et al., 2006; originally suggested by Bayer, 1955) and the Ellisellidae are not monophyletic. Most families sampled were polyphyletic; the few monophyletic families include Melithaeidae, Paralcyoniidae, Xeniidae, Paragorgiidae, Primnoidae, Isididae and Chrysogorgiidae (the latter three are likely monophyletic although this requires further analysis as an error in this analysis leaves them polyphyletic).

The two plexaurid genera, *Plexaurella* and *Swiftia* (Figure 3.2ii), fell within a clade dominated by the Gorgoniidae, as found in previous studies (Wirshing et al., 2005). These were far from the only genera of Plexauridae incongruent with morphological perceptions as 16 genera in this study fell across 9 different clades. Alcyoniidae are similarly polyphyletic (McFadden et al., 2006; 2010b), with 14 genera falling across 7 different clades (the genus *Alcyonium* being polyphyletic with *Alcyonium valdivae* in C1 and remaining *Alcyonium* sp. in C3).

3.6.2.2 Primnoidae

As Primnoidae were caught most frequently as by-catch, a more in-depth study of this family was possible. Thirteen genera were represented (two of which were undescribed genera identified morphologically) by 26 species (five of which are new species in existing genera).

Within Primnoidae, the BI and ML analyses differed in that the former yielded more structure in the BI analysis and the latter a polytomy. For example, in ML, *Dasystenella* is separate, however, it is found within a clade alongside *Fannyella* in BI analysis excluding *igr1* (Figure 3.3ii). Considering just BI, in the analysis excluding *igr1*, *Onogorgia nodosa* fell in a clade with *Primnoella chilensis* (Figure 3.3iii); in all-gene analysis, *O. nodosa* fell in a single clade with *P. chilensis* and *Digitogorgia* (Figure 3.2vi). In the all-gene analysis, *Thouarella grasshoffi* fell in a polytomy (Figure 3.2vii); in the analysis excluding *igr1* (Figure 3.3iv), it is found in a weakly-supported clade with *Ainigmaptilon edisto*. This unusual placement of *Thouarella grasshoffi* contributes to the conclusion that *Thouarella* is polyphyletic. Another notable result within *Thouarella* is the clear separation of *T. viridis*, and the close relationship between the so-called “Antarctic group” of *Thouarella* species (discussed in Chapter 2): *T. antarctica*, *T. parachilensis* and *T. crenelata*. These were not
separated genetically but form clear morphological species (Chapter 2). Within Primnoidae, the genera *Amphilaphis*, *Digitogorgia*, *Mirostenella*, *Dasystenella* and *Onogorgia* were monophyletic. *Amphilaphis* and *Mirostenella* were sister taxa. *Primnoella* was polyphyletic, with *P. antarctica* (which was a polyphyletic species and requires further morphological investigation) and *P. scotiae* recovered together, separate from *P. chilensis* that was resolved as a sister taxon to *Onogorgia nodosa* (Figure 3iii). *Plumarella* was polyphyletic with *P. undulata* and *P. diadema* in separate clades.

### 3.6.3 Species Delimitation results

Considering all the Octocorallia sequences, species from too many families showed no “barcoding gap” making methods to detect phylogenetic signals inappropriate (distance methods, mentioned previously, and MOTU_define.pl; Floyd and Blaxter, 2006). The phylogenetic tree was thus studied to evaluate the number of genera present (Blaxter, 2004). Phylogenetic analysis of by-catch from around South Georgia confirmed that it comprised a wide variety of Octocorallia spread across both C1 and C3 (no Pennatulacea were recovered as by-catch). There were at least 21 genera represented by at least 34 species within this phylogeny (Table 3.5).

The majority of sequences were of the family Primnoidae, as was the bulk of octocoral by-catch (Chapter 5). As these have been identified to species level, it was possible to utilise a new plug-in to Geneious that statistically tests whether putative species (from morphological examination) are monophyletic. Statistical tests include analysis of whether putative species are monophyletic relative to sister clades (under a null model of random coalescence, Rosenberg’s P), as well as statistics that characterise clade distinctiveness: the probability of a specimen being randomly distinct and an Intra/Inter ratio of within-species genetic differentiation (Intra Dist) to the nearest species (Near Dist) to estimate identification success (diagnostability) (Table 3.5; for full details see Masters et al., 2011).
Table 3.6 Octocoral specimens in by-catch from South Georgia. Those identified to at least genus were submitted to Genbank.

<table>
<thead>
<tr>
<th>Family and species</th>
<th>Genbank accession numbers</th>
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<td><em>msh1</em></td>
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<td><strong>Plexauridae</strong></td>
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<td><em>Bayergorgia vermidoma</em></td>
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</tr>
<tr>
<td><em>Paramuricea sp.</em></td>
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</tr>
<tr>
<td><strong>Paragorgiidae</strong></td>
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</tr>
<tr>
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</tr>
<tr>
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</tr>
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</tr>
<tr>
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</tr>
<tr>
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<td><strong>Isididae</strong></td>
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<td>Three unknown genera</td>
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</tr>
<tr>
<td>New genus 2</td>
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<tr>
<td><em>Convexella magelhaenica</em></td>
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<td><em>Digitogorgia brochii</em></td>
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</tr>
<tr>
<td><em>Dasystenella acanthina</em></td>
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</tr>
<tr>
<td><em>Fannyella kuekenthali</em></td>
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<tr>
<td><em>Plumarella diadema</em></td>
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<tr>
<td><em>Primnoella antarctica</em></td>
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</tr>
<tr>
<td><em>Primnoella chilensis</em></td>
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</tr>
<tr>
<td><em>Primnoella scotiae</em></td>
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Table 3.7 Species delimitations of putative morphological species using a Species Delimitation plug-in (Masters et al., 2011). * values in brackets are 95% CI truncated at 0 and 1.

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<th>Closest Sp.</th>
<th>Intra/Inter</th>
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<th>P ID(Liberal)*</th>
<th>P(Randomly Distinct)</th>
<th>Clade Support</th>
<th>Rosenberg's P(AB)</th>
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### CHAPTER THREE

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<td>15</td>
<td>17</td>
<td>0</td>
<td>0 (0, 0)</td>
<td>0.96 (0.83, 1.0)</td>
<td>NA</td>
<td>NA</td>
<td>2.60E-04</td>
</tr>
<tr>
<td><em>Ainigmaptilon edisto</em></td>
<td>16</td>
<td>17</td>
<td>0.06</td>
<td>0.56 (0.41, 0.71)</td>
<td>0.95 (0.79, 1.0)</td>
<td>0.05</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td><em>Amphilaphis abietina</em></td>
<td>17</td>
<td>18</td>
<td>0.33</td>
<td>0.42 (0.27, 0.57)</td>
<td>0.78 (0.62, 0.93)</td>
<td>0.11</td>
<td>1</td>
<td>0.03</td>
</tr>
<tr>
<td><em>Mirostenella articulata</em></td>
<td>18</td>
<td>19</td>
<td>0.66</td>
<td>0.26 (0.10, 0.41)</td>
<td>0.58 (0.42, 0.73)</td>
<td>0.4</td>
<td>0.75</td>
<td>0.11</td>
</tr>
<tr>
<td><em>Mirostenella new sp.</em></td>
<td>19</td>
<td>18</td>
<td>0.69</td>
<td>0.24 (0.08, 0.40)</td>
<td>0.56 (0.40, 0.72)</td>
<td>0.97</td>
<td>0.85</td>
<td>0.11</td>
</tr>
<tr>
<td><em>Plumarella undulata</em></td>
<td>20</td>
<td>17</td>
<td>0.27</td>
<td>0.83 (0.75, 0.92)</td>
<td>0.94 (0.89, 1.00)</td>
<td>0.05</td>
<td>1</td>
<td>2.80E-15</td>
</tr>
<tr>
<td><em>Plumarella diadema</em></td>
<td>21</td>
<td>20</td>
<td>0.36</td>
<td>0.77 (0.66, 0.87)</td>
<td>0.91 (0.85, 0.98)</td>
<td>0.05</td>
<td>1</td>
<td>1.85E-03</td>
</tr>
<tr>
<td><em>Plumarella new sp.</em></td>
<td>22</td>
<td>21</td>
<td>0.15</td>
<td>0.69 (0.51, 0.87)</td>
<td>0.92 (0.78, 1.0)</td>
<td>0.05</td>
<td>1</td>
<td>1.85E-03</td>
</tr>
<tr>
<td><em>Thouarella new sp.</em></td>
<td>23</td>
<td>20</td>
<td>0.76</td>
<td>0.74 (0.69, 0.79)</td>
<td>0.92 (0.90, 0.95)</td>
<td>0.05</td>
<td>1</td>
<td>9.10E-09</td>
</tr>
<tr>
<td><em>Thouarella variabilis</em></td>
<td>24</td>
<td>25</td>
<td>0.15</td>
<td>0.93 (0.86, 0.99)</td>
<td>0.98 (0.93, 1.0)</td>
<td>0.05</td>
<td>1</td>
<td>6.30E-12</td>
</tr>
<tr>
<td><em>Thouarella viridis T. antarctica / T. chilensis</em></td>
<td>25</td>
<td>27</td>
<td>0.41</td>
<td>0.84 (0.77, 0.91)</td>
<td>0.95 (0.91, 0.99)</td>
<td>0.05</td>
<td>1</td>
<td>1.30E-09</td>
</tr>
<tr>
<td><em>T. crenelata / T. parachilensis</em></td>
<td>26</td>
<td>27</td>
<td>0.58</td>
<td>0.70 (0.61, 0.79)</td>
<td>0.90 (0.85, 0.96)</td>
<td>0.05</td>
<td>0.83</td>
<td>6.40E-06</td>
</tr>
<tr>
<td><em>T. antarctica / T. parachilensis</em></td>
<td>27</td>
<td>26</td>
<td>0.38</td>
<td>0.76 (0.65, 0.86)</td>
<td>0.91 (0.85, 0.98)</td>
<td>0.05</td>
<td>1</td>
<td>6.40E-06</td>
</tr>
</tbody>
</table>
3.7 **Discussion**

### 3.7.1 Phylogeny of Octocorallia

All BI analyses and one ML analysis supported three major clades, providing strong evidence for these groupings. In all analyses, deep nodes were well-supported. BI analyses were more resolved than ML and this could be due to the modest number of bootstrap replicates that were possible (650-750). However, a conservative approach has been taken by examining relationships common to all trees.

The three clade phylogenetic tree presented here differed from the largest published mitochondrial phylogenetic tree of octocoral families as Pennatulacea and Ellisellidae (Calcaxonia; together being Group 2 in McFadden et al., 2006) did not fall within a mixed clade with many Calcaxonia (C3: see Table 3.4). However, previously the Pennatulacea were placed within a clade with Ellisellidae in a study by Sanchez et al. (2003). Other previous studies have also found that the Pennatulacea are basal within the Octocorallia (France et al., 1996; Song and Won, 1997). Sequences from Helioporacea or Subselliflorae were absent from our analyses, so their inclusion or expulsion from the original, large Pennatulacea/Calcaxonia clade (Group 2, McFadden et al. 2006) cannot be commented on. Similarly, it was not possible to include *Corallium, Anthomastus* or the other soft coral genera covered by McFadden et al. (2006), so the placement of these specimens within clades here, or as a separate fourth clade, was not possible. Considering the polyphyly found within Octocorallia, the different individual specimens from varying families included is likely responsible for differences between the research presented here and previous studies. Analysis of a wider selection of Pennatulacea alongside examples of *Anthemastus, Corallium*, Ellisellidae and a wide assortment of Alcyonacea is required. In addition, resolution at the base of the Octocorallia is poor and confounded by a lack of suitable taxa to root the tree (McFadden et al. 2006).

### 3.7.2 Primnoidae: By-catch species richness

Of the genera sequenced, *Callogorgia* and *Calyptrophora* were basal within the Primnoidae; polyps of both these genera face downwards. *Narella* species also have downward-facing polyps and this genus falls close to *Callogorgia* and *Calyptrophora* in a clade with, unusually, *Parastenella*, which has upward-facing polyps and is the
only genus with fluted marginal scales (Cairns and Bayer, 2009; Versluys, 1906). The placement of *Ainigmaptilon* deep within the Primnoidae clade is in stark contrast to a previous morphological phylogenetic study (Cairns and Bayer, 2009) that placed this genus towards the base of the Primnoidae clade.

Combined, all the genetic markers resolved many relationships within the Primnoidae at the genus level (in BI, Figure 3.2), and most at the species level. The “Antarctic group” of species, including *Thouarella antarctica*, *T. crenelata*, *T. chilensis* and *T. parachilensis*, were not successfully resolved. These species are morphologically very similar and either represent recently diverged species or one morphologically variable species (see Chapter 2 for morphological discussions). More precise markers are required to investigate these options. Apart from *Primnoella antarctica*, which was polyphyletic (morphological examination could not find any differences between specimens), and *T. grasshoffii* (discussed below), species of *Plumarella* and other *Thouarella* were also well-resolved. This is unusual within the Octocorallia as the identification of species from genetic data has proven difficult or impossible in previous studies (McFadden et al., 2010ab). The new species of *Thouarella* identified in this study is similar morphologically to *Thouarella variabilis* and it was the genetic separation that highlighted the small but consistent morphological differences found (Taylor et al., in prep.).

The Species Delimitation programme was useful to determine the “strength of phylogenetic evidence for species boundaries” (Masters et al., 2011, p.154). Although all species were considered monophyletic (see Table 3.6), and morphological evidence may say otherwise (particularly in the “Antarctica group”), the variation in the probability of specimens being randomly distinct –P(Randomly Distinct)- and the Intra Dist/Inter Dist (ID) Strict and Liberal probabilities were informative in exploring the relatedness of these species. The specimen of *Primnoella antarctica* that separated (Table 3.6, species 6) from the remaining *P. antarctica* specimens was considered monophyletic: this is understandable as the Species Delimitation process is tree-based and this species is polyphyletic in the phylogenetic trees shown here. The low probability of identification values Strict and Liberal scenarios for *Mirostenella* species and high Randomly Distinct probability value for *Mirostenella* new sp. (Table 3.6, species 19) would suggest perhaps these species are more similar than the clear
clade separation in the phylogenetic tree suggests. Two other very closely related species, *Plumarella undulata* and *P. diadema*, have high correct identification probability values and low probability of being randomly distinct, which indicates “clade distinctiveness is unlikely to be attributed to random coalescence” (Masters et al., 2011, p.154). Unusually, the distinct but morphologically variable species *Fannyella kuekenthali* (Bayer, 1998; Table 3.6, species 13) has a high Randomly Distinct probability value meaning it’s placement is likely to be attributed to random coalescence; this could be due to the placement of a new *Ophidogorgia* species at the base of this clade (Table 3.6, species 2). Given the polyphyletic nature of many genera within Primnoidae, the Rosenberg probability statistic was of less interest in this study.

Morphological and phylogenetic analysis combined with the clear and well-supported separation in Species Delimitation analysis (Table 3.6, species 23, 24), provides an example of the power of integrative taxonomy.

*Thouarella grasshoffi* is the only *Thouarella* in this study that had polyps in whorls (Group 2 in Chapter 2), perhaps indicating that a difference in polyp placement is a valid subgenus separator (Chapter 2). This subgenus is supported geographically, with the majority of species with polyps in whorls being found outside the sub-Antarctic region (the exception being *T. hicksoni* that occurs off the coast of South Africa and has isolated polyps; see Chapter 2); the remainder of *Thouarella* with isolated polyps are found in the sub-Antarctic (Chapter 2). The examination of more specimens of *Thouarella* with polyps in whorls is required to confirm whether this morphological difference is genetic in origin.

Primnoidae are commonly found in Antarctic waters and many of it’s genera are endemic to this region (López-González et al., 2002, Cairns and Bayer, 2009; Chapter 2). Primnoids were the most abundant and diverse octocorals within the by-catch examined throughout this research (see Chapter 5) and were the most species rich within successfully sequenced samples. Of the 230 described species of Primnoidae (numbers modified from Cairns and Bayer, 2009) 61 (27%) occur in the sub-Antarctic. By-catch included 11 of the 37 described genera of Primnoidae, making this the largest phylogenetic study of the family so far. The 25 Primnoidae species
resolved in the tree (over a third of all known sub-Antarctic Primnoidae) were, for the majority, supported by morphological and Species Delimitation analysis, making both methodologies useful in studying Primnoidae by-catch species richness. However, within the wider octocoral tree, families such as the Plexauridae and Clavulariidae (that were also regularly found in by-catch) require further morphological and molecular analysis.

### 3.8 Conclusions

Generally the gene combination used here (COI+igr1+msh1) resolved many relationships across Octocorallia although some results clash with taxonomic family designations. In the world of octocoral taxonomy, morphological species will continue to reign despite the plastic and complicated nature of Octocorallia morphology because of the need for new molecular markers that resolve the octocoral phylogenetic tree base and inform species-level differences. Until then, Octocorallia phylogeny and morphological taxonomy will clash. Unusually, within Primnoidae this gene combination does appear to resolve most species-level relationships and given the frequency and abundance with which Primnoidae occur as by-catch these genes form a useful tool to explore octocoral species richness. The value of utilising phylogenetics alongside morphology in an integrative manner has been shown here as without phylogenetic information one new species of Thouarella would have been incorrectly catalogued as T. variabilis.

### 3.9 Acknowledgements

This research was undertaken as part of NERC CASE studentship NE/F00785X/1 in collaboration with the Marine Resources Assessment Group Ltd, London, UK. Numerous observers are thanked for their time and efforts in collecting these specimens. Research was financially supported by the Lerner-Gray Grant for Marine Research and the Edith Mary Pratt-Musgrave Fund and samples were sequenced with NERC Molecular Genetics Facility grant (335); to all of whom I send our warmest thanks. At the Institute of Zoology, we would like to thank Dada Gottelli and Dr Kate Ciborowski for their invaluable advice and phylogenetic troubleshooting; Dr Oliver Pybus (University of Oxford) is too thanked for analytical advice.
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4 Using fisheries by-catch data to predict octocoral habitat suitability around South Georgia

4.1 Abstract

For many deep-sea fisheries globally there is an urgent management requirement for information on the presence of vulnerable marine ecosystems (VMEs). Gathering data from the deep sea using conventional means of scientific investigation can be expensive and time-consuming. One way of providing a rapid assessment of the presence of VMEs is to analyse by-catch data and samples gathered by fisheries observers, information arising from fisheries surveys or from historical observations. By-catch samples collected from fisheries observers from a wide area around South Georgia and Shag Rocks were studied. Octocorallia formed the majority of by-catch. To investigate octocoral habitat a terrain map of South Georgia was created using Benthic Terrain Modeller. Most by-catch was caught in narrow crest (an area that represents the shelf break and is associated with moraines) and steep (continental) slope terrains.

By-catch locations were combined with museum collection data and environmental layers to create an octocoral habitat suitability map using ecological-niche factor analysis (ENFA). Shelf-break areas were highlighted as highly suitable habitat for octocorals as are slopes around the gully between South Georgia and Shag Rocks, northwest of Shag Rocks and shelf-troughs. Three restricted impact areas were closed to fishing in 2009; this research confirms these areas as highly suitable octocoral habitat. However, as fishing is concentrated between 700-2000 m, longlining around South Georgia in unrestricted areas impacts a high proportion of habitat suitable to octocorals; 38% of highly suitable octocoral habitat is accessible to fishers.

This research demonstrates the potential for using by-catch data to create habitat suitability maps that can inform fisheries management and future research.

Keywords: Shag Rocks, Ecological-Niche Factor Analysis, ENFA, Benthic Terrain Modeller, troughs.
4.2 Introduction

The deep sea is the largest environment on Earth. It is also proportionally the least well known, sampled, and studied (Glover and Smith, 2003; Brandt et al., 2007) as research is costly and methods are inhibited, not least because instruments and viewing platforms need to withstand several hundred atmospheres of pressure beneath the ocean’s surface. Box corers, trawls and epibenthic sledges are common deep-sea sampling devices. In recent years remote operated vehicles (ROVs) equipped with cameras are a more precise, less invasive, but expensive and small-scale (in terms of the volume of samples procured), alternative method of sampling (with the drawback that species level identifications are less feasible from film, see Chapter 5). Technological advances in recent decades have opened up the deep sea to an increasing number of human activities such as gas and oil exploration (Hallock et al., 2004), submarine cable laying and, the most wide-spread industry, fishing (Koslow et al., 2000; Pauly et al., 2005; Roberts, 2002). Any sampling equipment, whether for industry or the advancement of science and our understanding of the deep sea, alters deep-sea habitats. Some, for instance trawls and dredges (Cryer et al., 2002; Watling and Norse, 1998; Gianni, 2004; Koslow et al., 2001; Kaiser et al., 2006; Williams et al., 2010), impact the deep sea more than others (e.g. traps, Eno et al., 2001; Chuenpagdee et al., 2003). These impacts may have very long-term, potentially permanent, impacts to benthic environments (Danovaro et al., 2001; reviewed in Davies et al., 2007; Kaiser et al., 2006).

Given that knowledge of the Antarctic deep sea, especially slope depths, is poor (Piepenburg et al., 2002; Brandt et al., 2007) and that systematically gathering data in the deep sea is generally only possible over limited areas, it is important to maximise the use of every source of biotic data. There is a relatively untapped wealth of data available in museum collections and country/expedition inventories. These ad-hoc data are primarily observations of particular species at a given date and location. They do not constitute a complete or systematic survey and are best analysed as species-presence data. However, this presence-only data (with no or unreliable information on species absence) is the most
difficult to transfer into statistical modelling methods that could expand species distributions and highlight diversity hotspots.

Vulnerable Marine Ecosystems (VMEs) include sponge fields, carbonate mounds, hydrothermal vents, cold seep communities, coral reefs and octocoral gardens (initially described in FAO, 2009; detailed list in Jones and Lockhart, 2011). This study utilises those deep-water octocoral locations in combination with data from museums, institutions and the literature to understand in what type of terrain octocorals and fishing occur. This is done by creating benthic megahabitat maps (Greene et al., 1999) of South Georgia and then undertaking an octocoral predictive habitat suitability modelling analysis (ecological-niche factor analysis, ENFA; Hirzel et al., 2002). The subsequent maps will inform fisheries managers of areas of potentially highly suitable octocoral habitat.

4.2.1 Study Location

South Georgia is the northernmost island in the Scotia Arc chain. It is located south of the Polar Front and lies within the zone influenced by the Antarctic Circumpolar Current (Orsi et al., 1995). Within Antarctica the water temperatures at South Georgia are the warmest and have the highest seasonal variability (Barnes et al., 2006). This, in combination with local current topography interactions (Meredith et al., 2003), and the fact that the South Georgia shelf also acts as a source of iron (Holeton et al., 2005) within a high nutrient, low chlorophyll region, make the waters around the island highly productive (Atkinson et al., 2001; Murphy et al., 2007) and biologically diverse in comparison to other sub-Antarctic locations (Barnes et al., 2006; Barnes, 2008; Ramos, 1999; Griffiths et al., 2008).

Much of the data in this study is from by-catch of the bottom-longline Patagonian toothfish, *Dissostichus eleginoides* Smitt, 1998, fishery that targets areas between 500 - 2000 m depth around South Georgia. Fisheries at South Georgia come under the direct jurisdiction of the Government of South Georgia and the South Sandwich Islands (GSGSSI), but the area is also within the area of application of CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources). Elsewhere in CCAMLR.
Bottom-longline camera deployment analysis

particularly the High Seas, areas are subject to conservation measures to control impacts on VMEs. The role of VMEs as potential fish habitat (Husebø et al., 2002; Stone, 2006; although the functional role of coral in fish life histories requires further investigation, see Auster, 2005) their intrinsic biodiversity value (Henry and Roberts, 2007; Jonsson et al., 2004) makes understanding their community structure, species distributions and identifying hotspots of VME diversity an important area of research. Although CCAMLR conservation measures for mitigation of impacts on VMEs, which were stimulated directly by UN General Assembly Resolutions on Sustainable Fishing on the High Seas 61-105 (UNGA, 2007), only apply to high sea waters, from which South Georgia is excluded, concern about impacts on benthos at South Georgia has given rise to several studies and management responses. For instance, bottom trawling around South Georgia is banned and bottom fishing using longlines has been prohibited in waters shallower than 500m since 2004 (extending to 700 m from 2011).

Bottom-longlines can be up to 13 km in length with 5,000-13,000 hooks (Agnew, 2004; MRAG, pers. comm.). Anecdotal information from fisheries observers about bottom-longline impacts on benthos around South Georgia has been collected since the late 1990s, however, Marine Stewardship Council (MSC) assessment of this fishery in 2004 initiated more specific studies of the extent and composition of benthic communities (Agnew et al., 2007; Wakeford et al., 2006). Octocorals were by far the most abundant benthic taxa caught as by-catch around South Georgia (Wakeford et al., 2006; see Chapter 5).

Based on research previously undertaken into by-catch from the Patagonian toothfish fishery (Agnew et al., 2007) a number of candidate areas around South Georgia were closed as restricted impact areas (RIAs) in 2009 (see Figure 4.2). These areas had high by-catch per unit effort of coral, macrourids and rays and closures also protected juvenile toothfish and spawning habitats (Agnew et al., 2007). Of these three (West Shag, West Gully and Northeast South Georgia) West Gully was expanded to almost one and a half times its original size in 2011 to protect toothfish spawning areas. The last research aim was to investigate the proportion of suitable octocoral habitat these RIAs protect.
4.3 Methods

4.3.1 Octocoral data

Benthic by-catch was collected between 2005-2009 by the Marine Resources Assessment Group (MRAG) as part of a wider study of fisheries by-catch from the bottom-longline Patagonian toothfish fishery around South Georgia. On each vessel Cnidaria specimens were collected from one randomly selected haul on one randomly chosen day each week. Samples were preserved in 70-90% ethanol and sent to the Zoological Society of London (ZSL) to be identified to the highest taxonomic level possible. Octocoral samples from by-catch were combined with a comprehensive literature search and data gathered from museums and expeditions to create a geo-referenced presence-only data set.

Each by-catch sample contained information about collection. If haul start and end depth were more than 400 m apart the data point was removed from analyses. By-catch data were investigated using R 2.11 (R Cored Development Team, 2010) with the ‘beanplot’ package (Kampstra, 2008) to show the distribution of depths.

4.3.2 Megahabitat map creation using Benthic Terrain Modeller (BTM)

Faunal distribution is generally dictated by both environmental and biological factors meaning species are often found in certain types of terrain and other conditions. Communities found in various habitats are likely a combination of both small (e.g. octocorals found on cobbles; Mortensen and Buhl-Mortensen, 2004; Stone, 2006) and large-scale features (e.g. canyons; De Leo et al., 2010). Large-scale features are possible to identify using available global data layers and there is evidence that octocorals are associated with large features such as shelf break (Bryan and Metaxas, 2007) and seamounts (Bryan and Metaxas, 2007; Yesson et al., in press). Delineating distinct terrain is therefore a valuable tool in defining habitat types.

Predicting habitat categories in deep-sea environments, beyond the continental shelf (~200 m depth), has rarely been undertaken even though these habitats are well suited to the task; being less accessible or open to direct observation. One way of doing this is to categorise areas into classes such as slope, flat, etc based on values derived from
bathymetry data for the area. These analyses work best with high-resolution bathymetry data as more features will be identified. Such data are available for the South Georgia area from Fretwell et al., (2009) who produced a 150m x 150m bathymetry grid based on acoustic sounding data (map projection EPSG:3762).

This fine-scale bathymetry layer was used to create a benthic habitat classification in Benthic Terrain Modeller (BTM) in ArcGIS 9.3.1 (Rinehart et al., 2004; Wright et al., 2005). The first step of the BTM process is to derive layers such as slope and Bathymetric Position Index (BPI, Weiss, 2001; Iampietro and Kvitek, 2002) from the original grid. In preliminary assessments of these derived layers there was an obvious distinction between areas based on high-resolution sounding data and those areas without high-resolution sampling that had been modelled. As such, it was necessary to smooth data by sub-sampling at a 450 m grid scale (in concurrence with scales discussed in Wilson et al., 2007). From this elevation grid a BPI was created by analyzing each grid cell in comparison to its neighbouring cells within a given annulus/circle (radii of 5-25; detailed method in Lundblad et al., 2006). The output has a range of positive and negative values; negative representing a cell lower than its neighbouring cells (valleys), positive was higher (ridges). Larger numbers characterise benthic features that are very different from surrounding cells. Flat areas or constant slopes have values close to zero.

The classification dictionary used was modified from a Hawaiian classification of habitats of 100-1000 m depth (Lundblad et al., 2006; details in Table 4.1). As South Georgia’s shelf break occurs deeper than Lundblad et al., (2006) 100 m depth this threshold was change to 300m for Shelf and Deep Shelf parameters.

<table>
<thead>
<tr>
<th>Habitat classification</th>
<th>Habitat classification characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Narrow Depression</td>
<td>Negative bathymetric position where both fine and broad terrain features are lower than surrounding seabed by position index values greater than one standard deviation from the mean in a negative direction</td>
</tr>
<tr>
<td>Broad Flat</td>
<td>Broad flat area where terrain has few, nested, fine scale features. Slope $\leq 5^\circ$</td>
</tr>
<tr>
<td>Shelf</td>
<td>As Broad Flat except shallower than a depth of 300m. Slope $\leq 5^\circ$</td>
</tr>
<tr>
<td>Escarpment</td>
<td>A steep slope of between 5-70°</td>
</tr>
<tr>
<td>Narrow Crest</td>
<td>Positive bathymetric position where both fine and broad terrain</td>
</tr>
</tbody>
</table>
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4.3.3 Predicted octocoral habitat suitability using Ecological-Niche Factor Analysis (ENFA)

Predictive habitat modelling has been used widely in terrestrial environments and is being used increasingly in the deep sea (marine fishes, Monk et al., 2010; sperm whales, Praca et al., 2009; gorgonians, Bryan and Metaxas, 2007; Lophelia pertusa, Davies et al., 2008; cold-water Scleractinia, Tittensor et al., 2009; 2010). By-catch specimens were combined with museum and marine institute inventory lists. The latter components extended data coverage into shallower waters where fishing is prohibited (Figure 4.2, yellow dots). Collectively this created an extensive presence-only data set. Together with environmental data and physical seascape factors for South Georgia these data were used to predict suitable octocoral habitat using ecological-niche factor analysis (ENFA; Hirzel et al., 2002). These models require both species distribution data and environmental layers for the area in question.

4.3.3.1 Identifying environmental layers

Topographic layers derived from bathymetry are useful environmental layers in habitat suitability modelling (Wilson et al., 2007; Woodby et al., 2009). Slope, aspect, curvature and relative position of features alongside rugosity (from BTM) were extracted from fine-scale bathymetry data (150 by 150 m; Fretwell et al., 2009). The local neighbourhood considered when calculating these layers can have a significant affect on the models (Wilson et al., 2007); these bathymetry-derived layers were therefore calculated across a variety of scales. Using Landserf (Wood, 2005), layers were created examining local neighbourhood windows of the following sizes: 3x3, 9x9, 33x33 (equivalent of 450m, 1350m and 4950m).

Additionally, environmental and chemical layers were derived from the World Ocean Atlas (WOA; Antonov et al., 2006; Garcia et al., 2006ab; Garcia et al., 2006ba; Locarnini et al., 2006) and GLODAP (Key et al., 2004) using the ‘cookie cutter’ upscaling method of Davies & Guinotte (accepted). This technique takes lower resolution depth-tiered
environmental layers (i.e. the 1 degree depth grids of WOA) and interpolates resolution values for the sea bottom at the resolution of the selected bathymetry grid. The temperature, salinity, silicate and phosphate layers of WOA and the total CO$_2$ and alkalinity layers of GLODAP were combined to model carbonate chemistry layers, omega calcite and omega aragonite using the R library seacarb (Lavigne and Gattuso, 2010). The full list of layers used in the analysis is provided in Appendices I and II.

Habitat suitability models can suffer from overfitting if too many environmental layers are incorporated into the analysis. Therefore a Principal Component Analysis (PCA) analysis of all layers was performed to identify correlation between layers (in Appendix I), as did the “cor” function in R (version 2.11.1; results in Appendix II). Salinity and alkalinity were highly correlated. Both correlation analyses showed all oxygen parameters and all bathymetry data to be highly correlated with aragonite and calcite; which were themselves highly correlated. Therefore, just one of these correlated parameters was included in the model: calcite. Calcite was used as it is important in coral structural development (as is aragonite; Macintyre et al., 2000) and has been previously found, in a global octocoral habitat suitability study, to be marginally better at explaining octocoral presence (Yesson et al., in prep). pH was correlated with oxygen, apparent oxygen utilisation (AOU), calcite, and aragonite so was excluded from the model. As nitrate and phosphate were only correlated with each other one was chosen to enter analyses: nitrate. A single layer from each depth derivative terrain class (Wilson et al., 2007) was used in the final model, with the exception of aspect which was broken down into east-west and north-south components using the cosine and sine trigonometric functions. The final set of environmental layers used for the analysis is listed in Table 4.2.
4.3.4 ENFA analysis

Environmental-niche factor analysis (Hirzel et al., 2002) was performed with a minimum 75% variation model using the selected environmental layers in openModeller version 1.1 (2010). The spatially unique filter was used to treat samples as presence-only data. Ten thousand background samples were selected to define the background data. Model performance was assessed using the area under curve (AUC) of the receiver operating characteristic (ROC; Fielding and Bell, 1997). Confidence intervals for the AUC were made by running 100 replicates of the model with each model trained with a random selection of 80% of the spatially unique data (spatially unique to the 150m² grid cells) with 20% of the data held back for model evaluation. Confidence intervals were based on the 2.5th and 97.5th percentiles of the 100 replicates. Areas were considered highly suitable for octocorals based on a prediction threshold determined by selecting the value that maximised the sum of sensitivity and specificity.

4.4 Results

4.4.1 Octocoral depth profiles

Initial identification of specimens was undertaken by MT and a portion of these verified by phylogenetic analysis (Chapter 3). 940 data points for Alcyonacea were procured. From a wider search of the Smithsonian Institution database, Natural History Museum samples and literature a further 40 data points were added to the dataset, creating a total of 980 geo-referenced data points with depth values (Figure 4.2).
The depths at specimen locations recorded by vessels were roughly comparable with depths derived from bathymetry at those same locations. Octocoral records occurred in three clear matching peaks at about 200m, 700m and 1300m (Figure 4.1). Discrepancies between the Fretwell et al. (2009) and fishing vessel depth data, particularly deeper than 1000m, may be due to a number of factors, including on ship instrumentation quality and the accuracy of position and depth data recording, but also operational considerations such as the choice of fishing position. The bathymetry dataset of Fretwell et al. (2009) was compiled using a variety of high quality and scientific data sources including multi- and single-beam swath bathymetry, and is likely to be more consistent across the entire area and depth profile of South Georgia. Accordingly, the Fretwell et al. (2009) dataset was used for all subsequent analyses in this chapter. Nevertheless, a preliminary analysis using fisheries depth data was undertaken and results were not substantially different from those presented here.

Figure 4.1 Beanplots showing abundance of octocoral data points across depth (black background represents abundance at specified depth), calculated using the start and end location of longline hauls with two different estimates of mean depth at which octocorals were caught: (a) mean (start and end of longline haul) depth data from fishing vessels and, (b) mean (start and end of longline haul) depth data from bathymetry layer. X axis is the number of octocoral records from a particular depth.
Figure 4.2 Map of South Georgia showing data points (red dots are by-catch samples and yellow dots are samples from museums, expeditions and the literature) and Restricted Impact Areas - West Shag, West Gully and Northeast South Georgia (NESG).
4.4.2 *Benthic megahabitats and fishing locations*

Of the original 13 habitat classes (Lundblad et al., 2006) 6 were present in the classification of South Georgia (Table 4.1). Most of the area beyond the shelf is broad shelf (shallow flat deep areas). There are a number of ridge areas (steep slope) and depressions found across this deep, flat seascape. A shallow sloping shelf surrounds both South Georgia and Shag Rocks, although cross shelf channels, or troughs, cut across the former, particularly to the north of the island; shown as deep shelf and escarpment in Figure 4.3. These are glacial features described in Graham et al. (2008). A distinct raised area before the shelf break (escarpment / steep slope; Figure 4.3) is thought to represent the glacial moraines described by Graham et al. (2008) and is mirrored by a narrow depression at the base of the slope. This depression, at the base of a steep slope, is possibly a strike valley, a result of ice scouring or a series of plunge pools (Lee et al., 2002); some depression areas perpendicular to the shelf towards the north of South Georgia likely represent outer continental shelf canyons (Graham et al., 2008).

<table>
<thead>
<tr>
<th>Megahabitat map terrain categories</th>
<th>All data (%)</th>
<th>Unique location data (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Narrow depression</td>
<td>6.44</td>
<td>6.71</td>
</tr>
<tr>
<td>Broad flat</td>
<td>6.03</td>
<td>6.28</td>
</tr>
<tr>
<td>Shelf</td>
<td>10.12</td>
<td>9.16</td>
</tr>
<tr>
<td>Steep slope</td>
<td>28.94</td>
<td>28.75</td>
</tr>
<tr>
<td>Narrow crest</td>
<td>45.5</td>
<td>46.22</td>
</tr>
<tr>
<td>Deep shelf</td>
<td>2.97</td>
<td>2.88</td>
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</tbody>
</table>

Table 4.3 Percentage of all and just uniquely located samples in each habitat category.
Figure 4.3 Megahabitat map of South Georgia and Shag Rocks (Shag Rocks being located in the centre of west shelf area) with octocoral sample data (red dots are by-catch samples and yellow dots are samples from museums, expeditions and the literature).
Octocoral habitat suitability

For ‘all data’, where there is some measure of abundance, narrow crest followed by steep slope are highlighted as terrains targeted by bottom-longline fishing vessels (Table 4.3). Considering just uniquely located samples (disregarding multiple samples per haul) the same remains true but these two terrains are more equally targeted. As most samples (96%) are by-catch from the longline fishing industry there is little difference between all samples and by-catch only samples.

The RIAs cover a variety of terrains: West Shag covers mostly narrow crest and slope with some broad and deep shelf to the south and narrow depression across the northern border; West Gully is similar to West Shag except with less broad shelf and narrow depression terrain; North East South Georgia covers deep shelf and narrow crest with some steep slope in the northeast corner.

4.4.3 Octocoral habitat suitability around South Georgia

The ENFA model retained four components that explained 78% of the variation. The AUC for the model was 0.82 (CI 0.78-0.85). A specialisation of more than 1 (1.19) would suggest octocorals are found within a narrow species niche (Hirzel et al., 2002). This value is similar to global predictions of octocoral habitat suitability (1.04; Yesson et al., in prep.). A marginality value of near to or more than 1 (1.11) indicates records were found in different conditions from the mean conditions across this area (Hirzel et al., 2002).

Predicted suitable octocoral habitat around South Georgia closely followed the shelf break, which often has a ridge of moraines (Graham et al., 2008), and narrow depression at the base of the shelf break (Figure 4.4). Steep slope is noticeable for its lack of octocoral habitat suitability. Fishing, and thus our by-catch data, was focused along the shelf/ narrow crest (Table 4.3; Wakeford et al., 2006).

Temperature had the highest loading for the marginality factor, followed by slope.
Table 4.4 Variance explained by the environmental variables in the ENFA model. Bold highlights the two highest overall loadings.

<table>
<thead>
<tr>
<th>Environmental layers</th>
<th>Specialisation factor 1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
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<tbody>
<tr>
<td>AOU</td>
<td></td>
<td>0.65</td>
<td>-0.73</td>
<td>0.56</td>
<td>-0.21</td>
<td>-0.08</td>
<td>-0.08</td>
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<tr>
<td>Aspect (cos)</td>
<td></td>
<td>0.07</td>
<td>-0.05</td>
<td>0.12</td>
<td>0.38</td>
<td>0.04</td>
<td>0.13</td>
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<td>-0.53</td>
<td>0.59</td>
<td>-0.65</td>
<td>-0.41</td>
<td>-0.16</td>
</tr>
<tr>
<td>Curvature</td>
<td></td>
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<td>-0.01</td>
<td>0.01</td>
<td>0.03</td>
<td>0.22</td>
<td>-0.43</td>
</tr>
<tr>
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<td>-0.15</td>
<td>-0.40</td>
<td>-0.22</td>
<td>-0.34</td>
</tr>
<tr>
<td>Slope</td>
<td><strong>0.44</strong></td>
<td>0.03</td>
<td>-0.01</td>
<td>0.10</td>
<td>-0.01</td>
<td>0.01</td>
<td>-0.47</td>
</tr>
<tr>
<td>Temperature</td>
<td><strong>0.70</strong></td>
<td>0.29</td>
<td>-0.43</td>
<td>0.27</td>
<td>-0.41</td>
<td>0.56</td>
<td>0.58</td>
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<tr>
<td>Aspect (sine)</td>
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<td>-0.24</td>
<td>0.00</td>
<td>-0.10</td>
<td>-0.10</td>
</tr>
</tbody>
</table>
Figure 4.4 South Georgia octocoral habitat suitability map with Restricted Impact Areas (RIA) from Figure 4.2 and octocoral sample data (red dots are by-catch samples and yellow dots are samples from museums, expeditions and the literature). Maps show logistic scores ranging from red=100=high suitability, to dark blue=0=low suitability.
CHAPTER FOUR

Using the Receiver Operating Characteristic (ROC) plot from which the AUC of the habitat suitability model is derived, the highest possible sensitivity and specificity was found at a model logistic score of 13 (Specificity=0.68, Sensitivity=0.85 see Appendix IV); the highest AUC value also corresponded to this score. This threshold was thus chosen to differentiate “highly suitable” octocoral habitat of which, there was 68874 km$^2$, 32.5% of that in the mapped extent; 25% was found between 200 and 300 m depth, 31% between 0-500 m, and 20% between 1500-2000 m (Figure 4.5).

The three RIAs presently in place protect large areas (over 90%) of predicted highly suitable octocoral habitat (see Appendix V).

![Figure 4.5 Bar chart showing percentage of predicted highly suitable octocoral habitat by depth.](image-url)
Table 4.5 Percentage of highly suitable octocoral habitat (HSOH) within fishable areas and areas under protection under various fishing restrictions. Total area = 212,056 km$^2$. 68,873 km$^2$ is highly suitable octocoral habitat (32% of the study area). 2000 m is an effective maximum fishing depth for operational reasons. *calculations for the RIAs are made on the basis of the size of the RIAs in 2011.

<table>
<thead>
<tr>
<th>Minimum fishing depth</th>
<th>700 m Current regulations</th>
<th>500 m Regulations from 2004</th>
<th>1000 m Scenario</th>
</tr>
</thead>
<tbody>
<tr>
<td>% of HSOH within fished area</td>
<td>42</td>
<td>46</td>
<td>35</td>
</tr>
<tr>
<td>% of HSOH in area shallower than minimum depth limit and therefore protected</td>
<td>38</td>
<td>34</td>
<td>45</td>
</tr>
<tr>
<td>% of HSOH deeper than depth limit but protected by an RIA</td>
<td>1.3</td>
<td>5</td>
<td>1.4</td>
</tr>
<tr>
<td>% of HSOH deeper than 2000m and therefore outside fishable depths</td>
<td>20</td>
<td>20</td>
<td>20</td>
</tr>
</tbody>
</table>

Around South Georgia the “fishable area” is between 700-2000 m (previously 500-2000 m, and 550-2000 m in 2009, however regulations lowered the upper limit depth to 700 m at the beginning of 2011). The 2000 m lower limit is not prescribed in law, but is an effective lower limit for fishing operations. In fact, most lines (85% of those from this study) are set in waters shallower than 1500 m. Nevertheless, 20% of highly suitable habitat is found deeper than 2000 m, and is therefore effectively outside the fishable area.

Thirty-eight percent (26,176 km$^2$) of all highly suitable octocoral habitat occurred in shallower waters (0-700 m) where fishing is prohibited, leaving 42% of highly suitable habitat (29,046 km$^2$) in areas that are deeper than 700 m (Table 4.5); most of this highly suitable habitat was around Shag Rocks (Figure 4.4). With West Gully expanding in size in 2011, RIAs protect 3563 km$^2$ (see Appendix V); an average of 94% of area inside the RIAs is considered highly suitable octocoral habitat. In total, with fishing depth regulations and RIAs, 28,858 km$^2$ (42%) of highly suitable octocoral habitat is protected, an additional 20% is deeper than is normally fished, and 38% is accessible to fishers.

Extension of protection down to 1000 m would protect an additional 7% of highly suitable octocoral habitat.
4.5 Discussion

4.5.1 Sampling bias and limitations
A global study of octocoral habitat suitability (Yesson et al., in prep.) found octocoral suborders had bimodal depth distributions (likely due to the current mismatch between morphological and molecular taxonomy meaning suborders contain a variety of relatively unrelated families; see Chapter 3 and reviewed in McFadden et al., 2010b). There is also an inherent bias in by-catch data as they are not collected randomly or systematically and are skewed towards fishing depths of 500-2000 m. So, although distributions here (Figure 4.1b) hint at a bimodal distribution similar to global analyses, the sampling skew to shallow depths makes this speculation. The additional data from other sources such as museum specimens helped counter this bias by providing information from shallower areas than those fished (where by-catch data originate).

A bimodal depth distribution can sometimes be difficult for habitat suitability model algorithms to handle (Sangermano and Eastman, 2007) and, should this be the case for all octocorals (rather than just within families), could result in low model performance. However, random samples from environmental layers (Appendix III) showed, for the majority, very similar results to octocoral location points inferring that samples spanned the entire environmental spectrum. To assess sampling bias and model robustness the model was run with 100 replicates using 80% training data that was cross-referenced against the remaining 20%; the resulting confidence intervals remained high (0.78-0.85).

4.5.2 Environmental factors and octocoral habitat suitability
Both temperature and slope have been previously identified as potentially important environmental parameters in deep-water Scleractinia (slope; Woodby et al., 2009) and octocoral distribution (slope; Bryan and Metaxas, 2007, temperature; Mortensen and Buhl-Mortensen, 2004) and results here support this. This research also supports previous studies showing complex topography as an important environmental factor for octocorals (Bryan and Metaxas, 2007). In particular the irregular topography of Shag Rocks, which is known to be a benthic biodiversity hotspot (Barnes, 2008), with low faunistic similarity to other Antarctic islands (Ramos, 1999), and the deep plateau at ~1000-1200 m depth,
Bottom-longline camera deployment analysis

west of Shag Rocks, are highlighted as the largest areas of highly suitable octocoral habitat around South Georgia (around half our samples came from this area as it is targeted by the fishing industry).

The complex topography between South Georgia and Shag Rocks is also highlighted as good octocoral habitat; again a historically important fishing ground. Around South Georgia Island bottom-longline fishing is focused on narrow crest and slope (700-2000 m), as seen in previous studies (Wakeford et al., 2006). These megahabitat categories coincide with shelf break areas, likely comprising moraines (Graham et al., 2008), and are predicted to be highly suitable octocoral habitat. These results (specifically listed in Table 4.5) indicate that there is a large overlap between fishing areas and areas suitable as octocoral habitat.

The biological parameters of calcite and AOU were most influential in determining octocoral habitat suitability. Aragonite saturation was found important in deep-water Scleractinia habitat suitability modelling (Tittensor et al., 2009) and this importance is unsurprising given the essential role aragonite (and calcite; which was highly correlated with aragonite) play in coral structure. On a wider scale, ocean acidification is predicted to affect the Southern Ocean more severely than other regions (Orr et al., 2005). Under several relatively modest “business as usual” IPCC scenarios, the aragonite saturation horizon in the Southern Ocean (which gets closer to the ocean surface as acidification intensifies), will reach the surface leaving the region completely undersaturated by 2100 (Caldeira and Wickett, 2005). Some studies have considered the effects of ocean acidification on deep-water Scleractinia corals (Guinotte et al., 2006; Tittensor et al., 2010), however, no papers, that these authors could locate at least, have so far studied the effects on deep-water Octocorallia. Given the varying composition of octocoral axes, from proteinaceous gorgonian to solidly calcitic or aragonite calcium carbonate (Bayer and Macintyre, 2001), the effect across all octocoral species uniformly is hard to determine. As calcite is less soluble, and the saturation horizon is thus deeper than aragonite, perhaps octocorals will be modestly buffered against ocean acidification, more so than Scleractinia. This area of octocoral biology requires much more research.
AOU was highly correlated with (Appendix III), and found to be highly determinate (Table 4.4) of, octocoral habitat suitability. A similar result in deep-sea Scleractinia (Davies et al., 2008; Tittensor et al., 2009) would suggest oxygen is just as important in octocorals with occurrence rare below approximately 3 ml l$^{-1}$ (Appendix IIIa), as was found for the scleractinian *Lophelia pertusa* (Linnaeus, 1758) (Dodds et al., 2007).

### 4.5.3 Octocoral distribution and fisheries

Within the sub-Antarctic, South Georgia has a very productive (Atkinson et al., 2001) and diverse (Griffiths et al., 2008; Barnes, 2008; Ramos, 1999) ecosystem. This, in conjunction with South Georgia’s age (Livermore et al., 2007), marine connectivity to Antarctica and the Falkland Trough (Griffiths et al., 2008; Barnes et al., 2006; Hofmann et al., 1998), and historical linkages to the South American mainland (Livermore et al., 2007), is likely responsible for the abundance and diversity of benthic life found there (Barnes, 2008; Griffiths et al., 2009). Although sea-ice impacts from 30-50 m (references in Clarke et al., 2004) result in limited three-dimensional habitat in this zone, below this depth, alongside sponges, anemones, ascidians and hydroids, octocorals are regular features of the seabed (Clarke et al., 2004, Barnes et al., 2006; Griffiths et al., 2008). Studies from the north of South Georgia (at 200, 500, 1000 and 1500 m depth) showed Cnidaria were relatively most abundant and had higher mass at 1000 and 1500 m (Griffiths et al., 2008). Although octocorals were not mentioned specifically it is likely (given the high frequency of gorgonians and alcyonarians within Cnidaria from other studies from the Scotia Arc; Ramos, 1999) that octocorals were common. Analysis of by-catch data shows octocorals occur down to 2000 m, and are caught more often than other benthos between 500-1000 m (Agnew et al., 2007; Wakeford et al., 2006); this contrasts with ecological studies (Ramos, 1999; Griffiths et al., 2008) where octocorals are more abundant deeper, and potentially infers a fishery selectivity towards octocorals (perhaps due to the features targeted). More research is required into the relative abundance of octocorals within benthic communities, octocoral distribution on a finer scale (e.g. octocorals are often found on boulders and drop stones; Oschmann, 1990) and longline...
Bottom-longline camera deployment analysis

gear selectivity (see Chapter 5), as this will further inform management about appropriate areas for protection.

The task of studying untouched deep-sea benthic communities around South Georgia is confounded by its long history of trawling and bottom-longlining; although trawling was for the majority limited to areas shallower than 500 m (D. Agnew, pers. comm.) and has been banned since the early 1990s. Given that pre-fishing habitat quantity and extent is unknown, estimating impacts of fishing activities is a difficult task with additional immeasurable elements such as by-catch lost off lines when hauling or the unseen damage caused by line interactions with corals (e.g. surface abrasions leading to infection and parasitism). Video investigation of benthic habitats is suggested to confirm and ground-truth these analyses. Preliminary work using cameras on bottom-longlines is presented in Chapter 5, however, remote-operated vehicles would be a more efficient and non-invasive platform for studies of the benthic environment around South Georgia and Shag Rocks.

Management actions taken by GSGSSI have effectively protected some 42% of suitable octocoral habitat. Recent deepening of the no-fishing contour around South Georgia from 500 m to 700 m has protected ~4% more highly suitable octocoral habitat and some areas of the shelf break. Further depth restrictions i.e. down to 1000 m, although protecting 7% more potentially highly suitable octocoral habitat (Table 4.5), may not be sensible for a number of reasons; firstly, most fishing currently takes place in the range 800-1500 m, and restricting fishing to a very small area within this range would concentrate impacts on a narrow depth band. Given that it is unknown whether some species of octocorals are unique to certain depths, this would effectively concentrate impacts at the expense of complete protection of other species groups in shallower water. Instead, the RIA approach taken helps to protect all benthos over the entire depth range.

In the shallows, where fishing is prohibited, cross-shelf troughs (Graham et al. 2008) are predicted to be suitable terrain for octocorals. The reduced fishing pressure and steep terrain would make this largely unexplored area relatively less impacted and may go
some way to explaining the relatively large volumes and high abundance of octocorals found in by-catch here (from experimental shallow fishing; MRAG, pers. comm.).

4.6 Conclusions

From by-catch data, which by its nature is presence-only, it is possible to create well-supported habitat suitability maps. In this way by-catch data are used to investigate the potential extent of octocoral habitat which supports management decisions with regard to reducing impacts on VMEs. RIAs in place around South Georgia, whose locations were partly based on abundance of octocoral by-catch (Agnew et al., 2007), would certainly appear to protect important octocoral habitat. This analysis also highlights highly suitable octocoral habitat from where there have been few research studies (e.g. the far northwest corner and cross-shelf troughs) and no octocoral data collected.

Ground-truthing of areas predicted to be highly suitable octocoral habitat, such as canyons, is encouraged as is future research in RIA areas where commercial fishing has now been prohibited. Such research would provide valuable density estimates which can be cross-referenced against habitat suitability values and provide a baseline, should the RIAs remain in place, where recovery of octocoral habitat from fishing impacts can be studied.

4.7 Acknowledgements

Numerous fisheries observers are thanked for their time and efforts in collecting these specimens. MT was sponsored by a Smithsonian Fellowship and NERC CASE Studentship, NE/F00785X/1, in partnership with the Marine Resources Assessment Group (MRAG), London. Chris Yesson provided advice on Habitat Suitability Modelling.
### Appendix I – Table showing PCA results from all environmental layers

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
</tr>
</thead>
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<td>0.14</td>
</tr>
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<td>0.22</td>
<td>0.03</td>
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<td>0.11</td>
<td>0.13</td>
</tr>
<tr>
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<td>0.04</td>
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</tr>
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<td>0.01</td>
<td>0.14</td>
</tr>
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</tr>
<tr>
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</tr>
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</tr>
<tr>
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<td><strong>0.35</strong></td>
<td>0.04</td>
<td>0.18</td>
</tr>
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</table>

*First three highest values highlighted in bold*
### 4.9 Appendix II - Table showing correlation values for all environmental layers.

| TCO2 | temp | Salinity | pH | phosphate | oxy | percentC02 | nitrate | Alk | AOU | calcite | aragonite | rugosity 450m | bathy 450m | bathy 1350m | aspect 450m (cos) | aspect 450m (sine) | aspect 1350m (cos) | aspect 1350m (sine) | aspect 1350m (sine) | aspect 450m (sine) | curvature 150m | curvature 1350m | slope 450m | slope 1350m |
|------|------|----------|----|-----------|-----|-------------|--------|-----|-----|--------|-----------|--------------|-----------|------------|---------------|----------------|----------------|----------------|----------------|----------------|----------------|-------------|-------------|-----------|-----------|
| 1.00 | 0.19 | 0.964    | 0.066 | 0.621 | 0.215 | 0.211 | 0.567 | 0.969 | 0.496 | 0.315 | 0.311 | 0.64 | 0.641 | 0.373 | 0.409 | 0.344 | 0.402 | 0.429 | 0.08 |
| 0.19 | 1.00 | 0.293 | 0.636 | 0.831 | 0.597 | 0.643 | 0.142 | 0.600 | 0.087 | 0.068 | 0.057 | 0.046 | 0.036 | 0.023 | 0.108 | 0.038 | 0.123 | 0.18 | 0.032 |
| 0.964 | 0.293 | 1.00 | 0.281 | 0.623 | 0.012 | 0.03 | 0.627 | 0.998 | 0.306 | 0.050 | 0.051 | 0.657 | 0.674 | 0.427 | 0.203 | 0.178 | 0.199 | 0.204 | 0.022 |
| 0.066 | 0.281 | 0.513 | 1.00 | 0.131 | 0.835 | 0.845 | 0.028 | 0.274 | 0.722 | 0.783 | 0.784 | 0.229 | 0.293 | 0.231 | 0.566 | 0.429 | 0.55 | 0.588 | 0.143 |
| 0.293 | 0.831 | 0.131 | 0.835 | 1.00 | 0.485 | 0.472 | 0.942 | 0.597 | 0.638 | 0.142 | 0.14 | 0.47 | 0.487 | 0.259 | 0.129 | 0.137 | 0.118 | 0.053 | 0.049 |
| 0.597 | 0.643 | 0.142 | 0.485 | 0.472 | 1.00 | 0.999 | 0.392 | 0.006 | 0.963 | 0.784 | 0.784 | 0.013 | 0.039 | 0.111 | 0.538 | 0.448 | 0.519 | 0.523 | 0.062 |
| 0.643 | 0.581 | 0.142 | 0.485 | 0.472 | 0.999 | 1.00 | 0.937 | 0.002 | 0.952 | 0.803 | 0.804 | 0.013 | 0.04 | 0.115 | 0.558 | 0.467 | 0.541 | 0.540 | 0.096 |
| 0.783 | 0.797 | 0.142 | 0.485 | 0.472 | 0.937 | 0.937 | 1.00 | 0.597 | 0.546 | 0.001 | 0.002 | 0.514 | 0.53 | 0.301 | 0.008 | 0.02 | 0.019 | 0.073 | 0.076 |
| 0.784 | 0.798 | 0.006 | 0.002 | 0.001 | 0.597 | 0.597 | 0.597 | 1.00 | 0.302 | 0.076 | 0.074 | 0.657 | 0.671 | 0.422 | 0.23 | 0.196 | 0.226 | 0.224 | 0.04 |
| 0.788 | 0.819 | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 | 0.597 | 1.00 | 0.011 | 0.003 | 0.514 | 0.53 | 0.301 | 0.008 | 0.02 | 0.019 | 0.073 | 0.076 |
| 0.789 | 0.847 | 0.011 | 0.016 | 0.016 | 0.016 | 0.016 | 0.016 | 0.011 | 1.00 | 0.053 | 0.054 | 0.118 | 0.118 | 0.38 | 0.149 | 0.139 | 0.139 | 0.139 | 0.091 |
| 0.786 | 0.845 | 0.016 | 0.016 | 0.016 | 0.016 | 0.016 | 0.016 | 0.011 | 0.053 | 1.00 | 0.054 | 0.054 | 0.118 | 0.118 | 0.38 | 0.149 | 0.139 | 0.139 | 0.139 | 0.091 |
| 0.784 | 0.845 | 0.016 | 0.016 | 0.016 | 0.016 | 0.016 | 0.016 | 0.011 | 0.054 | 0.054 | 1.00 | 0.054 | 0.054 | 0.118 | 0.118 | 0.38 | 0.149 | 0.139 | 0.139 | 0.139 | 0.091 |

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## Bottom-longline camera deployment analysis

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<th>2012 400-800 m</th>
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4.10 Appendix III – Scatter plots of octocoral habitat suitability values against environmental layers from (a) octocoral data and (b) 1000 randomly selected points across South Georgia
4.11 Appendix IV – Results of ROC curve analysis of ENFA results

Relative Operating Characteristic curves, ROC curves, are used to plot sensitivity (true positive rate) against specificity (false positive rate). Figure 4.A1 plots the fraction of true positives out of all positives (X = Specificity from Table 4.A1) against the fraction of false positives out of negatives (Y = 1- Sensitivity). Highest value (in bold) indicates threshold used for “highly suitable” octocoral habitat.

Table 4. A1. Results of ROC analysis

<table>
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<th>Score (Equal interval 0-100)</th>
<th>X = 1-Specificity</th>
<th>Y= Sensitivity</th>
<th>Specificity (1-X)</th>
<th>Sum of specificity &amp; sensitivity</th>
<th>1 value AUC</th>
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</tr>
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<td>0.213649852</td>
<td>0.9547</td>
<td>1.1683</td>
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</tr>
<tr>
<td>66.67</td>
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<td>0.9398</td>
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<td>0.6123</td>
</tr>
<tr>
<td>60.00</td>
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</table>

Figure 4.A1. ROC curve from ENFA model.
4.12 Appendix V – A close-up of habitat suitability in the three Restricted Impact Areas around South Georgia
CHAPTER FIVE
Chapter Five

5 Preliminary investigation of bottom-longline fishing interactions with coral around South Georgia using camera deployments

5.1 Abstract

Focused on the bottom-longline fishery around South Georgia for Patagonian toothfish, *Dissostichus eleginoides* Smitt, 1998, this study used video footage from a fixed camera array deployed on longline gear to survey density of octocorals and Stylasteridae (lace corals) and assess their vulnerability to damage from line impacts. As taxonomic identification beyond family was impossible from this video footage the density of different colony morphologies were compared to by-catch assemblages to investigate bottom-longline gear selectivity.

Three longline sets from relatively shallow water (500-550 m) were examined. High densities of octocoral and stylasterids were seen in the vicinity of the line. Stylasteridae were very fragile with 42% of interactions likely resulting in mortality through dislodgement, although only 6% of stylasterids within 0.45 m of the line were dislodged over all observations. When taut, above the seafloor, the longline interacted with benthic organisms less than when the line was dragged and thus in contact with the substratum. However, the sample size was not sufficient to determine whether this was a statistically significant effect or not. Octocoral morphology appears to play an important role in fragility with whip corals being less fragile than bushy or fan-shaped colonies.

Octocorallia made up the majority of by-catch from bottom-longline vessels studied from 2005-2009. Overall 10 families, 37 genera and at least 62 species of octocorals were caught as by-catch. For Primnoidae at least (which were seen most frequently in footage and by-catch), bushy corals were the most speciose morphology group and bottom-longline gear interacted with corals that have a bushy colony morphology, on average, more than whipped or fan-shaped corals.

*Keywords*: impacts; stylasterid; octocoral; autoline; by-catch; video, vulnerable marine ecosystem.
5.2 Introduction

Deep-sea vulnerable marine ecosystems (VMEs) include cold-water coral reefs, coral gardens and sponge reefs made up of VME indicators such as Scleractinia, Octocorallia and Porifera (FAO, 2009; detailed list in Jones and Lockhart, 2011). VMEs are potential fish habitat (Husebø et al., 2002; Stone, 2006), although the functional role of coral in fish population processes requires further investigation (Auster, 2005); this, in combination with their intrinsic value as habitat for many species (Krieger and Wing, 2002; Metaxas and Davis, 2005; Stone, 2006), makes researching octocoral diversity and fishing impacts very important.

The impact of some fishing gear, specifically bottom-longlines, on deep-sea benthos is poorly understood (Sharp et al., 2009). It is widely believed that fixed fishing gear (gill-nets, longlines, traps) has a lower impact than mobile fishing gear (bottom-trawls, dredges, rakes; Clark, 2010; Clark et al., 2010; Koslow et al., 2001; Watling and Norse, 1998). The impacts of bottom-trawls are well documented and severe (Clark and Rowden, 2009; Gage et al., 2005; Williams et al., 2010), with habitat recovery likely to take decades to centuries (Clark et al., 2010; Williams et al., 2010). However, the taxonomic selectivity of longlining has not previously been directly investigated. One reason is that video camera arrays capable of withstanding the temperature, pressure and lack of light at depths are expensive and bulky, making them difficult to deploy from fishing vessels. Also, cameras generally require power/operator control and thus necessitate tethering, whereas longlines generally are not tethered. Using specialist equipment capable of the above usually means deploying from a research, not a fishing, vessel (Kilpatrick et al., 2011). However, recent camera developments mean that autonomous video cameras can be attached to longlines (Kilpatrick et al., 2011), so for the first time the interaction of longline fishing gear and benthic habitat can be directly observed.

5.2.1 History of longline fisheries around South Georgia

Toothfish in late 1988, being joined later in the 1990s by Chilean, Bulgarian and Ukrainian vessels. Following intensive research in the mid-1990s, CCAMLR (Convention on the Conservation of Antarctic Marine Living Resources) changed the management approach to this fishery, requiring full observer coverage, the use of mitigation measures and a restriction to winter months from 1998 to protect birds that were being killed by longlines (Agnew, 2004). Today the Patagonian toothfish fishery involves between 5 and 13 vessels (the precise number varies annually depending on quota and licenses) covering between 700-2000 m depth (reduced from 550 m in 2011). Bottom-longlines can be up to 13 km in length with 5,000-13,000 hooks (Agnew, 2004; Marine Resources Assessment Group, MRAG, pers. comm.).

5.2.2 Vulnerable Marine Ecosystems (VMEs)

Measuring vulnerability of benthic habitats to disturbance is an essential element in understanding the immediate and long-term effects of fishing gear impacts. Unfortunately, a baseline pre-impact study is rarely available, in fact impact assessment generally commences long after a fishery has commenced making pre- and post-fishing comparisons very difficult.

Fisheries at South Georgia come under the direct jurisdiction of the Government of South Georgia and the South Sandwich Islands (GSGSSI), but are also within the area of application of CCAMLR. The waters around South Georgia, under GSGSSI jurisdiction, are not classified as high seas. Elsewhere in the CCAMLR area, fisheries in high seas areas are subject to conservation measures to control impacts on benthic habitats, particularly potential impacts on VMEs. Partly in response to the UN General Assembly Resolutions on Sustainable Fishing on the High Seas (61-105 and 64/72; UNGA, 2007; 2009) CCAMLR implemented conservation measures (CM22-06 and CM22-07) for high seas areas to identify potential VMEs from research and fishing data, and to limit the impact of fishing on those areas through temporary closures pending full analysis.

CCAMLR has also developed a detailed methodology for assessing the impact of bottom fishing on potential VMEs, including methods for estimating the footprint of longlines. Measuring the overall impact of one longline is a complicated and difficult task as longlines can move laterally as well as longitudinally (SC-CCAMLR, 2010,
p.127), there are historical impacts on the benthic environment from previous fishing, gear will interact with different benthic organisms differently, and distinct benthic organisms have varying productivity, dispersal, recovery capabilities (growth, susceptibility to disease etc) and levels of rarity (CCAMLR, 2009aa, SC-CCAMLR, 2010) and thus vulnerability.

A key concept in assessing the impact of fishing on benthos, and in particular VMEs, is the vulnerability of different organisms. CCAMLR considers vulnerability to be “[t]he susceptibility of a taxon or habitat to impact by a particular type of threat over time, without reference to the actual presence or intensity of the threat. Vulnerability incorporates fragility and resilience.” (p.51, SC-CCAMLR, 2010). Resilience is described by CCAMLR as “[t]he ability of a species or habitat to recover from impact over time, incorporating longevity, productivity/growth rate, dispersal and colonisation, rarity, patch size and spatial distribution, and ecological succession” (p.51, SC-CCAMLR, 2010). This chapter specifically considers fragility of corals. CCAMLR consider fragility to be “[t]he susceptibility of a taxon or habitat to impact (physical damage or mortality) arising from a particular interaction with a particular type of threat, e.g. bottom trawls or longlines. Fragility refers to an intrinsic physical property of the organism and the nature of the threat, without reference to the actual presence or intensity of the threat” (p. 51, SC-CCAMLR, 2010).

Identifying areas with VMEs in order to protect them from fishing impacts is difficult as the exact quantity/density of VME organisms necessary to designate a VME location is currently undefined (Jones and Lockhart, 2011; Post et al., 2010). “Move-on” rules, where a vessel is required to move a minimum distance when a threshold volume/weight of VME indicators are encountered, have been established in several Regional Fishery Management Organizations (Auster et al., 2011). Within CCAMLR exploratory fisheries, according to Conservation Measures (CM) 22-06 and 22-07 (CCAMLR, 2009bb), with by-catch of \( \geq 10 \text{ kg}/10 \text{ litres of VME}/1200 \text{ m}^2 \) would trigger a “move-on” where CCAMLR is notified of the location and there is a subsequent closure around the encounter of 1 nautical mile (b; CCAMLR, 2008ba).

Although CCAMLR conservation measures for VMEs do not apply in the non-High Seas areas of South Georgia, concern about impacts on benthos has given rise to
CHAPTER FIVE

several studies and management responses at South Georgia. Benthic interactions are reduced in South Georgia waters through the prohibition of bottom trawling, through the implementation of three Restricted Impact Areas (RIAs; in which commercial longlining is prohibited) and through the prohibition of fishing shallower than 500 m from 2004, and 700 m from 2011.

The history of these actions is important because the RIAs were implemented as a result of specific studies on benthic impacts. Anecdotal information from fisheries observers about longline impacts on benthos around South Georgia has been collected since the late 1990s. However, it was Marine Stewardship Council (MSC) assessment of the Patagonian toothfish fishery in 2004, which identified that deep water corals were being impacted by the fishery, and the importance placed on locating VMEs arising from the general discussions surrounding the 2007 UNGA resolutions, initiated more specific studies of benthic community location, extent and composition at South Georgia (Agnew et al., 2007; Wakeford et al., 2006). These initial studies resulted in identification of three areas with high coral catch per unit effort which were established as temporary RIAs, where fishing is excluded other than for research purposes. The RIAs provide protection for juvenile and spawning toothfish as well as other by-catch fish species in addition to protection for benthic communities (MRAG pers. comm.). In recent years further research has been undertaken into the species-level diversity of coral by-catch around South Georgia, the latest results of which are presented here (Figures 5.5 and 5.6; Appendix I).

The aims of this research were twofold: to provide information on octocoral and stylasterid fragility to assist with future calculations of benthic impacts; and to investigate the possibility of estimating the density of benthic organisms from a camera array attached to longline gear.

5.3 Methods

5.3.1 By-catch samples

Fisheries observers collected samples of by-catch caught on bottom-longline (using autoline gear) vessels fishing for Patagonian toothfish around South Georgia, from the years 2005-2009. On each vessel all Cnidaria specimens were collected from one
randomly selected haul on one randomly chosen day each week. Abundances were recorded and one example of everything considered by the trained observers to be a different species was preserved in 90% ethanol and sent to the Zoological Society of London (ZSL) to be identified to the highest taxonomic level possible (same specimens as in Chapter 3).

5.3.2 Video capture

As part of ongoing benthic research funded by GSGSSI, an MRAG observer deployed a Benthic Impacts Camera System (BICS, Figure 5.1) on 6 bottom autoline sets in 2009 between Shag Rocks and South Georgia. The BICS was designed by the Australian Antarctic Division (Kilpatrick et al., 2011). Four sets were six magazines (sections of line, see Figure 5.2) in length (with 1,200 hooks per magazine), one was four and half magazines and one was four magazines in length (see Figure 5.2). In addition, there was a 500 m section of hook-free line attached at either end of the anchors to reduce chances of hooked line entanglement after anchors land on the seafloor (Figure 5.2B).
Figure 5.2 Camera setting and hauling. A. Setting the line. B. Line in place. Image taken from WG-EMM 2010.

Footage from three camera deployments on bottom-longline gear are studied here (haul details in Table 5.1; haul locations in Figure 5.3). Hard bottom benthic habitat was observed in video footage from only the three shallowest sets (37, 40, 59), west of Shag Rocks, which were selected for further analysis (details in Table 5.1).

Table 5.1 Camera deployment bottom-longline haul details.

<table>
<thead>
<tr>
<th>Set no.</th>
<th>Start Depth (m)</th>
<th>End Depth (m)</th>
<th>Set start time</th>
<th>Set end time</th>
<th>Line Length (m)</th>
<th>Hooks Set</th>
<th>Camera magazine position</th>
<th>TOP §</th>
<th>Weight (kg)</th>
<th>VME taxa counts observed from by-catch*</th>
</tr>
</thead>
<tbody>
<tr>
<td>37</td>
<td>540</td>
<td>538</td>
<td>00:17</td>
<td>01:00</td>
<td>10800</td>
<td>7200</td>
<td>1st/2nd</td>
<td>ATX 9, GGW 8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>518</td>
<td>565</td>
<td>00:53</td>
<td>01:29</td>
<td>8100</td>
<td>5400</td>
<td>2nd/3rd</td>
<td>ATX 5, GGW 6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>59</td>
<td>525</td>
<td>538</td>
<td>20:14</td>
<td>20:44</td>
<td>7200</td>
<td>4800</td>
<td>1st/2nd</td>
<td>ATX 3, HQZ 1, GGW 7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>277</td>
<td>1434</td>
<td>1623</td>
<td>22:34</td>
<td>23:20</td>
<td>10800</td>
<td>7200</td>
<td>1st/2nd</td>
<td>505.08</td>
<td></td>
<td></td>
</tr>
<tr>
<td>284</td>
<td>1295</td>
<td>1210</td>
<td>22:54</td>
<td>23:43</td>
<td>10800</td>
<td>7200</td>
<td>1st/2nd</td>
<td>None</td>
<td></td>
<td></td>
</tr>
<tr>
<td>299</td>
<td>1200</td>
<td>1480</td>
<td>00:02</td>
<td>00:48</td>
<td>10800</td>
<td>7200</td>
<td>5th/6th</td>
<td>None</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

§ TOP – Patagonian toothfish
¥ - see Figure 3
*ATX – Actiniaria, GGW – Gorgonacea, HQZ – Hydrozoa
Based on megahabitat maps of South Georgia (Chapter 4) hauls 40 and 59 fall on narrow crest (slight rise) and haul 37 escarpment (steep slope). Megahabitat maps are made at a much larger scale than the footage viewed here covers. Areas seen in video footage were relatively flat with sporadic small ridges, large boulders and drop stones.

The author examined all video footage from these deployments. The deployed camera array was orientated around 70° to seafloor. A fixed window was placed over camera footage foreground (Figure 5.4a) within which an equal area each side of the longline could be observed. This unit area corresponded approximately to one snoods’ length (0.45 m) either side of the line and one snoods length along the line, or approximately 0.405 m². The camera tilted due to motion and drag, but area covered remained relatively constant irrespective of camera orientation. If camera orientation was exceedingly tilted this footage was disregarded. “Survey” speed was not constant so counts were based on the area of different sections not time. Sections were natural breaks in the video footage as hauling paused and restarted.
Visible coral benthos was split into four morphological categories based on what could be identified from footage: (1) Stylasteridae: generally very small colonies, usually white and highly reflective in camera light and thus clearly visible; Figure 5.4(d,iv); (2) bushy corals: generally octocorals such as Primnoidae, usually a light shade as covered in calcium carbonate scales; some may be Plexauridae; Figure 5.4(d,iii); (3) whip corals: again likely to be Primnoidae, lightly shaded; Figure 5.4(c)(d,ii); (4) fan corals: Primnoidae, lightly shaded, some Plexauridae; Figure 5.4(d,i). Sea urchin (Echinoidea: pen urchins, Cidaroida, and spiny urchins, Echinoida) occurrence was also recorded. Animals seen too infrequently in footage (or too frequently in the case of Euphausiacea, krill) to be enumerated include Porifera, Crinoidea, Brachyura (crabs), Ophiuroidea, and Asteroidea.

This study considers octocorals as non-Pennatulacea (of which none were recorded either in footage or by-catch) Octocorallia. The term ‘gorgonians’ is often used when describing such octocorals however the order Gorgonacea was abolished by Bayer, in
1981 and taxa transferred to Alcyonacea; which form the majority of taxa seen and recorded in this study.

Footage was viewed once to count the number of distance units (one unit being ~0.45 m) along which the line travelled, once for each morphological category (to estimate colony density), and once to count when each morphological category was touched by any of the line visible within the “transect” area. The latter viewing was undertaken with the window removed (but width markers remaining) as haul speed meant it was not possible to see the consequences (such as recovery or dislodgement) of some line touches when just the area within the window frame was visible.

5.3.2.1 Terminology used
Fragility was assessed by the type of contact that was visible in the video footage, classified as contacted or dislodged. *Contacted* defined actions where the organism was seen to be touched by the longline. *Dislodged* defined actions where a subsection of those contacted were seen to be removed from substrate/knocked over. If contact or dislodgement occurred out of the immediate window area but was still sustained within the length of the survey area it was recorded. This was necessary as there was often impact debris within the window impairing contact/dislodgement confirmation.

When viewing footage it became apparent that there were two distinct types of longline movement: *Taut*—bottom-longline held above the seafloor so hooks can hang down and be touching benthos but the line is not, and; *Dragged*—bottom-longline against benthos and being pulled across the seafloor. All Stylasterids that passed under a dragged longline were considered lethally impacted as, due to their rigid calcium carbonate skeleton, they are highly fragile (Heifetz et al., 2009) and if knocked over would likely die.

5.3.3 Analysis
The effect of different line tension was investigated as was the effect of colony morphology on the chances of dislodgement or contact by using a general linear model (GLM - dislodgement~line tension+coral morphology+haul). The GLM was fitted using a binominal error distribution and a logit link function in R (R Development Core Team, 2010).
5.3.4 Limitations

The black/white images meant identification of darker coloured benthos, such as Plexauridae, was difficult. This does skew results taxonomically towards Primnoidae, and Stylasteridae (which reflect in the camera light and are clearly visible), and Paragorgiidae (which are generally large). Overall this also means that estimates of benthos density produced here are likely to be conservative.

Camera and longline impacts on benthos often created a debris cloud that sometimes obstructed counts. Count estimates are thus, again, likely to be conservative.

Sample sizes used in these analyses were low so these results should be considered preliminary; further video research by GSGSSI and British Antarctic Survey is underway.

5.4 Results

5.4.1 By-catch from the South Georgia Patagonian toothfish fishery, 2005-2009

Previous investigations into by-catch found a wide taxonomic assortment of benthos although the vast majority was Octocorallia (Wakeford et al., 2006). To maintain the comparability of video and by-catch data only by-catch data from across Shag Rocks, west of 42.5°W, is shown in Figures 5.5 and 5.6. The extensive bottom-longline study of Patagonian toothfish fishery by-catch presented here also found that the vast majority was Cnidaria (80%; Figure 5.5) and within Cnidaria the majority were Octocorallia (72%, Figure 5.6). Within Octocorallia (from morphological identifications) the most prevalent family by far was Primnoidae (43% of all corals, 60% of all octocorals).

Phylogenetic studies (Chapter 3) of by-catch samples from the South Georgia Patagonian toothfish fishery found a large number of species across 8 families, at least 21 genera (of which two are new discoveries) composing of a minimum of 34 species. Including specimens that were not successfully sequenced i.e. all octocoral by-catch, figures rise to 10 families, 37 genera (three as yet to be described) and at least 62 species (of which 9 are new discoveries; listed in Appendix I).
5.4.2 Bottom-longline video footage

There were 26.5 minutes of useable footage that covered 113.83 m, representing 102.45 m$^2$ (see Table 5.3 for haul breakdown).

From video footage Primnoidae was the most frequently seen family. Of the 230 species of Primnoidae (numbers modified from Cairns and Bayer, 2009) 61 (27%) are known to occur in the sub-Antarctic. Of these 23 are bushy (38%), 21 fan-shaped
and 17 of a whip morphology (28%). The occurrence of categories and morphology types from video are presented in Table 5.2. Densities of corals were fairly constant across hauls (Table 5.3).

Table 5.2 Occurrence of categories/morphology types from video footage.

<table>
<thead>
<tr>
<th>Colony categories</th>
<th>Total no. of colonies identified in video footage</th>
<th>% of total</th>
<th>% considering just octocorals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bushy</td>
<td>585</td>
<td>14.38</td>
<td>58.91</td>
</tr>
<tr>
<td>Fan</td>
<td>161</td>
<td>3.96</td>
<td>16.21</td>
</tr>
<tr>
<td>Whip</td>
<td>247</td>
<td>6.07</td>
<td>24.87</td>
</tr>
<tr>
<td>Stylasteridae</td>
<td>3076</td>
<td>75.60</td>
<td>-</td>
</tr>
</tbody>
</table>

Table 5.3 Haul distances, area and breakdown of average benthic organism densities per haul (*number of colonies seen/colonies per m²). Sections were a natural break in footage e.g. haul paused so no movement. In brackets is number of sections that showed dragged/taut footage.

<table>
<thead>
<tr>
<th></th>
<th>Haul 37</th>
<th>Haul 40</th>
<th>Haul 59</th>
<th>All hauls</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance measured from footage (m)</td>
<td>63.1</td>
<td>33.81</td>
<td>16.91</td>
<td>113.83</td>
</tr>
<tr>
<td>Number of sections per haul</td>
<td>5</td>
<td>3</td>
<td>5</td>
<td>13</td>
</tr>
<tr>
<td>Area covered (m²)</td>
<td>56.9</td>
<td>30.43</td>
<td>15.22</td>
<td>102.45</td>
</tr>
<tr>
<td>Distance dragged/taut (m)</td>
<td>63.1/0</td>
<td>19.84 (1)/</td>
<td>0/16.91</td>
<td>82.94 / 30.88</td>
</tr>
<tr>
<td>All corals*</td>
<td>692/12.19</td>
<td>438/14.39</td>
<td>223/14.65</td>
<td>1353/13.2</td>
</tr>
<tr>
<td>Stylasterids*</td>
<td>515/9.07</td>
<td>227/7.46</td>
<td>157/10.32</td>
<td>899/8.77</td>
</tr>
<tr>
<td>Bushy corals*</td>
<td>79/1.39</td>
<td>160/5.26</td>
<td>40/2.17</td>
<td>279/2.65</td>
</tr>
<tr>
<td>Whip corals*</td>
<td>76/1.34</td>
<td>12/0.39</td>
<td>15/0.99</td>
<td>103/1</td>
</tr>
<tr>
<td>Fan corals*</td>
<td>22/0.39</td>
<td>39/1.28</td>
<td>18/1.18</td>
<td>79/0.77</td>
</tr>
<tr>
<td>Echinodermata*</td>
<td>65/1.14</td>
<td>36/1.18</td>
<td>11/0.72</td>
<td>112/1.09</td>
</tr>
</tbody>
</table>

For 13 of the 26.5 minutes of footage the bottom-longline was taut, above the seafloor. Taut line, as an average of all colonies seen, contacted less coral than a line dragged across the seafloor (Table 5.4). Anecdotally contacts from a taut line were seen to be mostly from hooks touching the seafloor. There is no known way to practically control whether a longline is taut or dragged on the bottom through long-line placement, techniques of hauling or retrieval (MRAG, pers. comm.).

Table 5.4 Total percentage of all colonies contacted across all haul area (includes dislodgement) from taut and dragged haul footage.

<table>
<thead>
<tr>
<th></th>
<th>Taut (%)</th>
<th>Dragged (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stylasterids</td>
<td>31.9</td>
<td>71.6</td>
</tr>
<tr>
<td>Bushy coral</td>
<td>51</td>
<td>12.39</td>
</tr>
<tr>
<td>Whip coral</td>
<td>4.26</td>
<td>9.17</td>
</tr>
<tr>
<td>Fan coral</td>
<td>12.8</td>
<td>6.88</td>
</tr>
</tbody>
</table>

These data were further analysed to investigate the drag/taut effect. Although overall percentages (Table 5.4) do suggest that coral morphology and line tension is likely to
influence the proportion of colonies contacted, because of the uneven sample sizes and the lack of crossover of data between two key variables – line tension (drag/taut) and separate line deployments – no consistent results were obtained from a binomial GLM over whether coral morphology or line tension were significant influences on the proportion of corals contacted.

Overall there were very few dislodged octocoral colonies (10 bushy corals, 4 fans, 1 whip) seen within the footage but 71 stylasterids; considering taut line footage alone there were even less (2 bushy, 1 whip and 7 stylasterids).

5.4.3 Fragility

The percentages of contacted corals that were impacted by line interactions differed substantially across coral categories (Table 5.5). Fan corals would appear to have much lower incidence of dislodgement than other categories/morphologies (Table 5.5). Fan corals recovered from 92% of all line interactions whereas Stylasteridae recovered from only 59% of contact interactions. Given Stylasteridae fragility, 42% of interactions likely resulted in colony mortality as the colony was dislodged (Table 5.7). A binomial GLM on the probability of dislodgement, once a coral has been contacted, suggested that coral type was a significant factor (Chi-squared test on a Binomial GLM, p<0.05, Table 5.6), although once again the model was unable to distinguish between line and tension effects due to the low number of examples.
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Table 5.5 Percentage of all colonies, by coral category and line interaction, that were contacted, contacted and dislodged and percentages of contacted corals that were dislodged. D = line dragged along seafloor, T = line taut, above seafloor, A = all line interactions.

<table>
<thead>
<tr>
<th></th>
<th>Bushy</th>
<th>Fan</th>
<th>Whip</th>
<th>Stylasteridae</th>
<th>All corals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>D</td>
<td>T</td>
<td>A</td>
<td>D</td>
<td>T</td>
</tr>
<tr>
<td>Number of colonies observed</td>
<td>151</td>
<td>121</td>
<td>272</td>
<td>49</td>
<td>30</td>
</tr>
<tr>
<td>Average % of colonies contacted</td>
<td>19.31</td>
<td>14.46</td>
<td>16.70</td>
<td>20.07</td>
<td>13.57</td>
</tr>
<tr>
<td>Average % of colonies dislodged</td>
<td>3.36</td>
<td>4.08</td>
<td>3.75</td>
<td>2.47</td>
<td>0</td>
</tr>
<tr>
<td>% contacted that were dislodged</td>
<td>17.41</td>
<td>28.23</td>
<td>22.46</td>
<td>12.30</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 5.6 Chi Squared test on Binomial GLM of the probability of dislodgement once a coral has been contacted. *** = 0-highly significant

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>NULL</td>
<td></td>
<td>33</td>
<td>58.967</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Line tension</td>
<td>1</td>
<td>0.1813</td>
<td>32</td>
<td>58.786</td>
<td>0.6702</td>
</tr>
<tr>
<td>Coral morphology</td>
<td>3</td>
<td>23.1100</td>
<td>29</td>
<td>35.676</td>
<td>3.831e-05 ***</td>
</tr>
<tr>
<td>Dragged/taut</td>
<td>1</td>
<td>2.6871</td>
<td>28</td>
<td>32.989</td>
<td>0.1012</td>
</tr>
</tbody>
</table>

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Final remarks

5.5 Discussion

5.5.1 Limitations

The total area surveyed was 102.44 m$^2$. Compared to other benthic video studies (e.g. 940.4 m$^2$, De Leo et al., 2010; 64,895 m$^2$, Heifetz et al., 2009) the area covered here is relatively small. And, given only three hauls (one of which was completely taut, one completely dragged and one with parts of each) were studied, it was not possible to separate the effects of taut/dragged from individual line effects. I measured each video in sections as once a haul had stopped and restarted there were sometimes different line behaviours that could affect what benthos is impacted. I suggest this method is sound however a laser or some precise measure of distance and thus size would aide statistical analysis by providing a fixed sample size. Nonetheless, this is the first investigation of bottom-longline selectivity using video deployment and an example of the diversity analyses and density estimates that are possible.

There was a cleared trough sometimes visible immediately adjacent to the longline, presumably created by the line passing through the substratum, but also perhaps the camera. Monitoring and measuring longline damage whilst having zero impact from camera deployment is a difficult task. The current array is certainly the most-streamlined design so far (see Figure 5.1; Kilpatrick et al. 2011) and I believe it had little impact as there was no evidence of coral damage coming into view after the camera had passed.

5.5.2 Coral densities

The habitat in footage is subjectively comparable to “medium density soft corals and gorgonian whip” communities in Post et al. (2010; Ross Sea). There are few examples of coral density estimates from the deep sea. This footage concentrated on three hauls where coral habitat was present making comparisons from general habitat surveys difficult. However if there was any coral at all it was included in analyses and there were areas with low or no corals present. Densities of all organisms were relatively similar across hauls (Table 5.3). Stone (2006) found coral on every transect and here I make some comparisons to the most diverse areas of that study from the Aleutian Islands, Alaska. Density estimates of all corals from footage here (13.2 /m$^2$; Table 5.3) were much higher than the highest seen (buttress habitat) for the Aleutian Islands:
a maximum of 6.53 corals per $m^2$ (0-350 m depth; Stone 2006). Hydrocorals (Stylasteridae) made up most of all corals in Stone (2006; 3.65 per $m^2$) however hydrocoral density found here were over double than in Alaska. Shallow areas of fjords in Chile have densities of stylasterids much higher than found off Shag Rocks; there stylasterids carpet the sea floor, with up to 80% cover (Häussermann and Försterra, 2007).

Octocoral (described as gorgonian) densities in Stone (2006) were highest in cobble fields (on the slope, 2.32/$m^2$, and shelf, 2.2/$m^2$). Anecdotally, video footage from South Georgia found corals were not uniformly present, but in patches; often on drop stones and outcrops, jutting above the seafloor. These raised zones of hard substratum seem to be refuges for corals (Oschmann, 1990), giving octocorals area to settle and height into faster flowing water that improves food catchment (Wainwright and Koehl, 1976).

Two previous studies have, using video footage, related coral density, albeit qualitatively (i.e. “sparse”, “medium” and “high” density categories), to the VME indicator units defined (arbitrarily) by CCAMLR ($\geq 10$ kg/10 l of VME/1200 $m^2$; CCAMLR, 2008b) and thus what would trigger VME locations under the CCAMLR Conservation Measures (Post et al., 2010; Jones and Lockhart, 2011). I believe a specific density threshold for VME indicator organisms that would define a VME needs to be developed. Camera deployment on bottom-longlines is a relatively non-invasive method of viewing VME organisms directly and potentially a more efficient method of calibrating longline hook data with benthic interactions. Ultimately, however, there are inherent sampling limitations in using longline hook recovery data (reviewed in Auster et al., 2011) and it would be useful to confirm the presence of VMEs with longline mounted, or other, camera systems alone. One problem with present CCAMLR conservation measures is that once an area is designated as a benthic impact protection area, no further fishing is permitted, so specific camera research would be required to confirm or deny the presence of a VME.

5.5.3 Gear selectivity

The complex three-dimensional shape of bushy corals would appear more “hookable” than the slender fingers of whip and fan corals as they appear more frequently in by-
catch. As observers have only been asked to return a single sample if many specimens are thought to be conspecific (Figure 5.4C: just one piece of one colony was collected from this by-catch), and by-catch counts are inherently conservative as colonies fall off longlines when being dragged and hauled (this was seen in footage), it was difficult to estimate abundance and thus proportions of different morphologies in by-catch. Generally, a higher proportion of bushy coral is caught in by-catch (70% of all by-catch west of Shag Rocks) than is seen on camera (59%; Table 5.2), although this is a relatively small difference. The opposite, however, is seen for whip corals, where the proportion seen on camera, 24%, is higher than that seen in by-catch, just 13%. Anecdotally, many whip and fan corals caught as by-catch are still attached to a small rock or piece of dead coral i.e. something that could be “hooked”. Fan corals are almost as diverse as bushy and make up a smaller portion of by-catch. Studies from the north of South Georgia (at 200, 500, 1000 and 1500 m depth) showed Cnidaria were relatively most abundant and had higher mass at 1000 and 1500 m (Griffiths et al., 2008). This would infer that the relatively high proportion of Cnidaria from by-catch is an effect of gear selectivity. That, and the research here, would agree with but not substantiate the logical expectation that longlines have an inherent selectivity bias towards bushy corals however, without species ranges and estimates of rarity as well as precise abundance figures of by-catch it is difficult to fully comprehend the extent and consequences of gear selectivity on octocoral diversity.

5.5.4 Coral by-catch: impacts and fragility

The long-term impact of longline contact on corals is unknown. Due to their rigid calcium carbonate skeleton, stylasterids are highly fragile (Heifetz et al., 2009); so although not explicitly known, dislodgement (the result of 42% of contacts, and affecting 6% of colonies in the sample area, Table 5.5) is very likely lethal for Stylasteridae. Any contact could result in sub-lethal damage that could later result in mortality, for instance through grazes that are open to infection or parasitism. This makes Stylasteridae vulnerable to fishing impacts (Heifetz et al., 2009). Sylasteridae resilience however is less understood and further investigations into the timing and frequency of Antarctic stylasterid reproduction, larval dispersal capabilities and growth are required as previous reproductive studies were focused on northern hemisphere habitats (Miller et al., 2004; Brooke and Stone, 2007). Stylasterids have been called “early colonizing species” (Clark et al., 2010, p. 266) and, if so, the
stylasterid littered seafloor seen in some footage could indicate this is an already heavily impacted environment showing wide, but low-level, recovery. Conversely, Stylasteridae from the Aleutian Islands have reproductive traits that would imply limited recolonising ability (Brooke and Stone, 2007), perhaps making stylasterids locally vulnerable. Nonetheless, there was no significantly higher impact seen in Stylasteridae compared to other coral categories/morphologies in the South Georgia study, and the impact area of longlines, both individually and collectively, is likely to be very small. The cumulative area of impact, calculated here by summing all line lengths set within the 500-1000 m depth band from 1995-2009 in the area west of Shag Rocks, where the three study lines were set, was 9% of the total area when assuming a 2 m wide footprint.

Similar to bottom-longline by-catch from the Ross Sea (Parker and Bowden, 2010), octocorals, specifically Primnoidae (and within Primnoidae, Thouarella) formed the majority of by-catch (Figures 5.5, 5.6). Octocorals have a more flexible scleroproteinaceous axis than Stylasteridae. This malleability meant dislodgement by longline was rarer (Table 5.5), confirming previous assumptions about octocoral/gorgonian low fragility (Parker and Bowden, 2010). Whip corals had higher average rates of recovery from dragged line contacts than fan or bushy corals (Table 5.5).

5.5.4.1 Growth rates
Relatively little is known about growth rates and age of deep-water corals. Corallium secundum Dana, 1846, is known to live for 71 ± 9 years with a radial growth rate of ~170 µm yr⁻¹ (Roark et al., 2006). A 112 year-old (not a fully grown colony) Primnoa resedaeformis (Gunnerus, 1763) was estimated to grow at 1.60 to 2.32 cm per year in height and approximately 0.36 mm per year in diameter (Andrews et al., 2002). A second colony (0.5–0.75 m tall) of Primnoa resedaeformis (Gunnerus, 1763) was aged at over 300 years with 0.044 mm.yr⁻¹, linear tip extension of 1.5–2.5 mm.yr⁻¹ (Risk et al., 2002). Within deep-water Stylasteridae even less is known. Estimates of growth rates varies from 7 mm/yr in New Zealand (Miller et al., 2004) to an average of 10 mm/yr in New Zealand (Chong and Stratford, 2002); the latter were both extending and suffering from regression through partial death (growth rates ranging between a regression of 15.6 mm yr⁻¹ and an extension of 18.3 mm yr⁻¹; Stratford,
268. Clearly these are long-lived, relatively slow-growing organisms that require decades, if not centuries, to recover from impacts.

5.5.5 *Recovery from fishing impacts*

Coral recovery from bottom-longline contact is dependent on life histories, growth rates, reproductive strategies and an ease in fishing pressure. Understanding the repeat occurrence of bottom-longlining on benthic habitats is near impossible given the limited understanding of lateral line movements, gear selectivity, total effort and constraints on specific fishing location, such as ice (Parker and Bowden, 2010). We do know that bottom-longline fishing around South Georgia is generally focused along the shelf break (Wakeford et al. 2006), a relatively small area of terrain highlighted as highly suitable octocoral habitat (see Chapter 4) and likely suitable habitat for a range of other organisms, such as hard corals and sponges, which are also reliant on hard substrata for holdfast attachment. In examples of trawled seamounts, intensive fishing on a concentrated area has been shown to have long-term effects on coral habitat with no recovery seen over 5 and 10 year periods (Williams et al., 2010) but these impacts are very much greater than would be expected with longlines. In the Williams *et al.* (2010) study, some taxa (including Chrysogorgiidae and solitary scleractinian corals) showed higher abundance in fished areas, contrary to the trend for most taxa, whose abundance had declined. This could be indicative of the ability of some corals to escape initial impacts (by residing in inaccessible refuges) or evidence of early colonisers (Williams *et al.*, 2010). In contrast to the complete removal of coral matrix associated with trawling, the fact that communities of octocorals are still apparent and, in some cases thriving, around South Georgia in areas with intense or long histories of bottom-longline fishing, suggests that areas subject to longlining either have much better recovery rates or lower initial impact, or both as communities of octocorals are still apparent. South Georgia’s RIA’s are an opportunity to test octocoral habitat recovery from longlining; this is research I strongly suggest fisheries management considers.

5.6 *Conclusions*

Although it was not possible to robustly estimate the impact of one bottom-longline it is known that coral by-catch regularly occurs (Agnew, 2004; Agnew *et al.*, 2007; Wakeford *et al.*, 2006) hence longlines must impact coral abundance. Although there
are some estimates of longline lateral movements (WG-EMM, 2010; and discussed in Sharp et al., 2009), a holistic estimate of damage is difficult without a view of the entire longline length, which is not practical. Investigations into online and offline (to the side of the longline in view) coral density estimates is one method of looking at individual longline impacts along a viewed section of longline. Although that has been shown to be ineffective in this study, as the sample size was too low to make any conclusions about overall impact, I suggest this as an important line of research to pursue. What is novel and important in this work is that along the path of the longline, corals were seen to be impacted, and from the comparison of by-catch versus video counted corals, it would seem that bushy octocorals and stylasterids were more likely to be impacted than slender whip and fan octocorals. With more deployments and a statistically robust analysis a clearer picture of longline impact on and the selectivity of benthos should be possible using these methodologies. Teasing historical impacts, given the long history and intensity of bottom-longline fishing (Wakeford et al. 2006) around South Georgia (examples of previous fishing impacts were intermittently visible offline e.g. Figure 4B), from the impact of a viewed longline will be more difficult.

Camera arrays are an excellent method of gathering information about immediate gear impacts and selectivity. Although truly independent observation would be ideal (camera on a separate line; Sharp et al., 2009), this camera array appears to have minimal impact (however this is an element of this study that should be investigated further), and produces ecologically informative footage that can be used to study coral diversity. Footage from a wider area could also be cross-referenced against predicted benthic habitat maps (see Chapter 4) as a ground-truthing exercise, and in wider deep-sea coral ecological studies to investigate coral preferences for different terrains, depths etc. Lastly, footage could be used to identify VME locations and this is being actively explored by other researchers (Jones and Lockhart, 2011). I suggest specific VME taxa density estimates are researched for this purpose.

Although it is impossible to know the full extent of longline impacts, or know what the South Georgia deep-sea benthic environment looked like pre-fishing, the footage seen was in stark contrast to images of habitats post-trawl, where the substratum is
denuded of structure (Clark et al., 2010); individual bottom-longlines have a far smaller and lighter footprint on the seafloor.

5.6.1 Suggestions for future camera longline arrays

There were limitations to what was possible to garner from video images given the black/white film, variable haul speed, lack of precise distance and size estimate, and camera motion. I thus made conservative counts and area estimates and explained the limitations we faced where necessary. I would advise future efforts to utilise at least two lasers to better estimate distance and area; colour film would greatly widen the number of organisms possible to identify and the taxonomic level of identification and collection of all benthos from bottom-longlines, even on a modest number of experimental lines, would compliment footage and allow for more precise estimates of gear selectivity. I see camera deployment as a very useful tool to inform the fishing industry and fisheries managers about habitats found in fishing areas and this supports efforts to fulfil UNGA resolutions 61/105 and 64/72 (UNGA, 2007; 2009).
Appendix I - List of all identified octocorals caught as by-catch from the longline Patagonian toothfish fishery around South Georgia from 2005-2009. ‘?’ indicates a tentative identification.

<table>
<thead>
<tr>
<th>Family</th>
<th>Genus and species</th>
<th>Family</th>
<th>Genus and species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthogorgiidae</td>
<td>Unknown genus</td>
<td>Primnoidae</td>
<td>Amphiphis abietina</td>
</tr>
<tr>
<td></td>
<td><em>Acanthogorgia</em></td>
<td></td>
<td><em>Amphiphis grandiflora</em></td>
</tr>
<tr>
<td>Alcyoniidae</td>
<td><em>Anathomastus</em></td>
<td>Primnoidae</td>
<td>Amphiphis plumacea</td>
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<tr>
<td></td>
<td><em>Convexella magelhaenica</em></td>
<td></td>
<td><em>Convexella new sp.</em></td>
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<td></td>
<td><em>Inflatocalyx infirmata?</em></td>
<td></td>
<td><em>Dasystenella acanthina</em></td>
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<tr>
<td></td>
<td>Unknown genus</td>
<td></td>
<td><em>Digitogorgia brochii</em></td>
</tr>
<tr>
<td>Clavulariidae</td>
<td>Unknown genus</td>
<td></td>
<td><em>Digitogorgia kuekenthali</em></td>
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<td></td>
<td><em>Digitogorgia new sp.</em></td>
<td></td>
<td><em>Digitogorgia new sp.</em></td>
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<tr>
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<td>Unknown genus</td>
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<td></td>
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<tr>
<td></td>
<td>Unknown genus</td>
<td><em>Fannyella (Cyanthogorgia)</em></td>
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<tr>
<td></td>
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<tr>
<td></td>
<td><em>Fannyella</em></td>
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<td><em>New Genus 3</em></td>
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<td><em>Mirostenella</em></td>
<td>Onogorgia nodosa</td>
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<td></td>
<td><em>Isidella</em></td>
<td>new sp.</td>
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<td></td>
<td><em>Keratoisis</em></td>
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<td></td>
<td><em>Mirostenella plumosa</em></td>
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<tr>
<td></td>
<td><em>New Genus 1</em></td>
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<td><em>New Genus 2</em></td>
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<td></td>
<td><em>New Genus 3</em></td>
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<tr>
<td>Keroeidididae</td>
<td><em>Ideogorgia</em>?</td>
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<td><em>Onogorgia nodosa</em></td>
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<td></td>
<td>new sp.</td>
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<td><em>Paragorgia</em></td>
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<td><em>Primnoella scotiae</em></td>
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<td></td>
<td><em>Paramuricea</em></td>
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<td><em>Thouarella andeep</em></td>
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<td><em>Thouarella antarctica</em></td>
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<td><em>Thouarella brucei</em></td>
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<td><em>Thouarella crenelata</em></td>
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<td><em>Thouarella new sp. 2</em></td>
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<td><em>Thouarella new sp. 3</em></td>
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<td><em>Thouarella parachilensis</em></td>
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<td><em>Thouarella pendalina</em></td>
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<td><em>Thouarella variabilis</em></td>
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<td><em>Scyphogorgia liouvillei</em></td>
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<td></td>
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<td></td>
<td><em>Tokoprymno anatis</em></td>
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CHAPTER SIX
6 Final remarks

The aims of this research were to investigate the species richness and diversity of octocorals caught as by-catch around South Georgia. This work developed beyond this remit into research to predict habitat suitable for octocorals in the wider South Georgia waters and investigations of specific longline impacts on benthic communities. Research presented here, although focused primarily on by-catch, examined octocorals around South Georgia from a species to suborder level using traditional taxonomic techniques, phylogenetics, habitat suitability modelling and by analysing underwater video footage.

6.1 Results, discoveries and implications

This research confirmed that octocorals form the majority of by-catch in the bottom-longline fishery for Patagonian toothfish around South Georgia. Primnoidae were the most frequently caught octocoral family. Primnoidae are found worldwide but are especially common in the sub-Antarctic (Cairns & Bayer, 2009). The revision of Thouarella, one genus of Primnoidae, was urgently required, having not been tackled in almost 80 years and, given the frequency and abundance of these corals in by-catch, an important undertaking. Species-level identifications are the building blocks of any diversity indices and the images and descriptions presented here will be useful to deep-sea octocoral taxonomists, fisheries observers, researchers and fisheries managers alike.

Deep-sea exploration and research produces many new species discoveries each year; in recent years, considering just octocorals, many new species have been described (Cairns, 2006; 2010; in press; López-González et al. 2002; Zapata-Guardiola & López-González, 2010a,b,c). It is likely that deep-sea species discoveries will continue in future years as there is heightened commercial interest in deep-sea areas (fisheries, mining, oil exploration etc.). Measuring the species richness of abundant and diverse groups of animals found in some areas of the deep-sea can be a difficult task as deep-sea communities are often poorly sampled and there remains relatively fewer deep-sea species to compare new discoveries to and embed them in a wider taxonomic picture than other ocean realms. One increasingly common technique to support species discovery is DNA barcoding (Herbert et al. 2003a,b; Vogler &
Monaghan, 2006), although species delineations on barcodes alone remain controversial (Moritz & Cicero, 2004; DeSalle et al. 2005; Ebach & Holdrege, 2005; Brower, 2006). In octocorals DNA barcoding is confounded by the unusually low genetic diversity in commonly used barcoding genes (COI; Herbert et al. 2003b) that makes utilisation of barcoding difficult (as it was for Primnoidae, unpublished data) and in many families impossible (McFadden et al. 2010a). For this reason this study focused on morphological taxonomy and phylogenetics to explore species richness.

Embedding species and specimens into a phylogenetic tree was seen as an informative method of looking at species richness and diversity (especially for those families of octocorals without morphological identifications). Within the phylogenetic tree presented here three major Octocorallia clades were resolved (in part supporting previous work by McFadden et al., 2006, however one clade separated differently) and pennatulids (sea pens) were again found basal to the majority of Octocorallia. Eight families, at least 21 genera (of which two are new discoveries) composed of a minimum of 34 species (including 9 new species) were caught as by-catch when both phylogenetic and morphological analyses are considered. The phylogenetic tree and markers used were effective at estimating the numbers of genera and species of the octocoral family Primnoidae and some other families of octocorals although not useful across the entire breadth of octocorals caught as by-catch. More complete sampling and morphological taxonomy is required to confirm these results. Given the scale of the need to understand fishing impacts on octocoral diversity (and other vulnerable marine ecosystems, VMEs), new genetic technologies should be utilised where possible and the value of an integrative approach (using morphology and phylogenetics) was shown here.

To compliment species richness investigations a wider study of octocoral habitat was undertaken. A bathymetry-derived megahabitat map of South Georgia was created. This map was useful in classifying geological features that may harbour different, distinct habitats, such as those preferred by octocorals. The map was cross-referenced against by-catch data and it was found that fishing is concentrated in shelf / narrow crest habitats. By-catch data was used for the first time to create a map of octocoral habitat suitability predictions. The habitat suitability model, based on presence-only location data, predicted shelf troughs, crest and slope areas as highly suitable.
octocoral habitat (which overlaps with fishing areas). More data from specific families will make it possible to tease apart the different habitats different families may occupy. The three restricted impact areas created in recent years by the Government of South Georgia and the South Sandwich Islands were found to contain highly suitable octocoral habitat and fishing regulations limiting fishing to below 700 m were also seen to protect more areas likely to be suitable habitat for octocorals.

This research has informed fisheries managers about the diversity of octocorals found in by-catch and provided a source of identification material for the most commonly caught genus, *Thouarella*. Around South Georgia management is very active meaning the habitat suitability maps form a useful tool that can inform about the effects future protection measures and regulations have on areas where one VME, octocoral, is predicted to have highly suitable habitat.

Many longline fishery managers are interested in understanding the physical effects a longline has on benthos; this is a difficult undertaking, given the length of longlines and the depths they are deployed in, but one now possible with cameras capable of withstanding the pressures of the deep-sea and specifically designed to be attached to longline gear. The preliminary analysis of video footage from such cameras has been useful in showing for the first time the interaction of longline gear with benthic communities. Although the amount of data was limited it was clear that utilising cameras on longlines is an informative method of gathering information on coral densities (which could be helpful in identifying VME locations), gear selectivity, and impacts.

### 6.2 Conclusions

Although direct comparisons to other geographical areas are difficult, given this relatively novel approach of utilising morphology and phylogenetics to identify octocorals from fisheries by-catch down to species level, it can be seen that octocoral species richness in by-catch from the South Georgia Patagonian toothfish fishery is high. The phylogenetic element of this research substantially added to present understanding of octocoral phylogeny, albeit with a focus on the abundant by-catch family of Primnoidae.
Morphological identifications were focused within Primnoidae (as they were the most prevalent in by-catch) and specifically the common bottlebrush genera of *Thouarella*. The revision presented here forms a useful identification guide and provides the breadth of detail about morphology required to understand and investigate species relationships within the genus. This morphological background and the species-level identifications carried out were essential in verifying the accuracy of phylogenetic markers used in Chapter 3.

Spatially embedding this new knowledge of South Georgia octocoral presence onto megahabitat maps and carrying out octocoral habitat suitability analyses was seen as an important step in informing fisheries management about the potential distribution of octocorals across the South Georgia shelf and slope. It was also possible to highlight highly suitable areas for octocorals found in Restricted Impact Areas and areas protected by fishing regulations (Chapter 4). Currently, Restricted Impact Areas protect habitats predicted to be highly suitable for octocorals, while fishing regulations protect 42% of all putative highly suitable octocoral habitat within the studied area.

The data from just three longlines were not sufficient to gain a full understanding of gear selectivity. The limitations of this work are fully acknowledged but I saw value in showing the data and analysis that could be extracted from video arrays attached to longlines. This pilot study has shown this method as having great promise. Moreover, although longline fishing had a greater impact on Stylasteridae, more so than other coral groups (such as octocorals), the footprint of a longline appears to be very small in comparison to other fishing methods (trawling for instance).

### 6.3 Future work

Phylogenetics methods, specifically barcoding, are being used more frequently in efforts to record the diversity of life on this planet (Blaxter, 2004; Blaxter et al., 2005; Hebert et al., 2003; Vogler and Monaghan, 2006). Phylogenetics has been key in understanding the evolutionary history of corals in shallow-water Scleractinia (Lindner et al., 2008), however, the current genetic markers at our disposal for octocorals are depauperate and often barcoding and phylogenetic analyses in octocorals fail to resolve species (McFadden et al., 2010a) or basal nodes (McFadden...
et al., 2006); hence the integrative approach alongside morphology presented here. I encourage future research into new octocoral markers. As the cost of high-throughput sequencing decreases, this method could bring many more variable markers to bear on the issue of Octocorallia phylogenetics. Specifically, markers to resolve basal nodes in Octocorallia and more sensitive markers for species differentiation would better elucidate the diversity of octocorals and help in the location of high-species richness areas. In addition to this, knowledge about deep-sea octocoral biology, physiology, reproduction, population size and range is very poor. These are essential in understanding the effects that climate change and, perhaps more importantly, ocean acidification could cause in deep-sea areas.

In a wider sense habitat suitability modelling and benthic terrain models combined with fisheries data can substantially improve knowledge about the potential location of VMEs. This is useful for many management purposes, not in the least assessing and limiting impacts on VMEs as dictated in the UN General Assembly Resolutions on Sustainable Fishing on the High Seas (61-105 and 64/72; UNGA, 2007; 2009). The South Georgia Patagonian toothfish fishery has observers on every vessel making comprehensive data collection possible. Such systematic collection of data means verification of said models is possible in fished areas, however, in non-fished areas, independent research into model results is advised.

Although preliminary video analysis from camera arrays attached to bottom-longlines did not reveal statistically significant gear selectivity towards any specific coral morphology (whip, bushy, fan) or group (Stylasteridae) of corals, I would encourage more videos to verify this result and investigate the link between a dragged/taut longline and impacts to benthic communities. I would also encourage research into the different interactions auto- and Spanish-longlines may have with benthos as it is believed these gears catch different volumes of coral by-catch (MRAG, pers. comm.). Suggestions on how to improve the data collection from video footage were listed at the end of Chapter 5. I would also be keen for managers to consider surveying the newly created Restricted Impact Areas to gather baseline information for long-term recovery of benthic communities from longline impacts; something I am not aware has been studied in any other longline fishery. Although the levels of previous impact are difficult to estimate this is an exciting opportunity and can be combined with
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research to groundtruth the octocoral habitat suitability models presented here. I also encourage research into the shallow-water troughs across South Georgia’s continental shelf that appear to be highly suitable octocoral habitats and are areas that have not been specifically surveyed or sampled.

On a small scale I hope this work has contributed to a greater understanding of octocoral species richness around South Georgia, the way longlines interact with benthic communities and highlighted potential areas of highly suitable octocoral habitat for future investigation.

6.4 References


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