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Dead man's fingers point to new taxa: two new genera of New Zealand soft corals (Anthozoa, Octocorallia) and a revision of *Alcyonium aurantiacum* Quoy & Gaimard, 1833

Gustav M. KESSEL[1,*], Philip ALDERSLADE[2], Jaret P. BILEWITCH[3], Kareen E. SCHNABEL[4], Jerry NORMAN[5], Romana TEKAHAROA POTTS[6] & Jonathan P.A. GARDNER[7]

[1,7]Victoria University of Wellington, Wellington, Aotearoa-New Zealand.
[2]CSIRO Oceans and Atmosphere, Hobart, Tasmania, Australia.
[3,4]National Institute of Water and Atmospheric Research Ltd., Wellington, Aotearoa-New Zealand.
[5,6]Ngāti Kurī, Tira Me Te Wā, Aotearoa-New Zealand.
[6]Te Wānanga o Aotearoa, Te Ringa Mauī / Ngāti Kurī / Te Ngaki, Aotearoa-New Zealand.

[*]Corresponding author: gustav.kessel@gmail.com
[2]Email: phil.alderslade@csiro.au
[3]Email: jaret.bilewitch@niwa.co.nz
[4]Email: kareen.schnabel@niwa.co.nz
[5]Email: jerrynorman.rotary@gmail.com
[6]Email: romana.potts@twoa.ac.nz
[7]Email: jonathan.gardner@vuw.ac.nz

[1]urn:lsid:zoobank.org:author:BDA5447C-03BF-4994-92E0-7BE0E87EC76
[2]urn:lsid:zoobank.org:author:93DC2CBE-C14F-4C64-BBD8-D02572886AB0
[3]urn:lsid:zoobank.org:author:38623569-6B57-4D79-AD6C-E4A92762DADD
[4]urn:lsid:zoobank.org:author:90CD9E5D-8E26-4E08-8A5F-3263CBE9D6BD
[5]urn:lsid:zoobank.org:author:6ABACFAA-E313-414B-A572-425841DD4898
[6]urn:lsid:zoobank.org:author:07A4AADF-0D7C-4092-8319-EAE030A189D9
[7]urn:lsid:zoobank.org:author:9F5C3217-34CD-41E7-9908-2CE2F01D0C6C

Abstract. The taxonomic status of *Alcyonium aurantiacum* Quoy & Gaimard, 1833, an octocoral endemic to New Zealand, was reviewed through morpho-molecular data comparisons in an integrative approach. Molecular phylogenetic analyses (nuclear *28S* and mitochondrial *mtMutS*) resolved New Zealand taxa as more closely related to other genera and nominal *Alcyonium* Linnaeus, 1758 from South America than to the genus' North Atlantic type species. Due to low genetic variation, species delimitation relied predominantly on identifying consistent differences in sclerite and colony morphology. The former *A. aurantiacum* is reassigned to *Kotatea* gen. nov. as *K. aurantiaca* gen. et comb. nov. and seven new species are described in this genus (*K. amicispongia* gen. et sp. nov., *K. lobata* gen. et sp. nov., *K. kapotaiora* gen. et sp. nov., *K. kurakootingotingo* gen. et sp. nov., *K. niwa* gen. et sp. nov., *K. raekura* gen. et sp. nov., and *K. teorowai* gen. et sp. nov.). Three new species in *Ushanaia* gen. nov. are also described (*U. ferruginea* gen. et sp. nov., *U. fervens* gen. et sp. nov. and *U. solida* gen. et sp. nov.). These descriptions increase our understanding of New Zealand's endemic octocoral diversity and contribute to ongoing systematic revisions of *Alcyonium*.

Keywords. Alcyonacea, integrative taxonomy, phylogenetics, species complex, species delimitation.

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Introduction

New Zealand's marine region harbours a diverse and distinctive octocoral assemblage characterised by high levels of endemism (Sánchez & Rowden 2006). At least 312 species have been inventoried, spanning 119 genera and 28 families, of which 58 (~20%) 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. Taxonomic progress has focused primarily on protected (Schedule 7A of the New Zealand Wildlife Act 1953 and 2010 amendment) deep-sea (> 200 m) calcaxonian and scleraxonian corals associated with vulnerable marine ecosystems, such as Isididae Lamouroux, 1812 (Dueñas *et al.* 2014), Paragorgiidae Kükenthal, 1916 (Sánchez 2005), and Primnoidae Milne Edwards, 1857 (Cairns 2012, 2016). This has left the state of species-level taxonomy for 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 & Gaimard, 1833 is a name 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 *Alcyonium digitatum* Linnaeus, 1758 from the North Atlantic. However, Philip Alderslade (unpublished research) 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 described scientifically from New Zealand during the *Astrolabe* expeditions of 1826–1829. Typically for the time, Quoy & 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 the description by Benham (1928), 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*, despite being highly variable in terms of colour, colony growth form and sclerite morphology (e.g., Morton & Miller 1973; Westerskov & Probert 1981; Grange *et al.* 1981, 2010; Goldberg *et al.* 1990; Morton 2004).

Doubt has also surrounded the species' generic placement, with *A. aurantiacum* poorly conforming to the characters of *Alcyonium* Linnaeus, 1758 sensu stricto as exhibited by the genus' type species, *A. digitatum* Linnaeus, 1758 (see Verseveldt 1973). Additionally, a DNA sequence (mitochondrial *ND2+mtMutS*) 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 & 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). The genus has been resolved as highly paraphyletic, with incongruence between morphological and molecular data (McFadden & van Ofwegen 2013a). Indeed, several new genera have been erected specifically to accommodate former members of *Alcyonium* (e.g., *Discophyton* McFadden & Hochberg, 2003; *Klyxum* Alderslade, 2000; *Lampophyton* Williams, 2000; *Lateothela* Moore, Alderslade & Miller, 2017; *Rhytisma* Alderslade, 2000).

Clearly, the taxonomic status of *A. aurantiacum* is in need of revision. Here, the phylogenetic relationships of *A. aurantiacum* are examined using molecular data (nuclear *28S* and mitochondrial *mtMutS* genes), which are compared to morphology in an integrative approach. As a result, evidence for two new genera endemic to New Zealand is presented – *Kotatea* gen. nov. with seven new species and *A. aurantiacum* reassigned as *K. aurantiaca* gen. et comb. nov., and *Ushanaia* gen. nov. with three new species. By revealing some of the hidden diversity among New Zealand's shallow-water soft corals, this research contributes to our understanding of this region's endemic marine biodiversity, as well as to ongoing taxonomic progress in the Octocorallia Haeckel, 1866 globally.

Material and methods

Specimens

Ninety-six relevant specimens collected from New Zealand were examined. Six specimens were loaned from the Auckland War Memorial Museum (AK) 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.

Morphological analysis

The morphological characteristics of colonies were recorded following established procedures described by Fabricius & 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 (Hadley 2020). All images were edited and assembled using GIMP ver. 2.8.22 (GIMP Development Team 2020).

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) (see Appendix). 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 & Hoover 2002) or mtMutS93F (Bilewitch & Degnan 2011) in combination with the reverse primer Mut-3458R (Sánchez *et al.* 2003) with PCR protocols following Bilewitch & Degnan (2011). *28S* was amplified using 28S-Far and 28S-Rab (McFadden & van Ofwegen 2013b) with a PCR protocol following Halász *et al.* (2014). PCR reactions of 25 µl contained 1 µl of

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 & Hoover (2002)
	mtMutS93F	AGTTCTATGAACTTTGGCATGAG	Bilewitch & Degnan (2011)
	Mut-3458R	TSGAGCAAAAGCCACTCC	Sánchez *et al.* (2003)
	94˚C/2 mins, (94˚C/60 secs, 58˚C/60 secs, 72˚C/60 secs) × 35, 72˚C/5 mins		
	mtMutS-GK-F	TAGAGGACTGTTCGGAGTTATC	This study
	mtMutS-GK-R	AATTTTAGCATTGGGTTCAGAYG	
	94˚C/2 mins, (94˚C/60 secs, 62˚C/60 secs, 72˚C/60 secs) × 35, 72˚C/5 mins		
28S	28S-Far	CACGAGACCGATAGCGAACAAGTA	McFadden & van Ofwegen (2013b)
	28S-Rab	TCGCTACGAGCTTCCACC AGTGTTT	
	94˚C/3 mins, (94˚C/30 secs, 50˚C/30 secs, 72˚C/60 secs) × 35, 72˚C/3 mins		
	28S-GK-F	GAAGCGAATGGAGTTAGCAATT	This study
	28S-GK-R	GCACATGTTAGACTCCTTGGT	
	94˚C/3 mins, (94˚C/30 secs, 47˚C/30 secs, 72˚C/60 secs) × 35, 72˚C/3 mins		

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.

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 (Geneious Development Team 2020) using the MAFFT ver. 7.450 plugin (Katoh *et al.* 2002; Katoh & 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 species of *Alcyonium* and associated taxa (McFadden *et al.* 2004, 2006b; McFadden & van Ofwegen 2013a, 2017; Moore *et al.* 2017) (Table 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 alignment accuracy (Wiens & Morrill 2011), and preliminary tests on the sequences 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 plus 21 sourced from GenBank) and was 1393 bp in length (*mtMutS* = 735 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 ver. 2.0 (Zwickl 2006), with 1000 replicates to generate bootstrap support values. BI analyses were run using MrBayes ver. 3.2.6

Table 2 (continued on next page). GenBank accession numbers for sequences used in phylogenetic analyses. A '+' in the voucher column indicates that sequences originating from two different voucher specimens were used.

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	NA
Anthothela grandiflora	NEREIDA 0610	KT366842	NA
Anthothela vickersi	NIWA 40439	KT366847	NA
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
Kotatea amicispongia gen. et sp. nov.	NIWA 154046	OM891002	OM976779
Kotatea amicispongia gen. et sp. nov.	NIWA 154129	OM891001	OM976778
Kotatea amicispongia gen. et sp. nov.	NIWA 156312	OM890999	OM976776
Kotatea amicispongia gen. et sp. nov.	NIWA 55958	OM891004	OM976780
Kotatea amicispongia gen. et sp. nov.	NIWA 57129	OM891000	OM976777
Kotatea aurantiaca gen. et comb. nov.	MAGNT C013957	OM891010	OM976787
Kotatea aurantiaca gen. et comb. nov.	MAGNT C015225	OM891011	OM976788
Kotatea aurantiaca gen. et comb. nov.	NIWA 12656	OM891014	OM976791
Kotatea aurantiaca gen. et comb. nov.	NIWA 54535	OM891009	OM976786
Kotatea aurantiaca gen. et comb. nov.	NIWA 54641	OM891008	OM976785
Kotatea aurantiaca gen. et comb. nov.	NIWA 54700	OM891005	OM976782
Kotatea aurantiaca gen. et comb. nov.	NIWA 54766	OM891016	OM976793
Kotatea aurantiaca gen. et comb. nov.	NIWA 55142	OM891007	OM976784
Kotatea aurantiaca gen. et comb. nov.	NIWA 55164	OM891006	OM976783
Kotatea aurantiaca gen. et comb. nov.	NIWA 57596	OM891015	OM976792
Kotatea aurantiaca gen. et comb. nov.	NIWA 75330	OM891013	OM976790
Kotatea aurantiaca gen. et comb. nov.	NIWA 75393	OM891012	OM976789
Kotatea kapotaiora gen. et sp. nov.	NIWA 3974	OM891026	OM976803
Kotatea kurakootingotingo gen. et sp. nov.	MAGNT C013955	OM891030	OM976807
Kotatea kurakootingotingo gen. et sp. nov.	MAGNT C015221	NA	OM976808
Kotatea kurakootingotingo gen. et sp. nov.	NIWA 101538	OM891029	OM976806
Kotatea lobata gen. et sp. nov.	AK 120774	OM891023	OM976800
Kotatea lobata gen. et sp. nov.	MAGNT C013956	OM891024	OM976801
Kotatea lobata gen. et sp. nov.	MAGNT C015227	OM891025	OM976802
Kotatea lobata gen. et sp. nov.	NIWA 101313	OM891022	OM976799
Kotatea lobata gen. et sp. nov.	NIWA 108960	OM891021	OM976798

Table 2 (continued). GenBank accession numbers for sequences used in phylogenetic analyses.

Taxon	Voucher	*mtMutS*	*28S*
Kotatea lobata gen. et sp. nov.	NIWA 142995	OM891020	OM976797
Kotatea niwa gen. et sp. nov.	MAGNT C015224	OM891027	OM976804
Kotatea niwa gen. et sp. nov.	MAGNT C015226	OM891028	OM976805
Kotatea raekura gen. et sp. nov.	AK 656516	OM891019	OM976796
Kotatea raekura gen. et sp. nov.	MAGNT C013954	OM891018	OM976795
Kotatea raekura gen. et sp. nov.	NIWA 101537	OM891017	OM976794
Kotatea teorowai gen. et sp. nov.	NIWA 27358	OM891003	OM976781
Ushanaia ferruginea gen. et sp. nov.	NIWA 156313	OM891038	OM976816
Ushanaia ferruginea gen. et sp. nov.	NIWA 24532	OM891033	OM976811
Ushanaia ferruginea gen. et sp. nov.	NIWA 24533	OM891032	OM976810
Ushanaia ferruginea gen. et sp. nov.	NIWA 54723	OM891036	OM976814
Ushanaia ferruginea gen. et sp. nov.	NIWA 54943	OM891034	OM976813
Ushanaia ferruginea gen. et sp. nov.	NIWA 55022	OM891035	OM976812
Ushanaia ferruginea gen. et sp. nov.	NIWA 55605	OM891031	OM976809
Ushanaia ferruginea gen. et sp. nov.	NIWA 56056	OM891039	OM976817
Ushanaia ferruginea gen. et sp. nov.	NIWA 57457	OM891037	OM976815
Ushanaia fervens gen. et sp. nov.	MAGNT C014322	OM891043	OM976821
Ushanaia fervens gen. et sp. nov.	MAGNT C014323	OM891041	OM976819
Ushanaia fervens gen. et sp. nov.	MAGNT C014988	OM891042	OM976820
Ushanaia fervens gen. et sp. nov.	MAGNT C014989	OM891044	OM976822
Ushanaia fervens gen. et sp. nov.	NIWA 156311	OM891045	OM976823
Ushanaia fervens gen. et sp. nov.	NIWA 3970	OM891040	OM976818
Ushanaia solida gen. et sp. nov.	NIWA 102133	OM891046	OM976824

(Huelsenbeck & 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 & 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 ver. 7.0.26 (Kumar *et al.* 2016) to support taxonomic decisions based on phylogenetic and morphological data.

Iwi engagement in naming

Kotatea gen. nov. and four of its new species were named by Ngāti Kurī, New Zealand's northernmost *iwi* (regional Māori tribe). These species were initially thought to be unique to the *rohe* (territory) of Ngāti Kurī, 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 Kurī Trust Board 2013). As *kaitiaki* (guardians/stewards), Ngāti Kurī seek to understand and protect the unique, nationally and internationally significant biodiversity of these sites, and to document the species inhabiting their *rohe*. Ngāti Kurī 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 Kurī 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 Kurī and taxonomists on the naming of seaweeds (Nelson *et al.* 2019; D'Archino *et al.* 2020) and fulfills recommendations outlined in the Waitangi tribunal report Wai 262 (2011), the UN Declaration on the

Rights of Indigenous Peoples (UNGA 2007) 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).

Repositories

NIWA = National Institute of Water and Atmospheric Research, Wellington, New Zealand
NIWA MITS = NIWA Marine Invasive Taxonomic Service collection, Wellington, New Zealand
AK = Auckland War Memorial Museum, Auckland, New Zealand
MAGNT = Museum and Art Gallery of the Northern Territory, Darwin, Australia

Results

Summary of taxonomic decisions

The differences in sclerite morphology and colony growth form were consistent between morphospecies and showed little variation, allowing all of the > 200 individual colonies comprising the available specimens to be unambiguously assigned to one of eleven groups. While genetic variation proved insufficient to corroborate the morphospecies groupings in most cases, morphology was deemed sufficient for the delineation of new species. Although several of the species are similar in some aspects, all are distinguishable from their most similar congeners using several diagnostic characters, which holds true across all of the examined specimens. Indeed, for species with restricted known distributions, collection region was easily predicted based only on the examination of a specimen's morphological characteristics. 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 proposed 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. nov., with seven new species, and *Ushanaia* gen. nov., with three new species. *Alcyonium aurantiacum* is reassigned to *Kotatea* gen. nov. as *K. aurantiaca* gen. et comb. nov.

Systematics

Phylum Cnidaria Hatschek, 1888
Class Anthozoa Ehrenberg, 1834
Subclass Octocorallia Haeckel, 1866
Order Alcyonacea Lamouroux, 1812
Family Alcyoniidae Lamouroux, 1812

Kotatea gen. nov.
urn:lsid:zoobank.org:act:89E20C47-8DAD-40C4-B7F7-58A4F8FE4F5A
Figs 1–4

Type species

Alcyonium aurantiacum Quoy & Gaimard, 1833, here designated = *Kotatea aurantiaca* (Quoy & Gaimard 1833) new combination.

Diagnosis

Azooxanthellate soft corals with an erect, lobate growth form. Colonies with finger-like lobes commonly displaying secondary and occasionally tertiary branching. Polyps monomorphic and fully retractile. True calyces absent, although retracted polyps may form low, rounded, mound-like protuberances of varying prominence depending on state of colony expansion. Anthocodial sclerites arranged as collaret and points, composed of slender, warty spindles, points contain thorny clubs distally. Tentacles contain irregular, warty, scale-like forms. Polyp neck contains mostly warty rod- and spindle-like forms. 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 their derivatives. Sclerites of the interior differ from those of the surface in being generally larger and 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 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. Additionally, *kota* (hardened shell) refers to the substrate on which some colonies grow, while *tea* (white) refers to the polyps, which together cling to this foundation and illustrate the importance of *whānau* (family), unity, and security. Ngāti Kurī 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* (family), then *hapū* (sub-tribe) and *iwi* (tribes). The word *awhi* (to embrace) is created from the first letters of *ahau*, *whānau*, *hapū*, and *iwi*. 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 limited to species possessing polyp sclerites in a collaret and points arrangement (McFadden & van Ofwegen 2013a, 2017), species in that genus tend to approach this arrangement only loosely (e.g., Stokvis & van Ofwegen 2006), and *A. digitatum* (the type of the genus) appears to possess few sclerites in the polyp head with a somewhat irregular and inconsistent arrangement (see Hickson 1895; Verseveldt 1973). Compared to *Kotatea* gen. nov., where the collaret and points are substantial and comprised of many sclerites, only the Chilean nominal species of *Alcyonium* appear to have polyp armatures approximating the same level of development, but unlike *Kotatea*, some of these taxa are said to possess calyces (see Verseveldt & 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 species of *Alcyonium*.

Unlike *Ushanaia* gen. nov., *Kotatea* gen. nov. 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* gen. nov. than in *Ushanaia*.

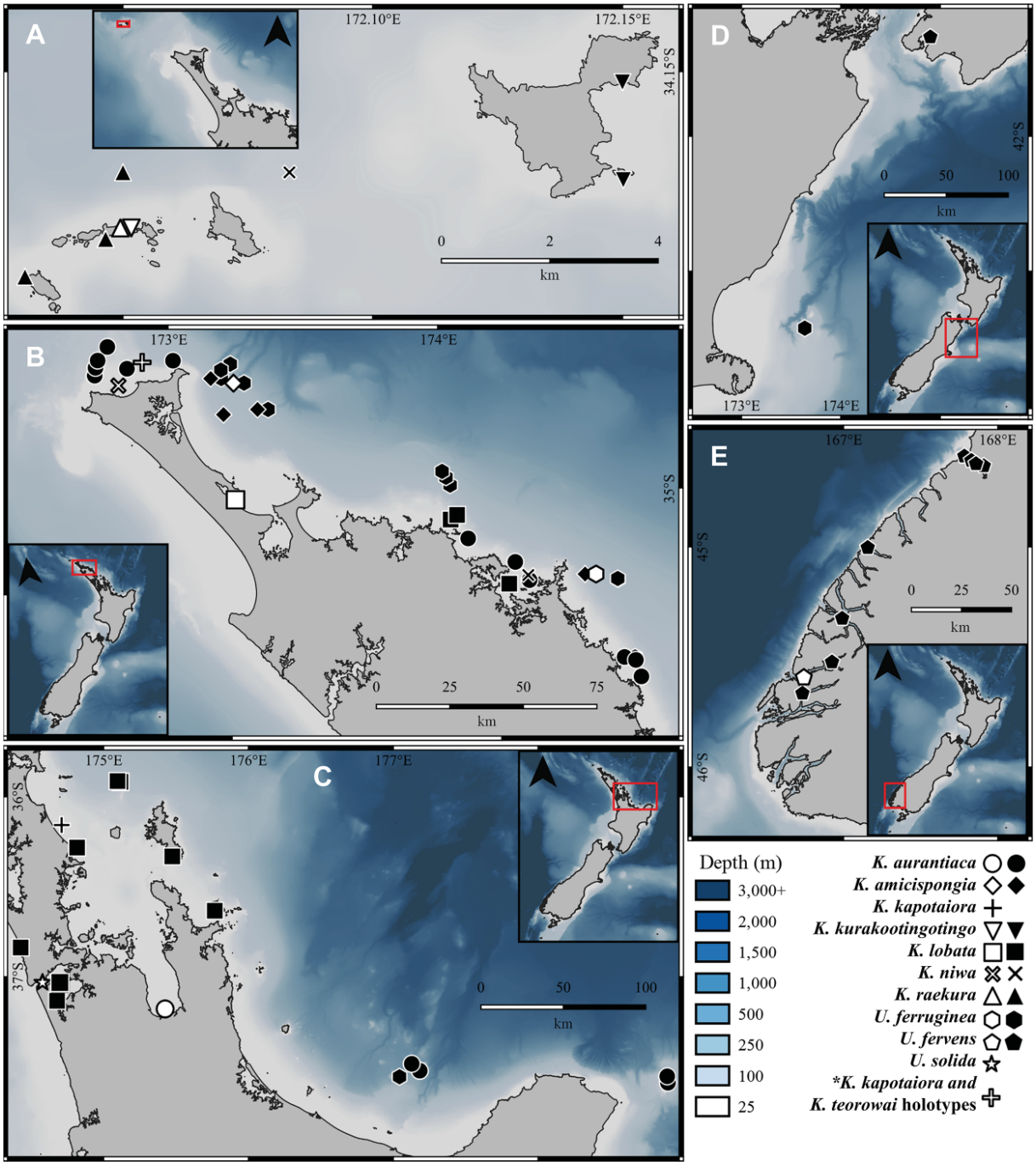

Fig. 1. Collection sites of specimens of *Kotatea* gen. nov. and *Ushanaia* gen. nov. Holotype collection sites are indicated by white symbols, paratypes and other material by black symbols. In the case of *K. aurantiaca* gen. et comb. nov., the type collection site refers to that described by Quoy & Gaimard (1833). **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 of *K. kapotaiora* gen. et sp. nov. and *K. teorowai* gen. et sp. nov. share the same collection site.

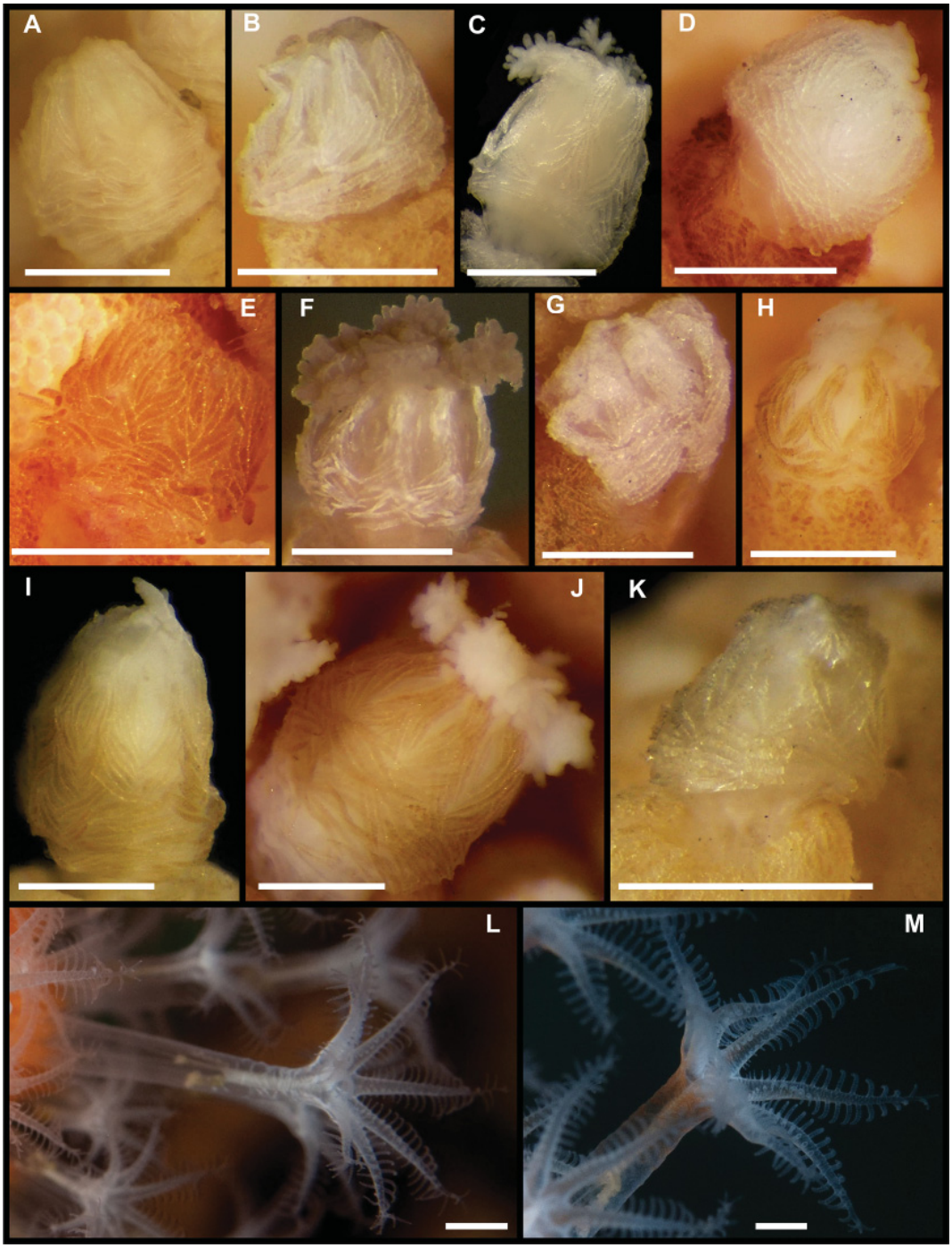

Fig. 2. Polyps. **A**. *Kotatea amicispongia* gen. et sp. nov., holotype (NIWA 156312). **B**. *K. aurantiaca* gen. et comb. nov. (NIWA 75330). **C**. *K. kapotaiora* gen. et sp. nov., holotype (NIWA 3974). **D**. *K. kurakootingotingo* gen. et sp. nov., holotype (NIWA 101538). **E**. *K. kurakootingotingo* gen. et sp. nov., paratype, small polyp with coloured collaret and points (MAGNT C015221). **F**. *K. lobata* gen. et sp. nov., holotype (NIWA 101313). **G**. *K. niwa* gen. et sp. nov., holotype (MAGNT C015226). **H**. *K. raekura* gen. et sp. nov., holotype (NIWA 101537). **I**. *Ushanaia ferruginea* gen. et sp. nov., holotype (NIWA 156313). **J**. *U. fervens* gen. et sp. nov., holotype (NIWA 156311). **K**. *U. solida* gen. et sp. nov., holotype (NIWA 102133). **L**. *K. aurantiaca* gen. et comb. nov., in situ (uncollected specimen), Poor Knights Islands, photo by Ian Skipworth (ianskipworth.com). **M**. *U. fervens* gen. et sp. nov., in situ (uncollected specimen), Fiordland, photo by Shane Geange. Scale bars = ~1 mm.

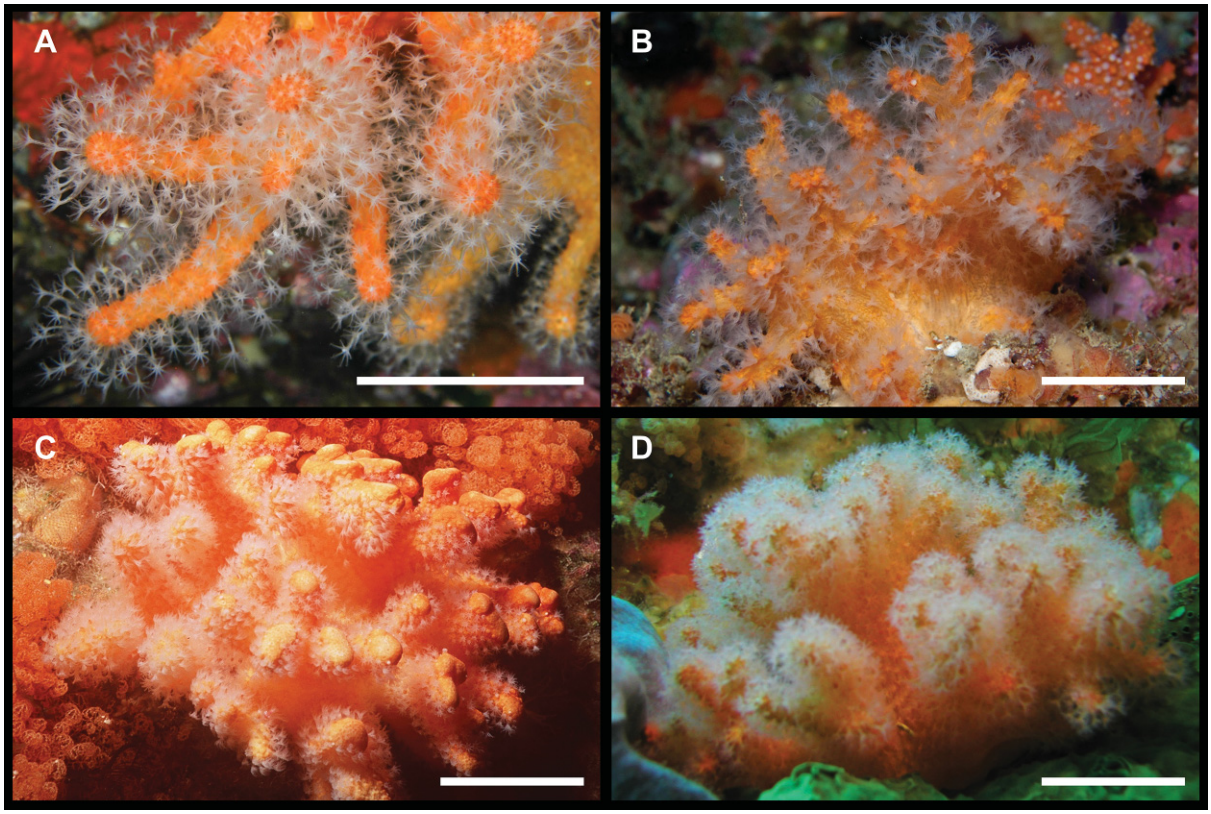

Fig. 3. In situ photographs of species of *Kotatea* gen. nov. usually possessing finger-like lobes. **A–B**. *K. aurantiaca* gen. et comb. nov. (uncollected specimens), expanded colonies with a contracted colony in upper right background of B, Poor Knights Islands, photos by Ian Skipworth (ianskipworth.com). **C**. *K. aurantiaca* gen. et comb. nov. (MAGNT C013957/NIWA 101181), large colony, Bay of Plenty, photo by Coral Reef Research Foundation. **D**. *K. raekura* gen. et sp. nov., holotype (NIWA 101537), Manawatāwhi/Three Kings Islands, photo by NIWA. Scale bars = ~3 cm.

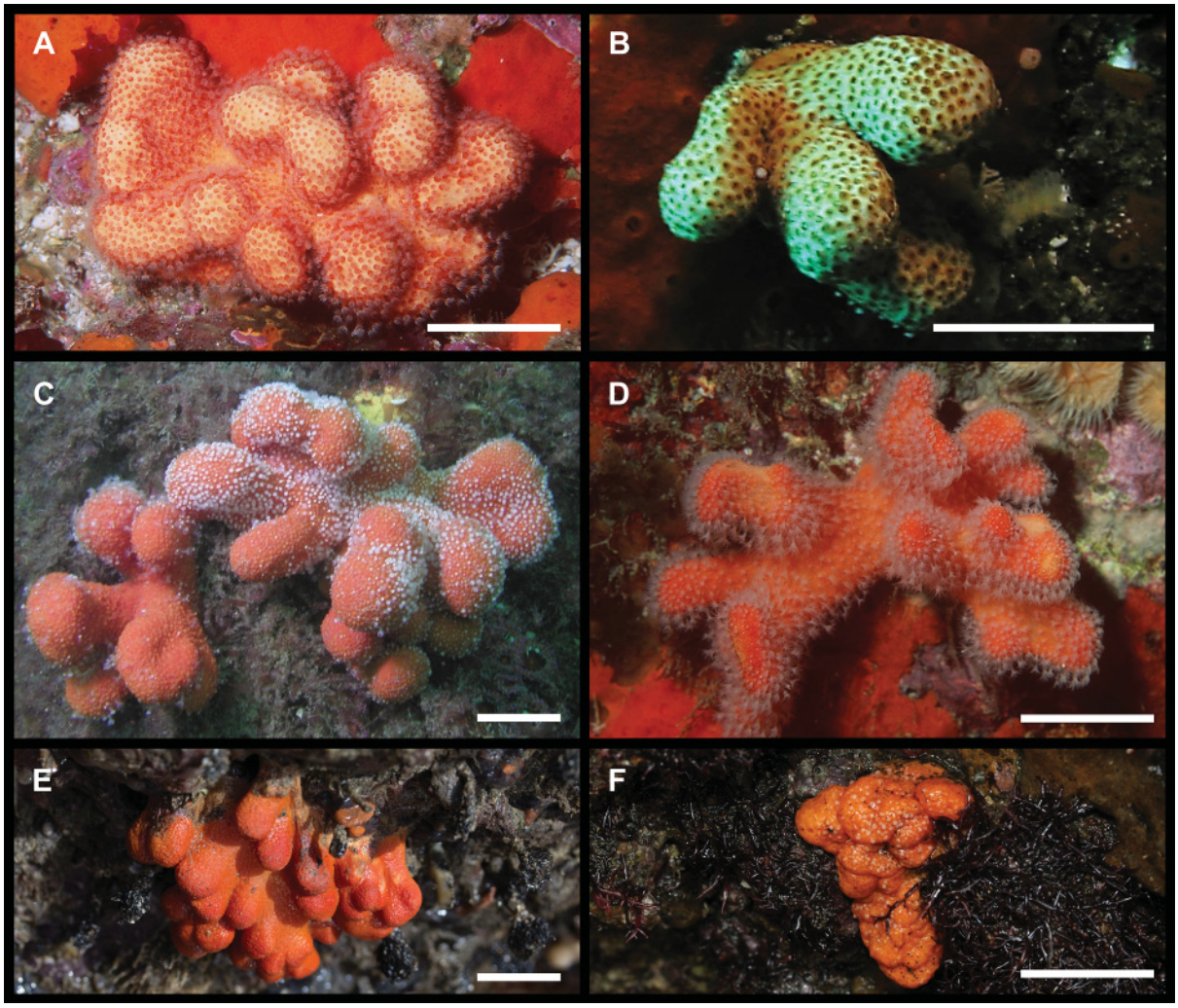

Fig. 4. In situ photographs of species of *Kotatea* gen. nov. usually possessing robust lobes. **A**. *K. kurakootingotingo* gen. et sp. nov., paratype (MAGNT C013955), Manawatāwhi/Three Kings Islands, photo by Coral Reef Research Foundation. **B**. *K. kurakootingotingo* gen. et sp. nov., holotype (NIWA 101538) with polyps retracted, Manawatāwhi/Three Kings Islands, photo by NIWA. **C**. *K. lobata* gen. et sp. nov., holotype (NIWA 101313), Houhora Harbour, photo by NIWA. **D**. *K. lobata* gen. et sp. nov. (paratype NIWA 101268 / MAGNT C013956), Mokohinau Islands, photo by Coral Reef Research Foundation. **E–F**. *K. lobata* gen. et sp. nov. exposed at low tide underneath rock overhangs, large colony (paratype, AK 120774) at Muriwai Beach (E) and small colony (uncollected specimen) at Whatipu Beach (F), photos by Wilma Blom, Auckland War Memorial Museum. Scale bars = ~3 cm.

Kotatea amicispongia gen. et sp. nov.
urn:lsid:zoobank.org:act:08A5B3CB-0D10-4203-BE1E-8011FC46D45D
Figs 1B, 2A, 5–6, 7A

Diagnosis

Yellow-orange colonies with white polyps, branching lobes, usually growing on a sponge. Collaret and points colourless, composed of slender, warty spindles and thorny clubs. Tentacles contain irregular, warty, scale-like sclerites. Polyp neck contains tuberculate to warty spindles. Polyp mounds contain thorny clubs. Lobe surface contains similar clubs, as well as spiny spindle-like sclerites and radiates. Base surface contains radiates, clubs and spheroids. Lobe and base interior contains spindles and radiates.

Etymology

The species name is a combination of the Latin '*amici*', meaning 'friend', and '*spongia*', meaning 'sponge', giving roughly 'friend of the sponge' and referring to the habit of specimens growing on sponges.

Material examined

Holotype

NEW ZEALAND • Northland, Great Exhibition Bay; 34.4650° S, 173.2115° E; depth 140–141 m; 13 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/134; NIWA 156312.

Paratypes

NEW ZEALAND • 5 specimens (and several small fragments); same collection data as for holotype; NIWA 56152 • 1 specimen; Northland, ~8 km SE of Cape Brett; 35.2160° S, 174.4033° E; depth 99–105 m; 6 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/38; NIWA 154129.

Additional material

NEW ZEALAND – **Northland, Great Exhibition Bay** • 1 specimen; 34.4398° S, 173.1297° E; depth 110–115 m; 15 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/181; NIWA 57129 • 1 specimen; 34.5562° S, 173.1562° E; depth 105–106 m; 12 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/126; NIWA 55958 • 2 specimens; 34.5570° S, 173.28533° E; depth 139–141 m; 13 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/132; NIWA 154046.

Description (holotype, NIWA 156312)

Colony form

The holotype is yellow-orange (ethanol-preserved), attached to a sponge fragment, and measures 2 cm tall by 3 cm wide (Fig. 7A). 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. 2A).

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. 5A–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 5A, 6C). The tentacles contain irregular warty, scale-like forms, often slightly to distinctly crescentic (~0.08–0.22 mm long) (Fig. 5C). The polyp neck contains some tuberculate to warty spindles (~0.08–0.15 mm long) (Fig. 5D). The polyp mounds and the lobe surface both contain

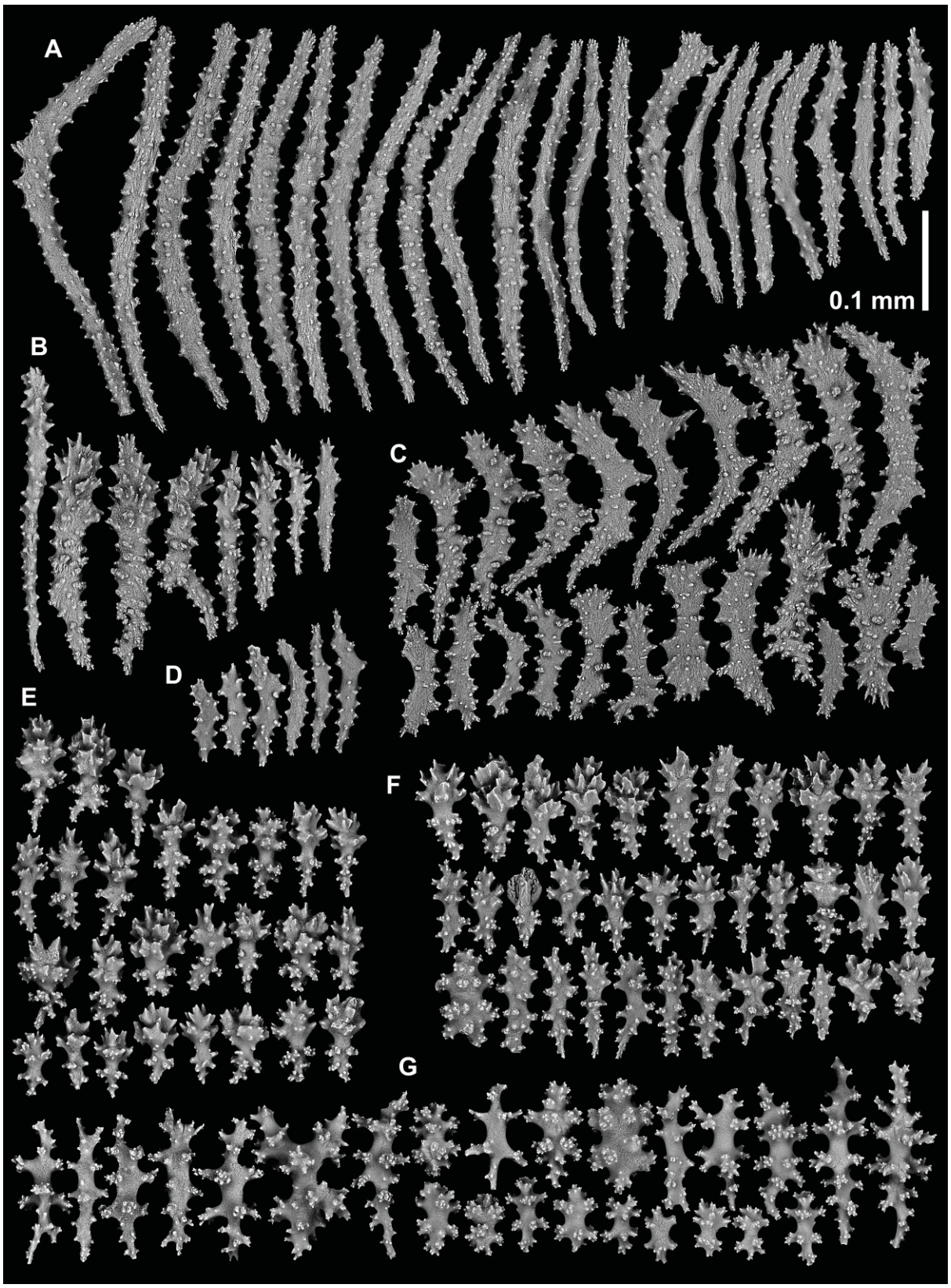

Fig. 5. *Kotatea amicispongia* gen. et sp. nov., holotype (NIWA 156312), SEMs of sclerites. **A**. Collaret and points. **B**. Distal points. **C**. Tentacles. **D**. Polyp neck. **E**. Polyp mound. **F**. Lobe surface. **G**. Lobe interior.

clubs with thorny and leaf-like processes (~0.06–0.12 mm long and up to ~0.06 mm wide) (Fig. 5E–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. 6A). 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. 5G). 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. 6B).

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. 7) and in sclerite size ranges, although the latter fell within the ranges described for the holotype in all cases (Figs 5–6).

Comparisons

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

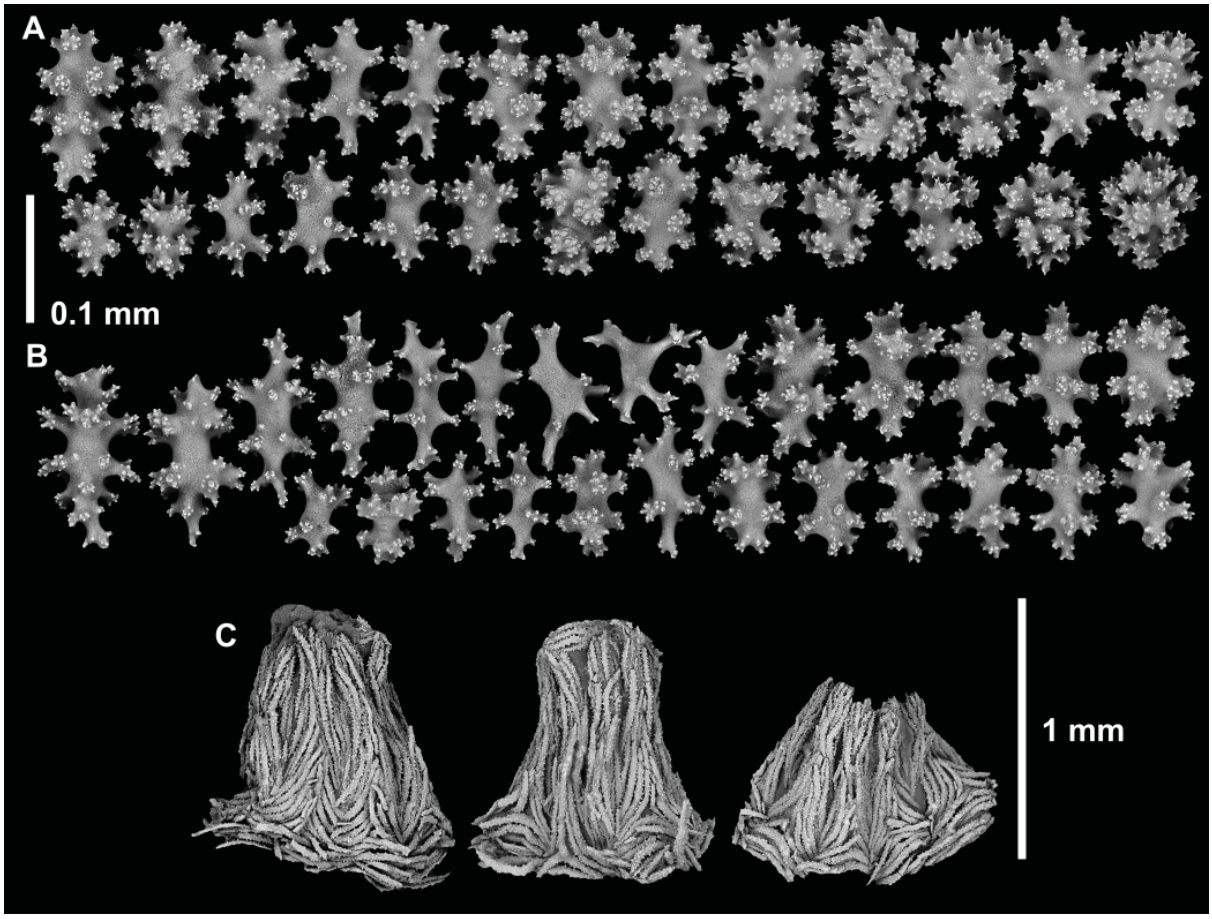

Fig. 6. *Kotatea amicispongia* gen. et sp. nov., holotype (NIWA 156312), SEMs of sclerites. **A**. Base surface. **B**. Base interior. **C**. Polyps (in situ).

All specimens of *Kotatea amicispongia* gen. et sp. nov. markedly differ from all specimens of *K. aurantiaca* gen. et comb. nov. in possessing far larger (and more abundant) clubs in their points (up to 0.28 mm long vs ~0.1 mm long, compare Figs 5B and 9B) and much wider polyp mound clubs (up

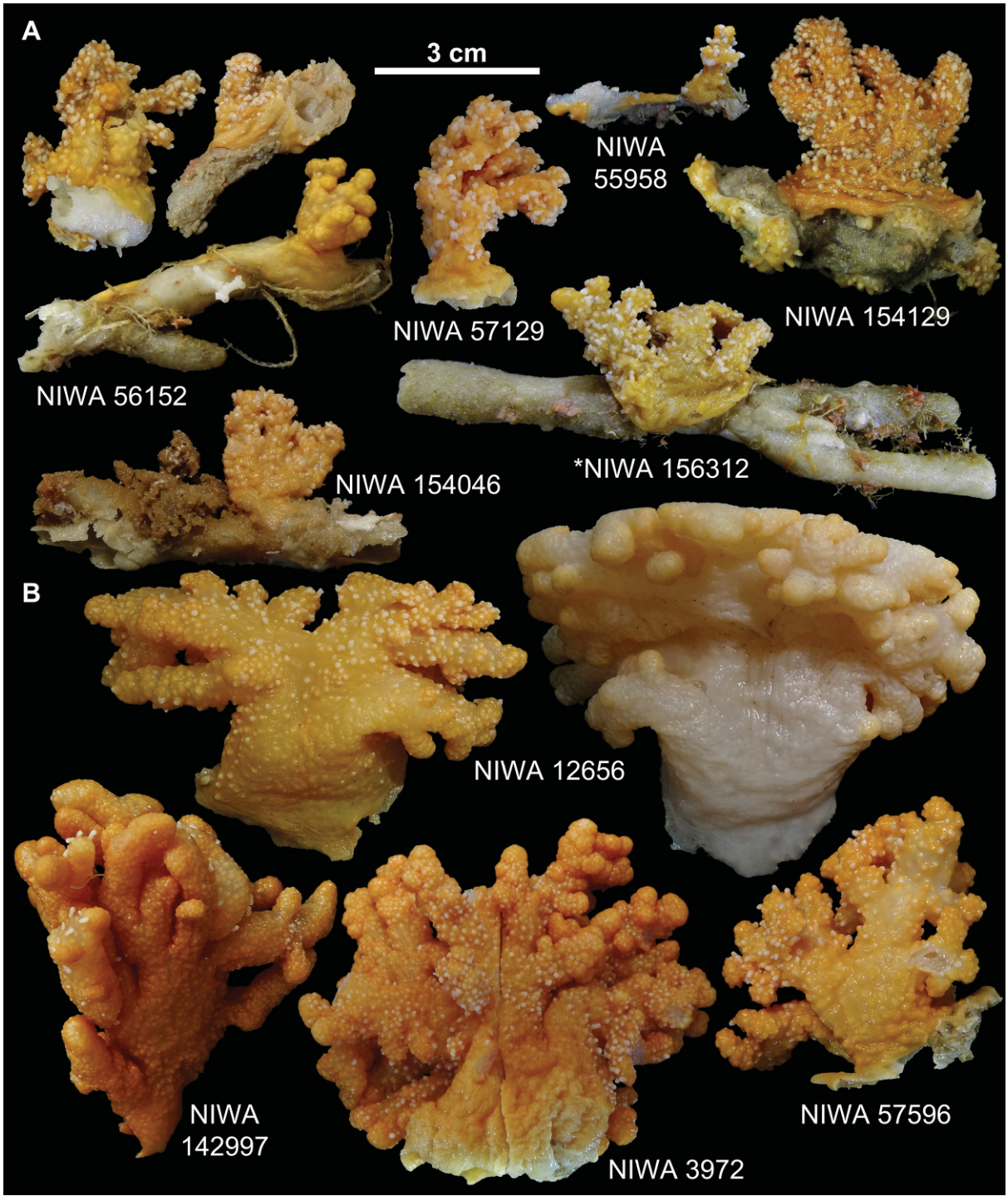

Fig. 7. Preserved specimens. **A**. *Kotatea amicispongia* gen. et sp. nov. **B**. *K. aurantiaca* gen. et comb. nov., expanded and stalked specimens. Note NIWA 154046 and NIWA 142997 contain additional fragments that are not depicted. * = holotype.

to 0.06 mm vs no more than ~0.03 mm, compare Figs 5E and 9E). Additionally, spindles of the collaret and points are overall smaller and more slender in *K. amicispongia* (compare Figs 5A and 9A), which is particularly apparent when polyp armatures are compared in situ (compare Figs 6C and 10B), 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 7A and 24B), a clear difference between *K. amicispongia* gen. et sp. nov. and *K. teorowai* gen. et sp. nov. is that specimens of *K. amicispongia* lack the leafy spheroids that form a distinctive component of the lobe surface in *K. teorowai* (compare Figs 5F and 27F). The two species are also distinct for their interior sclerites, which are far more abundant and more heavily ornamented in all specimens of *K. amicispongia* than in *K. teorowai*, being very rare (and absent towards the base) and sparsely ornamented in the latter (compare Figs 5G, 6B and 27H).

While the sclerites of *K. amicispongia* gen. et sp. nov. differ markedly from those of *K. kapotaiora* gen. et sp. nov. and *K. raekura* gen. et sp. nov. (compare Figs 5–6 with 12–13 and 25–26), specimens of *K. kapotaiora* 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*).

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. 1B). 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. et sp. nov. and the sponge fragment attached to NIWA 154129 is encrusted with small patches of this species.

Kotatea aurantiaca Quoy & Gaimard, 1833 gen. et comb. nov.
Figs 1B–C, 2B, L, 3A–C, 7B, 8–10, 11A–C, E

Alcyonum aurantiacum Quoy & Gaimard, 1833 [spelling of *Alcyonium* – lapsus calami]: 277, pl. 22 figs 16–18.

Alcyonium aurantiacum – Benham 1928 in part: 71–75, figs 6–11.
? *Alcyonium aurantiacum* – Powell 1947: 8, fig. 14. — Doak 1971: 44–46, pl. 20. —Westerskov & Probert 1981 in part: 111, pl. 28. — Grange *et al.* 2010 in part: 148.

non *Alcyonium aurantiacum* – McFadden *et al*. 2006b (= *Ushanaia fervens* gen. et sp. nov.): 517, 521, 523, figs 1, 3.

Diagnosis

Colonies with branching lobes, colour varying from pale to dark orange, with white polyps. Collaret and points colourless and composed of warty spindles and some irregular and branched forms, clubs rare and small. Tentacles contain irregular, warty, scale-like sclerites. Polyp neck contains spiny spindles and warty rod-like sclerites. Polyp mounds contain slender, spiny clubs and warty rod- and spindle-like sclerites. Lobe and base surface contains radiates, clubs, and occasionally leafy spheroids. Lobe and base interior contains slender spindles and radiates.

Etymology

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

Material examined

NEW ZEALAND – **Northland** • 1 specimen; ~14 km N of Piwhane/Spirits Bay; 34.3163° S, 172.7925° E; depth 68 m; 28 Jan. 1999; NIWA exped.; stn Z9702 (KAH9901/73); NIWA 3972 • 1 specimen; ~14 km NW of Piwhane/Spirits Bay; 34.3510° S, 172.7088° E; depth 57 m; 28 Jan. 1999; NIWA exped.; stn Z9697 (KAH9901/64); NIWA 3978 • 2 specimens; ~12 km NW of Piwhane/Spirits Bay; 34.3533° S, 172.7487° E; depth 55 m; 22 Apr. 1999; NIWA exped.; stn Z9753; NIWA 12656 • 1 specimen (cut into 2 fragments); ~3 km N of North Cape; 34.3668° S, 173.0003° E; depth 89 m; 27 Jan. 1999; NIWA exped.; stn Z9695 (KAH9901/59); NIWA 3979 • 1 specimen; ~8 km N of Piwhane/Spirits Bay; 34.3690° S, 172.8250° E; depth 55 m; 25 Jan. 1999; NIWA exped.; stn Z9677 (KAH9901/25); NIWA 3980 • 2 specimens; ~5.5 km NNE of Cape Reinga; 34.3745° S, 172.7013 ° E; depth 53 m; 27 Jan. 1999; NIWA exped.; stn Z9688 (KAH9901/47); NIWA 3977 • 1 specimen; ~7 km E of Takou Bay; 35.0750° S, 174.0183° E; depth 67–72 m; 19 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/245; NIWA 57596 • 1 specimen; Bay of Islands, ~1.5 km NE of Harakeke Island; 35.1457° S, 174.1517° E; depth 55 m; 7 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/57; NIWA 55142 • 2 specimens; same collection data as for preceding; NIWA 55164 • 1 specimen; Bay of Islands, ~500 m NW of Motutara Island; 35.2075° S, 174.1940° E; depth 23–27 m; 3 Sep. 2009; Oceans Survey 2020 exped.; stn KAH0907/195; NIWA 58551 • 1 specimen; ~4 km NE of Whananaki; 35.4858° S, 174.5012° E; depth 59–63 m; 5 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/21; NIWA 54641 • 1 specimen; same collection data as for preceding; NIWA 54700 • 2 specimens; ~6 km ENE of Whananaki; 35.5002° S, 174.5415° E; depth 64–66 m; 4 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/3; NIWA 54535 • 4 specimens; Matapouri, ~4 km NE of Matapouri Bay; 35.5525° S, 174.5525° E; depth 57 m; 5 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/25; NIWA 54766. – **Bay of Plenty** • 1 specimen; ~5 km NW of Whakaari/White Island; 37.4785° S, 177.1280° E; depth 12–17 m; 30 Apr. 1999; Coral Reef Research Foundation exped.; stn Z15884; MAGNT C013957 • 67 specimens; same collection data as for preceding; NIWA 101181 • 1 specimen; Whakaari/White Island, Volkner Rocks; 37.5167° S, 177.1833° E; depth 12–20 m; 30 Apr. 1999; J. Starmer leg.; MAGNT C015225 • 1 specimen; same collection data as for preceding; MAGNT C015231 • 1 specimen; same collection data as for preceding; MAGNT C015232 • 2 specimens; same collection data as for preceding; MAGNT C015233 • 1 specimen; same collection data as for preceding; MAGNT C015234 • 1 specimen; same collection data as for preceding; MAGNT C015235. – **East Cape** • 5 specimens; Ranfurly Bank; 37.5472° S, 178.8925° E; depth 68–70 m; 30 May 2011; Oceans Survey 2020 exped.; stn TAN1108/213; NIWA 75330 • 4 specimens; Ranfurly Bank; 37.5823° S, 178.8975° E; depth 42–48 m; 31 May 2011; Oceans Survey 2020 exped.; stn TAN1108/217; NIWA 75393. – **Unknown location** • 6 specimens; older than 1995; stn B5/96, no other data available; NIWA 142997.

Type locality

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

Preliminary remarks

Quoy & Gaimard's (1833) description alone lacks the detail needed to distinguish which of several species of *Kotatea* gen. nov. could be *A. aurantiacum*. However, when their original colour plate (Fig. 11A) and the photograph of the syntype specimens of *A. aurantiacum* (Fig. 11E) are considered in conjunction with the morphology and distributional range of all available specimens, the material here ascribed to *K. aurantiaca* gen. et comb. nov. is almost certainly conspecific with Quoy & Gaimard's (1833) species.

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

Description

Colony form

Kotatea aurantiaca gen. et comb. nov. produces irregularly branched, lobate colonies. Lobes are usually finger-like but can appear more robust when contracted (Figs 3A–C, 7B, 8). 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 7B, 8), 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. 8), or from a stalk (Fig. 7B). 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. 2B, 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. 9A–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 9A, 10C). 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. 9C), the polyp neck contains spiny spindles and warty rod-like forms (~0.06–0.15 mm long) (Fig. 9D), 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. 9E). 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. 9F, H). Surface sections may also occasionally include leafy spheroids (Fig. 9F). 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 9G, 10A). Interior sclerites are ~0.06–0.26 mm long.

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* gen. et comb. nov. can resemble *K. lobata* gen. et sp. nov. when highly contracted (compare NIWA 101181 in Fig. 8 to Fig. 18; 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 9–10).

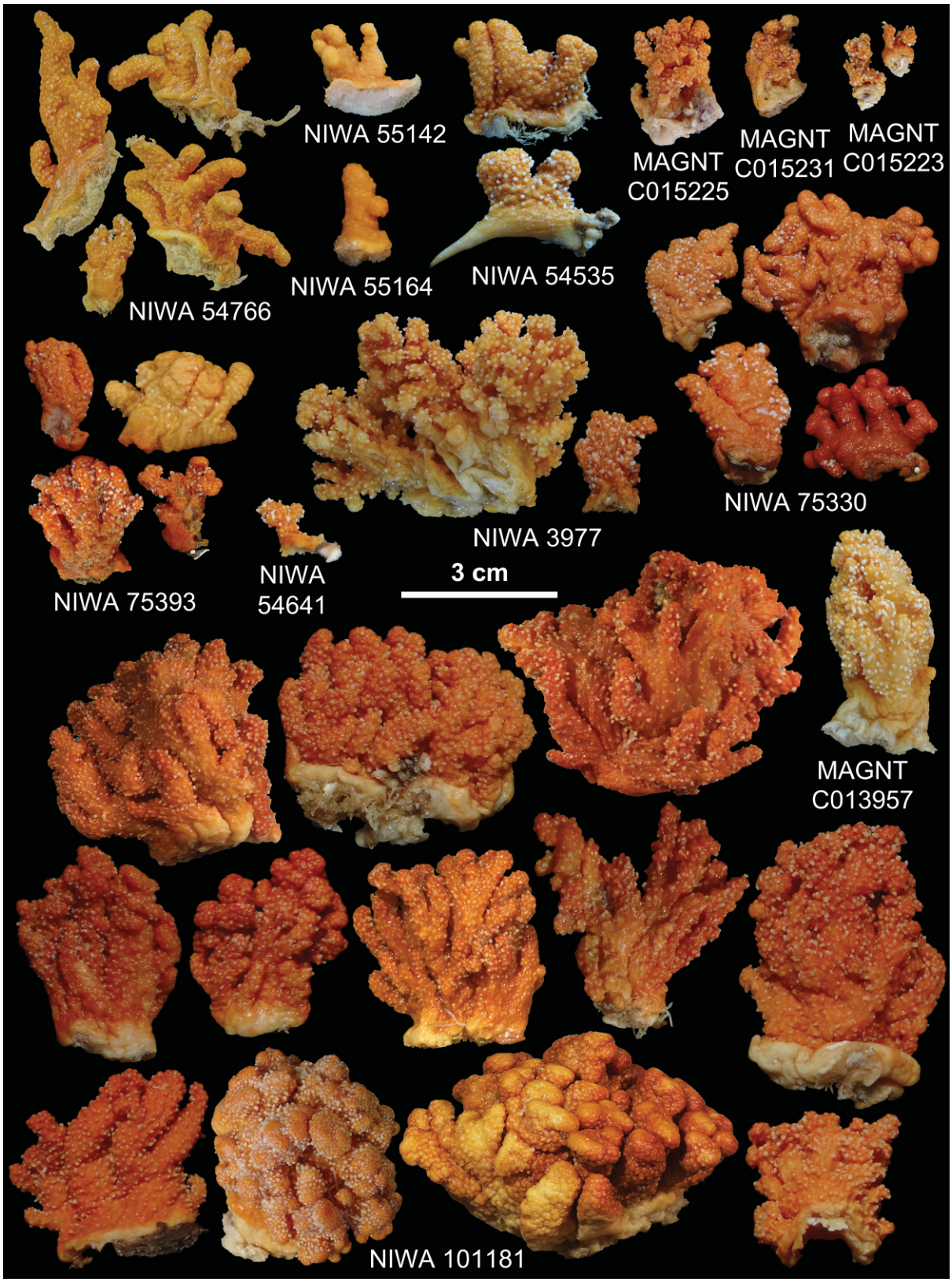

Fig. 8. Selected preserved specimens of *Kotatea aurantiaca* gen. et comb. nov. Note that most specimen lots include small additional fragments that are not depicted and NIWA 101181 comprises a total of 67 similar colonies, all of which were examined.

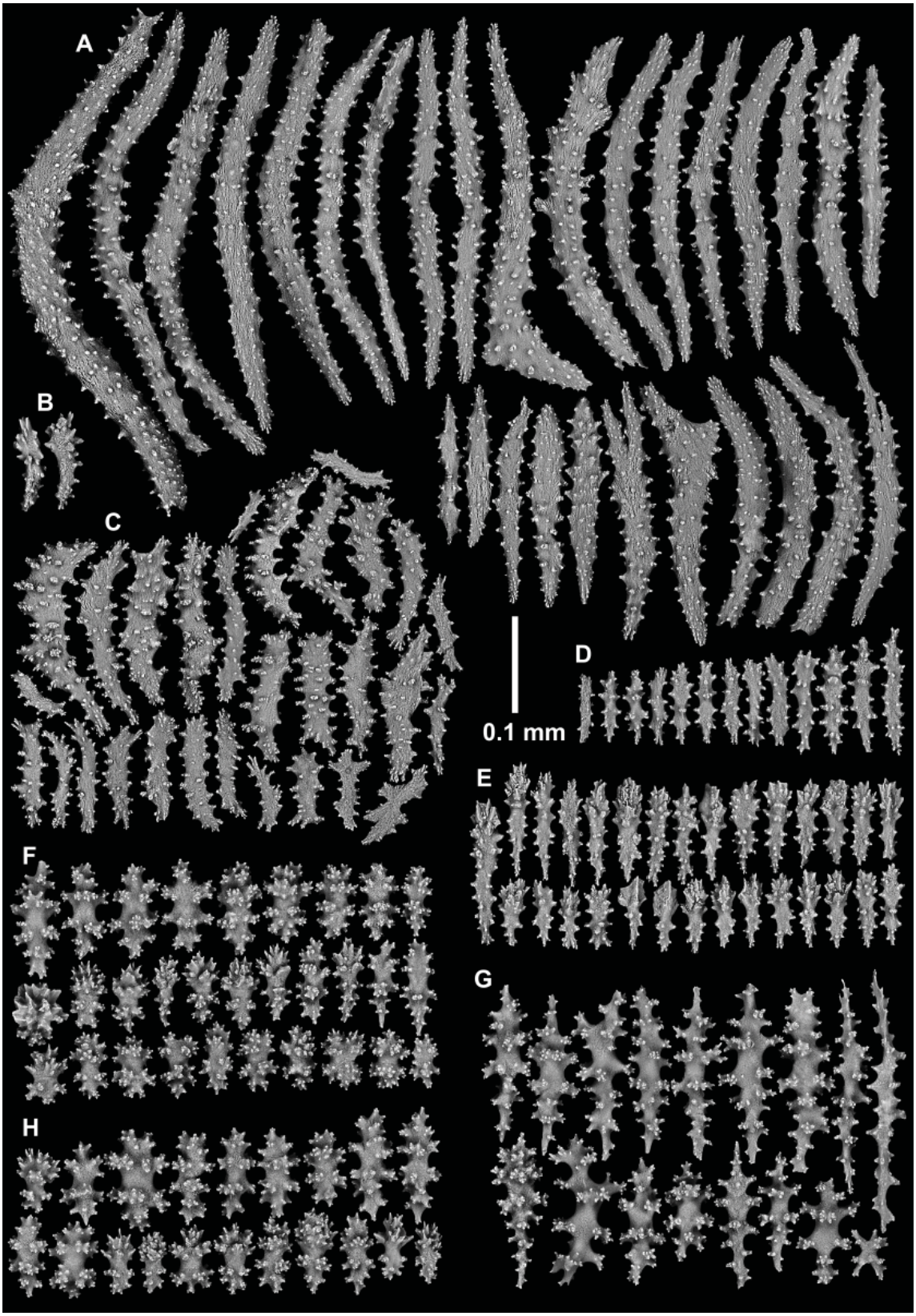

Fig. 9. *Kotatea aurantiaca* gen. et comb. nov. (NIWA 54766), SEMs of sclerites. **A**. Collaret and points. **B**. Distal points. **C**. Tentacles. **D**. Polyp neck. **E**. Polyp mound. **F**. Lobe surface. **G**. Lobe interior. **H**. Base surface.

Comparisons

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

Other than colour (compare Figs 7B, 8 and 14C), *Kotatea aurantiaca* gen. et comb. nov. specimens differ markedly from *K. kapotaiora* gen. et sp. nov. in lacking the latter's large and robust clubs in the lobe surface (compare Figs 9F and 12F), 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 9G, 10A and 12G, 13B).

Kotatea aurantiaca gen. et comb. nov. specimens can be easily differentiated from *K. raekura* gen. et sp. nov. 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* gen. et comb. nov. specimens being much smaller and more slender than the overall more robust sclerites found in *K. raekura* (compare Figs 9A, D–F, H and 25A, 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 *Kotatea kapotaiora* gen. et sp. nov., *K. aurantiaca* gen. et comb. nov. differs in colour from *K. teorowai* gen. et sp. nov. (compare Figs 7B, 8 and 24B). Notably, *K. teorowai* completely lacks the slender interior spindles that are present and abundant in all *K. aurantiaca* gen. et comb. nov. specimens, possessing only rare, irregularly branched radiates in its interior (compare Figs 9G, 10A and 27H). Additionally, while leafy spheroids are not common in any *K. aurantiaca* gen. et comb. nov. specimen, these sclerites are well-developed and feature conspicuously in the lobe surface of *K. teorowai* (compare Figs 9F and 27F).

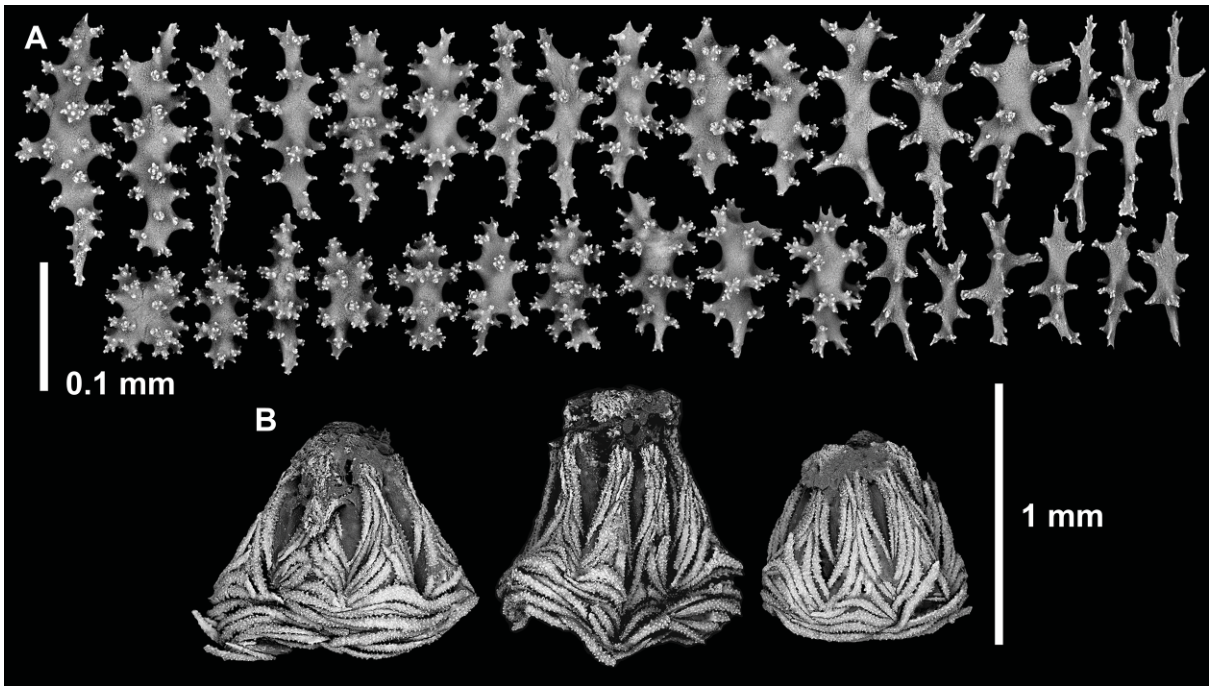

Fig. 10. *Kotatea aurantiaca* gen. et comb. nov. (NIWA 54766), SEMs of sclerites. **A**. Base interior. **B**. Polyps (in situ).

Kotatea aurantiaca gen. et comb. nov. and *K. lobata* gen. et sp. nov. are probably the most commonly encountered species of the genus. Specimens of *K. lobata* are distinctive in possessing very large, highly branched, antler-like sclerites in their interiors, especially in the lobes. By contrast, *K. aurantiaca* gen. et comb. nov. specimens entirely lack these sclerites, and their interiors are instead composed predominantly of slender spindles (compare Figs 9G, 10A and 20A, 21A). 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* gen. et comb. nov. (compare Figs 9F, H and 19F, 20B). Additionally, point clubs are more abundant in *K. lobata* specimens (compare Figs 9B and 19B).

While their growth forms are, in general, sufficiently distinct to allow for differentiation, in many cases colony-scale morphological overlap between *Kotatea aurantiaca* gen. et comb. nov. and *K. lobata* gen. et sp. nov. 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. 18 with some of the *K. aurantiaca* gen. et comb. nov. colonies of NIWA 101181 and NIWA 54535 in Fig. 8).

Habitat and distribution

Specimens were collected from northern New Zealand, between Piwhane/Spirits Bay and East Cape at depths of ~10–90 m (Fig. 1B–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.

Remarks

Quoy & 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. 11B) also shows these to be contracted.

Since Quoy & Gaimard's work, the only other taxonomic treatment of *Alcyonium aurantiacum* is that by Benham (1928), who described the morphology of three specimens and pointed out that Quoy & Gaimard's description omits the 'i' in *Alcyonium*. Again, Benham's descriptions have limited usefulness in

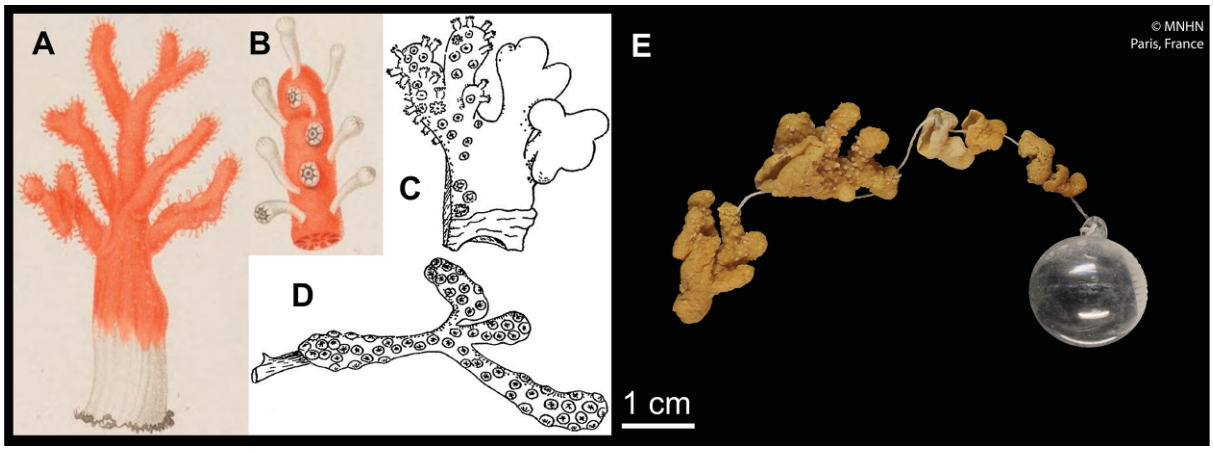

Fig. 11. A–B. Copies of Quoy & Gaimard's (1833) illustrations of "*A. aurantiacum*". **C–D**. Copies of the sketches of upright and encrusting specimens by Benham (1928), identified as *A. aurantiacum*. **E**. *A. aurantiacum* syntype, specimen MNHN-IK-2000-128 (photo by Marie Hennion).

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. 11C) may have been *K. aurantiaca* gen. et comb. nov., while an encrusting specimen collected in Dusky Sound and growing around a black coral fragment (Fig. 11D) almost certainly represents *Ushanaia fervens* gen. et sp. nov.

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 *Kotatea* gen. nov., but most likely not *K. aurantiaca* gen. et comb. nov., 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* or *Ushanaia* gen. nov. 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* gen. nov. colony, possibly *K. aurantiaca* gen. et comb. nov., from Fiordland, and Powell (1947) mentions having commonly dredged what is likely *K. aurantiaca* gen. et comb. nov. 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* gen. et comb. nov. 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 & Mackinnon, 1911. This species is *Alcyonium*-like and superficially similar in appearance as it is red when alive, but not related to *Kotatea* gen. nov. (Verseveldt & 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 & Miller 1973; Morton 2004; Grange *et al.* 2010), particularly among ascidians and sponges on moderately exposed shores (Westerskov & Probert 1981). Here, it has also been reported that the native nudibranch, *Tritonia incerta* Bergh, 1904, grazes on *A. aurantiacum* (Morton & Miller 1973; Westerskov & Probert 1981). However, intertidal observations are probably of *K. lobata* gen. et sp. nov., and not *K. aurantiaca* gen. et comb. nov.

Kotatea aurantiaca gen. et comb. nov. 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.

Kotatea kapotaiora gen. et sp. nov.
urn:lsid:zoobank.org:act:7816DF77-E0C6-4237-8CF9-F5CF95D028A8
Figs 1B–C, 2C, 12–13, 14C

Māori name

Kapo Taiora.

Diagnosis

Colonies laterally compressed with branching lobes, white with white polyps. Collaret and points colourless, composed of warty spindles and clubs, and some irregular, flattened, branched forms. Tentacles contain irregular, warty, scale-like sclerites. Polyp neck contains warty rod- and spindle-like

sclerites. Polyp mounds also contain similar forms, as well as thorny and leafy clubs. Lobe surface contains similar clubs and spiny radiates, with the latter also found in the base surface. Lobe and base interior contains distinct, irregular radiates with a few, thin, thorny, branched processes.

Etymology

The species name was composed by the Ngāti Kurī Tira Me 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 Kurī 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."

Material examined

Holotype

NEW ZEALAND • Northland, ~12 km NW of North Cape; 34.3570° S, 172.8850° E; depth 69 m; 29 Jan. 1999; NIWA exped.; stn Z9712 (KAH9901/88); NIWA 3974.

Paratype

NEW ZEALAND • 1 specimen; same collection data as for holotype; AK 73620.

Additional material

NEW ZEALAND • 1 specimen; Auckland, ~5 km E of Te Arai Point, Jellicoe Channel; 36.1580° S, 174.7100° E; depth 46 m; 22 Nov. 2020; NIWA exped.; stn KAH2006/13; NIWA 155300.

Description (holotype, NIWA 3974)

Colony form

The holotype consists of a white (ethanol-preserved), lobate colony (Fig. 14C), 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. 2C).

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. 12A–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 12A, 13C). The tentacles contain irregular, warty, scale-like forms that are often slightly curved and branched (~0.1–0.25 mm long) (Fig. 12C). The polyp neck contains warty rod- and spindle-like forms (~0.1–0.2 mm long) (Fig. 12D). 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. 12E). The surface of the lobes contains similar but more ornate clubs, as well as spiny radiates (~0.04–0.16 mm long) (Fig. 12F). In the interior of the lobes, irregular radiates with few, thin, thorny, branched processes predominate (~0.05–0.15 mm long) (Fig. 12G). The surface of the base lacks clubs but contains similar thorny radiates to the surface

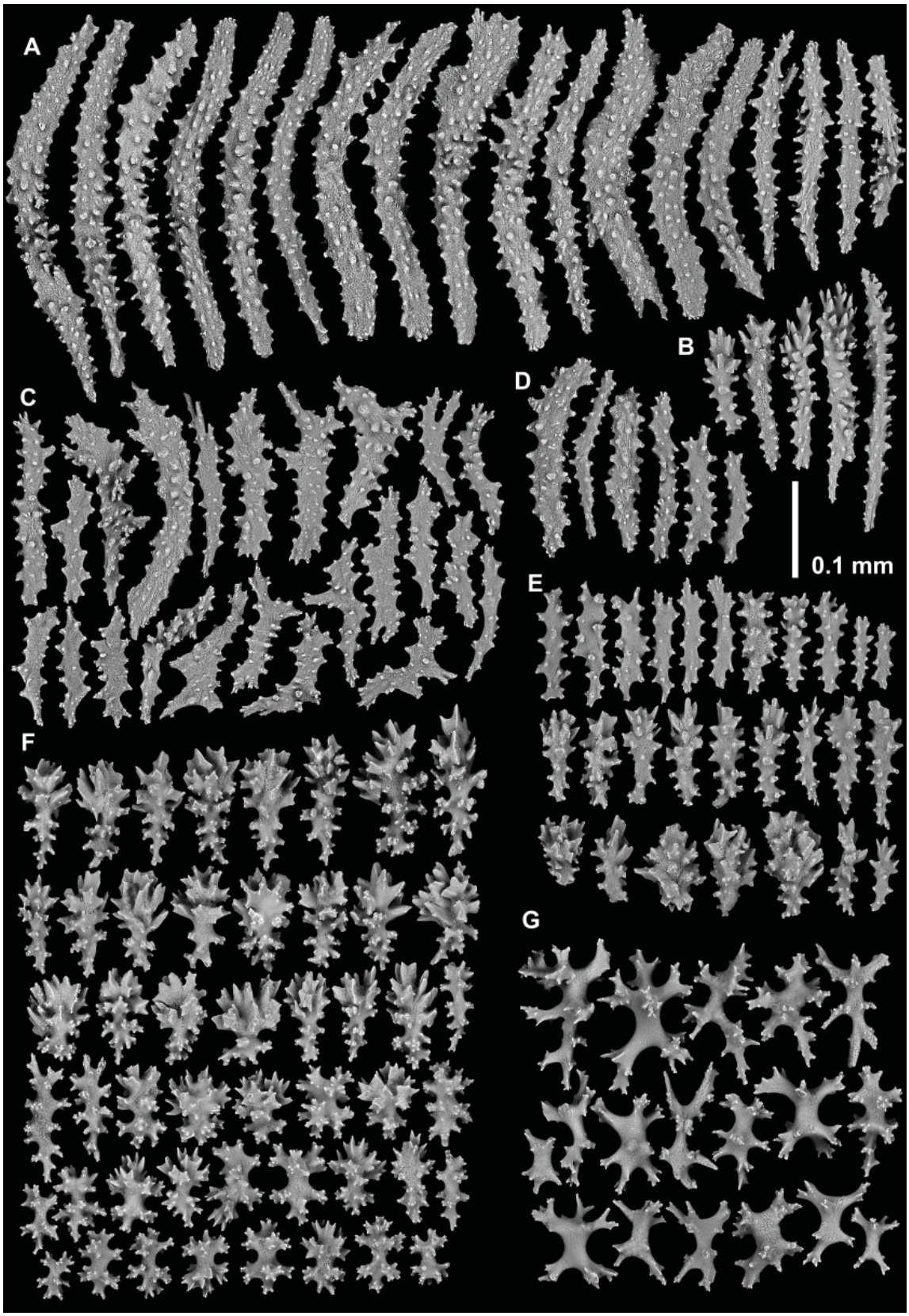

Fig. 12. *Kotatea kapotaiora* gen. et sp. nov., holotype (NIWA 3974), SEMs of sclerites. **A**. Collaret and points. **B**. Distal points. **C**. Tentacles. **D**. Polyp neck. **E**. Polyp mound. **F**. Lobe surface. **G**. Lobe interior.

of the lobes, although here these are generally smaller (~0.05–0.12 mm long) (Fig. 13A). 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. 13B).

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. 14C) and both the paratype and NIWA 155300 correspond very closely to the holotype in sclerite composition and size ranges (Figs 12–13).

Comparisons

Specimens of *Kotatea kapotaiora* gen. et sp. nov. 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 easily be differentiated from the rest of the genus by its characteristic, abundant interior radiates with few, thin, thorny branching processes (Figs 12G, 13B).

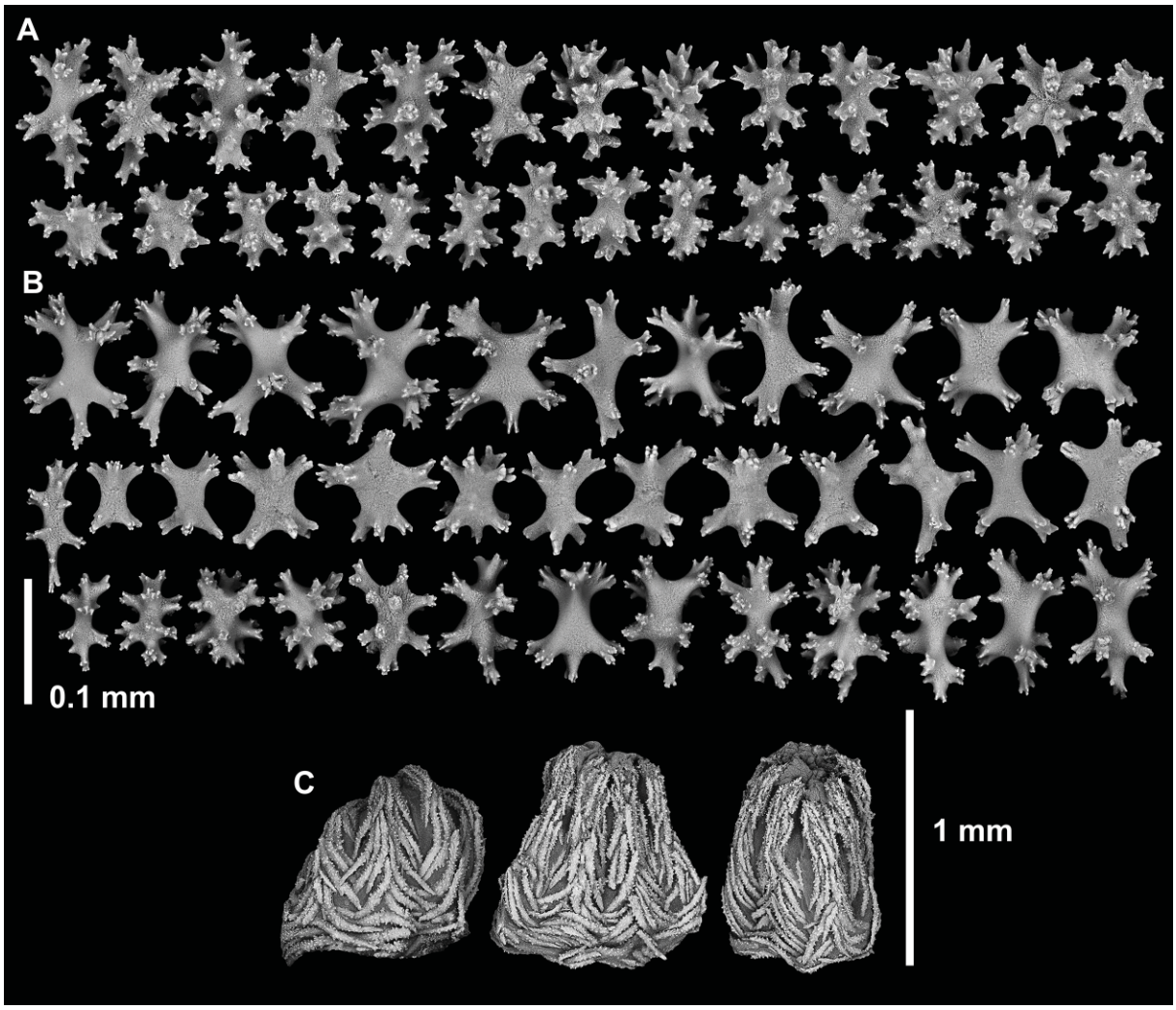

Fig. 13. *Kotatea kapotaiora* gen. et sp. nov., holotype (NIWA 3974), SEMs of sclerites. **A**. Base surface. **B**. Base interior. **C**. Polyps (in situ).

Habitat and distribution

The holotype and paratype, collected at 69 m north of North Cape, and one other colony, collected at a depth of 46 m near Te Arai Point, are the only known specimens of *K. kapotaiora* gen. et sp. nov. (Fig. 1B–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. 14C). *Kotatea kapotaiora* and *K. teorowai* gen. et sp. nov. can occur syntopically, as the holotypes for both species were collected together in the same sample.

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* gen. et sp. nov. That form is noted as rare and found at depths of 40–100 m. 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.

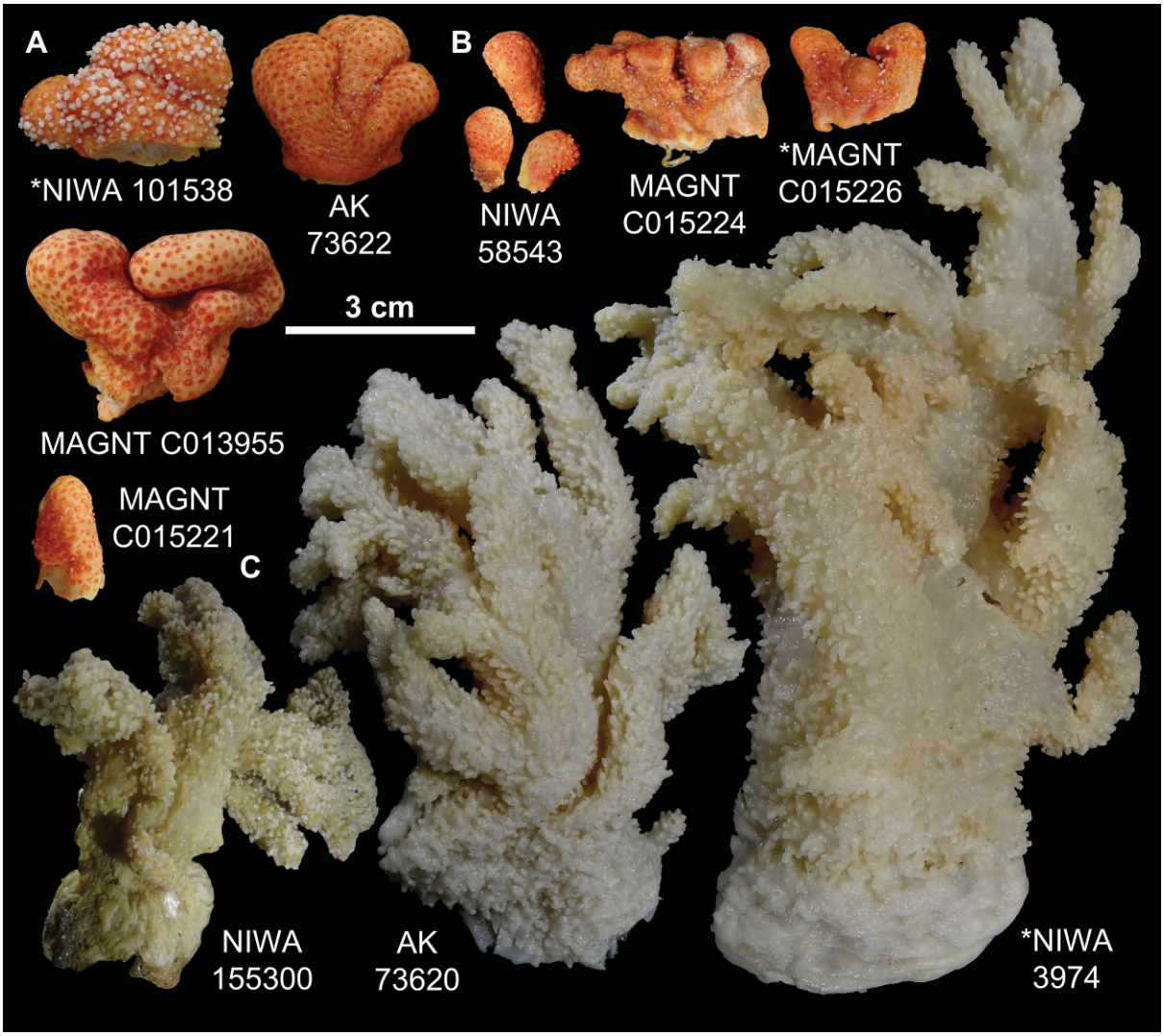

Fig. 14. Preserved specimens. **A**. *Kotatea kurakootingotingo* gen. et sp. nov. **B**. *K. niwa* gen. et sp. nov. **C**. *K. kapotaiora* gen. et sp. nov. Note that MAGNT C015224 and NIWA 58543 contain additional fragments that are not depicted. * = holotype.

Kotatea kurakootingotingo gen. et sp. nov.
urn:lsid:zoobank.org:act:EFF18A57-F73F-4434-9788-237264E59102
Figs 1A, 2D–E, 4A–B, 14A, 15–17

Māori name

Kura Kōtingotingo.

Diagnosis

Colonies robustly lobate and orange with distinct red or dark orange spots. Polyps white. Collaret and points may be colourless or dark orange, composed of warty to spiny spindles and well-developed thorny clubs. Tentacles contain irregular, warty, scale-like sclerites. Polyp neck contains warty rod-like forms. Polyp mounds contain similar sclerites, as well as cone-like clubs, spindle-like, rod-like and oval forms with warts in girdles. Lobe and base surface contains similar sclerites, but lacks well-developed clubs. Base surface also includes spheroids, a few clubs, and gradations between radiates and oval or rod-like forms with wart girdles and occasionally a narrow waist. Lobe and base interior contains highly sculptured rod-like, spindle-like and oval forms girdled with complex warts, spheroids particularly common in base interior.

Etymology

The species name was composed by the Ngāti Kurī Tira Me 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 Kurī provided the following *kōrero* (narrative): "Kura Kōtingotingo's spots are reminiscent of the dots on specific *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."

Material examined

Holotype

NEW ZEALAND • Manawatāwhi/Three Kings Islands, Princes Islands; 34.1759° S, 172.04949° E; depth 10–20 m; 24 Feb. 2002; NIWA exped.; stn Z15942; NIWA 101538.

Paratypes

NEW ZEALAND – **Manawatāwhi/Three Kings Islands** • 1 specimen; Manawatāwhi/Great Island; 34.15° S, 172.15° E; depth 7 m; 20 Apr. 1999; J. Starmer leg.; MAGNT C015221 • 1 specimen; Manawatāwhi/Great Island; 34.1662° S, 172.1502° E; depth 6 m; 20 Apr. 1999; Coral Reef Research Foundation exped.; MAGNT C013955 • 1 specimen; same collection data as for holotype; AK 73622.

Description (holotype, NIWA 101538)

Colony form

The holotype consists of a lobate colony, measuring 2.5 cm in height by 3.5 cm width (Figs 4B, 14A). 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. 2D), 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) (Fig. 15A–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. 15A). The number of collaret rows is variable depending on polyp size, but in large polyps this is approximately seven rows (Fig. 17C). The tentacles contain irregular, warty, scale-like forms, often slightly crescentic (~0.08–0.21 mm long) (Fig. 15C). The polyp neck contains many warty rod-like forms (~0.08–0.12 mm long) (Fig. 15D), 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. 16A). Between polyp mounds, the surface of the lobes contains similar sclerites (~0.1–0.18 mm long) but lacks well-developed clubs (Fig. 16B). 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. 17A). 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 16C, 17B).

Variability

Paratype MAGNT C013955 (Fig. 14A) consists of only a fragment and was originally part of a much larger colony, probably ~10 cm in width (Fig. 4A). Paratype MAGNT C015221 has mostly dark orange collaret and point sclerites (Fig. 2E) 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. 4A–B). The three paratypes correspond very closely to the holotype in their sclerite composition and size ranges (Figs 15–17).

Comparisons

Specimens of *Kotatea kurakootingotingo* gen. et sp. nov. are superficially similar to congeners with a robust, lobate growth form. However, *K. kurakootingotingo* and *K. lobata* gen. et sp. nov. 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 16B–C, 17A–B and 19F, 20, 21A). Conversely, specimens of *K. kurakootingotingo* lack the very large, highly branched, antler-like sclerites which are characteristic of interior sections in *K. lobata* (compare Figs 16C, 17B and 20A, 21A). Additionally, specimens of *K. lobata* are composed of smaller and much less robust sclerites overall (compare Figs 15–17 and 19–21).

Specimens of *Kotatea kurakootingotingo* gen. et sp. nov. differ from those of *K. niwa* gen. et sp. nov. 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 16B–C, 17A–B and 22F–G, 23A–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

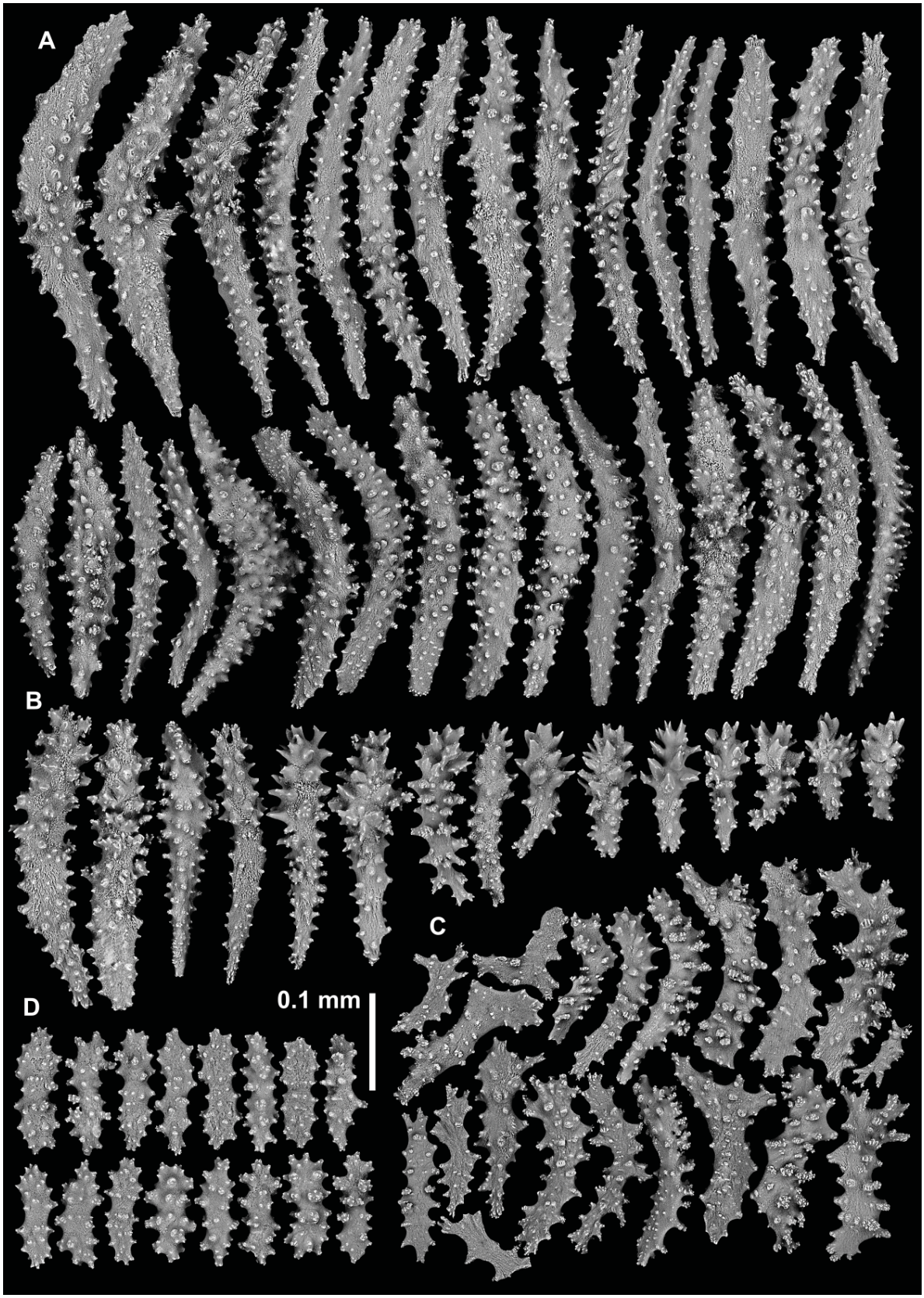

Fig. 15. *Kotatea kurakootingotingo* gen. et sp. nov., holotype (NIWA 101538), SEMs of sclerites. **A**. Collaret and points. **B**. Distal points. **C**. Tentacles. **D**. Polyp neck.

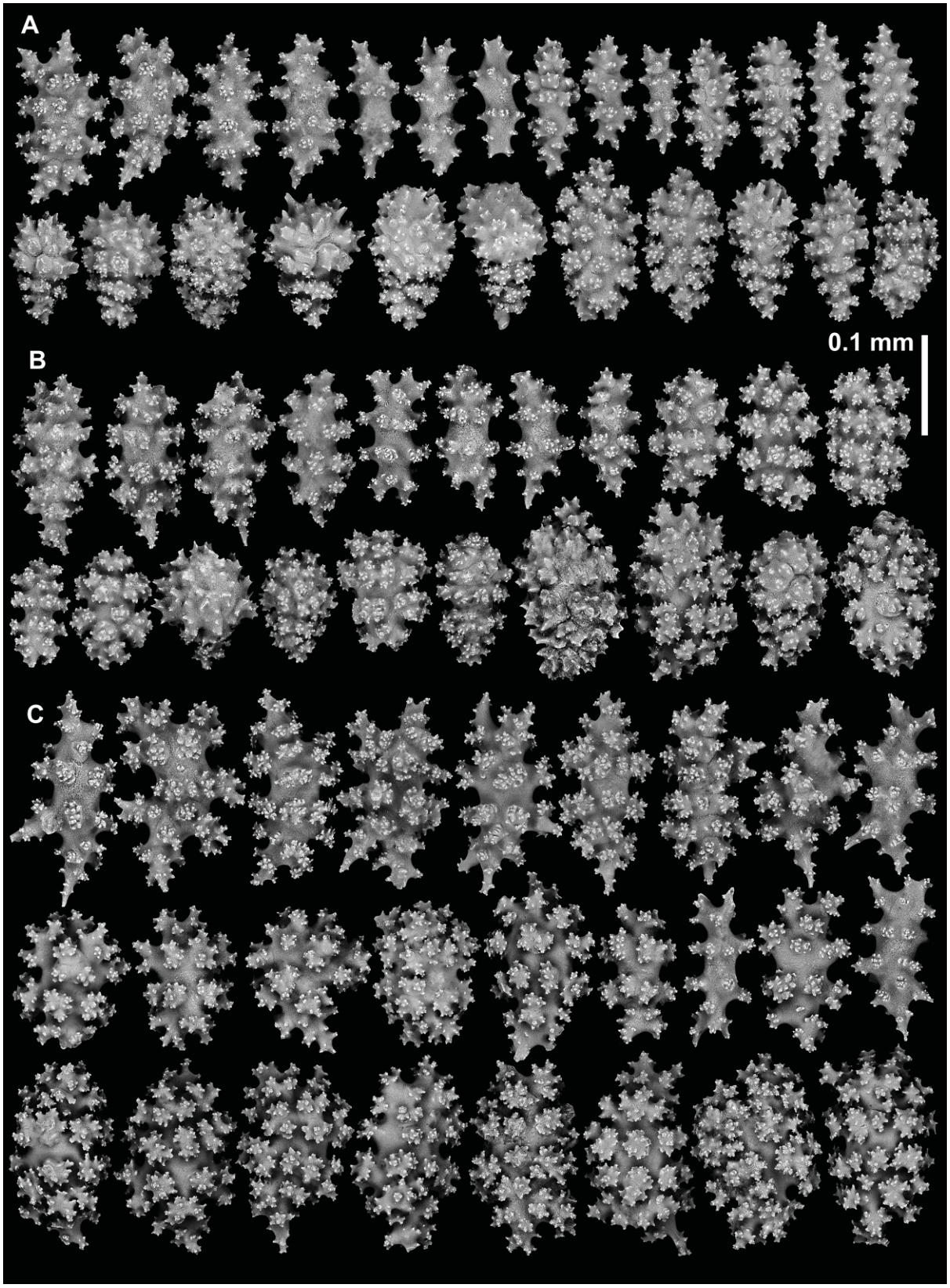

Fig. 16. *Kotatea kurakootingotingo* gen. et sp. nov., holotype (NIWA 101538), SEMs of sclerites. **A**. Polyp mound. **B**. Lobe surface. **C**. Lobe interior.

Figs 17C and 23C). Note also that these two species were each resolved as monophyletic by phylogenetic analyses of *mtMutS* and *28S* (Fig. 37).

Habitat and distribution

All specimens were collected at depths of ≤ 20 m at the Manawatāwhi/Three Kings Islands (Fig. 1A). Paratypes MAGNT C013955 and MAGNT C015221 were recorded as having been collected on a rocky reef.

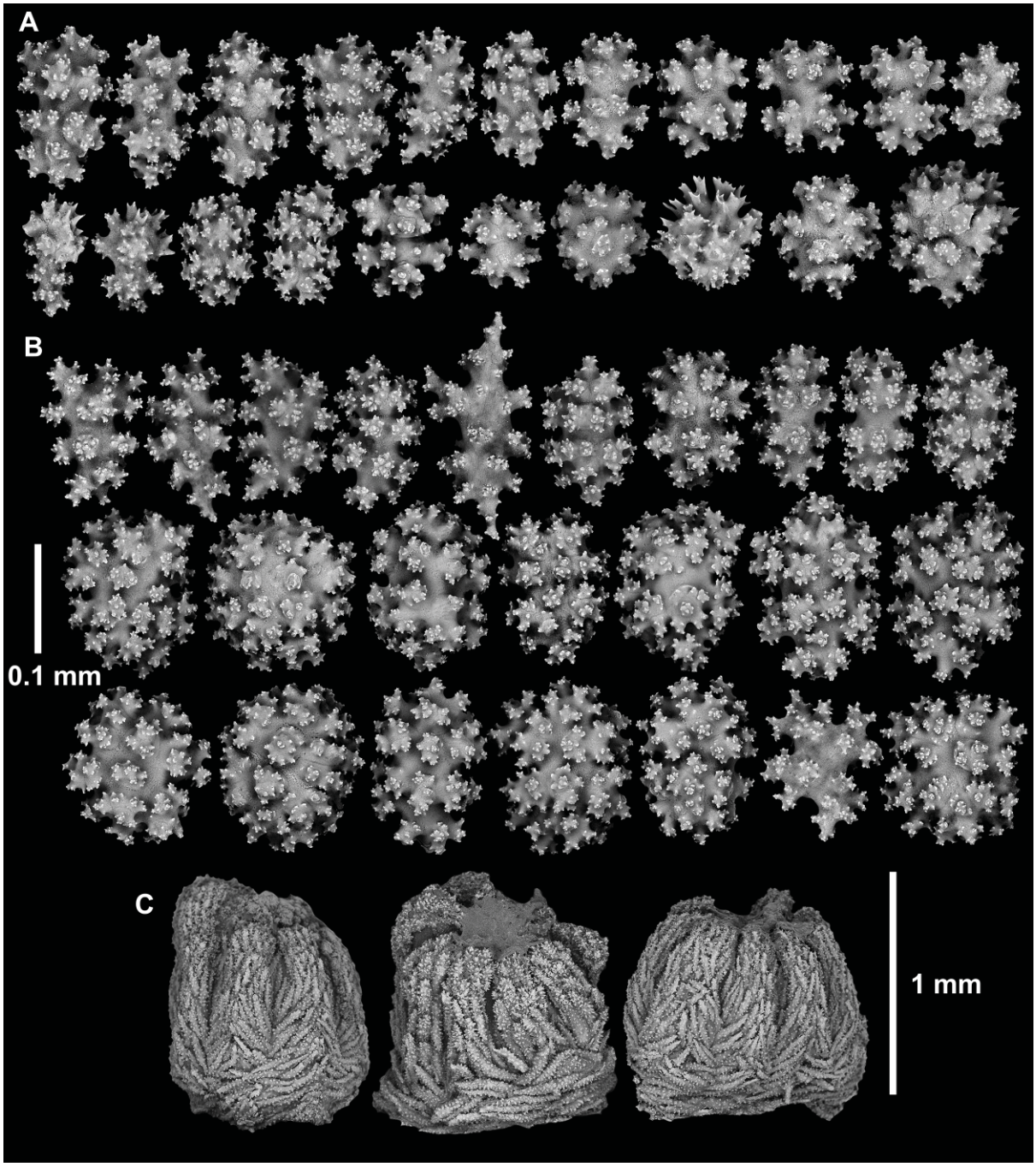

Fig. 17. *Kotatea kurakootingotingo* gen. et sp. nov., holotype (NIWA 101538), SEMs of sclerites. **A**. Base surface. **B**. Base interior. **C**. Polyps (in situ).

Kotatea lobata gen. et sp. nov.
urn:lsid:zoobank.org:act:DD060415-26EE-4549-A167-813E05D11323
Figs 1B, 2F, 4C–F, 18–21

? *Alcyonium aurantiacum* – Morton & Miller 1973: 154, 170, 272–274, pl. 6. — Westerskov & Probert 1981 in part: 111, pl. 28. — Morton 2004: 267; fig. 14.4. — Grange *et al.* 2010 in part: 148.

Diagnosis

Colonies robustly lobate and orange with white polyps. Collaret and points colourless with flattened, often slender, warty spindles and thorny clubs. Tentacles contain irregular, warty, scale-like sclerites. Polyp neck contains few tuberculate to warty rod-like forms, concentrated towards its base. Polyp mounds contain short, warty rod- and spindle-like forms and thorny clubs. Lobe surface contains similar thorny clubs, larger spindle-like forms and radiates. Base surface contains similar radiates, along with broad spindles, rod-like forms, clubs, and some leafy spheroids. Lobe and base interior contains distinctive, highly branched, irregular antler- and spindle-like forms.

Etymology

The species name is the Latin word '*lobata*' for 'lobed'.

Material examined

Holotype

NEW ZEALAND • Northland, Houhora Harbour; 34.8216° S, 173.1508° E; depth 3–10 m; 30 Nov. 2002; NIWA exped.; stn Z15913; NIWA 101313.

Paratypes

NEW ZEALAND – **Northland** • 1 specimen; Bay of Islands, Moturoa Island, Battleship Rock; 35.2087° S, 174.1167° E; depth 29–30 m; 7 Sep. 2009; Oceans Survey 2020 exped.; stn KAH0907/240; NIWA 58562 • 1 specimen; Mokohinau Islands, Flax Islands; 35.9128° S, 175.0954° E; depth 6–10 m; 23 Apr. 1999; Coral Reef Research Foundation exped.; stn Z15906; NIWA 101268. – **Auckland** • 8 specimens; Great Barrier Island/Aotea; 36.3330° S, 175.4740° E; 7 Jun. 2006; NIWA exped.; stn Z15978; NIWA 101740 • 10 specimens; Manukau Harbour; 37.0347° S, 174.6697° E; depth 8 m; 2 Feb. 1976; New Zealand Oceanographic Institute exped.; stn O8; NIWA 142995 • 2 specimens; Manukau Harbour; 37.1323° S, 174.6785° E; depth 8 m; 2 Feb. 1976; New Zealand Oceanographic Institute exped.; stn O4; NIWA 143082.

Additional material

NEW ZEALAND – **Northland** • 4 specimens; Cavalli Islands, Nukutaunga Island; 34.9750° S, 173.9635° E; depth 6 m; 12 Jun. 2017; S. Hannam leg.; stn Z17927; NIWA 108960 • 1 specimen; Cavalli Islands, Motukawanui Island; 34.9860° S, 173.9367° E; depth 5–17.5 m; 9 Apr. 2013; G. Wiren *et al.* leg.; stn TK2013-1-019; AK 656657 • 1 specimen; Mokohinau Islands, Flax Islands; 35.9128° S, 175.0955° E; depth 6 m; 23 Apr. 1999; Coral Reef Research Foundation exped.; MAGNT C013956 • 1 specimen; Mokohinau Islands, Flax Islands; 35.9167° S, 175.1167° E; depth 6–18 m; 23 Apr. 1999; J. Starmer leg.; MAGNT C015222 • 1 specimen; same collection data as for preceding; MAGNT C015227 • 1 specimen; same collection data as for preceding; MAGNT C015228 • 1 specimen; same collection data as for preceding; MAGNT C015229 • 1 specimen; same collection data as for preceding; MAGNT C015230 • 1 specimen; same collection data as for preceding; MAGNT C015250 • 1 specimen; same collection data as for preceding; MAGNT C015251. – **Auckland and Coromandel Peninsula** • 1 specimen; Cape Rodney, Leigh Reef; 36.2833° S, 174.8167° E; depth 20 m; Jan. 1978; P. Alderslade and K. Harada leg.; MAGNT C001022 • 1 specimen; same collection data as for preceding; MAGNT C001023 • 1 specimen; Cape Rodney, Leigh Reef; 36.2833° S, 174.8167° E; depth 0 m; 4 Feb. 1977;

P. Alderslade leg.; MAGNT C001693 • 1 specimen; Mercury Islands, Great Mercury Island/Ahuahu; 36.6347° S, 175.7675° E; depth 5–15 m; 6 Dec. 1988; Queensland Museum exped.; MAGNT C015219 • 1 specimen; Muriwai, Maukatia/Maori Bay; 36.8384° S, 174.4268° E; depth 0 m; 21 Jan. 2015; W.M. Blom leg.; AK 120774.

Description (holotype, NIWA 101313)

Colony form

The holotype consists of an orange (ethanol-preserved), lobate colony measuring 7 cm in height by 5 cm width (Fig. 18), 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. 2F).

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. 19A–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 19A, 21B). The tentacles contain flat, warty, scale-like forms with irregular but often curved shapes (~0.06–0.2 mm long) (Fig. 19C). 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. 19D). The polyp mounds are composed mostly of short, warty rod- and spindle-like forms and thorny clubs (~0.06–0.12 mm long) (Fig. 19E). 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. 19F). 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. 20B). 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. 20A), whereas the interior of the base possesses more antler-like sclerites (Fig. 21A).

Variability

The number of lobes can vary substantially between specimens (Figs 4C–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. 4C–E), and occasionally dull beige, which is the case for MAGNT C001022 and MAGNT C001693 (Fig. 18), 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 *Kotatea lobata* gen. et sp. nov. specimens a distinctive scaly appearance, which is especially clear in the holotype, NIWA 101313 (Fig. 18). 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. 18).

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 19–21). The size ranges of all specimens' sclerites also falls within those described for the holotype.

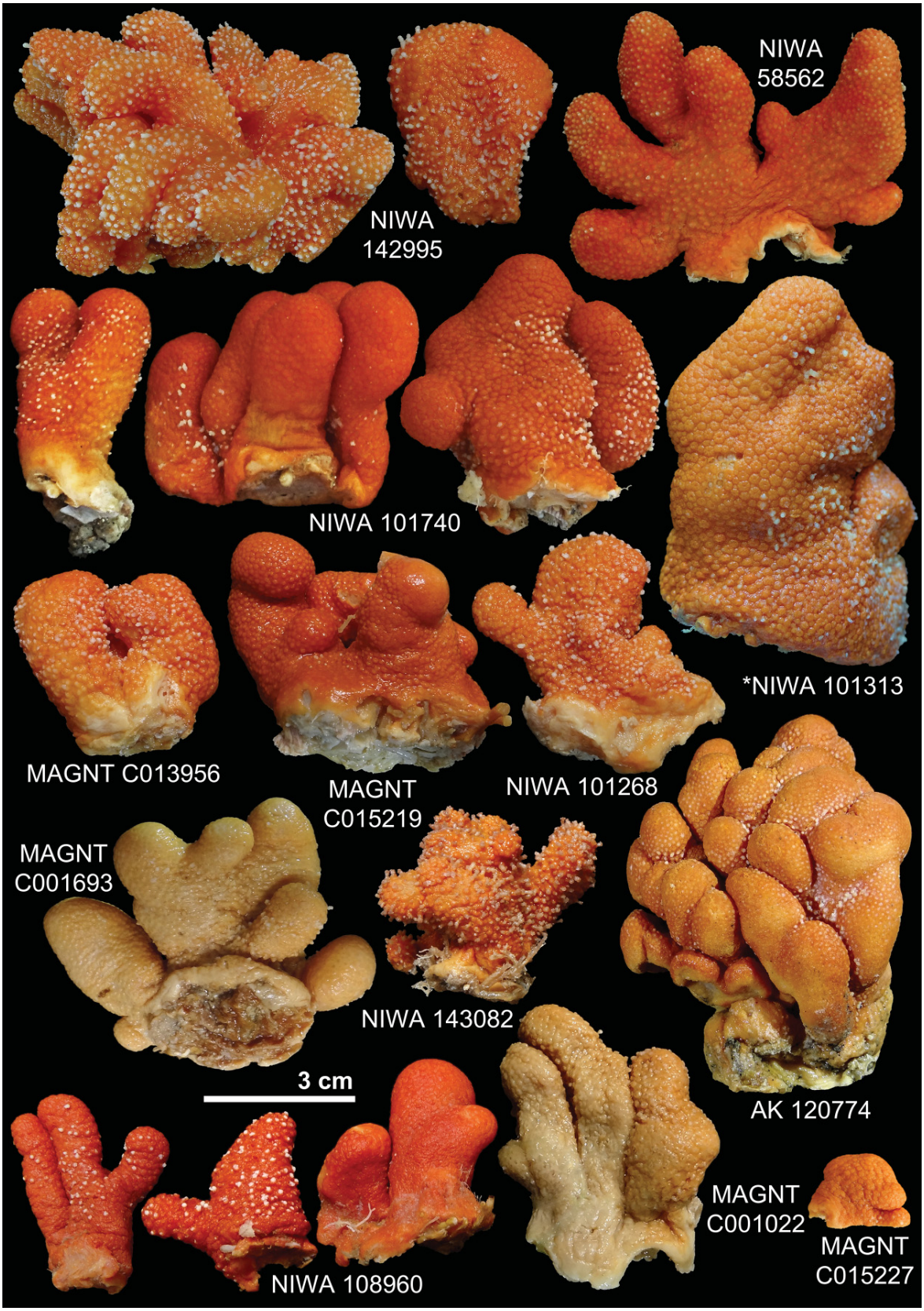

Fig. 18. Selected preserved specimens of *Kotatea lobata* gen. et sp. nov. Note that NIWA 142995, NIWA 101740 and NIWA 108960 contain additional fragments that are not depicted. * = holotype.

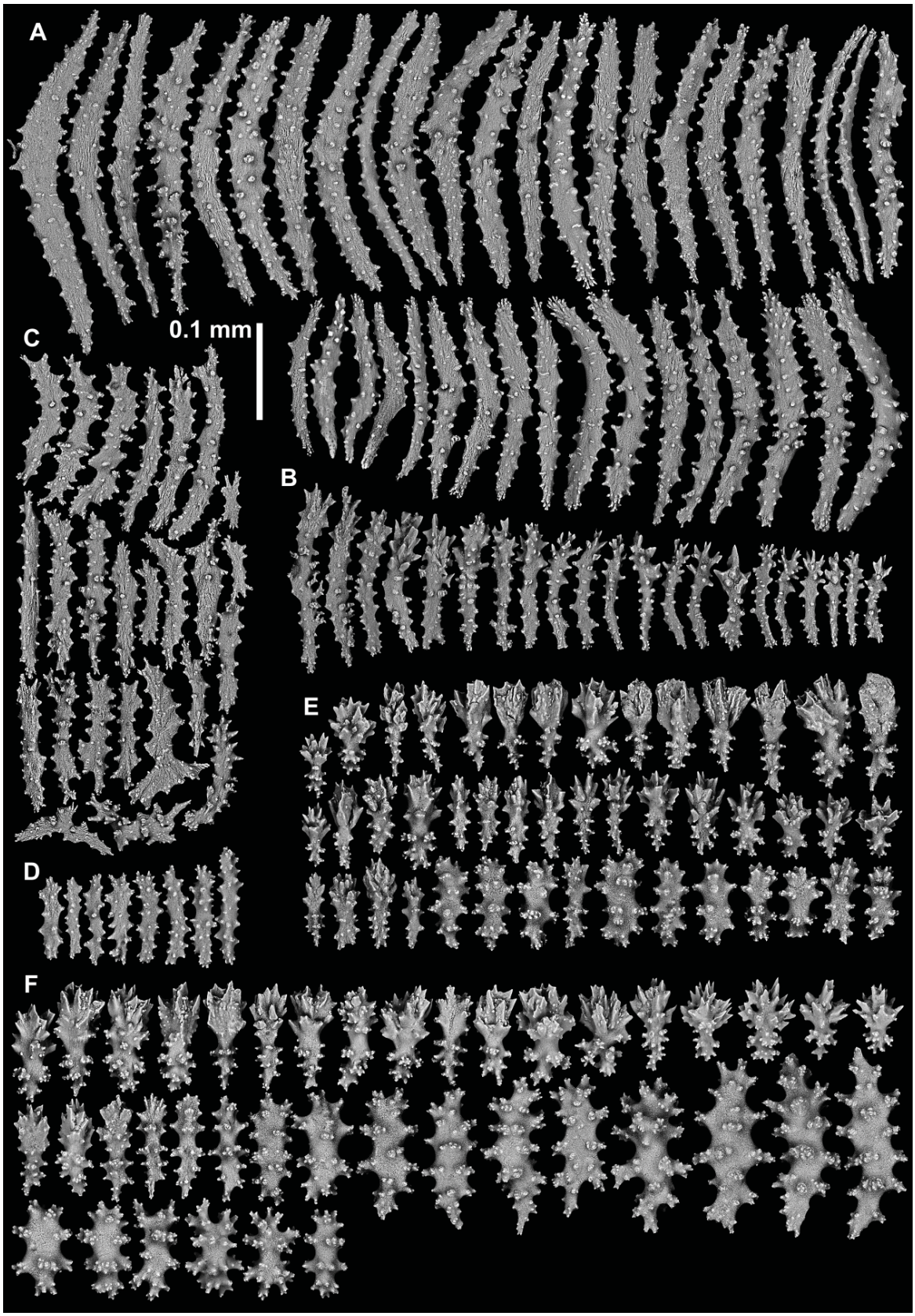

Fig. 19. *Kotatea lobata* gen. et sp. nov., holotype (NIWA 101313), SEMs of sclerites. **A**. Collaret and points. **B**. Distal points. **C**. Tentacles. **D**. Polyp neck. **E**. Polyp mound. **F**. Lobe surface.

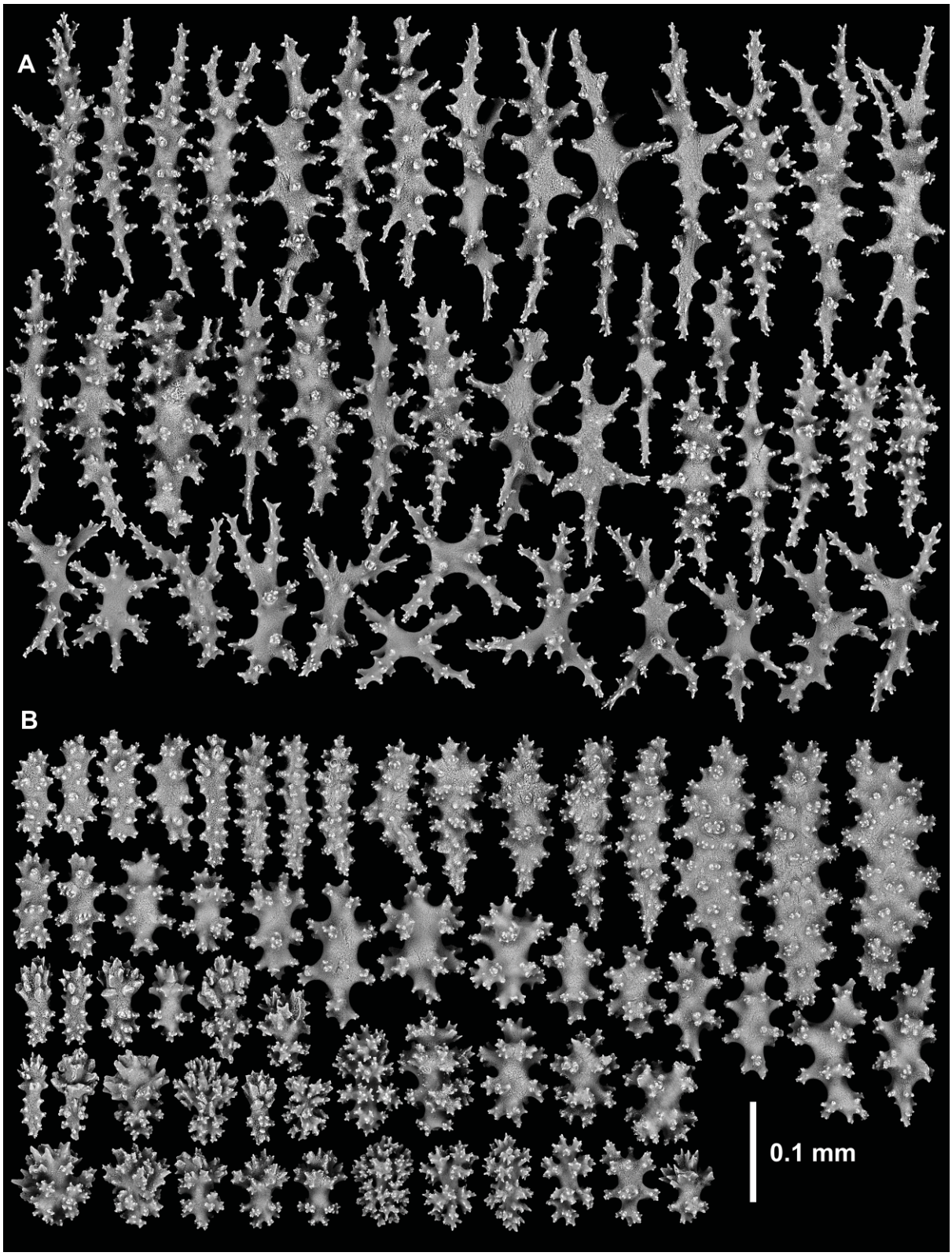

Fig. 20. *Kotatea lobata* gen. et sp. nov., holotype (NIWA 101313), SEMs of sclerites. **A**. Lobe interior. **B**. Base surface.

Comparisons

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

Specimens of *Kotatea lobata* gen. et sp. nov. are easily distinguished from those of *K. niwa* gen. et sp. nov. 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 20A, 21A and 22G, 23B). The sclerites of *K. lobata* are also overall smaller and less highly sculptured than those of *K. niwa*.

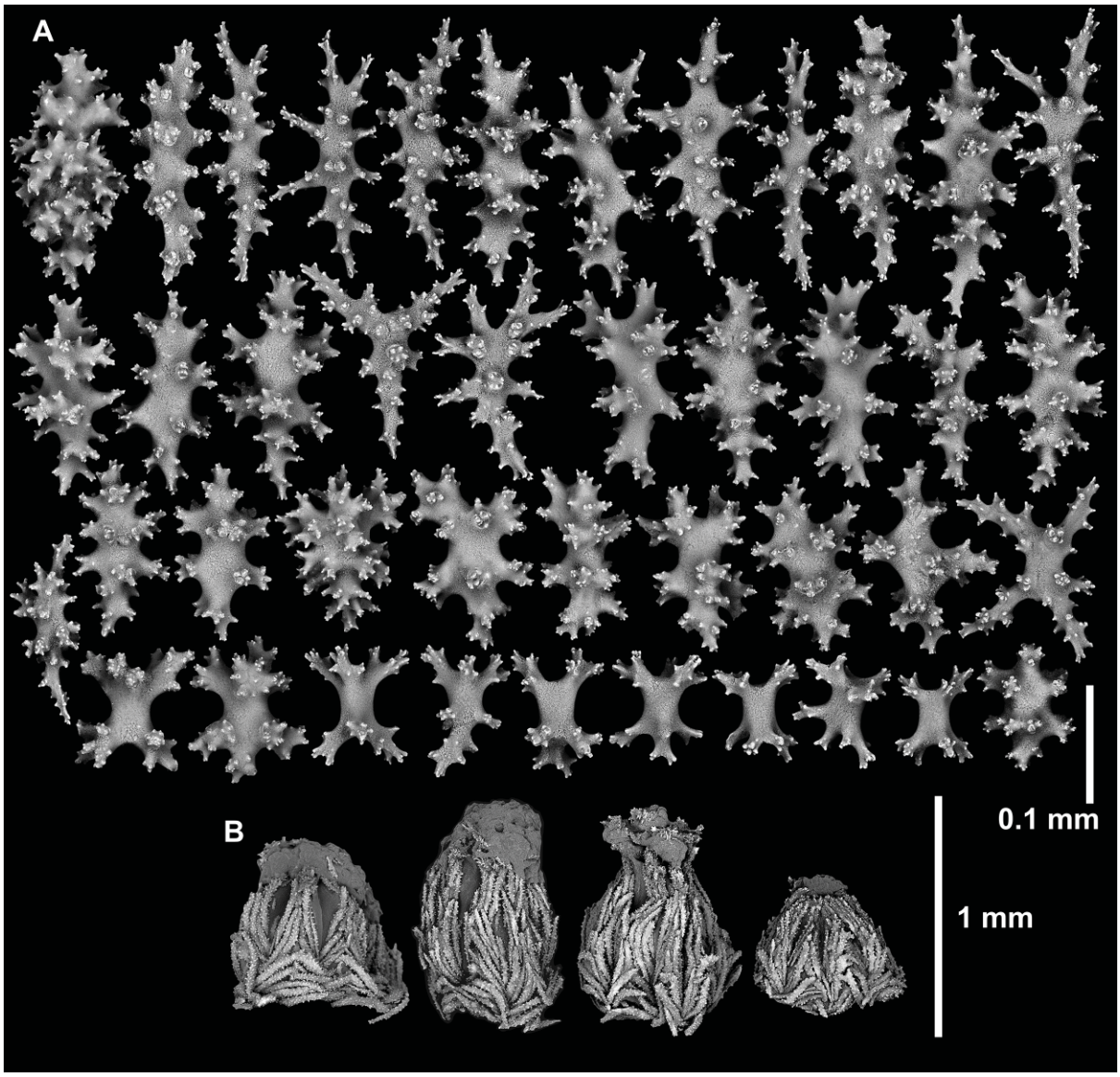

Fig. 21. *Kotatea lobata* gen. et sp. nov., holotype (NIWA 101313), SEMs of sclerites. **A**. Base interior. **B**. Polyps (in situ).

The fleshy lobes of *Ushanaia solida* gen. et sp. nov. superficially resemble those of *K. lobata* gen. et sp. nov., 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.

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. 1B–C). *Kotatea lobata* gen. et sp. nov. is also notable for occasionally being exposed at low tide, usually under boulders or overhangs (Fig. 4E–F). Many of the specimens were recorded as having been collected from under boulders and from rock faces.

Remarks

Intertidal observations of *Alcyonium aurantiacum* probably refer to *K. lobata* gen. et sp. nov. rather than *K. aurantiaca* gen. et comb. nov. (see remarks under *K. aurantiaca* gen. et comb. nov. above).

Kotatea niwa gen. et sp. nov.
urn:lsid:zoobank.org:act:21F82707-8C02-4C9E-A4B0-5672E5666601
Figs 1A–B, 2G, 14B, 22–23

Diagnosis

Colonies robustly lobate, orange with small red spots, and with white polyps. Collaret and points may be colourless or dark orange to red, and consist of warty, mostly flattened spindles and thorny clubs. Tentacles contain irregular, warty, scale-like sclerites. Polyp neck contains abundant warty rod-like forms. Polyp mounds contain similar sclerites and thorny clubs. Lobe surface contains thorny clubs and warty double-heads. Base surface contains warty radiates grading into double-heads, a few spheroids and tends to lack clubs. Lobe and base interior contains oval or rod-like forms girdled with warts, and highly sculptured spheroids and double-heads.

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.

Material examined

Holotype

NEW ZEALAND • Northland, Piwhane/Spirits Bay; 34.4167° S, 172.7833° E; depth 17–20 m; Apr. 1999; J. Starmer leg.; MAGNT C015226.

Paratype

NEW ZEALAND • 2 specimens; Manawatāwhi/Three Kings Islands, ~1 km NE of Moekawa/South West Island; 34.1667° S, 172.0833° E; depth 17 m; 20 Apr. 1999; J. Starmer leg.; MAGNT C015224.

Additional material

NEW ZEALAND • 5 specimens; Northland, Bay of Islands, ~1 km NW of Okahu Island; 35.1917° S, 174.1922° E; depth 37–40 m; 3 Sep. 2009; Oceans Survey 2020 exped.; stn KAH0907/194; NIWA 58543.

Description (holotype MAGNT C015226)

Colony form

The holotype is a lobate colony, measuring 1.5 cm in height by 2.5 cm width (Fig. 14B). The surface of the colony (ethanol-preserved) is orange with small red spots, which are produced by red polyp neck and

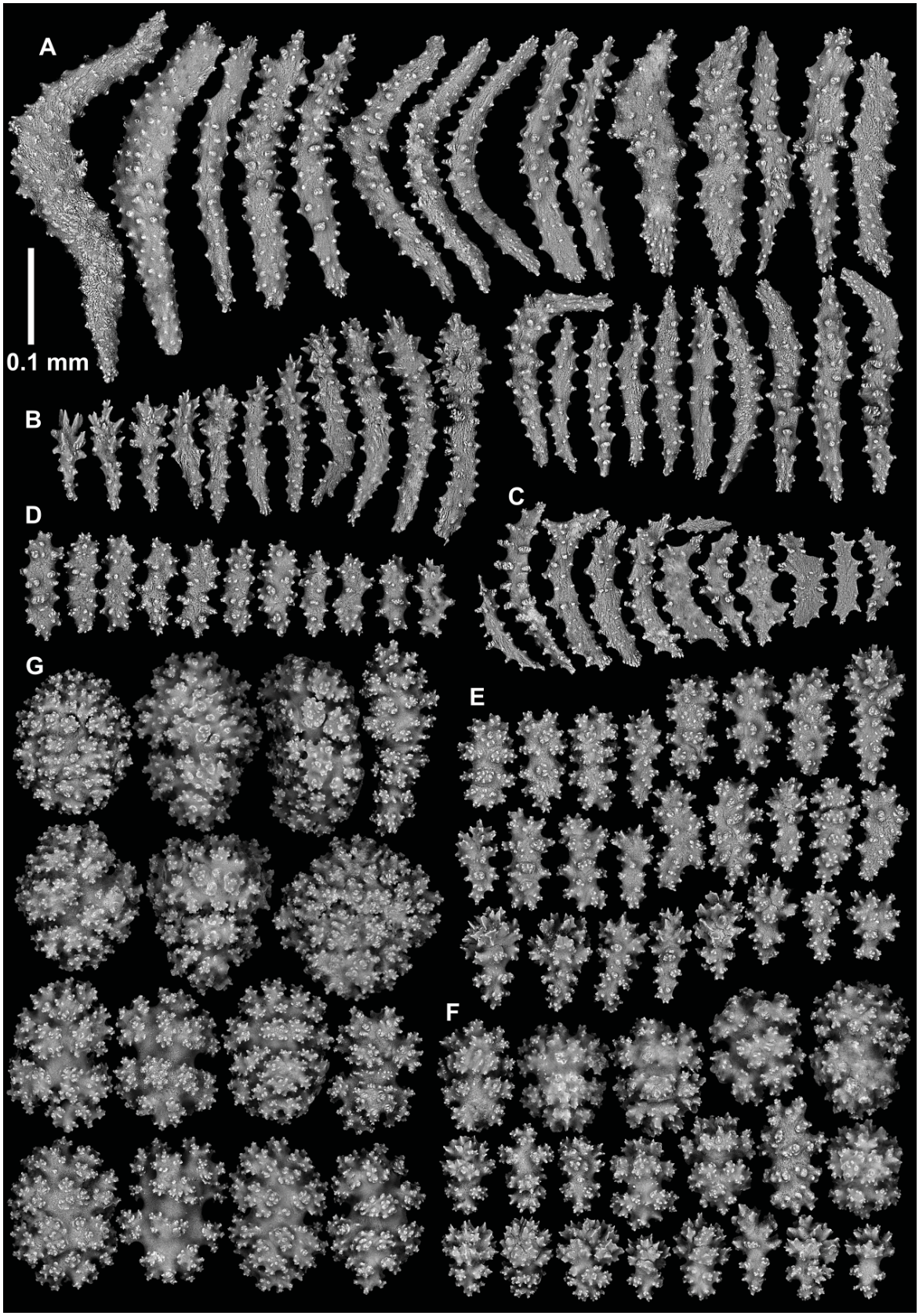

Fig. 22. *Kotatea niwa* gen. et sp. nov., holotype (MAGNT C015226), SEMs of sclerites. **A**. Collaret and points. **B**. Distal points. **C**. Tentacles. **D**. Polyp neck. **E**. Polyp mound. **F**. Lobe surface. **G**. Lobe interior.

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. 2G), but see variability section below.

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) (Fig. 22A–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. 22A). The number of collaret rows is variable depending on polyp size, but in large

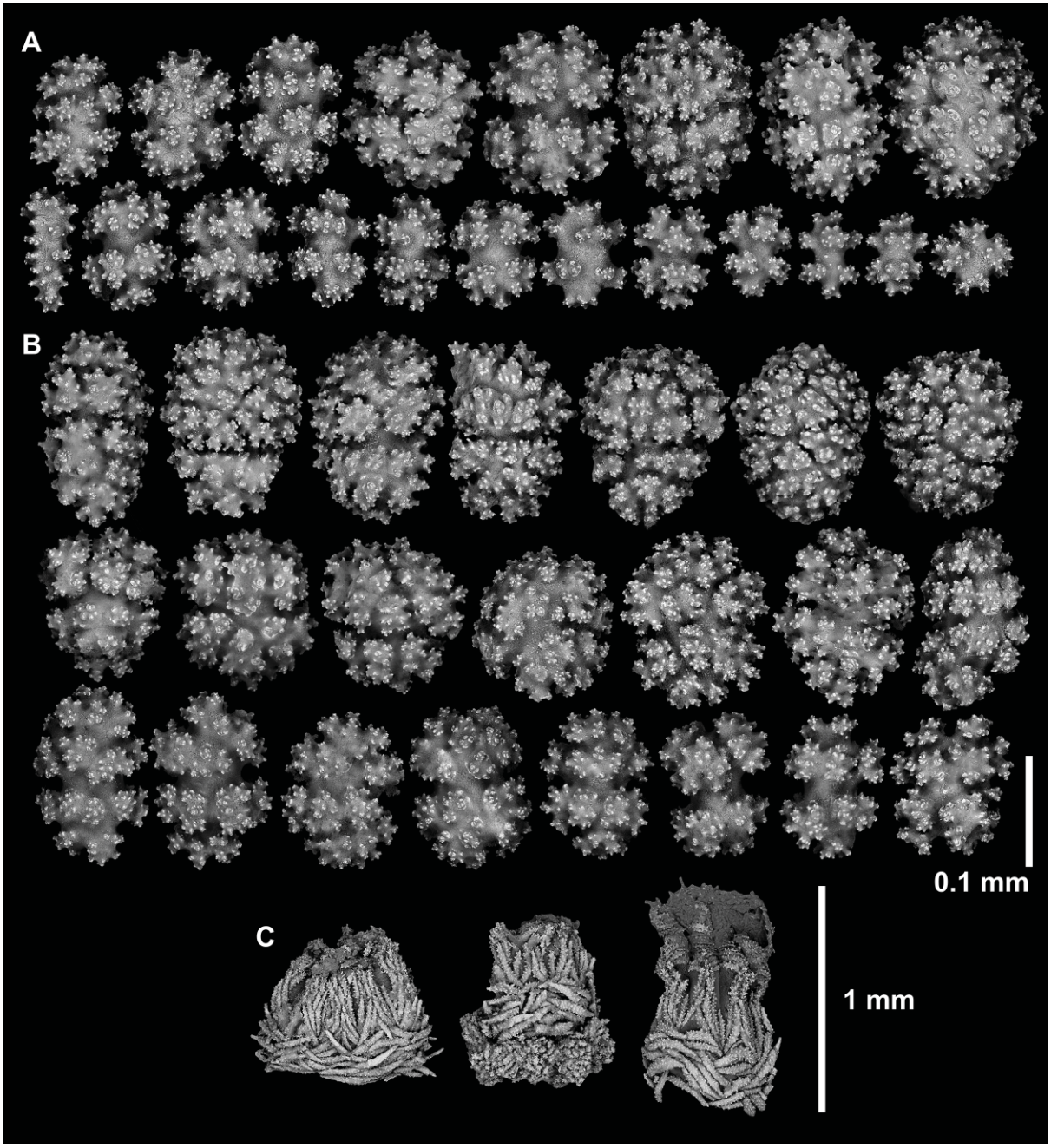

Fig. 23. *Kotatea niwa* gen. et sp. nov., holotype (MAGNT C015226), SEMs of sclerites. **A**. Base surface. **B**. Base interior. **C**. Polyps (in situ).

polyps this is approximately seven rows (Fig. 23C). The tentacles contain irregular, warty, scale-like forms, often slightly crescentic (~0.05–0.18 mm long) (Fig. 22C). The polyp neck contains abundant warty rod-like forms (~0.08–0.1 mm long) (Fig. 22D), which extend into the polyp mound, where they gradually give way to thorny clubs (~0.06–0.15 mm long) (Fig. 22E). 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. 22F). The surface of the base contains warty radiates grading into double-heads, and a few spheroids but tends to lack clubs (Fig. 23A). 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 22G, 23B).

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 lots are otherwise very similar in colony colour and growth form (Fig. 14B), and the paratype and NIWA 58543 correspond very closely to the holotype in terms of sclerite composition and size ranges (Figs 22–23).

Comparisons

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

Habitat and distribution

Specimens of *Kotatea niwa* gen. et sp. nov. were collected from the Manawatāwhi/Three Kings Islands, Piwhane/Spirits Bay and the Bay of Islands at depths between 17 and 40 m (Fig. 1A–B).

Kotatea raekura gen. et sp. nov.
urn:lsid:zoobank.org:act:5C90162B-2FE1-4A6C-93D5-BF309CA3C6D1
Figs 1A, 2H, 3D, 24A, 25, 26A–D

Māori name

Raekura.

Diagnosis

Colonies have branching lobes and are orange with white polyps. Collaret and points are orange and composed of warty, often flattened spindles and poorly developed thorny clubs. Tentacles contain irregular, warty, scale-like sclerites. Polyp neck contains warty rod-like forms. Polyp mounds contain thorny and warty clubs. Lobe surface contains similar clubs, as well as warty, girdled spindle-like forms. Base surface contains thorny clubs, radiates, and spindle-like forms girdled with spines or warts. Lobe and base interior contains irregular, branching, warty forms.

Etymology

The species name was composed by the Ngāti Kurī Tira Me 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 Kurī 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 and sub-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'."

Material examined

Holotype

NEW ZEALAND • Manawatāwhi/Three Kings Islands, Princes Islands; 34.1759° S, 172.0495° E; depth 10–20 m; 24 Feb. 2002; NIWA exped.; stn Z15942; NIWA 101537.

Paratypes

NEW ZEALAND • 1 specimen; same collection data as for holotype; AK 73621 • 2 specimens; Manawatāwhi/Three Kings Islands, Princes Islands; 34.1777° S, 172.0465° E; depth 6–11 m; 15 Apr. 1999; Coral Reef Research Foundation exped; stn Z15632; NIWA 100968.

Additional material

NEW ZEALAND – **Manawatāwhi/Three Kings Islands** • 1 specimen; Princes Islands; 34.1667° S, 172.0500° E; depth 5–10 m; 15 Apr. 1999; J. Starmer leg.; MAGNT C015223 • 1 specimen; Princes Islands; 34.1777° S, 172.0465° E; depth 10 m; 15 Apr. 1999; Coral Reef Research Foundation exped.; MAGNT C013954 • 2 specimens; Ōhau/West Island; 34.1839° S, 172.0304° E; depth 6–11 m; 12 Apr. 2013; S. Hannam *et al.* leg.; stn TK2013-25-276; AK 656516.

Description (holotype, NIWA 101537)

Colony form

The holotype (Fig. 24A) is a fragment of a larger colony (Fig. 3D) and measures 6 cm in 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. 2H). 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. 25A–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 5A, 26D). The tentacles contain irregular, warty, scale-like forms, often curved (~0.1–0.2 mm long) (Fig. 25C), and the polyp neck contains warty rod-like forms (~0.08–0.12 mm long) (Fig. 25D). Polyp mounds are composed mainly of thorny and warty clubs (~0.08–0.14 mm long) (Fig. 25E). The surface of lobes between mounds contains similar clubs along with numerous warty, girdled spindle-like forms (~0.08–0.18 mm long) (Fig. 25F). 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. 26B). 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. 26A, C).

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. 24A). 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 paratype lots and the three non-type lots correspond very closely with the sclerite composition and size ranges described for the holotype (Figs 25–26).

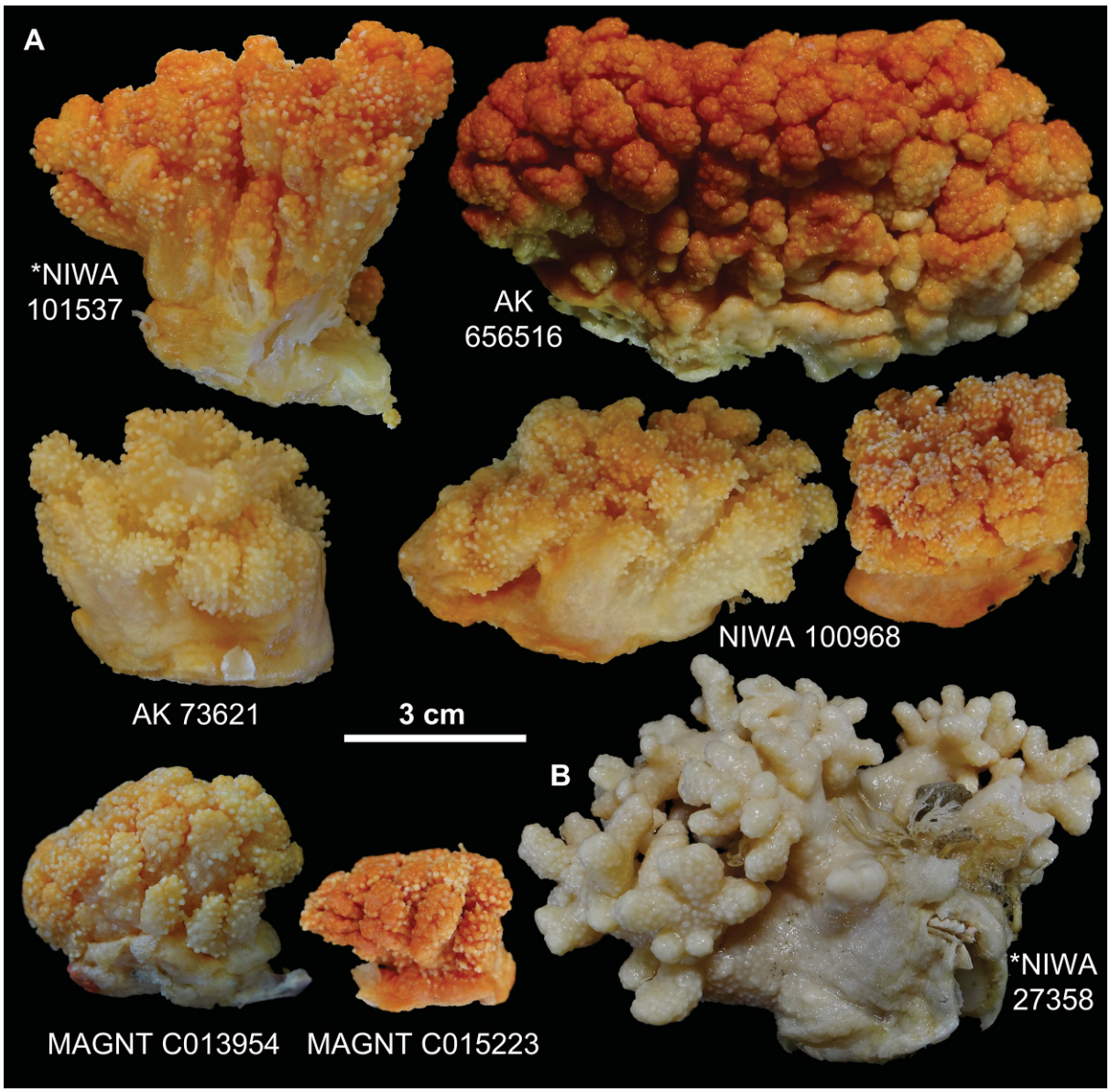

Fig. 24. Preserved specimens. **A**. *Kotatea raekura* gen. et sp. nov. **B**. *K. teorowai* gen. et sp. nov. Note that lot AK 656516 includes additional fragments that are not shown. * = holotype.

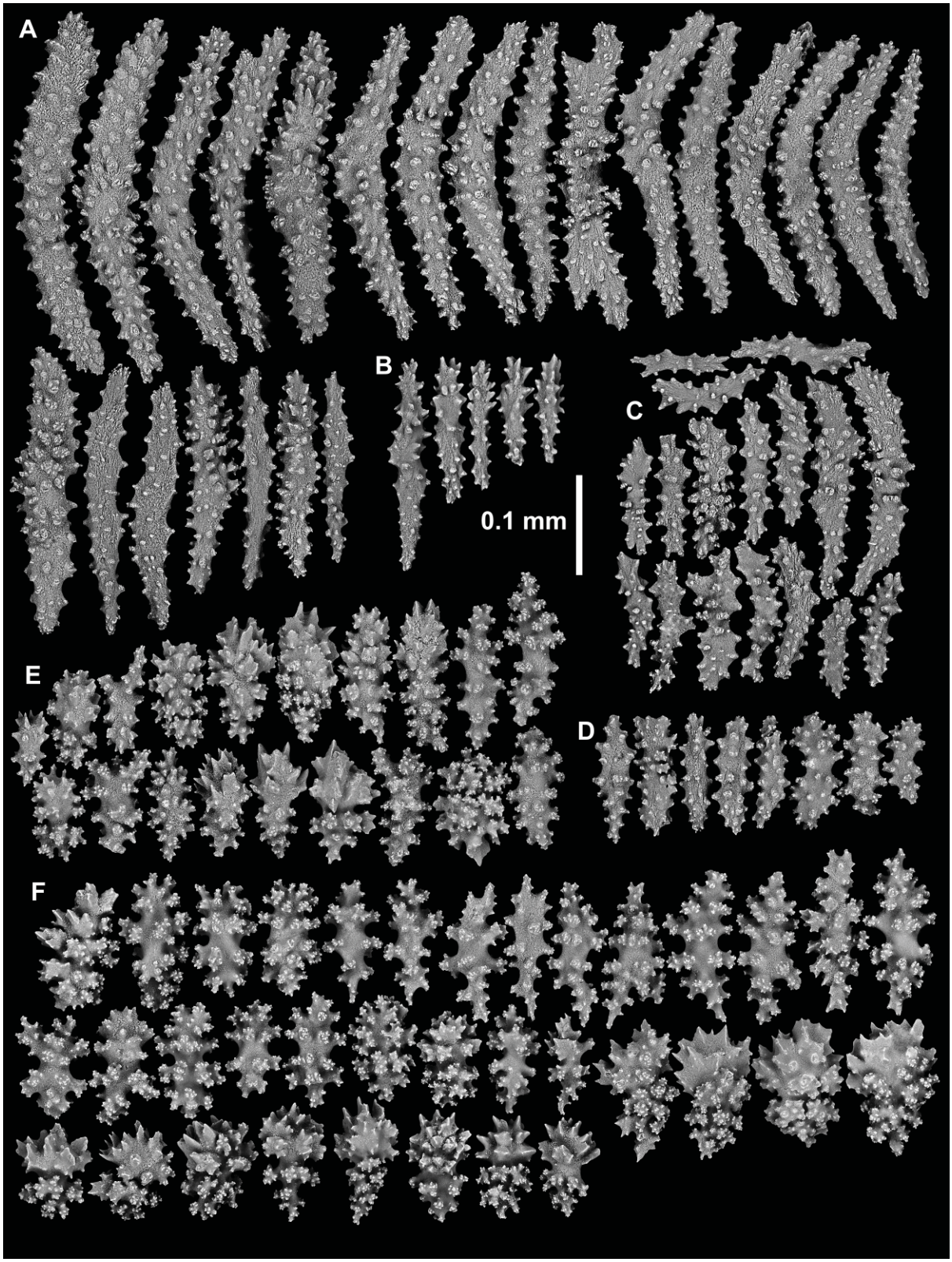

Fig. 25. *Kotatea raekura* gen. et sp. nov., holotype (NIWA 101537), SEMs of sclerites. **A**. Collaret and points. **B**. Distal points. **C**. Tentacles. **D**. Polyp neck. **E**. Polyp mound. **F**. Lobe surface.

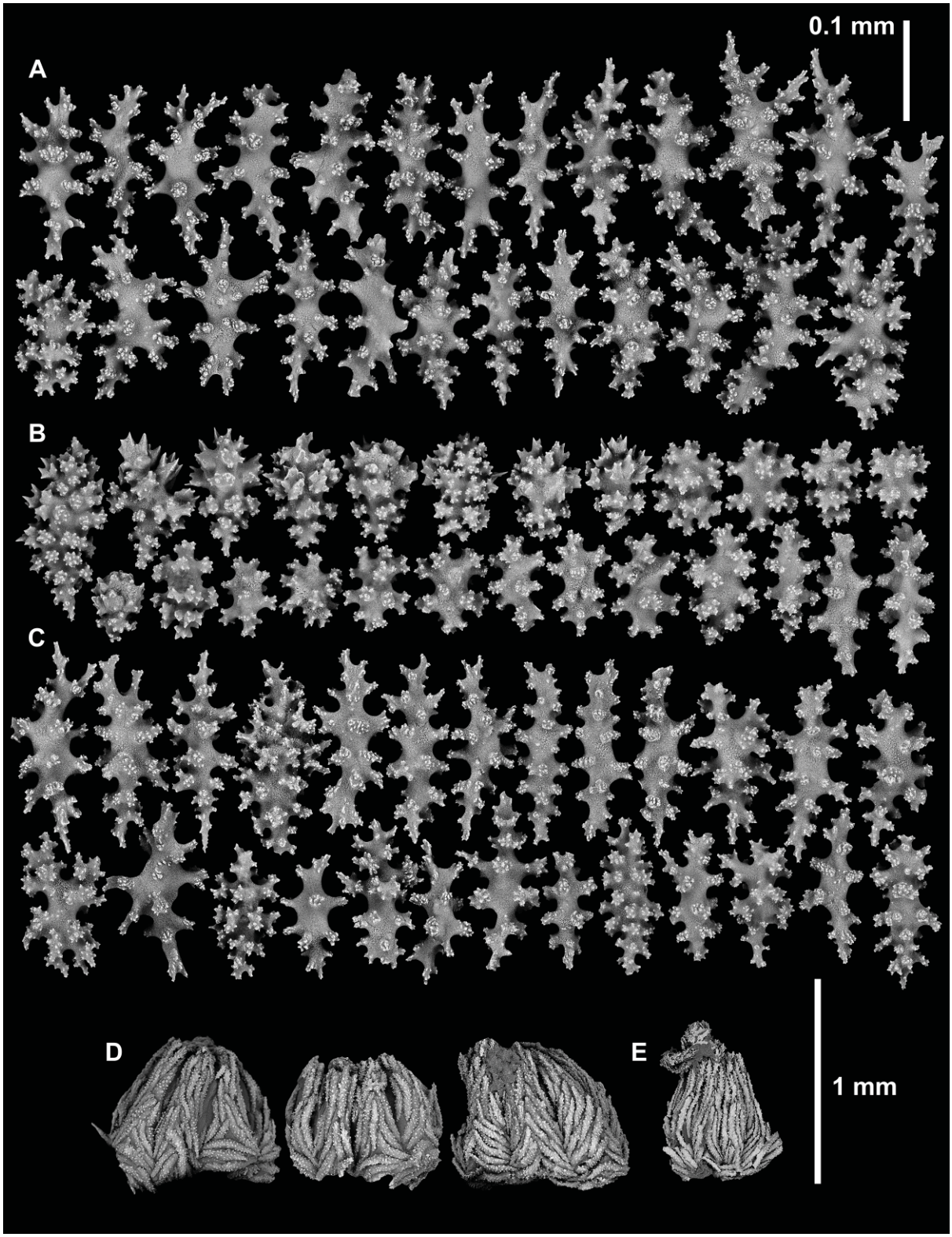

Fig. 26. A–D. *Kotatea raekura* gen. et sp. nov., holotype (NIWA 101537), SEMs of sclerites. **A**. Lobe interior. **B**. Base surface. **C**. Base interior. **D**. Polyps (in situ). — **E**. *K. teorowai* gen. et sp. nov., holotype (NIWA 27358), SEMs of sclerites, polyp (in situ).

Comparisons

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

Apart from containing sclerites that are overall far more robust (compare Figs 25–26 and 28), *Kotatea raekura* gen. et sp. nov. specimens further differ from *K. teorowai* gen. et sp. nov. 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 26A, C and 27H). The colour difference between these two species is also conspicuous (compare Fig. 24A and 24B), and *K. raekura* has so far only been collected from much shallower depths than *K. teorowai* (< 20 m vs ~70 m).

Habitat and distribution

All known specimens originate from shallow depths (≤ 20 m) at the Manawatāwhi/Three Kings Islands (Fig. 1A). MAGNT C013954 was recorded as growing on a rock wall.

Kotatea teorowai gen. et sp. nov.
urn:lsid:zoobank.org:act:0057DD86-BCD3-4CE2-8847-8F9E21D6AD0D
Figs 1B, 24B, 26E, 27

Māori name

Te Orowai.

Diagnosis

Colony white with branching lobes and white polyps. Collaret and points colourless and composed of slender, tuberculate spindles and well-developed thorny clubs. Tentacles contain irregular, warty, scale-like sclerites. Polyp neck contains warty rod-like and spiny spindle-like forms. Polyp mounds contain thorny clubs, radiates, spiny spindle-like and warty rod-like forms. Lobe surface contains radiates, spiny spindles and thorny clubs grading into leafy spheroids. Stalk surface contains spiny radiates and spindle-like forms. Interior contains irregularly branched or thorny radiates, but sclerites very sparse, especially towards base.

Etymology

The species name was composed by the Ngāti Kurī Tira Me Te Wā Taiao (Science) Collective, and is a combination of the Māori words *oro*, to resound, echo, resonate or rumble, and *wai*, water. Ngāti Kurī 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."

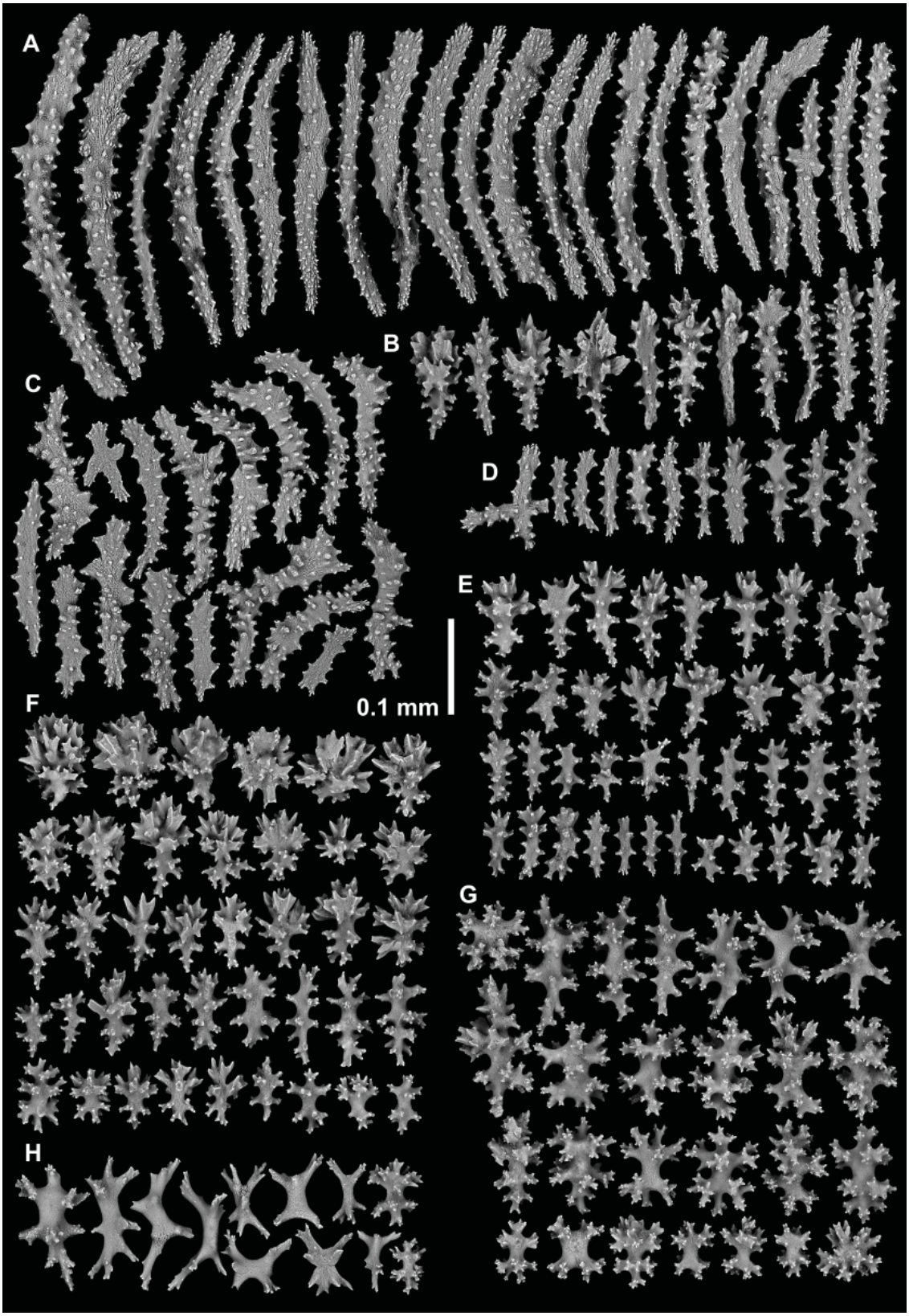

Fig. 27. *Kotatea teorowai* gen. et sp. nov., holotype (NIWA 27358), SEMs of sclerites. **A**. Collaret and points. **B**. Distal points. **C**. Tentacles. **D**. Polyp neck. **E**. Polyp mound. **F**. Lobe surface. **G**. Base surface. **H**. Lobe and base interior.

Material examined

Holotype

NEW ZEALAND • Northland, ~12 km NW of North Cape; 34.3570° S, 172.8850° E; depth 69 m; 29 Jan. 1999; NIWA exped.; stn Z9712 (KAH9901/88); NIWA 27358.

Description (holotype, NIWA 27358)

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. 24B). Several major lobes arise from a thick stalk, and divide into numerous smaller, rounded lobes of various thickness. Polyps are most densely packed at the 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. 27A–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 26E, 27A). The tentacles contain irregular, warty, scale-like forms, often slightly crescentic (~0.08–0.2 mm long) (Fig. 27C). 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. 27D). 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. 27E). 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. 27F). 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. 27G). 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. 27H).

Variability

The holotype is the only specimen of *K. teorowai* gen. et sp. nov. available at the time of writing.

Comparisons

Kotatea teorowai gen. et sp. nov. is most similar to *K. amicispongia* gen. et sp. nov., *K. aurantiaca* gen. et comb. nov. and *K. raekura* gen. et sp. nov., differences from which are discussed under each of these species.

Habitat and distribution

Kotatea teorowai gen. et sp. nov. can occur syntopically with *K. kapotaiora* gen. et sp. nov., as the holotypes for both species were collected together in the same sample.

Ushanaia gen. nov.

urn:lsid:zoobank.org:act:B76BD43C-D5C4-4B63-B304-14294AF62E37

Type species

Ushanaia fervens gen. et sp. nov., here designated.

Diagnosis

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

Etymology

The genus is named after the first author's partner.

Comparisons

As is the case for *Kotatea* gen. nov. (see comparisons for that genus), compared to *A. digitatum* and *Alcyonium* sensu stricto, *Ushanaia* gen. nov. 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 & van Ofwegen 2006). Compared to *A. haddoni* Wright & Studer, 1889 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 & van Ofwegen 1992; Casas *et al.* 1997; van Ofwegen *et al.* 2007).

Unlike *Kotatea* gen. nov., *Ushanaia* gen. nov. 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 & Försterra, 2006 (Clavulariidae Hickson, 1894) is found in a similar habitat in southern South American fjords and superficially resembles *Ushanaia* gen. nov. in its encrusting habit, but differs markedly in having no or very few polyp sclerites (van Ofwegen *et al.* 2006; McFadden & Van Ofwegen 2013b), whereas *Ushanaia* possesses strong collaret and points.

Ushanaia ferruginea gen. et sp. nov.
urn:lsid:zoobank.org:act:B82A7D8A-03FB-4B8B-93F8-B02DA463A319
Figs 1B, D, 2I, 28A, 29–30

Diagnosis

Colonies encrusting, orange with white polyps. Collaret and points may be colourless or orange and consist of slender, often flattened, warty spindles. Tentacles contain irregular, warty, scale-like sclerites. Polyp neck contains abundant tuberculate to warty rod-like sclerites. Polyp mounds contain larger warty rod-, spindle-, and club-like forms. Surface contains radiates, grading into more elongated warty clubs. Interior with warty radiates.

Etymology

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

Material examined

Holotype

NEW ZEALAND • Northland, ~8 km SE of Cape Brett; 35.2160° S, 174.4033° E; depth 99–105 m; 6 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/38; NIWA 156313.

Paratypes

NEW ZEALAND – **Northland** • 4 specimens (and several small fragments); ~16 km ESE of North Cape; 34.4650° S, 173.2115° E; depth 140–141 m; 13 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/134; NIWA 24533 • 3 specimens; ~27 km SE of North Cape; 34.5570° S, 173.28533° E; depth 139–141 m; 13 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/132; NIWA 56056 • 3 specimens; ~22 km NE of Whangaroa Bay; 34.8302° S, 173.8940° E; depth 149–151 m; 9 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/93; NIWA 55605 • 5 specimens (and several small fragments); same collection data as for holotype; NIWA 54984.

Additional material

NEW ZEALAND – **Northland** • 3 specimens; ~14 km E of North Cape; 34.4000° S, 173.1717° E; depth 249–252 m; 15 Oct. 1968; New Zealand Oceanographic Institute exped.; stn F933; NIWA 3976 • 4 specimens (and several small fragments); ~10 km E of North Cape; 34.4137° S, 172.1333° E; depth 133–210 m; 19 Apr. 1999; Coral Reef Research Foundation exped.; stn Z9742; NIWA 143081 • 2 specimens; ~8 km ESE of North Cape; 34.4398° S, 173.1297° E; depth 110–115 m; 15 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/181; NIWA 24532 • 3 specimens; ~16 km NE of Mahinepua/Stephenson Island; 34.8502° S, 173.9050° E; depth 132–134 m; 19 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/236; NIWA 57457 • 1 specimen; ~15 km NE of Mahinepua/Stephenson Island; 34.8760° S, 173.9158° E; depth 114–117 m; 19 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/235; NIWA 57364 • 2 specimens; ~15 km SE of Cape Brett; 35.2402° S, 174.4827° E; depth 135–139 m; 6 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/42; NIWA 55022 • 1 specimen; ~15 km SE of Cape Brett; 35.2417° S, 174.4833° E; depth 128–133 m; 6 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/36; NIWA 54943 • 1 specimen; ~3.5 km NE of Whananaki; 35.4858° S, 174.5012° E; depth 59–63 m; 5 Jul. 2009; Oceans Survey 2020 exped.; stn TAN0906/21; NIWA 54723. – **Bay of Plenty** • 2 specimens; ~18 km WSW of Whakaari/White Island, Rungapapa Knoll; 37.5497° S, 176.9707° E; depth 155–176 m; 5 Nov. 2000; NIWA exped.; stn KAH0011/40; NIWA 142902. – **NE coast of South Island** • 6 specimens; ~65 km E of Pegasus Bay, Pegasus Canyon; 43.4172° S, 173.5315° E; depth 115 m; 14 May 2011; Oceans Survey 2020 exped.; stn TAN1108/24; NIWA 74201.

Description (holotype, NIWA 156313)

Colony form

The holotype 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. 28A). 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. 2I). 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. 29A). Proximally, the spindles become larger and slightly more crescentic (~0.4–0.6 mm long),

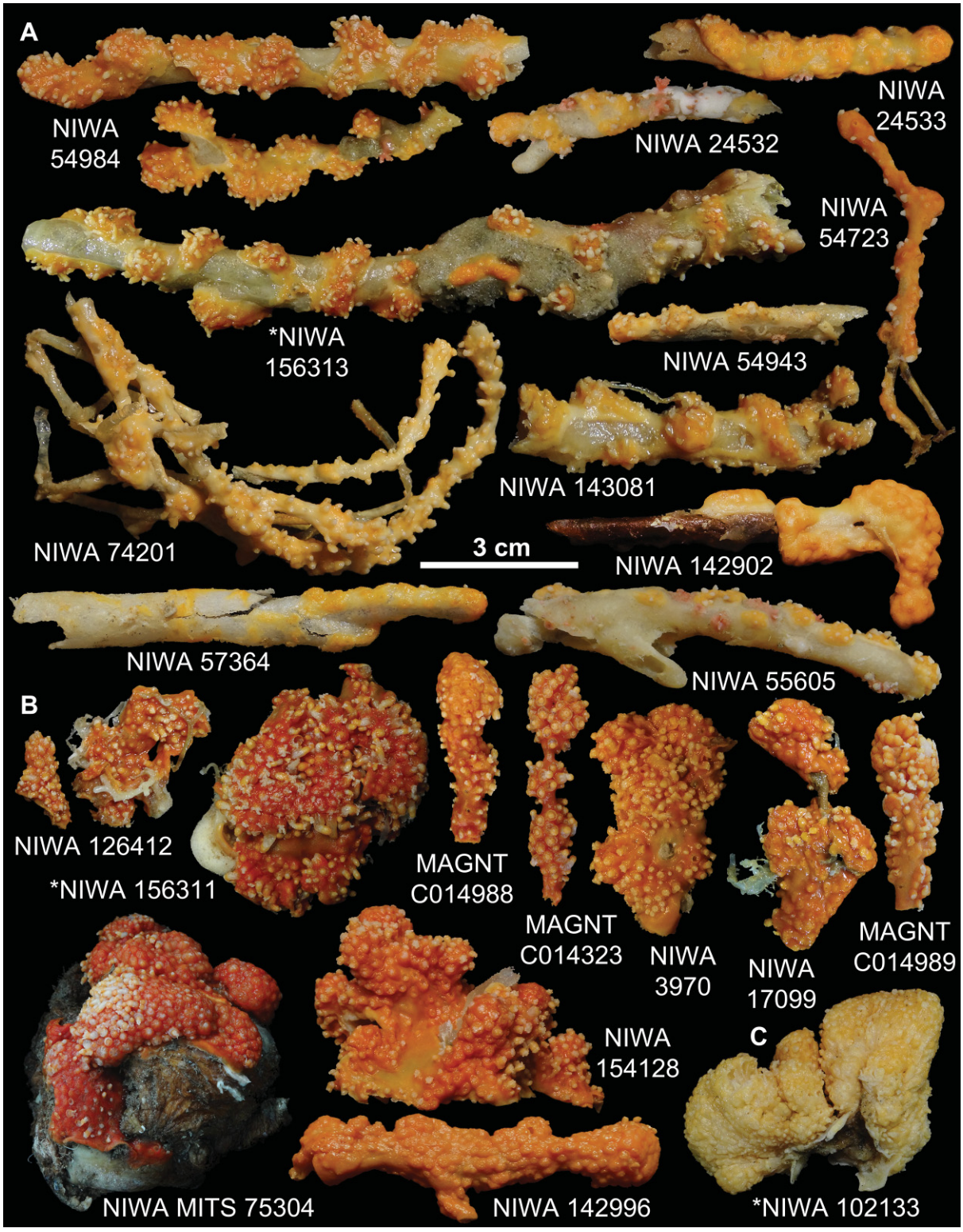

Fig. 28. Selected preserved specimens. **A**. *Ushanaia ferruginea* gen. et sp. nov. **B**. *U. fervens* gen. et sp. nov. **C**. *U. solida* gen. et sp. nov. Note that most specimen lots include additional fragments that are not depicted. * = holotype.

transitioning into a transverse orientation and merging with the collaret, which is usually around eight to twelve rows deep (Figs 2I, 29A, E). The tentacles contain irregular, warty, scale-like forms, often slightly crescentic (~0.1–0.25 mm long) (Fig. 29B). Tuberculate to warty rod-like sclerites (~0.08–0.18 mm long) are abundant in the polyp neck (Fig. 29C). Larger warty rod- and spindle-like forms

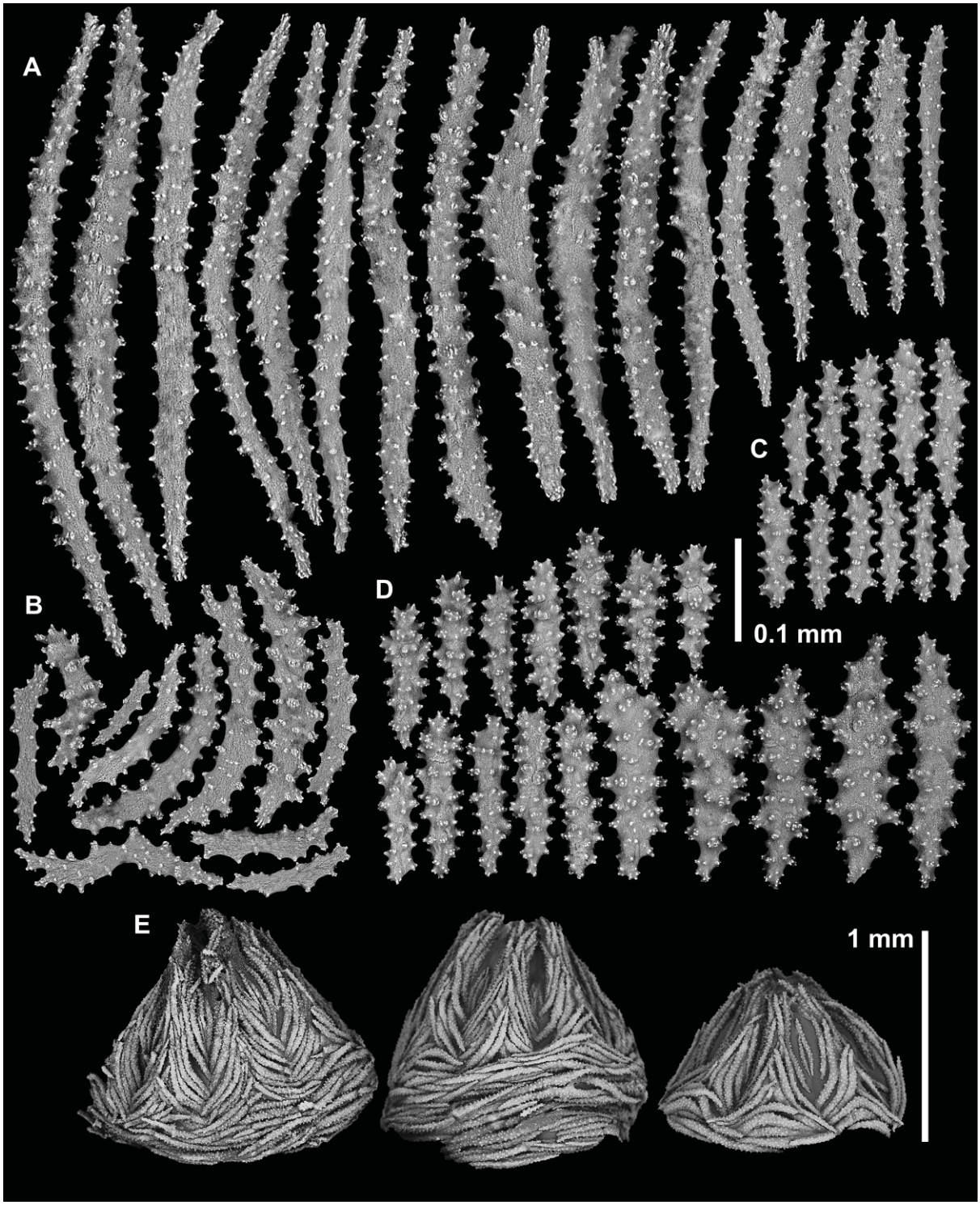

Fig. 29. *Ushanaia ferruginea* gen. et sp. nov., holotype (NIWA 156313), SEMs of sclerites. **A**. Collaret and points. **B**. Tentacles. **C**. Polyp neck. **D**. Polyp mound. **E**. Polyps (in situ).

(~0.12–0.25 mm long), some of which can be club-like, form a densely packed surface layer in the polyp mounds (Fig. 29D). 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. 30A). Sclerites of

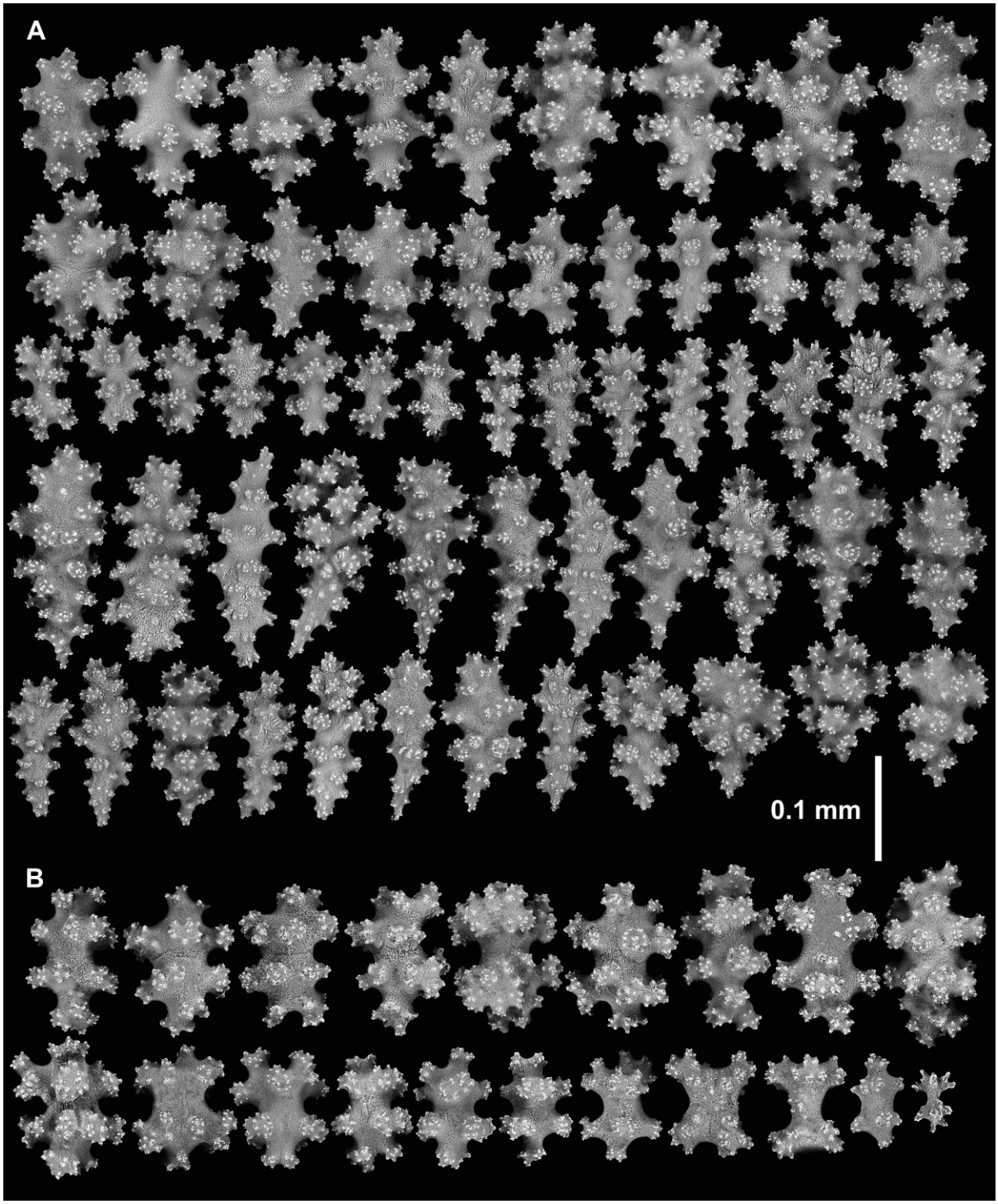

Fig. 30. *Ushanaia ferruginea* gen. et sp. nov., holotype (NIWA 156313), SEMs of sclerites. **A**. Surface (of thick, fleshy areas of colony). **B**. Interior (of thick, fleshy areas of colony).

the interior (of fleshy areas) are more uniformly comprised of warty radiates (~0.08–0.18 mm long) (Fig. 30B).

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 sponges. 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. 28A). All fifteen lots 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 29–30).

Comparisons

Ushanaia ferruginea gen. et sp. nov. can easily be distinguished from *U. fervens* gen. et sp. nov. by the far more brightly and conspicuously coloured collaret and point sclerites in the latter (compare Figs 2I–J, 28A and 2M, 28B, 31). Additionally, specimens of *U. ferruginea* lack distal clubs in their points, which are present in *U. fervens* (compare Figs 29A 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 29D and 33A). Beyond this, the surface and interior sclerites of specimens of *U. ferruginea* are overall noticeably more robust than those of *U. fervens* (compare Figs 30 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).

Specimens of *Ushanaia ferruginea* gen. et sp. nov. do not form fleshy lobes to the same extent as *U. solida* gen. et sp. nov., and also clearly differ 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 29A and 35A).

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 *Ushanaia ferruginea* gen. et sp. nov. may be widely distributed at depths of ~60–250 m around New Zealand (Fig. 1B–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* gen. et sp. nov., as several specimens of each were collected alongside the other.

Ushanaia fervens gen. et sp. nov.
urn:lsid:zoobank.org:act:D8AA094B-80EA-4BAE-A4A7-C93F44708100
Figs 1D–E, 2J, M, 11D, 28B, 31–33, 34A

Alcyonium aurantiacum – Benham 1928 in part: 71–75, figs 6–11. — McFadden *et al.* 2006b: 517, 521, 523, figs 1, 3.

? *Alcyonium aurantiacum* – Grange *et al.* 1981: 211–212, 214, 216, 224, figs 2, 4. — Westerskov & Probert 1981 in part: 111, pl. 28. — Goldberg *et al.* 1990: 99, fig. 4. — Grange *et al.* 2010 in part: 148.

Diagnosis

Colonies encrusting, red to orange with white polyps. Collaret and points bright orange and composed of slender, often flattened, warty to spiny spindles and thorny clubs. Tentacles contain irregular, warty, scale-like sclerites. Polyp neck contains warty rod- and spindle-like sclerites. Polyp mounds contain similar warty rod-like and spindle-like sclerites, which grade into clubs and irregularly branched forms. Surface contains warty radiates and spindle-like forms. The interior contains similar sclerites.

Etymology

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

Material examined

Holotype

NEW ZEALAND • Fiordland, Te Puaitaha/Breaksea Sound, Sunday Cove; 45.5952° S, 166.7422° E; depth 4 m; 16 Jan. 2018; R. Kinsey leg.; stn Z17956; NIWA 156311.

Paratypes

NEW ZEALAND • 3 specimens; Fiordland, Milford Sound/Piopiotahi; 44.6183° S, 167.8588° E; depth 25 m; 30 Mar. 1981; New Zealand Oceanographic Institute exped.; stn M773; NIWA 3970 • 4 specimens; same collection data as for holotype; NIWA 126412.

Additional material

NEW ZEALAND – **Wellington** • 1 specimen; Sorrento Bay, on wharf piles; 41.2547° S, 174.9012° E; 20 Jul. 2020; NIWA exped.; stn WLG31205-SF; NIWA MITS 75304. – **Fiordland** • 1 specimen; Milford Sound/Piopiotahi; 44.5833° S, 167.7833° E (estimated); depth 20 m; 2 Sep. 1996; stn Z10091; NIWA 154128 • 4 specimens (and several small fragments); Milford Sound/Piopiotahi; 44.6033° S, 167.8288° E; depth 27 m; 29 Mar. 1981; New Zealand Oceanographic Institute exped.; stn M763; NIWA 142996 • 3 specimens; Milford Sound/Piopiotahi, Harrison Cove, Underwater Observatory; depth 13 m; 16 Jun. 2003; K. Gowlett-Holmes leg.; MAGNT C014322 • 3 specimens (and several small fragments); Taitetimu/Caswell Sound; 45.0033° S, 167.1567° E; depth 30 m; 18 Apr. 1991; Chris N. Battershill and National Cancer Institute leg.; stn Q66C/Z7552; NIWA 17099 • 1 specimen; Doubtful Sound, Deep Cove; depth 12–14 m; 19 Jun. 2003; K. Gowlett-Holmes leg.; MAGNT C014323 • 1 specimen; Te Puaitaha/Breaksea Sound, Vancouver Arm; 45.5250° S, 166.9250° E; 21 Nov. 1999; M.S. Roy leg.; MAGNT C014989 • 1 specimen; Wet Jacket Arm/Moana Uta; 45.6667° S, 166.7333° E; 21 Nov. 1999; M.S. Roy leg.; MAGNT C014988.

Description (holotype, NIWA 156311)

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 (Figs 28B, 31). 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 2J, M, 29, 31B–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. 32A–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 2J, M, 32A, 34A). The tentacles contain irregular, warty, scale-like forms, often slightly crescentic (~0.1–0.3 mm long) (Fig. 32C). The polyp neck contains warty rod- and spindle-like sclerites (~0.1–0.22 mm long) (Fig. 32D). 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).

Variability

Preserved specimens of *Ushanaia fervens* gen. et sp. nov. 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. 28B). All specimens are otherwise similar in growth form. All eleven lots 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 *Ushanaia ferruginea* gen. et sp. nov. are discussed under that species.

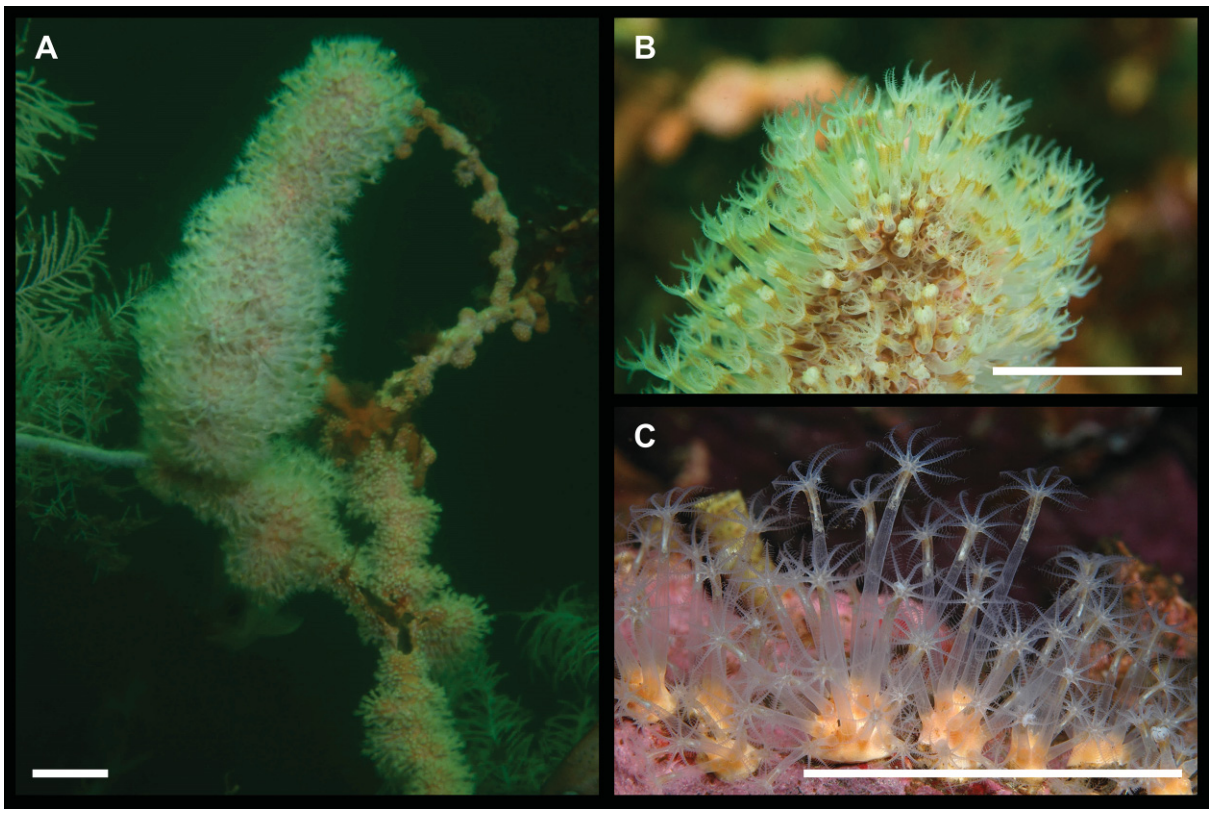

Fig. 31. In situ photographs of *Ushanaia fervens* gen. et sp. nov. **A–B**. Encrusting on black coral (uncollected specimen), Fiordland, photos by Richard Kinsey. **C**. Small colonies (uncollected specimens), Fiordland, photo by Ian Skipworth (ianskipworth.com). Scale bars = ~2 cm.

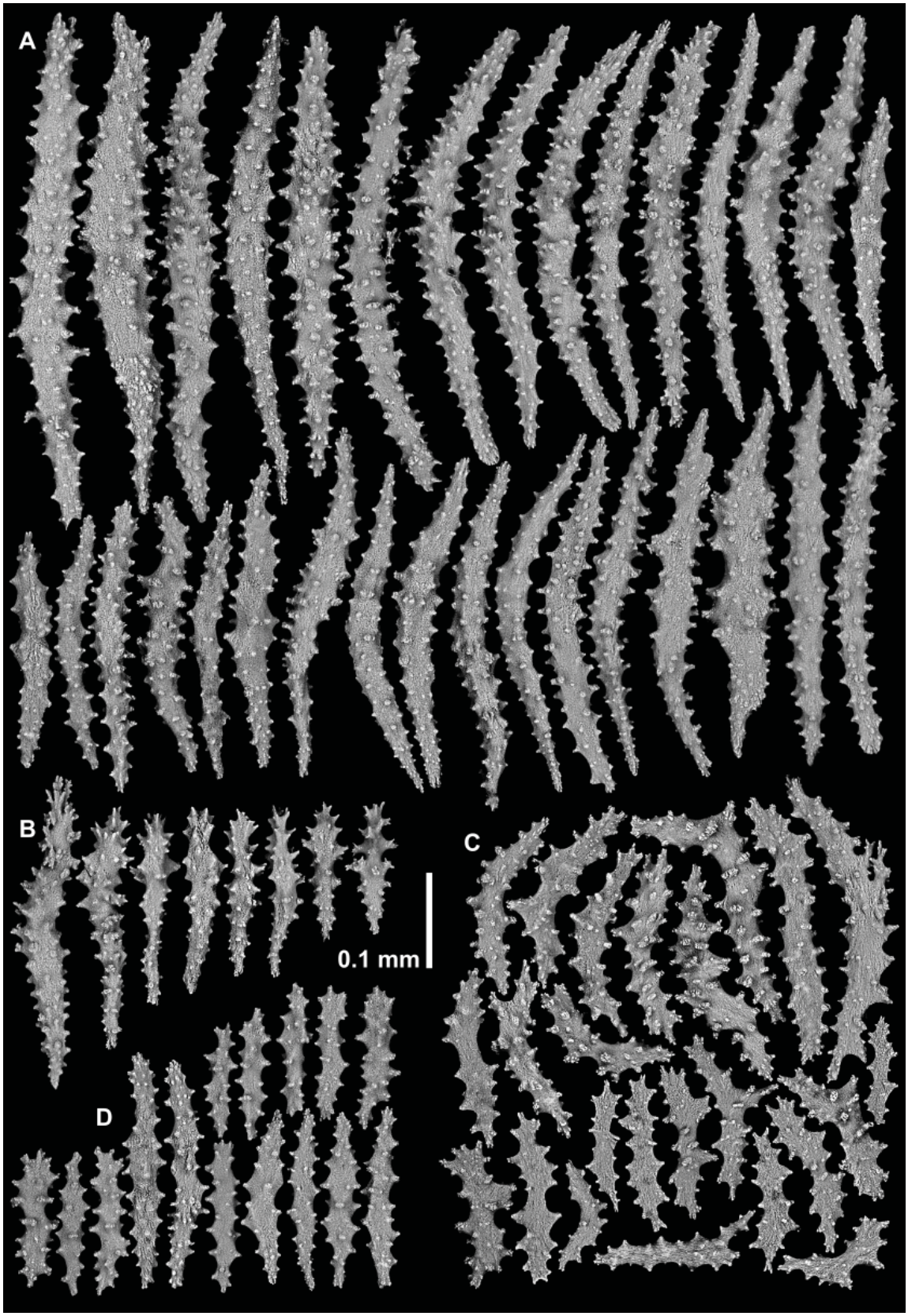

Fig. 32. *Ushanaia fervens* gen. et sp. nov., holotype (NIWA 156311), SEMs of sclerites. **A**. Collaret and points. **B**. Distal points. **C**. Tentacles. **D**. Polyp neck.

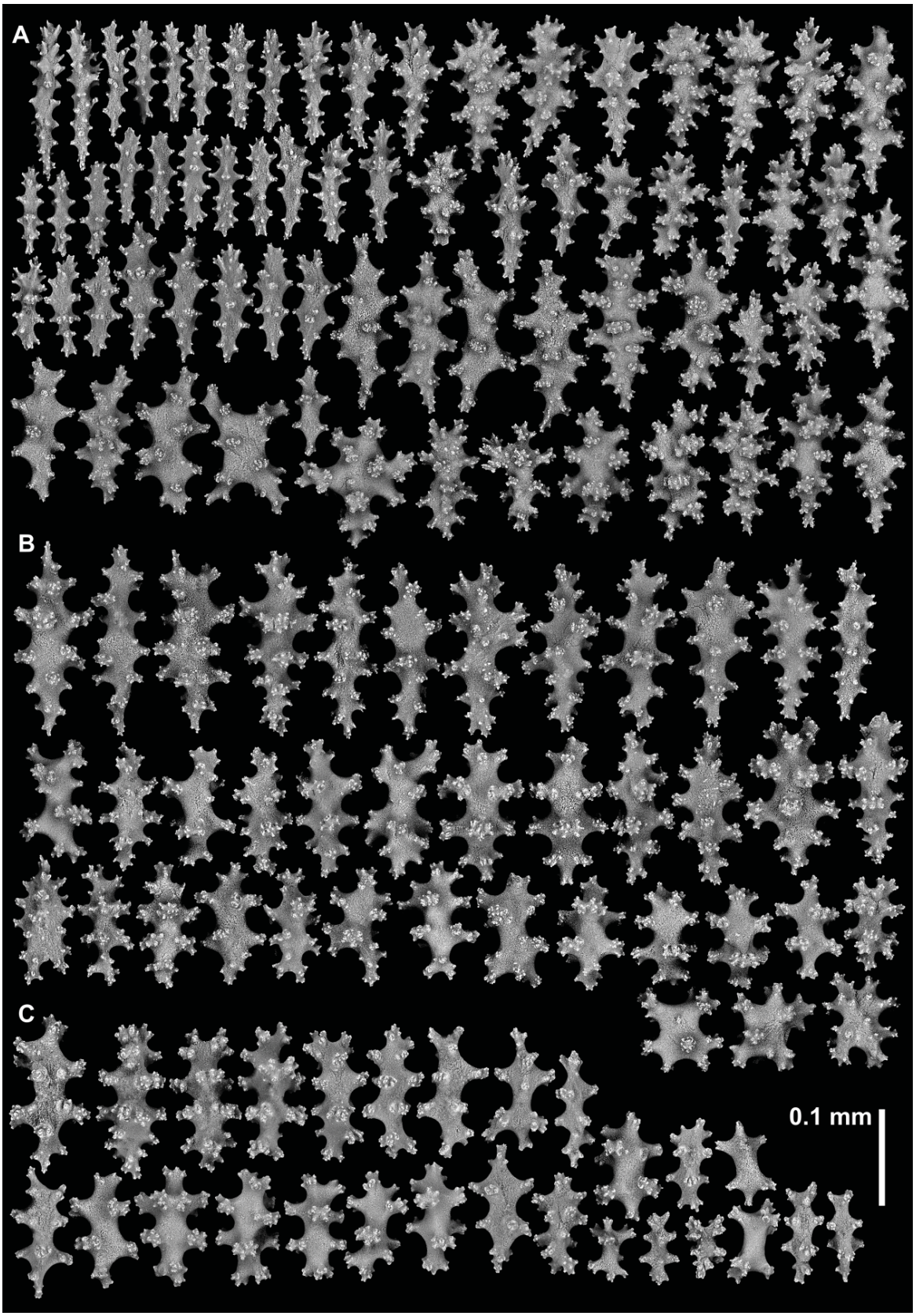

Fig. 33. *Ushanaia fervens* gen. et sp. nov., holotype (NIWA 156311), SEMs of sclerites. **A**. Polyp mound. **B**. Surface (of thick, fleshy areas of colony). **C**. Interior (of thick, fleshy areas of colony).

Much like *Ushanaia ferruginea* gen. et sp. nov., *U. fervens* gen. et sp. nov. clearly differs from *U. solida* gen. et sp. nov. 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). *Ushanaia fervens* also lacks the distinctive, broad, flattened collaret and point sclerites found in *U. solida* (compare Figs 32A and 35A). Conversely, *U. solida* lacks the conspicuous, bright collaret and points colouration which is characteristic of *U. fervens* specimens.

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. 1D–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.

Remarks

Having been collected in Fiordland, the encrusting specimen described by Benham (1928) was most likely a member of *Ushanaia fervens* gen. et sp. nov. 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* gen. nov. also inhabit this area. The *A. aurantiacum* illustrated by Westerskov & Probert (1981) likely also represents *U. fervens*.

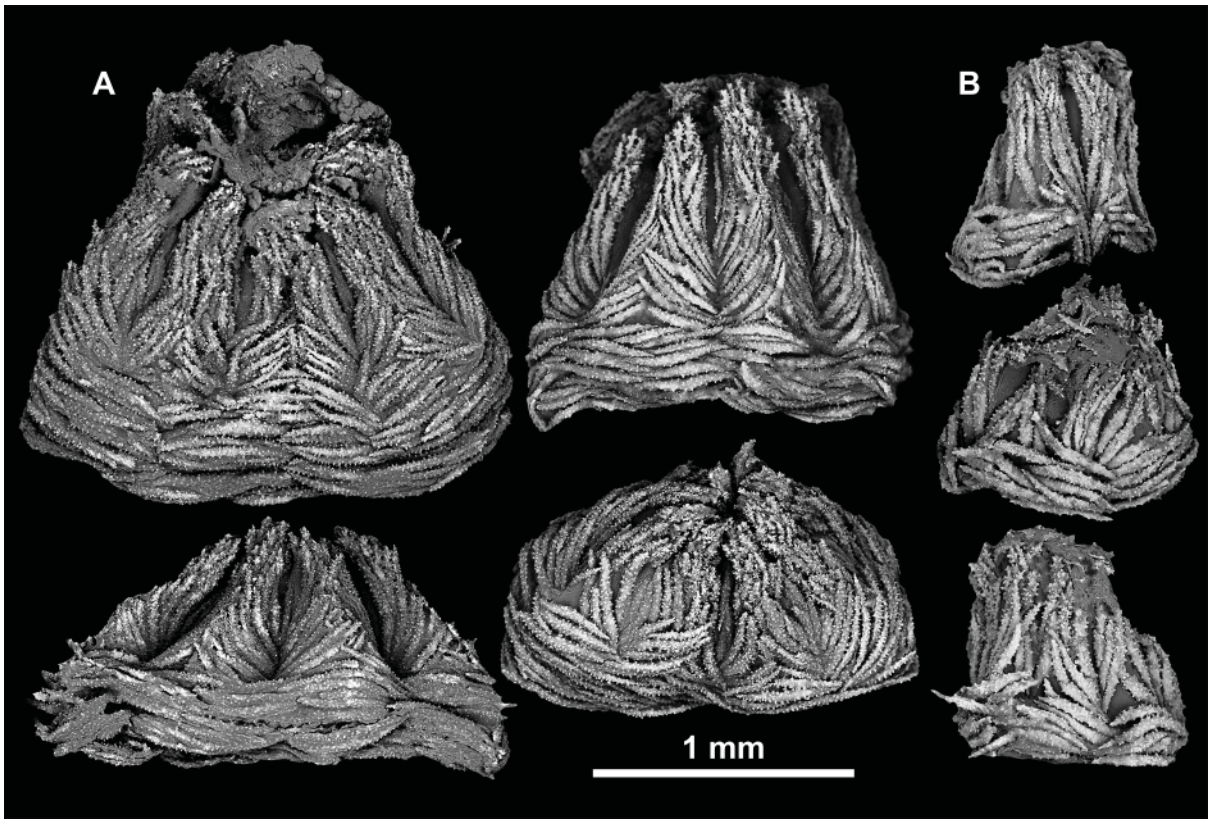

Fig. 34. SEMs of sclerites from polyps (in situ). **A**. *Ushanaia fervens* gen. et sp. nov., holotype (NIWA 156311). **B**. *U. solida* gen. et sp. nov., holotype (NIWA 102133).

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 *Ushanaia 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 *Ushanaia fervens* gen. et sp. nov. or a separate species.

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

Ushanaia solida gen. et sp. nov.
urn:lsid:zoobank.org:act:BC72CC9C-E954-4166-9DEB-6E17DF6A6E35
Figs 1C, 2K, 28C, 34B, 35–36

Diagnosis

Colony of loosely connected lobes, beige to pale orange with white polyps. Collaret and points hued orange and composed of tuberculate to warty spindles, often broad and flattened and irregular or branched, as well as thorny clubs and spindles. Tentacles contain irregular, warty, scale-like sclerites. Polyp neck contains warty to spiny rod-like sclerites. Polyp mounds contain similar warty to spiny rod- and spindle-like forms, grading into clubs. Surface and interior contains warty to spiny rod- and spindle-like forms, a few radiates and poorly developed clubs.

Etymology

The species name is the Latin word '*solida*', meaning 'solid' or 'three-dimensional' and referring to the substantially thicker, fleshier colony form of *Ushanaia solida* gen. et sp. nov. when compared to *U. ferruginea* gen. et sp. nov. or *U. fervens* gen. et sp. nov.

Material examined

Holotype

NEW ZEALAND • Auckland, Manukau Harbour; 37.0319° S, 174.6507° E (estimated); 11 Apr. 2003; stn Z18522; NIWA 102133.

Description (holotype, NIWA 102133)

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. 28C). 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. 2K).

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. 35A, 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, 35A). The tentacles contain irregular, warty, scale-like forms, which are often curved and branched (~0.06–0.24 mm long) (Fig. 35B). The polyp neck contains warty to spiny rod-like forms (~0.1–0.18 mm long) (Fig. 35C), 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. 36A). The sclerites of the surface of the lobes, both distal and proximal regions (relative to

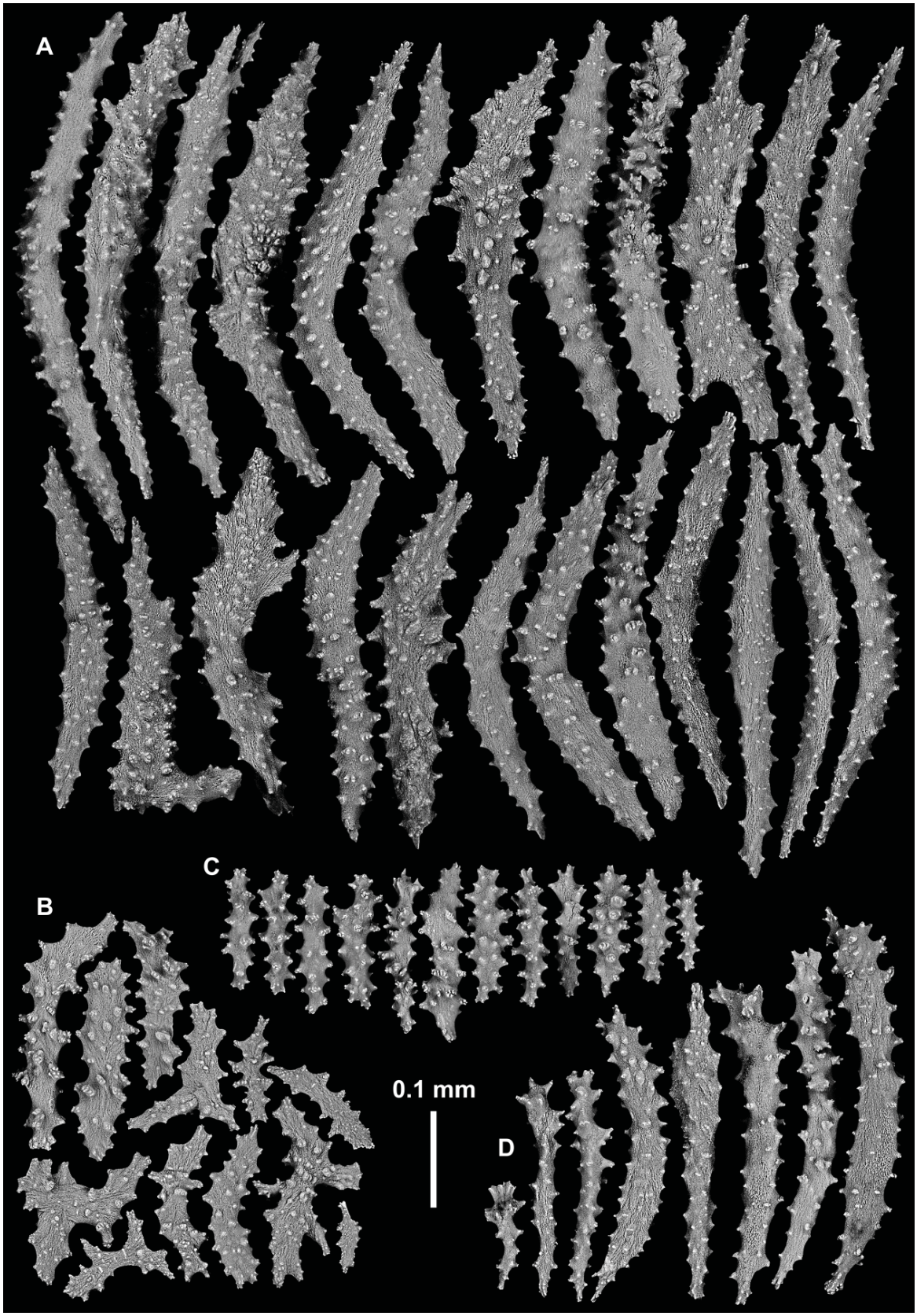

Fig. 35. *Ushanaia solida* gen. et sp. nov., holotype (NIWA 102133), SEMs of sclerites. **A**. Collaret and points. **B**. Tentacles. **C**. Polyp neck. **D**. Distal points.

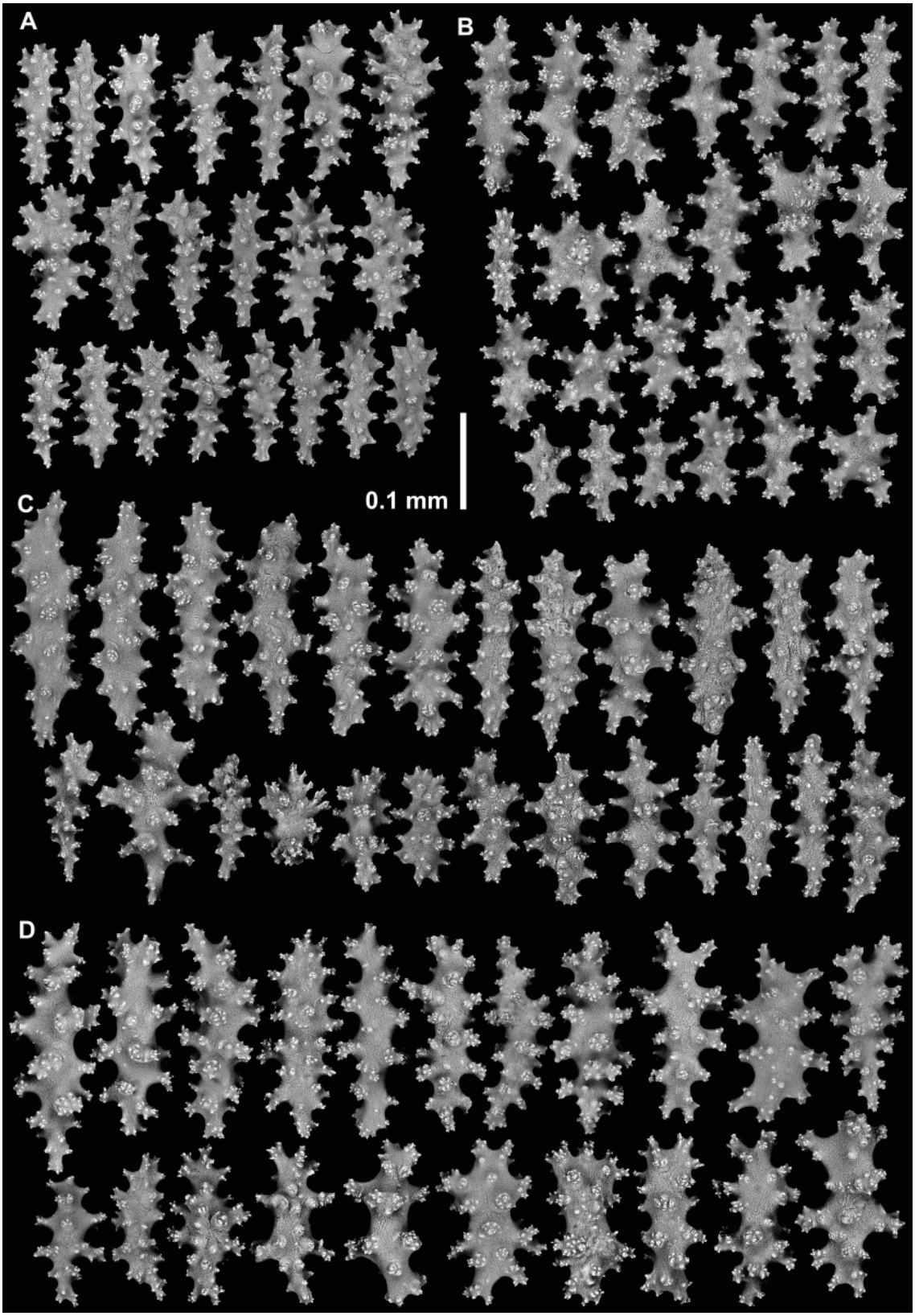

Fig. 36. *Ushanaia solida* gen. et sp. nov., holotype (NIWA 102133), SEMs of sclerites. **A**. Polyp mound. **B**. Lobe surface, proximal region (close proximity to substrate). **C**. Lobe surface, distal region. **D**. Interior.

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. 36B); distal lobe surface, ~0.12–0.26 mm long (Fig. 36C); interior, ~0.14–0.18 mm long (Fig. 36D).

Variability

The holotype is the only known specimen.

Comparisons

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

Habitat and distribution

The holotype was collected in Manukau Harbour (Fig. 1C). 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.

Morphological key to species of Kotatea gen. nov. and Ushanaia gen. nov.

1. Colonies erect and lobate in growth form with clubs abundant in polyp mounds, surface sclerites differ from interior sclerites markedly ..... 2 (***Kotatea*** gen. nov.)
– Colonies encrusting and/or clubs absent from polyp mounds; surface and interior sclerites do not differ in form ..... 9 (***Ushanaia*** gen. nov.)

2. 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
– Colonies not distinctly spotted in appearance; highly sculptured spheroids absent 4

3. Large polyps measure ~1.3 mm when expanded; interior sclerites not distinctly double-headed ..... ***K. kurakootingotingo*** gen. et sp. nov.
– Large polyps measure only ~0.75 mm when expanded; interior sclerites often distinctly double-headed ..... ***K. niwa*** gen. et sp. nov.

4. Collaret and point sclerites coloured orange (when preserved) ..... ***K. raekura*** gen. et sp. nov.
– Collaret and point sclerites colourless (when preserved) 5

5. Colonies white (when preserved) 6
– Colonies distinctly coloured yellowish or orange (when preserved), ranging from pale to dark shades 7

6. Colonies laterally compressed; interior sclerites abundant and composed predominately of radiates with few, thin, thorny branching processes ..... ***K. kapotaiora*** gen. et sp. nov.
– Colonies not laterally compressed; interior sclerites very scarce ..... ***K. teorowai*** gen. et sp. nov.

7. Sclerites in lobe interior very large (up to ~0.35 mm long), antler-like, and highly branched ..... ***K. lobata*** gen. et sp. nov.
– Sclerites in lobe interior are not as in 7A 8

8. 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. et sp. nov.
– 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. et comb. nov.

9. 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. et sp. nov.
– 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. Colonies never distinctly red (when preserved); well-developed point clubs absent ..... ***U. ferruginea*** gen. et sp. nov.
– Colonies may be distinctly red (when preserved); well-developed point clubs present ..... ***U. fervens*** gen. et sp. nov.

Phylogenetic analysis

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.

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 specimens of *Kotatea* gen. nov. and *Ushanaia* gen. nov. (data not shown). The only topological differences observed among these phylogenies were the placement of *Kotatea* and *Ushanaia* as sister clades rather than as a polytomy with the *A. haddoni* + *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* + *Alcyonium* spp. polytomy (*Eleutherobia* was placed as sister to these other taxa in the *28S* BI phylogeny while *A. dolium* McFadden & van Ofwegen, 2017 + *A. variabile* Thomson, 1921 took this position in the *mtMutS* 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. 37).

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 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 & van Ofwegen, 2013, plus representatives of *Anthothela*; a well-supported clade of *Kotatea* gen. nov.; and a strongly supported clade of *Ushanaia* gen. nov. Within *Kotatea*, *K. kurakootingotingo* gen. et sp. nov. and *K. niwa* gen. et sp. nov. also form monophyletic clades in a strongly supported sister clade to the rest of the genus. *Kotatea teorowai* gen. et sp. nov. and *K. kapotaiora* gen. et sp. nov. 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. Within both genera, genetic variation did not resolve species relationships.

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* gen. nov. and *Ushanaia* gen. nov. 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

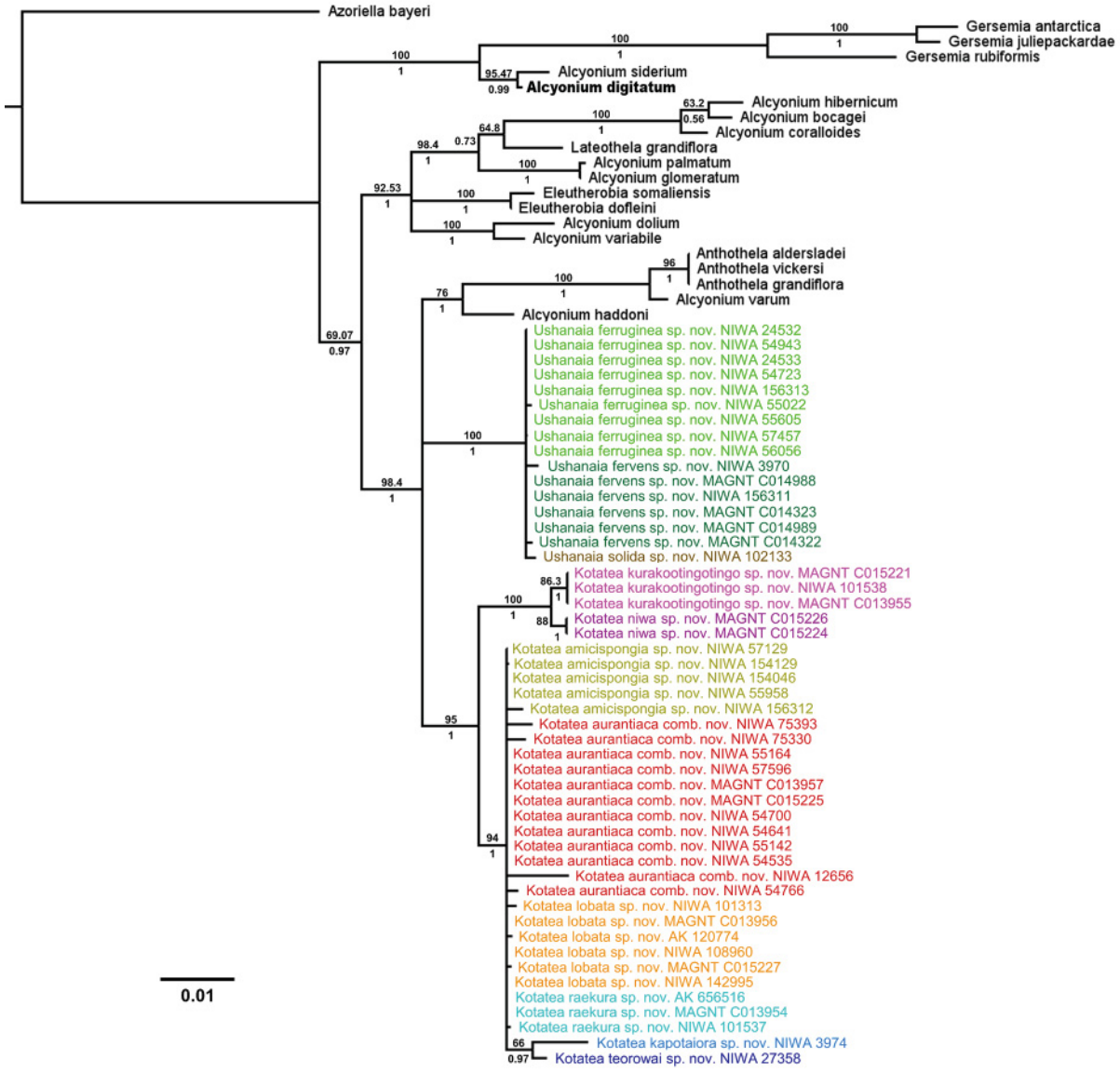

Fig. 37. Maximum likelihood phylogeny (identical in topology to Bayesian inference phylogeny) of *Kotatea* gen. nov., *Ushanaia* gen. nov., and associated taxa based on combined, partitioned analysis of *mtMutS* and *28S*. New species are identified by individual colours. The type species for *Alcyonium* Linnaeus, 1758 – *A. digitatum* Linnaeus, 1758 – appears in bold. ML bootstrap support values are given above each branch and BI posterior probabilities below.

Table 3. Mean interspecific genetic distances for species of *Kotatea* gen. nov. and *Ushanaia* gen. nov. 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* Linnaeus, 1758 identified by McFadden *et al.* (2014): 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.* (2014) also included *Igr1* and *COI*.

	K. aurantiaca gen. et comb. nov.	*K. kapotaiora* gen. et sp. nov.	*K. kurakootingotingo* gen. et sp. nov.	*K. lobata* gen. et sp. nov.	*K. niwa* gen. et sp. nov.	*K. raekura* gen. et sp. nov.	*K. teorowai* gen. et sp. nov.	*U. ferruginea* gen. et sp. nov.	*U. fervens* gen. et sp. nov.	*U. solida* gen. et sp. nov.
K. amicispongia gen. et sp. nov.	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 gen. et comb. nov.		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 gen. et sp. nov.			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 gen. et sp. nov.				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 gen. et sp. nov.					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 gen. et sp. nov.						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 gen. et sp. nov.							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 gen. et sp. nov.								0.036 **0.048** **0.028**	0.035 **0.046** **0.028**	0.035 **0.048** **0.027**
U. ferruginea gen. et sp. nov.									0.001 0.001 0.001	0.003 **0.006** 0.001
U. fervens gen. et sp. nov.										0.002 0.004 0.001

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*.

Based on thresholds for accurate species discrimination identified for *Alcyonium* species by McFadden *et al.* (2014) (i.e., 0.5% for *mtMutS* and 0.7% for *28S*) pairwise interspecific mean genetic 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* gen. et sp. nov. and *K. teorowai* gen. et sp. nov. for *mtMutS*, this was not the case between *K. kurakootingotingo* gen. et sp. nov. and *K. niwa* gen. et sp. nov., and there was little or no evidence to suggest separate species identities between *K. amicispongia* gen. et sp. nov., *K. aurantiaca* gen. et comb. nov., *K. lobata* gen. et sp. nov. and *K. raekura* gen. et sp. nov. (Table 3). Intraspecific genetic variation rarely exceeded interspecific genetic variation, with intraspecific mean distances falling below 0.002 in almost all instances.

Discussion

Taxonomic problems within *Alcyonium Linnaeus, 1758*

Alcyonium has had its morphological diagnosis discussed and incrementally amended many times. Essentially, diagnoses 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 1981; Groot & Weinberg 1982; Williams 1986a, 1986b, 1988, 1992; Verseveldt & 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 & 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 & van Ofwegen 2013a, 2017) – although *A. digitatum* seems to conform poorly to the latter (see Hickson 1895; Verseveldt 1973). 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 Verrill, 1879) than to *A. digitatum*, which itself is more closely associated with *Gersemia* (Nephtheidae Gray, 1862) than with some of its congeners (McFadden *et al.* 2006b; McFadden & van Ofwegen 2013a, 2017; Moore *et al.* 2017; and Fig. 37 herein).

Alcyonium (sensu lato) clearly constitutes a paraphyletic group that fails to contain all descendants of a recent common ancestor (e.g., Alderslade 2000; McFadden *et al.* 2006b; McFadden & van Ofwegen 2013a). It has been recommended that *Gersemia rubiformis* Ehrenberg, 1834 and *Eleutherobia somaliensis* Verseveldt & Bayer, 1988 would be better accommodated in *Alcyonium* (Williams & Lundsten 2009; McFadden & van Ofwegen 2013a), but *Anthothela* and *Lateothela* would then also need to be included to produce a monophyletic *Alcyonium* concept (Fig. 37 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 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* – morphologically, biogeographically and genetically – may be the best way of alleviating the frustrating state of the group's systematics. Accordingly, we have not placed New Zealand's *Alcyonium*-like soft corals within *Alcyonium*.

Separation of *Kotatea* gen. nov. and *Ushanaia* gen. nov. from *Alcyonium* sensu stricto

Kotatea gen. nov. and *Ushanaia* gen. nov. 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* gen. et sp. nov. (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 *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. 37). The nearly identical tree topologies that have been resolved repeatedly for this group using a range of genes (McFadden 2006b; Moore *et al.* 2017; Fig. 37 herein), strongly support excluding *Kotatea* and *Ushanaia* from *Alcyonium.*

Morphologically, the separation of *Kotatea* gen. nov. and *Ushanaia* gen. nov. 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. 37; McFadden *et al.* 2011; McFadden & 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 & van Ofwegen 2013a, 2017). Interestingly, the genus *Gersemia*, to which *A. digitatum* is closely allied, also lacks polyp collarets (Williams & 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 nonetheless provide a useful character for future revisions. 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* gen. nov. 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.

Separation of specimens into *Kotatea* gen. nov. and *Ushanaia* gen. nov.

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 clades of *Kotatea* gen. nov. and *Ushanaia* gen. nov. here resolved (Fig. 37) are also clearly discriminated by sclerite and colony growth form characteristics, corresponding to erect species (*Kotatea*) or encrusting species (*Ushanaia*). Furthermore, *Kotatea* and *Ushanaia* here formed a polytomy with the *Anthothela*/South American clade of *Alcyonium* (Fig. 37), 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 in the Anthothelidae (Moore *et al.* 2017), Isididae (Moore *et al.* 2016), Primnoidae (Baco & Cairns 2012), Nephtheidae and Xeniidae Ehrenberg, 1828 (McFadden *et al.* 2006a; McFadden & van Ofwegen 2012), and thus offer further support for their separation at genus-level.

Species delimitation

Genetic variation was not sufficient to resolve the morphological differences observed within *Kotatea* gen. nov. or *Ushanaia* gen. nov. 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.* 2003; Wirshing *et al.* 2005; Cairns & Bayer 2005; McFadden *et al.* 2006a, 2009; Cairns & Baco 2007). 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.* 2014), although admixture has recently been indicated between two such species from the Mediterranean Sea (Erickson *et al.* 2020).

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 species concepts is 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. 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 for *Alcyonium* by van Ofwegen *et al.* (2007), for *Primnoisis* Studer & Wright, 1887 by Moore *et al.* (2016), for *Thouarella* Gray, 1870 by Núñez-Flores *et al.* (2020) and for *Chrysogorgia* Duchassaing & Michelotti, 1864 by Xu *et al.* (2020) 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* gen. nov. and most of *Kotatea* gen. nov. 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* gen. et spp. nov. (the only two spotted species in the genus) and *K. kapotaiora*/*K. teorowai* gen. et spp. nov. (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* gen. nov. species (Fig. 37), potentially implicating colony colouration as an important identifier of intrageneric relationships in the genus. The separation of *K. kapotaiora*/*K. teorowai* gen. et spp. nov. was also supported by their interspecific mean p-distance for *mtMutS* (Table 3), which passed species discrimination thresholds recommended by McFadden *et al.* (2014). 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* May, 1898 (McFadden *et al.* 2009) and *Narella* Gray, 1870 (Cairns & Baco 2007).

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 & 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* gen. nov. or one of three in *Ushanaia* gen. nov.

Biogeographical considerations

The lack of any literature records of species from outside New Zealand which could be assigned to *Kotatea* gen. nov. or *Ushanaia* gen. nov. 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 species of *Alcyonium* 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. 37). 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 & 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* gen. nov., *Ushanaia* gen. nov. and other Southern Hemisphere taxa.

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.* 2015; Herrera & Shank 2016; Quattrini *et al.* 2019) coupled with species delimitation analyses – which have been successfully used in octocorals previously (e.g., Bayes Factor Delimitation, Herrera & Shank 2016; BPP and Structurama, 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* gen. nov. and *Ushanaia* gen. nov. 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 the use of 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* gen. nov. 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* gen. nov. 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.

Finally, further research into these new taxa may inform mechanisms of diversification in alcyoniids. Soft corals similar to *Kotatea* gen. nov. and *Ushanaia* gen. nov. 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* occurring syntopically around southern South American fjords and coasts (McFadden & van Ofwegen 2013b). This, in turn, raises questions about the drivers of speciation in soft corals. Incongruence between mitochondrial and nuclear gene trees implicates hybridisation and reticulate evolution as diversification mechanisms in some genera (McFadden *et al.* 2010), including *Alcyonium* (McFadden & 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* or *Ushanaia* may warrant future research.

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* gen. et sp. nov., *K. kurakootingotingo* gen. et sp. nov., *K. raekura* gen. et sp. nov. and *K. teorowai* gen. et sp. nov. 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 2007). Therefore, Māori names created through respectful collaboration should be represented among taxonomic binomials to a far greater extent than they currently are (Galbreath 2020). These taxa add to a growing body of new species names recently created through collaboration with Ngāti Kurī (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 & Wright 2020).

Conclusions

This taxonomic review and revision confirms 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* gen. nov. and *Ushanaia* gen. nov. 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 the biology of *Kotatea* and *Ushanaia*.

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Appendix

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)**.