Dead man's fingers point towards new species: A taxonomic revision of *Alcyonium aurantiacum* with statistical discrimination methods and a survey of integrative taxonomy in Octocorallia

by

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Abstract

Octocorals are a diverse group of sessile, colonial, filter-feeding anthozoan cnidarians, which form significant components of benthic marine communities worldwide. Globally, the most critical hurdle to the effective management of octocorals in the face of increasing anthropogenic pressure is the poor state of their species-level taxonomy, which hinders understanding of their biodiversity. New Zealand's octocoral assemblage is among the most diverse of any country and is characterised by high levels of endemism, yet over half of its octocoral species remain undescribed. While progress is being made, this has focussed almost exclusively on protected deep-sea gorgonian octocorals.

Unprotected coastal soft corals are less studied in New Zealand. This includes the endemic *Alcyonium aurantiacum* Quoy and Gaimard, 1833. Multiple, morphologically diverse forms have been attributed to this species. Here, the taxonomic status of *A. aurantiacum* is reviewed, and its phylogenetic relationships are examined using molecular data (nuclear *28S* and mitochondrial *MutS* genes), which is compared to morphology in an integrative approach. As a result, evidence for two new, endemic genera and ten new species is presented. *Alcyonium aurantiacum* is referred to *Kotatea* gen. n. (as *K. aurantiaca* comb. n.), which contains seven additional new species. A second genus, *Ushanaia* gen. n., contains three new species.

Of the new taxa described herein, *K. aurantiaca* and *K. lobata* sp. n. are the most commonly encountered and widespread, yet little is known regarding their biology. Both species co-occur in their natural habitat, could not be differentiated genetically with the tools used here, and can be difficult to distinguish without microscopic sclerite examinations. To facilitate the identification of these two similar species by non-taxonomists, a statistical model was developed that can discriminate them with up to 90% accuracy using easily obtainable measurements of gross colony morphology. Relationships between colony morphology and depth are also examined.

Considering the difficulties associated with species discrimination among octocorals, a literature survey was conducted to review the use of integrative taxonomy in this group since the start of the 21st century, focusing particularly on morpho-molecular data comparisons. This revealed that, while description rates at family, genus, and species levels over the last twenty-one years rank among the highest ever, integrative techniques have been applied unevenly across taxonomic groups and geographic regions and overall remain a minority compared to taxonomic research based solely on morphology. Implementation of the integrative approach is increasing, however,

as are the per-annum number of taxonomic publications and the total pool of authors associated with these publications.

It is hoped that the research presented herein can contribute to ongoing global efforts of revising octocoral systematics and that the examination of integrative practices in octocoral taxonomy will serve as a baseline against which future taxonomic progress can be compared and promoted. For New Zealand specifically, elucidating the taxonomy and variability of these endemic taxa will enable aspects such as their contribution to ecosystem functioning and management needs to be examined accurately for the first time, which in turn may lead to their recognition as organisms worthy of legal protection.

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Table of contents

List of figures

(captions abbreviated)

List of tables

(captions abbreviated)

Chapter 1.
General introduction

1.1 Introduction to Octocorallia

Octocorallia Haeckel, 1866 is a diverse subclass of sessile, mostly colonial, filter-feeding anthozoan cnidarians comprised of over 3,500 described species of soft corals and gorgonians (order Alcyonacea Lamouroux, 1812), sea pens (order Pennatulacea Verrill, 1865) and blue corals (order Helioporacea Bock, 1938). As the name suggests, this group is distinguished from its sister clade — the Hexacorallia Haeckel, 1896 — by the diagnostic apomorphy of eight-fold symmetry in its polyps, which bear eight internal mesenteries and eight, usually pinnate tentacles (Daly et al. 2007). Octocoral colonies are an ecologically significant component of benthic marine communities across virtually all latitudes and depths (Fabricius and Alderslade 2001). Soft corals are abundant on shallow coral reefs throughout the tropical Indo-Pacific region (Tursch and Tursch 1982; Dinesen 1983; Fabricius 1997), while sea rods and sea fans dominate many coral reefs in the Caribbean Sea (Sánchez et al. 1997, 1998). In general, shallow-living octocorals are poorly known in temperate regions, but some occupy significant proportions of the available substratum in the comparatively well-studied Mediterranean Sea (Weinberg 1977; Ballesteros 2006; Ambroso et al. 2013). However, it is in the deep sea where octocorals achieve their highest diversity, with around 75% of all species found below 50 m depth (Cairns 2007b; Roberts et al. 2009) and 67% of families below 200 m (Watling et al. 2011). Here, octocorals tend to form distinct habitats that do not overlap with those produced by other groups such as cold-water scleractinian reefs (Andrews et al. 2002), they display a high degree of endemism (Koslow et al. 2001; France and Hoover 2002), and are often regarded as ecosystem engineers whose presence increases the diversity of other organisms (Roberts et al. 2009).

Although octocorals are generally not reef-forming, the spiculite rock created by the accretion of basal sclerites in *Sinularia* May, 1898, for example, can contribute to reef growth in some areas (Schumacher 1997; Jeng et al. 2011). More characteristically for the group, however, are the high density single or multi-species assemblages they generate, which are commonly known as octocoral "gardens" or "forests" (Freiwald et al. 2004). This is an apt comparison since many species form tree-like structures that elevate their branches several metres above the seafloor. This forms not only a visually prominent element of the epifauna, but also a major source of three-dimensional biogenic habitat, offering shelter as well as feeding, spawning and nursery sites to a myriad of other organisms (Krieger and Wing 2002; Buhl-Mortensen and Mortensen 2004;

Metaxas and Davies 2005; Stone 2006; Etnoyer and Warrenchuk 2007; Mosher and Watling 2009; Buhl-Mortensen et al. 2010; Le Guilloux et al. 2010; Baillon et al. 2012; Quattrini et al. 2012).

Octocorals, particularly in the deep sea, are negatively impacted by destructive fishing practices (Althaus et al. 2009). Many octocorals are predisposed to fishing damage due to their upright morphology and often patchy but densely localised distributions, which may allow a single benthic trawl to significantly alter community composition (Koslow et al. 2001; Clark and Rowden 2009; Williams et al. 2010). Of greatest concern, however, is the very low expected recovery potential of deep-sea octocoral assemblages. Due to their slow growth, extreme longevity, fragility, and limited dispersal ability (Grigg 1988; Andrews et al. 2002; Risk et al. 2002), recovery times to a pre-exploitation state will most likely have to be measured in centuries (Goode et al. 2020). In addition to fishing, octocorals face a suite of other anthropogenic stressors globally, including deep-sea mining (Roberts et al. 2009), which is expected to begin at commercial scales in the near future, and damage from oil and gas exploration (De Leo et al. 2015).

Compounding these localised disturbances is the underlying threat of anthropogenic global climate change, particularly in shallow settings. Octocorals contain calcified micro-skeletal elements known as sclerites, which renders them vulnerable to ocean acidification (Gabay et al. 2013), although the soft tissues of some species may be capable of guarding sclerites against lowered pH levels (Gabay et al. 2014). Rising sea surface temperatures and thermal stress are already causing high mortality and/or bleaching among some octocorals in shallow temperate and tropical settings (e.g., Fabricius 1999; Bruno et al. 2001; Loya et al. 2001; Gambi et al. 2010; Lõhelaid et al. 2015; Dias and Gondim 2016), with subsequently slow recovery (Fabricius 1995; Cornish and DiDonato 2004). However, contrasting responses have been found in other octocorals. Following disturbance, some tropical soft corals are able to recruit and recolonise hard substrata rapidly and opportunistically to the point of monopolisation, thereby inhibiting the recovery of slow-growing and reef-building corals (Fox et al. 2003; Stobart et al. 2005; Tilot et al. 2008). Clearly, octocorals respond to anthropogenic stressors in many different ways, with some species benefitting while others suffer, and as a result, the collective ecological dynamics of the group may be shifting in ways that are difficult to predict.

Increasingly, octocorals are becoming a focus for global marine biodiversity conservation initiatives. Most notably, they are used as indicators in the identification of vulnerable marine ecosystems (VMEs) (Tracey et al. 2007), which are at significant risk of anthropogenic disturbance, particularly from fishing damage (FAO, 2009). International efforts to protect VMEs have

continued to gather momentum since the UN General Assembly Resolutions on Sustainable Fishing on the High Seas 61/105 and 64/72 called on nations and regional fisheries management organisations to protect VMEs by avoiding adverse bottom fishing practices (UNGA 2007a, 2009). As a consequence, octocorals now feature prominently in regulatory and spatial management policies (Parker et al. 2009). Despite these efforts, octocorals remain poorly known in many areas, and in order for meaningful safeguarding measures to be implemented, the current interest in their conservation must be backed by an improved understanding of their distributions, habitat associations, community structure and population connectivity (Taylor et al. 2013). However, the most critical hurdle to the global management of octocorals may be the poor state of their species-level taxonomy (Alderslade et al. 2014). Ironically, as our awareness of this group's importance to ecosystem functioning grows, there is a simultaneous realisation that we are poorly equipped to understand their responses to, and protect them from, rapid environmental change (Miller et al. 2009; Foley et al. 2010).

1.2 Octocoral taxonomy and current issues

Clearly defined species are necessary to accurately assess levels of endemism and abundance, determine population responses to environmental change, and formulate effective conservation strategies (Althaus et al. 2017). Yet this is a luxury that octocoral researchers and ecosystem managers are often forced to forgo, instead working only as far as genus or family level (e.g., Stone 2006; Fabricius and De'Ath 2008; Chanmethakul et al. 2010; Bridge et al. 2012), or simply discriminating amongst apparent morphospecies alphanumerically (e.g., van Oppen et al. 2005). This is due to the large number of undescribed species, the poor quality of many 19th and early 20th century descriptions, lost type material, the need for revisions in many groups, and the fact that octocoral identification is time-consuming and requires taxonomic expertise (Pérez et al. 2016).

While octocoral monophyly is well established, the ordinal, subordinal and familial organisation of the subclass has long frustrated taxonomists and is considered unstable (Bernston et al. 2001; Won et al. 2001; McFadden et al. 2006b, 2010; Daly et al. 2007). Most problematic is the order Alcyonacea. This group encompasses over 30 families, defined primarily by the morphological characters of colony growth form, skeletal axis structure (if present), and the shape and arrangement of sclerites (Fabricius and Alderslade, 2001). For taxonomic convenience Alcyonacea is currently divided into six sub-orders that reflect a progression from simple to complex morphologies, but which are widely acknowledged as representing different grades of colony construction rather than phylogenetic relationships (Bayer 1981a; Fabricius and Alderslade 2001; Daly et al. 2007). In the

monospecific Protoalcyonaria Hickson, 1894 the polyps are solitary, whereas those of all other sub-orders form colonies. In Stolonifera Thomson and Simpson, 1909, polyps are basally connected by ribbon-like stolons or membranes, while those in Alcyoniina Bayer, 1981(a) are embedded in a fleshy mass of coenenchymal tissue. These three groups all lack a supporting skeletal axis, and contain those families commonly referred to as soft corals (Daly et al. 2007). The remaining three sub-orders do produce a skeletal axis, the composition of which is used as a distinguishing characteristic. In Scleraxonia Studer, 1887, fused or unfused calcium carbonate sclerites make up the axis or axial-like layers. The axes in Calcaxonia Grasshoff, 1999 are composed of gorgonin (a proteinaceous, horn-like material unique to octocorals) with large amounts of non-scleritic calcite, whereas Holaxonia Studer, 1887 possess hollow and cross-chambered gorgonin axes with variable quantities of calcite (note though that this is a simplified summary and that these groups are highly diverse in their physiologies). These three groups are informally referred to as gorgonians, since most of their member taxa were historically placed in the now invalid order Gorgonacea Lamouroux 1816.

Crucially, this system is plagued by pervasive polyphyly (groups containing taxa that do not share an immediate common ancestor) and paraphyly (groups not containing all the descendants of a common ancestor) and because of this reclassification is necessary at virtually all taxonomic levels (Berntson et al. 2001; Sánchez et al. 2003a; McFadden et al. 2006b, 2010; McFadden and Ofwegen 2012b). This is the result of a paucity of useful morphological characters and more than two centuries of classification based on intraspecifically variable and homoplasious traits (Bayer 1981a; McFadden et al. 2006b; Bilewitch et al. 2010), exacerbated by a poor fossil record (Williams, 1997). Colony growth form and sclerite characteristics have traditionally served as the basis for taxonomic classification (Fabricius and Alderslade 2001; Daly et al. 2007). Sclerites are, however, highly variable in shape and size and change gradually across the different parts of individual colonies in most species, from base to branch and from inner to outer layers, for example. Furthermore, the sclerites in some species respond to environmental conditions, primarily depth (West et al. 1993; Prada et al. 2008), and biological processes such as predation (West 1997). The presence or pattern of colony branching can be similarly plastic (Rodríguez-Lanetty et al. 2003; Kim et al. 2004; Gori et al. 2012; Costantini et al. 2016; Calixto-Botía and Sánchez 2017). This morphological variability inevitably necessitates a certain degree of subjectivity in classification if the range of intraspecific polymorphism overlaps with interspecific variation (Prada et al. 2008). Additionally, homoplasy (independent origins of the same character state) has been demonstrated at all taxonomic levels by numerous molecular phylogenetic analyses through the repeated emergence of similar colony growth forms among distinct lineages (Sánchez et al. 2003a;

McFadden et al. 2006b; France 2007; Dueñas and Sánchez 2009; McFadden and van Ofwegen 2012b; Prada and Hellberg 2013; Bilewitch et al. 2014; Rowley et al. 2015; Yasuda et al. 2015; Ament-Velásquez et al. 2016). Clearly, the diagnostic merit and phylogenetic validity of morphological traits is doubtful in many cases.

The development of reliable molecular methods has also been challenging. Both nuclear and mitochondrial gene trees so far share a weak signal along the backbone of the Octocorallia phylogeny, suggesting that octocorals radiated rapidly and long ago (Berntson et al. 2001; McFadden et al. 2006b). Commonly used nuclear markers tend to perform poorly at resolving species-level relationships, as in the case of the *18S* ribosomal RNA gene (Berntson et al. 2001; Sánchez et al. 2003a), or tend to be affected by excessively high levels of intraspecific variation, as with internal transcribed spacer sequences (*ITS*) (Aguilar and Sánchez 2007). Moreover, mitochondrial nucleotide sequences are highly conserved and evolve 10–100 times slower than nuclear genes in all anthozoan cnidarians, but the resulting lack of variation in mitochondrial markers is particularly apparent in octocorals (France and Hoover 2002; Hellberg 2006; Chen et al. 2009). For example, the use of *16S* rDNA revealed only 2.7–6.3% sequence divergence for pairwise comparisons of octocoral families, but 16.1–26.3% for families of hexacorals (France et al. 1996). This reduced rate of variation has rendered the otherwise widely used animal barcode cytochrome oxidase subunit 1 (*COI*) unable to discriminate species accurately among and within genera (Shearer et al. 2002; Huang et al. 2008; Shearer and Coffroth 2008). Additionally, virtually no intraspecific variation has been found for *COI* in octocorals (Calderón et al. 2006), while pairwise genetic distance values between species of different families are generally lower than 10% (France and Hoover 2002). A lack of mutational variation appears to be a widespread feature of the octocoral mitochondrial genome, with similarly low values reported for other mitochondrial protein coding genes, including *ND3*, *ND4L* (France and Hoover 2001), *ND2*, and *ND6* (McFadden et al. 2004).

One exception is the mitochondrial gene *mtMutS*. This gene, previously referred to as *msh1*, is an apparent homolog of the prokaryotic mismatch repair gene *mut-S* (Pont-Kingdon et al. 1995, 1998), which entered the octocoral genome through an enigmatic horizontal gene-transfer event from a non-eukaryotic origin (Bilewitch and Degnan 2011). This gene represents a unique molecular synapomorphy (a shared derived character that distinguishes one clade from another) for Octocorallia, having been found in all examined octocoral families but no other metazoans (Culligan et al. 2000). Exhibiting approximately twice the variation of most other mitochondrial protein coding regions (France and Hoover 2001; van der Ham et al. 2009; McFadden et al. 2011),

mtMutS is the most systematically informative of all mitochondrial genes so far examined in Octocorallia (McFadden et al. 2010). It has therefore been widely used in phylogenetic studies at family, genus, and species levels (McFadden et al. 2010), although resolution at the species level is low within many genera (Sánchez et al. 2003b; Cairns and Bayer 2005; Wirshing et al. 2005). Despite this, the use of *mtMutS* as a genetic barcode has been useful in the classification of new species and revisionary systematics when used in isolation (McFadden et al. 2009) or in conjunction with other sequences, both nuclear (van Ofwegen and Groenenberg 2007) and mitochondrial (Sánchez and Cairns 2004; Herrera and Sánchez 2010), and has proved to be an invaluable tool for the detection of morphologically cryptic species (McFadden et al. 2006b, 2011; McFadden and van Ofwegen 2013b).

Our understanding of genetic species boundaries in octocorals is advancing rapidly, particularly through recent research on restriction site associated DNA (RAD) sequencing (Pante et al. 2015a; Herrera and Shank 2016; Quattrini et al. 2019) and ultraconserved elements (UCEs) (Quattrini et al. 2018; Erickson et al. 2020; Untiedt et al. 2021). However, these methods are not yet universally employed. Without their use, genetic differences can often not be found between morphologically distinct specimens (e.g., van Ofwegen et al. 2007; Moore et al. 2016; Núñez-Flores et al. 2020), and the question persists: do these constitute intraspecific polymorphism or sister taxa that can simply not be distinguished on a genetic basis due to inadequate molecular information? Defining and understanding species boundaries and the relevance of intraspecific variation from both morphological and molecular perspectives is currently perhaps the most pressing issue in octocoral taxonomy (Pérez et al. 2016). It is becoming increasingly clear that an integrative approach, encompassing both morphological and molecular techniques, is imperative to overcome such obstacles, obtain accurate descriptions of species, and revise the systematics of the Octocorallia (e.g., McFadden et al. 2017; Benayahu et al. 2018).

1.3 The New Zealand octocoral fauna

Bayer (2001) noted that while "… a monograph of world Octocorallia is still an impossible dream …", it is smaller regional revisions, that may be one of the most useful ways to achieve progress. New Zealand's Exclusive Economic Zone (EEZ) harbours one of the most diverse octocoral assemblages of any country (Sánchez and Rowden 2006) and is thus an ideal candidate for such an undertaking. Octocorals were among the first cnidarians described for New Zealand from material collected by the *Astrolabe* expedition in 1827 (Quoy and Gaimard 1833). This was followed by a small set of significant early octocoral records, including those of Kölliker (1880), Wright and

Studer (1889) and Dendy (1897), culminating with Hutton's (1904) list of all known species in the *Index Faunae Novae Zelandiae*. Since then, notable additions by New Zealand taxonomists include Benham (1928) and Brewin (1945), but the vast majority of recent taxonomic progress has been achieved by visiting overseas experts (e.g., Sánchez 2005; Williams 2007; Cairns 2012b, 2016; Dueñas et al. 2014; Moore et al. 2016). So far, at least 312 species divided among 119 genera and 28 families have been inventoried for New Zealand (Mills et al. 2019). Of these, roughly 20% are endemic and 60% are still undescribed (Cairns et al. 2009; Mills et al. 2019).

Octocorals have been recorded from the intertidal to depths of around 5,000 m in the New Zealand region. Very little is known about inshore octocorals inhabiting shallow depths (< 100 m) except that, uniquely, many taxa that are normally restricted to the deep sea can occasionally be observed at diveable depths, including sea pens and primnoids (Cairns et al. 2009). Most octocorals in New Zealand are known from deep waters, where the EEZ may host the highest species richness in the world for several families (including Isididae Lamouroux, 1812; Primnoidae Milne Edwards, 1857; and Chrysogorgiidae Verrill, 1883) (Sánchez and Rowden, 2006). Notably, New Zealand waters are home to the bubblegum coral *Paragorgia arborea* Linnaeus, 1758, which can reach up to 7 m in height and may be the planet's largest benthic invertebrate. Some very rare octocorals are also present, such as *Bathyalcyon robustus* Versluys, 1906 and the family Ifalukellidae Bayer, 1955. Another peculiarity of New Zealand's octocoral fauna is the endemic *Taiaroa tauhou* Bayer and Muzik, 1976 — the only octocoral that lives as a single, solitary polyp and the only extant member of the suborder Protoalcyonaria. This species' evolutionary distinctiveness is thus comparable to that of kiwi, tuatara and other emblems of New Zealand's more familiar terrestrial biodiversity.

The characteristic diversity within New Zealand's EEZ may be attributable in part to the geological isolation of seamount clusters acting as drivers of endemism (De Forges et al. 2000). Large octocorals are ecologically significant on seamounts throughout the region (Cairns et al. 2009), of which at least 800 have been identified in New Zealand waters (Rowden et al. 2005). Consequently, further sampling and analysis is predicted to yield still higher levels of endemism among octocorals in New Zealand (Sánchez and Rowden 2006). However, evaluations of the extent of endemism, along with the characterisation of octocoral distributions (Smith et al. 2004) — at all depths — remain constrained by the inadequate state of species-level taxonomy in New Zealand (Cairns et al. 2009; Mills et al. 2019; Tracey et al. 2019). This, in turn, is the result of limited sampling and a limited skill base, with no full-time cnidarian taxonomist presently active in New Zealand. Such limitations pose a severe hindrance to assessments of vulnerability to anthropogenic disturbance among octocorals in New Zealand (Consalvey et al. 2006).

Anthropogenic pressures have the potential to negatively impact benthic communities at all depths in New Zealand. In the deep sea, climate change, pollution, dumping, mining, and oil and gas exploration and extraction are serious concerns, but deep-sea bottom-trawling has been identified as the most severe threat (Key 2002). Increasingly sophisticated technology has facilitated a shift in fishing focus from flat areas to seamounts (Anderson and Dunn 2006). Due to their prevalence on seamounts and concordant association with aggregations of commercially fished species (Clark et al. 2010), octocorals — and seamount communities generally — have been heavily impacted by destructive fishing practices in New Zealand (Clark et al. 2019a). For example, 80% of known seamounts in the EEZ have been fished (Clark and O'Driscoll 2003) and octocorals feature heavily among bycatch in several fisheries (Blom et al. 2009; Clark et al. 2019b; Bilewitch and Tracey 2020), making up as much as 24% of bycatch in orange roughy trawls on the Chatham Rise (Probert et al. 1997). Meanwhile, there have been no quantitative assessments of threats faced by shallow-living octocorals in New Zealand, but climate change, severe weather events, sedimentation, dredging, anchoring, diver damage, and collection are regarded as likely sources of mortality (Freeman et al. 2019).

Clearly, New Zealand's octocoral fauna is threatened by ongoing and future anthropogenic activities, and therefore increased knowledge is needed to contribute to improved management practices. Greater resolution of species that allows threatened cryptic species to be distinguished from their relatives has been instrumental in boosting global conservation efforts for many taxa (reviewed by Morrison et al. 2009) such as birds (Zink et al. 2000), dolphins (Banguera-Hinestroza et al. 2002) and plants (Miller and Chambers 2006), and has been identified as a research priority for New Zealand octocorals (Consalvey et al. 2006; Cairns et al. 2009). Fortunately, there is no shortage of potential targets for taxonomic research among New Zealand octocorals.

The endemic and highly variable *Alcyonium aurantiacum* Quoy and Gaimard, 1833 is among the most commonly encountered shallow-living octocorals in New Zealand, but likely represents a complex of several undescribed species (Philip Alderslade, pers. comm.). While eight genera of soft coral have been identified at depths < 50 m (*Alcyonium* Linnaeus, 1758; *Capnella* Gray, 1869; *Cladiella* Gray, 1869; *Clavularia* de Blainville, 1830; *Dendronephthya* Kükenthal, 1905; *Efflatounaria* Gohar, 1939; *Sarcophyton* Lesson, 1834; and *Telesto* Lamouroux, 1812), five of these are confined to the subtropical Kermadec region (Duffy and Ahyong 2015). Currently, *A. aurantiacum* is one of only two described soft corals inhabiting such shallow depths around the mainland of New Zealand (Cairns et al. 2009; Grange et al. 2010), the other being *Clavularia novaezealandiae* Brewin, 1945. Although they can be a common component of benthic

communities, particularly in southern New Zealand's Fiordland (Grange et al. 1981), the distribution, ecology and species-level taxonomy of New Zealand's shallow-water soft corals are very poorly understood, even when compared to other octocorals (Tracey et al. 2019).

1.4 Thesis objectives and outline

First and foremost, the objective of this thesis is to re-evaluate the taxonomic status of the common, shallow-water octocoral species *Alcyonium aurantiacum* and expand our knowledge of New Zealand's endemic marine biodiversity. This is the focus of Chapter 2, where this nominal species is reassigned to one of two new genera and ten new species are described using an integrative approach comparing morphological and molecular data. The names of some of these taxa were formulated in consultation with Ngāti Kuri, New Zealand's northernmost *iwi* (regional Māori tribe), who have provided *kōrero* (cultural narratives) for inclusion in their etymology sections. The phylogenetic position of these new taxa and implications for the global systematics of problematic *Alcyonium*-associated octocorals are also discussed.

Virtually nothing is known regarding any aspect of these new taxa's ecology, life history or conservation management requirements. While a revised species-level taxonomy offers a crucial foundation for such research in the future, it quickly became apparent that several species are superficially very similar, overlapping in colony morphology, depth range and regional distribution, and that identification would require microscopic examination of sclerite characteristics. Therefore, to enable identification and facilitate research on these species for non-taxonomists, alternative identification methods were explored. In Chapter 3, statistical methods are described that differentiate between the two most common and most similar species with a high degree of accuracy based only on colony-scale morphological measurements.

While molecular data informed taxonomic decisions at the genus-level in Chapter 2, genetic resolution was insufficient to corroborate morphospecies in most cases, where species delimitation instead relied on morphological differences, which were explored further in Chapter 3. Evidently, although integrative taxonomy is often cited as the best way to produce robust species hypotheses and achieve progress in octocoral taxonomy, it is not so easily implemented. This realisation sparked an interest in the usage of this approach in octocoral taxonomy and led to the literature survey presented in Chapter 4, which aims to provide a comparative baseline for the evaluation of future progress in octocoral taxonomy.

Finally, Chapter 5 discusses the implications of this research for octocoral taxonomy in both New Zealand and global contexts. For New Zealand, the large scope for future research is emphasised, along with the importance of improved conservation measures and Māori inclusion in the taxonomic process. The value of the integrative approach, particularly morpho-molecular comparisons, for octocoral taxonomy and systematics is then discussed with commentary on the state of the discipline and possible future directions. It is hoped that this thesis can contribute to global taxonomic progress in the Octocorallia and significantly enhance our ability to protect shallow-water soft corals in New Zealand by elucidating their diversity and variability for the first time.

Chapter 2.
Taxonomic re-evaluation of *Alcyonium aurantiacum* Quoy & Gaimard, 1833 reveals two new genera and ten new species of New Zealand octocorals

2.1 Abstract

New Zealand's octocoral assemblage is diverse and characterised by high levels of endemism, yet over half of the species known from its oceanic region remain undescribed. While taxonomic progress is being made, this has been focused almost exclusively on protected deep-sea gorgonians, neglecting unprotected coastal soft corals. *Alcyonium aurantiacum* is an endemic and commonly encountered octocoral in New Zealand, but multiple morphologically diverse forms have been ascribed to this name. To review the taxonomic status of *A. aurantiacum* using an integrative approach, the morphology of 96 specimens was examined and 49 of these were included in phylogenetic analyses based on nuclear *28S* and mitochondrial *MutS* DNA sequence variation, together with DNA sequences from associated taxa for comparison. The New Zealand taxa were resolved as being more closely related to *Anthothela* and nominal *Alcyonium* from South America than to *A. digitatum*, the type species of *Alcyonium*. Here, they are ascribed to two new genera in the family Alcyoniidae based on comparisons of morphological and molecular data. Due to a lack of genetic variation at the *28S* and *mtMutS* regions, species delimitation relied predominantly on identifying consistent differences in sclerite morphology and colony growth form. The former *A. aurantiacum* is reassigned to *Kotatea* gen. n. as *K. aurantiaca* comb. n. and seven additional new species are described in this genus. Three new species in *Ushanaia* gen. n. are also described. A morphological key to the species of both genera is provided. The description of these taxa, all of which are endemic to New Zealand, increases our understanding of this region's octocoral diversity and will hopefully contribute to ongoing systematic revisions among this problematic group of *Alcyonium*-associated taxa.

2.2 Introduction

New Zealand's marine region harbours a diverse and distinctive octocoral assemblage characterised by high levels of endemism (Sánchez and Rowden 2006). At least 312 species have been inventoried, spanning 119 genera and 28 families, of which 58 species (roughly one fifth) are endemic (Mills et al. 2019). Another characteristic of New Zealand's octocoral fauna, however, is the poor state of its species-level taxonomy. Of the known species, 185 (~60%) remain undescribed, and it is estimated that around 75 more are yet to be sampled (Cairns et al. 2009; Mills et al. 2019), making octocorals some of New Zealand's least known seafloor macroinvertebrates. Although not necessarily the target of collecting expeditions, taxonomic progress has focused primarily on protected deep-sea (> 200 m) calcaxonian and scleraxonian corals associated with vulnerable marine ecosystems (e.g., Isididae, Dueñas et al. 2014; Paragorgiidae, Sánchez 2005; Primnoidae, Cairns 2012b, 2016), leaving the state of species-level taxonomy among coastal soft corals, which are not protected, particularly poor (Tracey et al. 2019). As one of only two described species of soft corals inhabiting depths less than 50 m around New Zealand's mainland, *Alcyonium aurantiacum* Quoy and Gaimard, 1833 is a name commonly applied to frequently observed soft corals of various growth forms and shades of orange, as is the common name "dead man's fingers", a moniker first applied to *A. digitatum* Linnaeus, 1758 from the North Atlantic. However, Philip Alderslade (pers. comm.) discovered that what was thought to be one commonly encountered species, based on sclerite differences, likely represents a complex of endemic species and genera (of which several have a very similar appearance) requiring a taxonomic review.

Alcyonium aurantiacum was among the first corals scientifically described from New Zealand during the *Astrolabe* expeditions of 1826–1829. Typically for the time, Quoy and Gaimard's original description is vague and based largely on characters that have little diagnostic value by modern standards. The only other taxonomic treatment of *A. aurantiacum* is Benham's (1928) description, which unfortunately further obscured the diversity among New Zealand's coastal soft corals by ascribing both lobate and encrusting specimens to this species. Consequently, several morphologically disparate forms have been identified as possibly belonging to *A. aurantiacum* ever since, despite being highly variable in terms of colour, colony growth form and sclerite morphology (e.g., Morton and Miller 1973; Westerskov and Probert 1981; Grange et al. 1981, 2010; Goldberg et al. 1990; Morton 2004).

Doubt has also surrounded the species' generic placement, with *A. aurantiacum* conforming poorly to the characters of *Alcyonium sensu stricto* as exhibited by the genus' type species, *A. digitatum*

(see Verseveldt 1973). Additionally, a DNA sequence (mitochondrial *ND2+MutS*) attributed to *A. aurantiacum* belonged to a clade separated from *A. digitatum* in a phylogeny by McFadden et al. (2006b). This is not surprising, since the taxonomy of species within *Alcyonium* is notoriously problematic, with this genus having long been treated as a repository for species that lack the characters indicative of more-narrowly defined alcyoniid genera (Daly et al. 2007; McFadden and van Ofwegen 2013a). As a result, *Alcyonium* has historically included virtually all possible growth forms observed in Alcyoniidae Lamouroux, 1812, from encrusting to lobate and digitate forms, as well as a plethora of sclerite shapes and arrangements (Williams 1988; Alderslade 2000). As currently defined, the genus distribution is circum-global and its reproductive strategies are incredibly diverse, including gonochorism, hermaphroditism and parthenogenesis, as well as either broadcast spawning or internally and externally brooded larvae (McFadden et al. 2001). Expectedly, the genus has been resolved as highly paraphyletic, with incongruence between morphological and molecular data (McFadden and van Ofwegen 2013a). Indeed, several new genera have been erected specifically to accommodate former members of *Alcyonium* (e.g., *Klyxum* and *Rhytisma*, Alderslade 2000; *Lampophyton*, Williams 2000; *Discophyton*, McFadden and Hochberg 2003; *Lateothela*, Moore et al. 2017).

Clearly, the taxonomic status of *A. aurantiacum* was in need of revision. Here, the aim was to achieve this through an integrative approach, utilising comparative assessments of morphological and molecular differences as congruent lines of evidence in order to produce more robust species hypotheses.

2.2.1 Iwi engagement in naming

The names of four of the new species described herein were formulated in consultation with Ngāti Kuri, New Zealand's northernmost *iwi* (regional Māori tribe). These species were initially thought to be unique to the *rohe* (territory) of Ngāti Kuri, although a specimen was also identified from a location further south for one of them late in the preparation of this manuscript. Specimens of these four species were collected predominantly from Manawatāwhi/Three Kings Islands and Piwhane/Spirits Bay, locations of deep spiritual and customary significance (Ngāti Kuri Trust Board 2013). As *kaitiaki* (guardians/stewards), Ngāti Kuri seek to understand and protect the unique, nationally and internationally significant biodiversity of these sites, and to document the species inhabiting their *rohe*. Ngāti Kuri contributed to the scientific naming of these four species through *mātauranga Māori* (Māori knowledge) and by crafting Māori names that bestow each with respect, history and spirituality. Ngāti Kuri also composed a *kōrero* (narrative) for each of these

species, which forms part of their etymology sections and explains the cultural significance and metaphorical meanings of their names. This partnership mirrors previous collaborations between Ngāti Kuri and taxonomists on the naming of seaweeds (Nelson et al. 2019; D'Archino et al. 2020) and fulfils recommendations outlined in the Waitangi tribunal report Wai 262 (2011), the UN Declaration on the Rights of Indigenous Peoples (UNGA 2007b) and by Veale et al. (2019). Reciprocity and exchanges of knowledge between *iwi* and taxonomists are mutually beneficial. Not only does this help to articulate *iwi* autonomy within their *rohe* (Nelson et al. 2019), it also allows for the co-production of new knowledge and realises the shared goal of increasing our understanding of *Aotearoa*'s (New Zealand's) natural *taonga* (treasures).

2.3 Materials and methods

2.3.1 Specimens

Ninety-six relevant specimens collected from New Zealand were examined. Six specimens were loaned from the Auckland War Memorial Museum (MA) in New Zealand and 29 from the Museum and Art Gallery of the Northern Territory (MAGNT), Darwin, Australia. The remaining 61 specimens are housed at New Zealand's National Institute of Water and Atmospheric Research (NIWA), Wellington, New Zealand, which includes the NIWA Invertebrate Collection and the Marine Invasive Taxonomic Service (MITS) collection. Regrettably, it was not possible to obtain or view in person the type material for *A. aurantiacum* held at the Muséum National d'Histoire Naturelle, Paris (MNHN), France, although photographs were provided (M. Castelin pers. comm.). Specimens in the "Material examined" sections are ordered by latitude.

2.3.2 Morphological analysis

The morphological characteristics of colonies were recorded following established procedures described by Fabricius and Alderslade (2001). Briefly, sclerites were obtained by dissolving polyps and small tissue fragments from the interior and exterior regions of colonies in 10% sodium hypochlorite. Sclerites were then observed and measured under various magnifications using a compound microscope. For selected specimens, sclerites were rinsed with ethanol followed by deionized water and pipetted onto Scanning Electron Microscopy (SEM) stubs, while polyps were carefully removed and also placed on stubs. Both were then allowed to dry for imaging using a benchtop SEM operated at 15 kV. *In situ* images of polyps were also obtained using an eyepiece

camera mounted to a stereo microscope. Montages of focus-stacked images were then generated using CombineZP. All images were edited and assembled using GIMP 2.8.22.

2.3.3 Molecular phylogenetic analysis

Total genomic DNA was extracted using either a modified Qiagen DNeasy Blood and Tissue Kit protocol or (for older, problematic specimens) a salting-out protocol modified from Jenkins et al. (2019) and Li et al. (2011) (Appendix 1). Fragments of mitochondrial *mtMutS* (formerly known as *msh1*) and the nuclear ribosomal *28S* gene were selected as loci for genetic analysis and were amplified using a combination of existing and novel primers (Table 1). The 5' end of *mtMutS* was amplified using either of the forward primers ND42599F (France and Hoover 2002) or mtMutS93F (Bilewitch and Degnan 2011) in combination with the reverse primer Mut-3458R (Sánchez et al. 2003b) with PCR protocols following Bilewitch and Degnan (2011). *28S* was amplified using 28S-Far and 28S-Rab (McFadden and van Ofwegen 2013b) with a PCR protocol following Halász et al. (2014). PCR reactions of 25 µl contained 1 µl of each primer (10 µM), 12.5 µl of MyTaq Red Mix (Bioline), 8.5 µl of deionized water and 2 µl of DNA template. Additionally, internal primers for both *mtMutS* (mtMutS-GKint-F/R) and *28S* (28S-GK-F/R) were designed for problematic specimens from which DNA sequences did not amplify successfully under the above protocols (Table 1), yielding smaller fragments of ~275 bp and ~410 bp for *mtMutS* and *28S*, respectively. For these primers, 25 µl PCR reactions were modified to contain a final $MgCl_2$ concentration of 4.5 mM, 9 µl of DNA template, and no water. Amplification products were sent to Sangon Biotech, Shanghai, China for sequencing.

Table 1. Primers and PCR protocols used in this study. PCR protocols are shown underneath their corresponding primer set.

Gene	Primer Name	Primer Sequence 5' → 3'	Reference
mtMutS	ND42599F	GCCATTATGGTTAACTATTAC	France and Hoover (2002)
	mtMutS93F	AGTTCTATGAACTTTGGCATGAG	Bilewitch and Degnan (2011)
	Mut-3458R	TSGAGCAAAAGCCACTCC	Sánchez et al. (2003b)
	94˚C/2mins, (94˚C/60secs, 58˚C/60secs, 72˚C/60secs) x35, 72˚C/5mins		
	mtMutS-GK-F	TAGAGGACTGTTCGGAGTTATC	This study
	mtMutS-GK-R	AATTTTAGCATTGGGTTCAGAYG	
	94˚C/2mins, (94˚C/60secs, 62˚C/60secs, 72˚C/60secs) x35, 72˚C/5mins		
28S	28S-Far	CACGAGACCGATAGCGAACAAGTA	McFadden and van Ofwegen (2013b)
	28S-Rab	TCGCTACGAGCTTCCACC AGTGTTT	
	94˚C/3mins, (94˚C/30secs, 50˚C/30secs, 72˚C/60secs) x35, 72˚C/3mins		
	28S-GK-F	GAAGCGAATGGAGTTAGCAATT	This study
	28S-GK-R	GCACATGTTAGACTCCTTGGT	
	94˚C/3mins, (94˚C/30secs, 47˚C/30secs, 72˚C/60secs) x35, 72˚C/3mins		

After BLASTn searching in GenBank to confirm their validity, *mtMutS* and *28S* sequences were assembled, edited, and aligned with additional sequences from closely related species and outgroup taxa in Geneious Prime 2020.1.1 using the MAFFT v7.450 plugin (Katoh et al. 2002; Katoh and Standley 2013). Closely related and outgroup sequences were sourced from GenBank and selected based on previously published phylogenies that included sequences identified as *A. aurantiacum* or from other nominal *Alcyonium* species and associated taxa (McFadden et al. 2006b, 2004; McFadden and van Ofwegen 2013a, 2017; Moore et al. 2017) (Appendix 2). For both loci, all missing data were replaced with 'N's (any nucleotide). Including missing data in such a way has been shown to have no significant effects on accuracy (Wiens and Morrill 2011), and preliminary tests on the sequences discussed herein consistently resulted in similar topologies across a wide range of phylogenetic analyses regardless of whether missing data were included as 'N's or not. The concatenated alignment included 70 sequences (49 generated here and 21 sourced from GenBank) and was 1,392 bp in length (*mtMutS* = 734 bp; *28S* = 658 bp).

Phylogenetic analyses were conducted using maximum likelihood (ML) and Bayesian inference (BI) on each locus individually and as a concatenated alignment. Models of evolution were selected based on Bayesian Information Criterion scores obtained in jModelTest2 (Darriba et al. 2012), yielding K2+G+I for 28S and GTR+G for *mtMutS*. ML analyses were run using GARLI 2.0 (Zwickl 2006), with 1,000 replicates to generate bootstrap support values. BI analyses were run using MrBayes 3.2.6 (Huelsenbeck and Ronquist 2001) for 5 million generations, with 4 heated chains and a burn-in of 25%. In both cases, analyses of the concatenated alignment were partitioned into two data subsets to incorporate the corresponding model for each gene. The phylogeny was rooted using the outgroup, *Azoriella bayeri* López-González and Gili, 2001, which was selected based on its placement relative to some of the included taxa in a phylogeny by Moore et al. (2017). Intergeneric, intrageneric, interspecific and intraspecific uncorrected p-distances were obtained using MEGA 7.0.26 (Kumar et al. 2016) to support taxonomic decisions based on phylogenetic and morphological data.

2.4 Results

2.4.1 Summary of taxonomic decisions

Genetic variation was insufficient to corroborate morphospecies in most cases. However, the distinct characteristics of sclerite morphology and colony growth form described in the taxonomic account below were so consistently different between morphospecies and showed so little variation

within them that all of the > 200 individual colonies comprising the available specimens could be assigned to one of eleven groups unambiguously. Morphology was therefore deemed sufficient for the delineation of new species. Although several of the species are similar in many regards, all are distinguishable from their most similar congeners by several identifying characters, which hold true across all the examined specimens. Identifying characters primarily include categorical differences in sclerite morphology and colony growth form, as well as distinctive colourations and the relative sizes of polyps and sclerites. Note that while only the sclerites of the holotypes are pictured, these holotypes were selected, illustrated and described (especially in terms of sclerite forms and size ranges) to reflect the relatively low degree of variation observed across all the examined specimens within the same species.

At the generic level, molecular phylogenetic placements were congruent with overall sclerite and colony growth form differences, dividing these New Zealand alcyoniid soft corals into a clade of erect forms and one of encrusting forms. These are described as two new genera in the family Alcyoniidae: *Kotatea* gen. n., with seven new species; and *Ushanaia* gen. n., with three new species. *Alcyonium aurantiacum* is reassigned to *Kotatea* as *K. aurantiaca* gen. n., comb. n.

2.4.2 Sequencing success

Of the 96 specimens examined, 48 were sequenced successfully for *mtMutS* (eight by using the internal primers), and 49 for *28S* (five by using the internal primers). Note that for one specimen (MAGNT C015221), the *mtMutS* sequence was thus entirely replaced with 'N's for the concatenated alignment. Most of the specimens for which target genes could not be amplified were known or suspected to have experienced historic exposure to formalin. The oldest specimen successfully sequenced was collected in 1976.

2.4.3 Phylogenetic relationships

ML and BI phylogenies generated by separate *mtMutS* and *28S* alignments were all largely congruent with one another and with concatenated ML and BI phylogenies in their placements of *Kotatea* and *Ushanaia* specimens. The only topological difference observed among these phylogenies were the placement of *Kotatea* and *Ushanaia* as sister clades rather than as a polytomy with the *A. haddoni* Wright and Studer, 1889 + *Anthothela* Verrill, 1879 clade in the *mtMutS* BI phylogeny, as well as some minor differences between the relative placements of taxa in the *Eleutherobia* Pütter, 1900 + *Lateothela* Moore, Alderslade and Miller, 2017 + *Alcyonium* spp.

polytomy (*Eleutherobia* was placed as sister to these other taxa in the *28S* BI phylogeny while *A. dolium* McFadden and van Ofwegen, 2017 + *A. variabile* Thomson, 1921 took this position in the *MutS* BI phylogeny). Both concatenated phylogenies, however, shared an identical topography and had much higher support values than single-gene phylogenies, and for these reasons only the concatenated, partitioned phylogenies are presented and discussed (Fig. 1).

Alcyonium was resolved as polyphyletic. *Alcyonium digitatum* (the type species of *Alcyonium*) from the northeastern Atlantic and *A. siderium* Verrill, 1922 from the northwestern Atlantic are here sister to the genus *Gersemia* von Marenzeller, 1878, which together form a strongly supported sister clade to all other included taxa. These other taxa are divided into two sister clades. One of these is a mixed clade composed of South African, Mediterranean, and other Atlantic species of *Alcyonium*, as well as representatives from the genera *Eleutherobia* and *Lateothela*. The other is a well-supported polytomy of three clades: a clade featuring the southern South American species *A. haddoni* and *A. varum* McFadden and van Ofwegen, 2013(a), plus representatives of *Anthothela*; a well-supported clade of *Kotatea* n. gen. spp.; and a strongly supported clade of *Ushanaia* n. gen. spp. Within *Kotatea*, *K. kurakootingotingo* sp. n. and *K. niwa* sp. n. also form monophyletic clades in a strongly supported sister clade to the rest of the genus. *Kotatea teorowai* sp. n. and *K. kapotaiora* sp. n. may also be more closely related to one another than they are to the remaining four species in *Kotatea*, which form an unresolved polytomy. *Ushanaia* consists of a single polytomy of three species. In both genera, genetic variation was insufficient to resolve species relationships any further.

2.4.4 Genetic distances

Genetic distances were low overall, as within both genera, several identical or near-identical haplotypes were shared between species as well as between specimens of the same species. The intergeneric mean p-distance between *Kotatea* and *Ushanaia* was 0.029 for the concatenated alignment, 0.037 for *mtMutS* and 0.024 for *28S*. For *Kotatea*, intrageneric mean p-distances were low at 0.007 for the concatenated alignment, 0.006 for *mtMutS* and 0.008 for *28S*, while p-distances were even lower for *Ushanaia* at 0.001 for the concatenated alignment, 0.002 for *mtMutS* and 0.001 for *28S*.

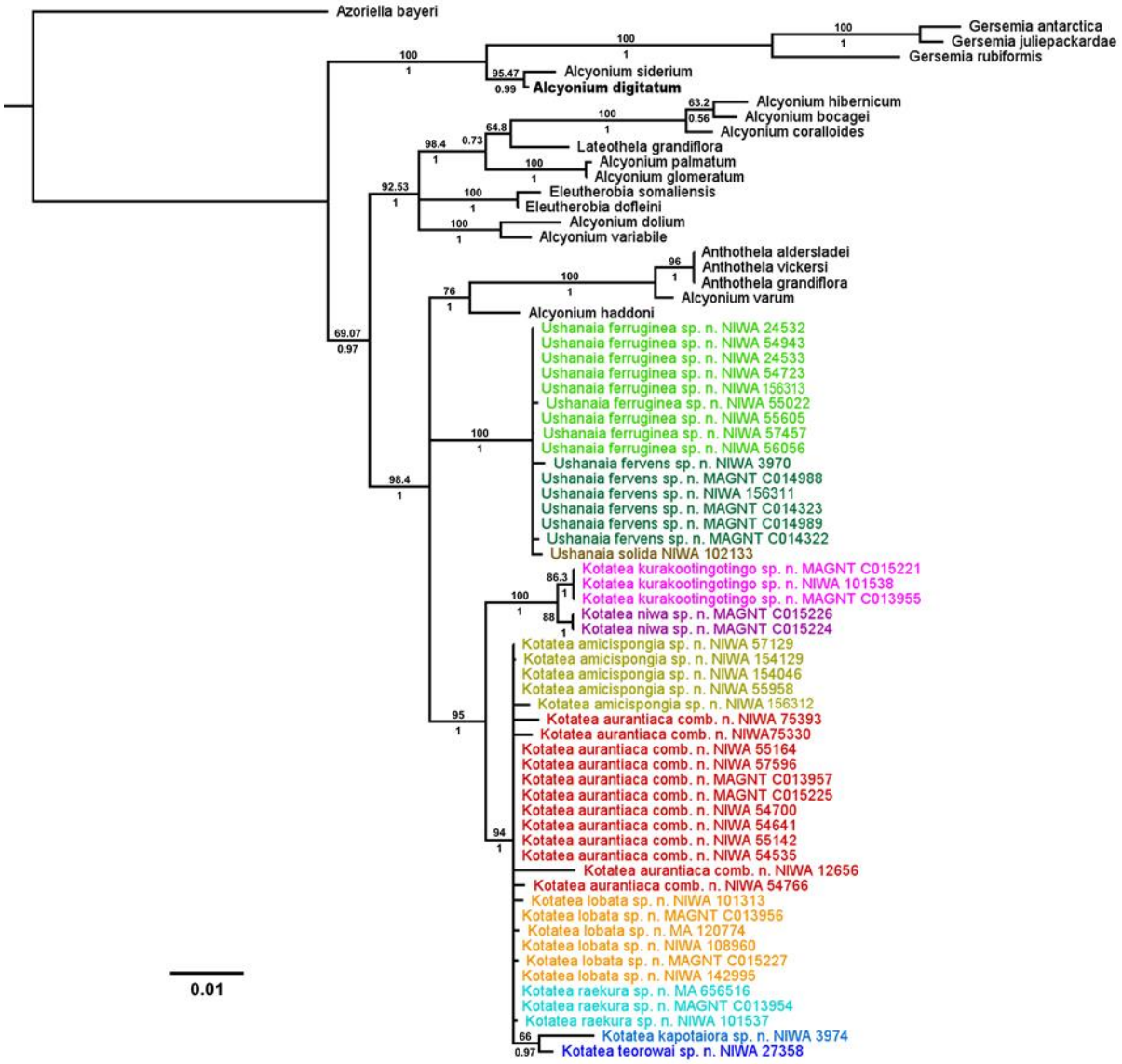

Figure 1. Maximum likelihood phylogeny (identical in topology to Bayesian inference phylogeny) of *Kotatea* gen. n., *Ushanaia* gen. n., and associated taxa based on combined, partitioned analysis of *mtMutS* and *28S*. New species are identified by individual colours. The type species for *Alcyonium*– *A. digitatum* appears in bold. ML bootstrap support values are given above each branch and BI posterior probabilities below.

Based on thresholds for accurate species discrimination identified for *Alcyonium* species by McFadden et al. (2014a) (i.e., 0.5% for *mtMutS* and 0.7% for *28S*) pairwise interspecific mean p-distances showed mixed results. In general, *mtMutS* p-distances were more informative, as there were no cases in which *28S* thresholds were met without those of *mtMutS* being met as well and *mtMutS* showed more significant thresholds overall. While a possible species-level difference was indicated by mean distances between *K. kapotaiora* and *K. teorowai* for *mtMutS*, this was not the case between *K. kurakootingotingo* and *K. niwa*, and there was little or no evidence to suggest separate species identities between *K. amicispongia* sp. n., *K. aurantiaca*, *K. lobata* sp. n. and *K.*

raekura sp. n. (Table 2). In general, intraspecific variation did not exceed interspecific variation, with intraspecific mean distances falling below 0.002 in almost all instances.

Table 2. Mean interspecific genetic distances for *Kotatea* and *Ushanaia* species. The mean uncorrected p-distance for each pairwise comparison is given for concatenated (*mtMutS+28S*) (top), *mtMutS* (middle) and *28S* (bottom) sequences. For comparison, mean p-distances appear in bold if they match or exceed the threshold for accurate discrimination of species in *Alcyonium* identified by McFadden et al. (2014a): 0.005 for *mtMutS*; 0.007 for *28S*. Note that the same comparison cannot be made for concatenated sequences, since those of McFadden et al. (2014a) also included *Igr1* and *COI*.

	K. aurantiaca	*K. kapotaiora*	*K. kurakootingotingo*	*K. lobata*	*K. niwa*	*K. raekura*	*K. teorowai*	*U. ferruginea*	*U. fervens*	*U. solida*
K. amicispongia	0.002 0.004 0.001	0.007 **0.018** 0.001	0.019 **0.008** **0.024**	0.002 0.003 0.001	0.017 **0.007** **0.026**	0.001 0.001 0.001	0.005 **0.013** 0.001	0.027 **0.037** **0.020**	0.029 **0.037** **0.023**	0.029 **0.041** **0.020**
K. aurantiaca		0.008 **0.020** 0.001	0.019 **0.009** **0.025**	0.002 **0.005** 0.001	0.017 **0.007** **0.027**	0.001 0.003 0.001	0.007 **0.017** 0.001	0.028 **0.036** **0.020**	0.029 **0.037** **0.023**	0.030 **0.041** **0.020**
K. kapotaiora			0.032 **0.026** **0.034**	0.008 **0.017** 0.001	0.031 **0.026** **0.035**	0.006 **0.016** 0.001	0.004 **0.011** 0.001	0.039 **0.056** **0.028**	0.038 **0.053** **0.027**	0.038 **0.056** **0.027**
K. kurakootingotingo				0.020 **0.008** **0.025**	0.005 0.002 0.006	0.021 **0.007** **0.027**	0.031 **0.022** **0.035**	0.030 **0.027** **0.031**	0.034 **0.028** **0.038**	0.031 **0.031** **0.031**
K. lobata					0.018 **0.007** **0.026**	0.001 0.002 0.001	0.006 **0.012** 0.001	0.027 **0.036** **0.020**	0.029 **0.036** **0.023**	0.029 **0.041** **0.020**
K. niwa						0.018 **0.006** **0.028**	0.030 **0.022** **0.035**	0.030 **0.029** **0.031**	0.033 **0.029** **0.037**	0.033 **0.036** **0.031**
K. raekura							0.005 **0.012** 0.001	0.028 **0.035** **0.022**	0.029 **0.035** **0.024**	0.030 **0.040** **0.022**
K. teorowai								0.036 **0.048** **0.028**	0.035 **0.046** **0.028**	0.035 **0.048** **0.027**
U. ferruginea									0.001 0.001 0.001	0.003 **0.006** 0.001
U. fervens										0.002 0.004 0.001

2.5 Taxonomic account

Order Alcyonacea Lamouroux, 1812

Family Alcyoniidae Lamouroux, 1812

***Kotatea* gen. n.**

Type species: *Alcyonium aurantiacum* Quoy and Gaimard, 1833, here designated, = *Kotatea aurantiaca* (Quoy and Gaimard, 1833) new combination

Diagnosis: Azooxanthellate soft corals with an erect, lobate growth form. Colonies with finger-like lobes commonly display secondary and occasionally tertiary branching. Polyps monomorphic and fully retractile. True calyces are absent, although retracted polyps may form low, rounded, mound-like protuberances of varying prominence depending on the colony's state of inflation and the level of polyp expansion. Anthocodial sclerites are arranged as a collaret and points. Both the collaret and points are composed of slender, warty spindles, and the distal part of the points also contains thorny clubs. The tentacles contain irregular, warty, scale-like forms. The polyp neck contains mostly warty rod- and spindle-like forms. The polyp mounds also contain rod- and spindle-like forms but tend to have mostly clubs. Surface samples also contain a mix of sclerite forms, including rod-like forms and clubs, but radiates tend to predominate. The latter are mainly eight-radiate capstans and derivatives of this form. Sclerites of the colony interior differ from those of the surface in being generally larger, as well as in displaying more complex branching processes. Interior sclerites can also be comprised of a mixture of forms, including radiates, rod- and spindle-like sclerites, spheroids and clubs. Sclerites can be pale to dark orange or colourless.

Etymology: *Kotatea* is the Māori word for red soft corals and is given as the genus name to acknowledge their original *te reo* (Māori language) names. *Ko* refers to a distant point in time, while *tatea* translates to offspring or progeny. Ngāti Kuri advised on the appropriateness of this name and provided the following ***kōrero* (narrative):** "*Kotatea* is all about *whānau* (family) and *whakapapa* (genealogy) and their physical, emotional and spiritual domains. *Whānau* means to give birth. *Whānau* first embraces the individual, *ahau*, then *whānau*, then *hapū* and *iwi* (tribes). They are all connected and interdependent through *whakapapa* and a common *tūpuna* (ancestor). *Whānau* can also mean to give birth to new realities, for example to new ideas (*ka whānau he whakaaro hou*). *Kotatea* embraces the many challenges of the undersea world to sustain its *whānau*."

Comparisons: Although *Alcyonium sensu stricto* has been defined as limited to species possessing polyp sclerites in the collaret and points arrangement (McFadden and van Ofwegen

2013a, 2017), species in this genus, and in particular *A. digitatum*, tend to contain few polyp sclerites and approach this arrangement only loosely when compared to *Kotatea*, where the collaret and points is substantial and comprised of many sclerites (see Hickson 1895; Verseveldt 1973; Stokvis and van Ofwegen 2006). Only the Chilean nominal *Alcyonium* species appear to have collaret and points arrangements approximating the level of development observed in *Kotatea*, but unlike *Kotatea* some of these taxa are said to possess calyces (see Verseveldt and van Ofwegen 1992; Casas et al. 1997; van Ofwegen et al. 2007). *Kotatea* also has a much greater variety of surface sclerites, including clubs and well-developed modifications of the eight-radiates than all other nominal *Alcyonium* species.

Unlike *Ushanaia*, *Kotatea* does not form encrusting colonies. Additionally, clubs constitute a predominant feature of polyp mounds, and surface and interior sclerites differ markedly in form, neither of which is the case for *Ushanaia*. Collaret spindles also tend to be smaller in *Kotatea* than in *Ushanaia*.

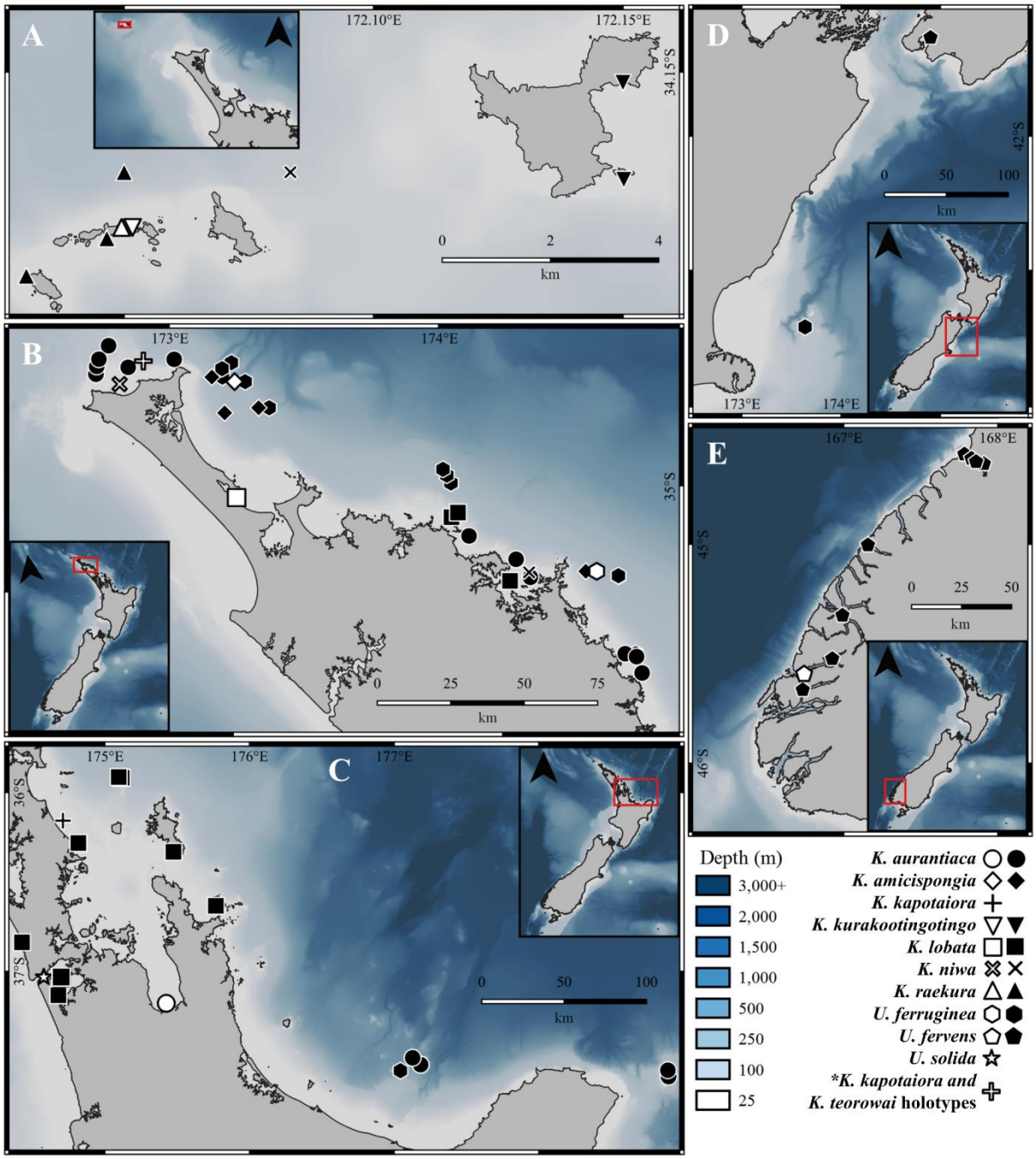

Figure 2. Collection sites of *Kotatea* gen. n. and *Ushanaia* gen. n. specimens. Holotype collection sites are indicated by white symbols, paratypes and other material by black symbols. In the case of *K. aurantiaca* gen. n., comb. n., the type collection site refers to that described by Quoy and Gaimard (1833). Collection sites at: **A.** Manawatāwhi/Three Kings Islands; **B.** Far northern NZ, from Piwhane/Spirits Bay to the Poor Knights Islands; **C.** Northern NZ, from the Mokohinau Islands to East Cape; **D.** Central NZ, Cook Strait to Banks Peninsula; **E.** South-East NZ, Fiordland. Note that the holotypes for *K. kapotaiora* gen. n., sp. n. and *K. teorowai* gen. n., sp. n. share the same collection site.

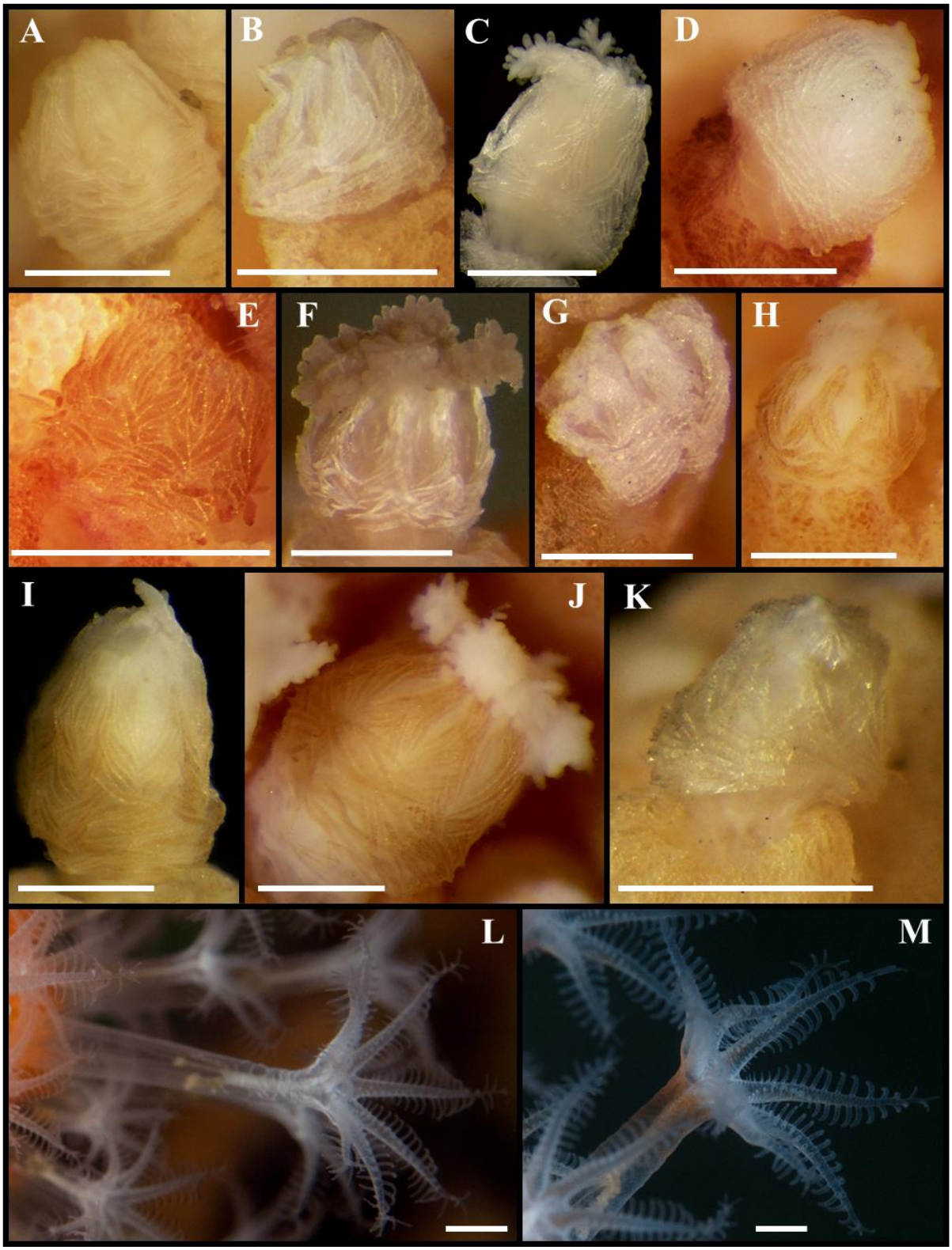

Figure 3. Polyps of: **A.** *Kotatea amicispongia* gen. n., sp. n. holotype (NIWA 156312); **B.** *K. aurantiaca* gen. n., comb. n. (NIWA 75330); **C.** *K. kapotaiora* gen. n., sp. n. holotype (NIWA 3974); **D.** *K. kurakootingotingo* gen. n., sp. n. holotype (NIWA 101538); **E.** *K. kurakootingotingo* gen. n., sp. n. paratype, small polyp with coloured collaret and points (MAGNT C015221); **F.** *K. lobata* gen. n., sp. n. holotype (NIWA 101313); **G.** *K. niwa* gen. n., sp. n. holotype (MAGNT C015226); **H.** *K. raekura* gen. n., sp. n. holotype (NIWA 101537); **I.** *Ushanaia ferruginea* gen. n., sp. n. holotype (NIWA 156313); **J.** *U. fervens* gen. n., sp. n. holotype (NIWA 156311); **K.** *U. solida* gen. n., sp. n. holotype (NIWA 102133); **[caption continues overleaf]**

[Figure 3. caption continued] L. *K. aurantiaca* gen. n., comb. n., *in situ* (uncollected specimen), Poor Knights Islands, photo by Ian Skipworth (ianskipworth.com); **M.** *U. fervens* gen. n., sp. n., *in situ* (uncollected specimen), Fiordland, photo by Vincent Zintzen. Scale bar = ~1 mm.

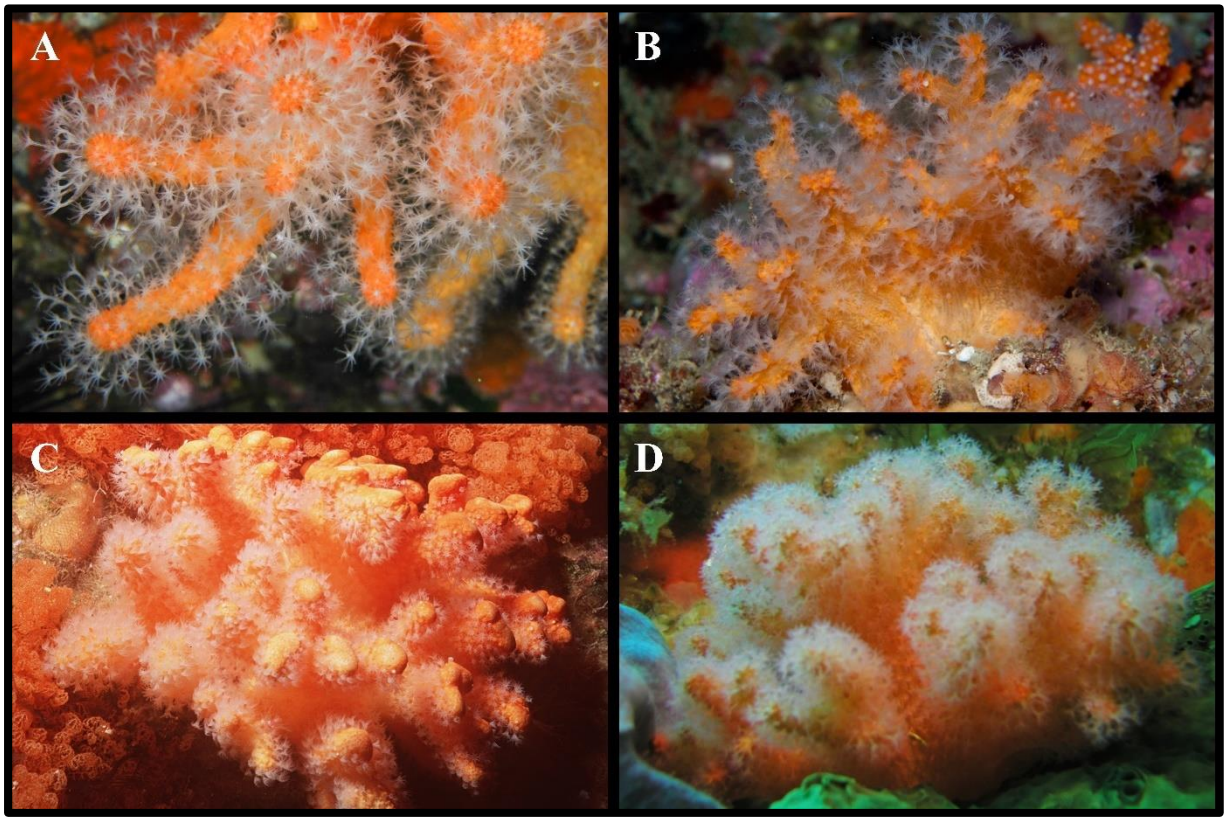

Figure 4. *In situ* photographs of *Kotatea* gen. n. species usually possessing finger-like lobes: **A–B.** *K. aurantiaca* gen. n., comb. n. (uncollected specimen), expanded colonies with a contracted colony in upper right background of **B**, Poor Knights Islands, photos by Ian Skipworth (ianskipworth.com); **C.** *K. aurantiaca* gen. n., comb. n. (MAGNT C013957/NIWA 101181), large colony, Bay of Plenty, photo by Coral Reef Research Foundation; **D.** *K. raekura* gen. n., sp. n. holotype (NIWA 101537), Manawatāwhi/Three Kings Islands, photo by NIWA.

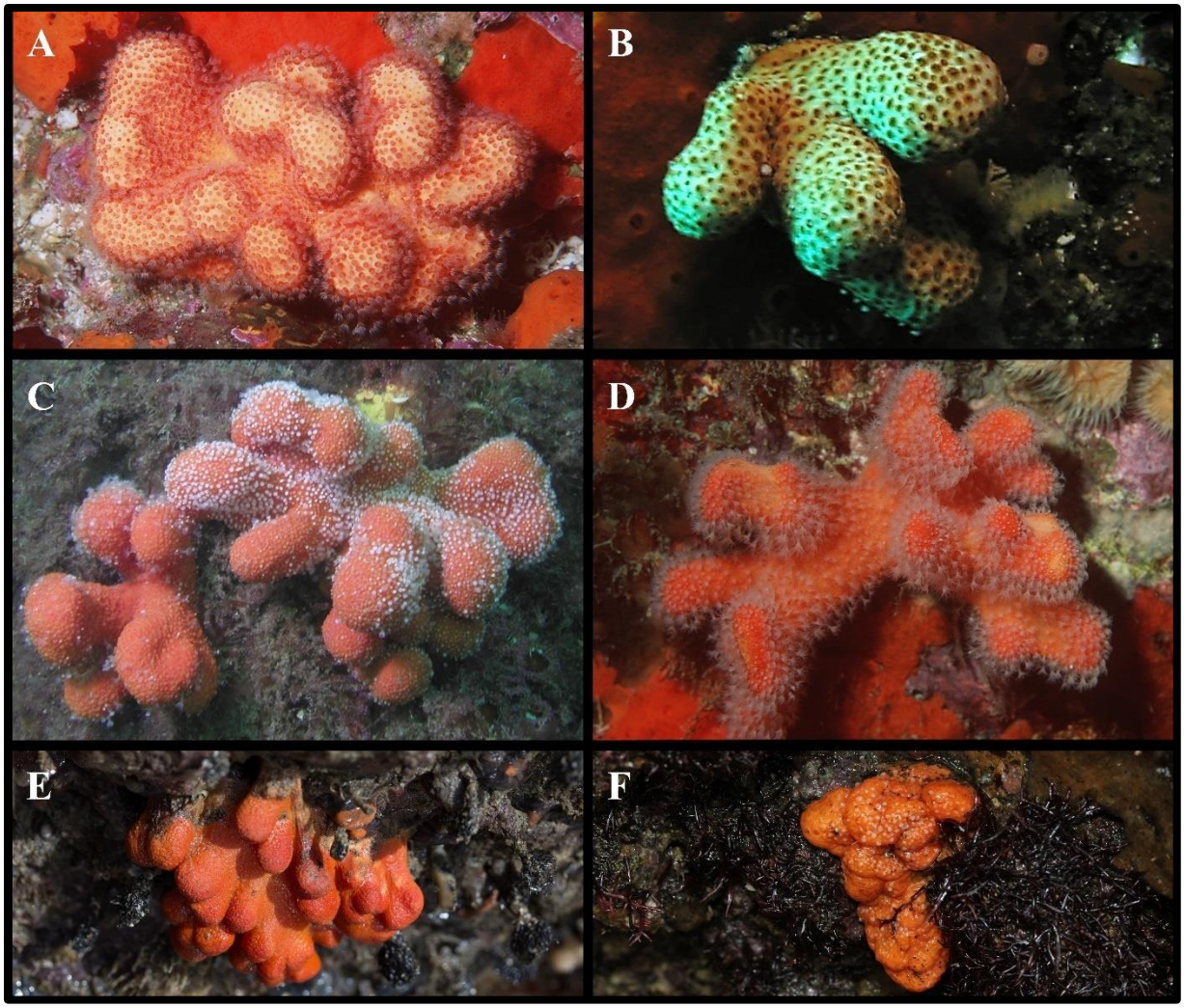

Figure 5. *In situ* photographs of *Kotatea* gen. n. species usually possessing robust lobes: **A.** *K. kurakootingotingo* gen. n., sp. n. paratype (MAGNT C013955), Manawatāwhi/Three Kings Islands, photo by Coral Reef Research Foundation; **B.** *K. kurakootingotingo* gen. n., sp. n. holotype (NIWA 101538) with polyps retracted, Manawatāwhi/Three Kings Islands, photo by NIWA; **C.** *K. lobata* gen. n., sp. n. holotype (NIWA 101313), Houhora Harbour, photo by NIWA; **D.** *K. lobata* gen. n., sp. n. (paratype NIWA 101268 / MAGNT C013956), Mokohinau Islands, photo by Coral Reef Research Foundation; **E–F.** *K. lobata* gen. n., sp. n. exposed at low tide underneath rock overhangs, large colony (paratype, MA 120774) at Muriwai Beach (**E**) and small colony (uncollected specimen) at Whatipu Beach (**F**), photos by Wilma Blom, Auckland War Memorial Museum.

***Kotatea amicispongia* gen. n., sp. n.**

Figs. 2B; 3A; 6; 7; 8A

Material examined.

Holotype: NIWA 156312, stn. TAN0906/134, Great Exhibition Bay, Northland, NZ, 34.4650˚S 173.2115˚E to 34.4690˚S 173.2153˚E, depth 140–141 m, coll. Oceans Survey 2020, 13th July 2009.

Paratypes: NIWA 56152, same data as holotype; **NIWA 154129**, stn. TAN0906/38, ~8 km SE of Cape Brett, 35.2160˚S 174.4033˚E to 35.2173˚S 174.4108˚E, depth 99–105 m, coll. Oceans Survey 2020, 6th July 2009.

Other material: Great Exhibition Bay, Northland, NZ: **NIWA 57129**, stn. TAN0906/181, 34.4398˚S 173.1297˚E to 34.4373˚S 173.1237˚E, depth 110–115 m, coll. Oceans Survey 2020, 15th July 2009; **NIWA 55958**, stn. TAN0906/126, 34.5562˚S 173.1562˚E to 34.5589˚S 173.1573˚E, depth 105–106 m, coll. Oceans Survey 2020, 12th July 2009; **NIWA 154046**, stn. TAN0906/132, 34.5570˚S 173.28533˚E to 34.5587˚S 173.2875˚E, depth 139–141 m, coll. Oceans Survey 2020, 13th July 2009.

Description of the holotype.

Colony form: The holotype is yellow-orange (ethanol-preserved), attached to a sponge fragment, and measures 2 cm tall by 3 cm wide (Fig. 8A). Three primary lobes emerge from a basal stalk, which is ~0.5 cm in height, and these each divide into several small lobules. The base of the colony forms a short membrane which partially encrusts the sponge substrate. Polyps grow all over the surface of the colony but are concentrated towards lobe tips and are rare on the basal membrane. Polyps are white, 0.5–1.5 mm tall when expanded, with colourless collaret and points (Fig. 3A).

Sclerites: Points are composed of slender, warty spindles (~0.18–0.28 mm long) and thorny clubs distally (~0.12–0.28 mm long) (Fig. 6A, B). Proximally, the spindles become larger and more crescentic (~0.12–0.28 mm long), transitioning into a transverse orientation and merging with the collaret, which is six to ten rows deep (Figs. 6A; 7C). The tentacles contain irregular warty, scale-like forms, often slightly to distinctly crescentic (~0.08–0.22 mm long) (Fig. 6C). The polyp neck contains some tuberculate to warty spindles (~0.08–0.15 mm long) (Fig. 6D). The polyp mounds and the lobe surface both contain clubs with thorny and leaf-like processes (~0.06–0.12 mm long and up to ~0.06 mm wide) (Figs. 6E, F), but the latter also contains some spiny spindle-like forms and radiates (~0.06–0.12 mm long). The surface of the base contains various radiates as well as some clubs and spheroids (~0.06–0.12 mm long) (Fig. 7A). The interior of the lobes contains slender spindles (~0.1–0.2 mm long) with branching processes and/or complex tubercles, as well

as radiates (~0.05–0.1 mm long) (Fig. 6G). The interior of the base contains similar sclerites, but the spindles tend to be smaller (~0.08–0.14 mm long) and the radiates larger (~0.06–0.12 mm long) (Fig. 7B).

Habitat and distribution: All specimens were collected off the east coast of far northern New Zealand, between Great Exhibition Bay and around Cape Brett, at ~100–140 m depth (Fig. 2B). NIWA 55958 and NIWA 57129 were collected from rocky sites, and NIWA 56152 from muddy sites. All specimens except NIWA 57129 are attached to sponge fragments, and NIWA 154046 was collected with mostly sponge material. Some of the specimens were collected along with specimens of *Ushanaia ferruginea* gen. n., sp. n., and the sponge fragment attached to NIWA 154129 is encrusted with small patches of this species.

Variability: All specimens are very similar, both in colony form and sclerite composition, varying only slightly in colour (note that all specimens are ethanol-preserved), colony size, the extent of the basal membrane (Fig. 8) and in sclerite size ranges, although the latter fell within the ranges described for the holotype in all cases (Figs. 6; 7).

Comparisons:

In growth form and sclerite morphology, *K. amicispongia* is most similar to *K. aurantiaca* and *K. teorowai*, and to a lesser extent resembles *K. kapotaiora* and *K. teorowai* (in growth form only). *Kotatea amicispongia* is easily distinguishable from *K. lobata*, *K. kurakootingotingo* and *K. niwa* by these species' more robustly lobed growth forms.

All *K. amicispongia* specimens differ markedly from all *K. aurantiaca* specimens in possessing far larger (and more abundant) clubs in their points (up to 0.28 mm long vs. ~0.1 mm long, compare Figs. 6B and 10B) and much wider polyp mound clubs (up to 0.06 mm vs. no more than ~0.03 mm, compare Figs. 6E and 10E). Additionally, spindles of the collaret and points are overall smaller and more slender in *K. amicispongia* (compare Figs. 6A and 10A), which is particularly apparent when polyp armatures are compared in *situ* (compare Figs. 7C and 11B), as this causes the collaret and points to appear much more crowded with sclerites than the more uniform arrangement typical in *K. aurantiaca*. Specimens of *K. amicispongia* also tend to have deeper collarets than those of *K. aurantiaca* (6–10 vs. 4–7 rows), and based on available material *K. amicispongia* may be restricted to deeper depths (> 100 m vs. < 100 m).

Other than colour (compare Figs. 8A and 25B), a clear difference between *K. amicispongia* and *K. teorowai* is that specimens of *K. amicispongia* lack the leafy spheroids that form a distinctive component of the lobe surface in *K. teorowai* (compare Figs. 6F and 28F). The two species are also distinct for their interior sclerites, which are far more abundant and more heavily ornamented in all *K. amicispongia* specimens than in *K. teorowai*, being very rare (and absent towards the base) and sparsely ornamented in the latter (compare Figs. 6G, 7B and 28H).

While the sclerites of *K. amicispongia* differ markedly from those of *K. kapotaiora* and *K. raekura* (compare Figs. 6–7 and 13–14 or 26–27), *K. kapotaiora* specimens can also be easily distinguished by their white colouration, and specimens of *K. raekura* by their orange-coloured collaret and points sclerites. Available material also suggests that *K. raekura* may be restricted to Manawatāwhi/Three Kings Islands and much shallower depths (collected at < 20 m vs. > 100 m in *K. amicispongia*).

Since *K. amicispongia* and *U. ferruginea* can occur within centimetres of one another, it is also worth noting that *K. amicispongia* appears to develop an upright growth form at small sizes and is therefore unlikely to be confused with this encrusting species, even without sclerite examination.

Etymology: The species name is a combination of the Latin *amici*, friend, and *spongia*, sponge, giving roughly "friend of the sponge", referring to the habit of *U. amicispongia* specimens of growing on sponge fragments.

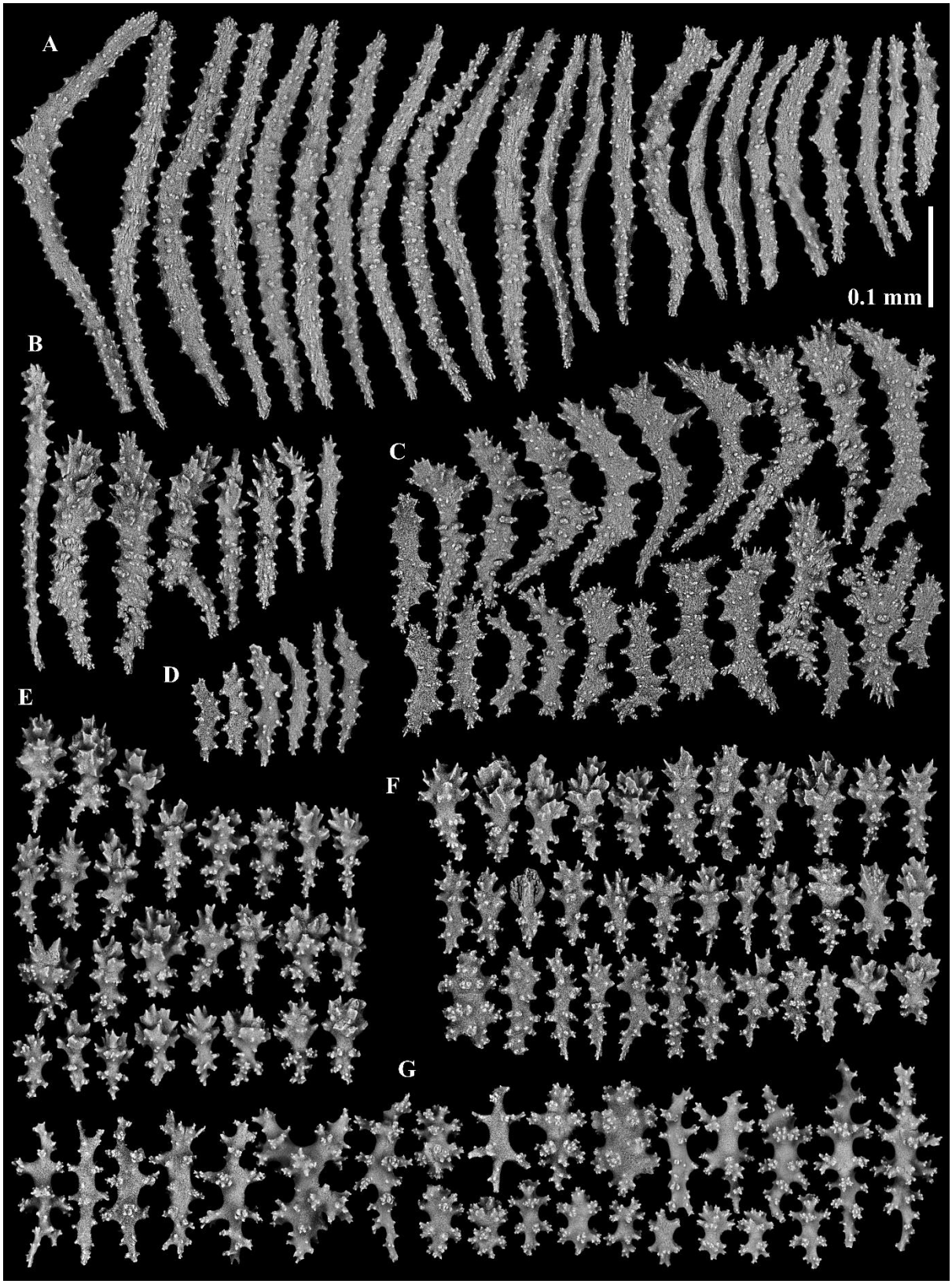

Figure 6. *Kotatea amicispongia* gen. n., sp. n. holotype (NIWA 156312), SEMs of sclerites from: **A.** Collaret and points; **B.** Distal points; **C.** Tentacles; **D.** Polyp neck; **E.** Polyp mound; **F.** Lobe surface; **G.** Lobe interior.

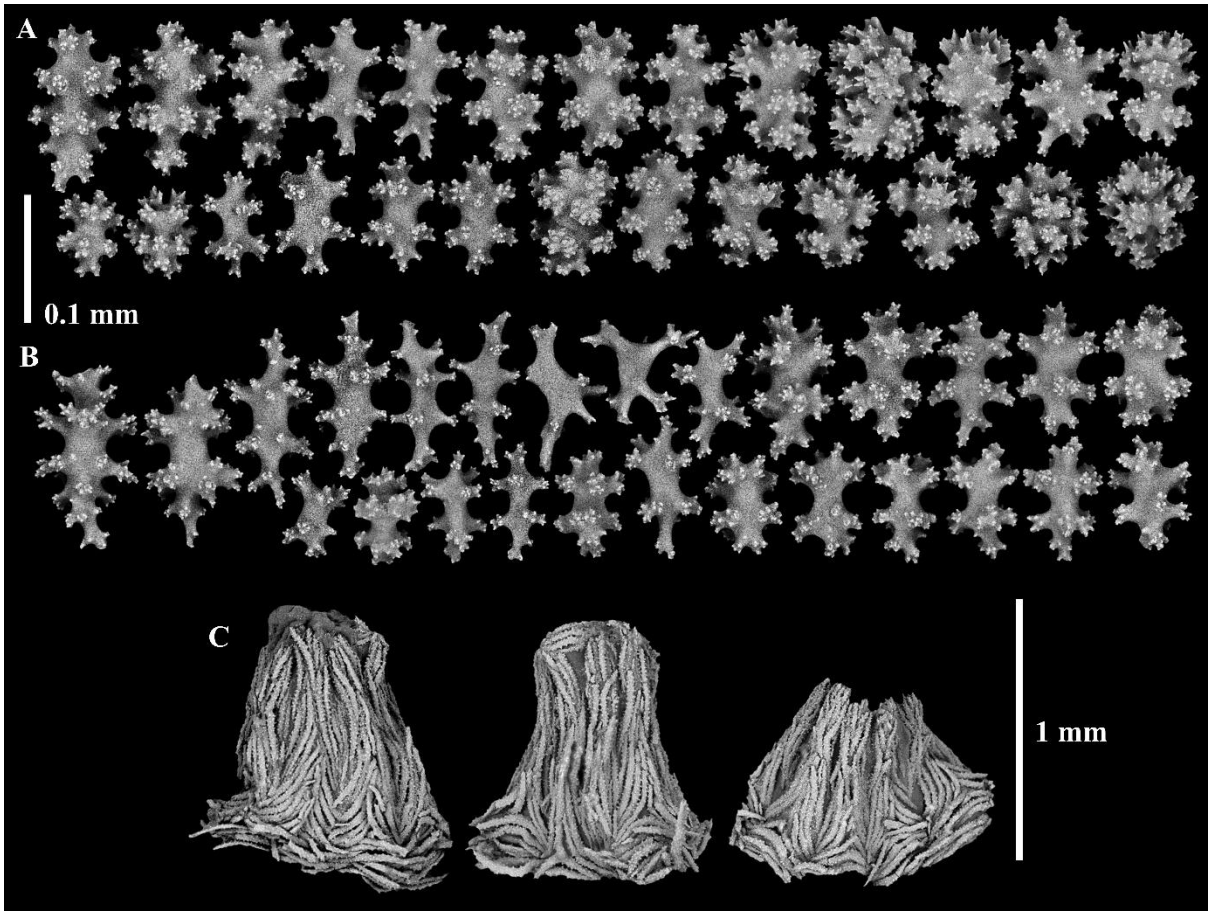

Figure 7. *Kotatea amicispongia* gen. n., sp. n. holotype (NIWA 156312), SEMs of sclerites from: **A.** Base surface; **B.** Base interior; **C.** Polyps (*in situ*).

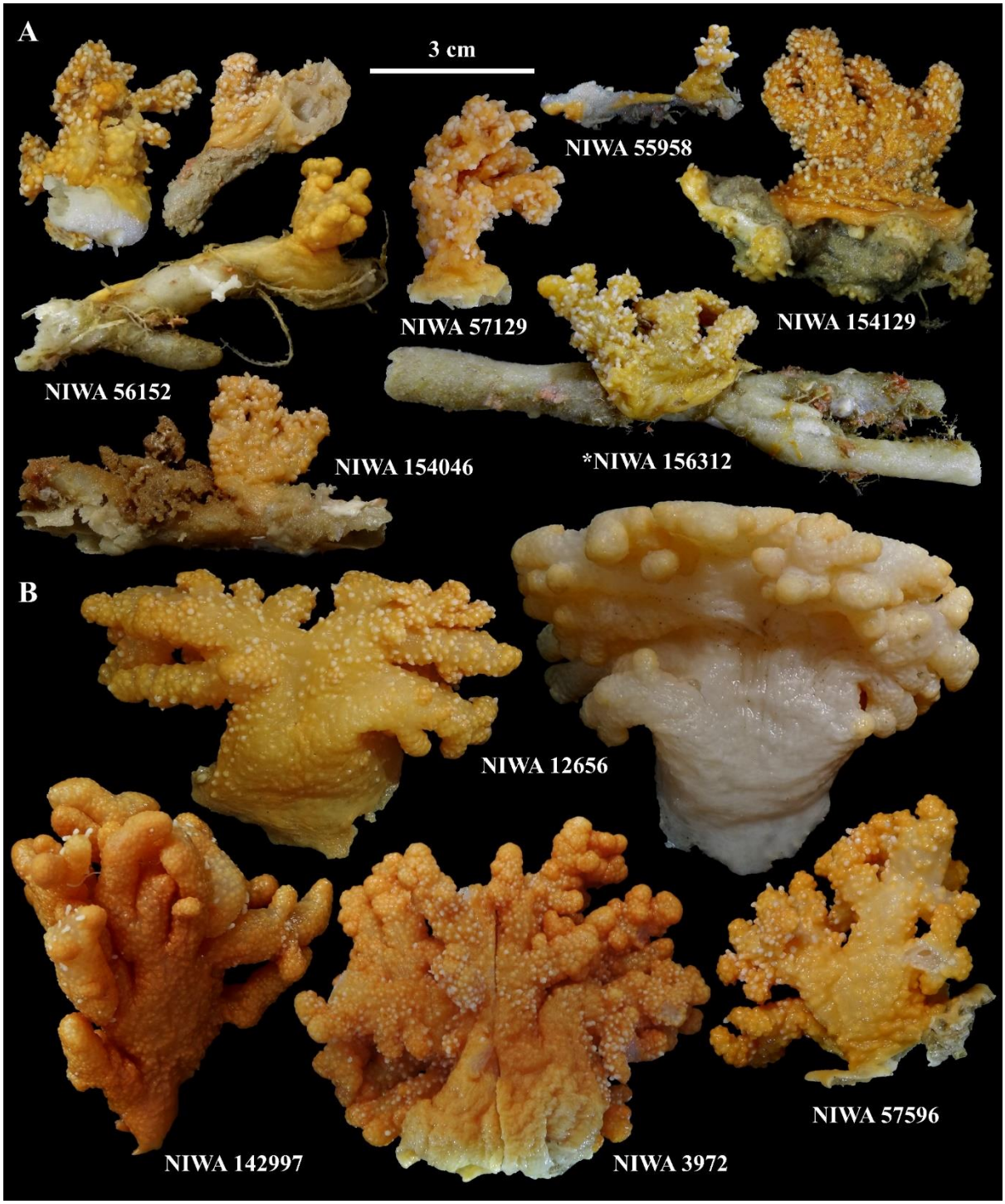

Figure 8. Preserved specimens of: **A.** *Kotatea amicispongia* gen. n., sp. n.; **B.** *K. aurantiaca* gen. n., comb. n., expanded and stalked specimens. Note NIWA 154046 and NIWA 142997 contain additional fragments that are not depicted. *Holotype.

***Kotatea aurantiaca* (Quoy and Gaimard, 1833) gen. n., comb. n.**

Alcyonum aurantiacum Quoy and Gaimard, 1833 [spelling of *Alcyonium — lapsus calami*]: pg. 277; figs. 16–18; plate 22

Alcyonium aurantiacum Benham 1928 in part: Pg. 71–75; Figs. 6–11

Not *Alcyonium aurantiacum* McFadden 2006b (= *Ushanaia fervens* gen. n., sp. n)

? Alcyonium aurantiacum Powell 1947: Pg. 8; Fig. 14

? *Alcyonium aurantiacum* Doak 1971: Pg. 44–46; Plate 20

? *Alcyonium aurantiacum* Westerskov and Probert 1981 in part: Pg. 111, Plate 28

? *Alcyonium aurantiacum* Grange et al. 2010 in part: Pg. 148

Figs. 2B, C; 3B, L; 4A–C; 8B; 9; 10; 11; 12A–C, E

Material examined.

Northland, NZ: **NIWA 3972**, stn. Z9702 (KAH9901/73), ~14 km N of Piwhane/Spirits Bay, 34.3163˚S 172.7925˚E, depth 68 m, coll. NIWA, 28th January 1999; **NIWA 3978**, stn. Z9697 (KAH9901/64), ~14 km NW of Piwhane/Spirits Bay, 34.3510˚S 172.7088˚E, depth 57 m, coll. NIWA, 28th January 1999; **NIWA 12656**, stn. Z9753, ~12 km NW of Piwhane/Spirits Bay, 34.3533˚S 172.7487˚E, depth 55 m, coll. NIWA, 22nd April 1999; **NIWA 3979**, stn. Z9695 (KAH9901/59), ~3 km N of North Cape, 34.3668˚S 173.0003˚E, depth 89 m, coll. NIWA, 27th January 1999; **NIWA 3980**, stn. Z9677 (KAH9901/25), ~ 8 km N of Piwhane/Spirits Bay, 34.3690˚S 172.8250˚E, depth 55 m, coll. NIWA, 25th January 1999; **NIWA 3977**, stn. Z9688 (KAH9901/47), ~5.5 km NNE of Cape Reinga, 34.3745˚S 172.7013 ˚E, depth 53 m, coll. NIWA, 27th January 1999; **NIWA 57596**, stn. TAN0906/245, ~7 km E of Takou Bay, 35.0750˚S 174.0183˚E to 35.0815˚S 174.0207˚E, depth 67–72 m, coll. Oceans Survey 2020, 19th July 2009; **NIWA 55142** and **NIWA 55164**, stn. TAN0906/57, ~1.5 km NE of Harakeke Island, Bay of Islands, 35.1457˚S 174.1517˚E to 35.1445˚S 174.1485˚E, depth 55 m, coll. Oceans Survey 2020, 7th July 2009; **NIWA 58551**, stn. KAH0907/195, ~ 500 m NW of Motutara Island, Bay of Islands, 35.2075˚S 174.1940˚E to 35.2123˚S 174.1895˚E, depth 23–27 m, coll. Oceans Survey 2020, 3rd September 2009; **NIWA 54641** and **NIWA 54700**, stn. TAN0906/21, ~4 km NE of Whananaki, 35.4858˚S 174.5012˚E to 35.4965˚S 174.5307˚E, depth 59–63 m, coll. Oceans Survey 2020, 5th July 2009; **NIWA 54535**, stn. TAN0906/3, ~6 km ENE of Whananaki, 35.5002˚S 174.5415˚E to 35.4955˚S 174.5393˚E, depth 64–66 m, coll. Oceans Survey 2020, 4th July 2009; **NIWA 54766**, stn. TAN0906/25, ~4 km NE of Matapouri Bay, Matapouri, 35.5525˚S 174.5525˚E to 35.5483˚S 174.5528˚E, depth 57 m, coll. Oceans Survey 2020, 5th July 2009.

Bay of Plenty, NZ: **MAGNT C013957** and **NIWA 101181**, stn. Z15884, ~5 km NW of Whakaari/White Island, 37.4785˚S 177.1280˚E, depth 12–17 m, coll. Coral Reef Research Foundation, 30th April 1999; **MAGNT C015225**, **MAGNT C015231**, **MAGNT C015232**, **MAGNT C015233**, **MAGNT C015234** and **MAGNT C015235**, stn. unknown, Volkner Rocks, Whakaari/White Island, 37.5167˚S 177.1833˚E, depth 12–20 m, coll. J. Starmer, 30th April 1999.

East Cape, NZ: **NIWA 75330**, stn. TAN1108/213, Ranfurly Bank, 37.5472˚S 178.8925˚E to 37.5455˚S 178.8880˚E, depth 68–70 m, coll. Oceans Survey 2020, 30th May 2011; **NIWA 75393**, stn. TAN1108/217, Ranfurly Bank, 37.5823˚S 178.8975˚E to 37.5852˚S 178.8937˚E, depth 42–48 m, coll. Oceans Survey 2020, 31st May 2011.

Unknown location: **NIWA 142997**, stn. B5/96, older than 1995, no other data available.

Type locality: Firth of Thames, North Island, NZ, depth ~14–18 m.

Preliminary remarks.

Quoy and Gaimard's (1833) description alone lacks the detail needed to distinguish which of several species of *Kotatea* gen. n. could be *A. aurantiacum*. However, when their original colour plate (Fig. 12A) and the photograph of the *A. aurantiacum* syntype specimens (Fig. 12E) are considered in conjunction with the morphology and distributional range of all available specimens, the material here ascribed to *K. aurantiaca* comb. n. is almost certainly conspecific with Quoy and Gaimard's (1833) species.

Apart from sclerites, *K. aurantiaca* specifically differs from all of its congeners as follows: *Kotatea amicispongia* sp. n. has only been collected from much greater depths than Quoy and Gaimard's (1833) material; *K. kapotaiora* sp. n. and *K. teorowai* sp. n. do not match the colour described for the original material as they are white rather than orange; *K. raekura* sp. n. is known only from Manawatāwhi/Three Kings Islands and not near the type locality; and *K. kurakootingotingo* sp. n., *K. lobata* sp. n., and *K. niwa* sp. n. all tend to differ in colony growth form. *Ushanaia* gen. n. also differs in growth form.

Description.

Colony form: *Kotatea aurantiaca* produces irregularly branched, lobate colonies. Lobes are usually finger-like but can appear more robust when contracted (Figs. 4A–C; 8B, 9). Preserved specimens vary in colour from very pale to dark orange and measure up to 7 cm in height and 7 cm in width (Figs. 8B; 9), but the species may attain larger sizes (see remarks below). Finger-like lobes emerge, often profusely, from a broad base that is usually lighter in colour than the rest of the colony, and which may be very short (Fig. 9), or from a stalk (Fig 8B). Polyps are most densely concentrated at lobe tips and tend to become sparser towards the base of the colonies, from which

they are usually absent. Polyps are white in preserved specimens, are 0.5–1 mm tall when expanded and have colourless collaret and points (Fig. 3B, L).

Sclerites: Points are composed of warty spindles (~0.15–0.4 mm long) and a few small clubs distally (~0.1 mm long) (Fig. 10A, B). Proximally, the spindles become larger and more crescentic (~0.3–0.5 mm long), transitioning into a transverse orientation and merging with the collaret, which is five to seven rows deep (Figs. 10A; 11C). Among the spindles, both the collaret and the points also contain some similarly sized, irregular, sometimes branched sclerites. The tentacles contain irregular, warty, scale-like forms that are often slightly crescentic (~0.06–0.2 mm long) (Fig. 10C), the polyp neck contains spiny spindles and warty rod-like forms (~0.06–0.15 mm long) (Fig. 10D), and the polyp mounds contain slender, spiny clubs and a few warty rod- and spindle-like forms (~0.06–0.15 mm long, clubs ~0.03 mm wide) (Fig. 10E). The surface of both the lobes and the base contains radiates and clubs (~0.05–0.12 mm long), with clubs being more common in the lobe surface (Fig. 10F, H). Surface sections may also occasionally include leafy spheroids (Fig. 10F). The interior of both the lobes and the base contains long, slender spindles with branches and/or complex tubercles, as well as radiates, with radiates being more common and spindles tending to be more branched in the interior of the base (Figs. 10G; 11A). Interior sclerites are ~0.06–0.26 mm long.

Habitat and distribution: Specimens were collected from northern New Zealand, between Piwhane/Spirits Bay and East Cape at depths of ~10–90 m (Fig. 2B, C). Many of the specimens were collected from rocky, gravelly and shelly substrates alongside seaweed, hydrozoans, ascidians, bryozoans and large numbers of various species of sponge.

Variability: Colonies of this species can expand and contract to a considerable degree. Consequently, the presence of a stalk may be difficult to discern, and although *K. aurantiaca* comb. n. can resemble *K. lobata* sp. n. when highly contracted (compare NIWA 101181 in Fig. 9 to Fig. 19; also see illustrations in Doak 1971), the material to hand indicates that the lobes of the latter are usually considerably longer and more robust.

Point clubs are overall more common in some specimens than in others and can be absent from some polyps. Additionally, leafy spheroids are present in low numbers in the surface sections of most colonies but may be absent. Beyond this, there is very little variability in the sclerites across all specimens, with size ranges falling within those described for the holotype in all cases (Figs. 10; 11).

Comparisons: *Kotatea aurantiaca* is most similar to congeners which commonly exhibit branching of the lobes: *K. amicispongia*, *K. kapotaiora, K. raekura,* and *K. teorowai*. Differences from *K. amicispongia* are discussed under that species.

Other than colour (compare Figs. 8B; 9 and 15C), *K. aurantiaca* specimens differ markedly from *K. kapotaiora* in lacking the latter's large and robust clubs in the lobe surface (compare Figs. 10F and 13F), and in possessing interior sclerites composed largely of slender spindles while those of *K. kapotaiora* specimens are distinct, irregular radiates with minimal branching processes (compare Figs. 10G; 11A and 13G; 14B).

Kotatea aurantiaca specimens can be easily differentiated from *K. raekura* by their colourless collaret and point sclerites, which are always coloured orange in *K. raekura*. Sclerites of the collaret and point, polyp neck, polyp mound and surface regions also clearly differ between the two species, with those in *K. aurantiaca* specimens being much smaller and more slender than the overall more robust sclerites found in *K. raekura* (compare Figs. 10A, D, E, F, H and 26A, D–F; 27B). Additionally, *K. raekura* specimens have shallower collarets (3–5 vs. 5–7 rows) and may be restricted to Manawatāwhi/Three Kings Islands judging from the available material.

As for *K. kapotaiora*, *K. aurantiaca* differs in colour from *K. teorowai* (compare Figs. 8B; 9 and 25B). Notably, *K. teorowai* completely lacks the slender interior spindles that are present and abundant in all *K. aurantiaca* specimens, possessing only rare, irregularly branched radiates in its interior (compare Figs. 10G; 11A and 28H). Additionally, while leafy spheroids are not common in any *K. aurantiaca* specimen, these sclerites are well-developed and feature conspicuously in the lobe surface of *K. teorowai* (compare Figs. 10F and 28F).

Kotatea aurantiaca and *K. lobata* are probably the most commonly encountered species of the genus. *Kotatea lobata* specimens are distinctive in possessing very large, highly branched, antler-like sclerites in their interiors, especially in the lobes. By contrast, *K. aurantiaca* specimens entirely lack these sclerites, and their interiors are instead composed predominantly of slender spindles (compare Figs. 10G; 11A and 21A; 22A). Equally characteristic are the very large spindle-like sclerites found in the surface sections (particularly of the base) of *K. lobata* specimens, which are again absent in *K. aurantiaca* (compare Figs. 10F, H and 20F; 21B). Additionally, point clubs are more abundant in *K. lobata* specimens (compare Figs. 10B and 20B). While their growth forms are, in general, sufficiently distinct to allow for differentiation, in many cases colony-scale morphological overlap between *K. aurantiaca* and *K. lobata* may prevent species identification by eye, especially in small or very contracted colonies and in areas where both species may be present (e.g., compare *K. lobata* specimen NIWA 108960 in Fig. 19 with some of the *K. aurantiaca* colonies of NIWA 101181 and NIWA 54535 in Fig. 9). The extent of morphological overlap between these two species and statistical methods for discrimination based on measurements of colony morphology are discussed in detail in Chapter 3.

Etymology: The species name is the feminine form of *aurantiacum*, the original species epithet (Quoy and Gaimard 1833).

Remarks: Quoy and Gaimard (1833) most likely did not observe the tentacles of their specimens in an expanded state, as they describe the tentacles as short and rounded and their plate (Fig. 12B) also shows these to be contracted.

Since Quoy and Gaimard's work, the only other taxonomic treatment of *A. aurantiacum* is that by Benham (1928), who described the morphology of three specimens and pointed out that Quoy and Gaimard's description omits the 'i' in *Alcyonium*. Again, Benham's descriptions have limited usefulness in distinguishing among the closely related species described here. However, judging from one of Benham's sketches, it is possible that one of his specimens collected from the Mahia Peninsula (reproduced here in Fig. 12C) may have been *K. aurantiaca*, while an encrusting specimen collected in Dusky Sound and growing around a black coral fragment (Fig. 12D) almost certainly represents *Ushanaia fervens* gen. n., sp. n.

The identity of Benham's third specimen, collected at Tasman Bay/Te Tai-o-Aorere, is unclear. This is described as stalked and lobed in growth form, with noticeably orange collaret sclerites, and so is likely a member of the genus *Kotatea*, but most likely not *K. aurantiaca*, which possesses colourless collaret sclerites. Benham (1928) also believed a specimen from the Auckland Islands was *A. aurantiacum*, and while the exact identity of this specimen cannot be ascertained from his descriptions, it points to the possible presence of *Kotatea* gen. n. or *Ushanaia* gen. n. in New Zealand's subantarctic islands, but at present, no samples are known from this far south.

Similarly, Grange et al. (2010) illustrate what appears to be a *Kotatea* colony, possibly *K. aurantiaca*, from Fiordland, and Powell (1947) mentions having commonly dredged what is likely *K. aurantiaca* from depths of ~10–15 m between Motuihe Island/Te Motu-a-Ihenga and Waiheke Island in the Hauraki Gulf/Tīkapa Moana. Additionally, observations recorded on iNaturalist (https://www.inaturalist.org. Accessed Jan 2021) of what appears to be *K. aurantiaca* indicate that it may reach at least as far south as Kaikōura. Therefore, this species and the genus in general may be (or have been) considerably more widely distributed around coastal New Zealand than available specimens would suggest.

Alcyonium aurantiacum occurring in southern Australia, as noted by Grange et al. (2010), is probably in reference to *A. etheridgei* Thomson and Mackinnon, 1911. This species is *Alcyonium*-like and superficially similar in appearance as it is red when alive, but not related to *Kotatea* (Verseveldt and Alderslade 1982; Alderslade pers. comm.), which should for now be considered endemic to New Zealand.

Alcyonium aurantiacum has previously been reported to grow intertidally (Morton and Miller 1973; Morton 2004; Grange et al. 2010), particularly among ascidians and sponges on moderately exposed shores (Westerskov and Probert 1981). Here, it has also been reported that the native nudibranch, *Tritonia incerta* grazes on *A. aurantiacum* (Morton and Miller 1973;

Westerskov and Probert 1981). However, intertidal observations are probably of *K. lobata*, and not *K. aurantiaca*.

Kotatea aurantiaca likely reaches a height of at least 30 cm when fully expanded *in vivo,* as noted by Grange et al. (2010) for *A. aurantiacum*. Present preserved material does not exceed ~7 cm in height.

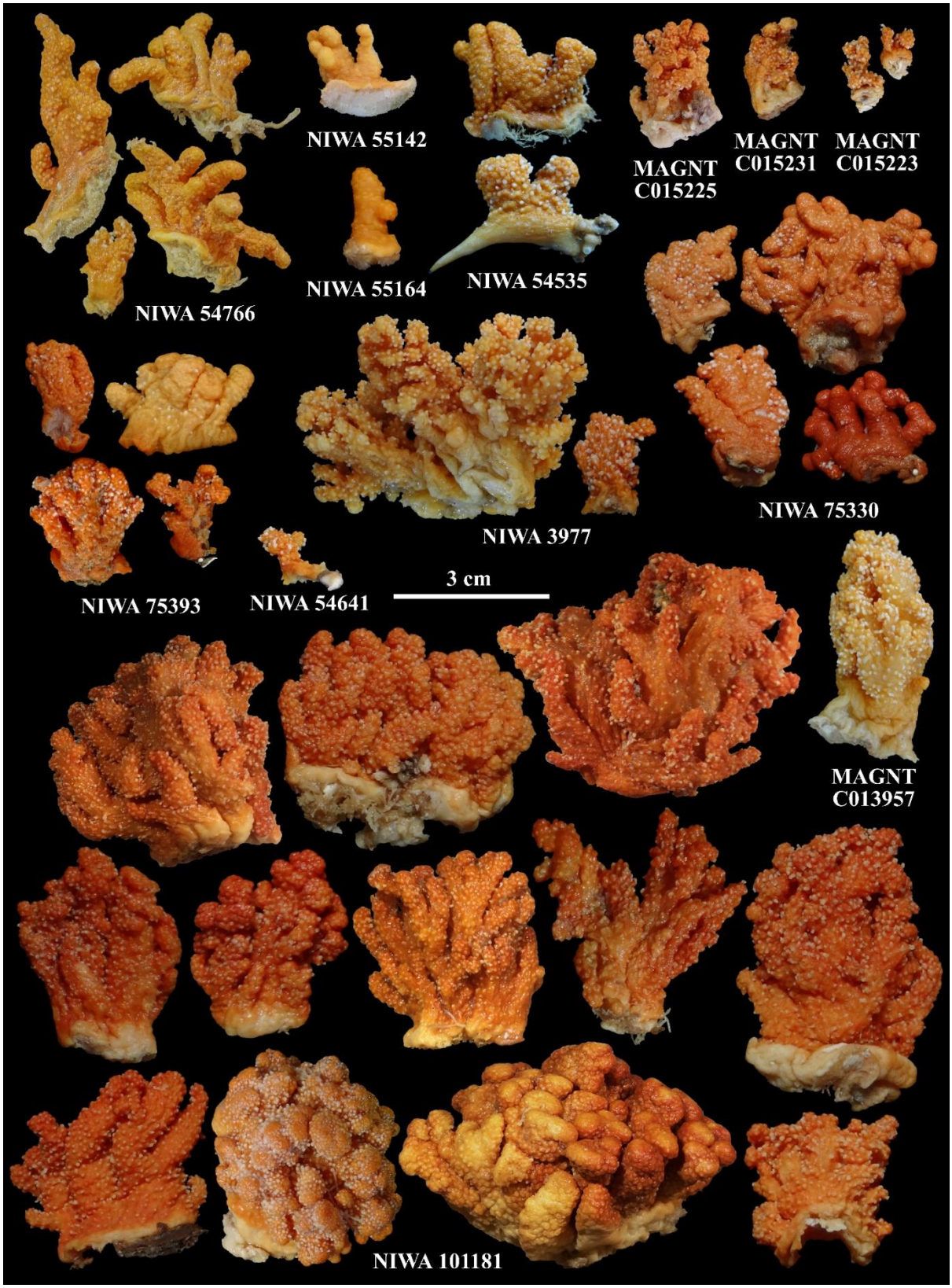

Figure 9. Selected preserved specimens of *Kotatea aurantiaca* gen. n., comb. n. Note that most specimen lots include small additional fragments that are not depicted and NIWA 101181 comprises a total of 67 similar colonies, all of which were examined.

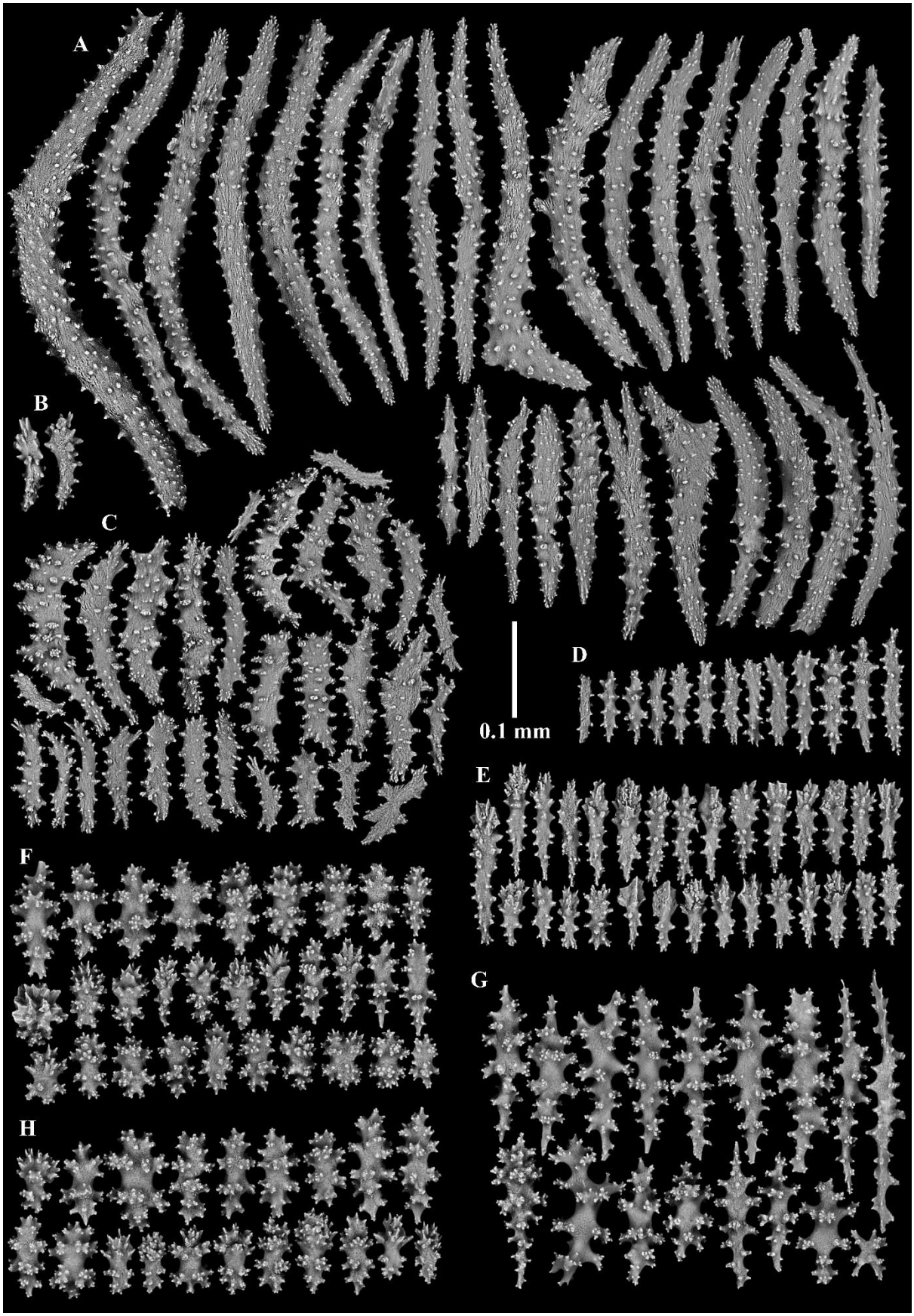

Figure 10. *Kotatea aurantiaca* gen. n., comb. n. (NIWA 54766), SEMs of sclerites from: **A.** Collaret and points; **B.** Distal points; **C.** Tentacles; **D.** Polyp neck; **E.** Polyp mound; **F.** Lobe surface; **G.** Lobe interior; **H.** Base surface.

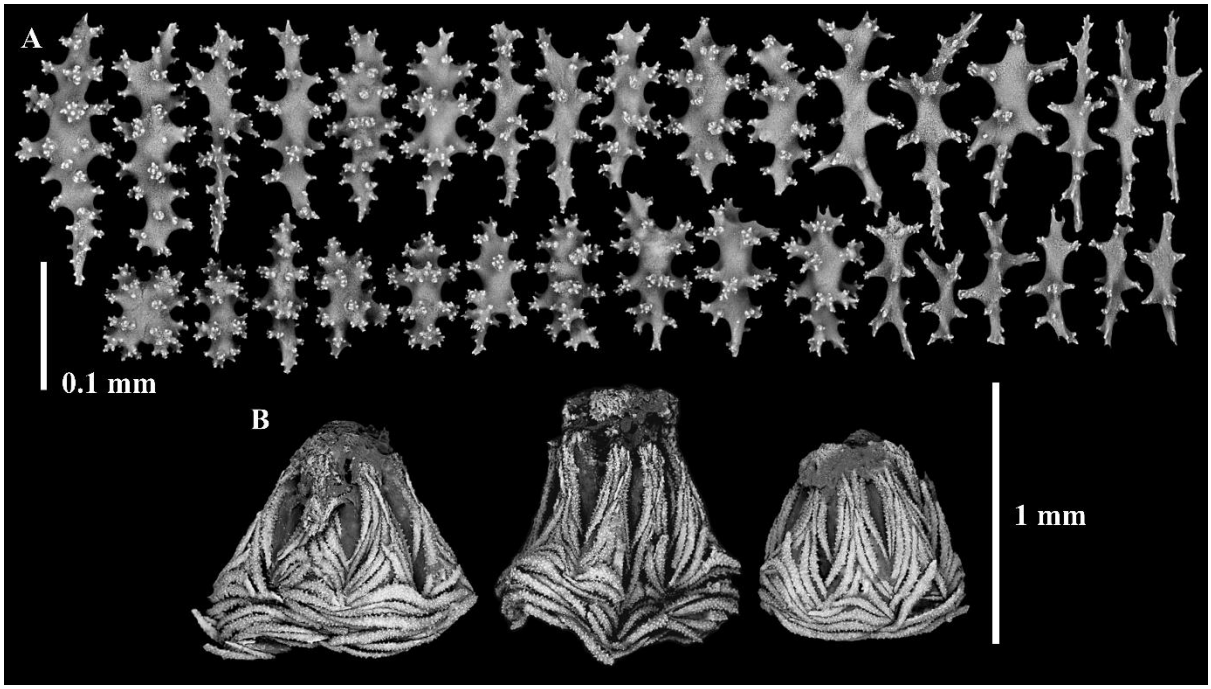

Figure 11. *Kotatea aurantiaca* gen. n., comb. n. (NIWA 54766), SEMs of sclerites from: **A.** Base interior; **B.** Polyps (*in situ*).

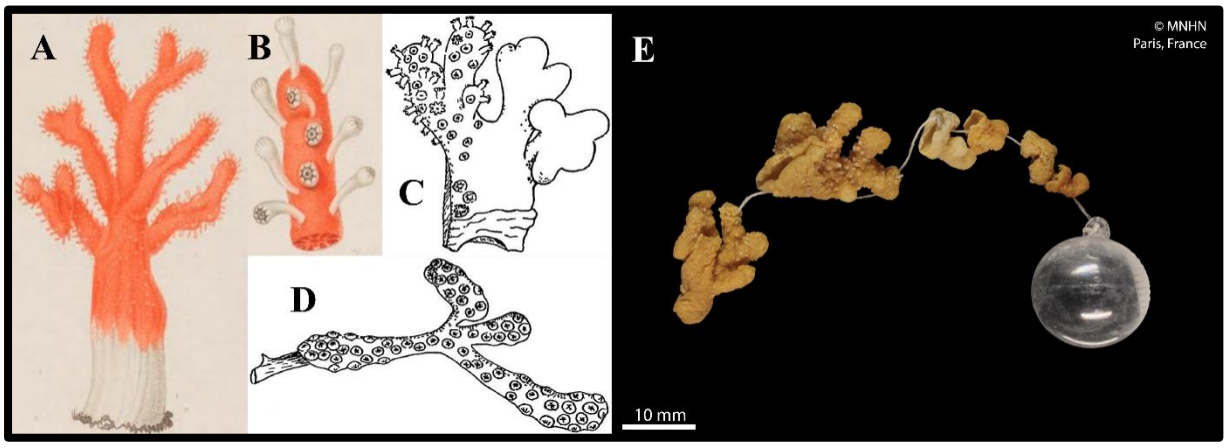

Figure 12. A–B. Copies of Quoy and Gaimard's (1833) illustrations of "*A. aurantiacum*"; **C–D.** Copies of Benham's (1928) sketches of upright and encrusting specimens, identified as *A. aurantiacum*; **E.** *A. aurantiacum* syntype, specimen MNHN-IK-2000-128 (photo by Marie Hennion).

***Kotatea kapotaiora* gen. n., sp. n.**

Figs. 2B–C; 3C; 13; 14; 15C

Māori name: Kapo Taiora

Material examined.

Holotype: NIWA 3974, stn. Z9712 (KAH9901/88), ~12 km NW of North Cape, Northland, NZ, 34.3570˚S 172.8850˚E, depth 69 m, coll. NIWA, 29th January 1999.

Paratype: MA 73620, same data as holotype.

Other material: NIWA 155300, stn. KAH2006/13, Jellicoe Channel, ~5 km E of Te Arai Point, Auckland, NZ, 36.1580˚S, 174.7100 ˚E, depth 46 m, coll. NIWA, 22nd November 2020.

Description of the holotype.

Colony form: The holotype consists of a white (ethanol-preserved), lobate colony (Fig. 15C), which is laterally compressed. Being roughly twice as wide as it is deep, it measures 15 cm in height by 8 cm width by 3.5 cm depth. Lobes emerge from a thick stalk, which is up to ~6 cm in height, and these branch into slender, finger-like lobes and small lobules. Polyps grow relatively uniformly over most of the colony but are absent from a short section of the base. Polyps are white, 0.5–1.5 mm tall when expanded, with colourless collaret and points (Fig. (Fig. 3C).

Sclerites: Points are composed of warty spindles (~0.18–0.25 mm long), as well as clubs distally (~0.1–0.28 mm long) (Fig. 13A, B). Proximally, the spindles transition into a transverse orientation and merge with the collaret, which is four to seven rows deep and composed of larger, usually curved, often flattened and sometimes irregular or branched sclerites (~0.2–0.4 mm long) (Figs. 13A; 14C). The tentacles contain irregular, warty, scale-like forms that are often slightly curved and branched (~0.1–0.25 mm long) (Fig. 13C). The polyp neck contains warty rod- and spindle-like forms (~0.1–0.2 mm long) (Fig. 13D). Warty rod-like forms are also abundant in polyp mounds (~0.06–0.1 mm long), where they gradually blend into thorny and leafy clubs (~0.06–0.12 mm long) (Fig. 13E). The surface of the lobes contains similar but more ornate clubs, as well as spiny radiates (~0.04–0.16 mm long) (Fig. 13F). In the interior of the lobes, irregular radiates with few, thin, thorny, branched processes predominate (~0.05–0.15 mm long) (Fig. 13G). The surface of the base lacks clubs but contains similar thorny radiates to the surface of the lobes, although here these are generally smaller (~0.05–0.12 mm long) (Fig. 14A). The interior of the base contains thorny radiates similar to those in the lobe interior along with smaller spiny forms (~0.06–0.12 mm long) (Fig. 14B).

Habitat and distribution: The holotype and paratype, collected at 69 m north of North Cape, and one other colony, collected at 46 m depth near Te Arai Point, are the only known

specimens of *K. kapotaiora* (Fig. 2B, C). None of the specimens are accompanied by habitat notes, but NIWA 155300 is attached to a large rock fragment heavily encrusted with bleached coralline algae (not shown in Fig. 15C). *K. kapotaiora* and *K. teorowai* can occur syntopically, as the holotypes for both species were collected together in the same sample.

Variability: The more recently collected NIWA 155300 is smaller and slightly more brownish in colour than the plain white holotype and paratype. Otherwise, all three specimens are very similar in growth form (Fig. 15C) and both the paratype and NIWA 155300 correspond very closely to the holotype in sclerite composition and size ranges (Figs. 13; 14).

Comparisons: *Kotatea kapotaiora* specimens are highly distinctive in appearance, forming large, white, laterally compressed colonies with slender lobes and a prominent stalk, and are unlikely to be confused for any other congeneric species. Additionally, *K. kapotaiora* can be easily differentiated from the rest of the genus by its characteristic, abundant interior radiates with few, thin, thorny branching processes (Figs. 13G; 14B).

Etymology: The species name was composed by the Ngāti Kuri Tira Ma Te Wā Taiao (Science) Collective, and is a combination of the Māori words *kapo*, to grasp, *tai*, the sea or tide, and *taiora*, nutrients. Ngāti Kuri provided the following ***kōrero* (narrative)**: "Clasping the sea, grabbing a hold of the ocean currents to ingest the life sustaining nutrients from its waters. Kapo Taiora shows strength and courage to withstand the ever-changing surges of different currents, *He punga tū moana* (the coral that stands steadfast in the face of all adversity). We need to stand up and grasp the deep tides of new knowledge presented to us by the natural world. Such tenacity also reminds us that our ancient knowledge from the peoples of the Pacific is never lost. We must allow the currents of creative thinking to surge forth and inspire our *whānau* (family) to seek knowledge and the truth of our science and of our world. Kapo Taiora inspires us all to bring to reality all yet to be discovered knowledge. Our ancient saying: '*Te au ō te moana ō naianei, nō onamataa*.' The ocean currents of today are from the ancient world."

Remarks: Grange et al. (2010) illustrate a large (up to 30 cm), white, digitate soft coral from Fiordland that, at least superficially, resembles *K. kapotaiora*. That form is noted as rare and found at 40–100 m depth. Since no specimens matching that description were available for examination, it remains unclear whether these observations represent *K. kapotaiora* living much further south than can currently be confirmed, or a separate species.

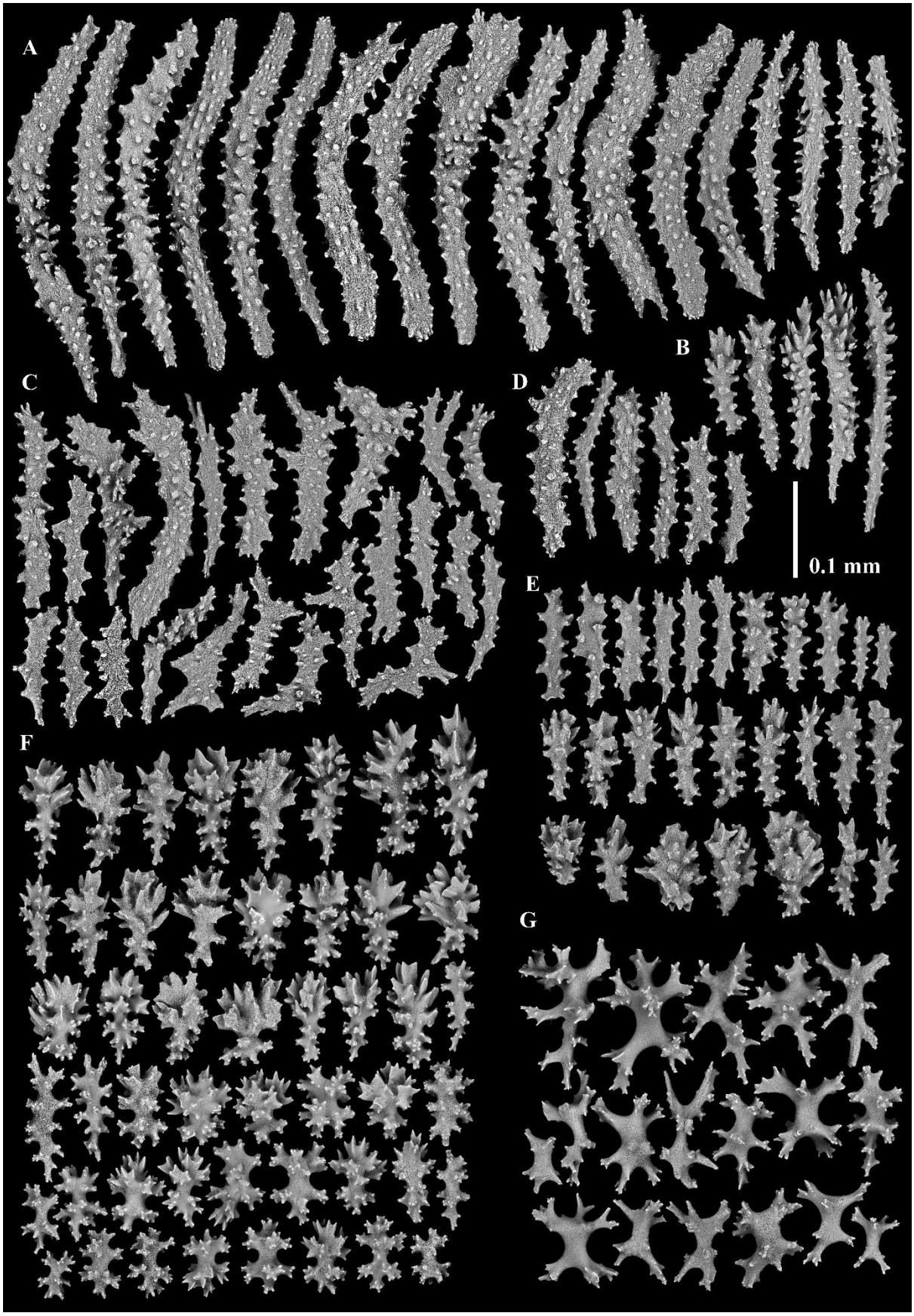

Figure 13. *Kotatea kapotaiora* gen. n., sp. n. holotype (NIWA 3974), SEMs of sclerites from: **A.** Collaret and points; **B.** Distal points; **C.** Tentacles; **D.** Polyp neck; **E.** Polyp mound; **F.** Lobe surface; **G.** Lobe interior.

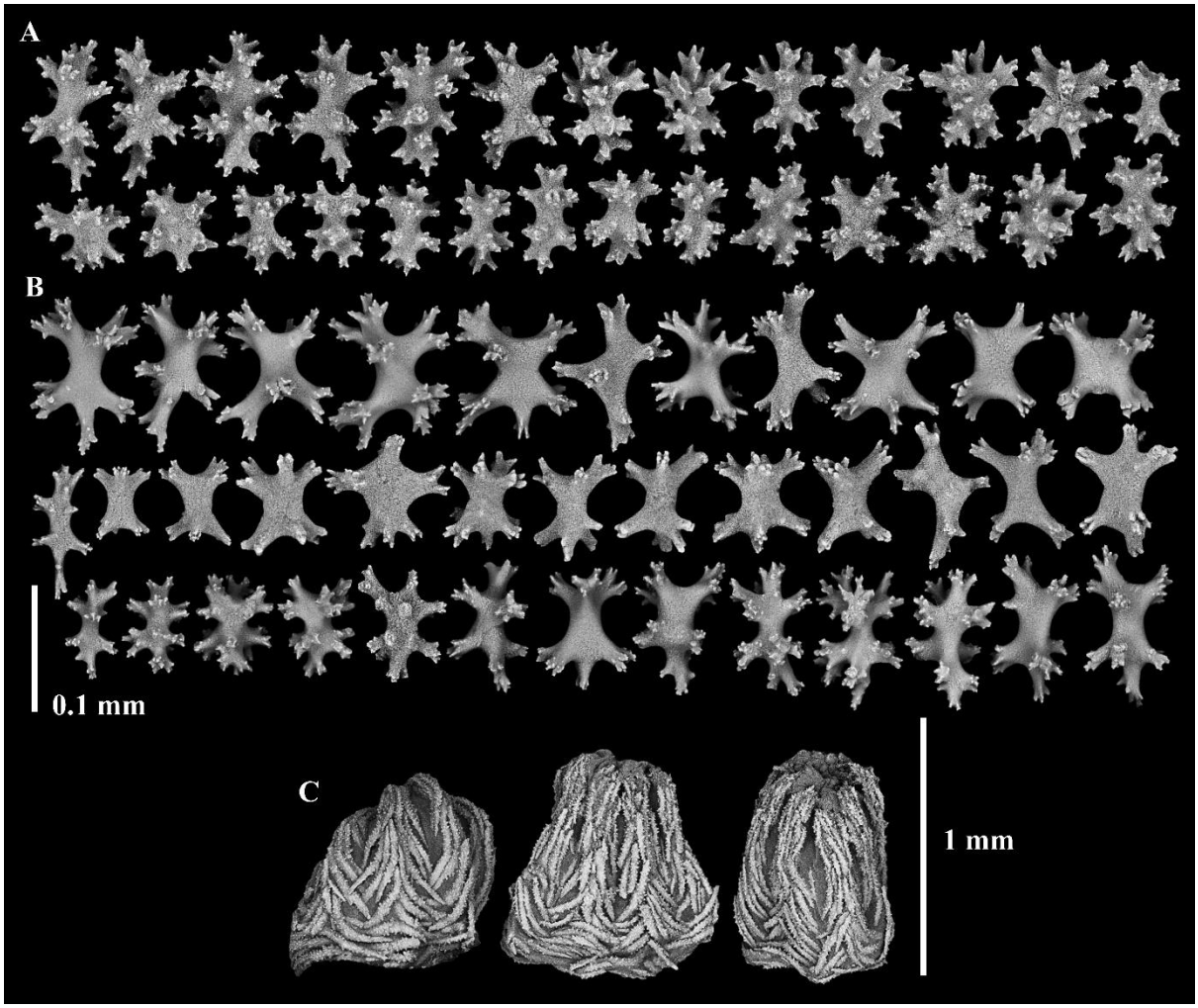

Figure 14. *Kotatea kapotaiora* gen. n., sp. n. holotype (NIWA 3974), SEMs of sclerites from: **A.** Base surface; **B.** Base interior; **C.** Polyps (*in situ*).

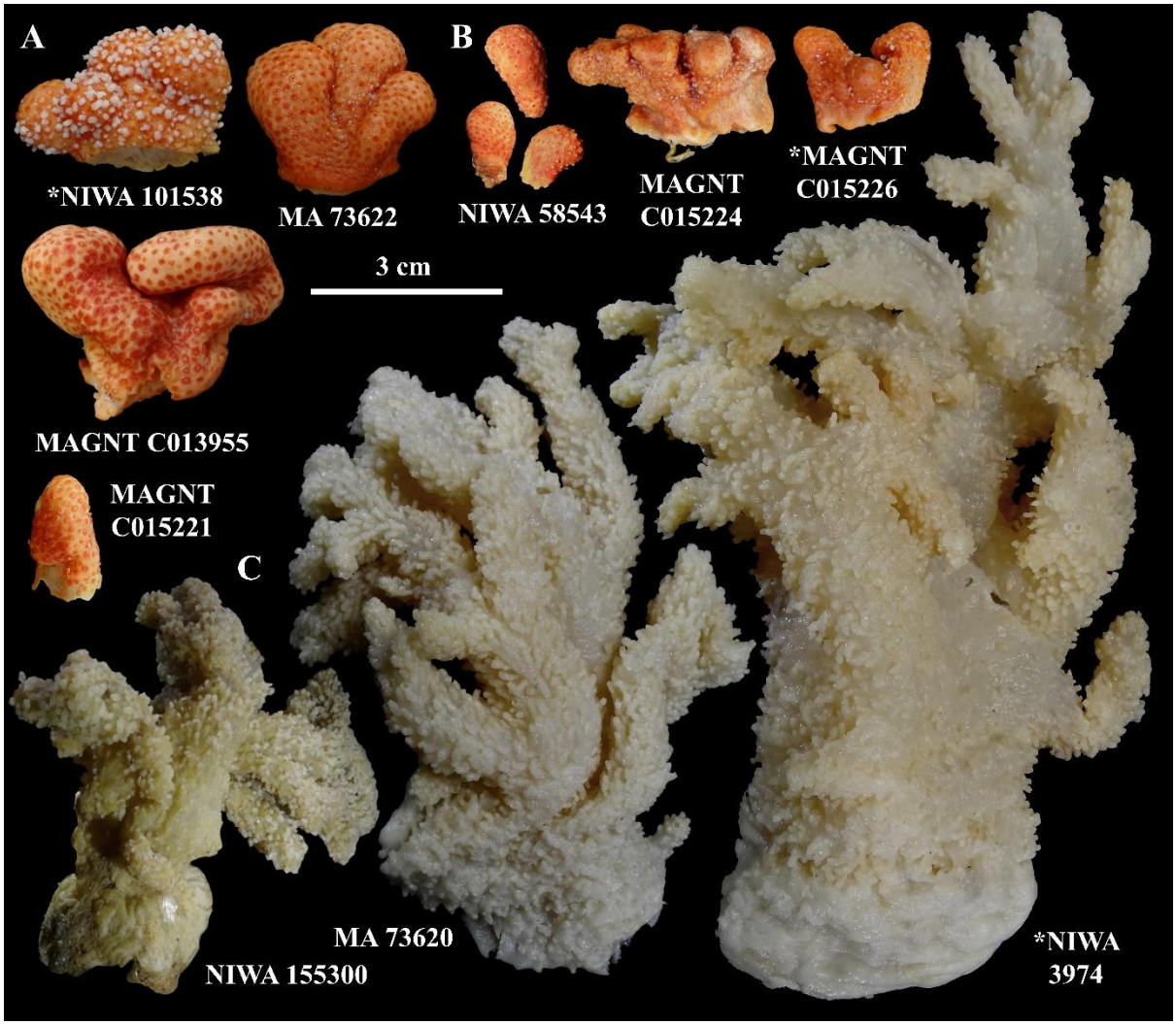

Figure 15. Preserved specimens of: **A.** *Kotatea kurakootingotingo* gen. n., sp. n.; **B.** *K. niwa* gen. n., sp. n.; **C.** *K. kapotaiora* gen. n., sp. n. Note that MAGNT C015226 contains an additional fragment that is not depicted. *Holotype.

***Kotatea kurakootingotingo* gen. n., sp. n.**

Figs. 2A; 3D, E; 5A–B; 15A; 16; 17; 18

Māori name: Kura Kōtingotingo

Material examined.

Holotype: NIWA 101538, stn. Z15942, Princes Islands, Manawatāwhi/Three Kings Islands, NZ, 34.1759˚S 172.04949˚E, depth 10–20 m, coll. NIWA, 24th February 2002.

Paratypes: Manawatāwhi/Three Kings Islands, NZ: **MAGNT C015221**, stn. unknown, Manawatāwhi/Great Island, 34.15˚S 172.15˚E, depth 7 m, coll. J. Starmer, 20th April 1999; **MAGNT C013955**, stn. unknown, Manawatāwhi/Great Island, 34.1662˚S 172.1502˚E, depth 6 m, coll. Coral Reef Research Foundation, 20th April 1999; **MA 73622**, same data as holotype.

Description of the holotype.

Colony form: The holotype consists of a lobate colony, measuring 2.5 cm height by 3.5 cm width (Figs. 5B; 15A). The surface of the colony (ethanol-preserved) is orange, while sclerites immediately surrounding the polyps and those in the polyp neck are red or dark orange, producing a conspicuously spotted appearance. There is no clearly discernible basal section and polyps are distributed more or less evenly across the entire surface of the colony. Polyps are white, 0.5–1.3 mm tall when expanded, with colourless collaret and points in the holotype (Fig. 3D) but see variability section below.

Sclerites: Points are composed of warty to spiny spindles and well-developed thorny clubs distally (~0.1–0.3 mm long) (Figs. 16A, B). Proximally, spindles become larger, more robust, and more crescentic (~0.25–0.45 mm long), transitioning into a transverse orientation and merging with the collaret (Fig. 16A). The number of collaret rows is variable depending on polyp size but in large polyps this is approximately seven rows (Fig. 18C). The tentacles contain irregular, warty, scale-like forms, often slightly crescentic (~0.08–0.21 mm long) (Fig. 16C). The polyp neck contains many warty rod-like forms (~0.08–0.12 mm long) (Fig. 16D), which extend some way into the polyp mound, where they grade into cone-like clubs, as well as spindle-like, rod-like and oval forms with warts arranged in girdles (~0.1–0.18 mm long) (Fig. 17A). Between polyp mounds, the surface of the lobes contains similar sclerites (~0.1–0.18 mm long) but lacks well–developed clubs (Fig. 17B). The surface of the base contains mostly smaller sclerites than the surface of the lobes, including spheroids, a few clubs, and a gradation between radiates and oval or rod-like forms, which are girdled with warts and some with a narrow waist (~0.08–0.14 mm long) (Fig. 18A). The interior of both the lobes and the base contains highly sculptured rod-like, spindle-like and oval forms that are girdled with complex warts, while spheroids are particularly common in the interior of the base. Generally, sclerites of the interior tend to be larger than those of the surface regions (~0.1–0.2 mm long) (Figs. 17C; 18B).

Habitat and distribution: All specimens were collected at ≤20 m depths at the Manawatāwhi/Three Kings Islands (Fig. 2A). Paratypes MAGNT C013955 and MAGNT C015221 were recorded as having been collected on a rocky reef.

Variability: Paratype MAGNT C013955 (Fig. 15A) consists of only a fragment and was originally part of a much larger colony, probably ~10 cm in width (Fig. 5A). Paratype MAGNT C015221 has mostly dark orange collaret and point sclerites (Fig. 3E) in its small polyps. All four preserved specimens are otherwise very similar in growth form and colour, matching the colouration of live colonies *in situ* (Fig. 5A, B). The three paratypes correspond very closely to the holotype in their sclerite composition and size ranges (Figs. 16–18).

Comparisons: *Kotatea kurakootingotingo* specimens are superficially similar to congeners with a robust, lobate growth form. However, *K. kurakootingotingo* and *K. lobata* specimens are easily distinguishable, as the latter are not spotted and completely lack the former's large, highly sculptured spheroids in surface and interior sections (compare Figs. 17B, C; 18A, B and 20F; 21; 22A). Conversely, *K. kurakootingotingo* specimens lack the very large, highly branched, antler-like sclerites which are characteristic of interior sections in *K. lobata* (compare Figs. 17C; 18B and 21A; 22A). Additionally, *K. lobata* specimens are composed of smaller and much less robust sclerites overall (compare Figs. 16–18 and 20–22).

Kotatea kurakootingotingo specimens differ from *K. niwa* in lacking the distinct double-heads of that species' lobe surface and interior, while conversely, *K. niwa* lacks the rod-like and spindle-like forms present in the interiors of *K. kurakootingotingo* (compare Figs. 17B, C; 18A, B and 23F, G; 24A, B). Additionally, the polyps of *K. kurakootingotingo* specimens are typically around twice as large as those in *K. niwa* (up to ~1.3 mm vs up to ~0.75 mm; compare Figs. 18C and 24C). Note also that these two species were each resolved as monophyletic by phylogenetic analyses of mitochondrial *MutS* and nuclear *28S* (Fig. 1).

Etymology: The species name was composed by the Ngāti Kuri Tira Ma Te Wā Taiao (Science) Collective, and is a combination of the Māori words *kura*, red, and *kōtingotingo*, spotted. Note that for the species epithet, the '*ō*' in *kōtingotingo* is replaced by 'oo' to indicate a long vowel sound without the use of a macron. Ngāti Kuri provided the following ***kōrero* (narrative)**: "Kura Kōtingotingo's spots are reminiscent of the spots on *kōwhaiwhai* patterns, which are used to represent ancestors and to serve as reminders to their *whānau* (family). The sacred red spots of Kura Kōtingotingo represent the sacred memory of our *tūpuna* (ancestors) and the legacy they leave for us in caring for nature. When they depart the living world, their *wairua* (spirits) rest awhile on Manawatāwhi. With teardrops of *aroha* (love), they look back for one last sight of *Aotearoa*, before continuing their journey to *Te Ao Wairua* (the spirit world), their final resting place. Our *tūpuna* remain forever etched into our memories. When you gaze upon the *kōwhaiwhai* patterns of the rafters in our *wharenui* (meeting house), the spots you see are symbols put there by the families. *Whakapapa* (genealogy) is celebrated in our rafter patterns. Look back on all our dots and enjoy the connectedness of *whānau* and *whakapapa*. *Whakapapa* is our map of infinite inter-connectedness with our *tūpuna* and our *taiao* (natural world), linked to our spiritual domain."

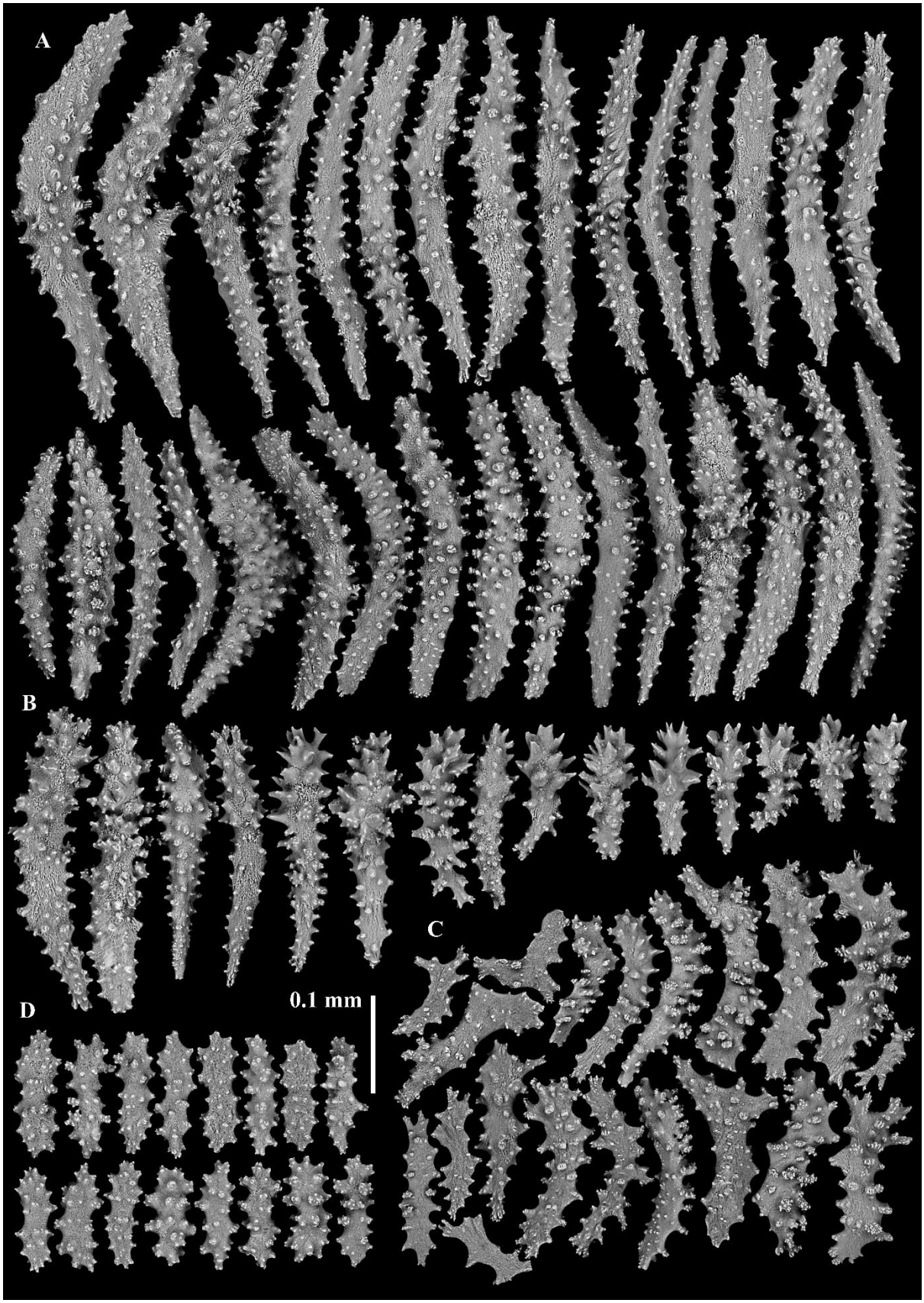

Figure 16. *Kotatea kurakootingotingo* gen. n., sp. n. holotype (NIWA 101538), SEMs of sclerites from: **A.** Collaret and points; **B.** Distal points; **C.** Tentacles; **D.** Polyp neck.

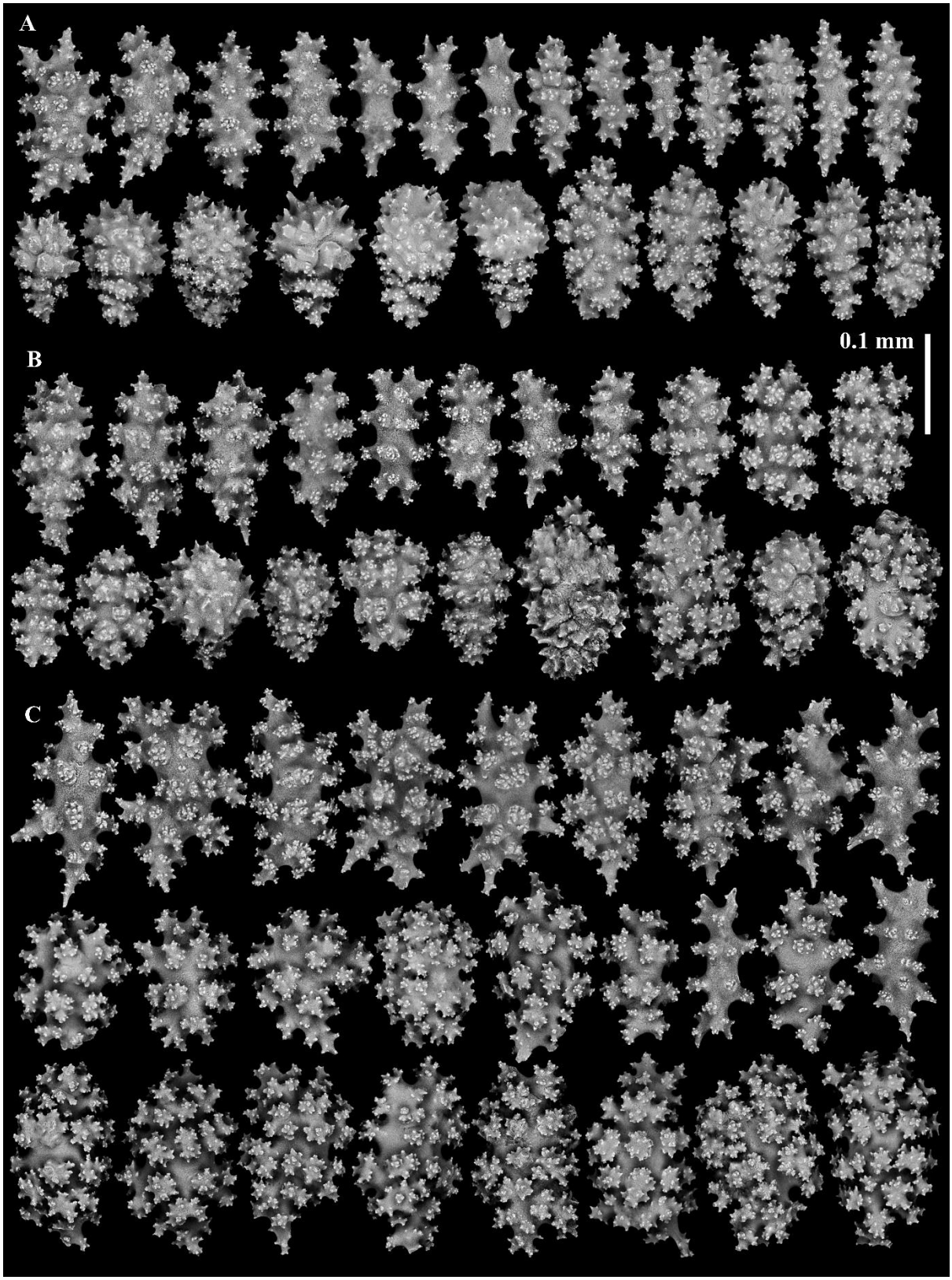

Figure 17. *Kotatea kurakootingotingo* gen. n., sp. n. holotype (NIWA 101538), SEMs of sclerites from: **A.** Polyp mound; **B.** Lobe surface; **C.** Lobe interior.

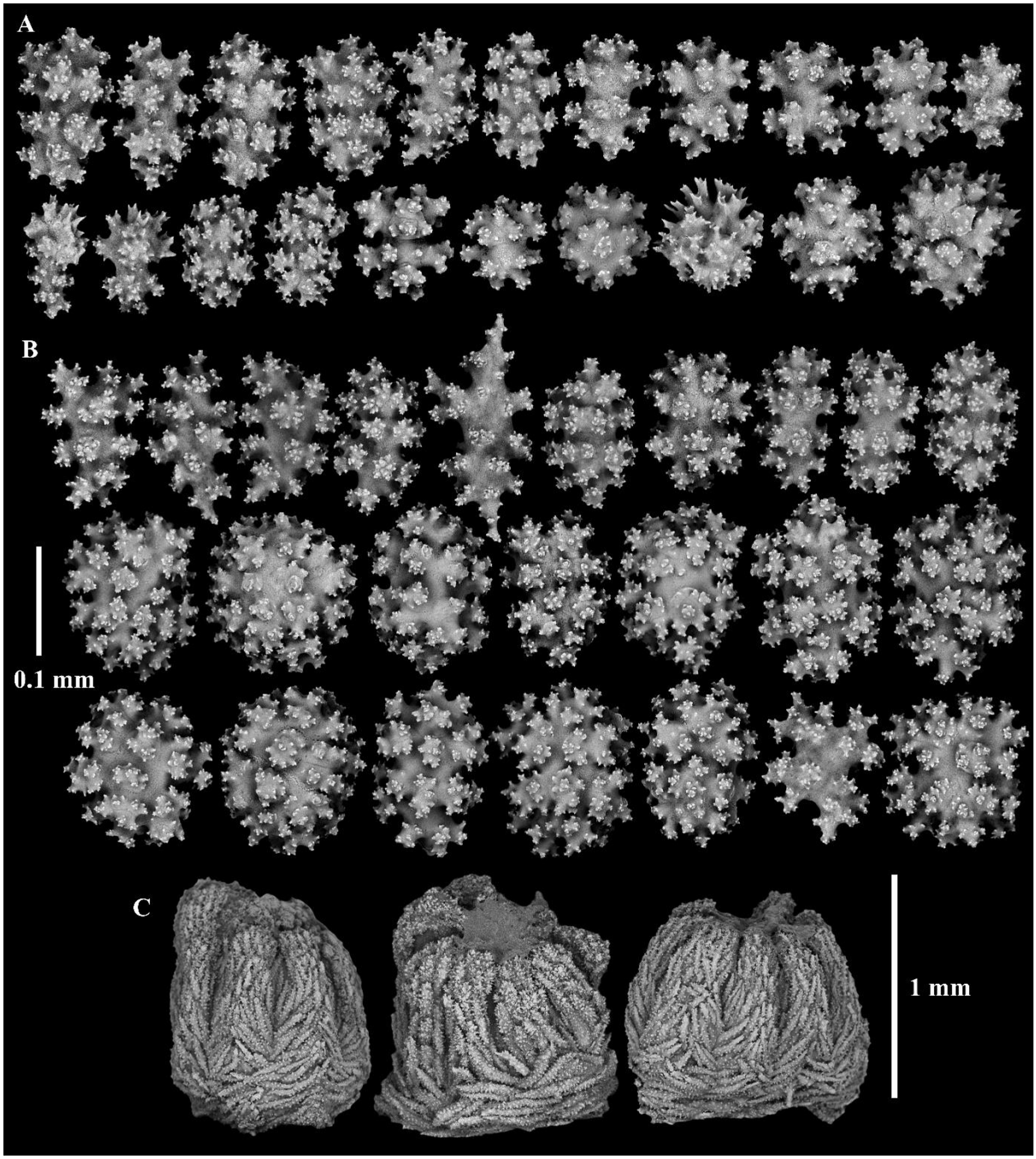

Figure 18. *Kotatea kurakootingotingo* gen. n., sp. n. holotype (NIWA 101538), SEMs of sclerites from: **A.** Base surface; **B.** Base interior; **C.** Polyps (*in situ*).

***Kotatea lobata* gen. n., sp. n.**

? *Alcyonium aurantiacum* Morton and Miller 1973: Pg. 154, 170, 272–274; Plate 6

? *Alcyonium aurantiacum* Westerskov and Probert 1981 in part: Pg. 111, Plate 28

? *Alcyonium aurantiacum* Morton 2004: Pg. 267; Fig. 14.4

? *Alcyonium aurantiacum* Grange et al. 2010 in part: Pg. 148

Figs. 2B; 3F; 5C–F; 19; 20; 21; 22

Material examined.

Holotype: NIWA 101313, stn. Z15913, Houhora Harbour, Northland, 34.8216˚S 173.1508˚E, depth 3-10 m, coll. NIWA, 30th November 2002.

Paratypes: Northland, NZ: **NIWA 58562**, stn. KAH0907/240, Battleship Rock, Moturoa Island, Bay of Islands, 35.2087˚S 174.1167˚E to 35.2140˚S 174.1172˚E, depth 29–30 m, coll. Oceans Survey 2020, 7th September 2009; **NIWA 101268**, stn. Z15906, Flax Islands, Mokohinau Islands, 35.9128˚S 175.0954˚E, depth 6–10 m, coll. Coral Reef Research Foundation, 23rd April 1999.

Auckland, NZ: **NIWA 101740**, stn. Z15978, Great Barrier Island/Aotea, 36.3330˚S 175.4740˚E, depth unknown, coll. NIWA, 7th June 2006; **NIWA 142995**, stn. O8, Manukau Harbour, Auckland, NZ, 37.0347˚S 174.6697˚E, depth 8 m, coll. New Zealand Oceanographic Institute, 2nd February 1976; **NIWA 143082**, stn. O4, Manukau Harbour, 37.1323˚S 174.6785˚E, depth 8 m, coll. New Zealand Oceanographic Institute, 2nd February 1976.

Other material: Northland, NZ: **NIWA 108960**, stn. Z17927, Nukutaunga Island, Cavalli Islands, 34.9750˚S 173.9635˚E, depth 6 m, coll. S. Hannam, 12th June 2017; **MA 656657**, stn. TK2013-1-019, Motukawanui Island, Cavalli Islands, 34.9860˚S 173.9367˚E to 34.9880˚S 173.9383˚E, depth 5–17.5 m, coll. G Wiren et al. 9th April 2013; **MAGNT C013956**, stn. unknown, Flax Islands, Mokohinau Islands, 35.9128˚S 175.0955˚E, depth 6 m, coll. Coral Reef Research Foundation, 23rd April 1999; **MAGNT C015222**, **MAGNT C015227**, **MAGNT C015228**, **MAGNT C015229**, **MAGNT C015230**, **MAGNT C015250** and **MAGNT C015251**, stn. unknown, Flax Islands, Mokohinau Islands, 35.9167˚S 175.1167˚E, depth 6–18 m, coll. J. Starmer, 23rd April 1999.

Auckland and Coromandel Peninsula, NZ: **MAGNT C001022** and **MAGNT C001023**, stn. unknown, Leigh Reef, Cape Rodney, 36.2833˚S 174.8167˚E, depth 20 m, coll. P. Alderslade and K. Harada, January 1978; **MAGNT C001693**, stn. unknown, Leigh Reef, Cape Rodney, 36.2833˚S 174.8167˚E, depth 0 m, coll. P. Alderslade, 4th February 1977; **MAGNT C015219**, stn. unknown, Great Mercury Island/Ahuahu, Mercury Islands, 36.6347˚S 175.7675˚E, depth 5–15 m,

coll. Queensland Museum, 6th December 1988; **MA 120774**, stn. unknown, Maukatia/Maori Bay, Muriwai, 36.8384˚S 174.4268˚E, depth 0 m, coll. W.M. Blom, 21st January 2015.

Description of the holotype.

Colony form: The holotype consists of an orange (ethanol-preserved), lobate colony measuring 7 cm height by 5 cm width (Fig. 19), composed of a single main lobe from which emerges a smaller, secondary lobe. The basal section is very short, reaching a maximum length of no more than a few millimetres. Polyps grow uniformly across most of the colony's surface, being absent only from the lowest edges of the base in close proximity to the substrate. Polyps are white, 0.5–1 mm tall when expanded, with colourless collaret and points (Fig. 3F).

Sclerites: Points are composed of flattened warty spindles (~0.16–0.2 mm long), many of which are slender, and thorny clubs distally (~0.08–0.24 mm long) (Fig. 20A, B). Proximally, the spindles become larger and more crescentic (~0.24–0.36 mm long), transitioning into a transverse orientation and merging with the collaret, which is four to six rows deep (Figs. 20A; 22B). The tentacles contain flat, warty, scale-like forms with irregular but often curved shapes (~0.06–0.2 mm long) (Fig. 20C). The polyp neck contains tuberculate to warty rod-like forms (~0.08–0.12 mm long), although these are few in number and occur mainly at its base (Fig. 20D). The polyp mounds are composed mostly of short, warty rod- and spindle-like forms and thorny clubs (~0.06–0.12 mm long) (Fig. 20E). The surface of the lobes between polyp mounds includes similar clubs as well as larger spindle-like forms and radiates (~0.09–0.2 mm long) (Fig. 20F). The surface of the base contains a few broad spindles (~0.25 mm long) but is mostly composed of similar radiates (although these can have more complex surface ornamentation than on the lobes), rod-like forms, clubs, and some leafy spheroids (~0.08–0.2 mm long) (Fig. 21B). The interior of both the lobes and the base are characterised by highly branched, irregular antler- and spindle-like forms (~0.08–0.35 mm long). The branched spindles are particularly common in the interior of the lobes (Fig. 21A), whereas the interior of the base possesses more antler-like sclerites (Fig. 22A).

Habitat and distribution: Specimens were collected from around the northern North Island of New Zealand, from Houhora Harbour to the Mercury Islands on the eastern coasts and from Muriwai to Manukau Harbour on the western coast between the intertidal and depths of ~30 m (Fig. 2B, C). *Kotatea lobata* is also notable for occasionally being exposed at low tide, usually under boulders or overhangs (Fig 5E–F). Many of the specimens were recorded as having been collected from under boulders and from rock faces.

Variability: The number of lobes can vary substantially between specimens (Figs. 5C–F; 19). The size of the colony and thickness of the lobes is also highly dependent on a colony's state of expansion. Examined contracted specimens measured up to 8 cm tall. In preserved specimens,

colour ranges from light to dark orange or even red (matching colouration of live specimens *in situ*, Fig. 5C–E), and occasionally dull beige, which is the case for MAGNT C001022 and MAGNT C001693 (Fig. 19), but this is probably due to initial fixation in formalin. Wherever polyps are retracted on contracted colonies the polyp mounds are often clearly visible and can give *K. lobata* specimens a distinctive scaly appearance, which is especially clear in the holotype NIWA 101313 (Fig. 19). Lobes always emerge from a short basal section but can be either cylindrical or somewhat flattened in one plane, as is the case for paratype NIWA 58562 (Fig. 19).

While minor variations in the relative frequencies of sclerite forms exist between specimens (e.g. one specimen may have more clubs and fewer radiates in its lobe surface compared to another), the composition of sclerite forms is consistent across all specimens (i.e. the lobe surface is always composed of clubs, radiates and large spindle-like forms), matching the holotype (Figs. 20–22). The size ranges of all specimens' sclerites also falls within those described for the holotype.

Comparisons: *Kotatea lobata* is most similar in appearance to the robustly lobed congeners *K. niwa* and *K. kurakootingotingo*, and to *K. aurantiaca*. Differences from the latter two species are discussed under their respective accounts above.

Kotatea lobata specimens are easily distinguished from *K. niwa* in lacking spots, but also in lacking the spheroids and distinctive interior double-heads found in this species. Conversely, the large, slender, antler-like spindles found in the interior of *K. lobata* are absent in *K. niwa* (compare Figs. 21A; 22A and 23G; 24B. The sclerites of *K. lobata* are also overall smaller and less highly sculptured than those of *K. niwa*.

The fleshy lobes of *Ushanaia solida* superficially resemble *K. lobata*, but *U. solida* is easily differentiated by a lack of the slender, highly branched, antler-like interior spindles which are characteristic of *K. lobata* specimens.

Etymology: The species name *lobata* is the Latin term for lobed.

Remarks: Intertidal observations of *A. aurantiacum* probably refer to *K. lobata* rather than *K. aurantiaca* (see remarks under *K. aurantiaca* above).

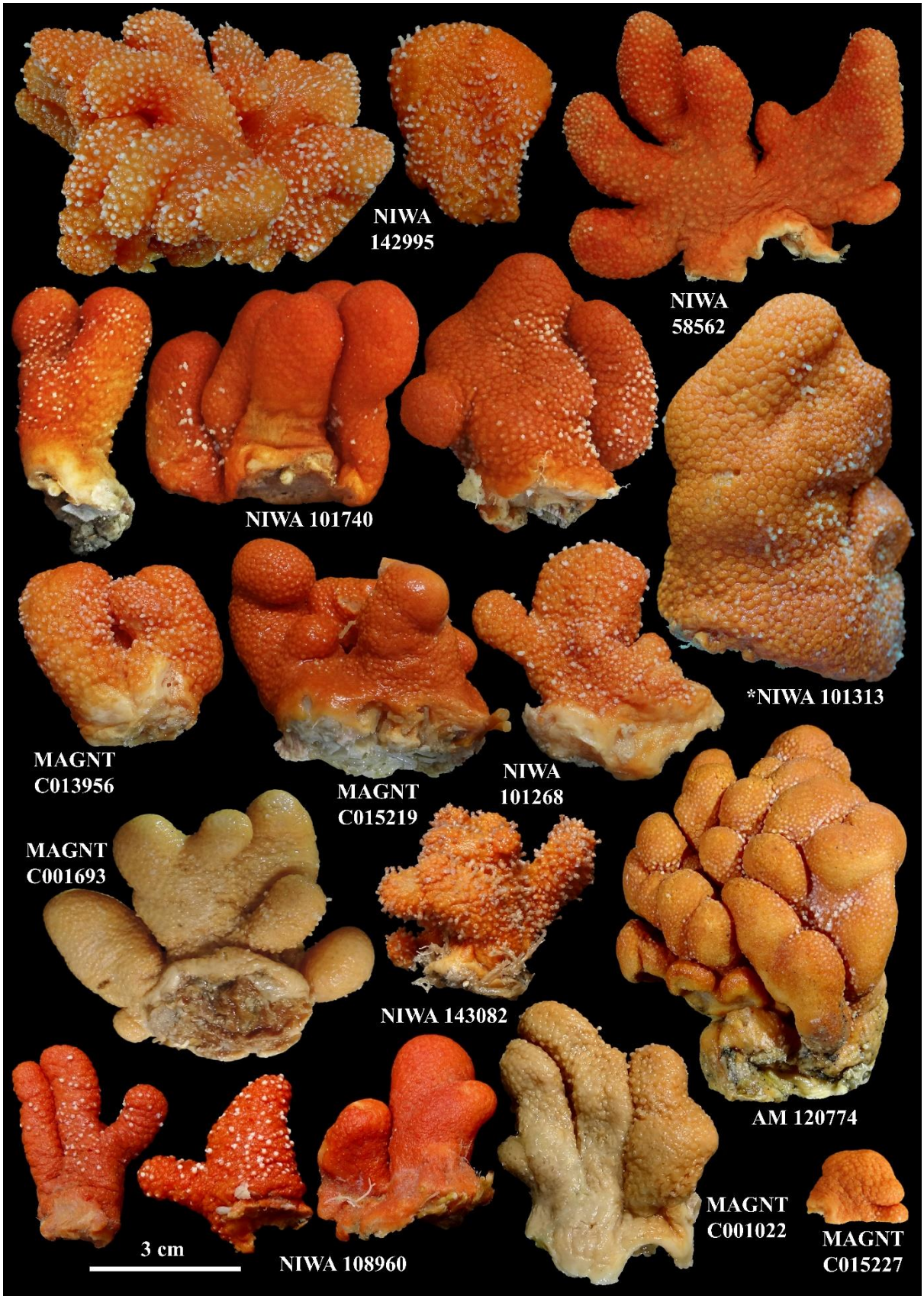

Figure 19. Selected preserved specimens of *Kotatea lobata* gen. n., sp. n. Note that NIWA 142995, NIWA 101740 and NIWA 108960 contain additional fragments that are not depicted. *Holotype.

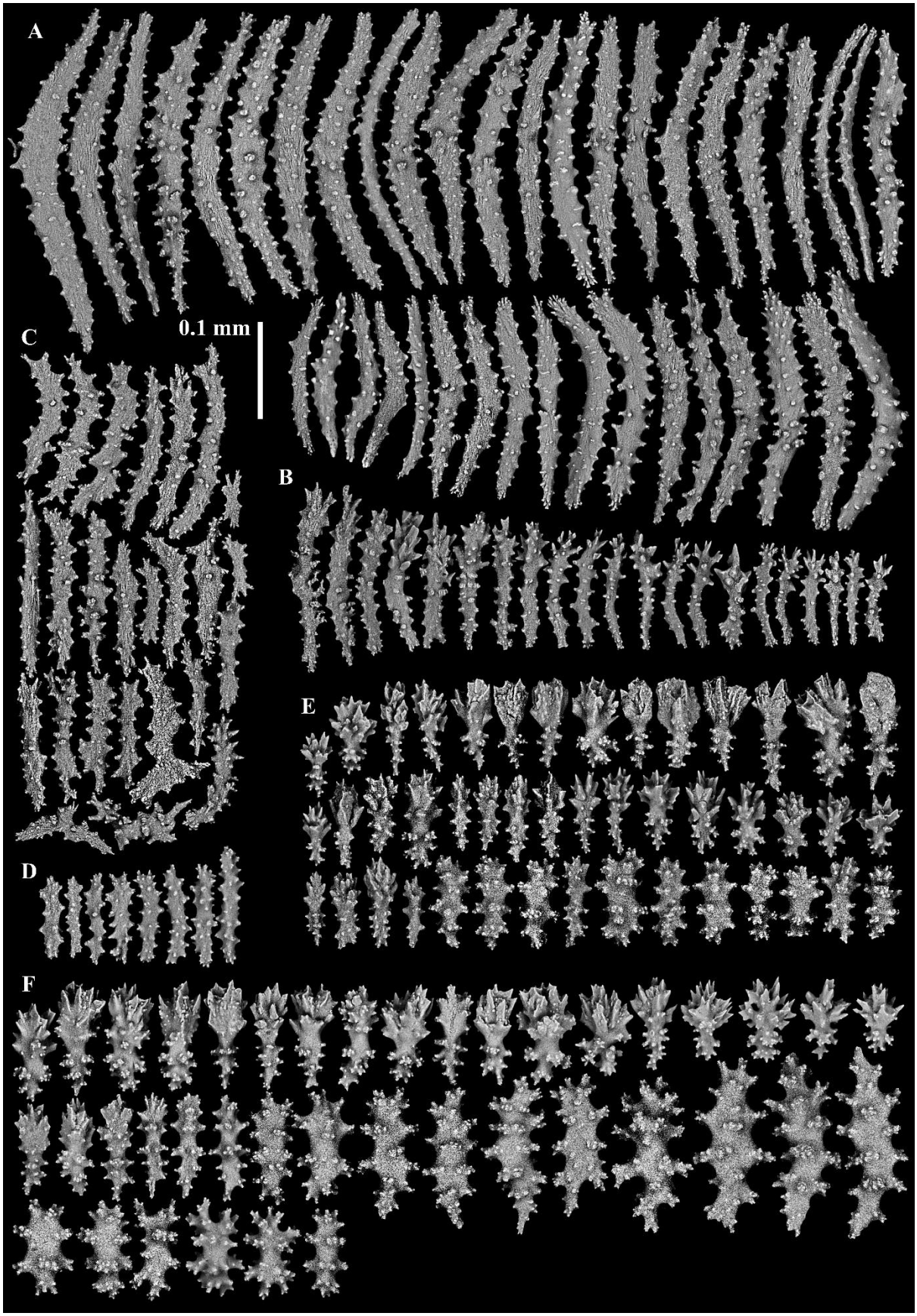

Figure 20. *Kotatea lobata* gen. n., sp. n. holotype (NIWA 101313), SEMs of sclerites from: **A.** Collaret and points; **B.** Distal points; **C.** Tentacles; **D.** Polyp neck; **E.** Polyp mound; **F.** Lobe surface.

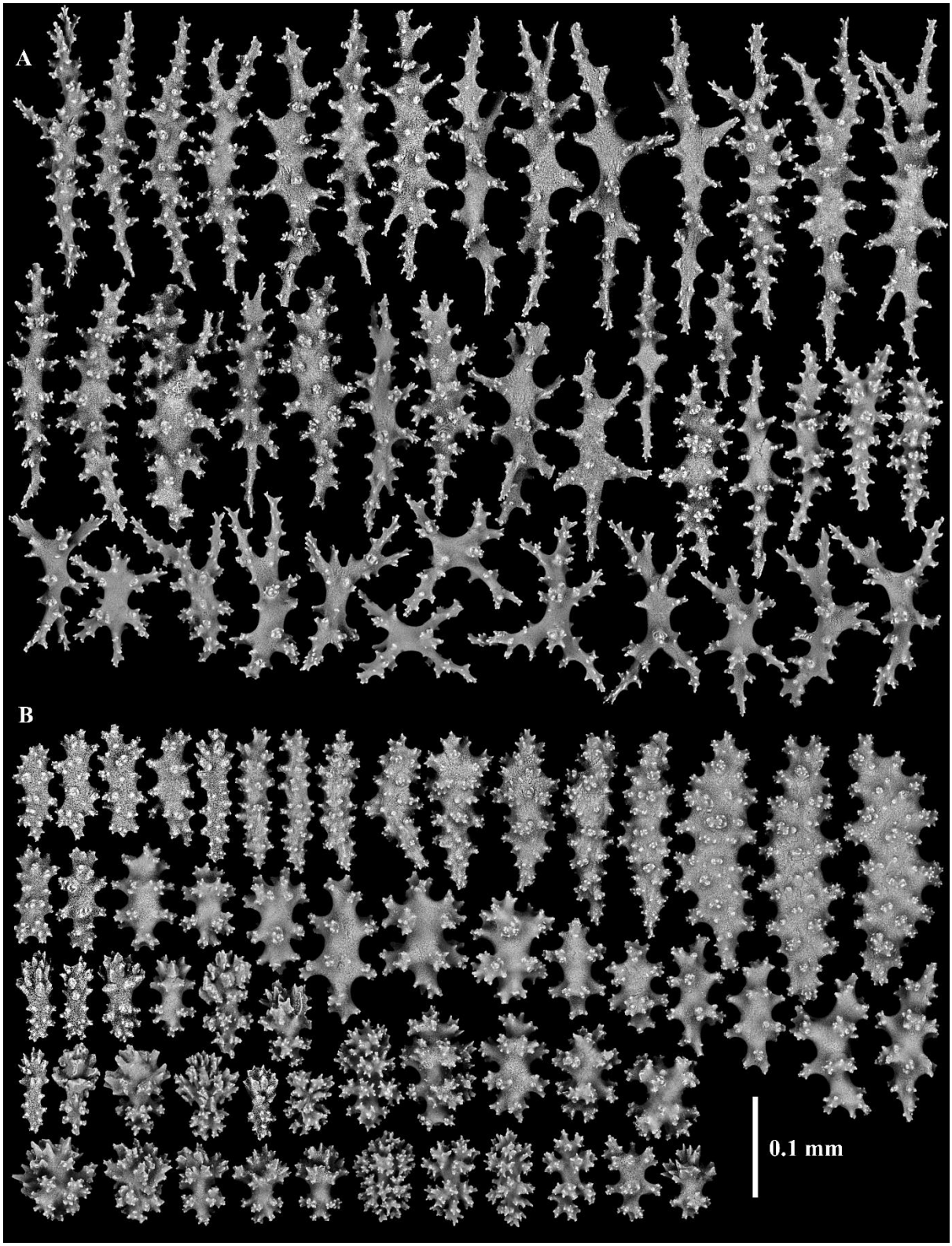

Figure 21. *Kotatea lobata* gen. n., sp. n. holotype (NIWA 101313), SEMs of sclerites from: **A.** Lobe interior; **B.** Base surface.

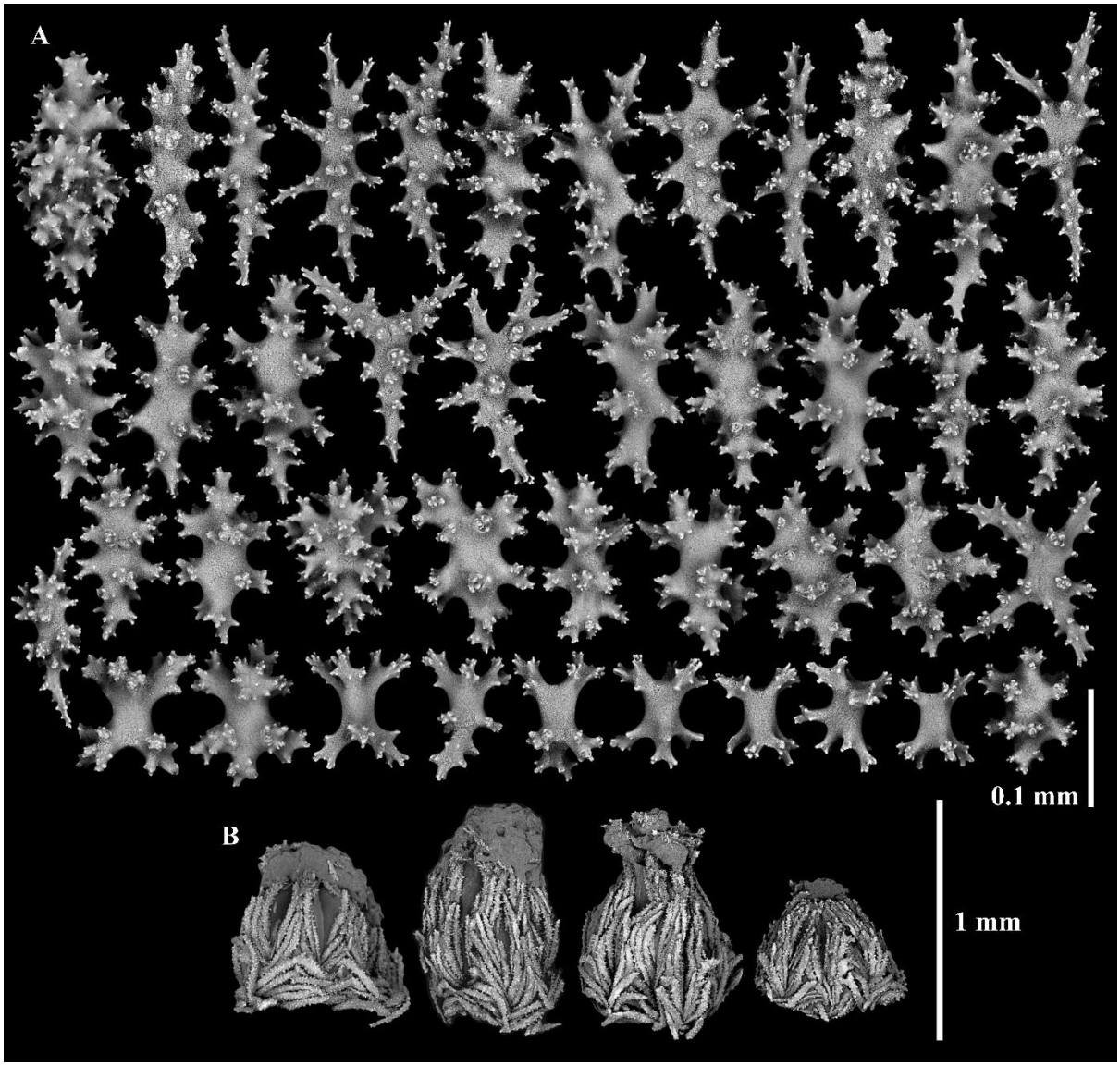

Figure 22. *Kotatea lobata* gen. n., sp. n. holotype (NIWA 101313), SEMs of sclerites from: **A.** Base interior; **B.** Polyps (*in situ*).

***Kotatea niwa* gen. n., sp. n.**

Figs. 2A–B; 3G; 15B; 23; 24

Material examined.

Holotype: MAGNT C015226, stn. unknown, Piwhane/Spirits Bay, Northland, NZ, 34.4167˚S 172.7833˚E, depth 17–20 m, coll. J. Starmer, April 1999.

Paratype: MAGNT C015224, stn. unknown, ~1 km NE of Moekawa/South West Island, Manawatāwhi/Three Kings Islands, NZ, 34.1667˚S 172.0833˚E, depth 17 m, coll. J. Starmer, 20th April 1999.

Other material: NIWA 58543, stn. KAH0907/194, ~1 km NW of Okahu Island, Bay of Islands, Northland, NZ, 35.1917˚S 174.1922˚E to 35.1962˚S 174.1903˚E, depth 37–40 m, coll. Oceans Survey 2020, 3rd September 2009.

Description of the holotype.

Colony form: The holotype is a lobate colony, measuring 1.5 cm height by 2.5 cm width (Fig. 15B). The surface of the colony (ethanol-preserved) is orange with small red spots, which are produced by red polyp neck and mound sclerites. Polyps occur all over the colony's surface but are sparser towards its base and absent from the very short basal section. Polyps are white, 0.5–0.75 mm tall when expanded, with colourless collaret and points (Fig. 3G).

Sclerites: Points are composed of warty spindles (~0.15–0.25 mm long), most of which are flattened, and thorny clubs distally (~0.08–0.22 mm long) (Figs. 23A, B). Proximally, the spindles become larger, more robust, and more crescentic (~0.2–0.38 mm long), transitioning into a transverse orientation and merging with the collaret (Fig. 23A). The number of collaret rows is variable depending on polyp size but in large polyps this is approximately seven rows (Fig. 24C). The tentacles contain irregular, warty, scale-like forms, often slightly crescentic (~0.05–0.18 mm long) (Fig. 23C). The polyp neck contains abundant warty rod-like forms (~0.08–0.1 mm long) (Fig. 23D), which extend into the polyp mound, where they gradually give way to thorny clubs (~0.06–0.15 mm long) (Fig. 23E). The surface of the lobes between polyp mounds contains a mixture of thorny clubs and warty double-heads (~0.08–0.15 mm long) (Fig. 23F). The surface of the base contains warty radiates grading into double-heads, and a few spheroids but tends to lack clubs (Fig. 24A). The interior of both the lobes and the base contains highly sculptured spheroids and double-heads, as well as some oval or rod-like forms girdled with warts, all of which are usually larger than the sclerites of the surface regions (~0.12–0.2 mm long) (Figs. 23G; 24B).

Habitat and distribution: *Kotatea niwa* specimens were collected from the Manawatāwhi/Three Kings Islands, Piwhane/Spirits Bay and the Bay of Islands at depths between 17 and 40 m (Fig. 2A, B).

Variability: Both the paratype and NIWA 58543 possess collaret and point sclerites which are coloured dark orange to red (colourless in holotype) in their smaller polyps. All three preserved specimens are otherwise very similar in colony colour and growth form (Fig. 15B), and the paratype and NIWA 58543 correspond very closely to the holotype in terms of sclerite composition and size ranges (Figs. 23; 24).

Comparisons: *Kotatea niwa* is most similar to *K. kurakootingotingo* and *K. lobata*, which share its robust, lobate growth form. Differences from these species are discussed under their respective accounts above.

Etymology: The species is named for NIWA, the National Institute of Water and Atmospheric Research in New Zealand, where the research described herein was conducted.

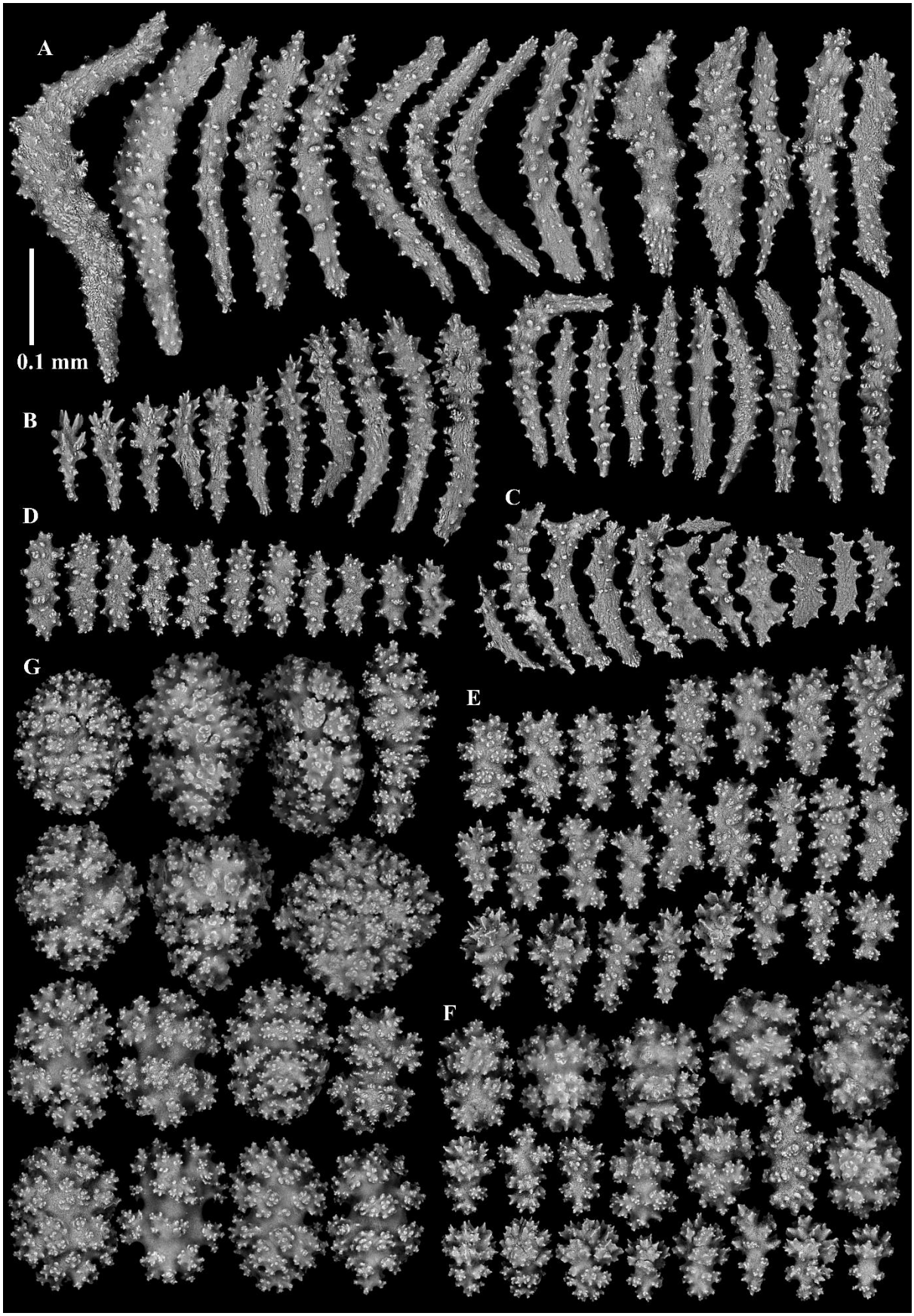

Figure 23. *Kotatea niwa* gen. n., sp. n. holotype (MAGNT C015226), SEMs of sclerites from: **A.** Collaret and points; **B.** Distal points; **C.** Tentacles; **D.** Polyp neck; **E.** Polyp mound; **F.** Lobe surface; **G.** Lobe interior.

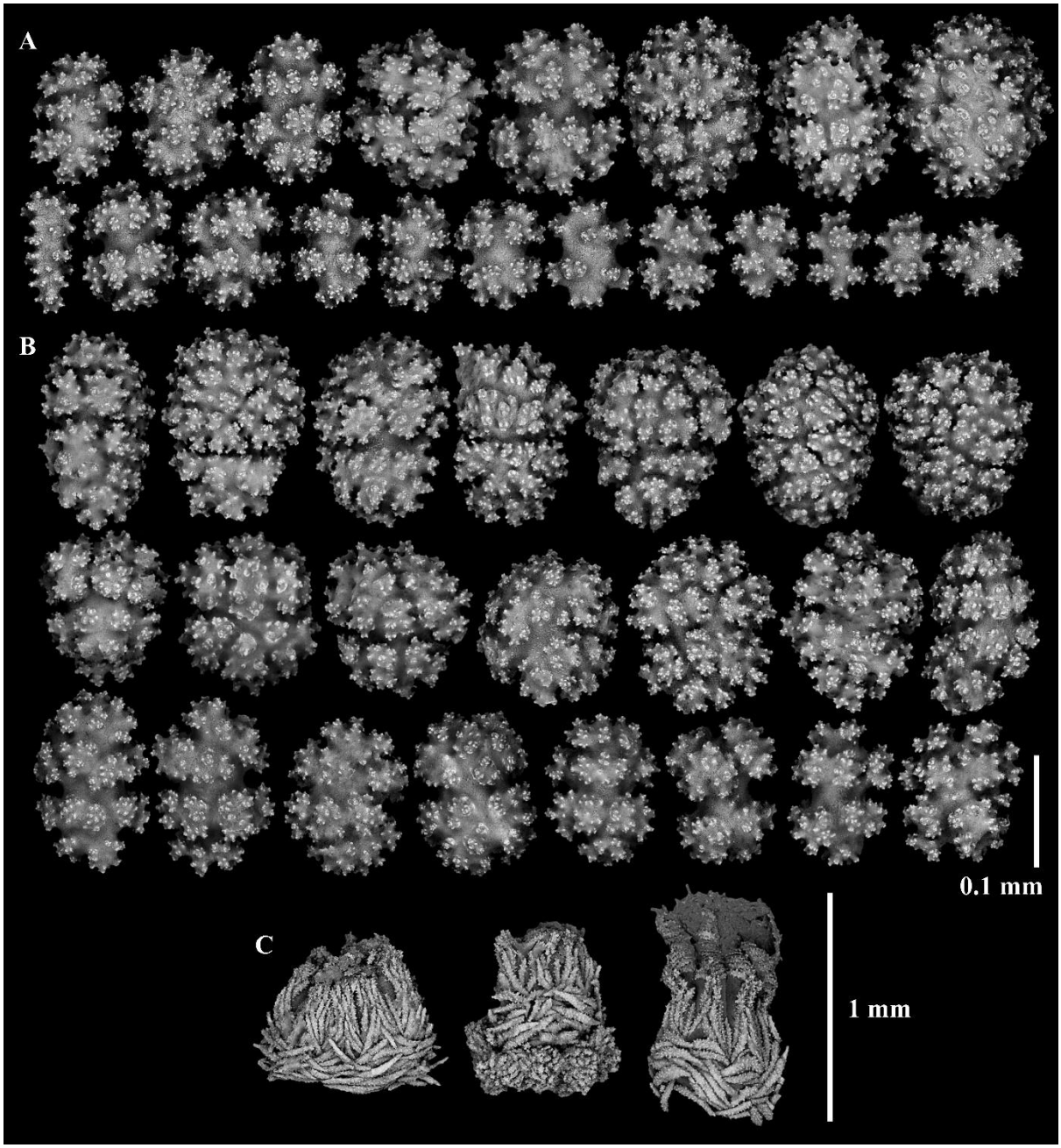

Figure 24. *Kotatea niwa* gen. n., sp. n. holotype (MAGNT C015226), SEMs of sclerites from: **A.** Base surface; **B.** Base interior; **C.** Polyps (*in situ*).

***Kotatea raekura* gen. n., sp. n.**

Figs. 2A; 3H; 4D; 25A; 26; 27A–D

Māori name: Raekura

Material examined.

Holotype: NIWA 101537, stn. Z15942, Princes Islands, Manawatāwhi/Three Kings Islands, NZ, 34.1759˚S 172.0495˚E, depth 10–20 m, coll. NIWA, 24th February 2002.

Paratypes: MA 73621, same data as holotype; **NIWA 100968**, stn. Z15632, Princes Islands, Manawatāwhi/Three Kings Islands, NZ, 34.1777˚S 172.0465˚E, depth 6–11 m, coll. Coral Reef Research Foundation, 15th April 1999.

Other material: Manawatāwhi/Three Kings Islands, NZ: **MAGNT C015223**, stn. unknown, Princes Islands, 34.1667˚S 172.0500˚E, depth 5–10 m, coll. J. Starmer, 15th April 1999; **MAGNT C013954**, stn. unknown, Princes Islands, 34.1777˚S 172.0465˚E, depth 10 m, coll. Coral Reef Research Foundation, 15th April 1999; **MA 656516**, stn. TK2013-25-276, Ōhau/West Island, 34.1839˚S 172.0304˚E, depth 6–11 m, coll. S. Hannam et al. 12th April 2013.

Description of the holotype.

Colony form: The holotype (Fig. 25A) is a fragment of a larger colony (Fig. 4D) and measures 6 cm height by 6 cm width. It is orange (ethanol-preserved), fading towards the base. Polyps are white, 0.5–1 mm tall when expanded, with orange collaret and points (Fig. 3H). They occur all over the lobes but are most densely packed at their tips and absent from the base, which is ~2 cm tall.

Sclerites: Points are composed of warty spindles (~0.18–0.26 mm long), which are rarely branched and often flattened, and poorly developed thorny clubs distally (~0.1–0.2 mm long) (Fig. 26A, B). Proximally, the spindles become larger, more robust, and more crescentic (~0.28–0.36 mm long), transitioning into a transverse orientation and merging with the collaret, which is three to five rows deep (Figs. 6A; 27D). The tentacles contain irregular, warty, scale-like forms, often curved (~0.1–0.2 mm long) (Fig. 26C), and the polyp neck contains warty rod-like forms (~0.08–0.12 mm long) (Fig. 26D). Polyp mounds are composed mainly of thorny and warty clubs (~0.08–0.14 mm long) (Fig. 26E). The surface of lobes between mounds contains similar clubs along with numerous warty, girdled spindle-like forms (~0.08–0.18 mm long) (Fig. 26F). The surface of the base contains thorny clubs along with some radiates and spindle-like forms girdled with spines or warts, which tend to have a simpler surface ornamentation and are smaller than those in the lobe surface (~0.06–0.14 mm long) (Fig. 27B). The sclerites in the interior of both the lobes and the

base are composed mainly of irregular forms with branches and very tall warts (~0.1–0.2 mm long) (Fig. 27A, C).

Habitat and distribution: All known specimens originate from shallow depths (≤20 m) at the Manawatāwhi/Three Kings Islands (Fig. 2A). MAGNT C013954 was recorded as growing on a rock wall.

Variability: All preserved specimens are similar in growth form, but colour can vary from one colony to another with some specimens being paler and some darker than the holotype (Fig. 25A). The colour of the collaret and points corresponds roughly to the overall colour of the colony, being paler in some specimens and darker in others, but never fully colourless. Both paratypes and the three non-type specimens correspond very closely with the sclerite composition and size ranges described for the holotype (Figs. 26; 27).

Comparisons: *Kotatea raekura* is most similar to *K. aurantiaca* and *K. teorowai*, but easily distinguished from both these species by its orange collaret and points. Further differences from *K. aurantiaca* are discussed under that species.

Apart from containing sclerites that are overall far more robust (compare Figs. 26; 27 and 28), *K. raekura* specimens further differ from *K. teorowai* in possessing abundant interior sclerites sculptured with tall warts. In contrast, the few interior sclerites present in *K. teorowai* have only minimal surface ornamentation (compare Figs. 27A, C and 28H). The colour difference between these two species is also conspicuous (compare Fig. 25A and B), and *K. raekura* has so far only been collected from much shallower depths than *K. teorowai* (< 20 m vs. ~70 m).

Etymology: The species name was composed by the Ngāti Kuri Tira Ma Te Wā Taiao (Science) Collective, and is a combination of the Māori words *rae*, forehead or ancient, treasured thoughts, and *kura*, which can mean red, but also red feathers used for decoration, treasure, sacred or precious possessions, divine law, philosophy and chief. Ngāti Kuri provided the following ***kōrero* (narrative):** "The forehead, the brain, this is where all pure thoughts are created and stored. Knowledge is passed on through *wānanga* (tribal knowledge and learning). Our *mātauranga* (knowledge) exists in both the visible and invisible universe. The *taiao* (natural world) says to us that we are simply guardians of a delicate balance of ecosystems. We need to continually create sustainable options to safeguard the future. We must listen to the voice of *Papatūānuku* (Earth mother). The orange crown at the top of Raekura's polyps symbolises *Te Ōpuawānanga* (the flowering of knowledge) that is prevalent in the teachings of our *tūpuna* (ancestors). We must continue to strive to seek new knowledge whilst holding on to our ancient knowledge. Raekura explores the many dimensions towards knowledge acquisition. Many *iwi* and *hapū* (tribes) have their unique complementing *mātauranga*. Dr Rangi Matamua of Tūhoe was given a manuscript from his grandfather to share the astronomical knowledge written by their *tūpuna* Te Kokau

Himiona Te Pikikotuku and his son Rawiri Te Kokau in the 19th century. His grandfather uttered these wise words: ‘Knowledge that isn’t shared isn’t knowledge’.”

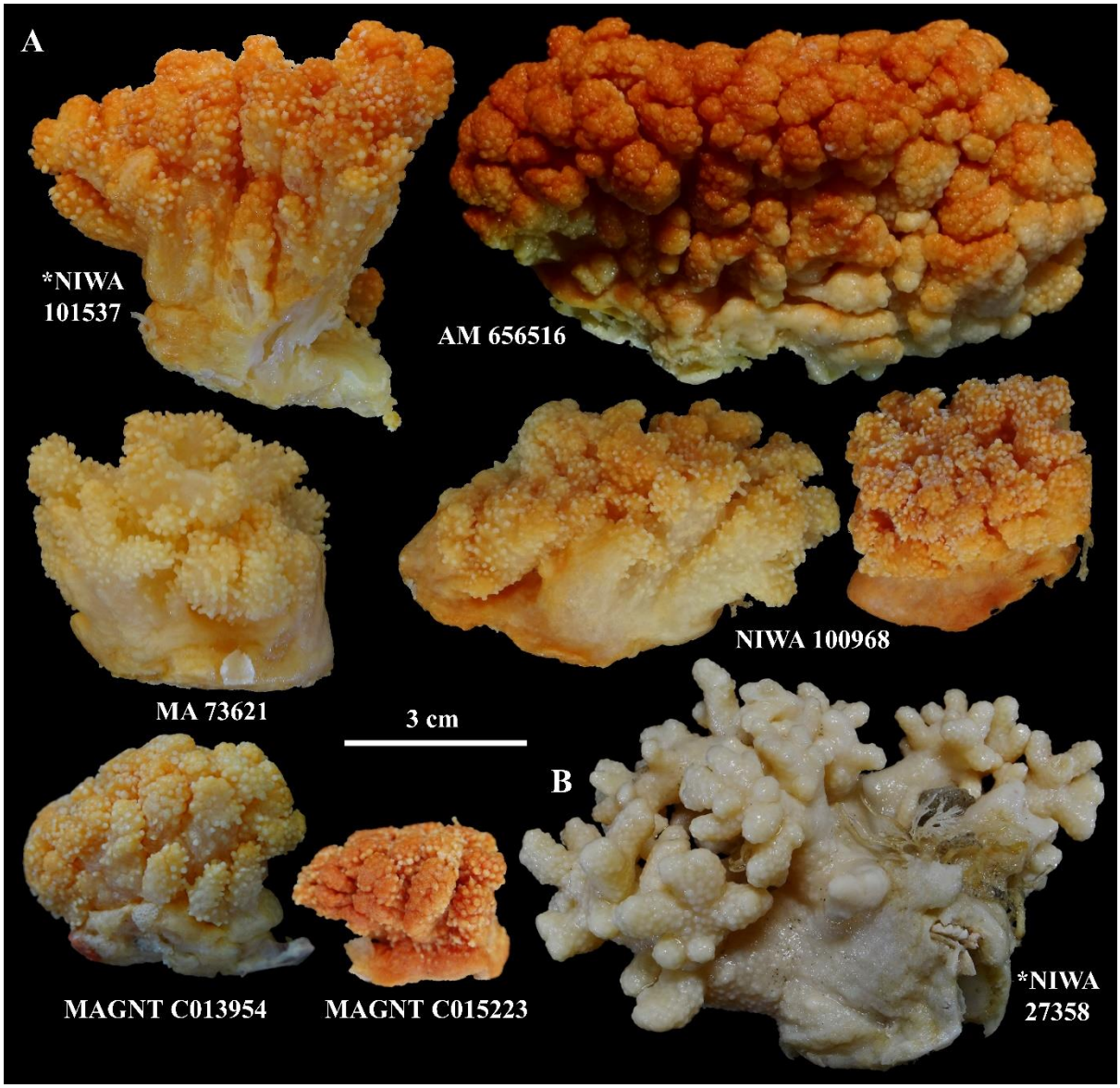

Figure 25. Preserved specimens of: **A.** *Kotatea raekura* gen. n., sp. n.; **B.** *K. teorowai* gen. n., sp. n. Note that lot AM 656516 includes additional fragments that are not shown. *Holotype.

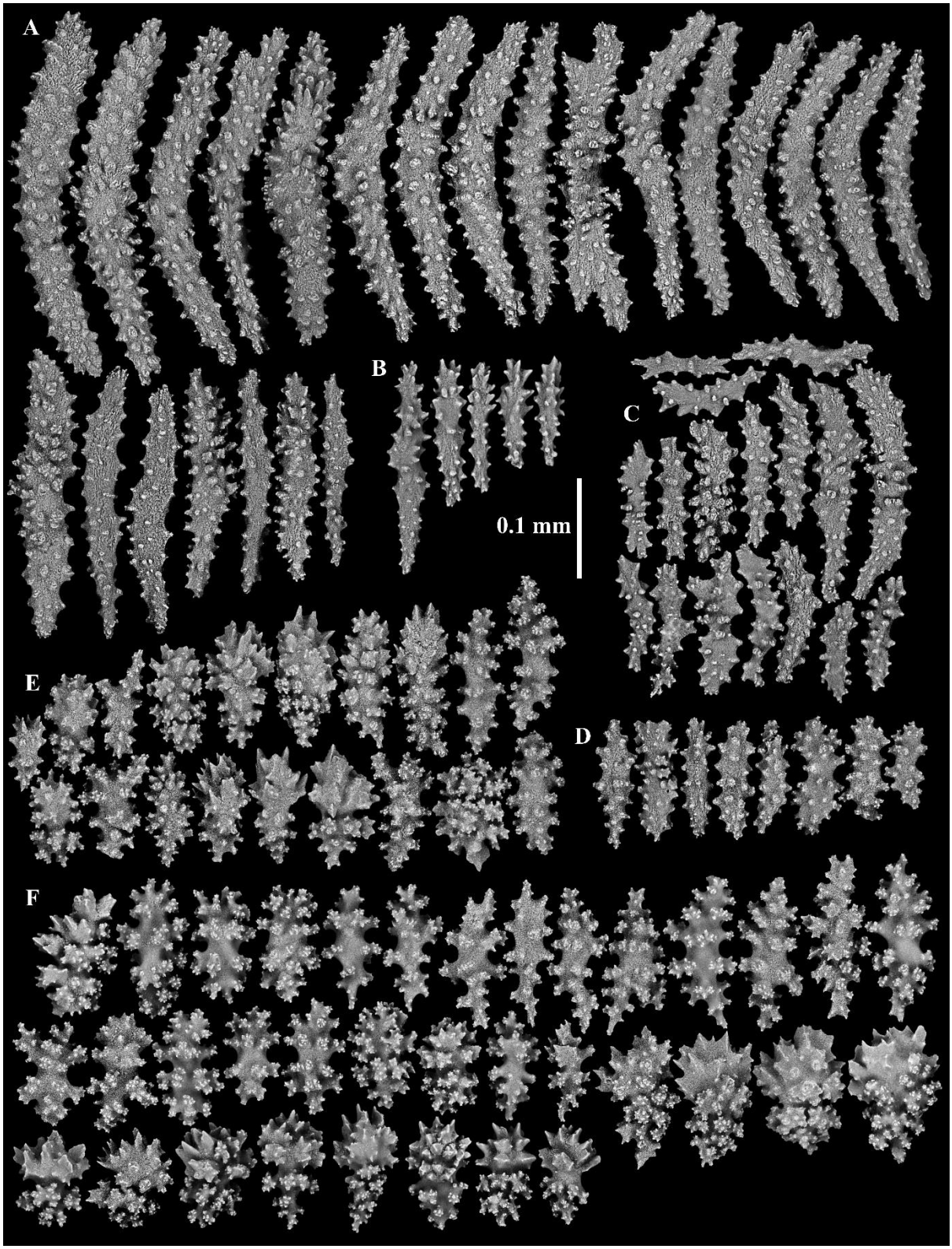

Figure 26. *Kotatea raekura* gen. n., sp. n. holotype (NIWA 101537), SEMs of sclerites from: **A.** Collaret and points; **B.** Distal points; **C.** Tentacles; **D.** Polyp neck; **E.** Polyp mound; **F.** Lobe surface.

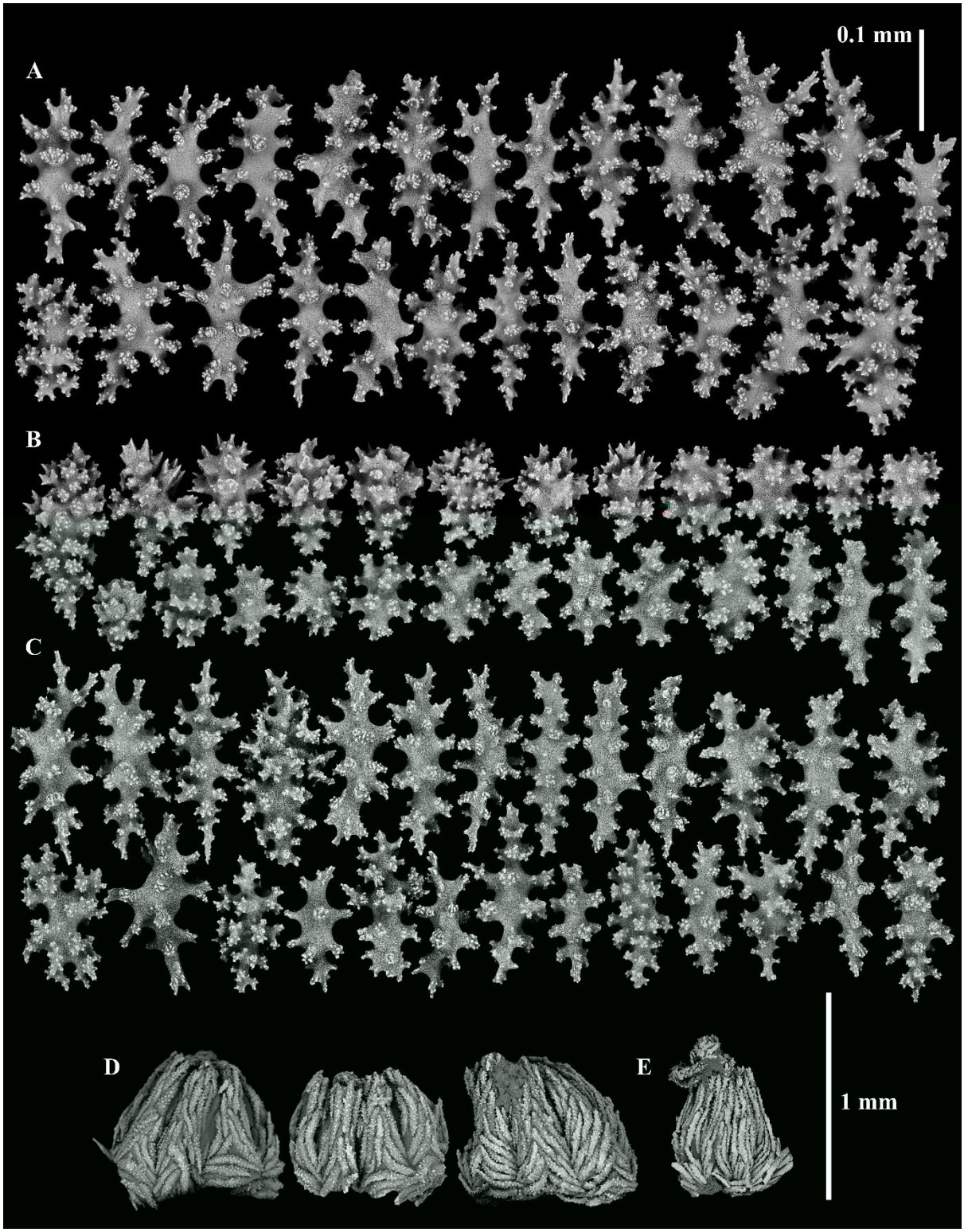

Figure 27. *Kotatea raekura* gen. n., sp. n. holotype (NIWA 101537) **(A–D)**, SEMs of sclerites from: **A.** Lobe interior; **B.** Base surface; **C.** Base interior; **D.** Polyps (*in situ*). *K. teorowai* gen. n., sp. n. holotype (NIWA 27358), SEMs of sclerites from: **E.** Polyp (*in situ*).

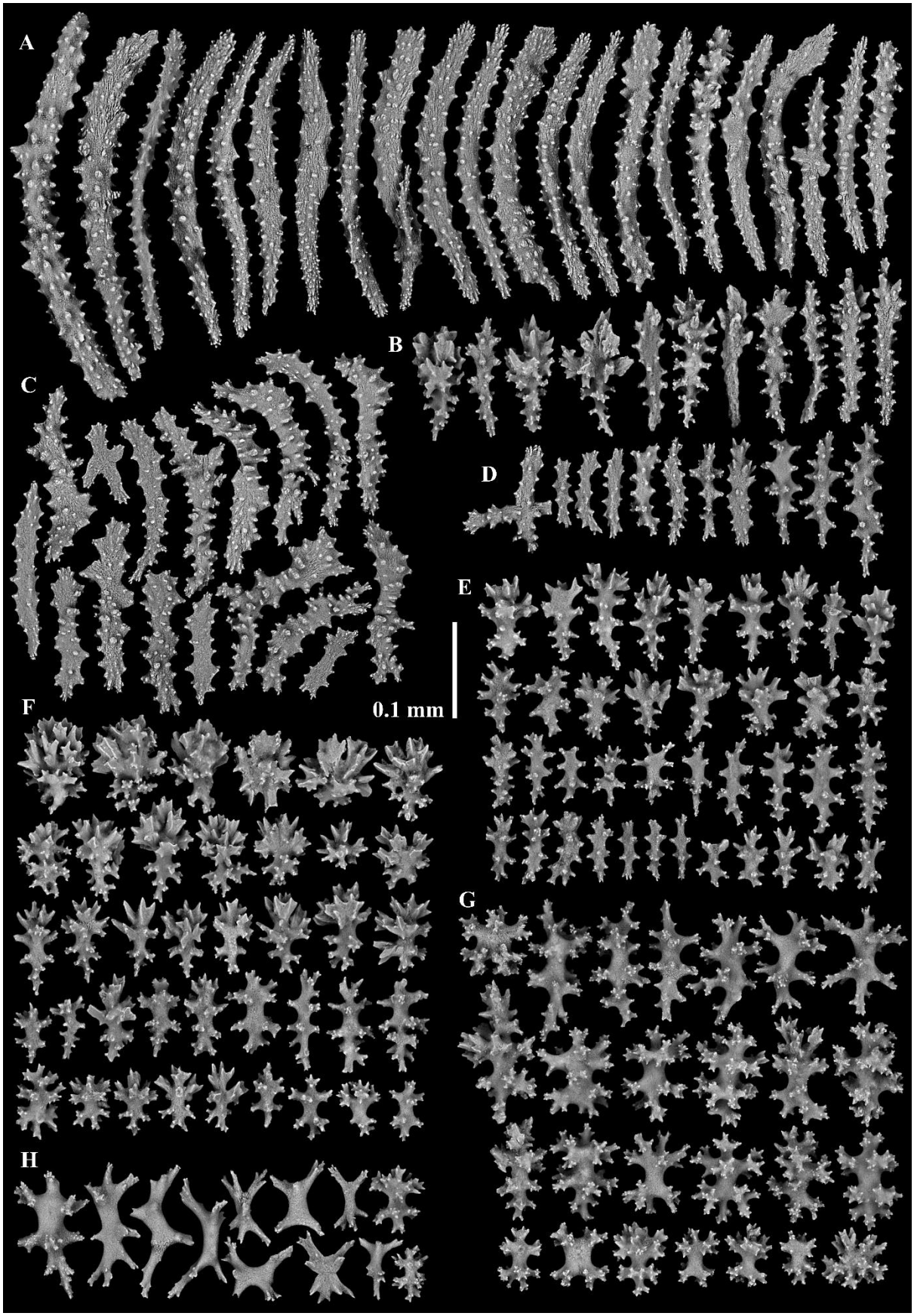

Figure 28. *Kotatea teorowai* gen. n., sp. n. holotype (NIWA 27358), SEMs of sclerites from: **A.** Collaret and points; **B.** Distal points; **C.** Tentacles; **D.** Polyp neck; **E.** Polyp mound; **F.** Lobe surface; **G.** Base Surface; **H.** Lobe and base interior.

***Kotatea teorowai* gen. n., sp. n.**

Figs. 2B; 25B; 27E; 28

Māori name: Te Orowai

Material examined.

Holotype: NIWA 27358, stn. Z9712 (KAH9901/88), ~12 km NW of North Cape, Northland, NZ, 34.3570˚S 172.8850˚E, depth 69 m, coll. NIWA, 29th January 1999.

Description of the holotype.

Colony form: The holotype consists of an entirely white, lobate colony (ethanol-preserved), measuring 6.5 cm in height by 9 cm in width (Fig. 25B). Several major lobes arise from a thick stalk, and divide into numerous smaller, rounded lobes of various thickness. Polyps are most densely packed at ends of the lobes but occur all over the colony, except for a ~1 cm proximal region of the base. The white polyps are all retracted and have colourless collaret and points.

Sclerites: Points are composed of slender, tuberculate spindles (~0.18–0.3 mm long), and often well-developed thorny clubs distally (~0.1–0.18 mm long) (Fig. 28A, B). Proximally, the spindles become slightly larger and more crescentic (~0.25–0.4 mm long), transitioning into a transverse orientation and merging with the collaret, which is six to eight rows deep (Figs. 28A; 27E). The tentacles contain irregular, warty, scale-like forms, often slightly crescentic (~0.08–0.2 mm long) (Fig. 28C). The polyp neck contains mostly warty rod-like and spiny spindle-like forms (~0.06–0.16 mm long), which become larger and more abundant towards the neck base (Fig. 28D). The polyp mounds mainly contain thorny clubs along with some radiates, and spiny spindle-like and warty rod-like forms (~0.06–0.08 mm long), which all grade into one another (Fig. 28E). The surface of the lobes between polyp mounds contains radiates, spiny spindles and thorny clubs grading into leafy spheroids (~0.06–0.1 mm long) (Fig. 28F). The surface of the stalk contains spiny radiates and spindle-like forms, some with long processes, which tend to be larger and more heavily branched than those in other regions of the colony (~0.08–0.15 mm long) (Fig. 28G). Interior sclerites are very sparse in the lobes and almost entirely absent in the lower sections of the base, occurring in any appreciable number only from around halfway up the colony stalk, and are comprised of irregularly branched or thorny radiates (~0.06–0.12 mm long) (Fig. 28H).

Habitat and distribution: *Kotatea teorowai* can occur syntopically with *K. kapotaiora*, as the holotypes for both species were collected together in the same sample.

Variability: The holotype is the only specimen of *K. teorowai* available at the time of writing.

Comparisons: *Kotatea teorowai* is most similar to *K. amicispongia*, *K. aurantiaca* and *K. raekura*, differences from which are discussed under each of these species.

Etymology: The species name was composed by the Ngāti Kuri Tira Ma Te Wā Taiao (Science) Collective, and is a combination of the Māori words *oro*, to resound, echo, resonate or rumble, and *wai*, water. Ngāti Kuri provided the following ***kōrero* (narrative)**: "The many surging currents are absorbed and deflected by the many branches of Te Orowai, thus creating the illusion of a symphony of sounds emanating from the depths of our oceans. There is a resonance of the many voices of the sea animals. *Te ha o Hinemoana* (the breath of Hinemoana) gives life and purpose to the many complementing sounds of the deep. The rhythm of the ocean is oft captured in the *hōhonu mātauranga* (deep and profound knowledge) of our *tūpuna* (ancestors). Our modes of learning are orchestrated by the ebb and flow of rhythmic patterns of nature. We create poetic imagery to memorise and recite our many varied *kōrero* (stories/narratives) and events through *mōteatea* (poetic chant), *waiata* (song), *haka* (dance), *whakataukī* (proverbs), *kōrero pūrakau* (the telling of myths and legends) and so on. Learning is a lifelong process, and we need to capture the diverse *mātauranga* (knowledge/wisdom) within the *taiao* (natural world) to allow nature to breathe life and knowledge into humanity. Te Orowai brings harmony and creative expression to our natural and celestial worlds."

***Ushanaia* gen. n.**

Type species: *Ushanaia fervens* sp. n., here designated.

Diagnosis: Azooxanthellate soft corals with a predominantly encrusting growth form, although fleshy, lobe-like processes can also occur. Polyps monomorphic and fully retractile. True calyces are absent, although retracted polyps may form low, rounded, mound-like protuberances of varying prominence depending on the state of expansion of the colony. Anthocodial sclerites are arranged as a collaret and points. Both the collaret and points are composed of tuberculate to warty spindles, although the distal part of the points may also contain thorny clubs. The tentacles contain irregular, warty, scale-like forms. The polyp neck contains tuberculate to warty rod- and spindle-like forms. The polyp mounds contain warty rod- and spindle-like forms, radiates and occasional club-like forms. Surface and interior sclerites include similar sclerites, mostly warty rod- and spindle-like forms, eight-radiate capstans and derivatives of this form, although clubs can also be present in the surface. Sclerites can be pale to dark orange or colourless.

Etymology: The genus is named after the author's partner, Ushana.

Comparisons: As is the case for *Kotatea* (see comparisons for that genus), compared to *A. digitatum* and *Alcyonium sensu stricto*, *Ushanaia* has far stronger collaret and points and a greater variety of surface sclerites, including clubs and well-developed radiates (see Hickson 1895; Verseveldt 1973; Stokvis and van Ofwegen 2006). Compared to *A. haddoni* and other South American nominal *Alcyonium* species, *Ushanaia* possesses a much more prominent radiate component among its surface and interior sclerites and does not have calyces (see Verseveldt and van Ofwegen 1992; Casas et al. 1997; van Ofwegen et al. 2007).

Unlike *Kotatea*, *Ushanaia* forms encrusting colonies. Additionally, *Ushanaia* has collaret spindles that tend to be larger than those found in *Kotatea* and lacks the clear presence of well-developed clubs in the polyp mounds and the marked difference between surface and interior sclerites that are observed in *Kotatea*.

The genus *Incrustatus* van Ofwegen, Häussermann and Försterra, 2006 (Clavulariidae) is found in a similar habitat in southern South American fjords and superficially resembles *Ushanaia* in its encrusting habit but differs markedly in having no or very few polyp sclerites (Van Ofwegen et al. 2006; McFadden and Van Ofwegen 2013b), whereas *Ushanaia* possesses strong collaret and points.

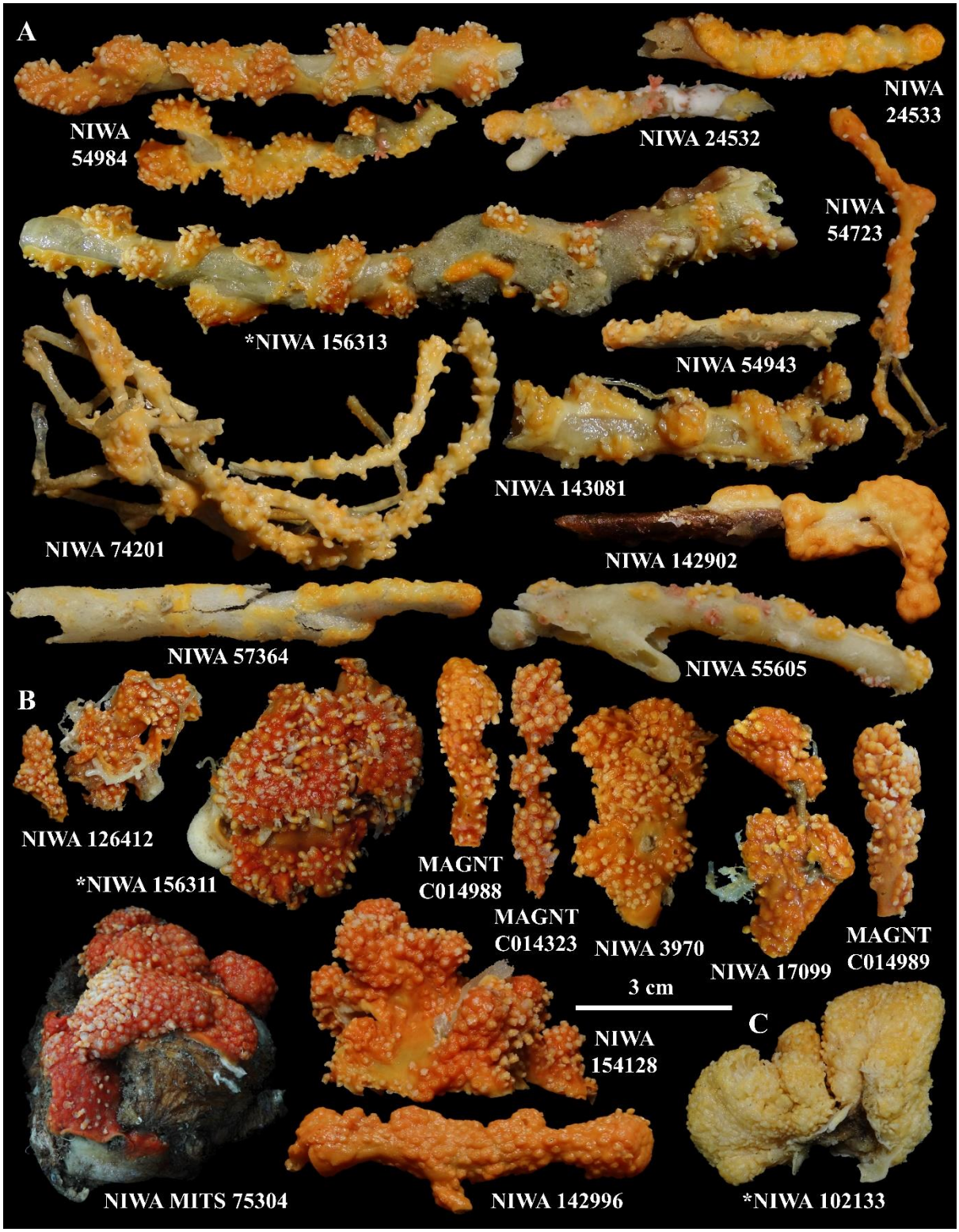

Figure 29. Selected preserved specimens of: **A.** *Ushanaia ferruginea* gen. n., sp. n.; **B.** *U. fervens* gen. n., sp. n.; **C.** *U. solida* gen. n., sp. n. Note that most specimen lots include additional fragments that are not depicted *Holotype.

***Ushanaia ferruginea* gen. n., sp. n.**

Figs. 2B, D; 3I; 29A; 30; 31

Material examined.

Holotype: NIWA 156313, stn. TAN0906/38, ~8 km SE of Cape Brett, Northland, NZ, 35.2160˚S 174.4033˚E to 35.2173˚S 174.4108˚E, depth 99–105 m, coll. Oceans Survey 2020, 6th July 2009.

Paratypes: Northland, NZ: **NIWA 24533**, stn. TAN0906/134, ~16 km ESE of North Cape, 34.4650˚S 173.2115˚E to 34.4690˚S 173.2153˚E, depth 140–141 m, coll. Oceans Survey 2020, 13th July 2009; **NIWA 56056**, stn. TAN0906/132, ~27 km SE of North Cape, 34.5570˚S 173.28533˚E to 34.5587˚S 173.2875˚E, depth 139–141 m, coll. Oceans Survey 2020, 13th July 2009; **NIWA 55605**, stn. TAN0906/93, ~22 km NE of Whangaroa Bay, 34.8302˚S 173.8940˚E to 34.8312˚S 173.8992˚E, depth 149–151 m, coll. Oceans Survey 2020, 9th July 2009; **NIWA 54984**, same data as holotype.

Other material: Northland, NZ: **NIWA 3976**, stn. F933, ~14 km E of North Cape, 34.4000˚S 173.1717˚E, depth 249–252 m, coll. New Zealand Oceanographic Institute, 15th October 1968; **NIWA 143081**, stn. Z9742, ~10 km E of North Cape, 34.4137˚S, 172.1333˚E, depth 133–210 m, coll. Coral Reef Research Foundation, 19th April 1999; **NIWA 24532**, stn. TAN0906/181, ~8 km ESE of North Cape, 34.4398˚S 173.1297˚E to 34.4373˚S 173.1237˚E, depth 110–15 m, coll. Oceans Survey 2020, 15th July 2009; **NIWA 57457**, stn. TAN0906/236, ~16 km NE of Mahinepua/Stephenson Island, 34.8502˚S 173.9050˚E to 34.8500˚S 173.8982˚E, depth 132–134 m, coll. Oceans Survey 2020, 19th July 2009; **NIWA 57364**, stn. TAN0906/235, ~15 km NE of Mahinepua/Stephenson Island, 34.8760˚S 173.9158˚E to 34.8792˚S 173.9103˚E, depth 114–117 m, coll. Oceans Survey 2020, 19th July 2009; **NIWA 55022**, stn. TAN0906/42, ~15 km SE of Cape Brett, 35.2402˚S 174.4827 to 35.2423˚S 174.4800˚E, depth 135–139 m, coll. Oceans Survey 2020, 6th July 2009; **NIWA 54943**, stn. TAN0906/36, ~15 km SE of Cape Brett, 35.2417˚S 174.4833˚E to 35.2420˚S 174.4770˚E, depth 128–133 m, coll. Oceans Survey 2020, 6th July 2009; **NIWA 54723**, stn. TAN0906/21, ~3.5 km NE of Whananaki, 35.4858˚S 174.5012˚E to 35.4965˚S 174.5307˚E, depth 59–63 m, coll. Oceans Survey 2020, 5th July 2009.

Bay of Plenty, NZ: **NIWA 142902**, stn. KAH0011/40, Rungapapa Knoll, ~18 km WSW of Whakaari/White Island, 37.5497˚S 176.9707˚E to 37.5495˚S 176.9772˚E, depth 155–176 m, coll. NIWA, 5th November 2000.

NE coast of South Island, NZ: **NIWA 74201**, stn. TAN1108/24, Pegasus Canyon, ~65 km E of Pegasus Bay, 43.4172˚S 173.5315˚E to 43.4152˚S 173.5245˚E, depth 115 m, coll. Oceans Survey 2020, 14th May 2011.

Description of the holotype.

Colony form: The holotype, which encrusts a ~15 cm long sponge fragment and consists of ~10 raised, fleshy mounds, which contain polyps and are joined together by ribbon-like membranes (Fig. 29A). These mounds range from a few millimetres up to several centimetres across, are up to ~5 mm thick, and range from pale to bright orange (ethanol-preserved), fading to beige towards their edges. The membranes are very thin (< 1 mm) and vary from pale-orange to beige. Polyps are concentrated towards the thicker parts of colony patches where they grow with a somewhat irregular spacing, but a few isolated polyps grow directly from the thin connective membranes between patches. Polyps are white, 0.75 mm to 2 mm tall when expanded, with collaret and points ranging from colourless to orange (Fig. 3I). Larger polyps tending to occur on thicker sections of the colony. Other polyp-bearing mounds encrusting the sponge that are not joined to the holotype are considered as paratypes.

Sclerites: Points are composed of slender, warty spindles (~0.25–0.45 mm long), many of which are flattened (Fig. 30A). Proximally, the spindles become larger and slightly more crescentic (~0.4–0.6 mm long), transitioning into a transverse orientation and merging with the collaret, which is usually around eight to twelve rows deep (Figs. 3I; 30A, E). The tentacles contain irregular, warty, scale-like forms, often slightly crescentic (~0.1–0.25 mm long) (Fig. 30B). Tuberculate to warty rod-like sclerites (~0.08–0.18 mm long) are abundant in the polyp neck (Fig. 30C). Larger warty rod- and spindle-like forms (~0.12–0.25 mm long), some of which can be club-like, form a densely packed surface layer in the polyp mounds (Fig. 30D). The rest of the surface layer (of fleshy areas) between polyp mounds contains radiates which grade into more elongated, warty clubs (~0.08–0.2 mm long) (Fig. 31A). Sclerites of the interior (of fleshy areas) are more uniformly comprised of warty radiates (~0.08–0.18 mm long) (Fig. 31B).

Habitat and distribution: While most specimens were collected off the east coast of far northern New Zealand, NIWA 142902, collected from the Bay of Plenty, and NIWA 74201, collected from Pegasus Canyon off the east coast of Waiponamou/South Island, suggest that *U. ferruginea* may be widely distributed at depths of ~60–250 m around New Zealand (Fig. 2B–D). Collection notes indicate that the species occurs in areas with a range of substrates, including muddy bottoms, gravels and shell debris, and is commonly associated with a high density of sponges and/or tube worms. *Ushanaia ferruginea* also occurs syntopically with *K. amicispongia*, as several specimens of each were collected alongside the other.

Variability: NIWA 54723, NIWA 55022, and NIWA 142902 are encrusting gorgonian fragments and NIWA 74201 is encrusting chaetopterid worm tubes. All other specimens are encrusting sponge. All preserved specimens are similar in growth form, varying only in the sizes of colony patches. In the examined specimens, colony patches reach up to ~8 cm long, with some

encircling their sponge substrates completely. Specimens vary only slightly in colour (Fig. 29A). All fifteen specimens are very similar in their sclerite compositions, varying only minimally in some size ranges, but these always fall within those described for the holotype (Figs. 30; 31).

Comparisons: *Ushanaia ferruginea* can be easily distinguished from *U. fervens* by the far more brightly and conspicuously coloured collaret and point sclerites in the latter (compare Figs. 3I, J; 29A and 3M; 29B; 35). Additionally, *U. ferruginea* specimens lack distal clubs in their points, which are present in *U. fervens* (compare Figs. 30A and 32B). *Ushanaia ferruginea* also possesses large, very uniform rod/spindle-like sclerites in polyp mounds, which are distinctly different from the irregular forms present in *U. fervens* (compare Figs. 30D and 33A). Beyond this, the surface and interior sclerites of *U. ferruginea* specimens are overall noticeably more robust than those of *U. fervens* (compare Figs. 31 and 33B, C). Note also that *U. ferruginea* has so far been collected only from considerably greater depths than *U. fervens* (~60–250 m vs. < 30 m).

Ushanaia ferruginea specimens do not form fleshy lobes to the same extent as *U. solida*, and also differ clearly from this species in having polyps that are typically around twice as large (up to 2 mm vs. up to 1 mm), and in lacking the distinctive, broad, flattened collaret and point sclerites found in *U. solida* (compare Figs. 30A and 36A).

Etymology: The species name is the Latin *ferruginea*, rusty or rust-coloured, referring to the colour and encrusting habit of the examined specimens.

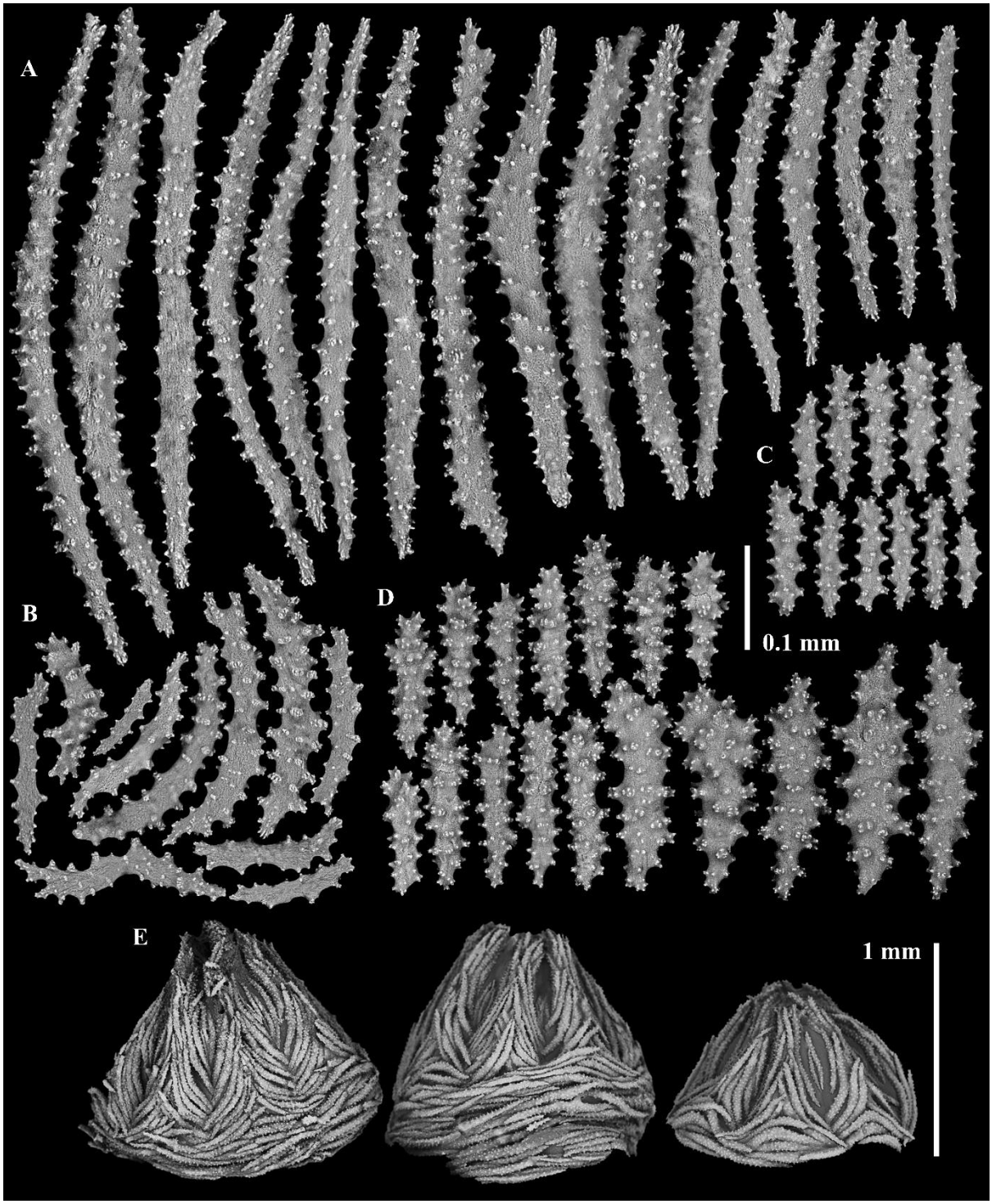

Figure 30. *Ushanaia ferruginea* gen. n., sp. n. holotype (NIWA 156313), SEMs of sclerites from: **A.** Collaret and points; **B.** Tentacles; **C.** Polyp neck; **D.** Polyp mound; **E.** Polyps (*in situ*).

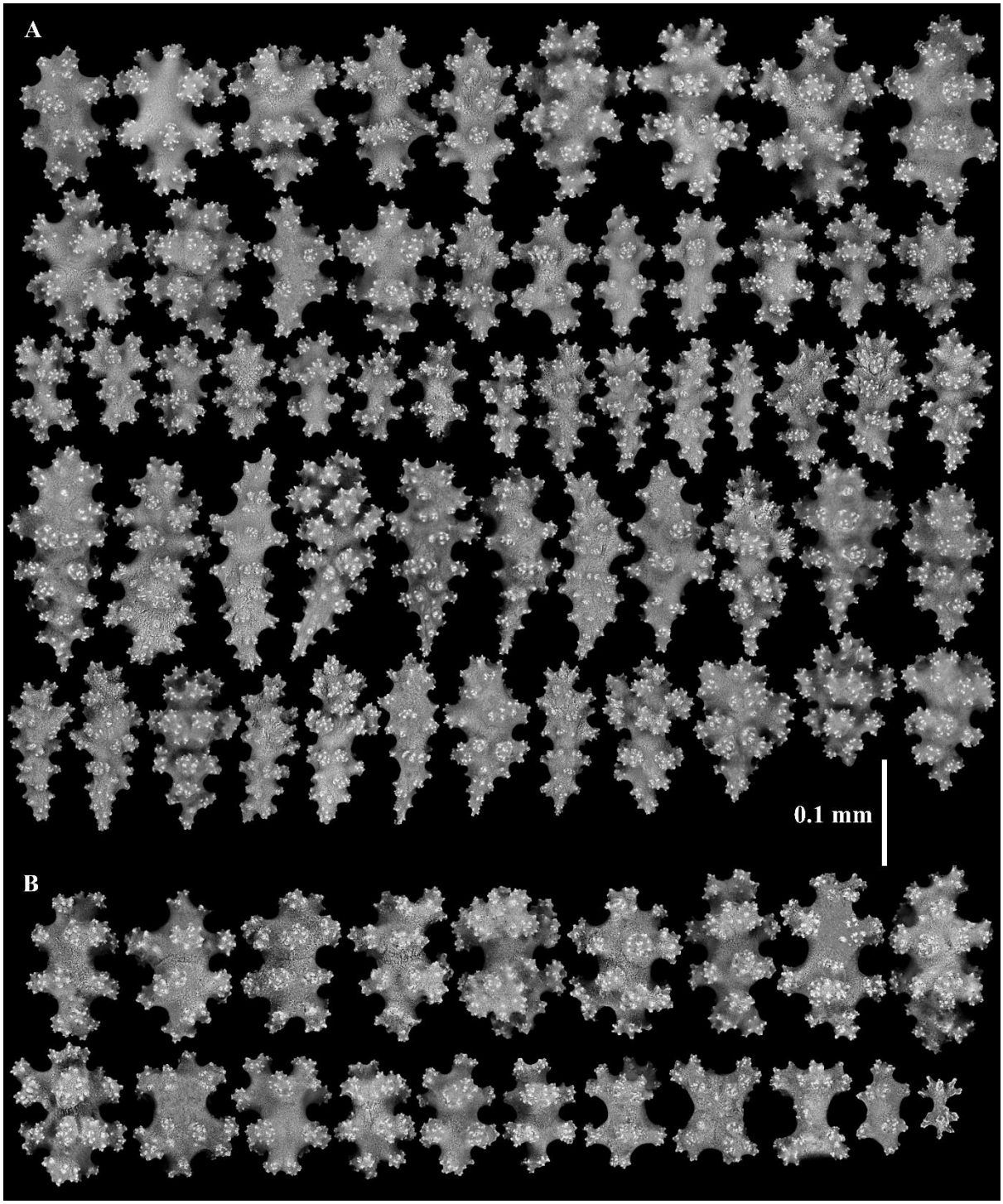

Figure 31. *Ushanaia ferruginea* gen. n., sp. n. holotype (NIWA 156313), SEMs of sclerites from: **A.** Surface (of thick, fleshy areas of colony); **B.** Interior (of thick, fleshy areas of colony).

***Ushanaia fervens* gen. n., sp. n.**

Alcyonium aurantiacum Benham 1928, in part: Pg. 71–75; Figs. 6–11

Alcyonium aurantiacum McFadden et al. 2006b: Pg. 517, 521, 523; Figs. 1, 3

? *Alcyonium aurantiacum* Grange et al. 1981: Pg. 211–212, 224, 214, 216; Figs. 2, 4

? *Alcyonium aurantiacum* Westerskov and Probert 1981 in part: Pg. 111, Plate 28

? *Alcyonium aurantiacum* Goldberg et al. 1990: Pg. 99; Fig. 4

? *Alcyonium aurantiacum* Grange et al. 2010 in part: Pg. 148

Figs. 2D–E; 3J, M; 12D; 29B; 32; 33; 34A; 35

Material examined.

Holotype: NIWA 156311, stn. Z17956, Sunday Cove, Te Puaitaha/Breaksea Sound, Fiordland, NZ, 45.5952˚S 166.7422˚E, depth 4 m, coll. R. Kinsey – Department of Conservation, 16th January 2018.

Paratypes: NIWA 3970, stn. M773, Milford Sound/Piopiotahi, 44.6183˚S 167.8588˚E, depth 25 m, coll. New Zealand Oceanographic Institute, 30th March 1981; **NIWA 126412**, same data as holotype.

Other material: Wellington, NZ: **NIWA MITS 75304**, stn. WLG31205-SF, Sorrento Bay, 41.2547˚S 174.9012˚E, depth unknown (but known to have been collected on wharf piles), coll. NIWA, 20th July 2020.

Fiordland, NZ: **NIWA 154128**, stn. Z10091, Milford Sound/Piopiotahi, 44.5833˚S 167.7833˚E (estimated), depth 20 m, coll. unknown, 2nd September 1996; **NIWA 142996**, stn. M763, Milford Sound/Piopiotahi, 44.6033˚S 167.8288˚E, depth 27 m, coll. New Zealand Oceanographic Institute, 29th March 1981; **MAGNT C014322**, stn. unknown, Underwater Observatory, Harrison Cove, Milford Sound/Piopiotahi, coordinates unknown, depth 13 m, coll. K. Gowlett-Holmes, 16th June 2003; **NIWA 17099**, stn. Q66C/Z7552, Taitetimu/Caswell Sound, 45.0033˚S 167.1567˚E, depth 30m, coll. Chris N. Battershill – NIWA/National Cancer Institute, 18th April 1991; **MAGNT C014323**, stn. unknown, Deep Cove, Doubtful Sound, coordinates unknown, depth 12–14 m, coll. K. Gowlett-Holmes, 19th June 2003; **MAGNT C014989**, stn. unknown, Vancouver Arm, Te Puaitaha/Breaksea Sound, 45.5250˚S 166.9250˚E, depth unknown, coll. M.S. Roy, 21st November 1999; **MAGNT C014988**, stn. unknown, Wet Jacket Arm/Moana Uta, 45.6667˚S 166.7333˚E, depth unknown, coll. M.S. Roy, 21st November 1999.

Description of the holotype.

Colony form: The holotype consists of a colony that measures ~4 cm by ~3 cm and up to ~3 mm thick, and encrusts a sponge fragment (Fig. 29B; 35). The holotype (ethanol-preserved) is dark red, fading to lighter shades of red or orange towards its edges or at thinner sections. Polyps are irregularly spaced, tending to concentrate towards the thicker, fleshier parts of the colony but also occasionally emerge from very thin sections. Polyps are white and 0.75 mm to 2 mm tall when expanded. Larger polyps tend to occur on thicker sections of the colony. The collaret and point sclerites are bright orange, contrasting against the white flesh of the polyps and the sometimes darker red or orange colour of the rest of the colony (Figs. 3J, M; 30; 35B–C).

Sclerites: Points are composed of slender, warty to spiny spindles (~0.2–0.3 mm long), many of which are flattened, and thorny clubs are present distally (~0.12–0.32 mm long) (Fig. 33A, B). Proximally, the spindles become larger and more crescentic (~0.12–0.28 mm long), transitioning into a transverse orientation and merging with the collaret, which is seven to ten rows deep (~0.2–0.55 mm long) (Figs. 3J, M; 33A; 34A). The tentacles contain irregular, warty, scale-like forms, often slightly crescentic (~0.1–0.3 mm long) (Fig. 33C). The polyp neck contains warty rod- and spindle-like sclerites (~0.1–0.22 mm long) (Fig. 33D). Close to the polyp neck, polyp mounds also contain abundant warty rod-like and spindle-like forms (~0.08–0.16 mm long), which grade into clubs and a few irregularly branched forms (~0.08–0.18 mm long) further away from the polyp (Fig. 33A). The surface between polyp mounds is dominated by warty radiates and spindle-like forms (~0.08–0.2 mm long) (Fig. 33B). Similar radiates and spindle-like forms are found in the interior of the thick, fleshy areas of the colony, although here they tend to be smaller (~0.06–0.16 mm long), less variable in shape and more sparsely ornamented (Fig. 33C).

Habitat and distribution: All specimens were collected in Fiordland, except NIWA MITS 75304, which was collected in Wellington Harbour, and all specimens (for which a depth was recorded) were collected at shallow depths of ≤30 m (Fig. 2D, E). MAGNT C014323 was collected on a rock wall and MAGNT C014988 and MAGNT C014989 are recorded as encrusting black coral. NIWA MITS 75304 was collected from a wharf pile.

Variability: Preserved *U. fervens* specimens are somewhat variable in overall colony colour, ranging from the dark red seen in the holotype and NIWA MITS 75304, to lighter red and orange in the other specimens (Fig. 29B). All specimens are otherwise similar in growth form. All eleven specimens are also very uniform in their sclerite compositions, with slight variations in size ranges representing the only appreciable difference between some individual colonies, but these always fall within the ranges described for the holotype (Figs. 32; 33).

Comparisons: Differences to *U. ferruginea* are discussed under that species.

Much like *U. ferruginea*, *U. fervens* clearly differs from *U. solida* in not forming fleshy lobes to the same extent as that species and in possessing polyps of around twice the size (up to 2 mm vs. up to 1 mm; Fig. 34). *U. fervens* also lacks the distinctive, broad, flattened collaret and point sclerites found in *U. solida* (compare Figs. 32A and 36A). Conversely, *U. solida* lacks the conspicuous, bright collaret and points colouration which is characteristic of *U. fervens* specimens.

Etymology: The species name is the Latin *fervens*, red-hot or burning, referring to the flame-like red and orange colour combination of the examined specimens.

Remarks: Having been collected in Fiordland, the encrusting specimen described by Benham (1928) was most likely a member of *U. fervens*. Similarly, the "*A. aurantiacum*" recorded by Grange et al. (1981) at depths of 4–20 m in Fiordland probably refers to this species, although it is unclear whether encrusting or upright-growing colonies were observed, and it may be that representatives of *Kotatea* also inhabit this area. The *A. aurantiacum* illustrated by Westerskov and Probert (1981) likely also represents *U. fervens*.

Notably, Goldberg et al. (1990) documented the formation of long, thread-like, defensive sweeper tentacles on black corals in Fiordland in response to encrusting epibionts identified as "*A. aurantiacum*". These observations can probably be attributed to *U. fervans* due to their encrusting habit.

As noted by Grange et al. (1981, 2010), a white octocoral also encrusts black corals in Fiordland, but since no specimens matching this description were available for examination it remains unclear whether these observations represent a form of *U. fervens* or a separate species.

The sequence identified as *Alcyonium aurantiacum* in McFadden et al. (2006b), belongs to *U. fervens* (MAGNT C014988).

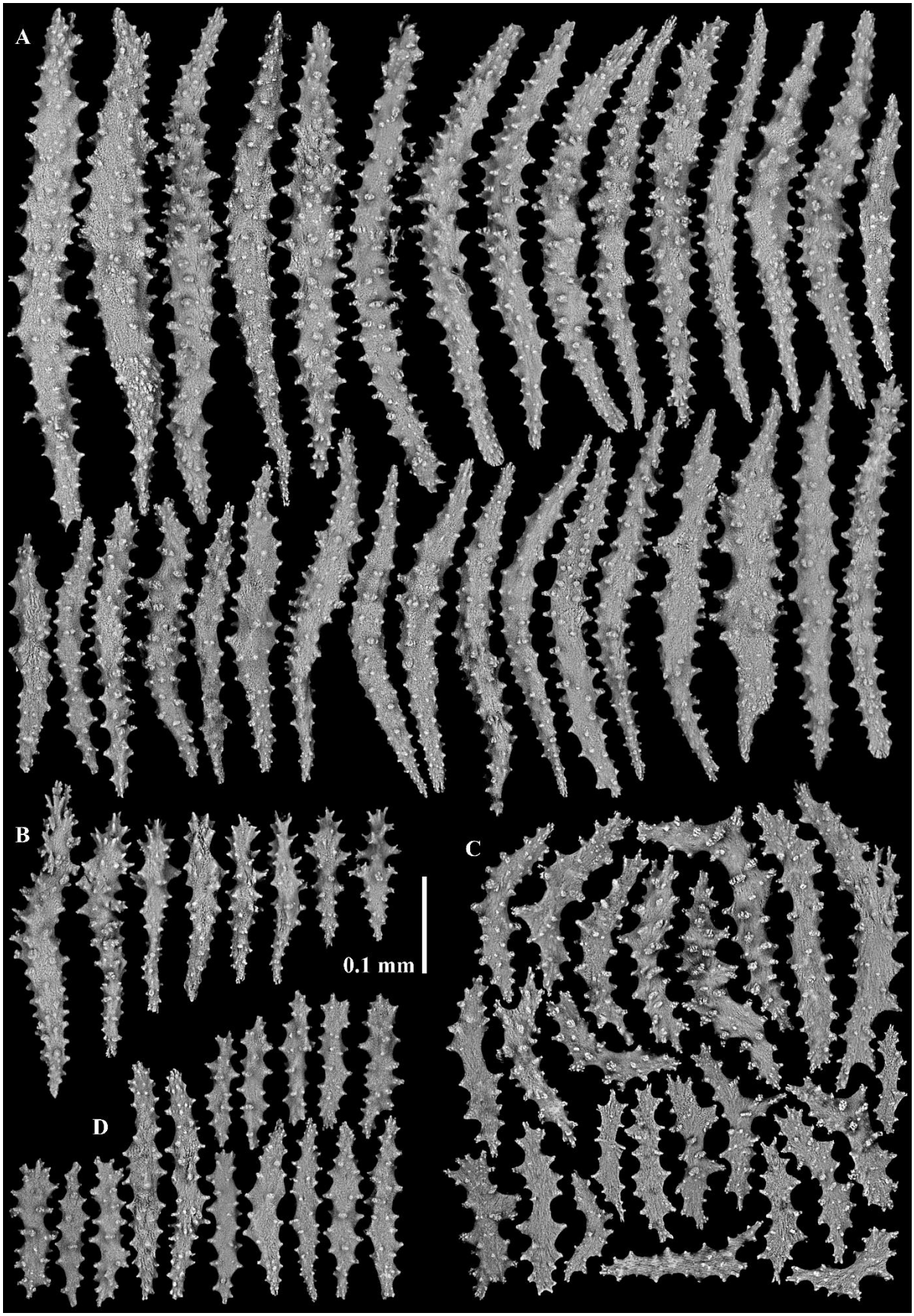

Figure 32. *Ushanaia fervens* gen. n., sp. n. holotype (NIWA 156311), SEMs of sclerites from: **A.** Collaret and points; **B.** Distal points; **C.** Tentacles; **D.** Polyp neck.

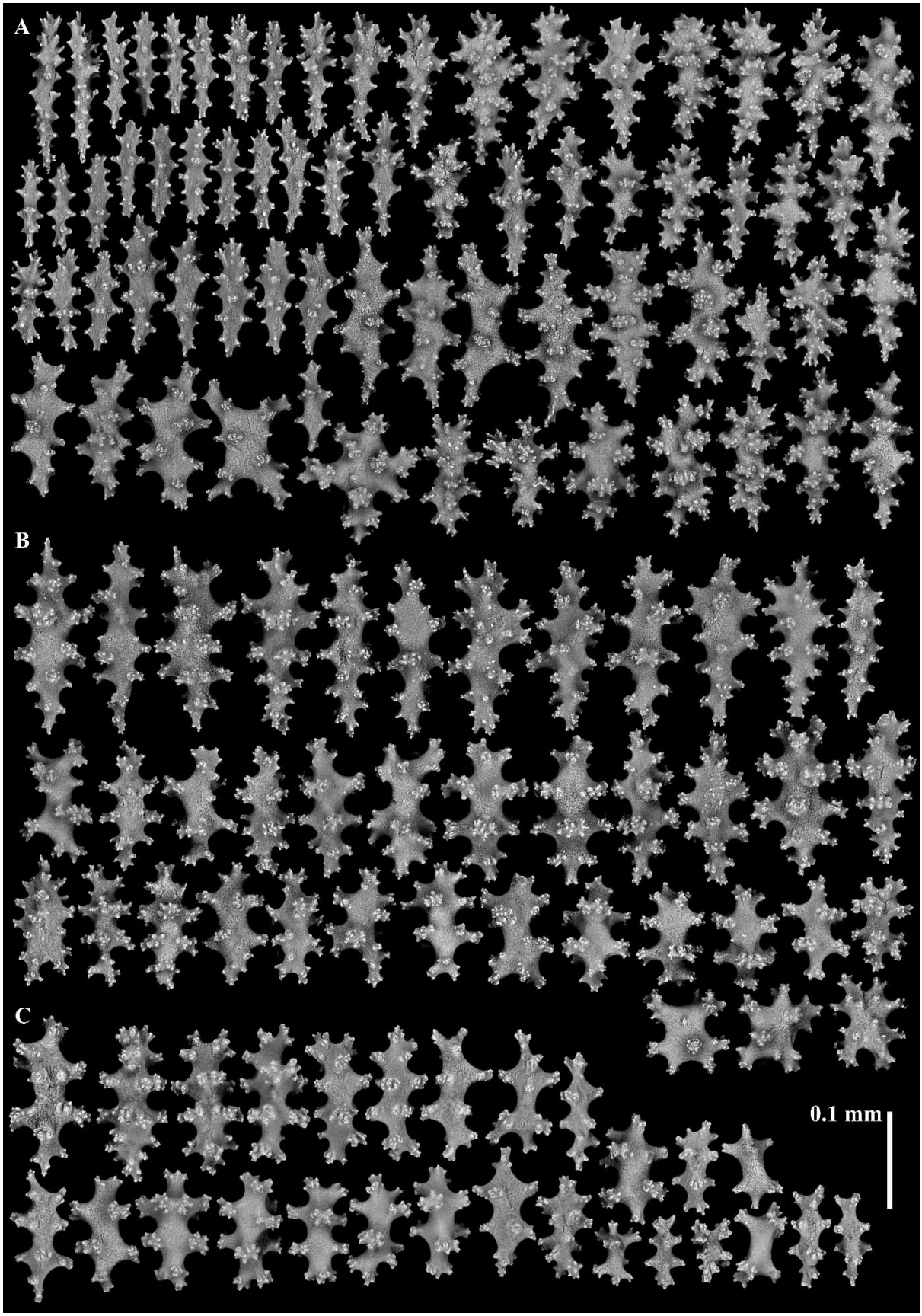

Figure 33. *Ushanaia fervens* gen. n., sp. n. holotype (NIWA 156311), SEMs of sclerites from: **A.** Polyp mound; **B.** Surface (of thick, fleshy areas of colony); **C.** Interior (of thick, fleshy areas of colony).

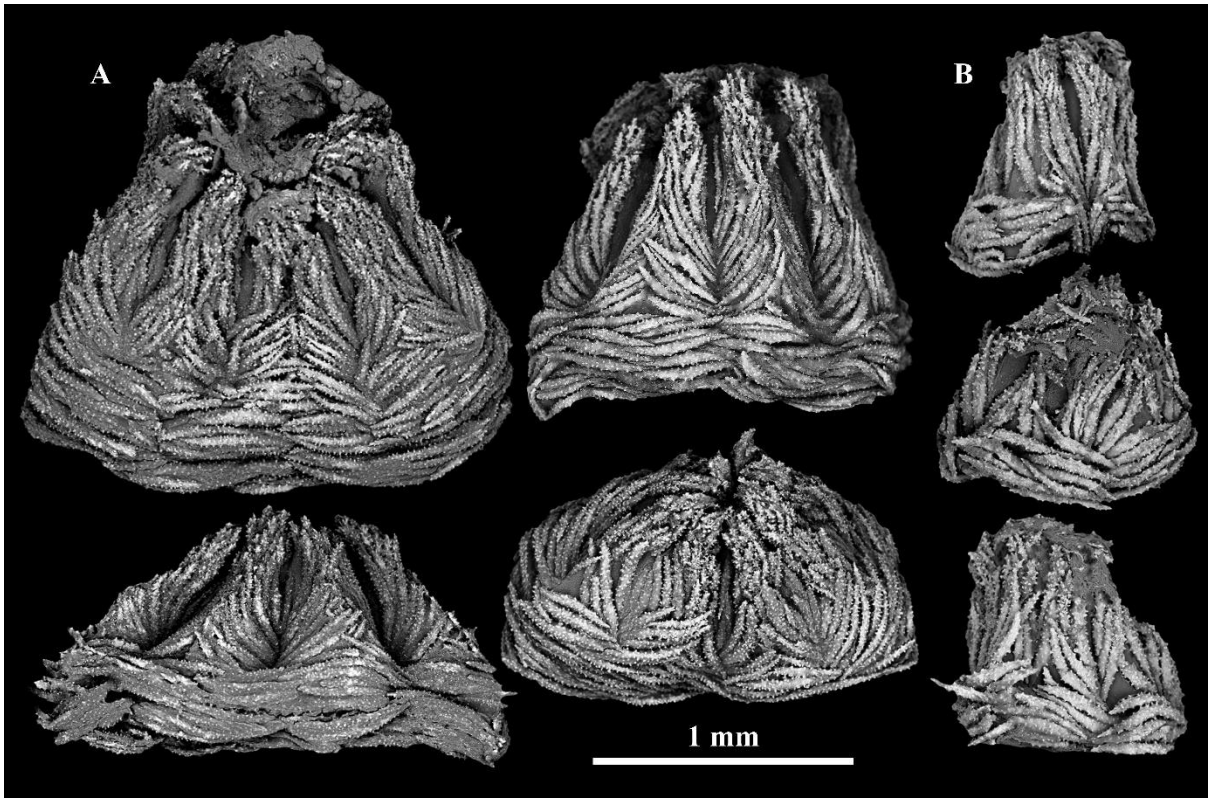

Figure 34. SEMs of sclerites from polyps (*in situ*) for: **A.** *Ushanaia fervens* gen. n., sp. n. holotype (NIWA 156311); **B.** *U. solida* gen. n., sp. n. holotype (NIWA 102133).

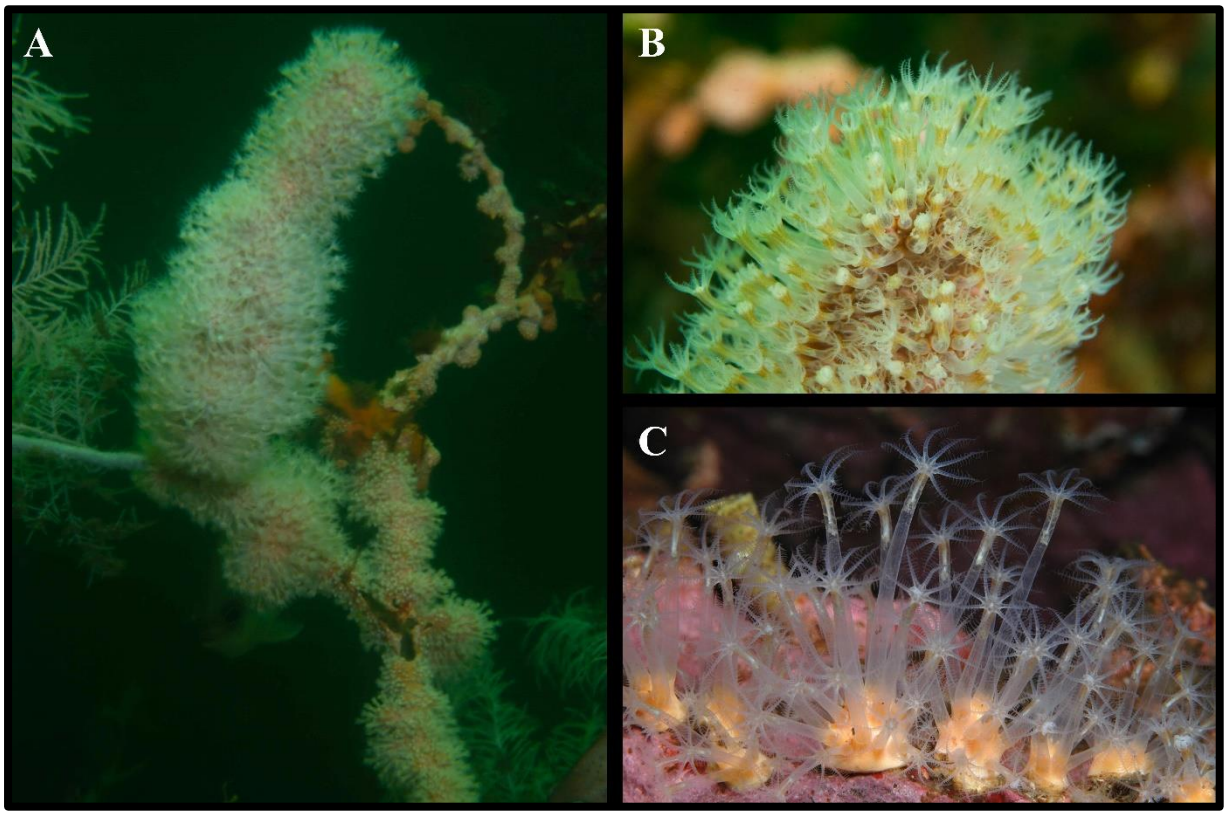

Figure 35. *In situ* photographs of *Ushanaia fervens* gen. n., sp. n.: **A–B.** Encrusting on black coral (uncollected specimen), Fiordland, photos by Richard Kinsey; **C.** Small colonies (uncollected specimens), Fiordland, photo by Ian Skipworth (ianskipworth.com).

***Ushanaia solida* gen. n., sp. n.**

Figs. 2C; 3K; 29C; 34B; 36; 37

Material examined.

Holotype: NIWA 102133, stn. Z18522, Manukau Harbour, Auckland, NZ, 37.0319˚S 174.6507˚E (estimated), depth unknown, coll. unknown, 11th April 2003.

Description of the holotype.

Colony form: The holotype is composed of three loosely connected main lobes, measures 4 cm in height and 5 cm in width, and is beige to pale orange (ethanol-preserved) (Fig. 29C). Polyps are densely arranged across the entire surface of the colony, white, 0.75 mm to 1 mm tall when expanded, and have collaret and point sclerites with a slight orange hue (Fig. 3K).

Sclerites: Points are composed of tuberculate to warty spindles, which are often broad and flattened and can be irregularly shaped and branched, and irregular, thorny clubs and spindles distally (~0.1–0.4 mm long) (Fig. 36A, D). Proximally, the spindles become more crescentic and slightly larger (~0.26–0.55 mm long), transitioning into a transverse orientation and merging with the collaret, which is five to seven rows deep (Figs. 34B; 36A). The tentacles contain irregular, warty, scale-like forms, which are often curved and branched (~0.06–0.24 mm long) (Fig. 36B). The polyp neck contains warty to spiny rod-like forms (~0.1–0.18 mm long) (Fig. 36C), although these are not abundant. Polyp mounds are composed of warty to spiny rod- and spindle-like forms, which grade into some club-like forms (~0.1–0.18 mm long) (Fig. 37A). The sclerites of the surface of the lobes, both distal and proximal regions (relative to the substrate), and of the interior are all very similar and consist of warty to spiny rod- and spindle-like forms, a few radiates and poorly developed clubs, and they essentially differ only in size: proximal lobe surface, ~0.12–0.26 mm long (Fig. 37B); distal lobe surface, ~0.12–0.26 mm long (Fig. 37C); interior, ~0.14–0.18 mm long (Fig. 37D).

Habitat and distribution: The holotype was collected in Manukau Harbour (Fig. 2C). No precise coordinates, depth or habitat information was recorded. From the remaining fragments of substrate on the colony's base, it appears to have been growing on encrusting coralline algae.

Variability: The holotype is the only known specimen.

Comparisons: *Ushanaia solida* is substantially more fleshy than *U. ferruginea* and *U. fervens*, differences to which are discussed further under these species. Differences to *K. lobata*, which may superficially resemble *U. solida*, are also discussed under that species.

Etymology: The species name is the Latin *solida*, solid or three-dimensional, referring to the substantially thicker colony form of *U. solida* when compared to *U. ferruginea* or *U. fervens*.

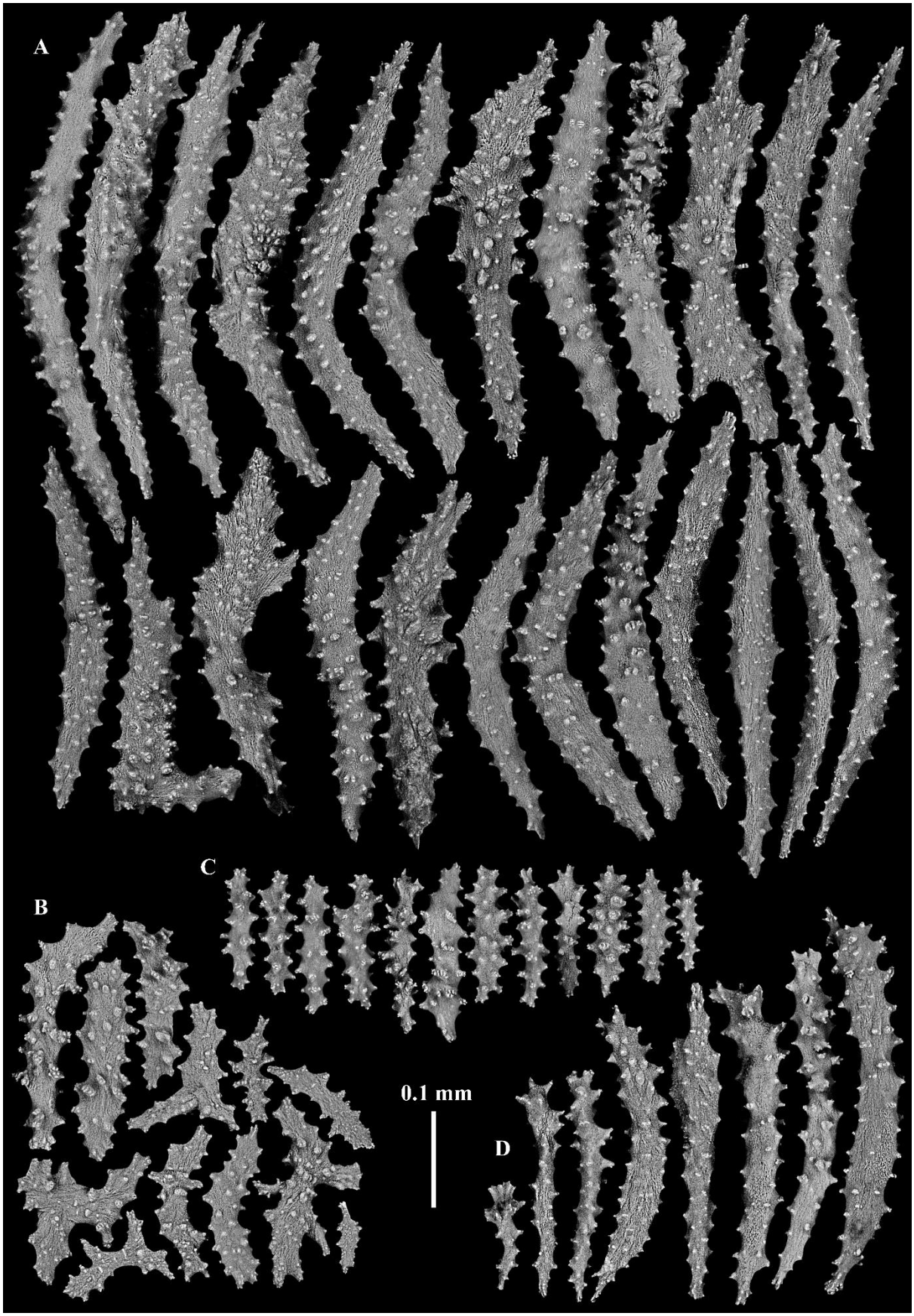

Figure 36. *Ushanaia solida* gen. n., sp. n. holotype (NIWA 102133), SEMs of sclerites from: **A.** Collaret and points; **B.** Tentacles; **C.** Polyp neck; **D.** Distal points.

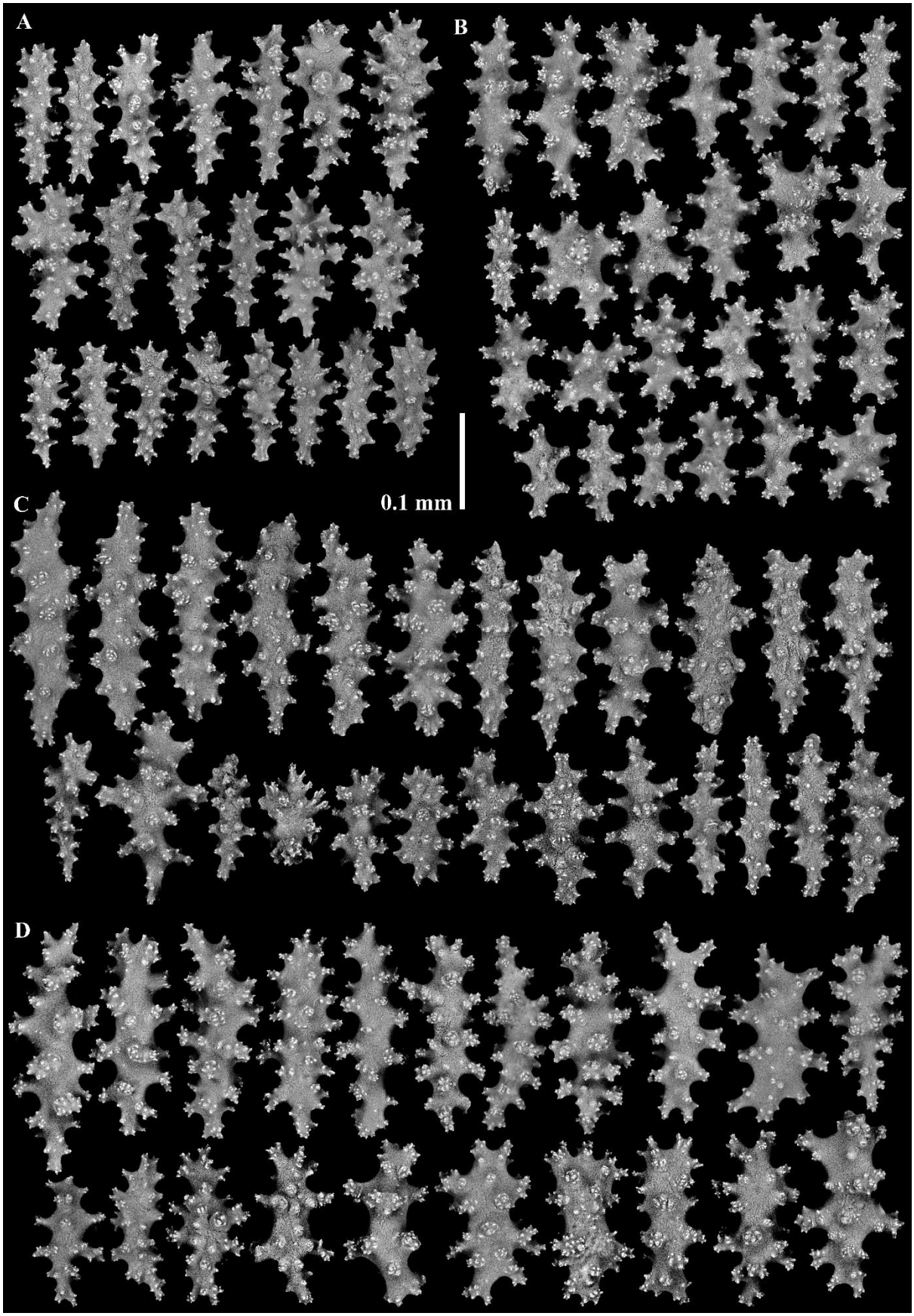

Figure 37. *Ushanaia solida* gen. n., sp. n. holotype (NIWA 102133), SEMs of sclerites from: **A.** Polyp mound; **B.** Lobe surface, proximal region (close proximity to substrate); **C.** Lobe surface, distal region; **D.** Interior.

Morphological key to species of *Kotatea* gen. n. and *Ushanaia* gen. n.:

1. A. Colonies erect and lobate in growth form with clubs abundant in polyp mounds, surface sclerites differ from interior sclerites markedly……...(*Kotatea* gen. n.) 2
   B. Colonies encrusting and/or clubs absent from polyp mounds, surface and interior sclerites do not differ in form……. (*Ushanaia* gen. n.) 9
2. A. Colonies distinctly spotted in appearance with thick lobes; large and robust, highly sculptured spheroids present in surface and interior sections; highly branched interior spindles absent……..……..3
   B. Colonies not distinctly spotted in appearance, highly sculptured spheroids absent..……..4
3. A. Large polyps measure ~1.3 mm when expanded, interior sclerites not distinctly double-headed.……...*K. kurakootingotingo* gen. n., sp. n.
   B. Large polyps measure only ~0.75 mm when expanded, interior sclerites often distinctly double-headed…….....*K. niwa* gen. n., sp. n.
4. A. Collaret and point sclerites coloured orange (when preserved)..…..*K. raekura* gen. n., sp. n.
   B. Collaret and point sclerites colourless (when preserved)…….……...…5
5. A. Colonies white (when preserved)…….…….……...6
   B. Colonies distinctly coloured yellowish or orange (when preserved), ranging from pale to dark shades…….…….....7
6. A. Colonies laterally compressed; interior sclerites abundant and composed predominately of radiates with few, thin, thorny branching processes.…….....*K. kapotaiora* gen. n., sp. n.
   B. Colonies not laterally compressed, interior sclerites very scarce.....*K. teorowai* gen. n., sp. n.
7. A. Sclerites in lobe interior very large (up to ~0.35 mm long), antler-like, and highly branched .....……*K. lobata* gen. n., sp. n.
   B. Sclerites in lobe interior are not as in 7A…….……8
8. A. Colonies yellowish orange (when preserved), clubs in points large (> 0.1 mm long) and abundant, collarets composed of ~6–10 rows of spindles.…*K. amicispongia* gen. n., sp. n.
   B. Colonies orange (not yellowish, when preserved), clubs in points small (< 0.1 mm long) and scarce, collarets composed of ~5–7 rows of spindles....*K. aurantiaca* gen. n., comb. n.
9. A. Large polyps measure only up to ~1 mm when expanded, collaret and point sclerites often distinctly flattened, collarets generally composed of seven or fewer rows of spindles ……..….*U. solida* gen. n., sp. n.
   B. Large polyps measure up to ~2 mm when expanded, distinctly flattened collaret and point sclerites absent, collarets generally composed of more than seven rows of spindles...….10

10. A. Colonies never distinctly red (when preserved), well-developed point clubs absent
……..……..….*U. ferruginea* gen. n., sp. n.

B. Colonies may be distinctly red (when preserved), well-developed point clubs present
…….…....*U. fervens* gen. n., sp. n.

2.6 Discussion

2.6.1 Taxonomic problems within *Alcyonium*

Alcyonium has had its morphological diagnosis discussed and incrementally amended many times. Essentially, these have included a broad range of upright and encrusting growth forms, combined with monomorphic polyps and sclerites in the form of tuberculate or thorny spindles, capstans, rods, clubs and needles (Bayer 1981a; Groot and Weinberg 1982; Williams 1986a, 1986b, 1988, 1992; Verseveldt and van Ofwegen 1992), with several subsequent attempts at refinement based on the characteristics of the type species *A. digitatum*. These included limiting *Alcyonium sensu stricto* to lobate or digitate growth forms (Benayahu and Schleyer 1995; Williams 2000), species that possess coenenchymal sclerites divided into a surface layer of mainly radiates, clubs and rods and an interior layer of straight or branched spindles and rods (Alderslade 2000), and most recently, to those species that possess polyp sclerites arranged as a collaret and points (McFadden and van Ofwegen 2013a, 2017). Despite the narrowing of its diagnosis over the years, many nominal species of *Alcyonium* remain encompassed by this definition, even though genetically they may have a much closer affinity to members of *Eleutherobia*, or even to the scleraxonian *Lateothela* and *Anthothela* (Anthothelidae) than to *A. digitatum*, which itself is more closely associated with *Gersemia* (Nephtheidae) than with some of its congeners (McFadden et al. 2006b; McFadden and van Ofwegen 2013a, 2017; Moore et al. 2017; and Fig. 1 herein).

Alcyonium (*sensu lato*) is clearly not monophyletic. Instead, it constitutes a paraphyletic group that fails to contain all descendants of a recent common ancestor and is based on homoplasious traits (e.g., Alderslade 2000; McFadden et al. 2006b; McFadden and van Ofwegen 2013a). While it has previously been specifically recommended, for example, that *Gersemia rubiformis* Ehrenberg, 1834 and *Eleutherobia somaliensis* Verseveldt and Bayer, 1988 would be better accommodated in *Alcyonium* (Williams and Lundsten 2009; McFadden and van Ofwegen 2013a), *Anthothela* and *Lateothela* would then also need to be included to produce a monophyletic *Alcyonium* based on their phylogenetic positions (Fig. 1 herein; Moore et al. 2017). However, the non-membranous representatives of these taxa feature a medulla and boundary canals that are highly derived and are

distinct from all other taxa phylogenetically associated with *Alcyonium* (Moore et al. 2017). Therefore, a broad genus definition that accommodates all these taxa would fail to reflect the diversity within this group.

Ultimately, *Alcyonium* currently has no workable diagnosis. Alderslade's (2000) assertion made more than two decades ago that the genus needs a total revision is still valid, as many of the more than 60 nominal species of *Alcyonium*, together with many of *Gersemia* and *Eleutherobia*, remain to be reassessed and are unrepresented in molecular phylogenies. Sequence data for a large proportion of these will likely need to be acquired before this deeply entangled group can finally be resolved, at least to genus level. In the meantime, regarding *Alcyonium* (*sensu lato*) as a complex of distinct genera and erecting new taxa wherever newly described species deviate from *A. digitatum* — both morphologically and genetically — may be the best way of alleviating the frustrating state of the group's systematics. Accordingly, New Zealand's *Alcyonium*-like soft corals were not placed in *Alcyonium*.

2.6.2 Separation of *Kotatea* and *Ushanaia* from *Alcyonium sensu stricto*

Kotatea and *Ushanaia* are separated from *Alcyonium sensu stricto*, as indicated by *A. digitatum*, through both their phylogenetic placement and morphological differences. Phylogenetically, a specimen identified as *A. aurantiacum*, now assigned to *U. fervens* (see *U. fervens* remarks section), was first resolved as forming a clade with *Anthothela* separate from *A. digitatum* by McFadden et al. (2006b) based on the *mtMutS* and *ND2* genes. More recently, Moore et al. (2017) showed that the southern South American *A. haddoni* and *A. varum* also form a separate clade with *Anthothela* based on *mtMutS* and *igr1–COI*. Here, using *mtMutS* and the nuclear *28S*, there is strong support to indicate that *Kotatea* and *Ushanaia*, along with South American nominal *Alcyonium* species and *Anthothela*, are more closely related to one another than to *A. digitatum* (Fig. 1). The nearly identical tree topologies that have been resolved repeatedly for this group using a range of genes, strongly support excluding *Kotatea* and *Ushanaia* from *Alcyonium.*

Morphologically, the separation of *Kotatea* and *Ushanaia* from *Alcyonium sensu stricto* is more difficult, as few differences can be gleaned from the available literature. Versevedt (1973) states that a collaret is absent in the polyps of *A. digitatum* (also see Hickson 1895), while *A. siderium* — the closest relative of *A. digitatum* (Fig. 1; McFadden et al. 2011; McFadden and van Ofwegen 2013a, 2017) — possesses a collaret of only about three rows but can also lack this feature entirely. This calls into question whether a collaret and points arrangement should form part of the diagnosis

of *Alcyonium* (as in McFadden and van Ofwegen 2013a, 2017). Interestingly, the genus *Gersemia*, to which *A. digitatum* is closely allied, also lacks polyp collarets (Williams and Lundsten 2009). In *Kotatea* and *Ushanaia*, by contrast, this feature is well-developed. While a collaret is shared by other nominal *Alcyonium* species as well, it may provide a useful character for future revisions in the group nonetheless. Additionally, Verseveldt (1973) depicts surface radiates for *A. digitatum* and *A. siderium* that are considerably less elongate and show far less variety than those seen in *Kotatea* and *Ushanaia*. Since no mention of neck or tentacle sclerites is made by Verseveldt (1973), it is unclear whether these are absent in *A. digitatum* and *A. siderium*, possibly presenting a key difference between *Alcyonium sensu stricto* and *Kotatea*/*Ushanaia*, or were simply overlooked.

Verseveldt's (1973) account is the most recent published work illustrating the sclerite characteristics of *A. digitatum*. Because this species has such a pivotal role in the re-classification of many related taxa, a detailed re-evaluation of the species using modern methods is needed. This would aid in the identification of morphological characters that are capable of delineating between *Alcyonium sensu stricto* and *Kotatea*/*Ushanaia* and may contribute to further new genera being erected from *Alcyonium sensu lato*. The diagnoses provided here for *Kotatea* and *Ushanaia* are thus likely to be amended by future investigations. Moreover, the placement of *Kotatea* and *Ushanaia* in Alcyoniidae, one of the most systematically heterogeneous families in Octocorallia (McFadden et al. 2006b, 2010), is necessarily tentative, and may also be subject to change pending further research into this group.

2.6.3 Separation of specimens into *Kotatea* and *Ushanaia*

Notwithstanding the ongoing taxonomic issues in *Alcyonium sensu lato*, the decision to separate the 11 species of New Zealand's *Alcyonium*-like soft corals identified here into two separate genera — rather than accommodating them in one — is well-supported by strong congruence between molecular and morphological data. The monophyletic, well-supported *Kotatea* and *Ushanaia* clades here resolved (Fig. 1) are also clearly discriminated by sclerite and colony growth form characteristics (see taxonomic section), corresponding to erect species (*Kotatea*) and encrusting species (*Ushanaia*). Furthermore, *Kotatea* and *Ushanaia* here formed a polytomy with the *Anthothela*/South American *Alcyonium* clade (Fig. 1), and thus sister relationships between these clades cannot conclusively be determined. This means that if united as a single genus, *Kotatea+Ushanaia* could become polytomous with the addition of more sequence data to phylogenetic analyses, but this possibility is pre-empted by the current arrangement. Additionally, intergeneric mean p-distances between *Kotatea* and *Ushanaia* (3.7% for *mtMutS* and 2.4% for *28S*)

are comparable to distances observed between genera in a range of octocoral families (including Anthothelidae, Moore et al. 2017; Isididae, Moore et al. 2016; Primnoidae, Baco and Cairns 2012; Nephtheidae and Xeniidae, McFadden et al. 2006a; McFadden and van Ofwegen 2012a) and thus offer further support for their separation at genus-level.

2.6.4 Species delimitation

Genetic variation was not sufficient to resolve the morphological differences observed within *Kotatea* or *Ushanaia* in most cases. This reflects results obtained throughout the Octocorallia generally. In this subclass, mitochondrial genes are considered to evolve at very slow rates when compared to other animals and are known to often lack the resolution needed to discriminate between congeneric species (e.g., Sánchez et al. 2003b; Wirshing et al. 2005; Cairns and Bayer 2005; Cairns and Baco 2007; McFadden et al. 2006a, 2009). The polytomous topologies within *Kotatea* and *Ushanaia* respectively are thus not unusual. Neither are their low intrageneric mean p-distances, as similarly low levels of variation — including identical haplotypes — have been found between some nominal species of *Alcyonium* for both *mtMutS* (McFadden et al. 2011) and *28S* (McFadden et al. 2014a).

The species concept employed in the description of new taxa is almost never discussed in the octocoral taxonomic literature (but see Herrera et al. 2012; McFadden et al. 2017). However, the use of phylogenetic or genetic concepts is invariably implicit when molecular data are presented as informative, as is the morphological species concept when such data are ambiguous or lacking, and the latter remains the case for the majority of descriptions (see Chapter 4). Indeed, when phylogenetic analyses are inconclusive, and a species concept based on the capability of exchanging genes or interbreeding is not testable, new octocoral species are nonetheless described based on clear and consistent morphological differences. For example, some of the new species described by van Ofwegen et al. (2007) for *Alcyonium*, Moore et al. (2016) for *Primnoisis* Studer and Wright, 1887, Núñez-Flores et al. (2020) for *Thouarella* Gray, 1870 and Xu et al. (2020) for *Chrysogorgia* Duchassaing & Michelotti, 1864 lacked monophyly but were deemed sufficiently distinct in morphology by the authors to warrant their description as separate taxa. Here too, unambiguous morphological data were critical in informing species-level differences within *Ushanaia* and most of *Kotatea* (see taxonomic section). The morphological species concept (see Zachos 2016) thus served as the basis for the description of a species, which is here defined as the smallest group that is consistently distinguishable by its distinct morphological characters.

Morphological differences were further supported by genetic evidence for distinctions between *K. kurakootingotingo/K. niwa* (the only two spotted species in the genus) and *K. kapotaiora*/*K. teorowai* (the only two white species in the genus). The species in both of these pairs were resolved as more closely related to one another than to the rest of the *Kotatea* species (Fig.1), potentially implicating colony colouration as an important identifier of intrageneric relationships in the genus. The separation of *K. kapotaiora*/*K. teorowai* was also supported by their interspecific mean p-distance for *mtMutS* (Table 2), which passed species discrimination thresholds recommended by McFadden et al. (2014a). Beyond this however, mean distances added no further support to species discrimination based on phylogenetic and morphological data, and for *mtMutS* generally fell within or below the ranges observed in other genera, such as *Sinularia* (McFadden et al. 2009) and *Narella* Gray, 1870 (Cairns and Baco 2007), for example.

The need to reconcile morphological variation with a lack of genetic divergence is a common challenge in Octocorallia, as distinct morphologies may represent intraspecific polymorphism, or conversely, target genes may simply lack the variation needed to distinguish between sister taxa (McFadden et al. 2010). Ascertaining which of these is the case can be problematic due to the prevalence of phenotypic plasticity among octocorals. For example, the form and abundance of sclerites can vary substantially within individual colonies and between individuals of different ages, or with the effects of predation and environmental conditions, with the latter also capable of influencing colony growth patterns as a whole (e.g., West et al. 1993; Brazeau and Harvell 1994; West 1997; Kim et al. 2004; Sánchez et al. 2007; Prada et al. 2008). Here however, observed differences in patterns of sclerite morphology and size, colony growth form, colouration, polyp size and ranges in collaret row numbers were consistent and served as reliable diagnostic characters to partition all examined specimens into one of eight species in *Kotatea* or one of three in *Ushanaia*.

2.6.5 Biogeographical considerations

The lack of any literature records of species from outside New Zealand which could be assigned to *Kotatea* and *Ushanaia*, indicates that these genera are endemic to New Zealand. Moreover, the molecular evidence suggests that they are more closely related to the southern South American *A. haddoni*, than to any other nominal *Alcyonium* species so far sequenced. *Alcyonium dolium* and *A. variabile* from South Africa, a region associated with high levels of genus and family-level endemism among octocorals (Williams 2000), are also more closely related to one another than to other nominal *Alcyonium* (Fig. 1). Hence, rather than constituting a single cosmopolitan genus, *Alcyonium sensu lato* may in the future be divided into several, regionally endemic genera, as has

previously been suggested for the South African clade by McFadden and van Ofwegen (2017). While intriguing, particularly for the Southern Hemisphere taxa, assessing their biogeography will require many more samples from African, Australian, Antarctic and South American species of *Alcyonium* (*sensu lato*) to be sequenced and new morphological comparisons between these taxa to be conducted.

Biogeographical patterns among deep-sea octocorals, including New Zealand taxa, have previously been explained with reference to the Antarctic Circumpolar Current, the formation and fluctuations of which have been identified as a key driver of diversification (Dueñas et al. 2016). Speculatively, similar large-scale processes, such as Southern Ocean hydrodynamics or the geological histories of landmasses with a Gondwanan origin (i.e., vicariance/dispersal) may account for the close phylogenetic relationships between *Kotatea*, *Ushanaia* and other Southern Hemisphere taxa.

2.6.6 Limitations and future research

Advanced genetic methodologies are now becoming more common and affordable, and their utilisation presents a promising way to test the validity of the species described here, which are hypotheses based on the weighting of diagnostic morphological over invariant molecular characters. For example, this could take the form of RAD-sequencing (e.g., Pante et al. 2015a; Herrera and Shank 2016; Quattrini et al. 2019) coupled with species delimitation analyses — which have been successfully used in octocorals previously (e.g., Bayes Factor Delimitation by Herrera and Shank 2016; BPP and Structurama by McFadden et al. 2017). However, this will necessitate the acquisition of additional, fresh material suitable for the extraction of high-quality sequence data, a key limitation that will likely require the targeted sampling of areas that *Kotatea* and *Ushanaia* species are now known to inhabit. Unfortunately, this was beyond the resources available to the current study, and only a handful of new specimens could be collected opportunistically since work began in 2017. Another, newer approach that can produce more informative genetic data from degraded specimens is target-capture enrichment of UCEs and exons (Erickson et al. 2020; Quattrini et al. 2018, 2020; Untiedt et al. 2021), but this technique penetrated the octocoral literature only after the molecular work presented here was already completed.

Regardless of these new taxa being subjected to more advanced genetic techniques in the future, the available evidence is clear in revealing a far more diverse octocoral fauna inhabiting New Zealand's shallow to mesophotic waters than was previously known. The clarified taxonomy presented here thereby opens up this virtually unstudied group to a myriad of new research avenues.

This includes research into basic aspects of each new species' biology, such as life history traits, feeding ecology and habitat preferences, as well as questions with a wider relevance to New Zealand and the Octocorallia globally. For example, at a regional scale within New Zealand, currently available material suggests that several species of *Kotatea* may possibly be restricted to two key hotspots of regional endemism, namely Manawatāwhi/Three Kings Islands (Grehan 2020) and Piwhane/Spirits Bay (Cryer et al. 2000). Although more material will need to be collected to confirm this, the presence of regionally endemic *Kotatea* species at these sites mirrors biodiversity patterns observed for other taxa, such as bryozoans (Rowden et al. 2004), and may contribute to a broader understanding of these sites' geological histories and the reasons for their biogeographic dissimilarity to the rest of New Zealand.

New Zealand soft corals are also promising candidates for exploration into novel natural products. Southern Ocean *Alcyonium* (*sensu lato*) species are rich in bioactive compounds (Núñez-Pons et al. 2013) and high epibiotic bacterial diversity in *A. digitatum* has led to the discovery of promising antimicrobial properties (Pham et al. 2016). Being evolutionarily similar to these other taxa, it is possible that *Kotatea* and *Ushanaia* might share these properties and harbour untapped potential for medical and industrial innovation in New Zealand.

Finally, further research into these new taxa may inform mechanisms of diversification in alcyoniids. Soft corals similar to *Kotatea* and *Ushanaia* routinely co-occur in other temperate regions, such as several species of *Alcyonium* occurring sympatrically throughout the Mediterranean Sea and north-east Atlantic Ocean (McFadden 1999) and two cryptic species of *Incrustatus* van Ofwegen, Häussermann and Försterra, 2007 occurring syntopically around southern South American fjords and coasts (McFadden and van Ofwegen 2013b). This, in turn, raises questions about the drivers of speciation in soft corals. Incongruence between mitochondrial and nuclear gene trees (although not observed in Chapter 2) implicates hybridisation and reticulate evolution as diversification mechanisms in some genera (McFadden et al. 2010), including *Alcyonium* (McFadden and Hutchinson 2004). Moreover, hybrids have been found to develop morphologies intermediate between parent species in *Alcyonium* (McFadden et al. 2005) and *Sinularia* (Quattrini et al. 2019), and the possible occurrence of hybridisation between morphologically similar congeners in *Kotatea* and *Ushanaia* may warrant future research.

2.6.7 Conclusions

This taxonomic review and revision confirm that *Alcyonium aurantiacum*, previously considered to be single species, is a complex composed of two new genera and at least 11 closely related species — ten of them new — that are endemic to New Zealand. Paraphyly and morphological differences support the exclusion of these new taxa from *Alcyonium sensu stricto* based on comparisons to *A. digitatum*, the type species of the genus. While genetic and morphological data were strongly congruent at the genus-level, species delimitation was in most cases based on consistent morphological differences alone. Based on phylogenetic analyses, a regional component (at a continental scale) appears to strongly influence the relationships within *Alcyonium sensu lato*, and future investigations may allow for the genus to be further divided into several regionally endemic genera.

The description and delineation of *Kotatea* and *Ushanaia* represents a significant increase in our understanding of New Zealand's octocoral fauna and will hopefully also contribute to the ongoing global systematic revisions within this problematic branch of the Octocorallia. Ultimately, the fact that New Zealand was host to only one described species of easily accessible, shallow-water *Alcyonium*-like soft coral for nearly two centuries emphasises how little is known about its regional marine biodiversity. Now, many new avenues of enquiry can be pursued for these newly described nearshore soft corals. Very little is known of their spatial distribution patterns, and virtually nothing regarding their ecology, reproduction, habitat associations or vulnerability to anthropogenic threats and change. It is hoped that this newly found diversity will stimulate further research into all aspects of *Kotatea* and *Ushanaia* biology.

Chapter 3.
Discrimination between two morphologically similar and phenotypically plastic New Zealand soft coral species

3.1 Abstract

In octocorals species discrimination is a resource-intensive task that routinely requires scanning electron microscopy, molecular techniques, and taxonomic expertise. In New Zealand, *Kotatea aurantiaca* and *K. lobata* are two common, endemic, and co-occurring soft corals that cannot currently be distinguished without microscopic examination of sclerites and of which virtually nothing is known regarding any aspect of their ecology or biology. Here, interspecific differences in macroscopic characters of colony morphology (mean lobe length, diameter and height, number of lobe tips, estimated volume) are quantified using MANOVA, which shows that whilst both species differ in terms of average character values, they overlap considerably in the range of every measured character. Nonetheless, a binary logistic regression model is developed by which these easily obtainable measurements can be used to reliably assign specimens to either species with up to 90% accuracy. Species assignment accuracy is highest when ratios formed from morphological measurements are used, rather than direct measurements. These ratios are used for the first time to account for the variability derived from the common habit among soft corals of altering their appearance by expanding and contracting the coelenteron with seawater. Relationships between colony morphology and depth are also examined, and it is suggested that phenotypic plasticity detected in *K. lobata*, causing it to resemble *K. aurantiaca* more closely at greater depths, may contribute to the morphological overlap observed between these species. It is hoped that this discrimination technique will facilitate future research on the ecology and biology of *K. aurantiaca* and *K. lobata*.

3.2 Introduction

Species represent the fundamental units on which many analyses in fields such as ecology, biogeography, evolutionary biology, and conservation are based (Guerra-García et al. 2008). Biological research thus often depends on the accurate identification and discrimination of species. However, for octocorals this can present a challenge. Identification keys based on features observable in the field or in preserved specimens can be produced for certain taxa or regions (e.g., Sánchez and Wirshing 2005), but in most cases species identification requires genetic comparisons or the extraction and examination of microscopic sclerites. These tasks are laborious, time-consuming, expensive and necessitate taxonomic and technical expertise. Consequently, the difficulty of species-level identification in octocorals may place it beyond the scope of some studies, such as those relying on field observations, which may then be restricted to identifications to higher taxonomic levels (e.g., Fabricius and De'Ath 2008; Chanmethakul et al. 2010). The conflict between the need to identify and discriminate between species and the resources this requires is problematic. As a consequence, the biology of most of the ~3500 currently recognised octocoral species (WoRMS 2021) remains unexamined in any detail (Bayer 1981b).

During taxonomic revision of the nominal species "*Alcyonium aurantiacum*" and its associated species complex (Chapter 2), it became apparent that two of the species involved, despite being separated by consistent sclerite differences, can be extremely difficult to distinguish based on macroscopic morphological characters. Specimens of *Kotatea aurantiaca* and the newly described *K. lobata*, can be similar in colony growth form and dimensions, as well as in the number and shapes of their lobes. Because genetic markers (mitochondrial *mtMutS* and nuclear *28S*) also failed to differentiate them, this raised concerns regarding how non-taxonomists could discriminate between the two species. *Kotatea aurantiaca* and *K. lobata* are two of the most commonly encountered inshore octocorals in New Zealand, where they are endemic, yet virtually nothing is known regarding any aspect of either species' biology, such as their ecologies or life history characteristics, their responses to anthropogenic pressures, and whether they require management. To fill these knowledge gaps, methods are required that enable these species to be distinguished reliably, quickly and cost-effectively, and without taxonomic training in octocorals.

In general, *K. aurantiaca* is digitate in growth form with more slender lobes, while *K. lobata* is lobate and tends to produce thicker and more robust lobes (Chapter 2). Critically however, both species are highly variable and these morphologies grade into one another (e.g., Chapter 2: compare *K. lobata* specimen NIWA 108960 in Fig. 19 with some of the *K. aurantiaca* colonies of NIWA

101181 and NIWA 54535 in Fig. 9). As a result, intraspecific and interspecific variation in macroscopic colony morphology overlap in these species, reflecting broad patterns of indistinct morphological species boundaries previously noted among octocorals (Prada et al. 2008; Dueñas and Sánchez 2009; McFadden et al. 2017). This is exacerbated by the common behaviour among soft corals in the suborder Alcyoniina to expand and contract the coelenteron with water and thereby change the size and shape of a colony, which may also be affected by collection and preservation method (Fabricius and Alderslade 2001; Hellström and Benzie 2011; Davis et al. 2015). This means that a given collection of specimens will invariably display a spectrum of expansion/contraction states that may complicate, for example, the differentiation of highly expanded *K. aurantiaca* and contracted *K. lobata* specimens.

While *K. aurantiaca* tends to occur at more southerly latitudes and deeper depths than *K. lobata*, the two species overlap in their geographic and bathymetric distributions (Fig. 38A, and see Figs. 2B, C in Chapter 2). Geographic overlap is particularly pronounced around Northland, in the northern North Island of New Zealand. Regarding depth, overlap occurs at ~30 m, which corresponds approximately to the minimum depth so far observed for *K. aurantiaca* and maximum depth for *K. lobata*. The true extent of overlap, however, is likely greater than can be inferred from the currently available material. Therefore, collection data may be of limited use in informing the species identity of a specimen. Moreover, phenotypic plasticity — defined as morphological responses to the environment that result in intraspecific variation (West-Eberhard 2003) — is common in octocorals, particularly along depth gradients (e.g., West et al. 1993; Rodríguez-Lanetty et al. 2003; Kim et al. 2004; Gori et al. 2012; Costantini et al. 2016; Calixto-Botía and Sánchez 2017), and may thus also contribute to the morphological variation observed in *K. aurantiaca* and *K. lobata*.

Currently, *K. aurantiaca* and *K. lobata* cannot be reliably discriminated without sclerite extraction and microscopy. The aim of the study presented here was to ascertain if — and in what ways — the colony growth forms of *K. aurantiaca* and *K. lobata* differ, and then to determine whether specimens could be reliably assigned to species based only on macroscopic measurements and their statistical analysis. The reliability of statistical species discrimination methods that are based directly on morphological measurements was compared with methods using ratios formed from these measurements. Ratios were used to produce variables that are independent of the actual size of a specimen and can thus account for the expansion/contraction state of colonies. This marks the first time that ratios of colony-scale morphological measurements have been used for this purpose in octocorals. It is hoped that this method of discriminating between these two common species

without the need for sclerite extraction will facilitate future research on other aspects of this understudied group's biology. Considering the lack of ecological information currently available for *K. aurantiaca* and *K. lobata*, phenotypic plasticity with depth was investigated in both species.

3.3 Materials and methods

3.3.1 Sample selection and measurements of colony morphology

Forty (preserved) colonies were selected from each of the *K. aurantiaca* and *K. lobata* specimens listed in Chapter 2. Nearly all *K. lobata* colonies available were included, barring the smallest and most degraded individuals. Since *K. aurantiaca* colonies were more numerous, the 40 most-intact individuals were selected to achieve balanced sample sizes and to correspond to the colony size range observed among the *K. lobata* samples. Maximum colony height, width and thickness (taken at 90˚ relative to the width measurement), as well as the length, diameter (at midpoint) and height (from colony base) of all primary lobes were measured (primary lobes were here treated as lobes arising directly from the base of the colony, not from other lobes — they can be "mother" lobes and give rise to "daughter" lobes *sensu* Sánchez 2004 in regards to branches, but may also lack daughter lobes) and the total number of terminal lobe tips was also recorded for each individual. This allowed five direct measurements of colony morphology to be obtained: 1) estimated volume (= colony height x width x thickness); 2) mean lobe length (mean length of primary lobes); 3) mean lobe diameter (mean diameter of primary lobes at midpoint); 4) mean lobe height (mean height of primary lobes from colony base); and 5) number of tips (total number of terminal lobe tips).

Three ratios were calculated using some of the above direct measurements to produce dimensionless values that are independent of a given colony's state of expansion/contraction. The following ratios were selected because they characterise key colony growth form attributes: 1) "LL:LD" (the ratio of mean lobe length to mean lobe diameter): an indicator of lobe thickness, where a high ratio represents a long and thin lobe and a low ratio represents a thick lobe; 2) "LH:CH" (the ratio of mean lobe height to colony height): an indicator of colony stalk development, where a high ratio represents a well-developed stalk and a low ratio represents a poorly developed stalk; 3) "Tips:LD" (the ratio of number of tips to mean lobe diameter): an indicator of tip development or lobe branching/splitting, where a high ratio represents much branching into daughter lobes and a low ratio represents little branching. Although the absolute number of tips present on a colony does not depend on its state of expansion/contraction, their

conspicuousness does increase with colony expansion, with tips being less discernible and more prone to miscounts on highly contracted specimens.

3.3.2 Statistical analyses

All statistical analyses were carried out in IBM SPSS 27 and PAST4 (Hammer et al. 2001).

3.3.2.1 Interspecific differences

First, two separate Hotelling's T^2 tests (a variation of one-way MANOVA where the independent variable has only two groups) were used to determine whether *K. aurantiaca* and *K. lobata* differ in either their direct measurements or their ratios of colony morphology. All five direct measurements were transformed to better meet the assumptions of the test, while the three ratios were untransformed and calculated from untransformed data. Estimated volume and number of tips were both inverse transformed (inv), mean lobe length and mean lobe diameter were both square root transformed (sqrt), and mean lobe height was log10 transformed. These transformations were carried out because they performed best overall at improving the fit of the data to statistical assumptions (data not shown). The same transformed data were used for all analyses described below.

Several assumptions of Hotelling's T^2 were violated and required further correction or consideration. Mean lobe height, estimated volume, and number of tips, as well as LH:CH and Tips:LD were non-normally distributed (Shapiro-Wilk test $p < 0.05$), but Hotelling's T^2 (and MANOVA in general) is considered robust to departures from normality (Weinfurt 1995). The number of tips and all three ratios violated homogeneity of variance (Levene's test $p < 0.05$), which was corrected for by using Welch's t-test for pairwise comparisons. The test on the three ratios did not exhibit homogeneity of variance-covariance matrices (Box's M test $p < 0.001$), but Hotelling's T^2 is considered robust to this violation when sample sizes are balanced (Tabachnick and Fidell 2014) — as is the case here — and Pillai's trace was used instead of Wilks' Λ (Olsen 1976). In both the Hotelling's T^2 tests (on direct measurements and on ratios), one multivariate outlier was detected for *K. aurantiaca* (assessed by Mahalanobis distance) as well as several univariate outliers for most variables in both species (assessed by boxplot), and although MANOVAs are regarded as sensitive to outliers (Tabachnick and Fidell 2014), these were retained in the analysis due to small sample sizes and to incorporate the true morphological variation observed (removal of outliers did not affect significance of results). In all other instances, all remaining assumptions were met.

Finally, pairwise comparisons between species were made using post-hoc independent-samples t-tests (or Welch's t-test) with a Bonferroni-adjusted α level of 0.01 for direct measurements (5 tests) and 0.017 for ratios (3 tests).

To further explore interspecific differences in the ratios, Spearman's rank-order correlations were used to assess the relationships between mean lobe length and mean lobe diameter, between mean lobe height and colony height, and between number of tips and mean lobe diameter for both species at a Bonferroni-adjusted α level of 0.008 (6 tests).

3.3.2.2 Species discrimination

Two separate binomial logistic regressions were used to classify individual colonies into species based on either the five direct measurements of colony morphology or the three ratios described above. For both analyses, all independent variables (measurements and ratios) were linearly related to the logit of the dependent variable (species), as assessed using the Box-Tidwell procedure (Box and Tidwell 1962; Fox 2016). For the regression incorporating the direct measurements as independent variables, one standardised residual with a value of −2.7 standard deviations was found but retained in the analysis. For the regression using the ratios as independent variables, two standardised residuals with values of −4.555 and −3.066 standard deviations were found but also retained in the analysis. These outliers were again retained due to small sample sizes and to incorporate the full range of morphological variation observed among the included specimens (removal of outliers did not affect significance of results).

For both analyses, ROC (receiver operating characteristic) curves were also calculated. In binomial logistic regression the area under the ROC curve is equivalent to the concordance statistic, which is the most common measure of a generalized linear model's ability to discriminate (Gönen 2007; Steyerberg 2009). ROC curve coordinates were used to inform cut-off values for species discrimination, which were deemed acceptable when sensitivity (% of *K. lobata* specimens correctly assigned) was $\geq$ 80% and 1−specificity (false positives or the % of *K. aurantiaca* specimens incorrectly assigned as *K. lobata*) was $\leq$ 20%.

Although the data violated critical assumptions of DFA (discriminant function analysis) and PCA (principal component analysis), both these tests were nonetheless performed as a comparison and to offer support to the logistic regression analyses. DFAs and PCAs were also performed once for direct measurements and once for ratios. For the PCAs, data showed an unacceptable overall KMO

measure of sampling adequacy (< 0.5) (Kaiser 1974), indicating that variables may be too highly correlated for PCA to be appropriate. For the DFA the same violations applied as for Hotelling's T^2 listed above. Because of this, the results of both these analyses were interpreted cautiously.

3.3.2.3 Intraspecific responses to depth

Spearman's rank-order correlations were used to test for an association between depth and morphological variables (direct measurements as well as ratios) within *K. aurantiaca* and *K. lobata*. The Bonferroni Correction was not used in this case because of its oft-criticised disadvantage of increasing the probability of false negatives (Rothman, 1990; Savitz and Olzhan, 1995; García, 2004) when a high number of comparisons are made (note that 16 tests — 8 variables for 2 species — would reduce the α level to 0.003).

3.4 Results

3.4.1 Interspecific differences

There was a statistically significant difference between *K. aurantiaca* and *K. lobata* in combined direct measurements of colony morphology ($F_{[5, 74]} = 15.143$, $p < 0.001$, Wilks' $\Lambda = 0.494$, partial $\eta 2 = 0.506$). Mean lobe length was significantly longer in *K. lobata* ($p < 0.001$), mean lobe diameter significantly thicker in *K. lobata* ($p < 0.001$), and *K. aurantiaca* had a significantly greater number of tips (Welch's t-test $p < 0.001$) (Fig. 38B–D), while estimated volume and mean lobe height did not differ significantly (Fig. 38E, F). A statistically significant difference was also found between *K. aurantiaca* and *K. lobata* in combined ratios of colony morphology ($F_{[3, 76]} = 24.018$, $p < 0.001$, Pillai's trace = 0.487, partial $\eta 2 = 0.487$), with LL:LD, LH:CH, and Tips:LD all being significantly greater in *K. aurantiaca* (Welch's t-test $p < 0.001$ in all cases) (Fig. 38G–I).

A statistically significant positive correlation was found between mean lobe length and mean lobe diameter for both *K. aurantiaca* ($r_{s[38]} = 0.645$, $p < 0.001$) and *K. lobata* ($r_{s[38]} = 0.602$, $p < 0.001$) (Fig. 39A). The correlation between mean lobe height and colony height was significant and positive for *K. aurantiaca* ($r_{s[38]} = 0.473$, $p = 0.002$), but non-significant for *K. lobata* ($r_{s[38]} = 0.321$, $p = 0.044$) (Fig. 39B). The correlation between number of tips and mean lobe diameter was significant and positive for *K. aurantiaca* ($r_{s[38]} = 0.588$, $p < 0.002$), while that for *K. lobata* was non-significant ($r_{s[38]} = 0.222$, $p < 0.169$) (Fig. 39C).

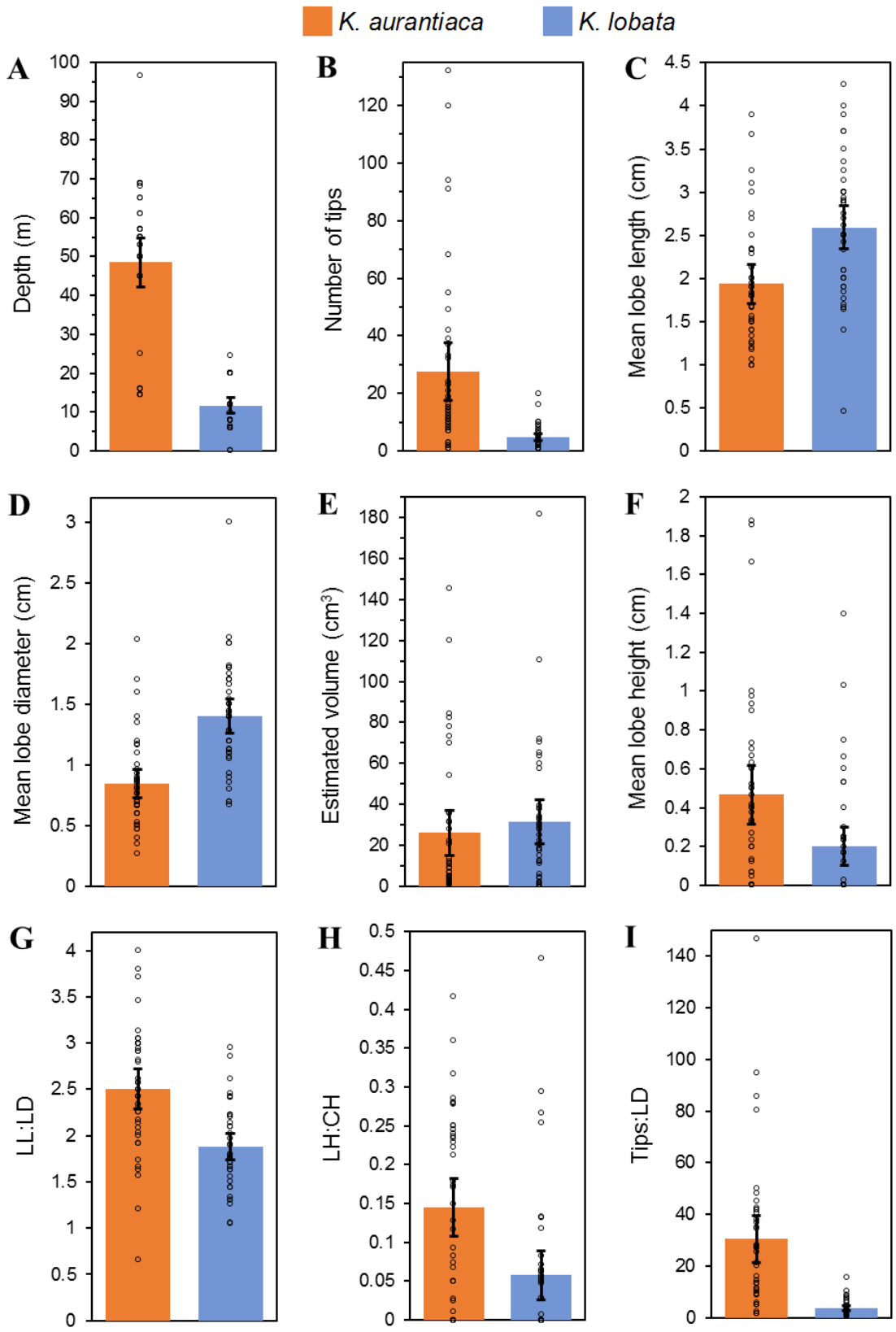

Figure 38. Mean differences between *K. aurantiaca* and *K. lobata* in depth (**A**) and all measured variables of colony morphology (**B–I**) ± 95% CI and individual data points.

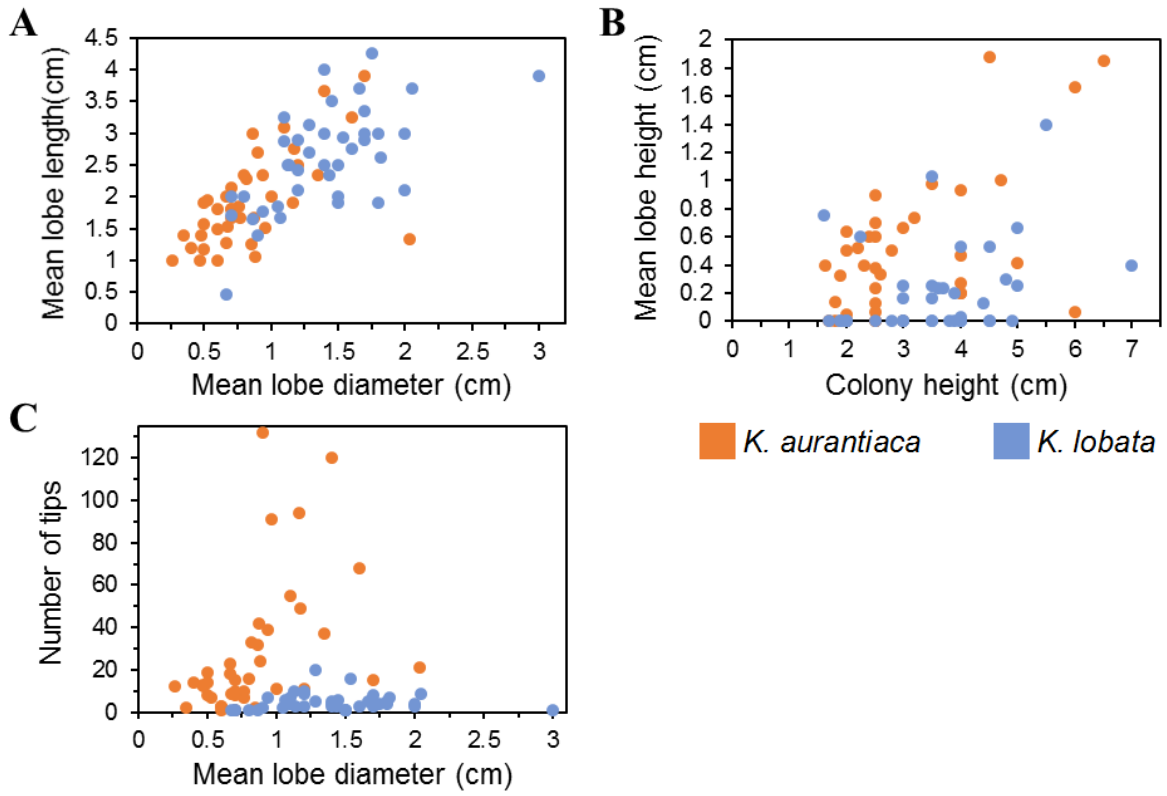

Figure 39. Correlations between the variables comprising each of the morphological ratios for *K. aurantiaca* and *K. lobata*: **A.** LL:LD; **B.** LH:CH; **C.** Tips:LD.

3.4.2 Species discrimination

For direct measurements of colony morphology, the logistic regression model was statistically significant ($\chi^2_{[5]} = 60.299$, $p < 0.001$) and explained 70.6% of the variance in species classification (Nagelkerke R^2). The model correctly classified 87.5% of cases, misclassifying five of 40 individuals for each species. Of the five predictor variables, only mean lobe diameter and number of tips were significant (Table 3), with increasing mean lobe diameter and decreasing number of tips (since the variable was inverse transformed) associated with an increased likelihood of classification as *K. lobata*.

For ratios of colony morphology, the logistic regression model was also statistically significant ($\chi^2_{[3]} = 70.313$, $p < 0.001$) and explained 78% of the variance in species classification (Nagelkerke R^2). This model correctly classified 90% of cases, misclassifying five *K. aurantiaca* individuals as *K. lobata*, and three *K. lobata* individuals as *K. aurantiaca*. All three ratios contributed significantly to the model (Table 3), with increasing LL:LD, LH:CH and Tips:LD ratios all associated with a decreased likelihood of classification as *K. lobata*. The area under the ROC curve for the analysis of direct measurements was 0.933 (95% CI, 0.878–0.988) and for the analysis of ratios was 0.952

(95% CI, 0.905–0.998), both indicating an "outstanding" level of discrimination (*sensu* Hosmer et al. 2013). Potentially acceptable cut-off values could only be produced for mean number of tips and mean lobe diameter (Table 4).

The logistic regression equation for direct measurements was:

$$\log(p/1\text{-}p) = -14.153 - 1.615*\text{Estimated volume[inv]} + 1.317*\text{Mean lobe length[sqrt]} + 9.723*\text{Mean lobe diameter[sqrt]} - 1.374*\text{Mean lobe height[log 10]} + 7.801*\text{Number of tips[inv]}$$

The logistic regression equation for ratios was:

$$\log(p/1\text{-}p) = 7.329 - 1.920*\text{LL:LD} - 8.431*\text{LH:CH} - 0.264*\text{Tips:LD}$$

Table 3. Logistic regression results. Note that for inverse transformed variables the true association is opposite to that displayed by the odds ratios. Statistically significant results are in bold. *B* = *B* coefficients (as log odds), used by regression equation to predict dependent variable from independent variables. SE = standard errors for *B*. Wald = Wald chi-square value used for determining significance of independent variable together with *p*. Odds Ratio = change in odds for a one-unit increase in independent variable.

Analysis Variable	***B***	**SE**	**Wald**	***df***	***p***	**Odds Ratio**	**95% CI for Odds Ratio**	
							Lower	**Upper**
Direct measurements								
Estimated volume (inv)	-1.62	1.86	0.75	1	0.385	0.20	0.01	7.63
Mean lobe length (sqrt)	1.32	1.75	0.57	1	0.450	3.73	0.12	114.17
Mean lobe diameter (sqrt)	9.72	3.15	9.54	1	**0.002**	16703.86	34.94	7984723.16
Mean lobe height (log 10)	-1.37	0.94	2.16	1	0.142	0.25	0.04	1.58
Number of tips (inv)	7.80	2.54	9.47	1	**0.002**	2442.21	17.00	350926.79
Constant	-14.15	3.57	15.73	1	< 0.001	< 0.001		
Ratios								
LL:LD	-1.92	0.78	6.09	1	**0.014**	0.15	0.03	0.67
LH:CH	-8.43	3.74	5.09	1	**0.024**	< 0.001	< 0.001	0.33
Tips:LD	-0.26	0.09	9.55	1	**0.002**	0.77	0.65	0.98
Constant	7.33	2.00	13.40	1	< 0.001	1524.60		

Table 4. Variables with (potentially) acceptable and near-acceptable cut-off values for assignment of a given specimen as *K. lobata* based on ROC curve coordinates. Sensitivity indicates % of *K. lobata* specimens correctly assigned, while 1−specificity indicates false positives or the % of *K. aurantiaca* specimens erroneously assigned to *K. lobata*.

Variable	**Cut-off value**	**Sensitivity**	**1−specificity**	**Untransformed value equivalent**
Mean lobe length (sqrt)	1.4317	70%	32.5%	> 2.05 cm
Mean lobe diameter (sqrt)	1.0123	82.5%	22.5%	> 1.02 cm
Number of tips (inv)	0.1339	82.5%	20%	< 7.5 tips

Both PCAs produced two components (PCs) with eigenvalues > 1. For direct measurements, these explained 44.4% (PC1) and 30.6% (PC2) of the total variance respectively. PC1 had strong loadings for mean lobe length and mean lobe diameter as well as a weaker loading for estimated volume, while PC2 had strong loadings for estimated volume and number of tips (Table 5). For ratios, the two PCs explained 51.5% and 31.4% of the total variance respectively. PC1's strongest loading was for LH:CH, and PC2's strongest was for Tips:LD. Both had similar, weaker loadings for LL:LD (Table 5). In both analyses, the two morphological components largely overlapped between the species (Fig. 40). No further components were included, as none had eigenvalues > 1 or reduced the level of overlap between species.

The DFA prediction model for direct measurements was statistically significant ($p < 0.001$) and correctly classified 86.25% of specimens overall, with 87.5% of *K. aurantiaca* specimens and 85.0% of *K. lobata* specimens correctly classified: mean lobe diameter and number of tips were the strongest predictors (Table 6). The DFA prediction model for ratios was also statistically significant ($p < 0.001$) and correctly classified 83.75% of specimens overall, with 72.5% of *K. aurantiaca* specimens and 95% of *K. lobata* specimens correctly classified and LL:LD and Tips:LD being the strongest predictors (Table 6).

Table 5. Rotated structure matrix for PCAs with Varimax rotation (major loadings > 0.5 and < −0.5 in bold). Communalities indicate the proportion of each variable's variance that is accounted for by the principal components.

Analysis Variable	**Component 1**	**Component 2**	**Communalities**
Direct measurements			
Estimated volume (inv)	**-0.555**	**0.724**	0.832
Mean lobe length (sqrt)	**0.882**	-0.091	0.785
Mean lobe diameter (sqrt)	**0.919**	0.097	0.854
Mean lobe height (log 10)	0.258	0.668	0.513
Number of tips (inv)	-0.112	**0.870**	0.769
Ratios			
LL:LD	**-0.606**	**0.601**	0.729
LH:CH	**0.937**	0.034	0.878
Tips:LD	0.032	**0.937**	0.879

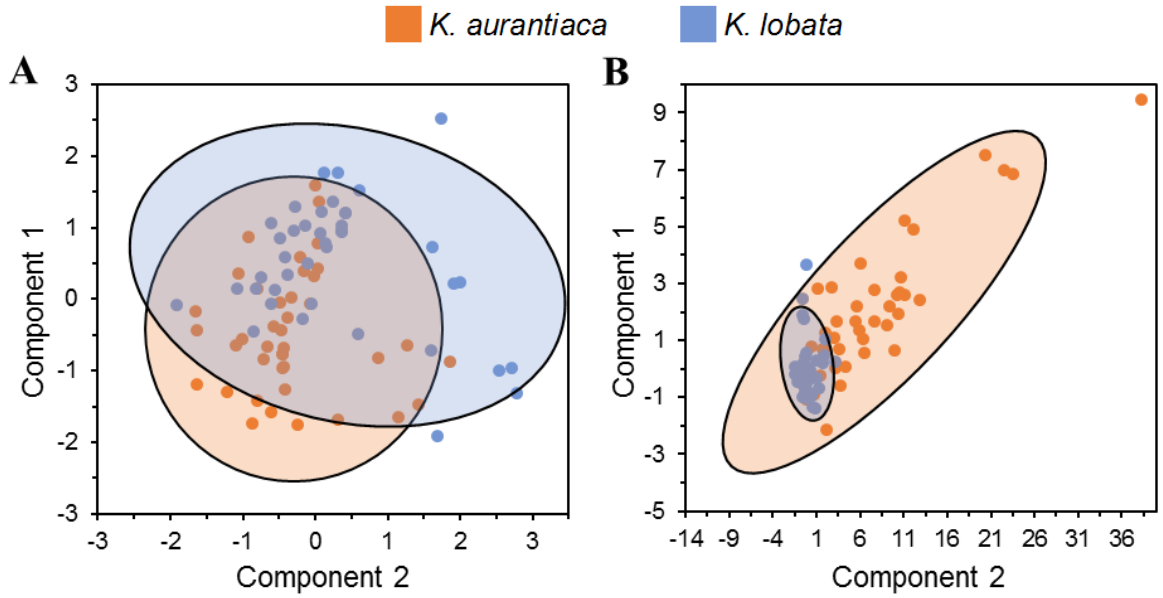

Figure 40. PCA plots (*K. aurantiaca* and *K. lobata*) with 95% ellipses for: **A.** Direct measurements of colony morphology; **B.** Ratios.

Table 6. Standardised canonical discriminant function coefficients for DFAs (strong predictors > 0.5 and < −0.5 in bold).

Analysis Variable	Discriminant function coefficients
Direct measurements	
Estimated volume (inv)	-0.022
Mean lobe length (sqrt)	0.195
Mean lobe diameter (sqrt)	**0.825**
Mean lobe height (log 10)	-0.256
Number of tips (inv)	**0.817**
Ratios	
LL:LD	**0.643**
LH:CH	0.485
Tips:LD	**0.664**

3.4.3 Intraspecific responses to depth

Statistically significant correlations were only found between depth and three of the morphological variables examined for *K. lobata*. These were all weak to moderate and include a positive correlation between depth and LL:LD ($r_{s[38]}$ = 0.329, p = 0.038) (Fig. 41A) and negative correlations between depth and mean lobe height ($r_{s[38]}$ = −0.459, p = 0.004) as well as LH:CH ($r_{s[38]}$ = −0.433, p = 0.005) (Fig. 41B, C). For *K. aurantiaca*, no statistically significant correlations were found between any of the examined variables and depth.

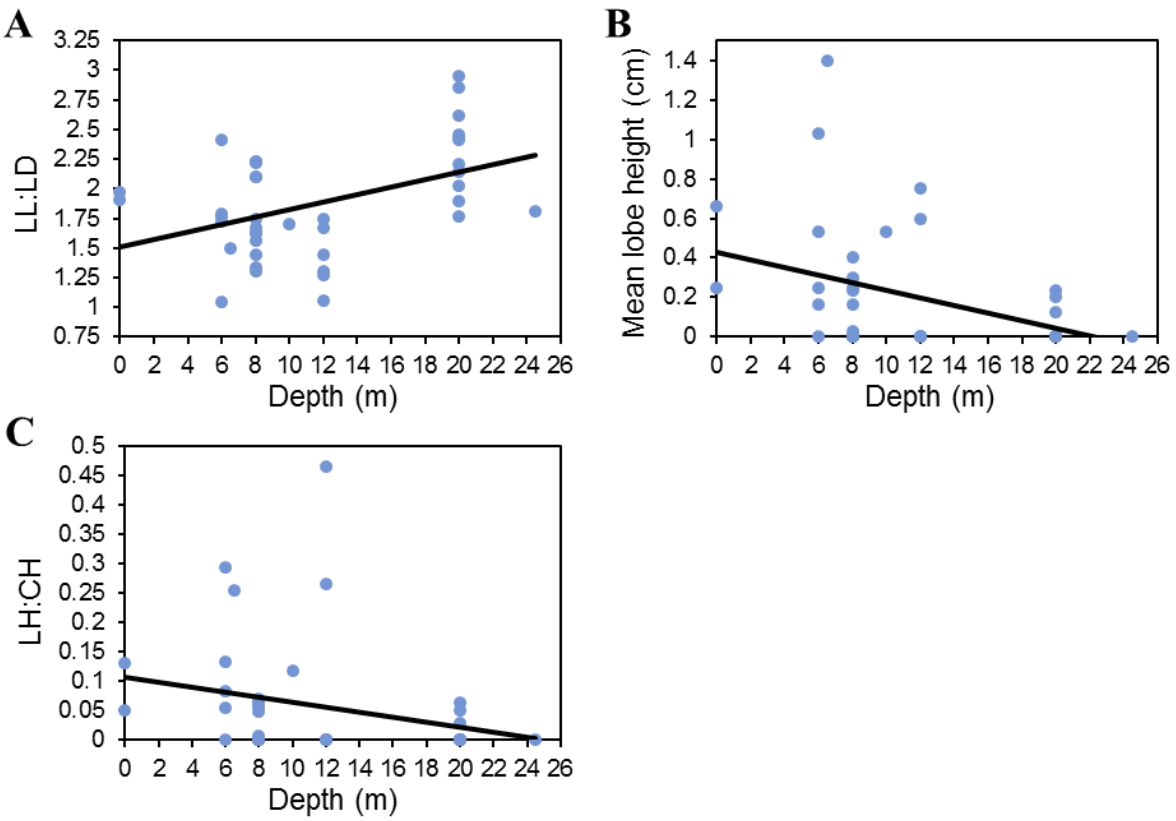

Figure 41. Significant correlations between morphological variables and collection depth (m) for *K. lobata*: **A.** LL:LD; **B.** Mean lobe height; **C.** LH:CH. Trendlines presented to help visualisation.

3.5 Discussion

3.5.1 Interspecific differences

Compared to *K. lobata*, *K. aurantiaca* tends to have more numerous terminal lobe tips and greater tip development, forms a more prominent stalk, and possesses primary lobes that are shorter, thinner and longer relative to their diameter. Further analysis of the variables comprising these ratios showed that, while primary lobe length increases with diameter in a similar way for both species, only in *K. aurantiaca* does lobe height increase with colony height and the number of terminal tips with average primary lobe diameter. This means that while primary lobes become thicker as they grow longer in both species, *K. aurantiaca* develops a stalk as the colony grows and continues to add terminal lobe tips, whereas *K. lobata* does not develop a stalk and grows mainly by progressively thickening its few lobes rather than by adding more. However, despite differences in means between the two species, the actual data points when superimposed (e.g., Fig. 38) illustrate clearly that *K. aurantiaca* and *K. lobata* overlap in every single measured morphological variable. These analyses thus serve to confirm the initial observations that general morphological differences

do exist between these species, but that these are difficult to discern for individual colonies due to a considerable degree of interspecific overlap.

3.5.2 Species discrimination

Determining how species can be discrimination is central to understanding biodiversity and the patterns and processes that drive it, as it allows us to recognise whether a given set of specimens constitute members of the same species or not (Dayrat 2005). Here, mean differences indicate that *K. aurantiaca* and *K. lobata* differ in colony morphology, and this makes it possible to discriminate between the species through the use of easily obtainable morphological measurements rather than relying on more resource-intensive methods such as sclerite extraction.

Morphometric analyses similar to those employed here are ubiquitous throughout comparative zoology (reviewed by Adams et al. 2004). In hexacorals and gorgonian octocorals, many more informative characters are available for interspecific comparison than in soft corals because these taxa do not exhibit colony expansion/contraction behaviour to the same degree. These include surface area, surface-to-volume ratio, inter-calyx distance, average distance between polyps, polyp density and branching angles (e.g., Weinbauer and Velimirov 1998; Prada et al. 2008; Einbinder et al. 2009; Soto et al. 2018), among many others. Doszpot et al. (2019) used 3D modelling to analyse "area of occupied space" in scleractinian corals, for example. None of these characters are reliable for interspecific comparisons in *Kotatea* species, and probably not within other Alcyoniina. Soft corals thus present an inherently difficult subject for examinations and taxonomic assessment based only on colony morphology.

Despite the observed morphological overlap, both logistic regression analyses were able to assign specimens correctly to species with a high degree of confidence. For the model based on direct measurements only two of five variables — mean lobe diameter and number of tips — were significant, and both were associated with extremely high odds ratios, indicating much higher odds of classification as *K. lobata* for each 1-unit increase in these variables. The reason for this is that the 1-unit increase used by the odds ratios covers almost the entire range of the transformed data, which is ~0.5–1.7 for the square root of the mean lobe diameter and ~0.01–1.00 for the inverse of the number of tips. Furthermore, the directions of the odds ratios are as would be expected based on the observed interspecific differences, namely that greater lobe diameter and fewer tips translate to greater odds of classification as *K. lobata*. It therefore follows that a 1-unit increase should necessarily be associated with greatly inflated odds of classification as *K. lobata* for these variables.

For the regression model based on ratios, all three variables were significant and, as would be expected from the observed interspecific differences, increases in all were associated with a decreased likelihood of classification as *K. lobata*. Overall, the fact that 90% of specimens were correctly classified using ratios compared to 87.5% using direct measurements, and considering the Nagelkerke R^2 and area under ROC curve values for both analyses, the regression model based on ratios performed slightly better. Misclassified specimens in both analyses were primarily composed of the smallest individuals, with correct assignment among these constituting the main difference in classification success between the two models. This may be because the smallest specimens tend not to exhibit much branching or very thick lobes and thus lack the features most useful to species discrimination. Regardless, this indicates that the ratios successfully controlled for a given specimen's state of expansion/contraction, and that species discrimination is less reliable when this is not taken into account. The three ratios improved the fit of the model compared to the two direct measurements (Table 3), suggesting that more useful morphological information can be extracted by forming meaningful ratios than by relying only on direct measurements. The use of morphometric ratios for species discrimination is firmly ingrained in the taxonomic study of many groups, from plants to arthropods (Baur and Leuenberger 2011). While ratios have been used in gorgonian octocorals (e.g., Brazeau and Lasker 1988), they have not been used in soft corals, among which colony morphology is typically regarded as relatively uninformative (e.g., McFadden et al. 2017). These new observations show that morphometric ratios may be useful for ongoing research into species boundaries in soft corals.

Here, cut-off values proved somewhat impractical to apply. Chiefly this is due to the extent of morphological overlap between *K. aurantiaca* and *K. lobata*. Table 4 presents the cut-off values with the best trade-off between sensitivity and specificity, or in other words, those with the best potential for use in species discrimination. Cut-off values for mean lobe diameter and number of tips, if implemented, result in ~80% correct species assignment. Such information could be incorporated into future identification guides as it shows potential utility for field measurements and may, for example, aid in preliminary identifications of newly collected material. The next best cut-off value was for mean lobe length, with misclassification rates of ~30%. Depending on the study, such rates could possibly be acceptable and taken into account when collecting data or designing experiments in the future. These cut-of values can all be refined in the future through the use of larger sample sizes, but even so, *K. aurantiaca* and *K. lobata* may simply be too variable to be discriminated based on any single measure of colony morphology at much higher rates than these.

Overall, the PCA and DFA results are less informative than the logistic regression models for species discrimination, but they nonetheless allow for valuable comparisons to be made between methods. The PCAs support the logistic regression results, as the variance explained was similar and ratios performed better than direct measurements in both analyses. Beyond this, the PCA again highlights the high degree of overlap that exists between the colony morphologies of the two species, particularly since all variables loaded strongly onto one of the two identified components for both analyses. Interestingly, and in contrast to the logistic regressions and PCA, the DFA based on direct measurements performed slightly better than that based on ratios, with 86.25% compared to 83.75% correct classifications overall. This may be because in the DFA using ratios, LH:CH was not identified as a particularly strong predictor of species, even though all three ratios added significantly to the logistic regression model, which, importantly, performed better. This indicates that while discrimination accuracy may be lost if the assumptions of DFA — which are more stringent compared to logistic regression — are not fully met (as was the case here), it can still be very high (> 80%). Thereby, the utility of the morphological characters described here for species discrimination in *K. aurantiaca* and *K. lobata* is further validated.

3.5.3 Phenotypic plasticity

Currently, one of the main issues facing octocoral taxonomy is the uncertainty surrounding the extent and relevance of intraspecific morphological variation coupled with insufficient interspecific variation among many commonly used molecular markers (Pérez et al. 2016), which makes it difficult to establish species limits (McFadden et al. 2010). In octocorals, phenotypic plasticity is often examined with the aim of reviewing the taxonomic status of two or more morphotypes, which may then be split into several species (e.g., Soler-Hurtado et al. 2017) or retained as one (e.g., Bilewitch et al. 2010). Here, however, depth-related phenotypic plasticity was examined for *K. aurantiaca* and *K. lobata* to address the lack of ecological information available for both of these commonly encountered New Zealand endemics. Evidence for phenotypic plasticity being associated with depth was only found for *K. lobata*, which is somewhat surprising, because *K. aurantiaca* occupies a much greater depth range. Interestingly, a near identical situation has been reported for two species of Mediterranean gorgonians, whereby plasticity in a usually shallower-living species has resulted in it being misidentified as a more morphologically stable and deeper-ranging species (Pica et al. 2018).

It may be that *K. lobata* exhibits phenotypic plasticity because this species tends to inhabit much shallower depths, extending even into the intertidal zone, where it may be subjected to greater

environmental variability than *K. aurantiaca*. This may include tidal water movement, wave stress, storm damage, and fluctuating light, salinity, temperature, and food availability — many of which are known to influence gorgonian colony form (e.g., Wainwright and Dillon 1969; Leversee 1976; Velimirov 1976; West 1997). *Kotatea lobata* has a higher LL:LD ratio at greater depths, equating to lobes that are longer and thinner, than at shallower depths. It may be that the thick and robust lobes of *K. lobata* are necessary for its colonies to withstand wave stress or to optimise water retention when exposed intertidally, while at deeper depths it can optimise surface area and food capture by forming colonies with thinner and more sprawling lobes, as has been reported for related soft corals (Sebens 1984). However, why mean lobe height and LH:CH should decrease with depth in *K. lobata* is unclear. This may be a plastic response related to sedimentation (Prada et al. 2008) or predation (West et al. 1993), but evidently, data incorporating a more complete range of depths and environmental conditions are needed to draw conclusions regarding the relationships between morphological variables and depth in both species.

Octocorals are highly species-specific in their responses to abiotic factors (Rodríguez-Lanetty et al. 2003), and thus it is difficult to compare the results and ecological interpretations presented by different studies. This is especially true for *K. aurantiaca* and *K. lobata*. While depth-related phenotypic plasticity has been recorded many times for gorgonians (e.g., West et al. 1993; Rodríguez-Lanetty et al. 2003; Kim et al. 2004; Gori et al. 2012; Costantini et al. 2016; Calixto-Botía and Sánchez 2017), this has not been reported for soft corals in the suborder Alcyoniina. Because of their contrasting colony architecture, the colony-scale morphometrics used in studies on gorgonians are (as explained above) uninformative in soft corals that exhibit colony expansion/contraction behaviour. As a result, the phenotypic plasticity observed in gorgonians cannot be directly compared to *K. aurantiaca* or *K. lobata* in most cases. Branch development is a notable exception, but comparisons of plasticity in this trait are also problematic as the vast majority of taxa in which this has been examined are zooxanthellate, whereas *K. aurantiaca* and *K. lobata* are azooxanthellate. For example, zooxanthellate gorgonians commonly exhibit decreased branch development at deeper depths (e.g., Lasker et al. 2003; Calixto-Botía and Sánchez 2017), which may minimise self-shading at reduced light levels (as postulated by Brazeau and Lasker 1988). *Kotatea lobata* shows an opposite pattern, tending to be more finely divided at greater depths, while *K. aurantiaca* is variable across its entire depth range. Clearly, zooxanthellate and azooxanthellate species contend with different selection-by-depth pressures and therefore express different phenotypic plastic responses.

3.5.4 The taxonomic status of *K. aurantiaca* and *K. lobata*

In light of the overlap in colony morphology described above and the lack of species-level monophyly in *K. aurantiaca* and *K. lobata* (see Fig. 1 in Chapter 2), it may be posited that these are not two but one species, with *K. lobata* and *K. aurantiaca* representing shallow and deep ecotypes respectively. Indeed, under this interpretation, observations made for *K. aurantiaca* and *K. lobata* would closely match results obtained by Prada et al. (2008), who demonstrated thicker branches and a tendency to grow in a single plane in a gorgonian species at shallower depths. Accordingly, *K. lobata* lives at shallow depths, can grow in a single-plane fashion (Chapter 2), and has thicker lobes than *K. aurantiaca*. However, this is unlikely to be the result of expansive phenotypic plasticity and in this case is better explained by interspecific variation based on fixed morphological differences. This is strongly supported by the consistent sclerite differences discussed in Chapter 2, which includes examinations of specimens from each species at comparable depths. *Kotatea aurantiaca* has larger collaret spindles overall than *K. lobata* (compare Figs. 10A and 20A) and much smaller and rarer point clubs (up to ~0.10 mm in *K. aurantiaca* vs. ~0.24 mm in *K. lobata*, compare Figs. 10B and 20B). Most notably, *K. aurantiaca* does not share the large spindle-like forms in its surface regions that can be found in *K. lobata* (compare Figs. 20F and 21B with Fig. 10F, H) and also lacks the distinctive, large, highly branched and irregular antler- and spindle-like forms which characterise the interior regions of *K. lobata* (compare Figs. 10G and 11A with Figs. 21A and 22A). Were both species part of a broader spectrum of phenotypic plasticity within a single species, one would expect to see less consistency in marked sclerite differences. Moreover, sclerite characteristics are generally regarded as more taxonomically informative than colony growth form attributes (Fabricius and Alderslade 2001). In terms of morphology, the overlap and phenotypic plasticity in colony-scale measurements presented above are outweighed by sclerite evidence and are therefore not deemed to offer sufficient support for the combination of *K. aurantiaca* and *K. lobata* as a single species.

Studies comparing morphological and genetic variation in octocorals have variously concluded distinct ecotypes to represent different species (e.g., Soler-Hurtado et al. 2017) or intraspecific variation (e.g., Gutiérrez-Rodríguez et al. 2009; Bilewitch et al. 2010) depending on whether genetic and morphological differences were concordant with one another. Occasionally, authors also express uncertainty regarding the taxonomic status of apparent ecotypes (e.g., Gori et al. 2012; Costantini et al. 2016). Here, the interpretation put forward in Chapter 2, that the lack of genetic variation between *K. aurantiaca* and *K. lobata* in mitochondrial *MutS* and nuclear *28S* simply indicates a lack of species-level resolution in the selected markers, is unchanged. It should be noted,

however, that *K. aurantiaca* and *K. lobata* met the proposed threshold for accurate discrimination of species in *Alcyonium* identified by McFadden et al. (2014a) for mean genetic p-distances in *mtMutS* (0.5%) (see Table 2 in Chapter 2). Mitochondrial *mtMutS* in particular often lacks the resolution needed to discriminate between congeneric species (e.g., Sánchez et al. 2003b; Wirshing et al. 2005; Cairns and Bayer 2005; Cairns and Baco 2007; McFadden et al. 2006a, 2009). Additionally, nominal species of *Alcyonium* have been shown to share identical haplotypes for both *mtMutS* (McFadden et al. 2011) and *28S* (McFadden et al. 2014a). Perhaps most importantly, in cases where morpho-molecular comparisons are inconclusive, clear and consistent morphological differences are commonly weighted more highly than a lack of phylogenetic resolution in new species descriptions (e.g., van Ofwegen et al. 2007; Moore et al. 2016; Núñez-Flores et al. 2020). This approach was followed in Chapter 2 and, considering that the balance of morphological evidence has not changed, should not be deviated from based on the results presented here.

3.5.5 Limitations and future research

Ideally, predictive models such as those discussed here should be trained and then tested on separate data sets. However, available material is not abundant enough for this method to be effective, and virtually all available specimens of *K. aurantiaca* and *K. lobata* were instead used in the building of the logistic regression models to include as much morphological information as possible. The techniques presented here could, of course, be replicated for other sets of similar soft coral species, but unfortunately, limited availability of specimens also prevented other species described in chapter 2 from inclusion in analyses. It should be noted, however, that the only other species with which *K. aurantiaca* and *K. lobata* (specimens with thinner lobes only) share a superficial resemblance are probably restricted to greater depths (*K. amicispongia*, > 100 m) or non-overlapping distributions (*K. raekura*, Manawatāwhi/Three Kings Islands), and are thus unlikely to be confused for these species even by non-taxonomists. Future collection of additional specimens will be necessary to test the performance of the models and to compare results obtained with preserved material against fresh samples or measurements taken from *in situ* photographs. Larger sample sizes based on targeted collections from a broader range of depths and locations will improve our ability to discern patterns relating to intraspecific variation and could allow for exploration into other environmental factors which may play a role in determining the morphologies of these species. Reciprocal transplant experiments (e.g., West et al. 1993; West 1997; Prada et al. 2008; Calixto-Botía and Sánchez 2017) or population-genetic analyses (e.g., Andras et al. 2012; Holland et al. 2017; Yesson et al. 2018) could be especially useful in re-

evaluating intraspecific variation in both species, as well as in confirming their separate species status.

3.5.6 Conclusions

Here it is shown that specimens can be assigned to *K. aurantiaca* and *K. lobata* with a high degree of confidence based only on measurements of colony morphology. This study marks the first use of ratios to control for the variable state of expansion/contraction among soft coral specimens, and since they performed slightly better at species classification, their use is recommended over direct measurements. Without the need for sclerite extraction or genetic comparisons, the logistic regression equations presented here will enable researchers not trained in octocoral taxonomy to fit their data to these models and investigate the ecology, life history, and conservation requirements of both species freely and without taxonomic confusion for the first time. It is hoped, therefore, that this species discrimination approach will stimulate further research on these New Zealand endemics, as well as on other sets of similar soft coral species for which this technique could be replicated.

Chapter 4.
The use of integrative taxonomy in octocorals: A literature survey

4.1 Abstract

Integrative taxonomy describes the simultaneous use of multiple lines of evidence, such as combinations of morphological and molecular data, for the delimitation and description of taxa. Since its formalisation in the literature in 2005, this approach has been broadly regarded as the most efficient way to produce robust species hypotheses. Octocorals constitute a significant component of benthic marine communities across most depths and latitudes worldwide, but the extent of their diversity is poorly known, and their systematics have long been regarded as poorly resolved. At the species level, the integrative approach is seen as a promising way to achieve taxonomic progress in this group, and it is thus worth assessing the extent of its usage. Here a literature survey was undertaken to gain an overview of taxonomic descriptions since the initiation of Linnaean taxonomy. This is followed by an analysis of published work from the years 2000–2020, for which the prevalence of integrative taxonomic techniques in descriptions is examined, in particular the combination of morphology and genetics. Description rates at family, genus and species levels over the last twenty-one years are found to be among the highest in the history of octocoral taxonomy. While for families and genera the formalisation of integrative taxonomy coincides with this acceleration, this was not observed for species. Moreover, the integrative approach has been applied unevenly across taxonomic groups and geographic regions and constitutes a minority for the octocoral literature. Its usage is increasing, however, as are the number of taxonomic publications and the total number of persons listed as authors per year. It is suggested that historically high description rates are being driven by research primarily based on morphology, which may be adding to the need for future revisionary studies. These data are intended to serve as a baseline by which future taxonomic progress can be evaluated.

4.2 Introduction

The term "integrative taxonomy" was formalised independently by two seminal papers in 2005 and was proposed primarily to reconcile the rift between morphology- and DNA-centric visions for the future of taxonomy that prevailed at the time (Dayrat 2005; Will et al. 2005). At its simplest, the integrative approach is predicated on the notion that the delimitation and description of taxa should be based on multiple, independent lines of evidence rather than selecting just one (Goulding and Dayrat 2016). Taxonomic decisions derived from this approach may combine morphological characteristics with, for example, developmental, molecular, ecological, or behavioural data sources. Since its inception, and despite some conceptual disagreements in its application, a formalised integrative approach has been broadly regarded as the most efficient and most objective way to produce robust species hypotheses (de Queiroz 2007; Padial et al. 2010; Schlick-Steiner et al. 2010; Yeates et al. 2011). Consequently, it is seen as a promising way to overcome the global taxonomic impediment, especially in light of the modern biodiversity crisis that threatens the extinction of species even before they can be described (Costello et al 2013a; Sheth and Thaker 2017; Vinarski 2020).

The application of integrative techniques is particularly urgent for taxa that are threatened by anthropogenic change and/or are poorly understood in terms of their diversity. Octocorals form ecologically significant and conspicuous components of benthic communities across most depths and latitudes worldwide (Fabricius and Alderslade 2001), but now face increasing pressure from disturbances (see Chapter 1) such as destructive fishing practices (Althaus et al. 2009), fossil fuel exploration (De Leo et al. 2015), ocean acidification (Gabay et al. 2013) and thermal stress due to rising sea surface temperatures (Fabricius 1999; Bruno et al. 2001; Loya et al. 2001; Gambi et al. 2010; Lõhelaid et al. 2015; Dias and Gondim 2016). Long seen as problematic, octocoral taxonomy remains in flux, and the effective future management of octocorals will hinge on improved understanding of species boundaries. For the most part, taxonomic difficulties in this group are due to a limited range of morphological characters forming the traditional basis for octocoral systematics, further exacerbated by homoplasy, intraspecific plasticity, and the enduring legacy of inadequate descriptions published during and before the early 20th century (Pérez et al. 2016). These factors have often led to incongruence between historical classifications and more recent molecular phylogenies — as is the case for many groups of marine invertebrates — and have highlighted the need for revisions throughout Octocorallia at all taxonomic levels (Daly et al. 2007).

Problems persist among genetic techniques as well, although their application has been instrumental in redressing confusion in octocoral taxonomy. Chiefly, many of the molecular markers chosen for phylogenetic analyses have shown limited variation at the species level (McFadden et al. 2010, 2011). This lack of fine-scale resolution among some taxa is further complicated by hybridisation and reticulate evolution, which convolute the diversification of some genera (McFadden and Hutchinson 2004; Quattrini et al. 2019). Additionally, progress in many groups is hampered by a dearth of material suitable for DNA extraction. Notwithstanding these challenges, recent advances such as the use of ultraconserved elements (Erickson et al. 2020) are encouraging, and the integration of genetic and morphological data is now often cited as key to alleviating the problematic state of octocoral taxonomy (Pérez et al. 2016; Núñez-Flores et al. 2020; Poliseno et al. 2021).

To date, the rate of taxonomic progress for Octocorallia has been reviewed only for certain groups, such as the sea pens (Williams 2011), or specific areas, such as Asia (Ramvilas et al. 2019), but has not been surveyed for octocorals as a whole. Neither has the use of integrative taxonomy. This means there is little by which to judge taxonomic progress in the octocoral literature or by which it may be compared to efforts on other organisms. Accordingly, the rate of progress and the impact of integrative techniques in octocoral taxonomy are here assessed through a literature survey focussing on the last twenty-one years. The aim is to elucidate how current description rates compare to historical rates and how the prevalence of the integrative approach in the literature varies across time, regions, and taxa. It is anticipated that this will provide a useful comparative baseline for octocoral taxonomy in the coming decades, and it is hoped that this will encourage more researchers to practice integrative methodologies.

4.3 Materials and methods

Firstly, records of all currently accepted (as of June 2021) extant species, genera and families in Octocorallia were downloaded from the World Register of Marine Species database (WoRMS 2021) using the advanced search function (search terms: status = “accepted”; rank = “is species”; belonging to “Octocorallia”; flags = “extant”) and compiled in a spreadsheet to compare description rates over time between 1755 (corresponding to the oldest octocoral species description listed in WoRMS) and 2020 (taxa described post-2020 were excluded). Note that synonymisations at any taxonomic level, although a key part in the taxonomy of octocorals, were omitted due to the sheer number of their implementation in Octocorallia and the logistical difficulty in accurately tracking synonymisation histories through WoRMS. The data presented here thus provide an approximation

of the rates (per annum) at which species, genera, and families of octocorals — going by currently accepted taxa — have been discovered. This should be borne in mind for results and discussions relating to 'description rates'.

Subsequently, to examine trends in the use of integrative taxonomic techniques, original published descriptions were retrieved for all species, genera and families described between and including the years 2000–2020 based on taxonomic authorities listed in the WoRMS database. Even though the concept of integrative taxonomy was formalised in 2005 (Dayrat 2005; Will et al. 2005), this timespan was chosen because genetic techniques were available and studies may have incorporated several lines of evidence in taxon descriptions prior to that year. This also offers a summary of taxonomic research on octocorals throughout the 21st century to date. Efforts were made to find, as near as possible, all other publications from 2000–2020 (which may not have been listed in WoRMS) featuring any of the following taxonomic actions pertaining to octocorals: new taxon descriptions at the species, genus or family level; resurrections of taxa at any of these levels; elevations (e.g., subfamily to family or subspecies to species); and transfers (e.g., species between genera or genera between families). This was done by searching the names of all octocoral taxa listed in the WoRMS database with the Web of Science research tool using the following fields: "Topic", taxon name; "Or"; "Title", taxon name; "And"; "Year Published", 2000–2020. The titles and abstracts of all publications in the search results were then viewed, and all judged to potentially include taxonomic actions on the searched-for taxa were retrieved. The relevant sections of all publications in the resulting list were then examined and each individual occurrence of any of the above taxonomic actions, the types of data used to support them, and the taxon to which they applied, were tallied in a spreadsheet. This formed the main dataset. Note that for currently accepted taxa which were elevated or resurrected, it is the date of first description, not the date of elevation or resurrection, which was treated as a 'new taxon description'. Geographical distribution can be considered to implicitly support taxonomic decisions, but it was excluded here (*sensu* Pante et al. 2015b).

Detailed statistical analyses are not feasible or appropriate in this case because of the relative newness of the formalised integrative taxonomic approach, which meant that these data cover a range of only twenty-one years and resulted in variable and, on occasion, small values. Instead, data were used directly to examine: general trends in the prevalence of integrative taxonomic techniques across time, regions and taxa; the total number of taxonomic publications per year; the proportion of publications employing an integrative approach; and trends relating to authorship including the proportions of publications by single, two, and three or more authors and the total

author pool per year (recorded as the number of different persons listed as authors for the whole year, with each person counted only once, regardless of how many publications they contributed to in that year).

4.4 Results

4.4.1 Description rates 1755–2020

Overall, 3,590 currently accepted octocoral species, 399 genera and 56 families were described between 1755 and 2020. For species, yearly description rates were highly variable, but peaked markedly in the years 1889, 1906 and 1908–1910 (Fig. 42). When plotted cumulatively, the first decade of the 20th century clearly stands out as a period of exceptionally high species description rates, followed by a long period of steady progress and slight acceleration in the late 1990s (Fig. 43A). Accordingly, when broken into 20-year intervals, the mean number of species descriptions per year was highest for the 1901–1920 period, while 2001–2020 showed the highest rates of species description since the turn of the 20th century (Fig. 44). For genera, description rates increased dramatically in the 1990s, reaching their highest ever rate (Fig. 43A), while family description rates spiked post-2005 to levels not seen since the mid-1800s (Fig. 43B).

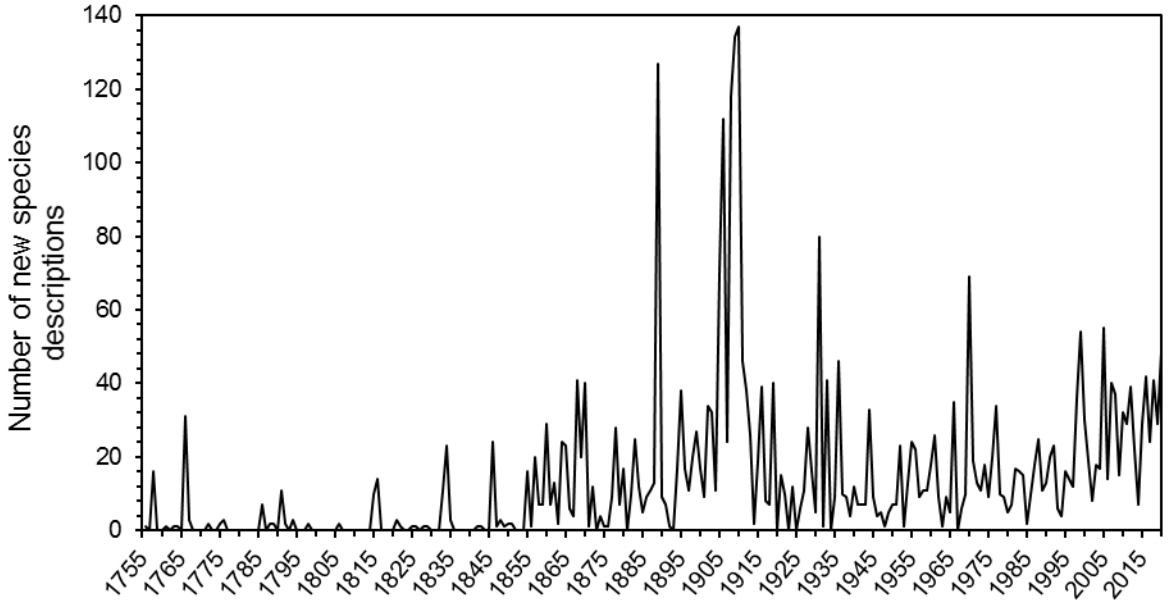

Figure 42. Number of new octocoral species descriptions per year, 1755–2020.

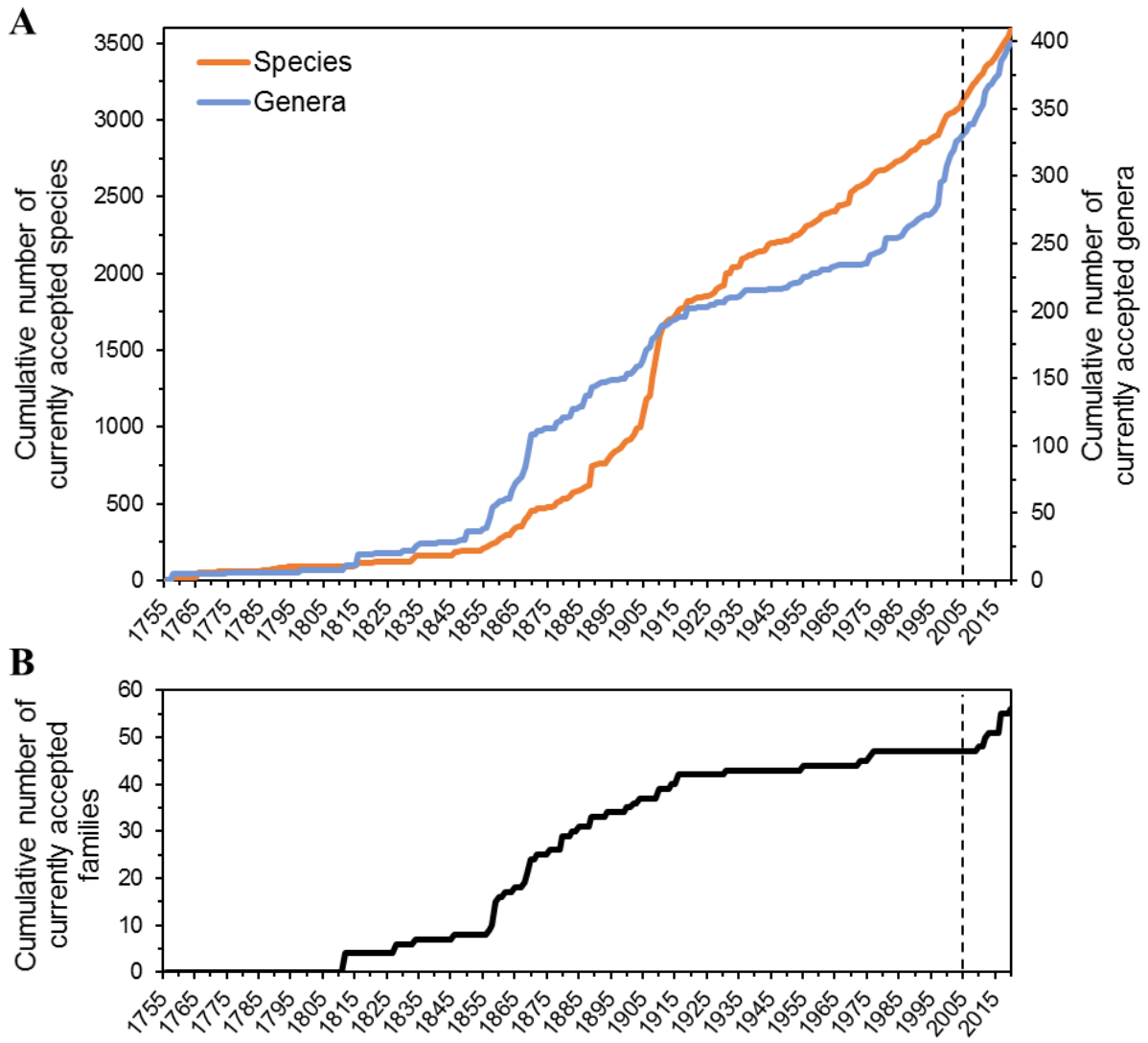

Figure 43. Cumulative number of octocoral species, genus, and family descriptions per year (1755–2020): **A.** Species and genera; **B.** Families. The formalisation of integrative taxonomy in 2005 is marked with a dashed line. Note different axis scales for species (primary y-axis in **A**), genera (secondary y-axis in A), and families (**B**).

4.4.2 Species descriptions 2000–2020

Between 2000 and 2020, 596 currently accepted species were described, 135 (23%) of which were described using an integrative taxonomic approach. Almost all integrative descriptions (134 of 135) included genetic evidence in addition to morphological data. Only two species descriptions included other forms of data — in this case reproductive traits (López-González and Gili 2000; Richards et al. 2018) — one of which did not include a genetic component.

The proportion of species described using an integrative approach (morpho-molecular comparisons in almost all cases) has fluctuated from year to year (Fig. 45). Pre-2007, this proportion was

uniformly close to zero. Post-2007 integrative descriptions were most often in the minority in comparison to morphology-only descriptions, but they did constitute a majority in 2014 and 2017, noticeably trending up overall (Fig. 45). This is confirmed when viewed in 5-year intervals, as the proportion of integrative species descriptions rose steadily: 2001–2005 = 117 new species, 2% integrative; 2006–2010 = 138 new species, 20% integrative; 2011–2015 = 126 new species, 29% integrative; 2016–2020 = 185 new species, 36% integrative. Between 2000 and 2020, there were also eight elevations to the species level from subspecies (one with an integrative approach) and seven species resurrections (two with an integrative approach).

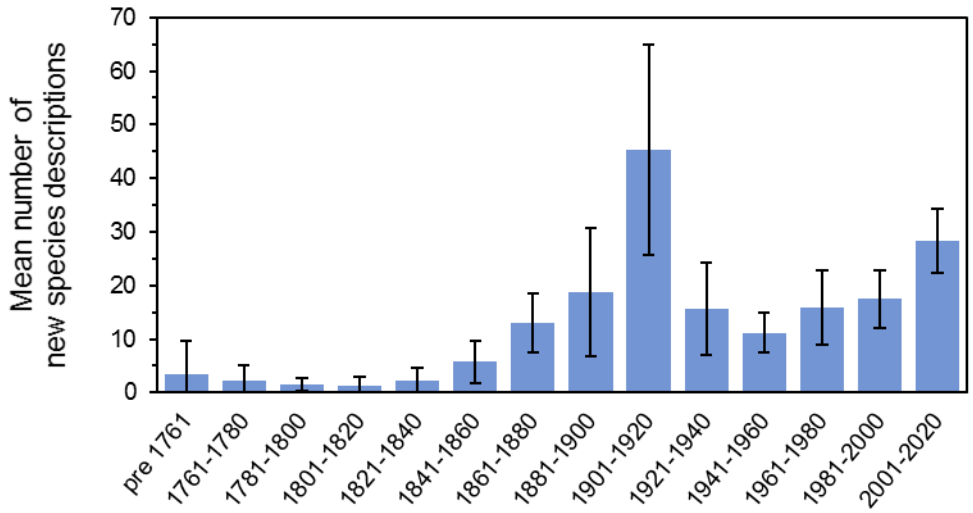

Figure 44. Mean number of octocoral descriptions per 20-year interval (1755–2020, ± 95% CI).

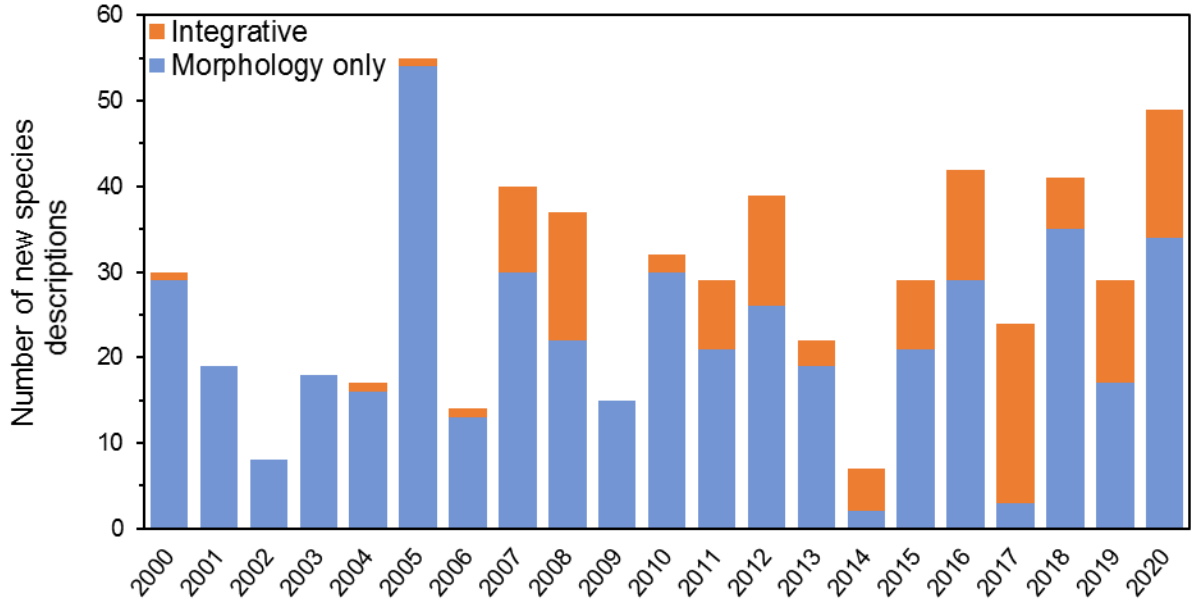

Figure 45. Number of new octocoral species descriptions per year (2000–2020) which used either an integrative approach or morphological data only.

4.4.3 Taxonomic actions at genus and family levels 2000–2020

At the genus level, there were 105 new descriptions from 2000 to 2020 (Fig. 43A), with 77 of these (73%) using an integrative approach. Two genera described as new in this period were subsequently subsumed into other genera, and both of these were initially described based only on morphological data. There were also seven genus resurrections, five with an integrative approach, and 359 instances of existing species being transferred to a different genus, with 54 of these (15%) using an integrative approach (note that some species were transferred between genera multiple times). Nine new families were described (Fig. 43B), eight (89%) with an integrative approach, and 36 species were transferred to a different family, with 12 of these transfers (33%) based on integrative evidence (note that a family-level change for a given species may or may not have coincided with a genus-level change). In terms of genera, 13 were transferred from one family to another, with 11 of these (85%) based on integrative evidence.

4.4.4 Trends by taxonomic group 2000–2020

Integrative techniques were not evenly applied in species descriptions across octocoral groups (Table 7). The use of integrative taxonomy was low among sea pens (Pennatulacea) and in the sub-order Holaxonia, but high in Stolonifera and Helioporacea (blue corals), although the latter was composed of only two new descriptions between 2000 and 2020 (Table 7). The families Primnoidae, Alcyoniidae and Nephtheidae saw the highest numbers of new species descriptions, but Alcyoniidae had by far the most with 32 integrative descriptions (Table 7). Chrysogorgiidae is notable for having both relatively high description numbers (31) and percentages of integrative descriptions (39%). Most families with higher percentages of integrative descriptions were represented by very few descriptions (Table 7).

4.4.5 Trends by geographic region 2000–2020

Similarly, both the number of species described, and the proportionate use of integrative techniques in their descriptions, varied widely between geographic regions (Table 8). Palau, South Africa and Western Pacific seamounts were the only regions from which a clear majority of the collected material was described using an integrative approach. In the regions of the Mediterranean, Papua New Guinea and Pacific South America, the proportion was around half, while that for most other regions was 10–30% (Table 8). In contrast, at the scale of whole oceanic regions, the usage of integrative taxonomy was relatively even, with around 20–25% of species descriptions following

this approach across material from the Atlantic, Indian, Pacific, and Southern oceans (Table 8). Oceans did, however, vary substantially in their number of species descriptions, with far more descriptions based on Pacific than Atlantic material, for example (Table 8).

Table 7. Octocoral species descriptions (2000–2020) by taxonomic groups.

Order Sub-order Family	Number of new species descriptions	Number of genera containing the new species	Number of new species described using integrative approach	% of new species described using integrative approach
Alcyonacea				
Alcyoniina				
Acrophytidae	4	2	1	25.0
Alcyoniidae	98	22	32	32.7
Aquaumbridae	1	1	1	100.0
Leptophytidae	2	2	2	100.0
Nephtheidae	72	5	4	5.6
Nidaliidae	4	2	3	75.0
Paralcyoniidae	6	2	0	0.0
Xeniidae	13	10	1	7.7
TOTAL	**200**	**46**	**44**	**22**
Calcaxonia				
Chrysogorgiidae	31	8	12	38.7
Ellisellidae	9	2	0	0.0
Huziogorgiidae	1	1	0	0.0
Isididae	16	8	11	68.8
Primnoidae	127	27	14	11.0
TOTAL	**184**	**46**	**37**	**20.1**
Holaxonia				
Acanthogorgiidae	11	4	0	0.0
Dendrobrachiidae	2	1	0	0.0
Gorgoniidae	43	6	5	11.6
Keroeididae	1	1	0	0.0
Plexauridae	47	23	3	6.4
TOTAL	**104**	**35**	**8**	**7.7**
Protoalcyonaria				
Haimeidae	1	1	0	0.0
Scleraxonia				
Anthothelidae	3	2	2	66.7
Briareidae	2	2	0	0.0
Coralliidae	12	2	6	50.0
Melithaeidae	14	2	3	21.4
Paragorgiidae	14	2	3	21.4
Spongiodermidae	1	1	1	100.0
Victorgorgiidae	6	1	5	83.3
TOTAL	**52**	**12**	**20**	**38.5**
Stolonifera				
Arulidae	5	4	5	100.0
Clavulariidae	20	13	15	75.0
Cornulariidae	1	1	0	0.0
incertae sedis	1	1	0	0.0
TOTAL	**27**	**19**	**20**	**74.1**
incertae sedis				
Acanthoaxiidae	1	1	0	0.0
Parasphaerascleridae	3	1	1	33.3
incertae sedis	1	1	0	0.0
TOTAL	**5**	**3**	**1**	**20.0**
Helioporacea	**2**	**2**	**2**	**100.0**
Pennatulacea	**21**	**15**	**3**	**14.3**
COMBINED TOTAL	**596**	**179**	**135**	**22.7**

Table 8. Octocoral species descriptions (2000–2020) by geographic origin of collected specimens.

Region	Number of new species descriptions	% of total number of species descriptions	Number of new species described using integrative approach	% of new species described using integrative approach
Atlantic Ocean				
Northern Atlantic coasts and seamounts	29	4.9	9	31.0
Caribbean	19	3.2	1	5.3
Coast of South America	13	2.2	2	15.4
Mediterranean	2	0.3	1	50.0
other western Atlantic	12	2.0	2	16.7
Mid-Atlantic ridge and seamounts	5	0.8	0	0.0
West coast of Africa	9	1.5	1	11.1
TOTAL	**89**	**14.9**	**16**	**18.0**
South Africa	**19**	**3.2**	**13**	**68.4**
Indo-West Pacific				
South-East Asia	33	5.5	10	30.3
South China Sea	5	0.8	1	20.0
Papua New Guinea and New Caledonia	11	1.8	5	45.5
Palau	16	2.7	15	93.8
Broad distribution and other	35	5.9	0	0.0
TOTAL	**152**	**25.5**	**39**	**25.7**
Indian Ocean				
East coast of Africa	15	2.5	5	33.3
Red Sea	24	4.0	4	16.7
Arabian Sea and Persian Gulf	11	1.8	1	9.1
TOTAL	**50**	**8.4**	**10**	**20.0**
Pacific Ocean				
Japan, Ryukyu Archipelago and Taiwan	43	7.2	10	23.3
Far northern Pacific	29	4.9	8	27.6
Western Pacific seamounts	10	1.7	10	100.0
Hawaii	16	2.7	2	12.5
Other Pacific Islands	21	3.5	0	0.0
Tasmania	7	1.2	2	28.6
New Zealand	40	6.7	4	10.0
North-eastern Pacific	28	4.7	3	10.7
Coast of Central America	40	6.7	6	15.0
Galapagos	10	1.7	0	0.0
Coast of South America	11	1.8	5	45.5
TOTAL	**255**	**42.8**	**50**	**19.6**
Southern Ocean and Tierra del Fuego	**30**	**5.0**	**7**	**23.3**
Undetermined	**1**	**0.2**	**0**	**0.0**
COMBINED TOTAL	**596**	**100.0**	**135**	**22.7**

4.4.6 Publication and authorship trends 2000–2020

In total, 255 octocoral publications were recorded as making taxonomic decisions between 2000 and 2020, of which 79 (30%) used an integrative approach. The 596 species descriptions published in this timespan appear in 231 of these publications, of which 66 (29%) included integrative taxonomic techniques. The remaining 24 publications included other decisions, such as genus transfers or species resurrections, and of these 16 (67%) were integrative. Only two of these combined morphological data with non-genetic evidence, including ecological niche differences (Bayer et al. 2014) and polyp pulsation behaviour (Halász et al. 2013). Overall, the total number of taxonomic publications on octocorals, the total author pool and the percentage of taxonomic

publications taking an integrative approach have all trended upwards over the last twenty-one years (Figs. 46; 47). In the case of the latter two this is especially clear since 2011, as post-2011 the lowest yearly author pool and the percentage of integrative publications are similar to or higher than the highest of these values pre-2011. For the total number of publications per year, increases are comparatively slight and obscured particularly by a dip in 2014 (Fig. 47). All data fluctuated from year to year, particularly the percentage of integrative publications (Fig. 46), which was zero in 2001, 2002, and 2009, but spiked in 2014 (but note low total publications), 2017 and 2020. Of the 79 total integrative papers, 4 were by single authors, 32 by two authors, and 43 by three or more. Of the 176 total non-integrative papers, 61 were by one author, 95 by two authors, and 20 by three or more.

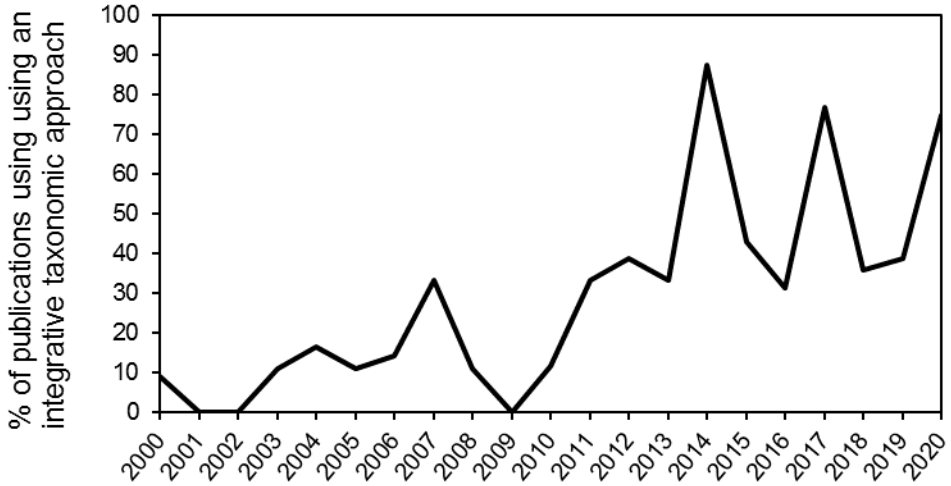

Figure 46. Percentage of all taxonomic publications on octocorals using an integrative approach per year (2000–2020).

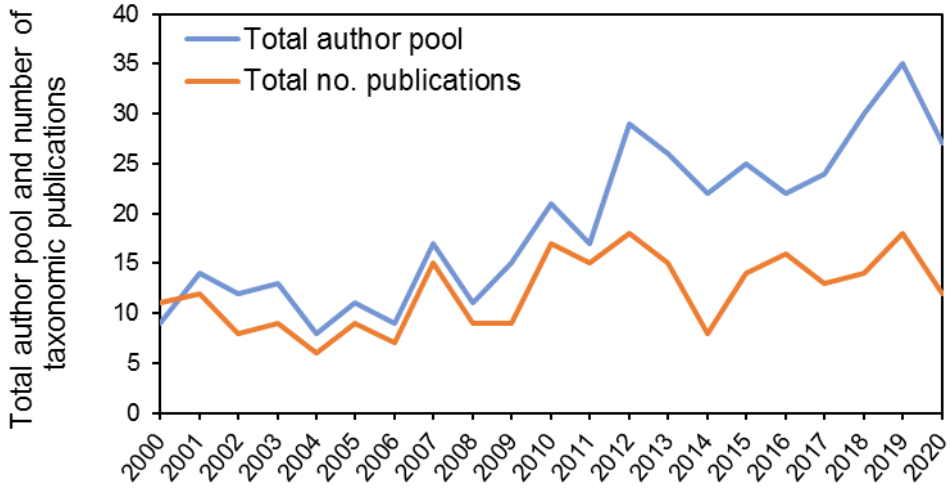

Figure 47. Total author pool and number of taxonomic publications on octocorals per year (2000–2020).

4.5 Discussion

4.5.1 Description rates and the use of integrative taxonomy

The exceptional pace of octocoral species descriptions around the turn of the 20th century is unsurprising as the same pattern has previously been identified for description rates concerning all life (Costello et al. 2012). For octocorals, this was driven by a number of major scientific expeditions operating round this time and the release of their reports (see Bayer 2001), which coincide precisely with the peaks in Fig. 42. This includes species collected, for example, during the H.M.S. *Challenger* (Wright and Studer 1889), R.I.M.S *Investigator* (Thomson and Henderson 1906; Thomson and Simpson 1909), *Valdivia* (e.g., Kükenthal 1906) and *Siboga* voyages (e.g., Versluys 1906; Nutting 1910). In part, the apparent rapidity of species accumulation during this period may also be due to many descriptions from this era still requiring revisions (Pérez et al. 2016), and thus the steepness of the curve in Fig. 43A may be somewhat softened in the future. Conversely, had descriptions been plotted for species which were later synonymised or are currently not accepted for other reasons, the steepness of cumulative species descriptions would probably have been more exaggerated in the early 1900s. Although beyond the scope of this study, the high number of synonymisations within Octocorallia may warrant further investigation regarding temporal, regional and taxonomic patterns of their implementation. By the measure of currently accepted taxa only, the last twenty-one years have seen higher species description rates than at any other point since the early 1900s. This may not hold true for all groups, however, as rates in sea pens (Pennatulacea), for example, showed a decline (Williams 2011).

Critically, the general acceleration in descriptions predates the formalisation of integrative taxonomy in the taxonomic literature (Dayrat 2005; Will et al. 2005). Taxonomy has integrated multiple lines of evidence for most of its long history (Valdecasas et al. 2008), but the coining of "integrative taxonomy" marked the most explicit call for the transformation of taxonomy and systematics into a multidisciplinary field and was widely expected to trigger a surge in new taxon descriptions over the following years (see Vinarski 2020). Yet for octocorals, description rates began to rise before this, in the late 1990s (see inflection in Fig. 43A). The inception of genetic applications in octocoral taxonomy coincides with this date (e.g., Lasker et al. 1996; McFadden 1999), but considering that morpho-molecular integration was rare prior to ~2007, this cannot account for the start of elevated description rates alone. Neither can the integration of other forms of data, since integrative taxonomy in octocorals is centred overwhelmingly on the combination of morphological and molecular data, with other forms being numerically negligible.

Regardless, integrative taxonomy, more or less exclusively in the form of morpho-molecular comparisons, continued to increase in prominence, reaching 36% of publications over the last five years (2016–2020). The integrative approach may thus have contributed to maintaining historically high species description rates among octocorals during this time, for example by uncovering cryptic species (McFadden and van Ofwegen 2013b), but it seems not to have directly caused the initial 1990s acceleration itself. Therefore, since 2005 the impact of integrative taxonomy on octocoral taxonomy at the species level is, for now, better characterised as adjuvant rather than revolutionary. This is not entirely surprising though, as it mirrors findings concerning all Animalia by Pante et al. (2015b) and suggests that for octocorals other factors drove up description rates late in the 20th century. This may include increases in revisions, sampling and the number of active researchers, or changes relating to the difficulty of publication.

At the genus level description rates also began to increase in the late 1990s. Unlike at the species level, however, a further acceleration is discernible post-2005 and descriptions then continued at their highest ever rates since the mid-1800s. The high proportion of integrative generic descriptions since 2000 (73%), also contrasts with the comparatively low prevalence of this approach at the species level (23%) and indicates that integrative morpho-molecular techniques were key in maintaining high genus description rates over the last twenty-one years. Further, the integrative approach has been applied nearly universally at the family level since the year 2000. The impacts of this, as well as improved genetic techniques, are clearly visible, and manifested as the steepest increase in description rates since the mid-1800s by around the year 2010. In general then, genus and family-level taxonomic descriptions are made using an integrative approach more frequently than at the species-level. This is most likely due to the difficulty of finding suitable species-level genetic markers in octocorals, meaning that higher taxa are more readily discernible by comparison (McFadden et al. 2011; also demonstrated in Chapter 2).

4.5.2 Trends by taxonomic group

The application of integrative species descriptions is very uneven across octocoral groups. No single overarching explanation can account for the observed patterns, which are probably caused by factors particular to each taxon. For example, in groups such as the family Clavulariidae, species tend to be small and inconspicuous, with similar morphologies that may necessitate data integration for robust species delimitation in most cases (e.g., McFadden and van Ofwegen 2012a; Lau and Reimer 2019). This would lead to a high proportion of integrative descriptions relative to other

taxa, which may have more diagnostic morphological features. Equally, patterns may reflect the opportunistic nature by which octocoral sampling is often carried out. In some groups, fresh specimens permitting an integrative approach may be more readily available, particularly those inhabiting easily accessible depths and environments, while others may be limited by the age and the state of preservation of archived material or the relative inaccessibility of their habitat. Similarly, patterns may reflect the personal preferences or expertise of the authors specialising in or focussing on different groups. For example, 70 of the 127 species added to Primnoidae since the year 2000 were described (without the use of genetic data) by Cairns (2006; 2007a, c; 2009; 2010; 2011; 2012a, b; 2015; 2018a, b).

Historically, taxa which are easily discernible as new may simply have been described earlier than more difficult ones. In other words, little 'low-hanging fruit' remains to be picked, leaving mostly cryptic taxa that require genetic data to be recognized and discriminated, particularly at genus and family levels. Accordingly, all groups associated with very high proportions of integrative species descriptions (80–100%) are made up of families or composed of genera that were described quite recently and for which genetic evidence was crucial, including Aquaumbridae (Breedy et al. 2012), Arulidae (McFadden and van Ofwegen 2012b), Leptophytidae (McFadden and van Ofwegen 2017) and Victorgorgiidae (Moore et al. 2017).

4.5.3 Trends by geographic region

Patterns relating to integrative taxonomy are similarly difficult to discern at the regional or national scale and, again, likely stem from each area's idiosyncrasies, such as its size, accessibility, underlying octocoral diversity, and resident expertise, as well as biases in where established institutions and experts choose to — or are able to — focus their efforts. The notably high usage of this approach in South Africa, for example, likely results from strong research interest due to its status as an important centre of endemism for octocorals (McFadden and van Ofwegen 2017). By contrast, when whole oceans are considered, the worldwide application of integrative taxonomy to species descriptions is roughly even at ~20%, despite the variability in absolute numbers of descriptions between oceans. Indeed, in terms of total species descriptions, the taxonomic literature is as scattered in geographic coverage now as it was when this was recognised by Bayer (1981b), and many of the same trends continue. Namely, regions with a long history of research, such as the Mediterranean, are considered more or less complete in their species inventories, while the octocoral diversity of the vast and species-rich Pacific and Indian oceans are comparatively poorly

known and continue to provide rich ground for species discovery (see overview by Pérez et al. 2016).

4.5.4 Authorship and other trends in the literature

Overall, the uptake of integrative taxonomy in octocorals was delayed following its formal introduction in the literature as a modern paradigm, and lags behind its usage in numerous other taxa (compare to Pante et al. 2015b; Vinarski 2020). Principally, this is likely because the years ~2000–2010 acted as a genetic discovery period for octocorals, during which markers were developed, explored and eventually employed as systematically informative data (France and Hoover 2001; McFadden et al. 2004, 2006a, 2011). This is supported by the percentage of integrative taxonomic papers on octocorals increasing only since ~2011. As most integrative taxonomic publications featured multiple authors, this, in turn, likely contributed heavily to the roughly concomitant increase in the total author pool. Together, this highlights the multidisciplinary nature of the approach and explains why yearly author pools have risen more sharply than the total number of taxonomic publications. The growing number of authors is thus an example of the "et al. effect" — an increase in authors per species named (*sensu* Costello et al. 2013b) — and illustrates a departure from the lone taxonomist stereotype in favour of modern standards, which require collaborations between experts with a range of skill sets.

4.5.5 One step forward, two steps back?

It is unclear why taxonomic researchers tend not to employ genetic techniques, as motivations for this are almost never stated. This may represent an enduring generational effect related to the preferences and expertise of long-established researchers (as noted above), available material may simply not be suitable for DNA extraction in many cases, or the funding and resources required may be prohibitive. Alternatively, reluctance may stem from a reputation for octocorals that even when attempted, genetic resolution is often insufficient to delimit species or incongruent with other data (e.g., Sánchez et al. 2003b; Wirshing et al. 2005; Cairns and Bayer 2005; Cairns and Baco 2007; McFadden et al. 2006a, 2009; also see Chapter 2). In either case, this is evidently not ideal.

Furthermore, where it is applied, the integrative approach revolves almost exclusively around morpho-molecular comparisons. By contrast, all other forms of data (e.g., reproductive traits, López-González and Gili 2000; Richards et al. 2018; polyp pulsation behaviour, Halász et al. 2013; ecological information, Bayer et al. 2014) constitute a very small minority in the taxonomic

literature (2000–2020) but may nonetheless prove highly useful in adjudicating cases of morphological and molecular incongruence in the future. The rarity of other data sources is probably a symptom of the fact that taxonomic research in this group — as in many others — tends to rely heavily on preserved specimens. In addition to possessing potentially degraded DNA, it may be difficult or impossible to glean ecological, reproductive, or behavioural data from such material, which may also be accompanied by little or no distributional or habitat context. It could be said then that, as a whole, octocorals are inherently difficult subjects for the integrative taxonomic approach, as indeed are many marine invertebrates (e.g., Wandeler et al. 2007; Zeng et al. 2019). Considering the scope of taxonomic problems within Octocorallia, the high rate of contemporary species descriptions, and the still gradual uptake of integrative taxonomy (as seen through proportions of integrative species descriptions and publications), this implies that we may currently be adding to the workload of instances requiring future revision faster than these are being resolved.

4.5.6 Limitations and future research

Ultimately, the "integrative future of taxonomy" (Padial et al. 2010) is only beginning to dawn for octocorals, but a new phase of discovery is well underway. Description rates at species, genus and family levels show no signs of slowing, and may be indicative of a large number of taxa still to be found. Bayer (1981b) estimated a total fauna of ~4000 species globally. This seems certain to be exceeded, especially considering that many genera have never been taxonomically revised and most of the world has never been systematically sampled (Pérez et al 2016). This, in turn, poses the question, how many species of octocoral are there? As a horizon of total species richness has not yet come into view, this will be difficult to answer. It may be useful to estimate this using species discovery curves (e.g., De Clerck et al. 2013; Edie et al. 2017). However, across a broad range of plant and animal taxa, species richness predictions are associated with extremely high margins of error in groups with highly incomplete inventories (Bebber et al. 2007). This means that until octocoral description rates begin to level off, it may be inappropriate to calculate discovery curves and attempt to predict a ceiling for the number of taxa in this group.

Examining how often the presence of unidentified species or species suspected of being undescribed is published may also contribute to future diversity estimates, although the difference between these two cases is difficult to extract from the literature in practice. Similarly, ascertaining how the use of integrative techniques in Octocorallia compares to specific other taxa could inform realistic timeframes for taxonomic progress, but this will require similar, focused literature surveys to be conducted for a range of taxa (beyond those by Pante et al. 2015b; Vinarski 2020 generalising

for all Animalia) and detailed direct comparisons cannot yet be made. Answers to these questions will be essential in shaping research priorities in octocoral taxonomy throughout the rest of the 21st century. Fundamentally though, this accumulation of biodiversity knowledge will require a substantial increase in the use of integrative practices to add to our understanding of octocoral phylogeny and systematics rather than adding to the burden of lingering taxonomic confusion.

Albeit speculative and in stark opposition to the perceived importance of integrative taxonomy, a future without the need for such an approach may now be possible. Whilst the universal animal *COI* barcode does not reliably distinguish between species of anthozoan cnidarians (McFadden et al. 2011), new methods can do so with increasing, unprecedented efficiency. Modern phylogenomics and RAD-sequencing in particular are proving revolutionary for species delimitation purposes (Herrera and Shank 2016; Erickson et al. 2020). Even species with no evident distinguishing morphological, ecological, or distributional characters can now be discriminated using only genetic data (McFadden et al. 2017). To inform this progress, it may be useful to quantify how the success of DNA at species delimitation and the emphasis of morphological or genetic evidence in cases of incongruence has changed over time. We could then be well-placed to ask: what will be the role of integrative taxonomy, let alone morphological methods, in a future where genomic capability is easily available to octocoral researchers? Perhaps integrative taxonomy is a transitional step between a discipline dominated by morphology in the past and genetics in the future. Without doubt, this carries profound philosophical implications for how we interpret different forms of data and choose from among many competing species concepts in the systematic delineation of species, and what data we incorporate into taxonomic descriptions and diagnoses. This will require collective introspection by the taxonomic community that is far beyond the scope of this study. Regardless, 134 species, 77 genera and 8 families were newly described using morpho-molecular comparisons over the last two decades. Few (perhaps none) of these new taxa could have been brought to light through morphology alone. For now, the contribution of integrative taxonomy to our understanding of octocoral diversity and systematics is thus clear, and the use of this approach is only set to grow.

4.5.7 Conclusions

The implementation of integrative taxonomy in octocorals has seen a marked increase in recent years. However, the integrative approach has been applied unevenly across taxonomic levels, taxonomic groups and geographic regions and, crucially, the majority of taxonomic decisions overall continue to be made solely based on morphological data. Moreover, description rates at

species, genus and family levels are currently among the highest ever seen for octocorals. Clearly, the early 21st century represents an exceptional period of discovery in the history of octocoral taxonomy and, encouragingly, this momentum is being carried forward by a growing field of authors.

Chapter 5.
General Discussion

5.1 Implications for octocoral research in New Zealand

The diversity and endemism of New Zealand soft corals, at all depths, has in the past been poorly studied (Tracey et al. 2019). The new genera and species described in this thesis present significant progress, adding to the existing tally of species, as well as to our understanding of endemism in the region. However, with over 200 undescribed octocoral species estimated to inhabit New Zealand's EEZ in total, a soberingly high proportion of New Zealand's octocorals still await description or remain unknown (Cairns et al. 2009; Mills et al. 2019) and it is perhaps not surprising to see New Zealand among the regions with the highest total number of octocoral species descriptions over the last twenty-one years (Table 8). Critically though, this accumulation of species must be accompanied by multi-disciplinary research efforts incorporating aspects such as habitat preference, distribution, abundance, population connectivity, species interactions and vulnerability to anthropogenic stressors if New Zealand is to effectively manage its unique marine biodiversity. Most such studies have tended to focus heavily on deep-sea and VME-associated taxa in New Zealand (e.g., Sánchez and Rowden 2006; Boschen et al. 2015; Anderson et al. 2016; Zeng et al. 2017), whilst globally, studies in this vein are generally rare for temperate, shallow soft corals (e.g., Holland et al. 2017), with the Mediterranean Sea being the basis of most examples (e.g., Weinberg 1977; McFadden 1999; Ambroso et al. 2013; Fiorillo et al. 2013; Topçu and Öztürk 2015; Teixidó et al. 2016).

With the taxonomic revision proposed here, the shallow-water soft coral species formerly reported as "*Alcyonium aurantiacum*" now encompasses eleven species in two genera with various geographic and bathymetric distributions around New Zealand. Some previous ecological observations attributed to *A. aurantiacum* could be reconciled with these new taxa, such as predation by nudibranchs likely referring to *Kotatea lobata* gen. n., sp. n. (Morton and Miller 1973; Westerskov and Probert 1981) and interactions with host antipatharians to *Ushanaia fervens* gen. n., sp. n. (Goldberg et al. 1990). However, most of the very limited ecological information historically associated with *A. aurantiacum* is difficult to transfer. Therefore, very little is known regarding the ecologies of any of these new species. Comparatively more is known for some similar soft corals elsewhere, such as *A. acaule* Marion, 1878 in the Mediterranean Sea. This species is a long-lived ecosystem engineer and can occur at densities as high as 18 colonies m^{-2} at comparable depths to *Kotatea* species (Weinberg 1977; Ballesteros 2006; Ambroso et al. 2013). If such

ecological significance were detected for New Zealand soft corals, this would clearly warrant protection. For now, however, soft corals — along with sea pens and zoanthids — are not protected in New Zealand under the Schedule 7A amendment (2010) to the Wildlife Act 1953 and have not been assessed in the New Zealand Threat Classification System (NZTCS) for marine invertebrates (Freeman et al. 2014). By contrast, one bamboo coral and one bubblegum coral have been assessed as threatened under the NZTCS, and many more gorgonians are considered. Furthermore, the collection or damaging of all "gorgonians", black corals, stony corals, and hydrocorals is illegal throughout New Zealand's EEZ, and numerous benthic protection areas have been closed to dredging and trawling to protect these corals and other benthic biodiversity (Freeman and Cryer 2019). *Kotatea* and *Ushanaia* collectively straddle the line between what is considered shallow and deep for corals, and at these intermediate or mesophotic depths research is scarce (Lesser et al. 2009, 2018; Bridge et al. 2012). Evidently, soft coral diversity, especially at depths between ~30–200 m, is far higher than previously thought in New Zealand, and in time we may find that their abundance and contribution to ecosystem functioning have also been underestimated.

Kotatea and *Ushanaia* — as well as many of the other unprotected corals — are unique to this country and, although understudied, are likely to be ecologically significant in some form. Their protection is thus fully in line with, and indeed aspired to, by the goals and objectives set out in the Aotearoa New Zealand Biodiversity Strategy (NZ Government 2020). The extent to which each of the *Kotatea* and *Ushanaia* species is represented in New Zealand's existing network of Marine Protected Areas (MPAs) is unknown and will require new surveying or additions to current monitoring programs. In New Zealand, full-protection MPAs are established based on the significance of unique ecosystems, habitats, or communities (Department of Conservation and Ministry of Fisheries 2005). Some *Kotatea* and *Ushanaia* species occur at sites known to harbour such assemblages or possess very high levels of endemism, including Fiordland, Manawatāwhi/Three Kings Islands (Grehan 2020), and Piwhane/Spirits Bay (Cryer et al. 2000), which are still not protected (or not fully so in the case of Fiordland). Their taxonomic descriptions therefore serve to strengthen the case for the protection of these areas, which if implemented would contribute substantially to the national coverage and biodiversity representation of New Zealand's MPA network. Unequivocally, it is time to specifically include soft corals in lists of government (e.g., Department of Conservation) research priorities and to reconsider their protection status in New Zealand. At the very least, efforts should be made to increase bycatch reporting for inshore fisheries where soft corals may be found, and to document soft coral diversity in commercial bycatch in a similar way as for protected corals (e.g., Bilewitch and Tracey 2020).

5.2 Cultural perspectives

Globally, the knowledge systems and worldviews of Indigenous cultures are increasingly recognised as beneficial and complementary to ecological and biodiversity research (e.g., Whyte et al. 2016). Biodiversity is deeply linked to Indigenous culture and language (Sutherland 2003; Maffi 2005). In New Zealand, the use of te reo Māori in science represents a critical contribution to its revitalisation as a language and to fostering the inclusion and representation of *mātauranga Māori* (Māori knowledge, values and philosophies) (McAllister et al. 2019). *Kotatea kapotaiora* sp. n., *K. kurakootingotingo* sp. n., *K. raekura* sp. n., and *K. teorowai* sp. n. offer a small step towards redressing the still widespread exclusion of Māori, either through ignorance of their interests or by design, in the process of describing and naming new species (Veale et al. 2019). Māori are recognised to hold *kaitiakitanga* (guardianship) over *taonga* (treasured species) and consultation is mandated by the Waitangi tribunal report Wai 262 as well as the UN Declaration on the Rights of Indigenous Peoples (UNGA 2007b). Therefore, Māori names created through respectful collaboration should be represented among taxonomic binomials to a far greater extent than they currently are (Galbreath 2020). This thesis adds to a growing body of new species names recently created through collaboration with Ngāti Kuri (e.g., Nelson et al. 2019; D'Archino et al. 2020). Hopefully, this partnership will be replicated by taxonomists working with other *iwi* throughout New Zealand as well as by researchers working on culturally significant organisms across the globe, and will contribute to the growing momentum this issue has received in the recent literature (see Gillman and Wright 2020).

5.3 The integrative approach and lingering problems in octocoral taxonomy

This thesis continues a long line of research that has incrementally improved on the composition and diagnosis of *Alcyonium* — one of the most taxonomically confounding genera in the Octocorallia (e.g., Bayer 1981a; Groot and Weinberg 1982; Williams 1986a, 1986b, 1988, 1992; Verseveldt and van Ofwegen 1992; Benayahu and Schleyer 1995; Alderslade 2000; Williams 2000 McFadden and van Ofwegen 2013a, 2017). Integrative taxonomy has contributed substantially to the delineation of species boundaries and the identification of homoplasious traits in many coral taxa (McFadden et al. 2017; Benayahu et al. 2018; Arrigoni et al. 2020). This thesis also forms part of a growing body of studies employing this approach (e.g., Núñez-Flores et al. 2020; Poliseno et al. 2021; Chapter 4). As seen in Chapter 2, the application of the integrative approach to octocoral research continues to be hampered by difficulties relating to molecular results, primarily the relatively low variance of mitochondrial genes (Huang et al. 2008; McFadden et al. 2011). Perhaps

this explains, at least in part, why traditional taxonomic studies relying only on morphology are still in the majority.

Although new or overlooked informative morphological characters are occasionally discovered (e.g., polyp sclerites in *Sinularia* by McFadden et al. 2009 and in *Anthothela* by Moore et al. 2017; branching characteristics in *Leptogorgia* Milne Edwards, 1857 by Soler-Hurtado et al. 2017; number of collaret rows in *Paramuricea* Kölliker, 1865 by Pica et al. 2018) and other lines of evidence are sometimes used for taxonomic decisions (e.g., polyp pulsation by Halász et al. 2013; reproductive characteristics by Richards et al. 2018), such cases are rare in the literature. Ultimately then, taxonomic progress will largely depend on continued improvements in genetic techniques. Many avenues have been explored over the last decade (e.g., haplotype distributions by Baco and Cairns 2012, Pante et al. 2012; microsatellites by Porto-Hannes and Lasker 2013; genetic distance thresholds by McFadden et al. 2014a, b; mitochondrial gene orders by Figueroa and Baco 2014; and SNPs by Moore et al. 2016). Currently, RAD-sequencing (Pante et al. 2015a; Herrera and Shank 2016; Quattrini et al. 2019), as well as target-capture enrichment of UCEs and exons (Erickson et al. 2020; Quattrini et al. 2018, 2020; Untiedt et al. 2021) shows promising resolution at all taxonomic levels. Despite the conceptual formalisation of integrative taxonomy in the taxonomic literature over 15 years ago, methodological improvements continue to be necessary, and it is because of this that two of the most enduring problems in octocoral taxonomy have not yet been solved: incongruence between morphological and molecular data, and the nebulous role of interspecific morphological variation in obscuring species boundaries.

Morphological and molecular lines of evidence are often not congruent with one another in many taxa (Carstens et al. 2013), and among octocorals variability in either may simply be insufficient to delimit species (e.g., Baco and Cairns 2012). It follows then, that the weighting and interpretation of evidence in such cases presents an ongoing challenge in octocoral taxonomy, and different studies emphasise either morphology or genetics in cases where DNA is insufficient to resolve putative species. For example, Moore et al. (2017) described new species that were genetically very similar or indistinguishable based on clear morphological differences further informed by geographic distribution. This is also the approach taken for some of the species described in Chapter 2. By contrast, Herrera et al. (2012) favoured genetic similarity as indicative of a single, morphologically variable and widespread species. Similar discrepancies in species recognition have been found for numerous other marine invertebrate taxa, including comparatively well-studied groups such as molluscs (reviewed by Knowlton 2000). Evidently, the integrative approach is difficult to implement consistently at the species level when morphological and molecular data are

not quantitatively analysed in conjunction (for examples see Hulsenbeck et al. 1996; Baker et al. 1998) and there are no definitive guidelines as to which of the above two interpretations (Moore et al. 2017 and Chapter 2 herein vs. Herrera et al. 2012) should be followed. Instead, for cases such as these (where putative species are morphologically distinct but genetically indistinct), conclusions regarding where species lines should be drawn are somewhat subjective and depend on taxonomic experience and assessments of the circumstances. There is currently no remedy for this, but additional lines of evidence (as per the integrative taxonomic approach) such as behavioural, reproductive, or ecological data could act as a deciding factor. Alas, due to the nature of octocoral sample collection and the environments they inhabit, this is probably rarely an option.

Species-level differences in all anthozoan cnidarians can be subtle, and assessments of species boundaries are often confused by morphological intraspecific variation and phenotypic plasticity (Kim et al. 2004; Prada et al. 2008; Forsman et al.; 2009; Marti-Puig et al. 2013; Paz-García et al. 2015; McFadden et al. 2017). This is exacerbated by a general lack of genetic markers capable of evaluating gene flow between populations and overlap between intra- and interspecific genetic distances among octocorals (McFadden et al. 2011). As a result, determining whether distinct forms represent environmentally induced phenotypic variations or reproductively isolated lineages poses a frequent challenge (e.g., Gutiérrez-Rodríguez et al. 2009; Bilewitch et al. 2010). Moreover, this difficulty in establishing consistent taxonomic units may lead to different species being lumped together, in turn causing underestimates of octocoral biodiversity (McFadden et al. 2011). Indeed, for a wide range of marine taxa, excessive lumping rather than splitting predominates (reviewed by Knowlton 2000). This is important because an inaccurate species-level taxonomy could potentially overlook threatened cryptic taxa. In turn, this would limit our understanding of the ecological roles octocorals play and fundamentally restrict the efficacy with which they, the ecosystems they inhabit, and by extension all other organisms with which they interact, are managed. The appropriate splitting of species has specifically been linked to improved protection outcomes (Morrison et al. 2009). Again, no panacea exists for this problem, but statistical analyses of morphometrics (as employed in Chapter 3) can provide additional, valuable information to aid species delimitation and reduce subjectivity (Gori et al. 2012; Soler-Hurtado et al. 2017; also see Mutanen and Pretorius 2007). Alternatively, the addition of morphological data directly into phylogenetic analyses may help, though this method is not often used in octocorals (Cairns and Wirshing 2018).

5.4 Comments on taxonomy as a discipline

Taxonomy has for decades been framed as a discipline in decline (Godfray 2002; Joppa et al. 2011), but in stark contrast to this image, analyses routinely show the opposite. Description rates as well as the number of active taxonomists and publications per year have been increasing over time — especially in aquatic taxa (Costello et al. 2006, 2012; Eschmeyer et al. 2010; De Clerck et al. 2013) — and Chapter 4 demonstrates that this is also the case for octocorals. Rather counterintuitively though, this rejuvenation of taxonomy may itself be cause for alarm as it hints at a large proportion of undiscovered biodiversity. For many taxa, including octocorals, no endpoint for values of species diversity is in sight, and this has severe implications for the amount of time required to discover and catalogue it. Known as the taxonomic impediment or "Linnean shortfall" (Wheeler 2004; Bini et al. 2006), overcoming this uncertainty is increasingly urgent in light of the modern biodiversity crisis. With tens of thousands of eukaryotic species becoming extinct on a yearly basis (Mora et al. 2011), undescribed taxa are being lost faster than they can be recognised (Costello et al. 2013a). The true magnitude of the Linnean shortfall is unknown and since it represents a lack of knowledge about the basic units of ecological and evolutionary study, this impediment creates others, including the Wallacean (distributions), Prestonian (abundance) and Darwinian (evolutionary patterns) shortfalls (Hortal et al. 2015). All apply to octocorals. Additionally, octocorals in general are increasingly vulnerable to anthropogenic pressures (discussed in Chapter 1) but are severely underrepresented in the IUCN red list, as are marine invertebrates overall (Chen 2021). To date, octocorals have been comprehensively assessed at a regional level only in the Mediterranean (Otero et al. 2017), where of 48 listed species one species is classified as critically endangered, two as endangered, and six as vulnerable, and of nine further species assessed globally one is endangered and two are vulnerable (IUCN 2021). Acknowledging that some described species of octocorals are in decline, this leads inevitably to the question: are undescribed species of octocorals being lost to extinction? In keeping with the pessimism that the "6th extinction" (Ceballos et al. 2015) so readily justifies, this is perhaps not unlikely. Integrative methods offer robust species hypotheses and lead to more accurate alpha-taxonomy, which is paramount to the effectiveness of global conservation efforts (Thomson et al. 2018). The literature trends identified in Chapter 4, showing increasing uptake of the integrative approach, thus offer a certain degree of optimism for the future of octocoral taxonomy.

5.5 Conclusions

For almost two centuries, the diversity of New Zealand's nearshore soft corals, along with that of most marine invertebrates, has been underestimated substantially. Due to an ambiguous original description, "*Alcyonium aurantiacum*" has until now been the only name available to which a host of superficially similar species could be ascribed. With the taxonomic revisions presented in Chapter 2, a significant new component of New Zealand's endemic marine biodiversity is illuminated. Using a modern integrative approach and comparing traditional morphological characters with molecular data, it was found that *A. aurantiacum* comprises two new genera. This includes *Kotatea*, which contains seven new species with lobate growth forms as well as the transferred *K. aurantiaca* comb. n., and *Ushanaia* with three new encrusting species. This newly clarified species-level taxonomy in turn revealed that some of the new species are difficult to distinguish without the microscopic examination of sclerites, precluding identification by most non-taxonomists. Since virtually nothing is known regarding any aspect of these species' ecologies, Chapter 3 provides a statistical discrimination method for two species of *Kotatea* based only on easily obtainable measurements of colony growth form. Overlap in inter- and intraspecific variation also obscures species boundaries in this case. Together, these chapters will enable new avenues of enquiry to be explored for these species (and others) for the first time. But beyond this, both chapters serve to highlight a key issue in modern octocoral taxonomy: the difficulty of establishing species boundaries when genetic differences are lacking. Integrative taxonomy is commonly regarded as a critical tool for taxonomic progress in the face of obstacles such as this. Chapter 4 thus assesses the use of integrative techniques — particularly morpho-molecular comparison — in the octocoral taxonomic literature and finds that while this approach is employed with growing frequency, its use remains in the minority. As descriptions at species, genus and family levels continue at some of their highest ever rates, the literature survey data presented in Chapter 4 provide a baseline against which to measure future progress. In aggregate, it is hoped that the research presented here can contribute to global taxonomic progress in the Octocorallia, and that the elucidation of their diversity and variability will offer a crucial first step in the continued research and future protection of these newly described New Zealand endemics.

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Appendices

Appendix 1. Protocols used for the extraction of genomic DNA from octocoral tissue.

(1) Modified Qiagen DNeasy Blood and Tissue Kit protocol.

Materials

- Buffer ATL
- Proteinase K (20 mg/ml)
- Buffer AL
- 100% ethanol
- Buffer AW1
- Buffer AW2
- Buffer AE

Equipment

- 1.5 ml microcentrifuge tubes
- Paper towels
- Plastic pestles (for use inside 1.5 ml microcentrifuge tubes)
- A larger pestle (for crushing and drying tissue)
- Vortexer
- Microcentrifuge
- DNeasy mini spin columns and collection tubes, or a substitute such as EconoSpin mini spin columns by Epoch Life Science Inc.

Protocol

Tissue preparation:

- Remove tissue sample (polyps and/or fragments of coenenchyme) from preservative and place on paper towel. Fold paper towel so that tissue sample is covered and press down on the tissue firmly using a pestle to expel as much ethanol as possible.
- Transfer the flattened and dried tissue sample (< 30 mg) to a 1.5 microcentrifuge tube.

Digestion:

- Add 180 µl of buffer ATL.
- Use a small pestle to break up the tissue as much as possible inside the microcentrifuge tube.
- Add 10 µl of proteinase K and mix by vortexing.
- Incubate at 56˚C for 4 hours or until completely lysed.
    - Add another 10 µl pf proteinase K after the first 2 hours, vortex and return to incubation.

Sclerite removal:

- Centrifuge at 6,000 g for 3 minutes.
- Pipette out as much liquid as possible (~ 195 µl), being careful to avoid the sclerites, and transfer this to a new 1.5 ml microcentrifuge tube.

Removal of proteins and cellular debris:

- **(►)** Add 200 µl of buffer AL and mix by vortexing.
- Incubate at 56˚C for 10 minutes.
- Add 200 µl of 100% ethanol and mix by vortexing.
- Transfer this mixture (595 µl) into a mini spin column placed in a 2 ml collection tube.
- Centrifuge at 6,000 g for 1 minute and discard the collection tube containing the flow-through.
- **(X)** Place the mini spin column in a new 2 ml collection tube and add 500 µl buffer AW1.
- **(X)** Again, centrifuge at 6,000 g for 1 minute and discard the collection tube containing the flow-through.
- Place the mini spin column in another new 2 ml collection tube and add 500 µl buffer AW2.
- Centrifuge at 20,000 g for 3 minutes and discard the collection tube containing the flow-through.

Elution:

- Place the mini spin column in a new 1.5 ml microcentrifuge tube and add 50 µl of buffer AE to the centre of the mini spin column's membrane.
- Incubate at 56˚C for 5 minutes.
- Centrifuge at 6,000 g for 3 minutes.
- Add another 50 µl of buffer AE to the centre of mini spin column's membrane.
- Repeat the above incubation and centrifuge steps and discard the spin column.

(2) Salting-out protocol for problematic specimens.

Modified from Jenkins et al. (2019), originally based on Li et al. (2011).

Materials

- Proteinase K (20 mg/ml)
- 1% SDS cell lysis buffer
- 0.5 M EDTA
- 100% isopropanol
- 7.5 M ammonium acetate
- 70% ethanol
- Deionized water

Equipment

- 1.5 ml microcentrifuge tubes
- Paper towels
- Plastic pestles (for use inside 1.5 ml microcentrifuge tubes)
- A larger pestle (for crushing and drying tissue)
- Vortexer
- Microcentrifuge

Protocol

Tissue preparation:

- Same as in protocol 1 above.

Digestion:

- Add 350 µl of 1% SDS cell lysis buffer.
    - First, add only 150 µl and use a small pestle to break up the tissue as much as possible inside the microcentrifuge tube, then add the remaining 200 µl.
- Add 42 µl of 0.5 M EDTA.
- Add 10 µl proteinase K and mix by vortexing.
- Incubate at 56˚C for 4 hours or until completely lysed.
    - Add another 5 µl pf proteinase K after the first 2 hours, vortex and return to incubation.

Removal of proteins and cellular debris:

- Place 100% isopropanol in a -20˚C freezer before starting the below steps to allow it to cool.
- **(►)** Add 140 µl of 7.5 M ammonium acetate and mix by vortexing.
- Incubate in 4˚C fridge for 10 minutes.
- Centrifuge at 12,000 g for 10 minutes.
- Transfer ~ 500 µl of the supernatant, being careful to avoid debris (containing sclerites), to a new 1.5 ml microcentrifuge tube.
- Repeat once from ammonium acetate stage above **(►)**.

DNA precipitation:

- Add 680 µl of cold 100% isopropanol.
- Mix by gently inverting the microcentrifuge tube 5 times.
- Centrifuge at 20,000 g for 5 minutes.
- Pipette out all liquid (1,180 µl), leaving only the DNA pellet and being careful to avoid contact with it.
- Mark tubes which do not contain visible pellets, these will be treated slightly differently during rehydration.

Washing the DNA:

- Add 400 µl of 70% ethanol and invert the microcentrifuge tube a few times.
- Centrifuge at 20,000 g for 1 minute.
- Pipette out all liquid (400 µl), again leaving only the DNA pellet and being careful to avoid contact with it.
- Allow the pellet to air dry for 10 – 20 minutes, being careful to avoid over-drying.

Rehydrating the DNA:

- Add 50 µl of deionized water, or 30 µl if no pellet was visible after DNA precipitation, to re-suspend the dried pellets.
- Mix by inverting a few times and spin down.
- Incubate in 4˚C fridge over night or at room temperature for 30 minutes, then store at -20˚C.

Final DNA cleaning:

- Add 150 µl of deionized water, or 170 µl if no pellet was visible after DNA precipitation, to bring the volume of the DNA extract to 200 µl.
- Then continue from the buffer AL stage **(►)** in protocol 1 above, but skipping the buffer AW1 stages **(X)**.

Appendix 2. GenBank accession numbers for sequences of related taxa and out-groups used in phylogenetic analyses. Where sequences originating from two different voucher specimens had to be used this is indicated by a "+".

Taxon	Voucher	*mtMutS*	*28S*
Alcyonium bocagei	SAG AC2 + RMNH Coel. 39672	GU355960	KF728088
Alcyonium coralloides	RMNH Coel. 39678	GQ342465	JX203640
Alcyonium digitatum	SBMNH 360700	GQ342466	JX203641
Alcyonium dolium	RMNH Coel. 40204	MG053055	MG053011
Alcyonium glomeratum	GLE AG23 + RMNH Coel. 39666	GU355964	KF728091
Alcyonium haddoni	ZSM 20061191	GU355974	JX203642
Alcyonium hibernicum	RMNH Coel. 39661	AY607771	KF728089
Alcyonium palmatum	RMNH Coel. 39685	GQ342467	JX203643
Alcyonium siderium	NAH SR1.1	GU355972	KF728090
Alcyonium variabile	RMNH Coel. 40800	GQ342470	JX203645
Alcyonium varum	ZSM 20061195	GQ342468	JX203644
Anthothela aldersladei	WAM Z31463	KT366839	N-coded
Anthothela grandiflora	NEREIDA 0610	KT366842	N-coded
Anthothela vickersi	NIWA 40439	KT366847	N-coded
Eleutherobia dofleini	WAM Z13252	HG970080	HG970067
Eleutherobia somaliensis	WAM Z12201	HG970079	HG970066
Gersemia antarctica	C59	GQ342473	JX203646
Gersemia juliepackardae	VEN 3208-A3	JX203768	JX203647
Gersemia rubiformis	ZS1	GQ342474	JX203648
Lateothela grandiflora	NTNU-VM 67147	KT366858	N-coded
Azoriella bayeri (outgroup)	RMNH Coel. 40806	GQ342486	JX203672