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Stoloniferous octocorals (Anthozoa, Octocorallia) from South Africa, with descriptions of a new family of Alcyonacea, a new genus of Clavulariidae, and a new species of *Cornularia* (Cornulariidae)

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Abstract. We describe a new family and genus of stoloniferous octocorals (Alcyonacea) and a new genus of Clavulariidae from material collected in South Africa in 2008. Arulidae, fam. nov., is characterised by polyps whose tentacles are fused proximally to form an expanded oral membrane, and sclerites of a type ('table-radiates') that has not been recorded previously in Octocorallia. One species, *Arula petunia*, gen. nov., sp. nov., is described, and the possible existence of congeners elsewhere in the Indo-Pacific is discussed. *Inconstantia*, gen. nov., is erected for three new species of Clavulariidae that have no or only weak anthocodial armature. *I. pannucea*, sp. nov., and *I. procera*, sp. nov., both have tall, cylindrical calyces, while *I. exigua*, sp. nov., has low, retractile calyces. Despite these morphological differences that would normally place them in different subfamilies, all three species are nearly identical genetically. We also describe *Cornularia pabloi*, sp. nov., a new species of Cornulariidae from South Africa, and discuss an unidentified species of *Carijoa* with an unusual colony growth form. A molecular phylogenetic analysis of 130 octocoral taxa, including 15 genera of stoloniferans, supports the distinctions of these new taxa from existing families and genera, and highlights the polyphyletic distribution of the taxa attributed to family Clavulariidae.

Additional keywords: molecular phylogenetics, COI, mtMutS, 28S rDNA, endemism, new species.

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Introduction

The Agulhas Bioregion of southern South Africa spans the ~1700 km of coastline from the Cape Peninsula east to southern Natal province (Griffiths *et al*. 2010). Located at the confluence of the warm-temperate Agulhas and cold, upwelled Benguela currents, this biogeographic region supports high marine biodiversity, and, most notably, high levels of endemism in many marine taxa (Gibbons *et al*. 1999; Awad *et al*. 2002; Griffiths *et al*. 2010). Octocorals are among the taxa that are especially diverse and rich in endemics in this region (Williams 1992*a*, 2000*a*; Gibbons *et al*. 1999; Awad *et al*. 2002). Over 200 species of octocorals have been reported from South Africa, greatly exceeding estimates for other comparably sampled marine ecosystems including the tropical Caribbean (Williams 1992*a*); estimates of endemicity range from 30% (Awad *et al*. 2002) to over 50% (Gibbons *et al*. 1999) of species, and 14% of genera (Williams 2000*a*).

Williams (1990, 1992*a*, 1992*b*, 1992*c*) catalogued the species diversity of all octocorals reported to occur in South Africa, including sea pens, soft corals, gorgonians, and stoloniferans. Subsequently, several additional species and genera of soft corals and one new gorgonian species have been described from the Agulhas Bioregion (Bayer 1995; Benayahu and Schleyer 1995; van Ofwegen and Schleyer 1997; Williams and Lindo 1997; Williams 2000*a*, 2000*b*; Williams and Starmer 2000; Williams and Little 2001). Compared with the soft corals, however, the stoloniferan octocorals of this region have received relatively little attention (Ocaña and van Ofwegen 2003).

Stolonifera is a loosely defined, phylogenetically heterogeneous assemblage of octocoral families that are characterised by a relatively simple colony growth form in which the polyps are united basally by a stolon or membrane rather than being embedded within a common coenenchymal mass (Fabricius and Alderslade 2001; Daly *et al*. 2007).

Six families of Alcyonacea are typically considered to belong to this group. The largest and best-known stoloniferan family is Clavulariidae Hickson, 1894, which comprises ~25 genera and 60 or more species. The other five families (Acrossotidae Bourne, 1914; Coelogorgiidae Bourne, 1900; Cornulariidae Dana, 1846; Pseudogorgiidae Utinomi & Harada, 1973; and Tubiporidae Ehrenberg, 1828) are all either monospecific or monogeneric but with no more than a few described species.

Although the genus *Tubipora* (Tubiporidae) has been reported to occur on the subtropical coral reefs of northern Natal (Williams 1992*a*, 1992*b*; Benayahu and Schleyer 1993), to date only the family Clavulariidae is known from the cold-temperate Agulhas Bioregion. Seven genera of Clavulariidae have been recorded, including one species each of *Bathytelesto* Bayer, 1981, *Denhartogia* Ocaña & Ofwegen, 2003 (recorded by Williams as *Sarcodictyon* Forbes, 1847 but subsequently reassigned), *Scleranthelia* Studer, 1878, and *Scyphopodium* Bayer, 1981. These four genera are well defined morphologically and are not diverse; only two species each of *Scleranthelia* and *Bathytelesto* are known worldwide, and the other two genera are both monotypic. The other three clavulariid genera reported from South Africa, *Carijoa* F. Müller, 1867, *Clavularia* Blainville, 1830, and *Telestula* Madsen, 1944, are poorly defined and greatly in need of revision, making identification of the South African material to species difficult or impossible.

Here we describe a new stoloniferous family and genus of Alcyonacea and a new genus of Clavulariidae from recent collections in southern South African waters. Molecular phylogenetic analyses support the separation of these morphologically distinct groups from other families and genera of stoloniferous octocorals. In addition, we report the first confirmed record of the genus *Cornularia* and family Cornulariidae outside of the Mediterranean and North Atlantic Oceans, and discuss the identity of a species of *Carijoa* with an atypical colony growth form.

Methods

Collection and deposition of specimens

Specimens were collected in March 2008 during the 'Assembling the Cnidarian Tree of Life' expedition to South Africa. All specimens were collected at depths of 10–25 m using SCUBA. Material was preserved in 70% EtOH, with small pieces of tissue stored in 95% EtOH for DNA studies. Vouchers and type material have been deposited at the Netherlands Centre for Biodiversity Naturalis, formerly Rijksmuseum van Natuurlijke Historie, Leiden (RMNH) and the USA National Museum of Natural History, Washington, DC (USNM). Material for comparison was obtained from the Museum and Art Gallery of the Northern Territory, Darwin, Australia (NTM).

Morphological analysis

Sclerites were obtained by dissolving tissues from the upper and lower regions of a colony in 10% sodium hypochlorite (household bleach). Sclerites were rinsed well with deionised water, dried, and mounted on stubs for SEM. They were imaged using a JEOL JSM-6480LV scanning electron microscope operated at 10 kV. Details of the preserved specimens were photographed using a motorised Zeiss Discovery V12 stereomicroscope with Axiocam MRc5 camera system and AxioVision 4.8 multifocus imaging software.

Molecular phylogenetic analysis

Extraction of DNA from ethanol-preserved tissue samples, PCR amplification, and sequencing of the *mtMutS* (*msh1*) and COI genes followed the protocols published in McFadden *et al*. (2011). In addition, we sequenced an ~810 nt fragment of the 28S nuclear ribosomal gene using primers 28S-Far (5′-CACGAGACCGATAGCGAACAAGTA-3′) and either 28S-Rar (5′-TCATTTCGACCCTAAGACCTC-3′) or 28S-Rab (5′-TCGCTACGAGCTTCCACCAGTGTTT-3′), and the same PCR protocol used for COI. Sequence data were proofread using LaserGene software, and the L-INS-i method in MAFFT (Katoh *et al*. 2005) was used to align sequences to a reference dataset of 130 octocoral taxa including representatives of 15 genera of stoloniferans (Table 1). Pairwise measures of genetic distance (uncorrected P) among sequences were computed using MEGA ver. 5 (Tamura *et al*. 2011). Modeltest 3.0 (Posada and Crandall 1998) was used to select appropriate models of evolution for maximum-likelihood analyses that were run using GARLI 2.0 (Zwickl 2006). The 28S rDNA and mitochondrial gene (*mtMutS* + COI) datasets were analysed separately, and in a combined analysis with different models of evolution applied to each data partition (mt genes: TVM+I+G; 28S: GTR+I+G). Bayesian analyses were run using MrBayes ver. 3.2.1 (Ronquist *et al*. 2012) with the same data partitions; because MrBayes does not support the TVM model, a GTR+I+G model was applied separately to each partition. Analyses were run for 4 million generations (until standard deviation of split partitions <0.01) with a burn-in of 25% and default Metropolis coupling parameters. Members of three hexacorallian orders for which COI and 28S rDNA sequences were both available were included as outgroup taxa in all analyses: *Leiopathes* sp. (Antipatharia), *Nematostella vectensis* (Actiniaria), *Metridium senile* (Actiniaria) and *Montastraea franksi* (Scleractinia) (Table 1).

Results

mtMutS (~735 nt), COI (~878 nt) and 28S rDNA (~810 nt) sequences were obtained for all South African stoloniferan specimens, and for those reference taxa for which sequence data were not already available in GenBank (Table 1). Separate maximum-likelihood analyses of the mitochondrial and 28S rDNA datasets resulted in trees that were highly congruent (with the exception of some relationships within Pennatulacea), supporting a combined analysis. Maximum likelihood and Bayesian analyses of the combined, partitioned data yielded identical tree topologies, and differed only in levels of support for some of the deeper nodes within the tree (Fig. 1).

Genera of stoloniferous octocorals were distributed throughout the tree in nine well supported and well separated clades (Fig. 1). The polyphyletic nature of family Clavulariidae, already recognised from previous phylogenetic analyses (McFadden *et al*. 2006*a*), is clearly evident here, with genera of Clavulariidae falling into seven of those clades. South African species belonged to four clades:

(1) Genus *Cornularia* (family Cornulariidae) is the sister group to all other Octocorallia, having diverged before the split between the two major clades of Octocorallia recognised in previous studies (Calcaxonia–Pennatulacea and Holaxonia–Alcyoniina) (McFadden *et al*. 2006*a*). A South African species of *Cornularia* is the sister taxon to *C. cornucopiae* (Pallas, 1766) from the North Atlantic, although the two species are quite divergent genetically (Fig. 1). All of the

Table 1. Voucher specimens and GenBank accession numbers for octocoral taxa used in phylogenetic analysis

Stoloniferan taxa are highlighted in boldface. CRCNI = Palau International Coral Reef Center; CSM = laboratory of C. S. McFadden, to be deposited in curated collections following completion of ongoing studies; MNHN = Museum National d'Histoire Naturelle, Paris; NIWA = National Institute of Water and Atmospheric Research (New Zealand); NTM = Museum and Art Gallery of the Northern Territory; OCDN = Coral Reef Research Foundation (Palau); RMNH = Netherlands Centre for Biodiversity; SBMNH = Santa Barbara Museum of Natural History; UF = Florida Natural History Museum; USNM = National Museum of Natural History (Smithsonian Inst.); ZMTAU = Zoological Museum, Tel Aviv University; ZSM = Zoologische Staatssammlung München; n.a., not available

Family	Genus/species	Specimen voucher	GenBank accession no		
			COI	*mtMutS*	28S rDNA
Acanthoaxiidae	*Acanthoaxis wirtzi*	RMNH Coel. 39502	JX203816	JX203764	JX203635
Acanthogorgiidae	*Acanthogorgia breviflora*	ZMTAU CO34194	GQ342378	GQ342464	JX203636
Acrossotidae	***Acrossota amboinensis***	RMNH Coel. 40798	GQ342379	DQ985956	JX203637
Alcyoniidae	*Acrophytum claviger*	RMNH Coel. 40222	JX203823	JX203770	JX203655
Alcyoniidae	*Alcyonium coralloides*	RMNH Coel. 39678	GQ342380	GQ342465	JX203640
Alcyoniidae	*Alcyonium digitatum*	SBMNH 360700	GQ342381	GQ342466	JX203641
Alcyoniidae	*Alcyonium haddoni*	ZSM 20061191	GU355958	GU355974	JX203642
Alcyoniidae	*Alcyonium palmatum*	RMNH Coel. 39685	GQ342382	GQ342467	JX203643
Alcyoniidae	*Alcyonium roseum*	ZSM 20061195	GQ342383	GQ342468	JX203644
Alcyoniidae	*Alcyonium variabile*	RMNH Coel. 40800	GQ342385	GQ342470	JX203645
Alcyoniidae	*Anthomastus ritteri*	RMNH Coel. 40802	JX203824	DQ302816	JX203761
Alcyoniidae	*Cladiella sphaerophora*	ZMTAU CO34132	GQ342386	GQ342471	JX203653
Alcyoniidae	*Discophyton rudyi*	CSM-DIRU15	GQ342387	DQ302808	JX203659
Alcyoniidae	*Eleutherobia aurea*	RMNH Coel. 40799	JX203817	JX203766	GQ377454
Alcyoniidae	*Eleutherobia flammicerebra*	MNHN TER708.12	JX203818	JX203765	JX203638
Alcyoniidae	*Eleutherobia grayi*	NTM C14902	JX203871	DQ302809	n.a.
Alcyoniidae	*Eleutherobia rotifera*	UF3890	GQ342388	GQ342472	JX203639
Alcyoniidae	*Klyxum utinomii*	ZMTAU CO34127	GQ342392	GQ342476	JX203654
Alcyoniidae	*Lampophyton planiceps*	RMNH Coel. 40201	GQ342393	GQ342477	JX203656
Alcyoniidae	*Lobophytum pauciflorum*	UF2856	GQ342394	DQ280575	JX203649
Alcyoniidae	*Malacacanthus capensis*	RMNH Coel. 40801	GQ342395	DQ302811	JX203660
Alcyoniidae	*Nephthyigorgia* sp.	RMNH Coel. 40819	JX203864	JX203804	JX203732
Alcyoniidae	*Paraminabea aldersladei*	NTM C14895	JX203819	JX203767	JX203763
Alcyoniidae	*Protodendron bruuni*	CSM-SAF361	GQ342434	GQ342507	JX203658
Alcyoniidae	*Rhytisma fulvum*	ZMTAU CO34124	GQ342396	GQ342478	JX203728
Alcyoniidae	*Sarcophyton ehrenbergi*	NTM C14455	JX203821	DQ280516	JX203650
Alcyoniidae	*Sarcophyton trocheliophorum*	NTM C14854	JX203822	JX203769	JX203651
Alcyoniidae	*Sinularia querciformis*	ZMTAU CO34096	GQ342399	FJ621469	JX203652
Alcyoniidae	*Thrombophyton coronatum*	SBMNH 145123	GQ342400	DQ302814	JX203661
Anthothelidae	*Alertigorgia* sp.	NTM C14528	JX203825	JX203771	JX203662
Anthothelidae	*Diodogorgia nodulifera*	RMNH Coel. 40803	JX203826	JX203772	JX203663
Anthothelidae	*Erythropodium caribaeorum*	RMNH Coel. 40829	GQ342401	GQ342480	JX203664
Anthothelidae	*Homophyton verrucosum*	RMNH Coel. 40805	GQ342403	GQ342482	JX203666
Anthothelidae	*Iciligorgia* sp.	RMNH Coel. 40040	GQ342402	GQ342481	JX203665
Anthothelidae	*Ideogorgia capensis*	RMNH Coel. 40804	GQ342428	GQ342502	JX203667
Anthothelidae	*Solenocaulon* sp.	RMNH Coel. 40033	GQ342404	GQ342483	JX203668
Arulidae, fam. nov.	***Arula petunia*, gen. nov., sp. nov.**	RMNH Coel. 40188	JX203827	JX203773	JX203670
Arulidae, fam. nov.	***Arula petunia*, gen. nov., sp. nov.**	USNM 1178392	JX203828	JX203774	JX203671
Briareidae	*Briareum asbestinum*	RMNH Coel. 40825	GQ342405	GQ342484	JX203669
Chrysogorgiidae	*Radicipes gracilis*		HM590861	DQ297424	n.a.
Chrysogorgiidae	*Stephanogorgia faulkneri*	NTM C14927	GQ342406	GQ342485	JX203718
Chrysogorgiidae	*Trichogorgia capensis*	RMNH Coel. 40817	JX203863	JX203798	JX203719
Clavulariidae	***Azoriella bayeri***	RMNH Coel. 40806	GQ342407	GQ342486	JX203672
Clavulariidae	***Carijoa riisei***	RMNH Coel. 40807	JX203829	JX203775	JX203673
Clavulariidae	***Carijoa* sp. (South Africa)**	RMNH Coel. 40189	JX203830	n.a.	JX203675
Clavulariidae	***Carijoa* sp. (South Africa)**	CSM-SAF336	JX203831	JX203777	n.a.
Clavulariidae	***Carijoa* sp. (West Papua)**	RMNH Coel. 40031	JX203832	JX203776	JX203674
Clavulariidae	***Carijoa* sp. (Palau)**	RMNH Coel. 40808	JX203833	n.a.	JX203676
Clavulariidae	***Cervera atlantica***	RMNH Coel. 40838	JN620805	JN620804	JX203677
Clavulariidae	***Clavularia inflata***	NTM C11542	n.a.	DQ302799	JX203679
Clavulariidae	***Clavularia* sp.**	RMNH Coel. 40809	JX203834	JX203778	JX203678
Clavulariidae	***Cryptophyton goddardi***	RMNH Coel. 40810	GQ342409	JX203779	JX203680

(*continued next page*)

Table 1. (*continued*)

Family	Genus/species	Specimen voucher	GenBank accession no		
			COI	*mtMutS*	28S rDNA
Clavulariidae	***Inconstantia exigua*, gen. nov., sp. nov.**	RMNH Coel. 40191	JX203870	JX203790	JX203690
Clavulariidae	***Inconstantia pannucea*, gen. nov., sp. nov.**	RMNH Coel. 40192	JX203840	JX203789	JX203689
Clavulariidae	***Inconstantia pannucea*, gen. nov., sp. nov.**	RMNH Coel. 40193	JX203841	JX203788	JX203688
Clavulariidae	***Inconstantia procera*, gen. nov., sp. nov.**	RMNH Coel. 40044	JX203837	JX203781	JX203682
Clavulariidae	***Inconstantia procera*, gen. nov., sp. nov.**	RMNH Coel. 40194	JX203842	JX203784	n.a.
Clavulariidae	***Inconstantia procera*, gen. nov., sp. nov.**	RMNH Coel. 40195	JX203835	JX203783	JX203684
Clavulariidae	***Inconstantia procera*, gen. nov., sp. nov.**	RMNH Coel. 40196	JX203843	JX203785	JX203685
Clavulariidae	***Inconstantia procera*, gen. nov., sp. nov.**	USNM 1178386	JX203838	JX203782	JX203683
Clavulariidae	***Inconstantia procera*, gen. nov., sp. nov.**	USNM 1178387	JX203836	JX203780	JX203681
Clavulariidae	***Inconstantia procera*, gen. nov., sp. nov.**	USNM 1178388	JX203839	JX203786	JX203686
Clavulariidae	***Inconstantia procera*, gen. nov., sp. nov.**	USNM 1178389	JX203844	JX203787	JX203687
Clavulariidae	***Incrustatus comauensis***	RMNH Coel. 33872	GQ342391	GQ342475	JX203691
Clavulariidae	***Knopia octocontacanalis***	NTM C15392	GQ342410	GQ342488	JX203692
Clavulariidae	***Paratelesto* sp.**	RMNH Coel. 40019	GQ342411	GQ342489	JX203693
Clavulariidae	***Phenganax parrini***	CSM-NB2	GQ342412	GQ342490	JX203694
Clavulariidae	***Rhodelinda* sp.**	NTM C10034	n.a.	DQ302799	n.a.
Clavulariidae	***Rhodelinda* sp.**	NTM C12792	JX203845	n.a.	JX203695
Clavulariidae	***Telesto* sp.**	NTM C12710	n.a.	DQ302802	JX203696
Clavulariidae	***Telestula* sp.**	NTM C14984	JX203846	DQ302803	JX203697
Clavulariidae	***Telestula* cf. *spiculicola***	OAS-28	FJ264917	GU563311	n.a.
Clavulariidae	***Trachythela rudis***	REH221–1	FJ264909	GU563310	n.a.
Coelogorgiidae	***Coelogorgia palmosa***	NTM C14914	GQ342413	DQ302805	JX203698
Coralliidae	*Corallium kishinouyei*		n.a.	n.a.	GQ293268
Coralliidae	*Corallium konojoi*		AB595190	AB595190	n.a.
Cornulariidae	***Cornularia cornucopiae***	CSM-PLG	JX203848	n.a.	JX203760
Cornulariidae	***Cornularia pabloi*, sp. nov.**	RMNH Coel. 40197	n.a.	JX203791	n.a.
Cornulariidae	***Cornularia pabloi*, sp. nov.**	USNM 1178390	JX203847	JX203792	JX203699
Echinoptilidae	*Actinoptilum molle*	RMNH Coel. 40822	GQ342414	GQ342491	JX203738
Ellisellidae	*Dichotella gemmacea*	NTM C14929	GQ342415	GQ342492	JX203701
Ellisellidae	*Ellisella* sp.	RMNH Coel. 40811	JX203849	n.a.	JX203700
Ellisellidae	*Ellisella* sp.	RMNH Coel. 40812	JX203850	JX203793	JX203702
Ellisellidae	*Verrucella* sp.	RMNH Coel. 40030	JX203851	n.a.	JX203704
Ellisellidae	*Viminella* sp.	RMNH Coel. 40032	JX203852	JX203794	JX203703
Ellisellidae	*Viminella* sp.	RMNH Coel. 40813	GQ342416	GQ342493	JX203705
Gorgoniidae	*Eugorgia multifida*	UABCS-013	GQ342417	GQ342494	JX203706
Gorgoniidae	*Eunicella tricoronata*	RMNH Coel. 40814	JX203853	JX203795	JX203707
Gorgoniidae	*Gorgonia flabellum*	RMNH Coel. 40827	GQ342418	GQ342495	JX203708
Gorgoniidae	*Guaiagorgia anas*	NTM C14545	GQ342419	GQ302851	n.a.
Gorgoniidae	*Leptogorgia rigida*	UABCS-008	GQ342420	GQ342496	JX203709
Gorgoniidae	*Pacifigorgia media*	UABCS-015	GQ342421	GQ342497	JX203710
Gorgoniidae	*Pinnigorgia flava*	RMNH Coel. 40815	GQ342422	GQ342498	JX203711
Gorgoniidae	*Pseudopterogorgia bipinnata*	RMNH Coel. 40828	GQ342423	GQ342499	JX203712
Gorgoniidae	*Pseudopterogorgia elisabethae*	RMNH Coel. 40831	JX203854	JX203796	JX203713
Gorgoniidae	*Pterogorgia anceps*	RMNH Coel. 40837	GQ342424	GQ342500	JX203714
Gorgoniidae	*Rumphella* sp.	RMNH Coel. 40816	JX203855	JX203797	JX203715
Halipteridae	*Halipteris finmarchica*	NTM C14596	GQ342425	DQ302868	JX203741
Helioporidae	*Heliopora coerulea*	CRCNI 577	GQ342426	DQ302872	JX203716
Ifalukellidae	*Ifalukella yanii*	UF4139	GQ342427	GQ342501	JX203717
Isididae	*Acanella eburnea*		EF672731	EF672731	n.a.
Isididae	*Keratoisidinae* sp. BAL208.1		EF622534	EF622534	n.a.
Kophobelemnidae	*Kophobelemnon macrospinum*	NTM C14985	GQ342429	DQ302937	JX203742
Melithaeidae	*Acabaria erythraea*	ZMTAU CO34216	GQ342430	GQ342503	JX203720
Melithaeidae	*Acabaria sinaica*	ZMTAU CO34200	GQ342431	GQ342504	JX203721
Melithaeidae	*Clathraria rubrinodis*	ZMTAU CO34054	GQ342432	GQ342505	JX203722
Melithaeidae	*Melithaea* sp.	RMNH Coel. 40049	JX203856	JX203799	JX203723
Melithaeidae	*Mopsella* sp.	RMNH Coel. 40034	JX203857	JX203800	JX203724
Melithaeidae	*Wrightella coccinea*	RMNH Coel. 40041	JX203858	JX203801	n.a.
Nephtheidae	*Dendronephthya sinaiensis*	ZMTAU CO34163	GQ342433	GQ342506	JX124349

(*continued next page*)

Table 1. (*continued*)

Family	Genus/species	Specimen voucher	GenBank accession no		
			COI	*mtMutS*	28S rDNA
Nephtheidae	*Eunephthya thyrsoidea*	RMNH Coel. 40182	JX124384	JX124364	JX124340
Nephtheidae	*Gersemia antarctica*	CSM-C59	GQ342473	GQ342390	JX203646
Nephtheidae	*Gersemia juliepackardae*	CSM-VEN3208-A3	JX203820	JX203768	JX203647
Nephtheidae	*Gersemia rubiformis*	CSM-ZS1	GQ342390	GQ342474	JX203648
Nephtheidae	*Lemnalia* sp.	RMNH Coel. 40818	JX203859	JX203802	JX203726
Nephtheidae	*Nephthea elatensis*	ZMTAU CO34112	GQ342435	GQ342508	JX203725
Nephtheidae	*Paralemnalia thyrsoides*	ZMTAU CO34087	GQ342436	GQ342509	JX203727
Nephtheidae	*Scleronephthya corymbosa*	ZMTAU CO34159	GQ342438	GQ342511	JX124350
Nephtheidae	*Stereonephthya cundabiluensis*	ZMTAU CO34204	GQ342439	GQ342512	JX124351
Nidaliidae	*Chironephthya* sp.	ZMTAU CO34203	GQ342440	GQ342513	JX203730
Nidaliidae	*Nidalia* sp.	ZMTAU C014876	GQ342441	DQ302828	JX203729
Nidaliidae	*Pieterfaurea khoisanianum*	CSM-SAF183	GQ342437	GQ342510	JX203657
Nidaliidae	*Siphonogorgia godeffroyi*	RMNH Coel. 40833	JX203860	JX203803	JX203731
Paragorgiidae	*Paragorgia arborea*		FJ264900	GQ293312	GQ293260
Paralcyoniidae	*Ceeceenus quadrus*	UF2858	GQ342442	GQ342514	JX124346
Paralcyoniidae	*Paralcyonium spinulosum*	RMNH Coel. 40820	JX124389	DQ302833	JX124347
Paralcyoniidae	*Studeriotes* sp.	RMNH Coel. 40043	GQ342443	GQ342515	JX124348
Pennatulidae	*Gyrophyllum sibogae*	NOR89/53	JX203865	DQ302869	JX203740
Plexauridae	*Astrogorgia* sp.	RMNH Coel. 40018	JX203861	JX203805	JX203733
Plexauridae	*Bebryce* sp.	RMNH Coel. 40821	JX203862	JX203806	JX203734
Plexauridae	*Echinogorgia* sp.	RMNH Coel. 40020	GQ342450	GQ342522	JX203737
Plexauridae	*Eunicea tourneforti*	RMNH Coel. 40835	GQ342445	GQ342517	n.a.
Plexauridae	*Euplexaura* sp.	ZMTAU CO34220	GQ342446	GQ342518	JX203735
Plexauridae	*Menella* sp.	RMNH Coel. 40038	GQ342447	GQ342519	JX203736
Plexauridae	*Muricea atlantica*	RMNH Coel. 40834	GQ342448	GQ342520	JX203747
Plexauridae	*Muriceopsis flavida*	RMNH Coel. 40830	GQ342449	GQ342521	JX203744
Plexauridae	*Plexaura kuna*	RMNH Coel. 40836	JX203866	JX203807	JX203748
Plexauridae	*Plexaurella nutans*	RMNH Coel. 40826	GQ342451	GQ342523	JX203745
Plexauridae	*Pseudoplexaura wagenaari*	RMNH Coel. 40832	GQ342452	GQ342524	JX203746
Primnoidae	*Callogorgia formosa*	NTM C14593	GQ342453	GQ342525	JX203749
Primnoidae	*Thouarella grasshoffi*	USNM 1078188	FJ268636	GQ868334	n.a.
Protoptilidae	*Distichoptilum gracile*	NTM C14561	GQ342454	DQ302866	JX203739
Renillidae	*Renilla* sp.	UF4000	GQ342455	GQ342526	n.a.
Subergorgiidae	*Annella mollis*	NTM 14924	GQ342456	JX203808	JX203750
Subergorgiidae	*Subergorgia suberosa*	NTM C14930	GQ342457	JX203809	JX203762
Taiaroidae	*Taiaroa tauhou*	NIWA 28679	JX203867	JX203810	JX203751
Tubiporidae	***Tubipora* sp.**	ZMTAU CO34116	GQ342458	JX203811	JX203752
Virgulariidae	*Virgularia schultzei*	RMNH Coel. 40823	GQ342459	GQ342527	JX203743
Xeniidae	*Anthelia glauca*	ZMTAU CO34183	GQ342460	JX203812	JX203753
Xeniidae	*Asterospicularia randalli*	UF2851	GQ342461	DQ302836	JX203754
Xeniidae	*Cespitularia erecta*	OCDN-8504C	JX203869	JX203813	JX203755
Xeniidae	*Heteroxenia fuscescens*	ZMTAU CO34118	GQ342462	GQ342528	JX203756
Xeniidae	*Sarcothelia edmondsoni*	CSM-SKB	JX203868	JX203814	JX203757
Xeniidae	*Sympodium caeruleum*	ZMTAU CO34185	GU356009	JX203815	JX203758
Xeniidae	*Xenia hicksoni*	ZMTAU CO34072	GQ342463	GQ342529	JX203759
Scleractinia	*Montastraea franksi*		NC007225	n.a.	AY026375
Actiniaria	*Metridium senile*		AF000023	n.a.	n.a.
Actiniaria	*Nematostella vectensis*		n.a.	n.a.	AY345871
Antipatharia	*Leiopathes* sp.		FJ597644	n.a.	FJ626241

other South African stoloniferans sequenced here belong to the Holaxonia–Alcyoniina clade.

(2) *Carijoa* falls in a clade with the membranous genus *Cryptophyton* Williams, 2000*c*. These two genera are the sister group to the holaxonian family Acanthoaxiidae Ofwegen & McFadden, 2010, and are not closely related to any of the other stoloniferans included in the tree. A *Carijoa* species from South Africa is nearly indistinguishable genetically from *Carijoa* species from other geographic regions.

(3) The three species of *Inconstantia*, gen. nov., described below are sister taxa to the membranous South American genus *Incrustatus* Ofwegen, Häussermann & Försterra, 2006. The [*Incrustatus* + *Inconstantia*] clade is also not close

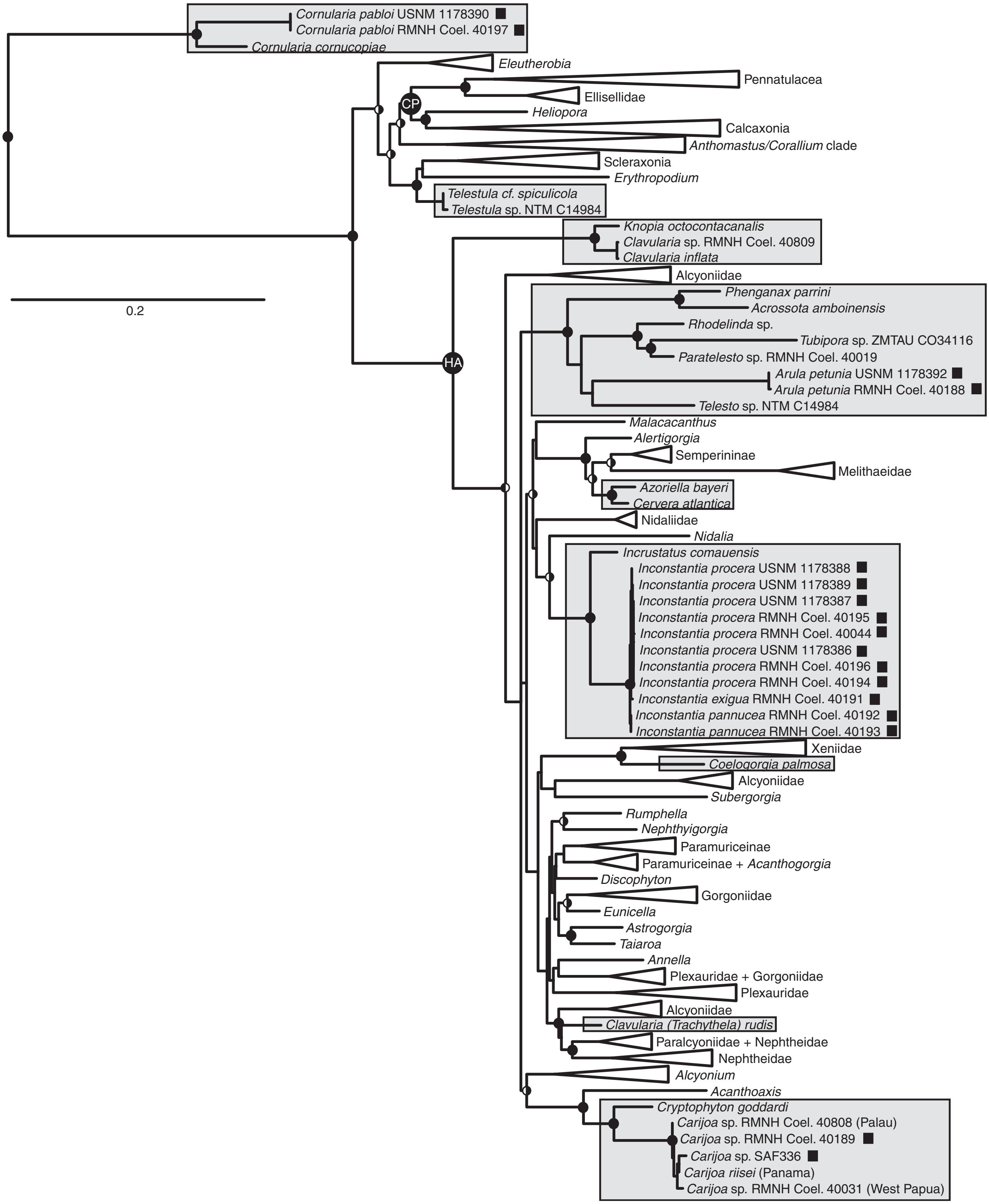

Fig. 1. Phylogenetic relationships among South African stoloniferan specimens (solid squares), and 130 octocoral reference taxa (stoloniferan genera enclosed in shaded boxes). Solid circles at nodes indicate strong support from both maximum-likelihood (bootstrap value >70%) and Bayesian (posterior probability >90%) analyses; split circles indicate strong support from one analysis only (left half solid: supported by ML; right half solid: supported by Bayesian analysis). Strongly supported clades that include no stoloniferan taxa have been collapsed. HA = Holaxonia–Alcyoniina clade; CP = Calcaxonia–Pennatulacea clade (McFadden *et al*. 2006*a*). Hexacorallian outgroup taxa used to root tree are not shown.

genetically to any other stoloniferan genera. The sister taxon to this group is, however, unclear due to a lack of support for the deeper nodes within the tree.

(4) *Arula*, gen. nov., falls within a well supported clade of stoloniferan taxa that includes the families Acrossotidae and Tubiporidae as well as representatives of four genera of Clavulariidae (*Paratelesto* Utinomi, 1958, *Phenganax* Alderslade & McFadden, 2011, *Rhodelind*a Bayer, 1981, and *Telesto* Lamouroux, 1812). The branches within this clade are all relatively long, indicating that members of these morphologically disparate taxa are not close genetically, despite their monophyletic relationship.

The remaining genera of stoloniferans included within the phylogenetic analysis fall into an additional five clades, none of which is closely related to others (Fig. 1). *Coelogorgia* (Coelogorgiidae) is the sister taxon to a clade of soft corals that includes the family Xeniidae Ehrenberg, 1828. The clavulariid genera *Cervera* López-González *et al.*, 1995 and *Azoriella* López-González & Gili, 2008 are embedded within a clade of scleraxonian gorgonians, and *Trachythela* Verrill, 1922 (a genus Deichmann (1936) synonymised with *Clavularia* without discussion) falls within a clade of soft corals that includes the families Nephtheidae and Paralcyoniidae. *Clavularia* and *Knopia* Alderslade & McFadden, 2007 belong to a clade that is sister to all remaining Holaxonia–Alcyoniina. Genus *Telestula* Madsen, 1944 falls outside of Holaxonia–Alcyoniina, belonging to a clade of mostly scleraxonian gorgonians that lies at the base of Octocorallia (Fig. 1). No South African species (of those we analysed) belong to any of these five clades.

Taxonomy

Order **ALCYONACEA** Lamouroux

ARULIDAE, fam. nov.

Diagnosis

Alcyonacea with polyps arising from a narrow, tubular stolon. Tentacles fused proximally to form a broad, circular oral membrane. Sclerites in the form of table-radiates.

Type genus

Arula, gen. nov, here designated.

Remarks

The majority of stoloniferan octocorals have been placed in Clavulariidae Hickson, 1894, a family that currently comprises 60 or more species in ~25 genera. In contrast, the other five families of stoloniferans are all either monospecific or monogeneric. Three of these families are distinguished from Clavulariidae by unique aspects of the colony growth form: in Coelogorgiidae a very long axial polyp gives rise to secondary polyps that in turn produce lateral polyps, in Pseudogorgiidae an axial polyp gives rise to lateral polyps that are embedded within coenenchyme, and in Tubiporidae the polyps are housed within calcareous tubes that are connected to one another by raised stolonic platforms. The other two families, Acrossotidae and Cornulariidae, are distinguished from Clavulariidae (and from all other octocoral families) by unique characteristics of the polyps. In Acrossotidae the polyp tentacles lack pinnules, while in Cornulariidae the polyp is covered by a theca-like chitinous envelope. The oral membrane of *Arula*, gen. nov., is as unique and distinctive a structure as those that characterise each of these families, and thus we propose a new family for the genus. The sclerites found in the calyx and stolons of *Arula* are also of a unique form that has not been found in any other family of octocorals.

Molecular phylogenetic analyses support the distinctiveness of the genus *Arula. Arula* belongs to a clade of stoloniferans that includes the families Tubiporidae and Acrossotidae. *Arula* is, however, more distinct genetically from those two families than either *Acrossota* or *Tubipora* is from members of other genera currently classified in Clavulariidae: *Acrossota* is close to *Phenganax*, and *Tubipora* falls in a clade with *Paratelesto* and *Rhodelinda* (Fig. 1). The combination of unique morphological features and phylogenetic distance from other stoloniferan families supports the status of Arulidae as a new family.

Genus ***Arula***, gen. nov.

Type species

Arula petunia, sp. nov., by original designation.

Diagnosis

Colony with polyps connected by narrow, tubular stolons; anthocodiae retractile into cylindrical to clavate calyces. Adjacent tentacles fused proximally to form broad, circular oral membrane. Sclerites of anthocodia are smooth rods. Sclerites of calyx and stolon are small 6-radiates and table-radiates. Sclerites colourless. Zooxanthellate.

Etymology

From the Latin *arula*, a little altar, denoting the shape of the sclerites in the calyx and stolons, which resemble altar tables. Gender: feminine.

Arula petunia, sp. nov.

Figs 2*a–d*, 3, 4

Clavularia capensis non (Studer, 1878): Tixier-Durivault, 1954: 124–126.

?*Clavularia* sp.: Williams, 1989: 142; 1992b: 255.

Clavularia sp.: Branch *et al*. 2010: 34, fig. 10.6

Material examined

Holotype. South Africa, Kwazulu-Natal, Park Rynie, Howard's Castle (30°16.862′S, 30°48.555′E), depth 16–21 m, 19.iii.2008, coll. C. S. McFadden [SAF362] (RMNH Coel. 40188).

Paratypes. Two colonies, same data as holotype: [SAF362] (USNM 1178391); [SAF372] (USNM 1178392).

Description

Colony of ~100 polyps attached to piece of hard substrate 4.5 cm by 3.0 cm (Fig. 2*a–c*). Polyps spaced 1.0–2.5 mm apart,

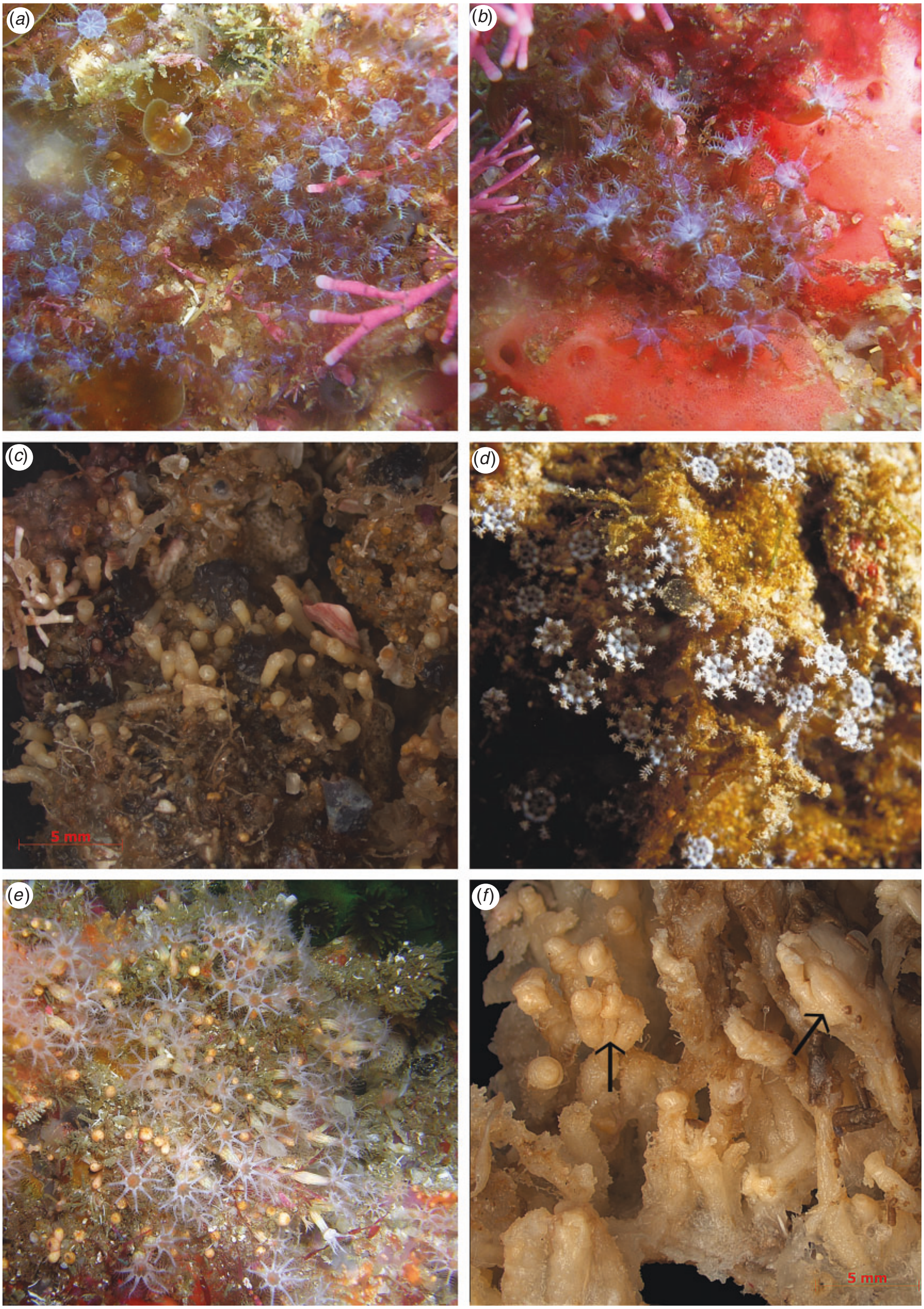

Fig. 2. (*a*, *b*) *Arula petunia*, holotype, RMNH Coel. 40188, photographed *in situ*; (*c*) *A. petunia*, holotype, RMNH Coel. 40188, preserved colony; (*d*) *Arula* sp. photographed on a coral reef in Bali, Indonesia; (*e*) *Carijoa* sp. photographed *in situ*; (*f*) RMNH Coel. 40189, preserved specimen of *Carijoa* sp., with arrows indicating clusters of secondary polyps arranged around the axis of a primary polyp.

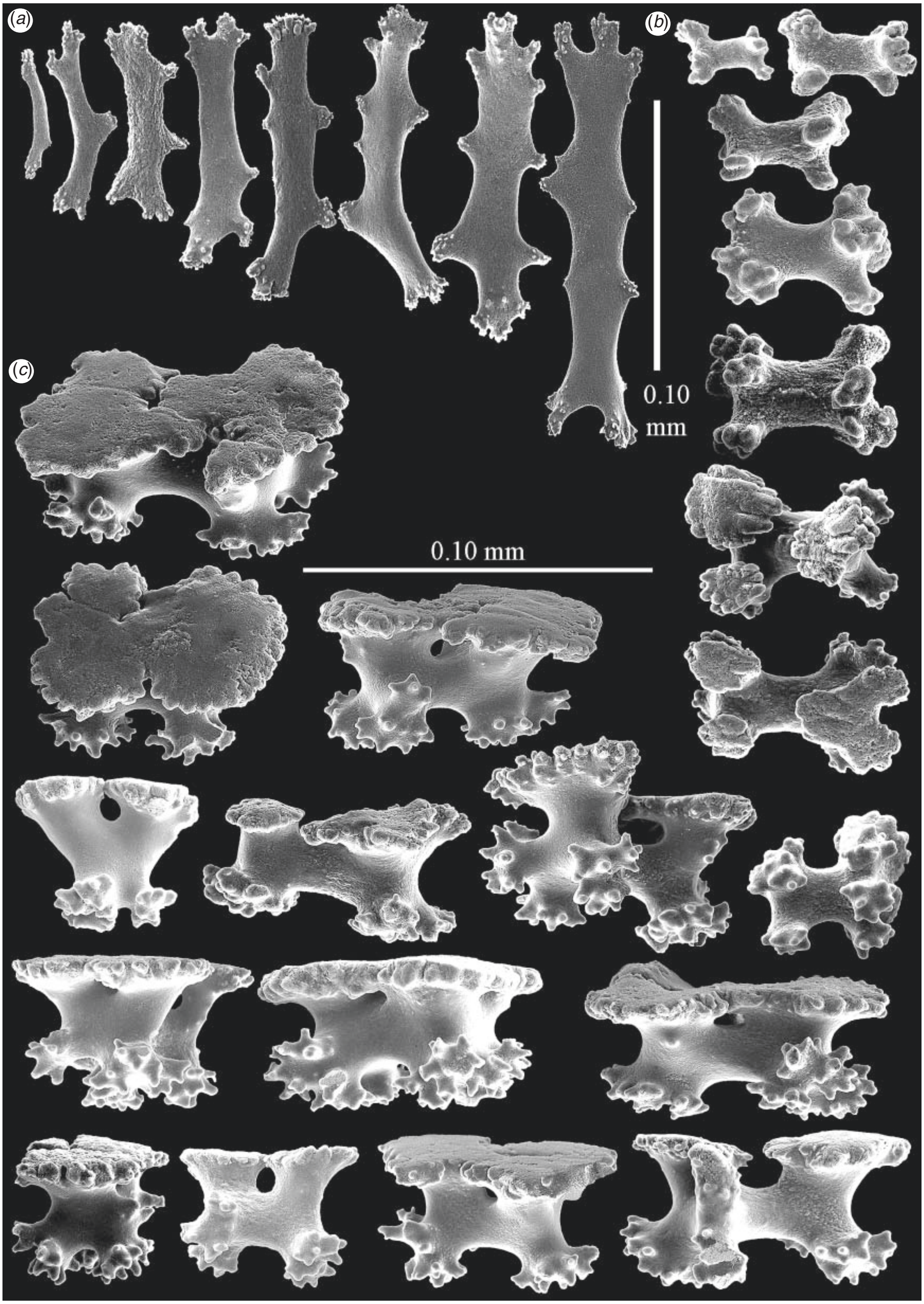

Fig. 3. *Arula petunia*, holotype, RMNH Coel. 40188: (*a*) anthocodial sclerites; (*b*) 6-radiates of calyx; (*c*) table-radiates of calyx, lateral views.

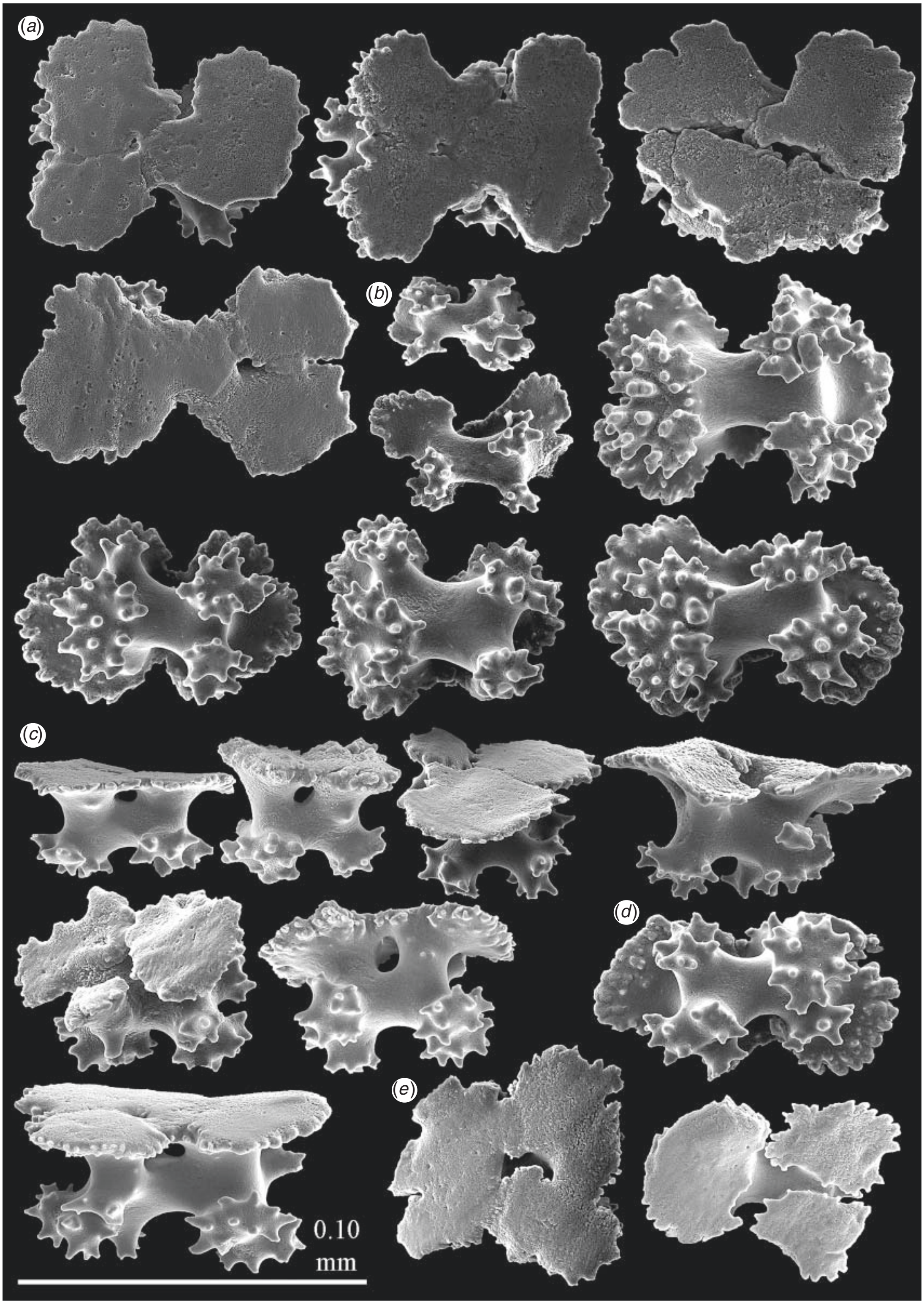

Fig. 4. *Arula petunia*, holotype, RMNH Coel. 40188: (*a*) table-radiates of calyx, top views; (*b*) table-radiates of calyx, bottom views; (*c*) table-radiates of stolons, lateral views; (*d*) table-radiate of stolons, bottom view; (*e*) table-radiates of stolons, top views.

connected by stolons that are 0.3 mm in diameter and circular in cross-section. Most polyps have anthocodia retracted into calyx 2–3 mm tall and 0.9 mm diameter at widest point; calyces slightly club-shaped, wider near distal end than at proximal point of attachment to stolon. Surface of calyx covered by dense layer of small sclerites giving it a slight granular appearance.

Oral disk expanded into broad circular membrane by fusion of proximal regions of adjacent tentacles (Fig. 2*a*, *b*). Margin of oral membrane with eight broad lobes, eight deep furrows running from intertentacular margin to mouth of polyp; oral disk of polyp thus resembling tubular flower with eight floral rays. Distal two-thirds of tentacles extending from fused margins of oral membrane. Tentacles long and thin,10–13 pairs of widely spaced pinnules arranged in single row on either side of rachis.

Anthocodial sclerites smooth rods, 0.05–0.16 mm long, with sparse simple tubercles around margins (Fig. 3*a*); arranged on anthocodia in eight longitudinal tracts extending to bases of tentacles and transversely on tentacle rachis. Wall of calyx containing small 6-radiates, 0.03–0.06 mm long (Fig. 3*b*), and unique radiate-derivatives (‘table-radiates’) with one broad, flat side (Figs 3*c*, 4). Stolons with table-radiates of same shape and size as calyces, 0.04–0.09 mm long by 0.03–0.07 mm wide (Fig. 4).

Oral disk and tentacles blue in life (Fig. 2*a*, *b*), yellowish-white in EtOH.

Distribution

East coast of South Africa from Transkei to northern Natal (see remarks). The same species or a congener perhaps occurring further north along African coast (Zanzibar) and in Bali, Indonesia (Fig. 2*d*).

Remarks

Sclerites of the type found in *A. petunia*, sp. nov., are unique among octocorals, and have never been described previously, nor has the unique structure of its oral disk ever been discussed. It appears, nonetheless, that this species was recorded by Tixier-Durivault (1954), who misidentified it, and perhaps also by Williams (1989, 1992*b*), who reported it as an undetermined species of *Clavularia*. A colour photo of what is clearly *A. petunia* is shown in Branch *et al*. (2010), labelled *Clavularia* sp. Tixier-Durivault (1954) presented a detailed description of a specimen collected from Port St Johns, Transkei, that she identified as *Clavularia capensis* (Studer, 1878). Her material is not, however, Studer’s species, which he described as cinnamon-red in colour with non-retractile polyps and sclerites in the form of rods with weak ornamentation. Instead, Tixier-Durivault’s description closely matches that of *A. petunia*. The smooth rods (0.03–0.08 mm long) and radiate-like sclerites (0.04–0.125 mm long) she illustrates closely resemble the sclerites of *A. petunia* as seen through a light microscope, in which the unique table-top form is difficult to discern. Her depiction of the colony form and the calyces is also an accurate likeness of *A. petunia*; she does not mention the structure of the oral disk, but it is difficult to see in contracted, preserved material. The only aspect of Tixier-Durivault’s description that does not match our material is the height of the polyps, which she reports as 9–10 mm; in our preserved material, the calyces are only 2–3 mm tall. Williams (1989) also reports what may be this same species from Sodwana and Kosi Bays, northern Natal. Although he mentions the blue tentacles of the living material, he does not remark upon the unusual structure of the oral disk or the unique form of the sclerites. A species with a very similar oral membrane, undoubtedly either the same species or a congener, has been photographed on the coral reefs of Bali, Indonesia (Fig. 2*d*).

Several previously described species of *Clavularia* also share some characters with *A. petunia*, but it is not clear from the original descriptions if they have sclerites of the same unique form. Thomson and Henderson (1906*a*) described *Clavularia margaritiferae* from the Gulf of Manaar and later identified the same species from Zanzibar (Thomson and Henderson 1906*b*). Many aspects of their description fit *A. petunia*, and their illustration of a colony (Thomson and Henderson 1906*a*: plate III, fig. 8) looks very much like our material. *C. margaritiferae* has polyps that are 3 mm tall and 0.9 mm in diameter, spaced 2–2.5 mm apart on stolons that are 0.4–0.6 mm in diameter and never form membranes. Their description of the polyps states that ‘the expanded tentacles are seen in a few forms as if rising on a narrower neck from within a broader funnel’ (Thomson and Henderson 1906*b*: 404), a plausible description of the oral membrane of *A. petunia*. Their description of the sclerites in the calyx as ‘substantial rods bearing blunt wart-like projections often in a whorl of four towards each end’ (Thomson and Henderson 1906*a*: 273) does not, however, correspond to the sclerites seen in *A. petunia*. *C. repens* Thomson & Henderson, 1906*b* is described as being very similar to *C. margaritiferae*, but with minute capstans in the calyx (0.03–0.05 mm long) as well as ‘quadrangular forms with an axial cross (0.05 × 0.05),’ which unfortunately are not illustrated. *C. racemosa* Utinomi, 1950 likewise has calyces 2–4.5 mm tall arranged 1–3 mm apart on a stolon that is cylindrical in cross-section and 0.4–1.0 mm in diameter. The anthocodial sclerites are rods that bear a strong resemblance to those of *A. petunia*, and the sclerites of the calyx and stolons are described as capstans and irregularly shaped derivatives of capstans, 0.03–0.04 mm long. There is no mention or illustration of a unique oral disk structure, however, although it is clear from his description that Utinomi (1950) had observed live material. Examination of type material will be necessary to determine whether any of these species might be additional members of *Arula*, gen. nov.

Etymology

New Latin: *petunia*, a genus of plants whose broad, tubular flowers resemble the oral membrane of this species.

Family **CLAVULARIIDAE** Hickson

Genus ***Carijoa*** F. Müller, 1867

Carijoa sp.

Figs 2*e*–*f*, 5

Material examined

South Africa, Kwazulu-Natal, Park Rynie, Lander’s Reef (30°19.973′S, 30°47.523′E), 22–28 m depth, 18.iii.2008, coll. C. S. McFadden, [SAF306] (RMNH Coel. 40189); same data as RMNH Coel. 40189,

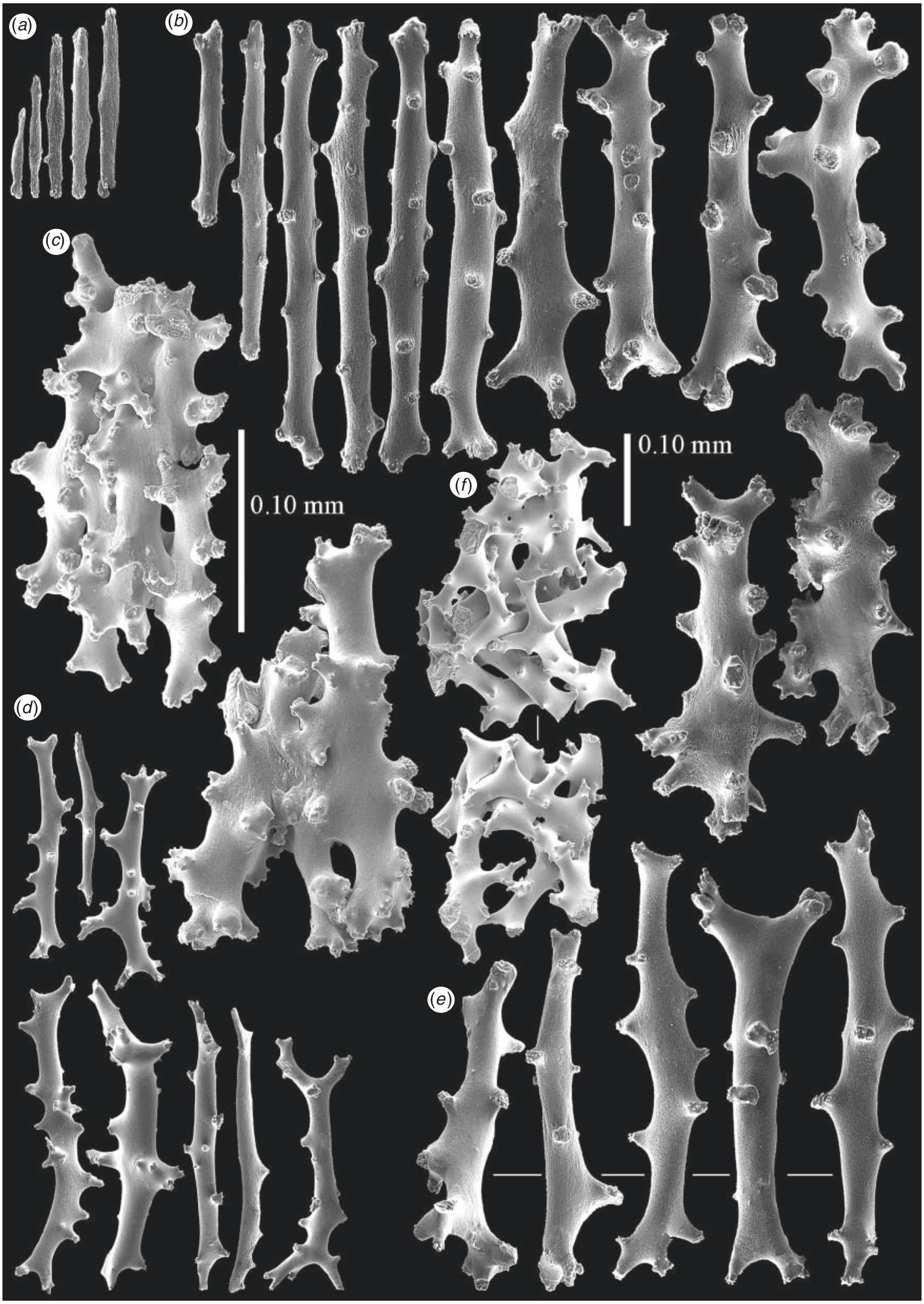

Fig. 5. *Carijoa* sp., RMNH Coel. 40189: (*a*) tentacle sclerites; (*b*) polyp sclerites; (*c*) fused clump of polyp sclerites; (*d*) stolon sclerites; (*e*) stolon sclerites (higher magnification); (*f*) fused clumps of stolon sclerites. Scale at (*f*) applies to (*f*) only.

[SAF307] (RMNH Coel. 40190); South Africa, Kwazulu-Natal, Aliwal Shoal, NE Pinnacles (30°15.599′S, 30°49.724′E), 12–16 m depth, 19.iii.2008, coll. C. S. McFadden [SAF336].

Description

Colonies of tall, branched polyps connected to one another by basal stolonal network (Fig. 2*e, f*). Stolons are flat ribbons, 0.4–1.6 mm wide, anastomosing to form reticulated network. Axial (primary) polyps arising from stolonal network at intervals of 0.5–3.5 mm, ranging from 2.5 mm tall with no secondary polyps to 20 mm tall with maximum of 6 secondary polyps. Secondary polyps arising from axial polyp at irregular intervals, two or three often budding at same height from opposite sides of axis (Fig. 2*f*). Secondary polyps closely appressed to axial polyp, oriented vertically with axes parallel to primary axis. Polyp clusters resembling candelabra, with several secondary polyps of similar height surrounding each axial polyp (Fig. 2*f*).

Polyp sclerites smooth rods, 0.10–0.23 mm long, with sparse, simple tubercles; some with side branches or forked (Fig. 5*b*). Also robust tuberculate rods, 0.2 mm long, that may be fused into clumps (Fig. 5*c*). Tentacles with smooth, unornamented rods, 0.05–0.09 mm long (Fig. 5*a*). Sclerites in stolons similar to those in polyp but somewhat larger: smooth rods, 0.16–0.35 mm long, often forked, with sparse, simple tubercles (Fig. 5*d*, *e*), often fused into tangled clumps (Fig. 5*f*).

Remarks

This material can be identified to the genus *Carijoa* F. Müller, 1867 by the form of the sclerites, but revisions of that genus and the morphologically similar *Telesto* Lamouroux, 1812 are necessary before a species-level identification can be made. *Carijoa* and *Telesto* are two very old genera of stoloniferous octocorals with a long and confused history. Wright and Studer (1889) first united several species that had been described in various other genera under the umbrella of *Telesto*, a genus defined by a growth form in which long axial polyps give rise to secondary polyps. They divided the genus into subgenera *Telesto* and *Carijoa*, distinguished by *Telesto* (*Telesto*) having relatively short axial polyps giving rise to secondary polyps of similar size, while *Telesto* (*Carijoa*) has very long axial polyps that give rise to much shorter secondary polyps. They described the sclerites of subgenus *Telesto* (*Telesto*) as ‘broad dentate discs, or ramified, irregular bodies, whose spines interlock’; in contrast, in *Telesto* (*Carijoa*) the sclerites ‘are rod-like, with few spines’ and are bound together by ‘a horny substance’ (pp. 260–262). Subsequent authors (e.g. Kükenthal 1913; Deichmann 1936) made no distinction between these subgenera, and continued to assign species of both types to *Telesto*.

In his treatise on Caribbean octocorals, Bayer (1961: 32) remarked that he believed that the West Indian species of *Telesto* belonged to two separate genera, one with ‘elongate, often branching, rodlike, colorless sclerites in the body walls’ and the other with ‘ovate, sometimes pebble-like bodies in the polyp walls’. He also noted a difference in the arrangement of anthocodial sclerites between the two groups. Bayer (1961) declined to formally separate them, however, citing as a difficulty the fact that Lamouroux’s type species, *Telesto aurantiaca*, is too poorly known to be certain to which group it belongs. He suggested, however, that *T. aurantiaca* probably belongs to the group with ovate sclerites, and that *Carijoa* F. Müller, 1867 would therefore be available as a name for the group with branched rods. In several later papers, Bayer (1981*a*, 1981*b*) listed *Telesto* and *Carijoa* as separate genera without further comment. The name *Carijoa* has subsequently been adopted for several species, but a complete revision of genus *Telesto* has yet to be made.

The sclerites of the South African species are very similar in form to those described for the Caribbean species of *Carijoa* (Bayer 1961), and it is very similar genetically to *Carijoa* species collected from the Caribbean and the Indo-Pacific (uncorrected *P* distance = 0.2–0.6% for *mtMutS*, 0–0.1% for COI, 0.6–1.3% for 28S rDNA) (Fig. 1). The growth form of the South African species is, however, very different from that of Caribbean material and from one or more species that have been reported from Hawaii and elsewhere in the Indo-Pacific. Those species all have very long axial polyps with numerous, much shorter secondary polyps that arise at regular intervals and nearly right angles to the axial polyp, and form upright, bushy colonies (see photos in Fabricius and Alderslade 2001; Concepcion *et al*. 2008). *In situ* this low-growing South African species is typically overgrown by sponges and other encrusting organisms, and individual polyps protrude through the epifauna (Fig. 2*e*); as a result, the branched nature of the polyps is generally not evident in the field, and the colony looks much like other low, encrusting species such as those described below.

On the basis of their original descriptions, the two species of *Telesto* that have been recorded previously from South Africa, *T. arborea* Wright & Studer, 1889 and *T. trichostemma* (Dana, 1846) both belong to genus *Carijoa* (Wright and Studer 1889). Some aspects of the growth form of the species we collected fit Wright and Studer’s (1889: 265) description of material they assigned to *C. trichostemma*, with secondary polyps ‘appressed to the ascending axial polyps on the stem portion’ with ‘mouth directed upward’. Whether or not our material or other material recorded previously from South Africa belongs to this or any other described species of *Carijoa* (or *Telesto*) cannot, however, be determined without examination of type material.

Genus ***Inconstantia***, gen. nov.

Type species

Inconstantia pannucea, sp. nov., by original designation.

Diagnosis

Clavulariidae with polyps connected by ribbon-like stolons or broad membranes. Polyps may be fused to one another at base of calyx, but secondary polyps not produced. Polyps retractile into cylindrical calyces that may be tall or may contract nearly flush with stolon. Retractile portion of polyp (anthocodia) with no sclerites or with few small rods and crosses. Sclerites of calyx and stolon may include radiates and their derivatives, tuberculate spindles, small rods and crosses. Sclerites colourless.

Remarks

The species included in *Inconstantia*, gen. nov., display a remarkable diversity of colony growth forms and sclerite types that would normally preclude assigning them to the same genus. Genetically, however, they form a remarkably homogeneous group (Fig. 1), separated from one another by genetic distances (uncorrected *P*) ranging from only 0.1% (COI) to 0.6% (*mtMutS*), values that are in the lower half of the range typical of differences among congeneric species of octocorals (McFadden *et al*. 2011). The three species of *Inconstantia* described below are, however, well separated genetically from their closest sister taxon, *Incrustatus* (uncorrected *P* = 1.1–1.2% for COI, 2.3–2.7% for *mtMutS*, 9.1–9.2% for 28S rDNA), and are not close phylogenetically to any other genera of stoloniferous octocorals (Fig. 1).

Bayer (1981*a*) divided those genera of Clavulariidae that lack secondary polyps into two subfamilies, Clavulariinae for genera with tall, tubular calyces, and Sarcodictyinae for those with low calyces that retract almost completely into the stolons. By his system of classification, *Inconstantia* includes species belonging to both of these subfamilies. The species with tall, cylindrical calyces are most similar morphologically to genus *Clavularia*, while the species with low, fully retractile calyces and a membranous growth form most closely resembles *Incrustatus* and *Cryptophyton*. The latter two genera are morphologically quite similar to one another but phylogenetically distant (Fig. 1).

The three species of *Inconstantia* described below are distinguished from most species currently included within *Clavularia* by the form and distribution of sclerites in the polyps and stolon. Most *Clavularia* species have the retractile part of the polyp (anthocodia) heavily armed either with a well developed collaret and points of spindles, or, in the absence of transverse sclerites forming a collaret, eight longitudinal bands of sclerites ending in points that may extend onto the tentacle rachis. In contrast, species of *Inconstantia* entirely lack sclerites in the anthocodiae or have only a few small rods and crosses. The sclerites of most *Clavularia* species are large spindles, typically from 0.4 mm to over 1.0 mm in length, arranged longitudinally in the calyx and often lengthwise in the stolons. Two of the three species of *Inconstantia* described here lack spindles entirely, and have only radiates and their derivatives in both the calyx and stolon.

Clavularia crassa (Milne Edwards, 1848) a species from shallow water in the Mediterranean, shares with *Inconstantia* relatively small spindles (up to 0.26 mm long) in the calyx and few sclerites in the anthocodia (Weinberg 1978). Unpublished sequence data for *C. crassa* suggest, however, that it does not belong to *Inconstantia* (P. López-González, pers. comm.). The descriptions of many of the other species that have been placed in *Clavularia* are poor and poorly illustrated, and information about the degree and arrangement of anthocodial armature is often lacking. It is possible, therefore, that other species attributed to *Clavularia* will be found to belong to *Inconstantia*.

Like *Inconstantia*, both *Cryptophyton* and *Incrustatus* have anthocodiae with no or only very sparse, small rod-like sclerites. In *Cryptophyton*, however, the sclerites found in the membrane are robust rods and irregular oval forms rather than radiates or spindles (Williams 2000*c*). *Incrustatus* does have predominantly radiates and their derivatives in the calyces and membrane, but they have distinctive tubercular ornamentation that distinguishes them from *Inconstantia* (van Ofwegen *et al*. 2006). Molecular phylogenetic analyses suggest that *Incrustatus* is the sister taxon to *Inconstantia*, and neither genus is closely related to *Cryptophyton* (Fig. 1).

Etymology

Latin: *inconstantia*, meaning changeability or fickleness, in recognition of the diversity of sclerites and growth forms observed within the genus. Gender: feminine.

Inconstantia exigua, sp. nov.

Figs 6*a*, *b*, 7

Material examined

Holotype. South Africa, Cape Peninsula, Oudekraal (33°58.930′S, 18°21.564′E), intertidal, 24.iii.2008, coll. C. S. McFadden, [SAF460] (RMNH Coel. 40191).

Description

Membranous colony covering distal half of mussel shell (Fig. 6*a*), size ~20 cm^2 with ~100 polyps. Polyps embedded within thin membrane, spaced 0.5–2.5 mm apart; some areas of membrane devoid of polyps, others overgrown by encrusting sponges. Some polyps partially expanded with tips of tentacles protruding from mouth (Fig. 6*b*); squat cylinders, 2.5 mm tall with diameter of 1.6 mm. Other polyps with anthocodia withdrawn into low, conical calyx, or with calyx fully retracted into membrane, visible only as small mound (Fig. 6*a*).

Anthocodiae devoid of sclerites. Calyx with radiates, 0.06–0.10 mm long, with complex tubercles, and tuberculate spheroids, 0.10–0.12 mm long (Fig. 7*a*). Membrane containing radiates and derivatives of radiates, 0.08–0.18 mm long, with complex tubercles (Fig. 7*b*).

Colour greyish-brown in EtOH.

Distribution

Cape Peninsula, South Africa.

Remarks

The growth form of *I. exigua*, sp. nov., in which short, conical calyces can be contracted flush with the basal membrane, is very different from that of the other two species of *Inconstantia*, both of which have tall, non-contractile, cylindrical calyces. Instead, *I. exigua* most closely resembles *Cryptophyton goddardi* Williams, 2000 and *Incrustatus comauensis* Ofwegen, Häussermann & Försterra, 2006. Both of those species have a membranous growth form, low calyces that can be contracted flush with the membrane, no or very few anthocodial sclerites, and sclerites in the membrane that are radiates or their derivatives. In *C. goddardi*, however, the sclerites are much more irregular in form than those of *I. exigua*, and in *I. comauensis* the radiates have much larger tubercles with dense sculpture. The radiates in the calyces and membrane of *I. exigua* are most similar in form to those of *I. pannucea*, sp. nov. (Fig. 9*b*, *c*), although they have denser tubercular ornamentation. *I. exigua* differs from the other two species of *Inconstantia* by only 0.1–0.4% at *mtMutS*, and 0.2–0.4% at 28S rDNA; at COI it differs from *I. pannucea*, sp. nov., by 0.1%, and has a haplotype identical to that of *I. procera*, sp. nov.

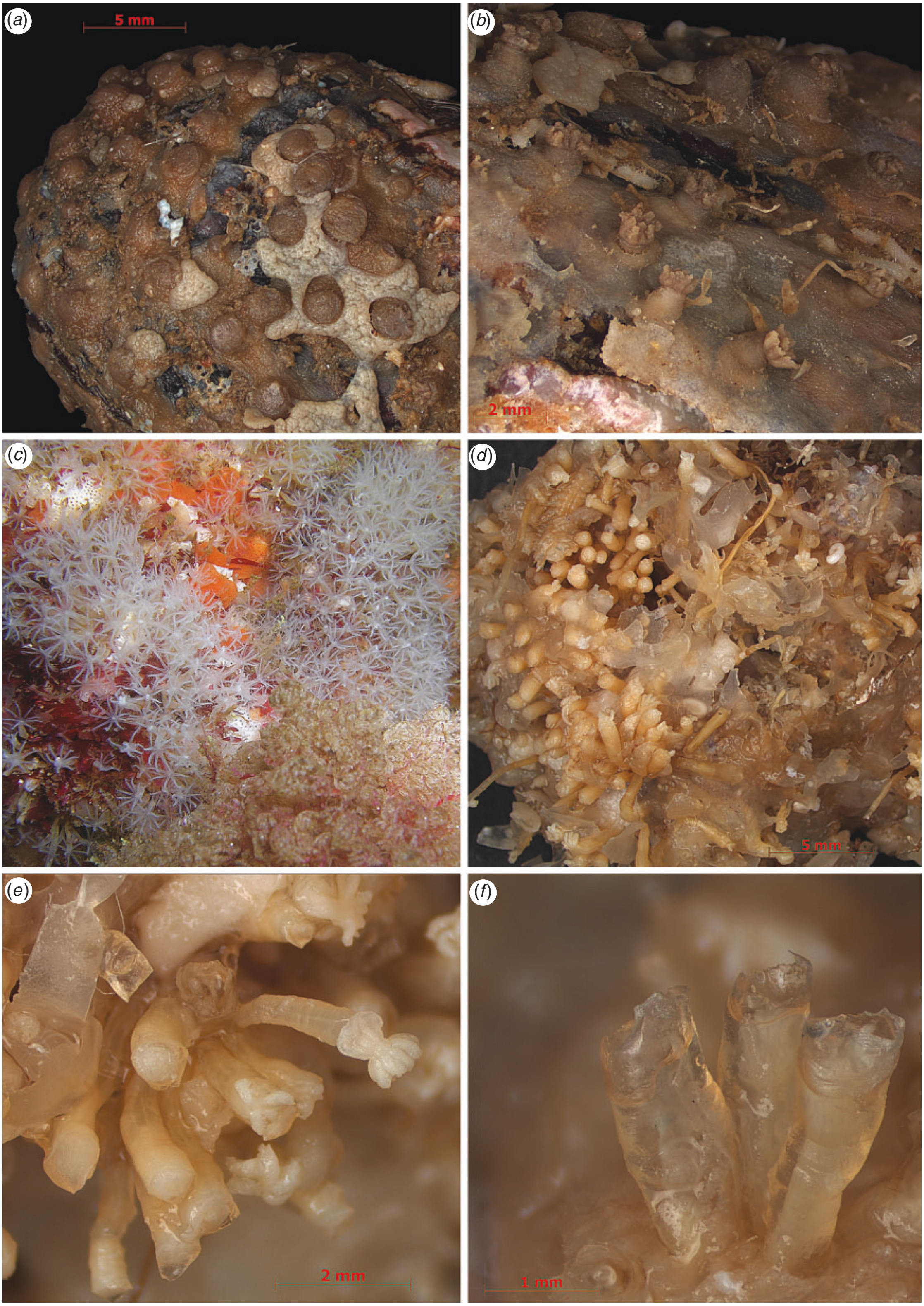

Fig. 6. *Inconstantia exigua*, holotype, RMNH Coel. 40191: (*a*) preserved colony; (*b*) close-up of same. *Cornularia pabloi*, sp. nov.: (*c*) a colony *in situ. Cornularia pabloi*, holotype, RMNH Coel. 40197: (*d*) preserved colony; (*e*) close-up of polyps in varying degrees of retraction; (*f*) polyps retracted within cuticular envelope.

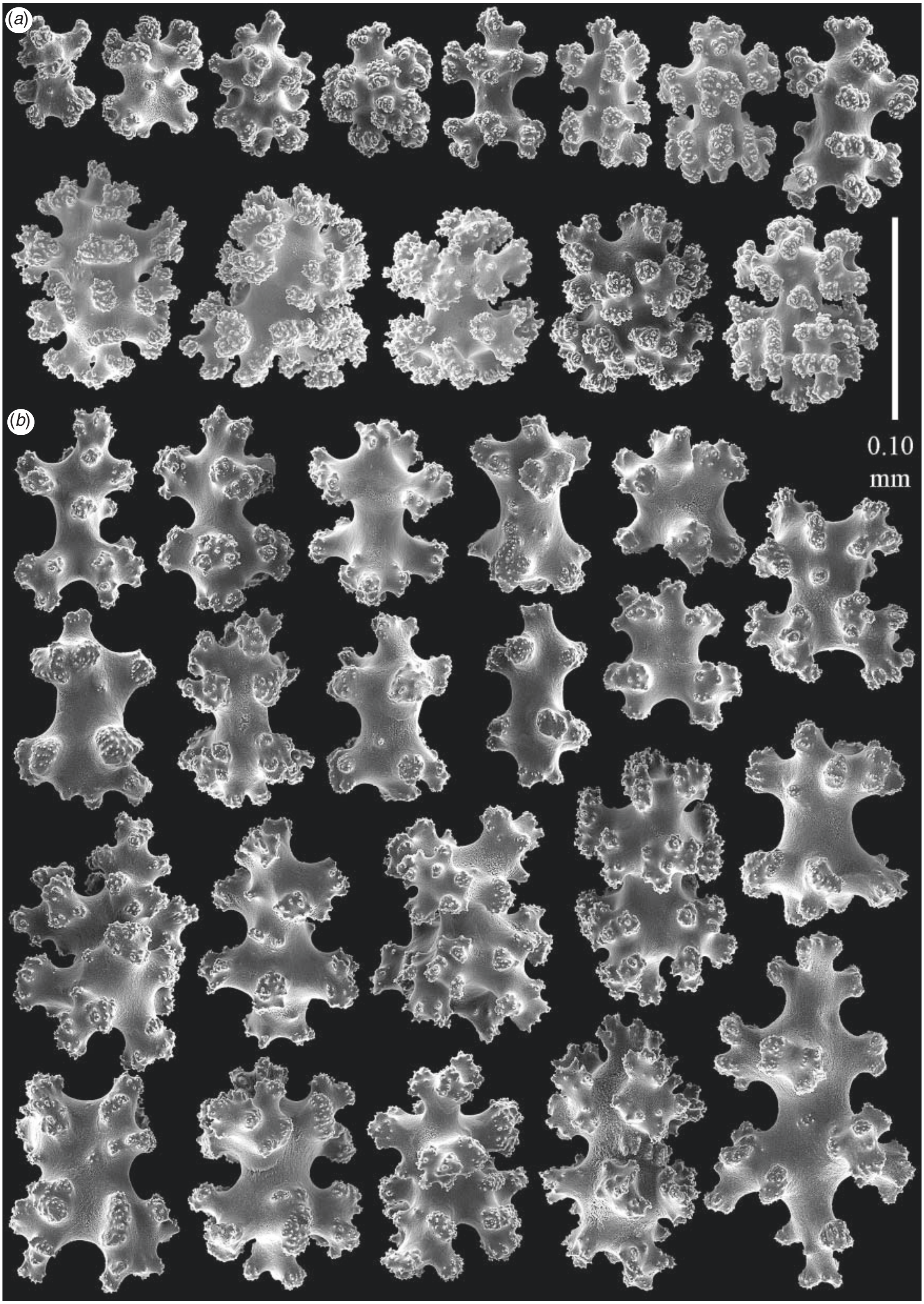

Fig. 7. *Inconstantia exigua*, holotype, RMNH Coel. 40191: (*a*) sclerites of calyx; (*b*) sclerites of membrane.

Etymology

Latin: *exiguus*, meaning small, in reference to the short calyces of this species relative to other species in the genus.

Inconstantia pannucea, sp. nov.

Figs 8*a–c*, 9

Material examined

Holotype. South Africa, Cape Peninsula, Vulcan Rock (34°03.970′S, 18°18.627′E), depth 15–27 m, 23.iii.2008, coll. C. S. McFadden, [SAF389] (RMNH Coel. 40192).

Paratype. Same data as holotype, [SAF387] (RMNH Coel. 40193).

Description

Holotype 3 cm by 2 cm, attached to fragment of calcareous substrate (Fig. 8*a, b*). Approximately 50 polyps arising from common membrane; membrane overgrown by encrusting sponges and bryozoans and difficult to discern. Polyps set very close to one another, some adjacent polyps fused along proximal half of calyx. Some polyps with anthocodia retracted within calyx, others with anthocodia and tentacles partially expanded (Fig. 8*b*). Calyces up to 10 mm tall, diameter 1.4–1.8 mm. Calyces slightly flared, widest at distal end. Calyx covered by thin cuticle, transparent in preserved material and very wrinkled (Fig. 8*c*); longitudinal ridges marking surface of calyx result from wrinkling of cuticle. Expanded anthocodia transparent and clearly demarcated from opaque, yellowish-brown calyx (Fig. 8*a*). Calyx ~$^1/_3$ to $^1/_2$ total height of expanded polyp. 10–13 pairs of pinnules arranged in single row on either side of tentacle rachis. Spherical gametes, 0.3–0.6 mm in diameter, visible in bases of damaged polyps.

Sclerites of anthocodiae are flat rods, 0.06–0.10 mm long (Fig. 9*a*), and small crosses (not shown), relatively few in number and not arranged to form collaret or points. Calyx wall containing small, blunt spindles, crosses, and derivatives of radiates, 0.07–0.12 mm long, with complex tubercles (Fig. 9*b*). Stolon sclerites are plate-like forms and derivatives of radiates, 0.11–0.20 mm long, with complex tubercles (Fig. 9*c*).

Colour in life transparent with yellowish calyx, white in EtOH.

Distribution

Cape Peninsula, South Africa.

Remarks

The paratype is a colony fragment ~1.5 cm by 1.5 cm with 30 polyps; it has been removed from the original substrate, but the basal membrane is entirely obscured by an encrusting sponge. It is similar to the holotype in all respects.

Superficially, *I. pannucea*, sp. nov., resembles its congener *I. procera*, sp. nov., and the two may be difficult to distinguish in the field. In preserved material, however, the two species can easily be separated by differences in the degree of calcification of the calyces. In *I. procera* the calyces are heavily armored with longitudinally arranged spindles that may appear as eight distinct ribs on the calyx surface (Fig. 8*e*). In contrast, the calyces of *I. pannucea* are much less heavily armored, and their surfaces appear flabby and wrinkled as a result of the overlying cuticle (Fig. 8*c*). The radiate-like sclerites of *I. pannucea* are more similar to those of *I. exigua* than to the much larger spindles found in *I. procera*.

Etymology

Latin: *pannuceus*, meaning wrinkled, describing the wrinkled cuticle that covers the surface of the calyx.

Inconstantia procera, sp. nov.

Figs 8*d–f*, 10–12

Material examined

Holotype. South Africa, Port Elizabeth, Algoa Bay, Bell Buoy 3 (33°58.816′S, 25°41.577′E), depth 12–15 m, 14.iii.2008, coll. C. S. McFadden [SAF249] (RMNH Coel. 40194).

Paratypes. Same data as holotype except coll. B. Picton [SAF263] (RMNH Coel. 40196); South Africa, Port Elizabeth, Algoa Bay, Philips Reef (33°15.933′S, 25°41.768′E), 10–12 m depth, 10.iii.2008, coll. C. S. McFadden [SAF068] (USNM 1178387); South Africa, Port Elizabeth, Algoa Bay, White Sands 15 (33°59.900′S, 25°42.522′E), depth 14–16 m, 12.iii.2008, coll. C. S. McFadden [SAF179] (USNM 1178386) [SAF178] (RMNH Coel. 40044); South Africa, Port Elizabeth, Algoa Bay, Table Top (33°58.920′S, 25°41.590′E), depth 10–12 m, 13.iii.2008, coll. C. S. McFadden [SAF219] (RMNH Coel. 40195); South Africa, Cape Peninsula, False Bay, Simon's Town, A-Frame (34°12.477′S, 18°27.649′E), 5–6 m depth, 26.iii.2008, coll. C. S. McFadden [SAF467] (USNM 1178388) [SAF468] (USNM 1178389).

Description

Holotype of five fragments removed from common substrate, each bearing 3–9 polyps (Fig. 8*e, f*); stolons that originally connected fragments have been severed. Polyps within each fragment connected basally by broad, flat ribbon-like stolon, usually 2–5 mm wide but with some broader membranous expansions; stolon overgrown by encrusting sponges, bryozoans and ascidians, and thus difficult to follow. Most polyps arising directly from stolon, immediately adjacent to one another or up to 3 mm apart. Some polyps directly connected to one another at base of calyx (Fig. 8*f*). Calyces cylindrical, 3–16 mm tall, 2 mm in diameter. Eight ribs formed by longitudinally oriented rows of sclerites visible on calyx surface (Fig. 8*e*). All polyps with anthocodiae retracted within calyces. Expanded anthocodiae transparent and clearly demarcated from opaque calyx, which is often overgrown by red alga (Fig. 8*d*). Calyx ~$^1/_2$ to $^2/_3$ total height of expanded polyp. 9–11 pairs of pinnules arranged in single row on either side of tentacle rachis.

Sclerites in anthocodiae are rods, 0.08–0.13 mm long, with simple tubercles (Fig. 10*a*), relatively few in number and not arranged to form collaret or points. Calyx with wide, blunt spindles, 0.11–0.27 mm long and up to 0.08 mm wide, with prominent complex tubercles (Fig. 10*b*). Some irregular plates and cross-like forms up to 0.13 mm long also found in calyx (Fig. 10*b*). Sclerites in stolon similar to those of calyx but smaller: blunt spindles up to 0.17 mm long by 0.06 mm wide, flattened spindles, 0.10–0.16 mm long, with sparse tubercles, and small rods and crosses, 0.06–0.09 mm long, with simple tubercles (Fig. 10*c*).

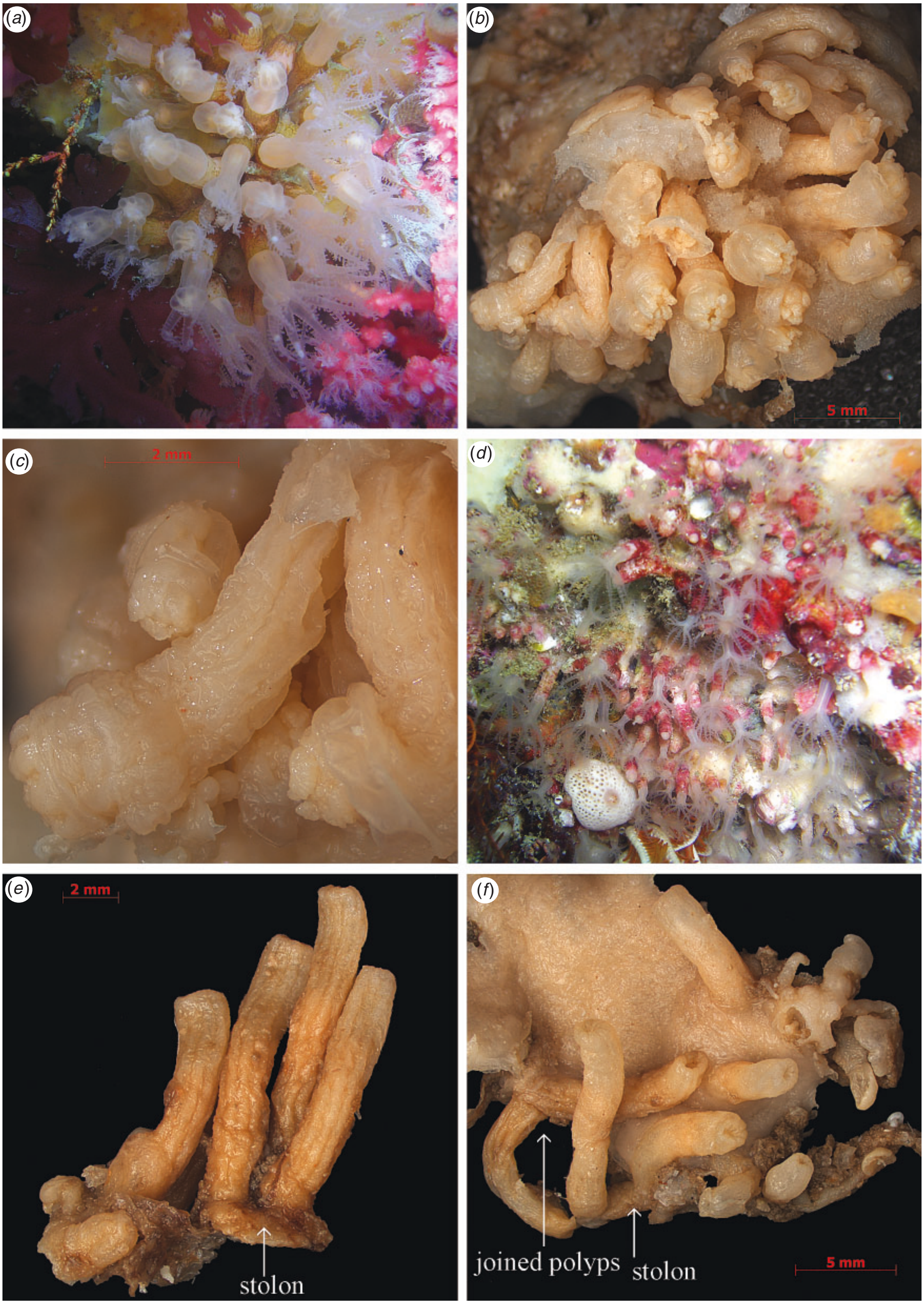

Fig. 8. *Inconstantia pannucea*, holotype, RMNH Coel. 40192: (*a*) colony *in situ*; (*b*) preserved colony; (*c*) polyps, showing wrinkled periderm. *Inconstantia procera*, holotype, RMNH Coel. 40194: (*d*) colony *in situ*; (*e*) fragment of preserved colony; (*f*) fragment of preserved colony.

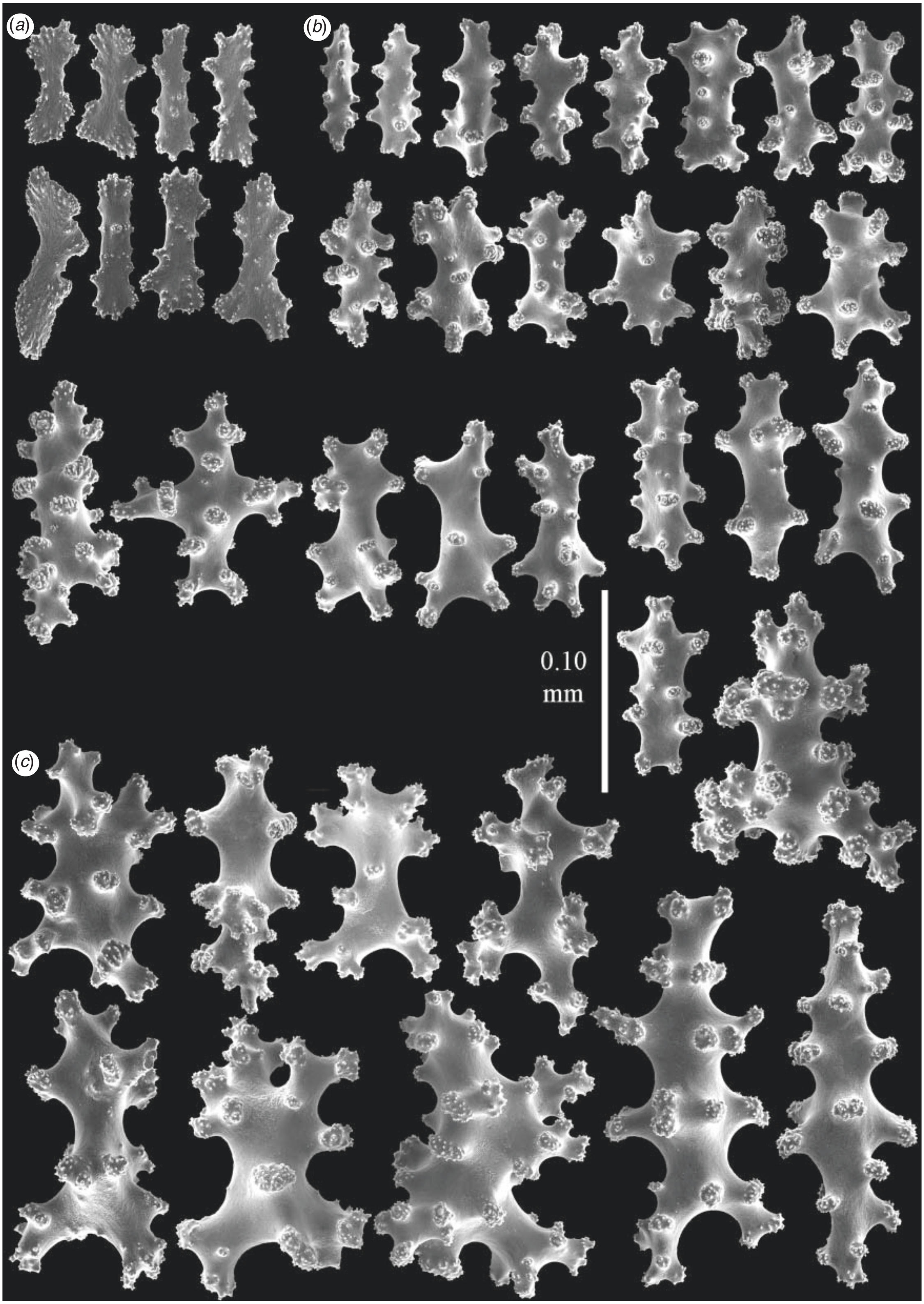

Fig. 9. *Inconstantia pannucea*, holotype, RMNH Coel. 40192: (*a*) anthocodial sclerites; (*b*) sclerites of calyx; (*c*) sclerites of stolon.

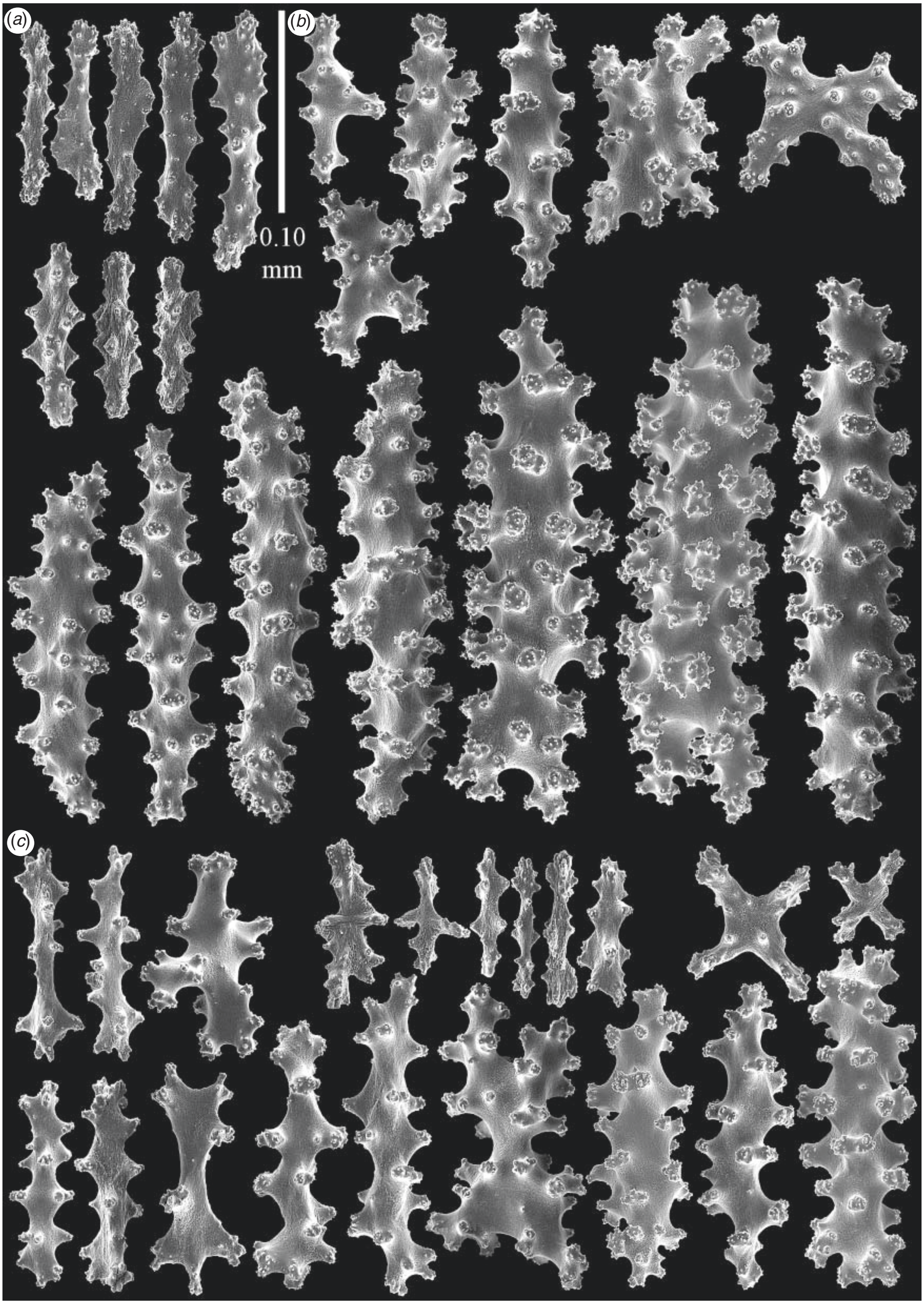

Fig. 10. *Inconstantia procera*, holotype, RMNH Coel. 40194: (*a*) anthocodial sclerites; (*b*) sclerites of calyx; (*c*) sclerites of stolon.

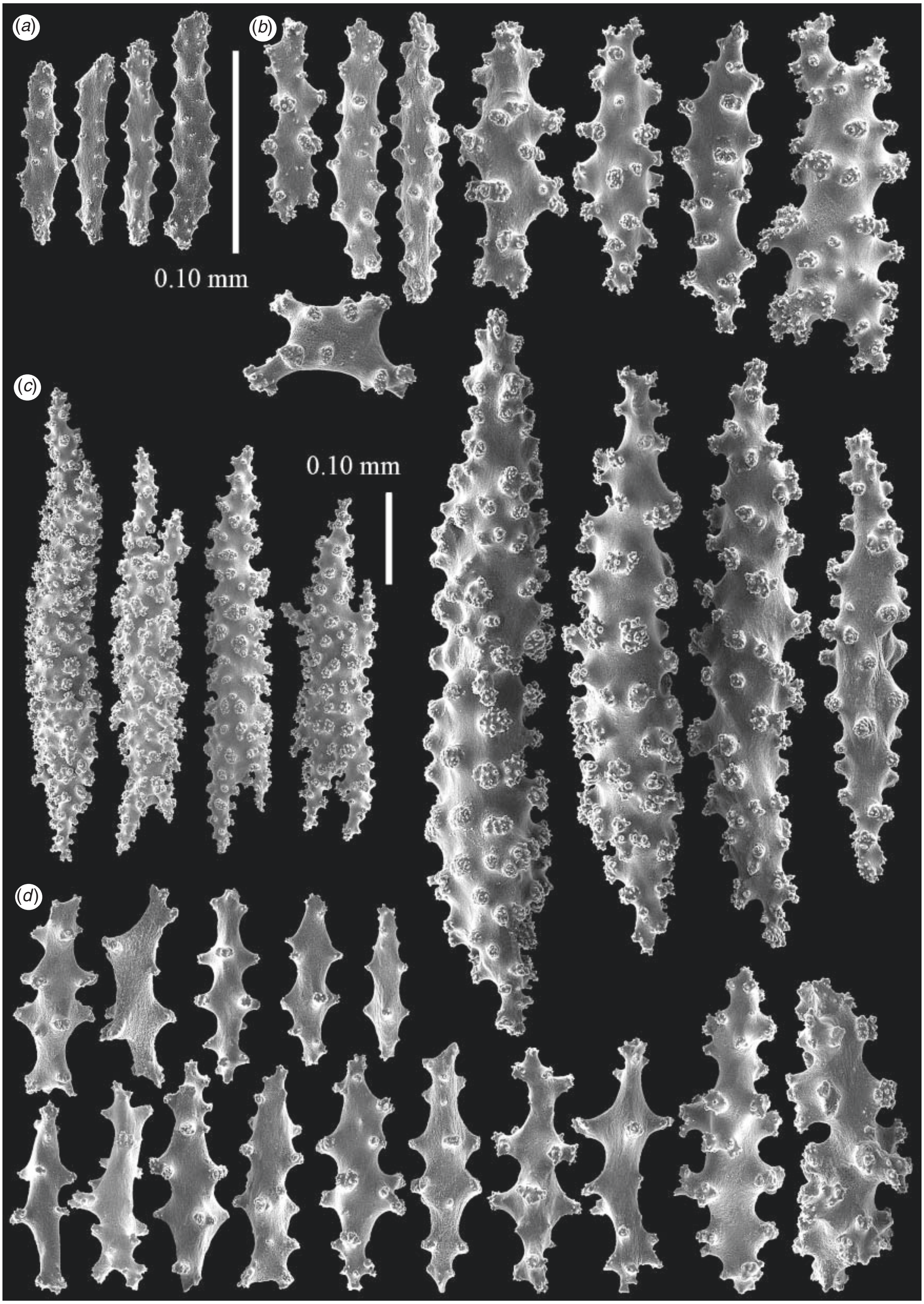

Fig. 11. *Inconstantia procera*, paratype, USNM 1178386: (*a*) anthocodial sclerites; (*b*) sclerites of calyx; (*c*) sclerites of calyx, different scale; (*d*) sclerites of stolon. Scale at (*b*) applies to (*a*) and (*d*).

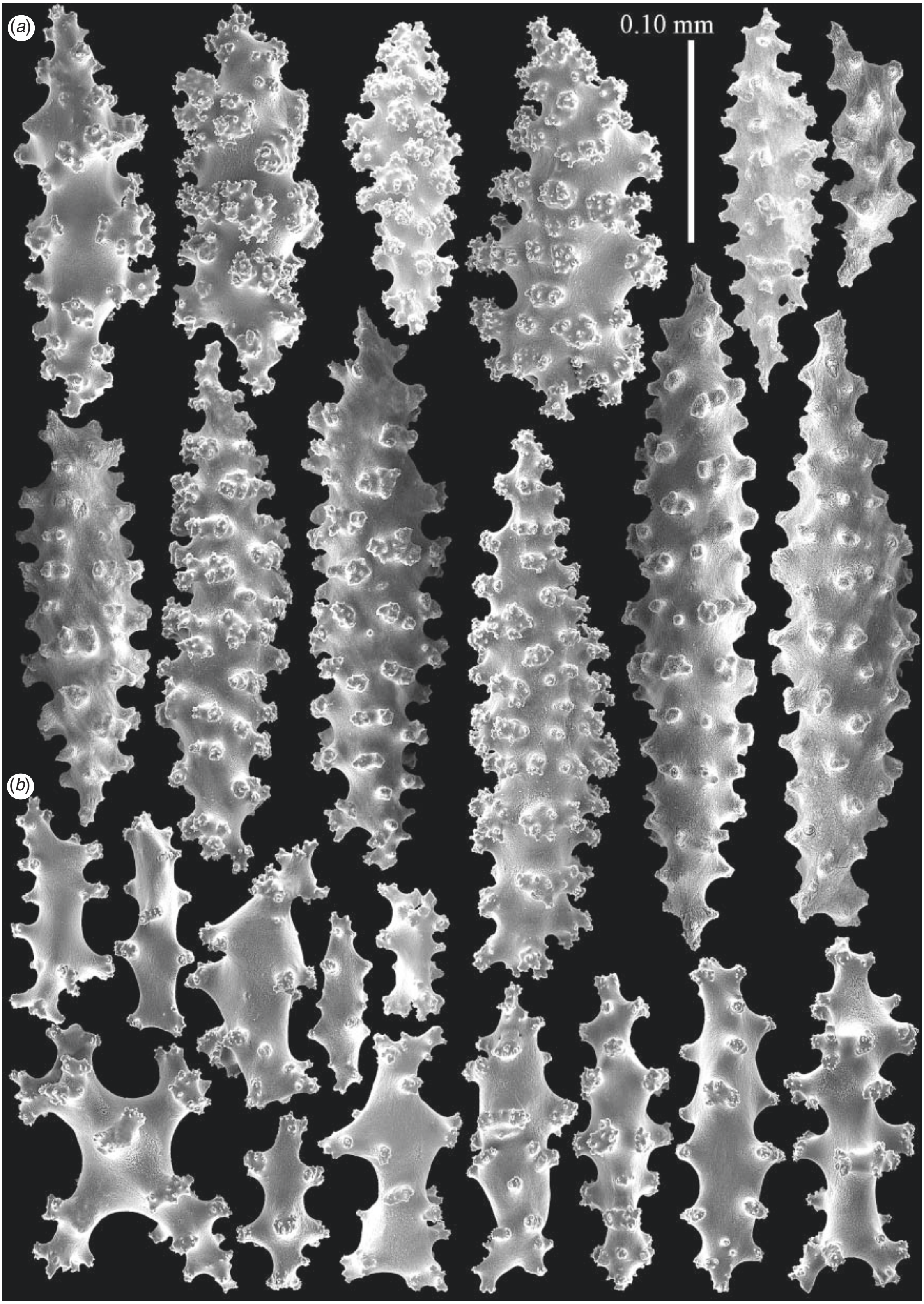

Fig. 12. *Inconstantia procera*, paratype, RMNH Coel. 40044: (*a*) sclerites of calyx; (*b*) sclerites of stolon.

Colour in life transparent; calyx yellowish-brown but often appearing reddish due to overgrowth by algae. In EtOH, cream to white.

Distribution

Southern South Africa from Cape Peninsula to Algoa Bay, Eastern Cape Province.

Remarks

The paratypes are similar to the holotype but in general have shorter calyces, up to 6 mm tall. Some of the paratypes have sclerites very similar to the holotype in size and form, while others have larger spindles (Figs 11, 12). USNM 1178386 has spindles up to 0.52 mm long and 0.08 mm wide, and the larger sclerites have dense tubercular ornamentation and side branches (Fig. 11*c*). RMNH Coel. 40044 has spindles up to 0.34 mm long, including some very stout forms to 0.12 mm wide (Fig. 12*a*). The sclerites found in the anthocodiae and stolons of these specimens (Figs 11*a, d*, 12*b*) are very similar to those of the holotype (Fig. 10*a, c*). Despite the variability in the size and form of spindles in the calyx, all specimens are genetically identical at 28S rDNA and COI, and differ by <0.3% at *mtMutS*.

I. procera, sp. nov., and *I. pannucea*, the two species of *Inconstantia* with tall calyces, resemble superficially many of the species that have been assigned to genus *Clavularia*. Only four species of *Clavularia* have been reported previously from South Africa (Williams 1992*b*), however, and none of them match the material we have described here. *C. diademata* Broch, 1939, described from Table Bay, Cape Peninsula, has a unique anthocodial armature consisting of a collaret and 16 points, and the stolon sclerites are long, slender needles up to 0.6 mm long. Thomson (1921) identified a species from Cape Infanta as *C. elongata* Wright & Studer, 1889, which he designated var. *africana* without providing a description. *C. elongata* from the type locality (Azores) has anthocodial sclerites arranged in a collaret and points, and the sclerites in the calyx are large spindles and clubs up to 0.83 mm long. *C. cylindrica* Wright & Studer, 1889, reported from False Bay by Thomson (1923) and from 547 m depth by Tixier-Durivault (1954), lacks a collaret and points, but has spindles up to 0.2 mm long in the tentacles. Finally, *C. parva* Tixier-Durivault, 1964, described from a depth of 590 m in southern Mozambique, has very low, mound-like calyces that are spaced well apart on a narrow stolon, and sclerites arranged en chevron in eight longitudinal rows on the distal portion of the anthocodia. None of the three species of *Inconstantia* described here match these descriptions or those of any other described species of *Clavularia* apart from the Mediterranean species mentioned above.

Of the three species of *Inconstantia* described here, *I. procera* appears to be the most common and widespread. We encountered it at several sites in Algoa Bay as well as in False Bay, Cape Peninsula. In contrast, *I. exigua* and *I. pannucea* were each encountered only once, in the Cape Peninsula region.

Etymology

Latin: *procerus*, meaning tall, in reference to the tall calyces of this species relative to others in the genus.

Family **CORNULARIIDAE** Dana

Genus ***Cornularia*** Lamarck

Cornularia pabloi, sp. nov.

Fig. 6*c–f*

Material examined

Holotype. South Africa, Port Elizabeth, Algoa Bay, Riy Banks 1 (33°59.097′S, 25°51.774′E), depth 15–20 m, 11.iii.2008, coll. C. S. McFadden [SAF089] (RMNH Coel. 40197).

Paratypes. Same data as holotype [SAF095] (USNM 1178390). [SAF096]

Other material examined. *Cornularia cornucopiae* (Pallas, 1766), Spain, Cádiz, El Chato (36°31′N, 6°16′W), intertidal, 9.ii.1990 (RMNH Coel. 23137); *C. cornucopiae*, Spain, Cádiz, Caños de Meca (36°11′N, 6°2′W), intertidal, 11.ii.1990 (RMNH Coel. 23138); *C. cornucopiae*, Spain, Cádiz, La Caleta, 6 m depth, 2012, coll. P. López-González.

Description

Colonies of small polyps (Fig. 6*c, d*) connected by thin, tubular stolons, 0.2 mm in diameter. Stolons covered by yellowish cuticle. Polyps surrounded by clear, gelatinous-looking cuticular envelope, 2–3 mm tall and flared at distal end, with an opening 0.8 mm in diameter (Fig. 6*e, f*). Most polyps retracted into cuticular envelope, appearing flat-topped due to straight upper margins of cuticle (Fig. 6*e*); upper portion of envelope appearing empty in some very deeply retracted polyps (Fig. 6*f*). Some polyps with anthocodia and tentacles partially expanded, up to 5 mm tall. Polyps with 13–15 pairs of pinnules arranged in single row along each side of tentacle rachis. No sclerites.

Distribution

Algoa Bay, Eastern Cape Province, South Africa.

Remarks

The genus *Cornularia* is unique among octocorals in having the polyps covered by a theca-like chitinous envelope into which they can be withdrawn. The well known European species *C. cornucopiae* (Pallas, 1766) has been redescribed and illustrated well in recent years by Weinberg (1978) and López-González *et al*. (1995). *C. cornucopiae* is common in the western Mediterranean (e.g. Betti *et al*. 2011) and has also been recorded from sites in the north-eastern Atlantic, including France, Spain, Portugal and the Azores (López-González *et al*. 1995). We compared *C. pabloi*, sp. nov., to RMNH Coel. 23137 and 23138, specimens of *C. cornucopiae* from Spain that were examined and described by López-González *et al*. (1995), and to newly collected material from the same locality, also provided by P. López-González.

A complete lack of sclerites in all parts of the colony limit the taxonomic characters available to describe and compare species of *Cornularia*, and the South African specimens were not preserved appropriately for histological examination. Relative to the Spanish specimens of *C. cornucopiae*, *C. pabloi* has slightly larger calyces (on average 2.5 mm tall by 0.8 mm wide compared with 1.9 mm tall by 0.5 mm wide) and a much higher density of polyps. These traits have, however, been reported to vary both geographically as well as seasonally in Mediterranean populations; for instance, Betti *et al*. (2011) documented seasonal variation in average calyx height from 1.5 to 2.6 mm and a 15-fold annual change in polyp density in one Italian population of *C. cornucopiae*. The differences we observed between *C. cornucopiae* and *C. pabloi* in these traits are, therefore, unlikely to be taxonomically meaningful. Weinberg (1978) reported 13–15 pairs of pinnules per tentacle, and López-González *et al*. (1995) reported 14–18 in *C. cornucopiae*, both estimates that overlap our estimates of 13–15 in *C. pabloi*. On the basis of gross colony morphology, therefore, there appear to be few if any diagnostic differences between *C. cornucopiae* and *C. pabloi*.

Comparison of DNA sequences for COI and 28S rDNA, however, indicate that there are large genetic differences between the Mediterranean and South African *Cornularia* populations (uncorrected *P* distance, COI: 5.8%, 28S: 4.7%) (Fig. 1). Intraspecific genetic distance values at COI are typically <1.0% in octocorals, and distances as great as 5% among congeneric species are rare (McFadden *et al*. 2011). The high values we obtained (>5%) clearly support the status of *C. pabloi* as a distinct species.

The disjunct biogeographic distribution of the North Atlantic/Mediterranean and South African *Cornularia* populations also supports their status as separate species: to date, none of the species of alcyonacean octocorals whose identity and occurrence in South Africa have been verified have geographical distributions that include the North Atlantic or Mediterranean regions (Williams 1992*a*). *C. cornucopiae* has not been reported from south of the Strait of Gibraltar (although most of the western coast of Africa has been inadequately explored). The only other species possibly attributable to genus *Cornularia* is *C. australis*, Busk, 1867 from Australia, although its validity is questionable (Utinomi 1955).

Etymology

Named in honour of octocoral researcher Pablo López-González for his contributions to the study of stoloniferous octocorals, and for kindly providing us with material of *C. cornucopiae* for comparison.

Discussion

Our records of new taxa add two families, Arulidae and Cornulariidae, to the 26 families of octocorals previously documented to occur in the Agulhas Bioregion of South Africa. Three genera are newly recorded, one of which – *Inconstantia*, gen. nov. – is known so far only from southern South Africa, increasing the number of octocoral genera that are endemic to that biogeographic region to 13. *Cornularia* also occurs in the Mediterranean and north Atlantic, and we suspect that *Arula* will be found in other parts of the Indo-Pacific (e.g. Fig. 2*d*). With additional molecular phylogenetic analyses and family-level revisions it is likely, however, that the number of higher taxa known to be endemic to the unique Agulhas Bioregion of South Africa will continue to increase (e.g. McFadden and van Ofwegen 2012).

The South African species we describe here illustrate the lack of correspondence between morphological characters, which are sparse in these simple stoloniferous octocorals, and their phylogenetic relationships. Within *Inconstantia*, for example, we find three species that differ greatly in calyx height and sclerite form despite their apparent genetic homogeneity. Within Clavulariidae, the height of the calyx has been proposed as a subfamilial character (Bayer 1981*a*, 1981*b*), and genera have been divided into separate groups based on whether they have tall, non-contractile calyces or short calyces that can be contracted more-or-less flush with the coenenchyme. Both morphologies are represented within *Inconstantia*, and the two species with the most extreme differences in calyx height – *I. procera* and *I. exigua* – are extremely similar genetically for the markers we sequenced here (Fig. 1). The differences in sclerite form between these two species would also normally justify classifying them in separate genera. Species with spindles such as those found in the calyx and stolons of *I. procera* would typically be placed in *Clavularia*, while the possession of radiates or plate-like sclerites, as seen in both *I. exigua* and *I. pannucea*, typify a variety of the clavulariid genera with low calyces such as *Sarcodictyon*, *Azoriella*, and *Rolandia* Lacaze-Duthiers, 1900. The three species of *Inconstantia* illustrate clearly the evolutionary lability of both calyx height and sclerite form, and the consequent unreliability of these morphological traits as genus-level taxonomic characters in Clavulariidae.

The phylogenetic distribution of genera of Clavulariidae within subclass Octocorallia illustrates clearly the polyphyletic nature of this family, and the repeated independent evolution of the stoloniferous growth form. Representatives of only half (13 of 26) of the described genera of Clavulariidae are included in our analysis, yet they belong to seven different clades (Fig. 1), most of them more closely related to non-stoloniferan families than to other clades of Clavulariidae. As exemplified at the species level by *Inconstantia*, phylogenetic affinities of genera also do not appear to be predicted by morphology: morphologically similar genera fall into phylogenetically disparate clades, while morphologically disparate genera display close phylogenetic affinities. For example, the four genera *Carijoa*, *Paratelesto*, *Telesto* and *Telestula*, united by a similar growth form in which secondary polyps arise from an axial polyp (Bayer 1981*a*), belong to four phylogenetically distant clades. *Telestula* is the only stoloniferan genus known so far to belong to the Calcaxonia–Pennatulacea clade of octocorals. In contrast, *Carijoa* belongs to Holaxonia–Alcyoniina, and is close phylogenetically to *Cryptophyton*, a membranous genus without secondary budding, and with low calyces and entirely different types of sclerites than those found in *Carijoa. Cryptophyton*, in turn, is very similar morphologically (in both growth form and sclerite type) to *Incrustatus*, which is found in a very different clade, allied with the morphologically highly variable *Inconstantia*.

Although it is obvious that family Clavulariidae is in need of complete revision, and that several new families will need to be defined to reflect adequately the phylogenetic distribution of stoloniferous genera, such a revision is still somewhat premature. Additional molecular phylogenetic analyses that include a more complete representation of genera of Clavulariidae and species of the large genus *Clavularia* will be necessary before we can begin to interpret fully the morphological distinctions among clades. As has been the case for some genera of Alcyoniidae (McFadden *et al*. 2006*b*, 2009), a knowledge of phylogenetic affinities, poorly predicted by the morphological characters traditionally used for taxonomy, may guide us to a different morphological character set that better reflects the phylogenetic relationships among and within genera.

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