Phylogenetic reconstruction of scleraxonian octocorals supports the resurrection of the family Spongiodermidae (Cnidaria, Alcyonacea)

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Abstract. The Scleraxonia are a group of octocorals that share similarities of their axis morphology. However, molecular phylogenetic analyses have shown this group to be largely polyphyletic. As a result, there is a significant lack of understanding of what constitutes distinct evolutionary units among members of this group, particularly at the family level. Prompted by the discovery of an unknown spongiodermid scleraxonian octocoral (Anthothelidae) from shallow water off the Pacific coast of lower Baja California, a phylogenetic analysis of the undescribed specimen, together with members of six scleraxonian families and an additional 29 non-scleraxonian octocorallian families was performed. Two mitochondrial loci (*mtMutS* and *COI*) and one nuclear locus (*28S*) supported a monophyletic spongiodermid clade (*Homophyton*, *Callipodium*, *Diodogorgia*, *Titanideum* and *Sclerophyton*, gen. nov.) at the family-level. The unknown scleraxonian was supported as a new genus and species within the spongiodermid clade, sister to the western Atlantic genus *Titanideum*. A morphological examination of the taxa within this clade revealed shared morphological similarities in solenial (boundary) canals, and medullar and cortical sclerites. A revision, with illustrations, of the Spongiodermidae was performed. Similar to previous studies, this study underscores the importance of combined morphological and molecular analyses in order to resolve unstable systematic relationships among octocorals.

Introduction

Octocorals are a taxonomically diverse group of mostly colonial benthic marine organisms that are found worldwide, from shallow water to the deep sea (Daly *et al*. 2007). They possess polyps with eight tentacles, and produce skeletal components that are mostly comprised of calcitic material. The Scleraxonia is a group of gorgonian (or branching) octocorals consisting of seven families that are recognised by the presence of an axis composed of fused or unfused sclerites (microscopic biomineralised skeletal components) (Bayer 1981; Fabricius and Alderslade 2001; Daly *et al*. 2007). Within the Scleraxonia, members of the family Anthothelidae Broch, 1916 belong to three subfamilies (Anthothelinae, Semperininae and Spongiodermatinae) (*sensu* Bayer 1981) that are characterised by an axis that contains two layers, an inner medulla and an outer cortex, separated by boundary canals (Daly *et al*. 2007). Phylogenetic analyses of the Scleraxonia have revealed this group to be largely polyphyletic (Sanchez *et al*. 2003; McFadden *et al*. 2006). For example, many anthothelid taxa are spread throughout the octocorallian tree, and members of the anthothelid subfamilies Semperininae (*Iciligorgia*, *Solenocaulon*) and Anthothelinae (*Anthothela*) group within a large clade consisting of many taxa from the Holaxonia and Alcyoniina ('Holaxonia–

Alcyoniina' clade; McFadden *et al*. 2006). In addition, scleraxonians from the families Coralliidae and Paragorgiidae group in a separate '*Anthomastus–Corallium*' clade, while *Briareum* (Briareidae) and *Erythropodium caribaeorum* (Anthothelidae) fall outside the three principal octocorallian clades (*sensu* McFadden *et al*. 2006; see also McFadden and van Ofwegen 2012, 2013).

The discovery of an undescribed shallow-water scleraxonian octocoral from the lower Baja Peninsula (Pacific Ocean), similar in morphology to the western Atlantic spongiodermid *Titanideum* (Anthothelidae), prompted the need for a morphological and phylogenetic analysis of the subfamily Spongiodermatinae in the context of a larger comprehensive octocorallian phylogeny. In order to confirm the identity and phylogenetic placement of the undescribed scleraxonian, a phylogenetic analysis was performed using representatives of six of the eight putative scleraxonian families (Briareidae, Anthothelidae, Subergorgiidae, Paragorgiidae, Coralliidae and Melitheidae) together with members of 29 non-scleraxonian octocorallian families. In addition, a revision of the resurrected family Spongiodermidae Wright & Studer, 1889 was completed, and a new genus and species, *Sclerophyton bajaensis*, gen. nov., sp. nov., are described.

Materials and methods

Samples for genetic analyses

Scleraxonian colonies were sampled from the collections of the Smithsonian National Museum of Natural History (NMNH). Representatives from six of the eight putative scleraxonian families (Briareidae, Anthothelidae, Subergorgiidae, Paragorgiidae, Coralliidae and Melitheidae) were included with the exception of Parisididae and Dendrobrachiidae (Table 1). Members of the latter two families were either unavailable or were not suitable for genetic analysis. If members of a particular taxonomic group did not yield suitable amounts of genomic DNA for downstream analyses, sequences from GenBank were used, if available. In order to robustly interpret phylogenetic relationships among the Scleraxonia, members of 29 octocorallian families representing the three octocorallian orders (Pennatulacea, Helioporacea and Alcyonacea) and alcyonacean suborders or 'grades/' (Scleraxonia, Holaxonia, Calcaxonia, Stolonifera and Alcyoniina, with the exception of Protoalcyonaria) (Daly *et al.* 2007) were used for phylogenetic analyses.

Molecular analyses – DNA extraction, amplification, sequencing

Three to four polyps, or ~4–5 mm^3 of tissue were used for DNA extraction using a DNeasy blood and tissue kit (Qiagen, Inc., Valencia, CA, USA). Final elution was in 60 µL of manufacturer-provided AE buffer, and samples were stored at −20°C. Dried or ethanol-preserved colonies (70% to 95% EtOH) were used, although higher DNA yields were generally obtained from colonies collected within 10 years and/or stored in 95% EtOH. For colonies collected >10 years ago and stored in 70% EtOH, dried colonies of the same taxa tended to be better suited for DNA extraction. The polymerase chain reaction (PCR) was used to amplify two mitochondrial loci – *mtMutS*, AnthoCorMSH: 5′-AGG AGA ATT ATT CTA AGT ATG G-3′ (Herrera *et al.* 2010), Mut3458R: 5′-TSG AGC AAA AGC CAC TCC-3′ (France and Hoover 2001); and *COI*, COI-LA-8398-F: 5′-GGA ATG GCG GGG ACA GCT TCG AGT ATG TTA ATA CGG-3′, COIoct-R: 5′-ATC ATA GCA TAG ACC ATA CC-3′ (McFadden *et al.* 2011) – and one nuclear locus – *28S*, Far: 5′-CAC GAG ACC GAT AGC GAA CAA GTA-3′, Rab: 5′-TCG CTA CGA GCT TCC ACC AGT GTT T-3′ (McFadden and van Ofwegen 2012).

Polymerase chain reaction amplifications used final concentrations of 3 pmol of each primer, 500 µM dNTPS, 3 mM MgCl and 1–5 µL of genomic DNA (varying final elution concentrations) using 0.05 U µL^{-1} of Biolase DNA polymerase (Bioline, Inc., Taunton, MA, USA) and manufacturer-provided buffers. Sterile DNA-grade water was added to make final reaction volumes of 10 or 20 µL. Thermal cycler reaction parameters included an initial denaturing step of 94°C for 3 min, followed by 35 or 40 rounds of 94°C for 30 s, annealing temperatures of either 48°C, 50°C or 55°C for 30 s or 1 min, an extension at 74°C for 30 s or 1 min, and a final extension step of 72°C for 5 min. Polymerase chain reaction products were neutralised using ExoSAP-IT (Affymetrix, Santa Clara, CA, USA), and prepared for sequencing using BigDye Terminater v3.1 (Applied Biosystems, Grand Island, NY,

USA). Cycle-sequenced products were purified using Sephadex G-50 Fine (GE Healthcare, Piscataway, NJ, USA), and DNA sequencing was performed on an ABI 3730 at the Laboratories of Analytical Biology (NMNH). Sequence contigs were collated and edited using Geneious Pro 7.1.7 (Biomatters; http://www.geneious.com/).

Phylogenetic analyses

Nuclear and mitochondrial loci were analysed separately to determine if the phylogenetic signal between the two datasets were similar. The two mitochondrial loci were analysed together as a single concatenated dataset (*mtMutS+COI*), and the nuclear locus (*28S*) was examined alone. Because many of the museum-extracted scleraxonian samples did not amplify well for *28S*, resulting in a limited dataset for this locus compared with the mitochondrial dataset, a complete concatenated analysis was not performed. Protein coding mitochondrial loci were aligned using MUSCLE (multiple sequence comparison by log-expectation) (Edgar 2004), and rDNA was aligned using MAFFT (Katoh and Kuma 2002). MrAIC (Nylander 2004), using the Akaike information criterion (AIC), was used to determine the best model of nucleotide sequence evolution for each locus – GTR+G+I for all loci.

Phylogenetic reconstruction was performed on two datasets, *mtMutS+COI* and *28S*, using Bayesian inference (BI) performed with MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003), maximum likelihood (ML) with RAxML (Stamatakis 2006), and maximum parsimony (MP) with PAUP* v4.0b10 (Swofford 2004). All analyses were run on the Topaz Cluster, which is maintained at the Smithsonian NMNH. Bayesian inference analyses consisted of two independent runs with four chains, with trees sampled every 100th generation. Markov chain Monte Carlo (MCMC) runs were carried out for 12 million generations for the *mtMutS+COI* dataset, and 10 million generations for the *28S* dataset. The *mtMutS+COI* dataset was partitioned into character sets for each locus, and the model of sequence evolution chosen by MrAIC applied to each partition. All model parameters (tratio, statefreq, shape, pinvar) were unlinked, and the rate prior (prset ratepr) was set to 'variable'. To increase the efficiency with which the four chains exchanged information (up to 62% for *mtMutS+COI*, and 50% for *28S*), the heating parameter (lset temp) was set to 0.04 and 0.08, respectively. Convergence was determined when the average standard deviation of split frequencies was <0.01 and the potential scale reduction factor (PSRF) was 1.00. Tracer v1.5 (Rambaut and Drummond 2009) was used to confirm the stationarity of the runs, and to verify that an adequate number of trees were sampled from the posterior distribution (effective sample size (ESS) > 4500 for all parameters). To calculate posterior probabilities, a 'burn-in' of 25% adequately removed trees before convergence. Maximum parsimony analyses using PAUP* v4.0b10 utilised heuristic searches with default options. Maximum likelihood with RAxML was run using rapid bootstrap analysis and search for best-scoring ML tree (-f m) and the GTRGAMMA model (-m). One thousand bootstrap replicates were performed with MP and ML.

Three outgroups were used for each dataset. *Montastraea franksi* (Scleractinia) (GenBank accession # NC007225),

Table 1. Taxonomic information and GenBank accession numbers for octocoral taxa and outgroups used for phylogenetic analyses

Taxa in bold represent newly sequenced individuals (this study); voucher numbers for these specimens are in parentheses following their genus/species identification

Family	Genus/species	GenBank accession		
		COI	_mtMutS_	_28S_ rDNA
Acanthoaxiidae	_Acanthoaxis wirtzi_	JX203816	JX203764	JX203635
Acanthogorgiidae	_Acanthogorgia breviflora_	GQ342378	GQ342464	JX203636
Acrossotidae	_Acrossota amboinensis_	GQ342379	DQ985956	JX203637
Alcyoniidae	_Acrophytum claviger_	JX203823	JX203770	JX203655
Alcyoniidae	_Alcyonium coralloides_	GQ342380	GQ342465	JX203640
Alcyoniidae	_Anthomastus ritteri_	JX203824	DQ302816	JX203761
Alcyoniidae	_Cladiella sphaerophora_	GQ342386	GQ342471	JX203653
Alcyoniidae	_Discophyton rudyi_	GQ342387	DQ302808	JX203659
Alcyoniidae	_Eleutherobia aurea_	JX203817	JX203766	GQ377454
Alcyoniidae	_Klyxum utinomii_	GQ342392	GQ342476	JX203654
Alcyoniidae	_Lampophyton planiceps_	GQ342393	GQ342477	JX203656
Alcyoniidae	_Lobophytum pauciflorum_	GQ342394	DQ280575	JX203649
Alcyoniidae	_Malacacanthus capensis_	GQ342395	DQ302811	JX203660
Alcyoniidae	_Nephthyigorgia_ sp.	JX203864	JX203804	JX203732
Alcyoniidae	_Paraminabea aldersladei_	JX203819	JX203767	JX203763
Alcyoniidae	_Rhytisma fulvum_	GQ342396	GQ342478	JX203728
Alcyoniidae	_Sarcophyton ehrenbergi_	JX203821	DQ280516	JX203650
Alcyoniidae	_Sinularia querciformis_	GQ342399	FJ621469	JX203652
Alcyoniidae	_Thrombophyton coronatum_	GQ342400	DQ302814	JX203661
Anthothelidae	_Alertigorgia_ sp.	JX203825	JX203771	JX203662
Anthothelidae	**_Anthothela_ cf. _grandiflora_ (USNM1095147)**	KP714035	KP713985	KP714021
Anthothelidae	**_Anthothela_ sp. (USNM1139023)**	KP714036	KP713986	KP714022
Anthothelidae	**_Anthothela_ sp. (USNM83402)**	KP714037	KP713987	KP714023
Anthothelidae	_Erythropodium caribaeorum_	GQ342401	GQ342480	JX203664
Anthothelidae	**_Erythropodium caribaeorum_ (USNM1017543)**	KP714048	KP713998	n/a
Anthothelidae	**_Erythropodium caribaeorum_ (USNM81337)**	KP714049	KP713999	n/a
Anthothelidae	**_Iciligorgia brunnea_ (USNM86848)**	KP714050	KP714000	KP714024
Anthothelidae	_Iciligorgia_ sp.	GQ342402	GQ342481	JX203665
Anthothelidae	_Solenocaulon_ sp.	GQ342404	GQ342483	JX203668
Arulidae	_Arula petunia_	JX203827	JX203773	JX203670
Briareidae	_Briareum asbestinum_	GQ342405	GQ342484	JX203669
Briareidae	**_Briareum asbestinum_ (USNM1122631)**	KP714038	KP713988	n/a
Chrysogorgiidae	_Radicipes gracilis_	HM590861	DQ297424	n/a
Chrysogorgiidae	_Stephanogorgia faulkneri_	GQ342406	GQ342485	JX203718
Chrysogorgiidae	_Trichogorgia capensis_	JX203863	JX203798	JX203719
Clavulariidae	_Azoriella bayeri_	GQ342407	GQ342486	JX203672
Clavulariidae	_Carijoa riisei_	JX203829	JX203775	JX203673
Clavulariidae	_Cervera atlantica_	JN620805	JN620804	JX203677
Clavulariidae	_Clavularia_ sp.	JX203834	JX203778	JX203678
Clavulariidae	_Inconstantia exigua_	JX203870	JX203790	JX203690
Clavulariidae	_Incrustatus comauensis_	GQ342391	GQ342475	JX203691
Clavulariidae	_Knopia octocontacanalis_	GQ342410	GQ342488	JX203692
Clavulariidae	_Paratelesto_ sp.	GQ342411	GQ342489	JX203693
Clavulariidae	_Telestula_ sp.	JX203846	DQ302803	JX203697
Coelogorgiidae	_Coelogorgia palmosa_	GQ342413	DQ302805	JX203698
Coralliidae	**_Corallium medea_ (USNM1110365)**	KP714040	KP713990	n/a
Coralliidae	**_Corallium rubrum_ (USNM45614)**	KP714041	KP713991	n/a
Coralliidae	**_Paracorallium tortuosum_ (USNM1072445)**	KP714051	KP714001	n/a
Coralliidae	**_Paracorallium tortuosum_ (USNM1196760)**	KP714052	KP714002	KP714025
Cornulariidae	_Cornularia pabloi_	JX203847	JX203792	JX203699
Ellisellidae	_Ellisella_ sp.	JX203850	JX203793	JX203702
Ellisellidae	_Viminella_ sp.	JX203852	JX203794	JX203703
Gorgoniidae	_Eugorgia multifida_	GQ342417	GQ342494	JX203706
Gorgoniidae	_Eunicella tricoronata_	JX203853	JX203795	JX203707
Gorgoniidae	_Gorgonia flabellum_	GQ342418	GQ342495	JX203708
Gorgoniidae	_Leptogorgia rigida_	GQ342420	GQ342496	JX203709

Table 1.   (*continued*)

Family	Genus/species	COI	mtMutS	28S rDNA
		COI	*mtMutS*	*28S* rDNA
Gorgoniidae	*Pacifigorgia media*	GQ342421	GQ342497	JX203710
Gorgoniidae	*Pinnigorgia flava*	GQ342422	GQ342498	JX203711
Gorgoniidae	*Pseudopterogorgia bipinnata*	GQ342423	GQ342499	JX203712
Gorgoniidae	*Pterogorgia anceps*	GQ342424	GQ342500	JX203714
Gorgoniidae	*Rumphella* sp.	JX203855	JX203797	JX203715
Helioporidae	*Heliopora coerulea*	GQ342426	DQ302872	JX203716
Ifalukellidae	*Ifalukella yanii*	GQ342427	GQ342501	JX203717
Isididae	*Acanella eburnea*	EF672731	EF672731	n/a
Melithaeidae	*Acabaria erythraea*	GQ342430	GQ342503	JX203720
Melithaeidae	*Acabaria sinaica*	GQ342431	GQ342504	JX203721
Melithaeidae	*Clathraria rubrinodis*	GQ342432	GQ342505	JX203722
Melithaeidae	*Melithaea* sp.	JX203856	JX203799	JX203723
Melithaeidae	*Wrightella coccinea*	JX203858	JX203801	n/a
Nephtheidae	*Eunephthya thyrsoidea*	JX124384	JX124364	JX124340
Nephtheidae	*Gersemia rubiformis*	GQ342390	GQ342474	JX203648
Nephtheidae	*Paralemnalia thyrsoides*	GQ342436	GQ342509	JX203727
Nidaliidae	*Chironephthya* sp.	GQ342440	GQ342513	JX203730
Nidaliidae	*Pieterfaurea khoisanianum*	GQ342437	GQ342510	JX203657
Paragorgiidae	**Paragorgia alisonae (USNM1126251)**	KP714053	KP714003	n/a
Paragorgiidae	**Paragorgia arborea (USNM1092768)**	KP714054	KP714004	KP714026
Paragorgiidae	**Paragorgia arborea (USNM1120404)**	KP714055	KP714005	KP714027
Paragorgiidae	**Paragorgia johnsoni (USNM73767)**	KP714056	KP714006	KP714028
Paragorgiidae	**Paragorgia regalis (USNM1072340)**	KP714057	KP714007	n/a
Paragorgiidae	**Paragorgia sp. (USNM1075751)**	n/a	n/a	KP714031
Paragorgiidae	**Paragorgia sp. (USNM1075751)**	KP714059	KP714009	n/a
Paragorgiidae	**Paragorgia sp. (USNM1123838)**	KP714060	KP714010	n/a
Paragorgiidae	**Paragorgia sp. (USNM1164628)**	KP714058	KP714008	n/a
Paragorgiidae	**Sibogagorgia cauliflora (USNM54831)**	KP714062	KP714012	n/a
Paragorgiidae	**Sibogagorgia dennisgordoni (NIWA3328)**	KP714063	KP714013	n/a
Paralcyoniidae	*Paralcyonium spinulosum*	JX124389	DQ302833	JX124347
Paralcyoniidae	*Studeriotes* sp.	GQ342443	GQ342515	JX124348
Pennatulidae	*Gyrophyllum sibogae*	JX203865	DQ302869	JX203740
Plexauridae	*Astrogorgia* sp.	JX203861	JX203805	JX203733
Plexauridae	*Bebryce* sp.	JX203862	JX203806	JX203734
Plexauridae	*Eunicea tourneforti*	GQ342445	GQ342517	n/a
Plexauridae	*Menella* sp.	GQ342447	GQ342519	JX203736
Plexauridae	*Muricea atlantica*	GQ342448	GQ342520	JX203747
Plexauridae	*Muriceopsis flavida*	GQ342449	GQ342521	JX203744
Plexauridae	*Plexaura kuna*	JX203866	JX203807	JX203748
Plexauridae	*Plexaurella nutans*	GQ342451	GQ342523	JX203745
Plexauridae	*Pseudoplexaura wagenaari*	GQ342452	GQ342524	JX203746
Primnoidae	*Callogorgia formosa*	GQ342453	GQ342525	JX203749
Primnoidae	*Thouarella grasshoffi*	FJ268636	GQ868334	n/a
Protoptilidae	*Distichoptilum gracile*	GQ342454	DQ302866	JX203739
Renillidae	*Renilla* sp.	GQ342455	GQ342526	n/a
Spongiodermatidae	**Callipodium (YPM8594)**	KP714039	KP713989	n/a
Spongiodermatidae	**Diodogorgia ceratosa (USNM1147814)**	KP714042	KP713992	n/a
Spongiodermatidae	*Diodogorgia nodulifera*	JX203826	JX203772	JX203663
Spongiodermatidae	**Diodogorgia nodulifera (USNM59128)**	KP714043	KP713993	n/a
Spongiodermatidae	**Diodogorgia nodulifera (USNM78673)**	KP714044	KP713994	n/a
Spongiodermatidae	**Diodogorgia nodulifera (USNM1147817)**	KP714045	KP713995	n/a
Spongiodermatidae	**Diodogorgia nodulifera (USNM1147822)**	KP714046	KP713996	n/a
Spongiodermatidae	**Diodogorgia nodulifera (USNM1147872)**	KP714047	KP713997	n/a
Spongiodermatidae	*Homophyton verrucosum*	GQ342403	GQ342482	JX203666
Spongiodermatidae	**Sclerophyton bajaensis (colony 1a) (USNM1246058)**	KP714067	KP714017	KP714030
Spongiodermatidae	**Sclerophyton bajaensis (colony 1b) (USNM1246058)**	KP714068	KP714018	n/a
Spongiodermatidae	**Sclerophyton bajaensis (colony 2) (USNM1246058)**	KP714069	KP714019	n/a
Spongiodermatidae	*Titanideum frauenfeldii*	FJ264916	GU563314	n/a

(*continued next page*)

Table 1.   (*continued*)

Family	Genus/species	GenBank accession		
		COI	*mtMutS*	*28S* rDNA
Spongiodermatidae	**Titanideum frauenfeldii (USNM49587)**	KP714065	KP714015	n/a
Spongiodermatidae	**Titanideum frauenfeldii (USNM60410)**	KP714066	KP714016	n/a
Subergorgiidae	**Annella mollis (USNM76231)**	KP714032	KP713982	n/a
Subergorgiidae	**Annella ornata (USNM75884)**	KP714033	KP713983	KP714020
Subergorgiidae	**Annella reticulata (USNM100821)**	KP714034	KP713984	n/a
Subergorgiidae	*Annella mollis*	GQ342456	JX203808	JX203750
Subergorgiidae	**Rosgorgia inexpetata (USNM1013161)**	KP714061	KP714011	KP714029
Subergorgiidae	**Subergorgia suberosa (USNM75340)**	KP714064	KP714014	n/a
Subergorgiidae	*Subergorgia suberosa*	GQ342457	JX203809	JX203762
Tubiporidae	*Tubipora* sp.	GQ342458	JX203811	JX203752
Virgulariidae	*Virgularia schultzei*	GQ342459	GQ342527	JX203743
Xeniidae	*Sarcothelia edmondsoni*	JX203868	JX203814	JX203757
Xeniidae	*Xenia hicksoni*	GQ342463	GQ342529	JX203759
Outgroups				
Actiniaria	*Metridium senile*	AF000023	n/a	n/a
Actiniaria	*Nematostella vectensis*	n/a	n/a	AY345871
Antipatharia	*Leiopathes glaberrima*	FJ597644	n/a	
Antipatharia	*Leiopathes* cf. *expansa*	n/a	n/a	FJ626241
Scleractinia	*Montastraea franksi*	NC007225	n/a	AY026375

Leiopathes glaberrima (Antipatharia) (FJ597644) and *Metridium senile* (Actiniaria) (AF000023) were used for the *MutS*+*COI* dataset. For *28S*, *Nematostella vectensis* (Actiniaria) (AY345871), *Montastraea franksi* (Scleractinia) (AY026375) and *Leiopathes* cf. *expansa* (Antipatharia) (FJ626241) were used.

Morphological analyses

Standard morphological terminology for octocorals is used, based on the glossary of Bayer *et al*. (1983). In addition, the abbreviation L : D is used to indicate the ratio of the length to diameter of a sclerite.

Results

Genomic DNA (gDNA) yields from NMNH scleractinian octocorals varied considerably. The greatest yields tended to be from samples stored in 95% EtOH and/or collected within 10 years. Genomic DNA was reliably recovered from dried specimens >10 years old; however, fungal contamination was common, and likely contributed to higher total gDNA yields as fungal nuclear rDNA was often preferentially amplified in many dried specimens. As a result, many scleraxonian specimens were not sequenced for octocoral-specific *28S*.

Phylogenetic reconstruction – Scleraxonia

Analyses of mitochondrial (*mtMutS*+*COI*) and nuclear (*28S*) loci each recovered phylogenies congruent with previous studies (e.g. McFadden *et al*. 2006; McFadden and van Ofwegen 2012 2013) (Fig. 1). Both phylogenies contained supported clades consistent with the 'Holaxonia–Alcyoniina' (HA), 'Anthomastus–Corallium' (AC) and 'Calcaxonia–Pennatulacea' (CP) clades discussed in McFadden *et al*. (2006); however, the AC and CP clades were unresolved with *28S* (Fig. 1*B*). Neither dataset recovered a monophyletic Scleraxonia, but instead scattered many of the families and genera throughout the octocorallian phylogeny. For example,

members of the families Subergorgiidae (*Subergorgia*, *Annella* and *Rosgorgia*) and Anthothelidae (*Erythropodium*, *Anthothela*, *Solenocaulon*, *Iciligorgia* and *Alertigorgia*) were both polyphyletic, with the anthothelid genera distributed within and outside the HA clade. Members of the Coralliidae and Paragorgiidae grouped within a well-supported clade that showed a close phylogenetic affinity to *Anthomastus ritteri* (Alcyoniidae) and *Paraminabea aldersladei* (Alcyoniidae) (*sensu* AC clade; McFadden *et al*. 2006) with the *mtMutS* +*COI* dataset (only *Anthomastus ritteri* with *28S*). With *mtMutS*+*COI*, the representative paragorgiids were not monophyletic; both species of *Sibogagorgia* (*S. dennisgordoni* and *S. cauliflora*) did not group with the *Paragorgia* spp., but were sister to a clade containing the *Paragorgia* species and the coralliids *Paracorallium tortuosum*, *Corallium rubrum* and *C. medea* (Fig. 1*A*).

Members of the anthothelid subfamily Anthothelinae (*Anthothela*, *Alertigorgia* and *Erythropodium*) were polyphyletic with both datasets. The *Anthothela* species grouped together within the HA clade but did not group with *Alertigorgia* sp., and *Erythropodium caribaeorum* was an unresolved lineage outside the HA clade. Members of another anthothelid subfamily, Semperininae (*Iciligorgia* and *Solenocaulon*), showed a close mutual phylogenetic relationship, and together with *Azoriella bayeri* and *Cervera atlantica* (both clavulariids) were sister to a monophyletic melithaeid clade. *Briareum asbestinum* (family Briareidae) fell outside the HA clade and grouped as a sister taxon to members the Spongiodermidae (formerly in the anthothelid subfamily Spongioderminae).

Spongiodermidae Wright & Studer, 1889 (resurrected family)

With both mitochondrial and nuclear datasets, members of the family Spongiodermidae (*Callipodium*, *Diodogorgia*, *Homophyton*, *Titanideum* and *Sclerophyton*, gen. nov.)

formed a well-supported clade outside the HA clade that was sister to *Briareum asbestinum*. This clade was unresolved among the other octocorallian taxa at deeper nodes with *mtMutS+COI* (Fig. 1*A*), but was sister to the HA clade with *28S* (Fig. 1*B*). Phylogenetic relationships among the Spongiodermidae with *mtMutS+COI* were largely consistent across all the reconstruction methods, and differed only with the placement of *Homophyton verrucosum* with maximum parsimony (MP) and likelihood (ML and MB) analyses (Fig. 2). For example, with BI and ML (Fig. 2*A*), *H. verrucosum* was sister to all of the spongiodermid genera. With MP (Fig. 2*B*), *H. verrucosum* was sister to a clade containing *Callipodium pacificum* and *Diodogorgia nodulifera*. The remaining taxa, *Titanideum frauenfeldii* and *Sclerophyton bajaensis*, sp. nov., grouped in a separate sister clade. With all methods, *Sclerophyton bajaensis*, sp. nov. was sister to *Titanideum frauenfeldii*, and *Callipodium pacificum* was sister to *Diodogorgia nodulifera*.

Discussion

Phylogenetic analysis of taxa representing six scleraxonian families recovered several polyphyletic clades scattered throughout a larger octocorallian phylogeny. However, one of the clades was consistent with a monophyletic Spongioderminae (subfamily within the Anthothelidae), but was resolved at the family level. In addition, this clade was sister to *Briareum asbestinum*, a member of the family Briareidae. This relationship could be interpreted as *B. asbestinum* belonging to a more inclusive Spongiodermidae (resurrected family). However, the genetic distance (uncorrected p) of *B. asbestinum* relative to the other spongiodermids was 3.9%, a value that may seem low, but can be interpreted as relatively high for mitochondrial DNA in octocorals (McFadden *et al*. 2011; see also Shearer *et al*. 2002). Additionally, the sclerite morphology of *B. asbestinum* is generally distinct from those of the spongiodermids. Therefore, these two indices suggest that *B. asbestinum* most likely belongs to an evolutionary lineage that is sister to, but separate from, the spongiodermids at the family level.

The pairwise genetic distance between *S. bajaensis*, sp. nov. and its sister taxon, *Titanideum*, was 0.9%. This value is above what is generally found for intraspecific variation in octocorals (0.5%), but within the range of what can be considered as separate congeneric species (McFadden *et al*. 2011). This suggests that *S. bajaensis*, sp. nov. could be a species of *Titanideum*; however, the genetic distance between *Callipodium* and *Diodogorgia*, also inter-oceanic taxa and with greater morphological differentiation, was 0.6%. Thus, although a strict interpretation of an octocoral 'barcode' suggests minimal taxonomic diversity among these four genera (*Titanideum*, *Sclerophyton*, *Callipodium* and *Diodogorgia*), the presence of discernable contrasting morphologies, most notably among

their boundary canal systems in cross section (Fig. 3), more likely points to a lack of genetic resolution, or 'false negatives' (McFadden *et al*. 2011), among these taxa. However, the minimal variation among sclerite morphologies between *Sclerophyton* and *Titanideum* makes these taxa difficult to distinguish (see 'Taxonomy'). Nevertheless, keeping *S. bajaensis*, sp. nov. in a separate genus sister to *Titanideum* is likely a better representation of the biodiversity and evolutionary history within the Spongiodermidae.

In addition to the spongiodermids, and similar to other studies (e.g. Aguilar-Hurtado *et al*. 2012; McFadden and van Ofwegen 2012, 2013; Reijnen *et al*. 2014), the melithaeids also formed a monophyletic clade. This clade was part of a larger well-supported clade containing three anthothelid taxa (*Iciligorgia*, *Solenocaulon* and *Alertigorgia*) and two alcyoniids (*Azoriella* and *Cervera*), and suggests a close phylogenetic relationship among these morphologically disparate taxa. Increased taxon sampling, specifically with the addition of the monotypic melithaeid genus *Asperaxis* (*sensu* Reijnen *et al*. 2014), and additional morphological analyses need to be performed to clarify the relationships among the taxa found in this clade.

Like other studies that have examined upper-level systematic relationships among octocorals (e.g. McFadden *et al*. 2006), this study highlights the limitation, yet relative usefulness, of standard molecular markers and well-sampled taxa to resolve enigmatic systematic relationships among octocorals. Undoubtedly, the addition of novel markers, most likely through the use of next-generation sequencing techniques, will help resolve many of the recalcitrant groups within the octocorallian phylogeny and enhance our understanding of this ecologically important and biologically diverse group of marine organisms.

Taxonomy

Order **ALCYONACEA**

Subordinal group **SCLERAXONIA**

Family **SPONGIODERMIDAE** Wright & Studer, 1889

Spongioderminae Wright & Studer, 1889: xxxi (in part: not *Iciligorgia*).
    Briareidae: Kükenthal, 1924: 9 (in part).
    Spongiodermatidae Aurivillius, 1931: 16 (in part: not *Suberia*).
    Spongiodermatinae Bayer, 1955: 208; 1956: F196; 1981: 945.—
        Williams, 1992*a*: 186.
    Type genus: *Spongioderma* Kölliker, 1871 (=*Homophyton*).

Diagnosis

Monomorphic Scleraxonia with its medulla surrounded by a ring of longitudinal solenial (boundary) canals; a secondary

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Fig. 1. Molecular phylogenies: (*A*) *mtMutS+COI*; (*B*) *28S*. Scleraxonian taxa are colour coded by family (see legend), and newly sequenced individuals contain their USNM ID. Each phylogeny was generated using Bayesian inference (BI), maximum likelihood (ML) and maximum parsimony (MP). Node support for BI, ML and MP is shown from left to right. Clades with support <50 for maximum likelihood and parsimony, and <0.80 for Bayesian posterior probabilities were collapsed to the next well-supported clade; '–' represents less than the threshold for that method or not following the branching topology for that method.
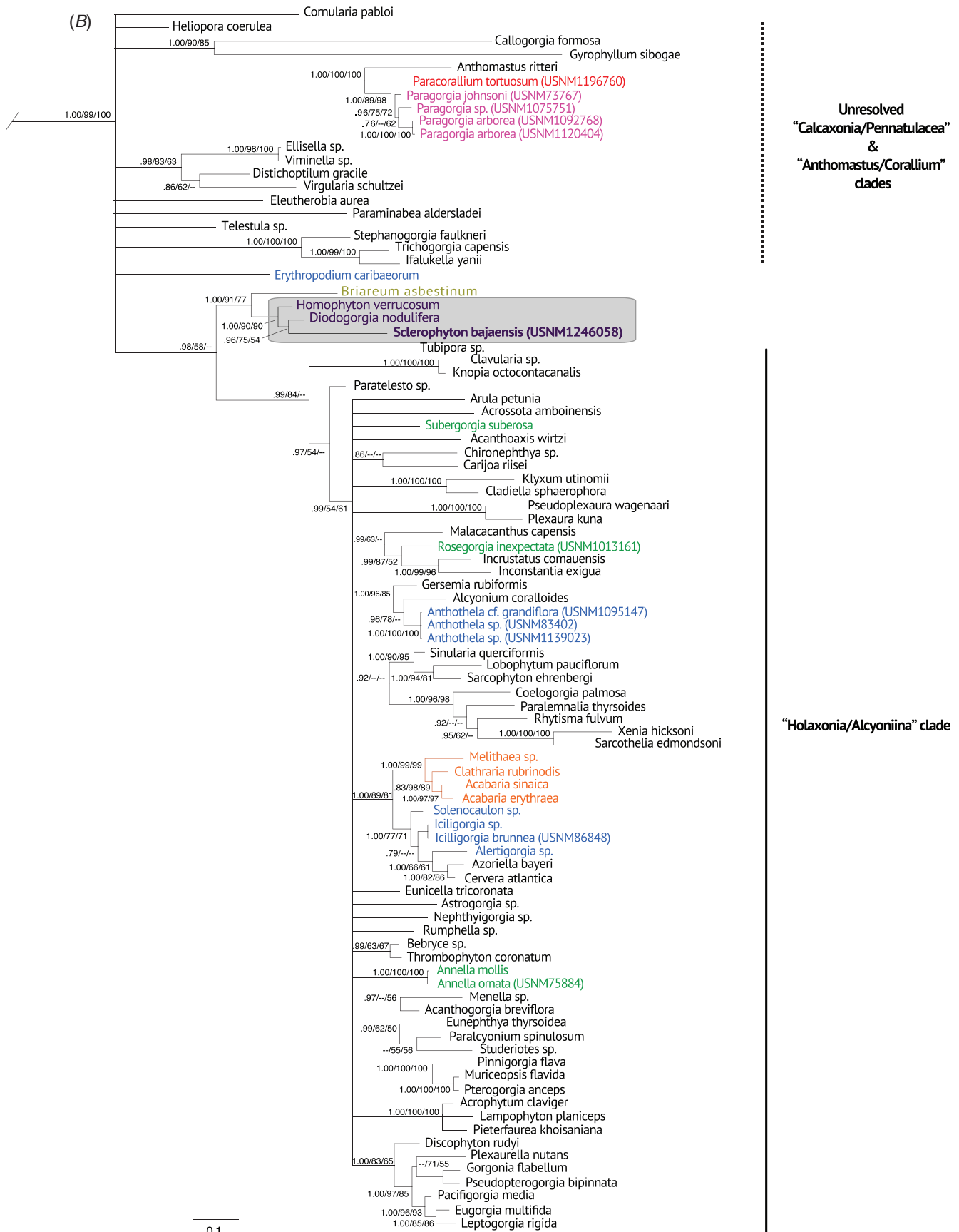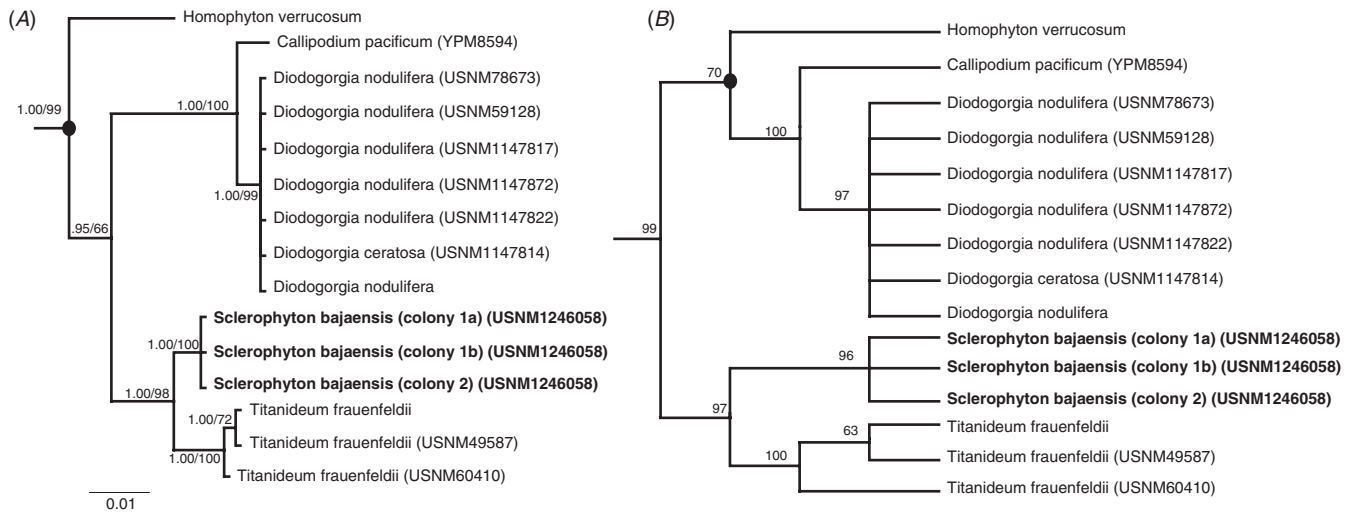
Fig. 1. (*continued*)

Fig. 1.   (*continued*)

Fig. 2. Phylogenies depicting phylogenetic relationships among the Spongiodermidae with the *mtMutS+COI* dataset. (*A*) Phylogram generated by Bayesian inference (BI) and maximum likelihood (ML). (*B*) Cladogram generated by maximum parsimony (MP). With BI and ML, *Homophyton verrucosum* was sister to all of the spongiodermid genera. With MP, *H. verrucosum* was sister to a clade containing *Callipodium pacificum* and *Diodogorgia nodulifera*. See Fig. 1 for node support explanation.

ring canal system may also separate inner from outer cortex. Medullar sclerites stout rods, often bifurcate, branched, and/or spiny; cortical sclerites always include radiates, and may include spindles, ovals and double heads.

Remarks

Three of the five previously known spongiodermid genera were described between 1864 and 1869, another in 1919, and the fifth in 1955, thus the generic complement of the family has been fairly stable for a long time and subject to the evaluation of the four comprehensive revisions of the Octocorallia, i.e. Wright and Studer (1889), Kükenthal (1924) and Bayer (1956, 1981). Nonetheless, Kölliker (1871) was the first to notice the resemblance of *Titanideum* and *Spongioderma* (=*Homophyton*), but placed them in the associated scleraxonian family Briareidae.

In the first comprehensive classification of the Octocorallia, Wright and Studer (1889) divided the scleraxonian section of the Gorgonacea into four families, one of these four families, the Briareidae, with two subfamilies, the Briareinae and the Spongioderminae, the latter containing *Titanideum*, *Spongioderma* (=*Homophyton*) and *Iciligorgia*. Thus, the proper authorship of the family-group name Spongiodermidae should be attributed to Wright and Studer (1889), not Aurivillius (1931), as is common. Subfamily Briareinae was distinguished from the Spongioderminae by having solenial canals in the medulla, the latter not. A similarity to *Callipodium* was mentioned, but that encrusting genus was placed by Wright and Studer (1889) in the rather distant family Cornulariidae in the order Alcyonacea.

Kükenthal's (1924) revision of the Gorgonaria was somewhat of a step backwards in that he lumped 14 scleraxonian genera into the Briareidae, including those now assigned to the Spongiodermidae, Briareidae, Anthothelidae and Paragorgiidae, the character distinguishing this family from the other three

scleraxonian families being the unconsolidated axis (medulla) of its genera.

The first modern account of the scleraxonian families was that of Aurivillius (1931), who divided the suborder into eight families or subfamilies, a classification that is currently used. He also provided useful keys to the scleraxonian families and genera within each family. He elevated the spongiodermids to the family rank for the first time and considered it to be a new family, but according to the International Code of Zoological Nomenclature, this must be considered as an elevation of Wright and Studer's (1889) subfamily Spongioderminae and thus take Wright and Studer's name and date. The correct spelling of the elevation to family status would then be Spongiodermidae, not Spongiodermatidae, as later advocated by Aurivillius (1931) and Bayer (1956). Aurivillius (1931) defined the family as having monomorphic polyps, an axis (medulla) that was non-jointed, not cemented together and not penetrated by solenial canals (instead the canals form rings in the cortex), and with at least some cortical radiate sclerites.

Despite Aurivillius' reasoning, Bayer (1955, 1956, 1981), without explanation, downgraded the spongiodermids to the subfamily grade, sharing the family Anthothelidae with the subfamilies Anthothelinae and Semperininae. Essentially he distinguished the Spongioderminae from the other two subfamilies by its cortical radiates and branching medullar rods. Contemporary classifications (e.g. Williams and Cairns 2014) have followed that classification.

However, as discussed above, genetic analysis of mitochondrial and nuclear loci support the spongiodermid genera (with the exception of *Tripalea*, not used in this study) as a monophyletic clade at the family level, that is sister to the family Briareidae. Thus, the family level taxon Spongiodermidae is resurrected, as first suggested by Wright and Studer (1889). There are now nine families considered to fall within the scleraxonian group: six families with an unconsolidated axis (Briareidae, Anthothelidae, Spongiodermidae, Subergorgiidae, Paragorgiidae
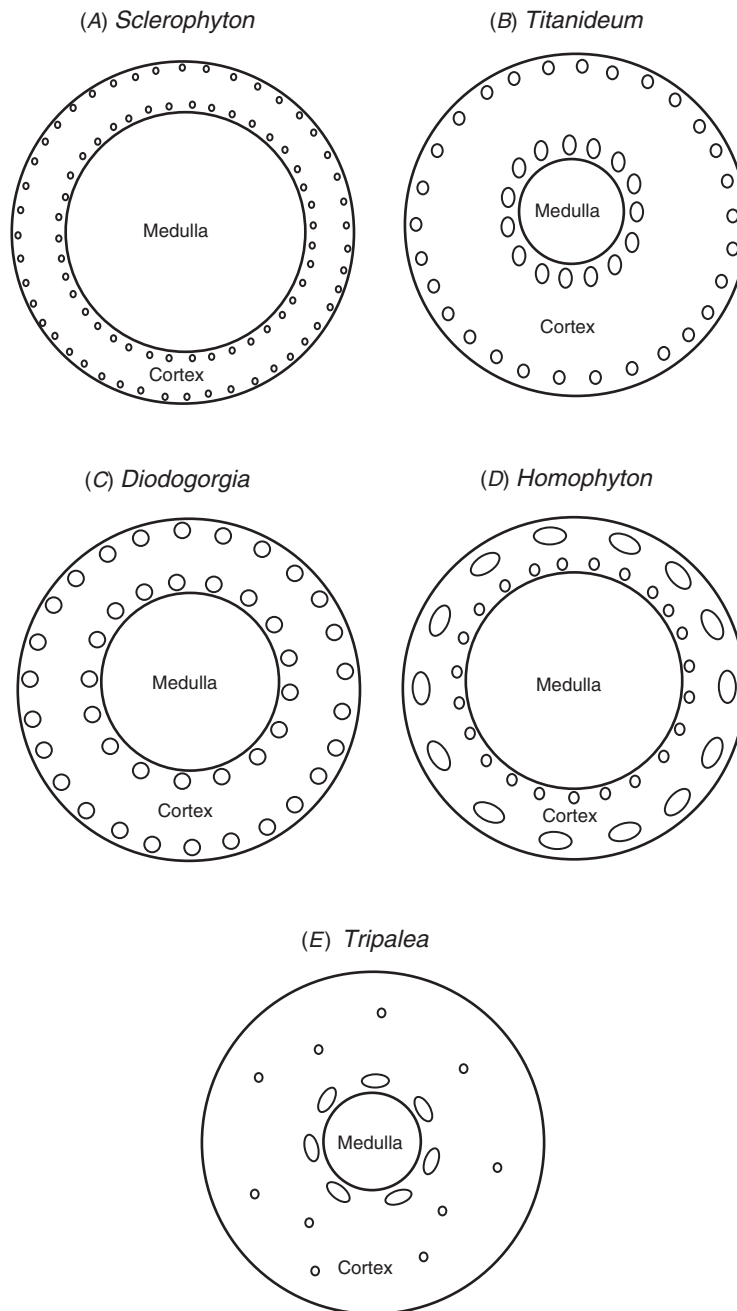
(*A*) *Sclerophyton*

(*B*) *Titanideum*

(*C*) *Diodogorgia*

(*D*) *Homophyton*

(*E*) *Tripalea*

Fig. 3. (*A–E*) Diagrammatic representations of the relative sizes and positions of the medulla, cortex, and inner and outer circles of ring canals.

and Sibogagorgiidae (resurrected family; Figueroa and Baco 2015)) and three with consolidated axes (Coralliidae, Melithaeidae and Parisididae).

Genus *Sclerophyton*, gen. nov.

Type species: *Sclerophyton bajaensis*, here designated. urn:lsid:zoobank.org:act:15B67DCE-7ED8-47E2-B565-87F030 CC37A4

Diagnosis

Colonies unbranched or sparsely branched in dichotomous fashion. Outer cortex composed of 3- to 8-radiates; inner cortex composed of larger 4-, 5-, 6-, 7- and 8-radiates, often with an elongate neck region connecting sets of tubercles. Medulla composed of closely packed longitudinally arranged rods, often with bifurcating tips and occasional side branches; contiguous medullar sclerites often fused. Two longitudinal rings of boundary canals present, one delimiting outer from inner cortex, the other delimiting the inner cortex from the medulla.

Remarks

The morphological differences between *Titanideum* and *Sclerophyton* are small, primarily a slight difference in the sclerite component of the cortex (i.e. *Titanideum* has double heads and *Sclerophyton* does not). Also, *Sclerophyton* often has fused medullar sclerites (*Titanideum* does not), and the longitudinal canals of the two ring systems of *Sclerophyton* are uniform in diameter, whereas those of the inner ring of *Titanideum* appear to be slightly larger. Morphologically, it is a subjective opinion whether the new taxon should be a new species of *Titanideum* or a separate genus. There is no quantitative morphological measure to support either option – just a feeling borne of experience working with octocorals and shared by taxonomists such as Deichmann, Bayer, Verrill, Kükenthal, Stiasny, Kölliker and Verseveldt. However, the genetic distance for *mtMutS+COI* between *Sclerophyton* and *Titanideum* (0.9%) is greater than that between *Callipodium* and *Diodogorgia* (0.6%) (see 'Discussion'), the latter two taxa with more discernable morphological differences. Therefore, the molecular evidence suggests that *Sclerophyton* and *Titanideum* are most likely two separate genera.

Other species

Monotypic.

Distribution

Pacific side of southern Baja California, 15–18 m.

Etymology

From the Greek root *scleros* (meaning hard, and also the basis for the suborder Scleraxonia) + *phyton* (meaning plant, a common suffix in scleraxonian genera). A fungus has the same name *Sclerophyton* Eschw., 1824, but the name is still available for an animal taxon.

Sclerophyton bajaensis, sp. nov.

(Figs 3*A*, 4*B, C*, 6*A–G*)

urn:lsid:zoobank.org:act:195BE748-591F-4EEB-A1E5-9238
8BB26AD1

Material examined

Holotype: Turtle Bay, Baja California (Pacific side, approx. 27°38′N, 114°54′W), MEXICO, 15–18 m, xi.1959, USNM 1246057, coll. James Stewart. *Paratypes*: from type locality, six colonies and 23 branches, USNM 1246058; Punta Hughes, Baja California (Pacific side, near Magdalena Bay), MEXICO, 18 m, viii.1957, three colonies, USNM 1246059, coll. James Stewart.

Type locality

Turtle Bay, Baja California (Pacific side), Mexico, 15–18 m.

Description

Colonies unbranched (Fig. 4*B*) or sparsely, dichotomously branched (Fig. 4*C*), the latter with U-shaped axils, and in both cases the colony reaches up to 28 cm in height. Branch tips blunt to slightly clavate. Colonies have a thin encrusting base, the

diameter of the lower stem reaches up to 12 mm. Calyces flush with branch. Colonies pinkish-orange in colour, but a thin encrusting sponge (Fig. 6*C*) gives most of colony a white patina. Thin outer cortex (Fig. 6*B, C, E*) densely packed with 3- to 8-radiates, but primarily 3- and 4-radiates that are 0.068–0.110 mm in length; inner cortex (Fig. 6*F*) composed of larger (0.106–0.172 mm long) 4- to 8-radiates, but somewhat elongate, sets of tubercles separated by a short neck region; L : D ratio up to 1.6. Medullar region composed of densely packed, longitudinally arranged rods (Fig. 6*D, G*) 0.18–0.27 mm in length. These rods usually distally bifurcate and may also have short lateral branches; they are relatively smooth, with few tubercles. Contiguous medullar sclerites often laterally fused (Fig. 6*D*) conferring a greater strength to branch axis. Cortical sclerites orange, whereas medullar sclerites colourless. Outer ring canal system (Figs 3*A*, 6*A–C*) lies just beneath (0.18 mm) branch surface and is fairly well defined. Inner ring system (Figs 3*A*, 6*C*), which encircles medulla, sometimes indistinct but always present. Canals of both systems of same relatively small size: 0.10–0.14 mm in diameter.

Distribution

As for the genus.

Etymology

Named for the region from which it was collected.

Genus *Titanideum* Verrill, 1864

(Figs 3*B*, 4*D*, 7*A–H*)

Titanideum Verrill, 1864*a*: 10; 1864*b*: 39; Kölliker, 1871: 16; Wright & Studer, 1889: xxxiii; Kükenthal, 1919: 81, 82; 1924: 30; Deichmann, 1936: 83; Bayer, 1956: F196; 1961: 77; 1981: 945.

Type species: *Gorgonia suberosa* Ellis & Solander, 1786, by monotypy (=*Solanderia frauenfeldii* Kölliker, 1865). The name of *G. suberosa* Ellis & Solander, 1786 is not nomenclaturally available because it is a junior homonym of *Gorgonia suberosa* Pallas, 1766 (=*Subergorgia suberosa*). The next available junior synonym is *Solanderia frauenfeldii* Kölliker, 1865.

Diagnosis

Colonies unbranched or sparsely branched from basal region, with long ascending branches. Outer cortex composed of 3- and 4-radiates and double heads; inner cortex composed of 4-, 5-, 6-, 7- and 8-radiates, these sclerites often elongate with a neck region connecting sets of tubercles. Medulla composed of closely packed longitudinally arranged rods, often with bifurcate tips and occasionally short medial branches. Two longitudinal rings of boundary canals present, one delimiting outer from inner cortex, the other delimiting the inner cortex from the medulla.

Description of type species

Colonies unbranched or sparsely branched, most long ascending branches originating near colony base (Fig. 4*D*); colonies reach up to 31 cm in height and 15 mm in basal branch diameter. Calyces usually flush with branch surface. Colonies usually uniformly yellow or orange, the latter sometimes with pale yellow calyces, or pinkish-red, or rarely white. Cortex sclerites pink, medullar sclerites colourless. Thin outer cortex densely
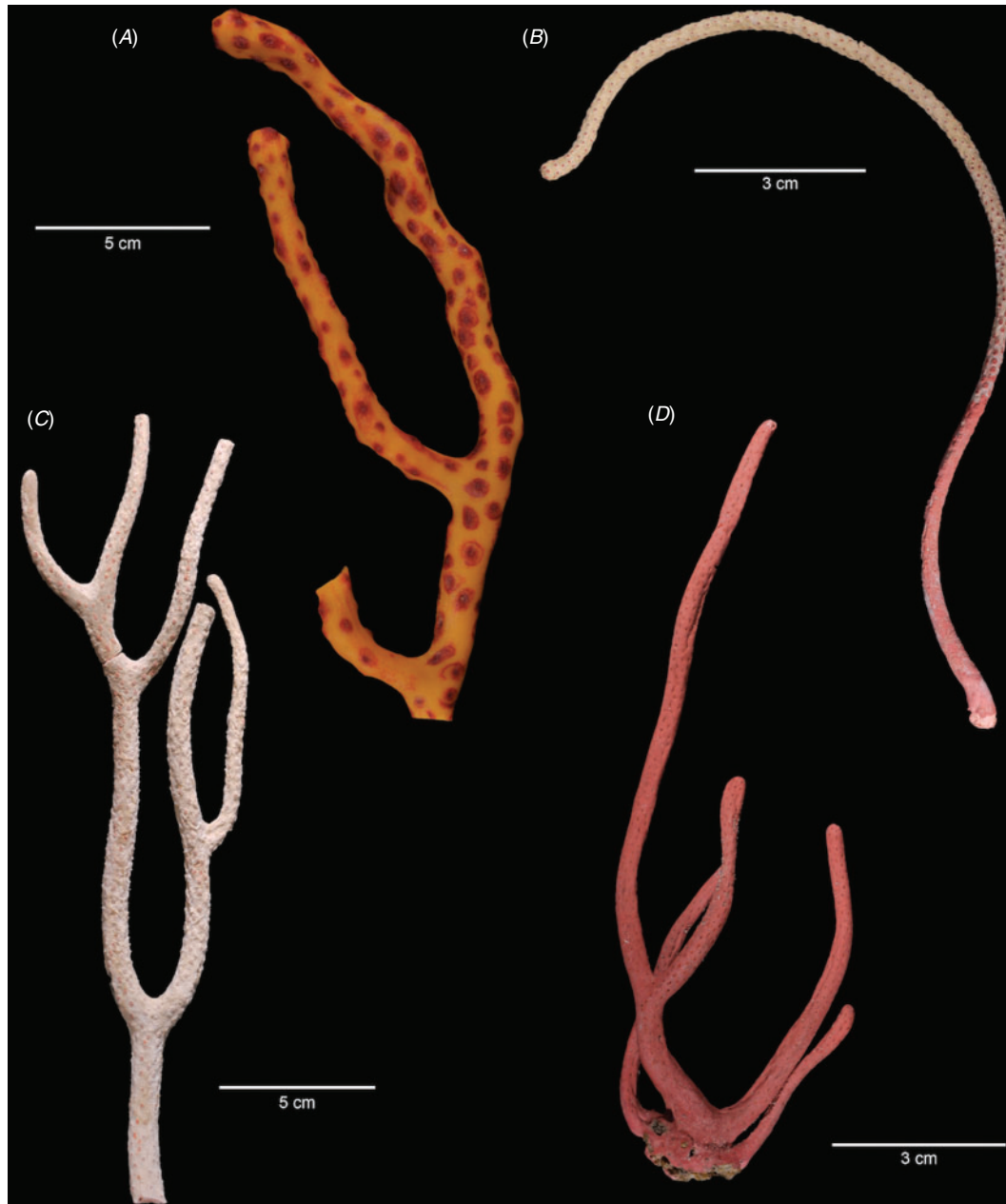
Fig. 4. (*A*) *Diodogorgia nodulifera*, USNM 49705, Palm Beach, Florida, 73 m. (*B*) *Sclerophyton bajaensis*, USNM 1246059, paratype. (*C*) *Sclerophyton bajaensis*, USNM 1246057, holotype. (*D*) *Titanideum frauenfeldii*, USNM 60410, Cape Hatteras, beach.

packed with 3- and 4-radiates (Fig. 7*C, F*) and double heads (Fig. 7*G*), the former 0.038–0.09 mm in length, the latter 0.044–0.068 mm in length. Inner cortex composed of larger 4- to 8-radiates (0.11–0.19 mm in length), the tubercles often separated by a short neck region and thus approximating a tuberculate spindle (Fig. 7*H*); these sclerites have an L : D ratio of up to 1.6. Relatively small medullar region composed of densely packed longitudinally arranged rods (Fig. 7*B, D, E*) 0.22–0.36 mm in length. These rods usually distally bifurcate and may also have short lateral branches; rods relatively smooth and have few tubercles. Inner ring canal system well defined

(Figs 3*B*, 7*B*), consisting of 10–12 contiguous, relatively large (0.15 mm in diameter) canals that border the medulla. Outer ring canal system somewhat indistinct (Figs 3*B*, 7*A*), consisting of more numerous, smaller (0.075–0.10 mm in diameter), non-contiguous canals lying only ~0.15 mm beneath branch surface, distinguishing outer from inner cortex.

Remarks

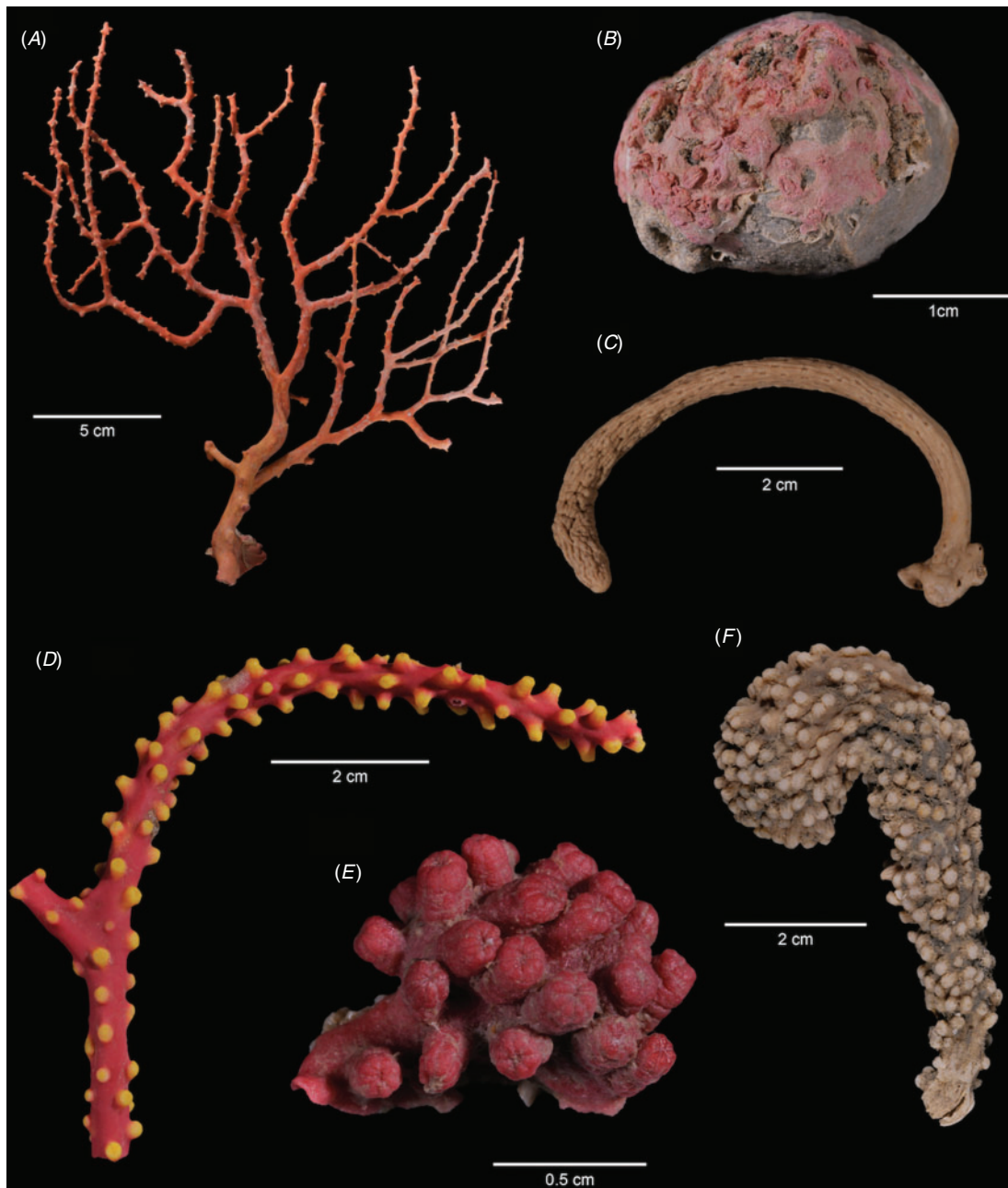Among the four spongiodermid genera with two longitudinal ring canal systems (Table 2), *Titanideum* is unique in having

Fig. 5. (*A*) *Diodogorgia nodulifera*, USNM 1147814, Discovery Bay, Jamaica, 82 m. (*B*) *Callipodium pacificum*, YPM 588, Panama, syntype. (*C*) *Tripalea clavaria*, USNM 43421, 36°42′S, 56°23′W, 21 m. (*D*) *Homophyton verrucosum*, USNM 1091355, 29°27′S, 31°31′E, 68 m. (*E*) *Callipodium rubens*, USNM 50523, off Freeport, Texas, 9.1 m. (*F*) *Tripalea clavaria*, MNRJ 5478, –23°58'06.0000", -045°29'26.4000" 23°58.1′S, 45°29.44′W, 45 m.

double heads in its outer cortex. It is further compared to *Sclerophyton* in the account of that genus.

Useful descriptions, comments and/or illustrations of the type species can be found in: Verrill (1864*a*), Kükenthal (1919, 1924), Deichmann (1936), Bayer (1961), Cairns and Bayer (2009), and DeVictor and Morton (2010). Its distribution is: North Carolina to Cuba, and south-east Gulf of Mexico, 13–293 m.

The genus *Paratitanideum* Kükenthal, 1919: 84 (in part, type species *Titanideum friabilis* Nutting, 1911, by subsequent designation (Kükenthal 1924)) was placed in the Semperinidae by Aurivillius (1931).

Other species

?*Titanideum obscurum* Thomson, 1927: Azores, 1250 m. Although not examined, the illustrations in the original
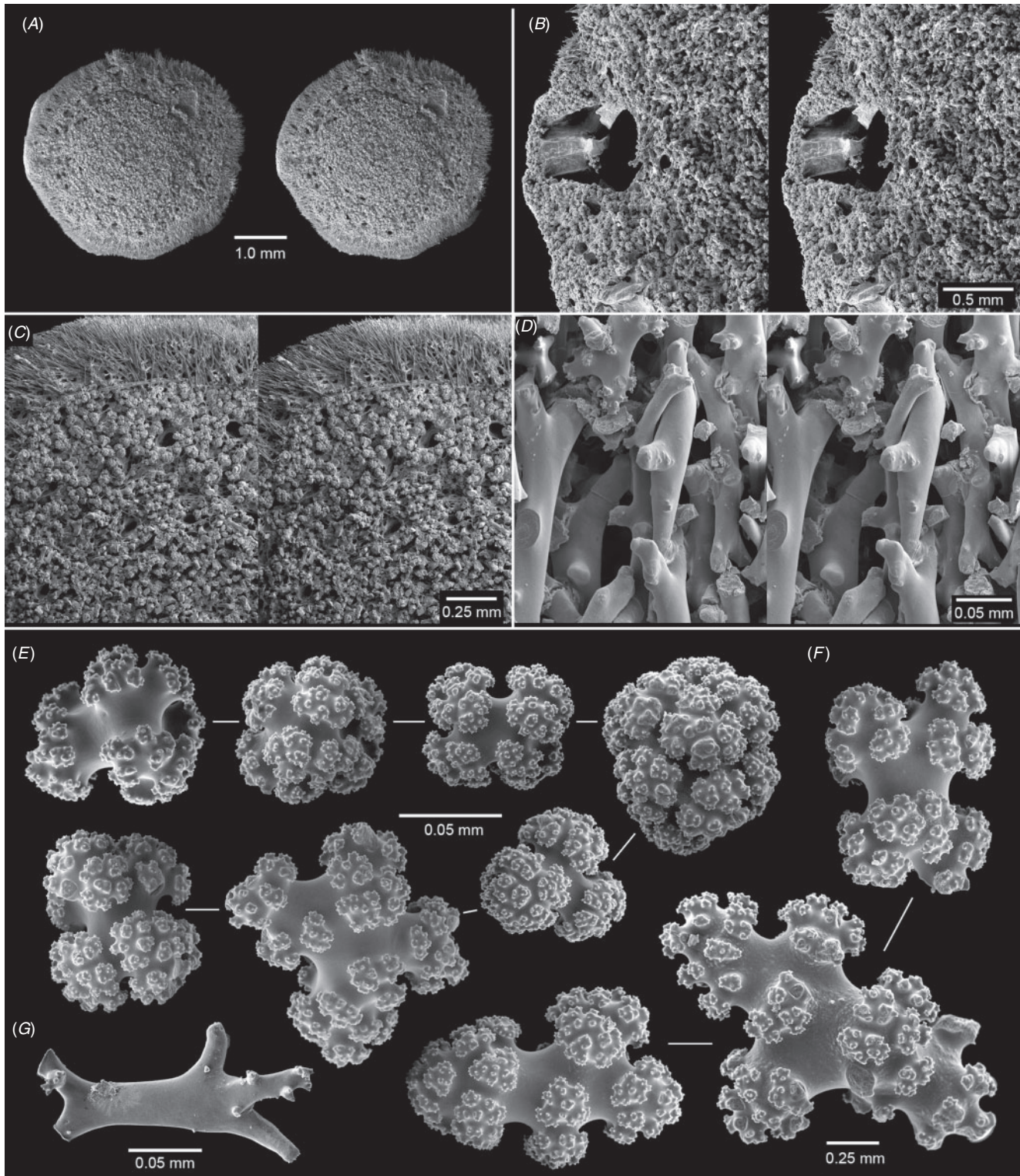
Fig. 6.   (*A–G*) *Sclerophyton bajaensis*, paratype, USNM 1246058: (*A*) stereo view of branch cross section showing inner and outer ring canals; (*B*) stereo view of polyp cross section in the outer cortex; (*C*) stereo view of branch cross section showing cortex, medulla, ring canals and sponge sclerites encrusting the branch; (*D*) stereo view of interlocking branched medullar rods; (*E*) 3- to 8-radiates from outer cortex; (*F*) 4- to 8-radiates with a short neck region, from inner cortex; (*G*) medullar sclerite.
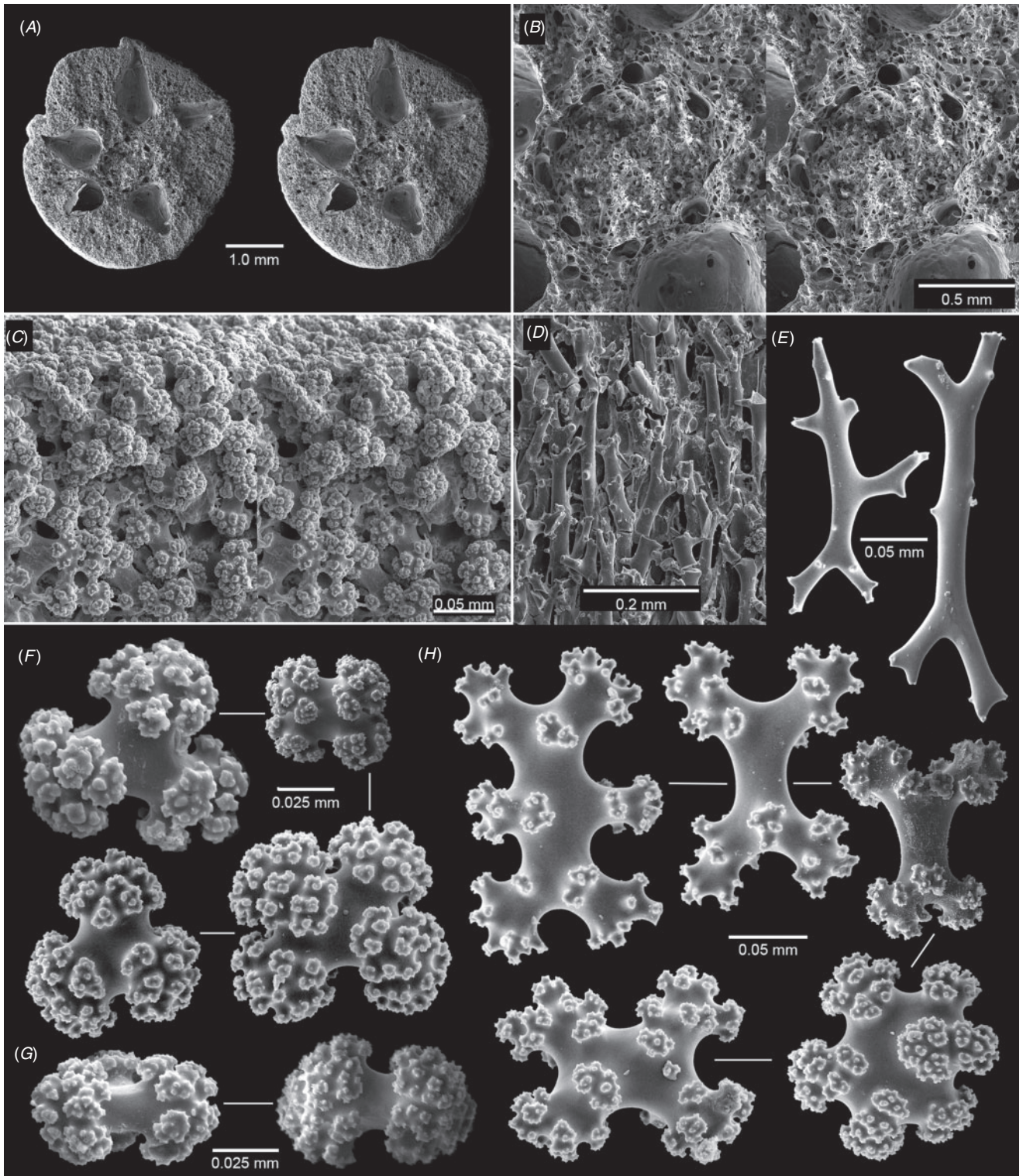
Fig. 7. (*A–G*) *Titanideum frauenfeldii*, USNM 49587, off Little River Reef, Florida, 14 m; USNM 8348, 35°12′30″N, 75°25′W (Cape Hatteras), 88 m: (*A*) stereo view of branch cross section showing inner and outer ring canals and longitudinal section of five polyps; (*B*) stereo view of medulla surrounded by inner ring canal; (*C*) stereo view of radiates in outer cortex; (*D*) branched medullar rods *in situ*; (*E*) branched medullar rods; (*F*) 3- and 4-radiates from outer cortex; (*G*) double heads from outer cortex; (*H*) 4- to 8-radiates with neck region from inner cortex.

Table 2.   Comparison of the spongiodermatid genera

	Sclerophyton	*Titanideum*	*Diodogorgia*	*Homophyton*	*Tripalea*	*Callipodium*
Colony shape	Sparse dichotomous	Unbranched or sparsely branched from base	Dichotomous, planar	Unbranched or sparsely branched	Unbranched, clavate	Encrusting
Outer cortex	3- to 8-radiates (2- or 4-radiates most common)	3-, 4-radiates; double heads	3-, 4-, 5-, 6-radiates; tuberculate spindles; spheroids	3- to 8-radiates, spheroids	Tuberculate spindles, spheroids	Girdled and branched spindles (L:W up to 3.8); ovals; 7-, 8-radiates (no distinction between layers)
Inner cortex	4- to 7-radiates, with neck region (L:W up to 1.6)	4- to 8-radiates with a neck region (L:W up to 1.55)	Long tuberculate spindles (L:W up to 5.6)	Ovals (L:W ~2)	Spiny spindles (L:W up to 5.5), vacuous	
Medulla	Bifurcate rods, sometimes fused	Bifurcate rods	Rods, rarely bifurcate	Short, bifurcate rods	Bifurcate rods	Bifurcate rods
Longitudinal canals	Two rings, outermost indistinct	Two discrete rings, inner ring canals large	Two discrete rings	Two rings: inner ring indistinct with small diameter canals, outer ring distinct and canals much larger	One inner ring	No ring canals

description show elongate spindles in the cortex and no radiates, which would not be consistent with this genus. It is also quite deep for this family.

Distribution

Western Atlantic (North Carolina to Cuba, Gulf of Mexico), ?Azores, 13–293-?1250 m.

Genus *Diodogorgia* Kükenthal, 1919

(Figs 3*C*, 4*A*, 5*A*, 8*A–H*)

Diodogorgia Kükenthal, 1919: 96, 97; 1924: 36; Aurivillius, 1931: 16, 18, 19; Deichmann, 1936: 85, 86; Stiasny, 1937: 67; Bayer, 1956: F196; Bayer, 1961: 71, 72; Bayer, 1981: 945; Williams, 1992*a*: 193.

Type species: *Diodogorgia ceratosa* Kükenthal, 1919, by subsequent designation (Kükenthal, 1924) (=*Solandaria nodulifera* Hargitt in Hargitt & Rogers, 1901 (senior synonym); =*Solanderia cristata* Hargitt in Hargitt & Rogers, 1901; =*Diodogorgia cervicornis* Kükenthal, 1919; =*Corallium vanderbilti* Boone, 1933).

Diagnosis

Colonies regularly and dichotomously branched in a flabellate fashion, or unbranched (i.e. *D. capensis*). Outer cortex composed of small 3-, 4-, 5- and 6-radiates, tuberculate spheroids, and short tuberculate spindles; inner cortex composed of longer tuberculate spindles. Medulla composed of closely packed, longitudinally arranged rods, only rarely bifurcate at tips. Two well-defined longitudinal rings of solenial boundary canals present in branches, one ring between outer and inner cortex (termed the 'lateral canals' by Verseveldt 1940), the other between the inner cortex and medulla (termed the 'median canals' by Verseveldt 1940).

Description of type species

Colonies abundantly and dichotomously branched (Figs 4*A*, 5*A*); branches often slightly clavate. Individual colonies up to 25 cm in height, with a basal branch diameter up to 15 mm. Calyces form small protuberances even when contracted, thus the name *nodulifera*. Most common colour of corallum yellow with red or purplish-red polyps, but other variations include uniformly yellow, red or pink. Most sclerites red, those of calyces usually yellow. Thin outer cortex densely packed with 4-, 5- and 6-radiates 0.065–0.110 in diameter (Fig. 8*D*), even smaller tuberculate spheroids (Fig. 8*F*) ~0.050 mm in diameter, and short tuberculate girdled spindles (Fig. 8*E*) up to 0.15 mm in length. Rather abruptly at outer (lateral) boundary ring canal, the sclerite composition changes to larger tuberculate spindles (Fig. 8*G*) some of which are up to 0.60 mm in length and with an L:D ratio of up to 5.5. Inner medullar region composed of densely packed, longitudinally oriented rods (Fig. 8*A–C, H*) 0.23–0.57 mm in length and rarely if ever bifurcate. Medullar rods smooth compared with cortical spindles, but do occasionally have superficial tubercles. Medullar rods do not fuse, except within holdfast, where they form a somewhat continuous foundation. Polyp sclerites similar to those of outer cortex. Two rings of longitudinal solenial canals well defined and their adjacent canals within a ring are closely spaced (Figs 3*C*, 8*A–C*), canals of both rings circular to elliptical in outline and
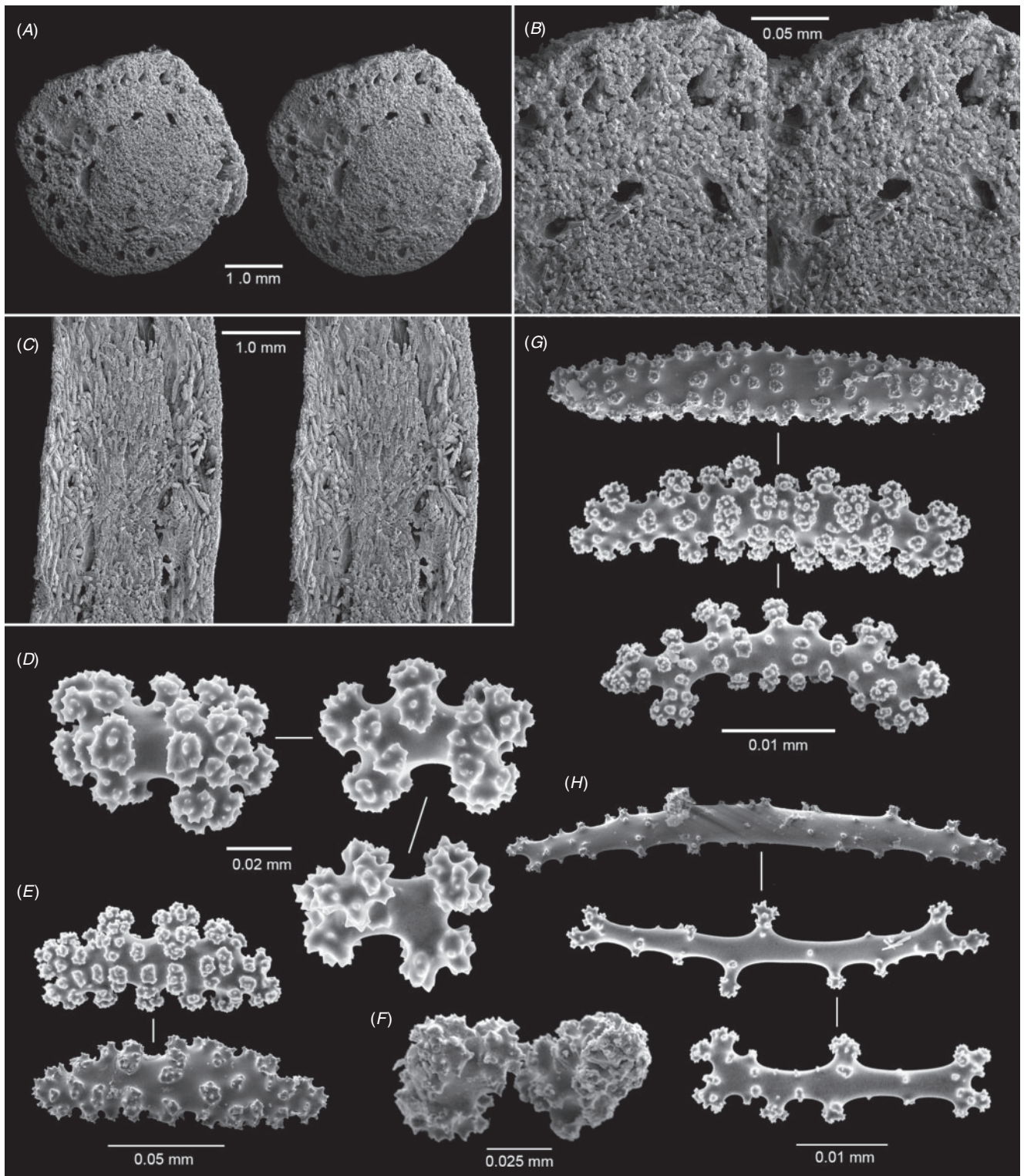
Fig. 8. (*A, B, D, G, H*) *Diodogorgia nodulifera*, USNM 49705 (see above – *C, E, F*, USNM 59128) off Little Cayman, 21.3 m: (*A*) stereo view of branch cross section showing inner and outer ring canals, cortex and medulla; (*B*) stereo view of enlargement of cortex and part of inner and outer ring canal system; (*C*) stereo view of branch longitudinal section showing cortex and medulla; (*D*) 3- to 6-radiates from outer cortex; (*E*) tuberculate spindles from outer cortex; (*F*) two tuberculate spheroids from outer cortex; (*G*) elongate tuberculate spindles from inner cortex; (*H*) medullar rods.

about the same size in both rings, i.e. 0.18–0.20 mm in greater diameter.

Remarks

Among the four spongiodermid genera with two longitudinal ring canal systems (Table 2), *Diodogorgia* differs in having well-developed tuberculate spindles in its cortex, as well as various classes of radiates.

Useful descriptions, comments and/or illustrations of the type species can be found in: Kükenthal (1919), Deichmann (1936), Stiasny (1937), Verseveldt (1940), Bayer (1959, 1961), Cairns and Bayer (2009), and DeVictor and Morton (2010). The account by Verseveldt (1940) is by far the most exhaustive. Indeed, this is one of the better known and discussed octocoral species in the western Atlantic. DeVictor and Morton (2010) were the first and only to illustrate sclerites with SEM, which we add to with stereo views of the ring canal, sclerites *in situ*, and the various sclerite types. Its distribution includes, from north to south: Jacksonville, Florida, Bahamas, Greater and Lesser Antilles, Panama and the northern coast of South America to Surinam (Bayer 1961) at depths of 36–183 m.

Other species

Diodogorgia capensis (Thomson, 1911): off South Africa, 80–90 m (see Williams 1992b: 397, fig. 23A).
?*Diodogorgia sibogae* Stiasny (1941: 67): South Africa, Indonesia, 73 m.

Distribution

Western Atlantic (from Florida throughout Greater and Lesser Antilles, eastern Gulf of Mexico, Panama, northern coast of S. America to Surinam), South Africa, ?Indonesia; 36–183 m.

Genus *Homophyton* Gray, 1866

(Figs 3D, 5D, 9A–F)

Solanderia: Möbius, 1861: 3.
Homophyton Gray, 1866: 27, fig. 2; Bayer, 1981: 945; Williams, 1992a: 186, 187.
Spongioderma Kölliker, 1871: 14 (type species: *Solanderia verrucosa* Möbius, 1861, by monotypy); Wright & Studer, 1889: xxxiv; Kükenthal, 1919: 89–91; 1924: 34; Aurivillius, 1931: 18; Bayer, 1956: F196.
Type species: *Homophyton gattyiae* Gray, 1866, by monotypy (=*Solanderia verrucosa* Möbius, 1861, the senior synonym).

Diagnosis

Colonies unbranched or sparsely dichotomously branched. Outer cortex composed of small 3- to 8-radiates and tuberculate spheroids; inner cortex composed of much larger ovals. Medulla composed of closely packed longitudinally arranged rods, often bifurcate at their ends. Two longitudinal rings of boundary canals present, the inner ring indistinct.

Description of type species

Colonies unbranched or sparsely branched in a dichotomous fashion (Fig. 5D), colonies attaining a height of 42 cm with a basal branch diameter of 15 mm. Branch tips attenuate to blunt (not clavate). Calyces often protuberant (Fig. 5D), expressed as

cylinders up to 3 mm in height and ~1.7 mm in diameter, and often of a different colour from branch, but they may also be flush with branch surface when retracted. Colonies uniformly yellow, pinkish-white, reddish-orange or dark red; calyces either white, yellow or red (Williams 1992a). Thin outer cortex (Fig. 9A, B) composed of 3- to 8-radiates (Fig. 9D) 0.048–0.12 mm in length or diameter. Inner cortex composed of much larger and thicker sclerites called ovals (Fig. 9C, E) up to 0.28 mm in length and with an L : D ratio of only 2. Large medullar region (Fig. 9A) composed of relatively short (0.12–0.29 mm in length), densely packed, longitudinally arranged rods (Fig. 9F) that are relatively smooth and often distally bifurcate. Inner ring canal system that occurs at boundary of medulla and inner cortex is indistinct, the small diameter canals measuring only ~0.16 mm in diameter. The outer ring canal system, which separates the inner from the outer cortex, quite distinct (Figs 3D, 9A, B), composed of large (up to 0.5 mm in diameter) canals.

Remarks

Among the four spongiodermid genera with two longitudinal ring canal systems (Table 2), *Homophyton* is distinguished by having ovals in its inner cortex, and much larger diameter canals in its outer ring than its inner ring.

Homophyton was resurrected by Bayer (1981) to replace *Spongioderma*, based on priority of description.

Useful descriptions, comments and/or illustrations of the type species can be found in: Möbius (1861), Gray (1866), Kükenthal (1919, 1924) and Williams (1992a, 1993), the most complete accounts provided by Kükenthal (1919) and Williams (1992a).

Other species

The genus is monotypic. *Juncella elongata* var. *capensis* Hickson, 1904, once placed in *Spongioderma*, is now placed in *Ideogorgia* (see Williams 1992a), and *Spongioderma chunii* Kükenthal, 1908 is considered to be a junior synonym of *H. verrucosum*.

Distribution

South Africa, southern Mozambique, 0–168 m (Williams 1992b: 397, fig. 24b).

Genus *Tripalea* Bayer, 1955

(Figs 3E, 5C, F, 10A–F)

Suberia Studer, 1878: 666 (in part: *S. clavaria*); Kükenthal, 1919: 85 (in part); 1924 (in part).
Tripalea Bayer, 1955: 208, 209; Bayer, 1956: F196; 1961: 70; 1981: 911, 945.
Type species: *Suberia clavaria* Studer, 1878, by original designation.

Diagnosis

Colonies unbranched, branch tips clavate. Outer cortex composed of tuberculate spheroids and tuberculate and girdled spindles; inner cortex spongy, composed of spiny spindles. Medulla composed of closely packed longitudinally arranged rods, often bifurcate at their ends. Only one longitudinal ring canal system, located at the boundary of medulla and inner cortex.
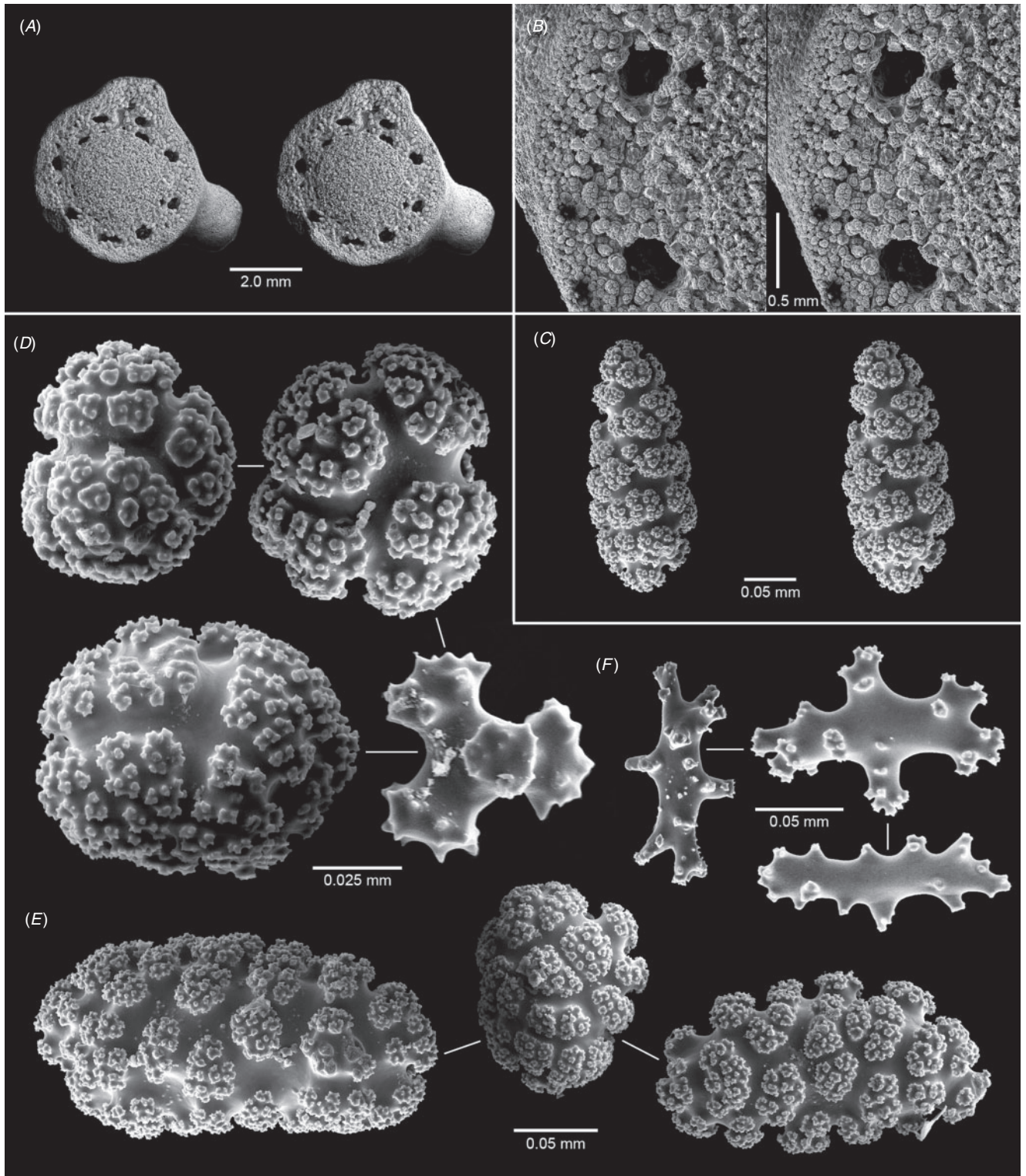
Fig. 9. (*A–E*) *Homophyton verrucosum*, USNM 1091355 (see above), (*F*) USNM 53882, 31°38′48″S, 29°34′24″E, 48 m. (*A*) Stereo view of branch cross section showing large canals of outer ring and much smaller canals of inner ring, and central medulla; (*B*) Ssereo view of branch cross section showing boundary between outer and inner cortex and two large longitudinal ring canals of outer ring; (*C*) stereo view of an inner cortex oval; (*D*) 3- to 8-radiates from outer cortex; (*E*) ovals from inner cortex; (*F*) medullar rods.
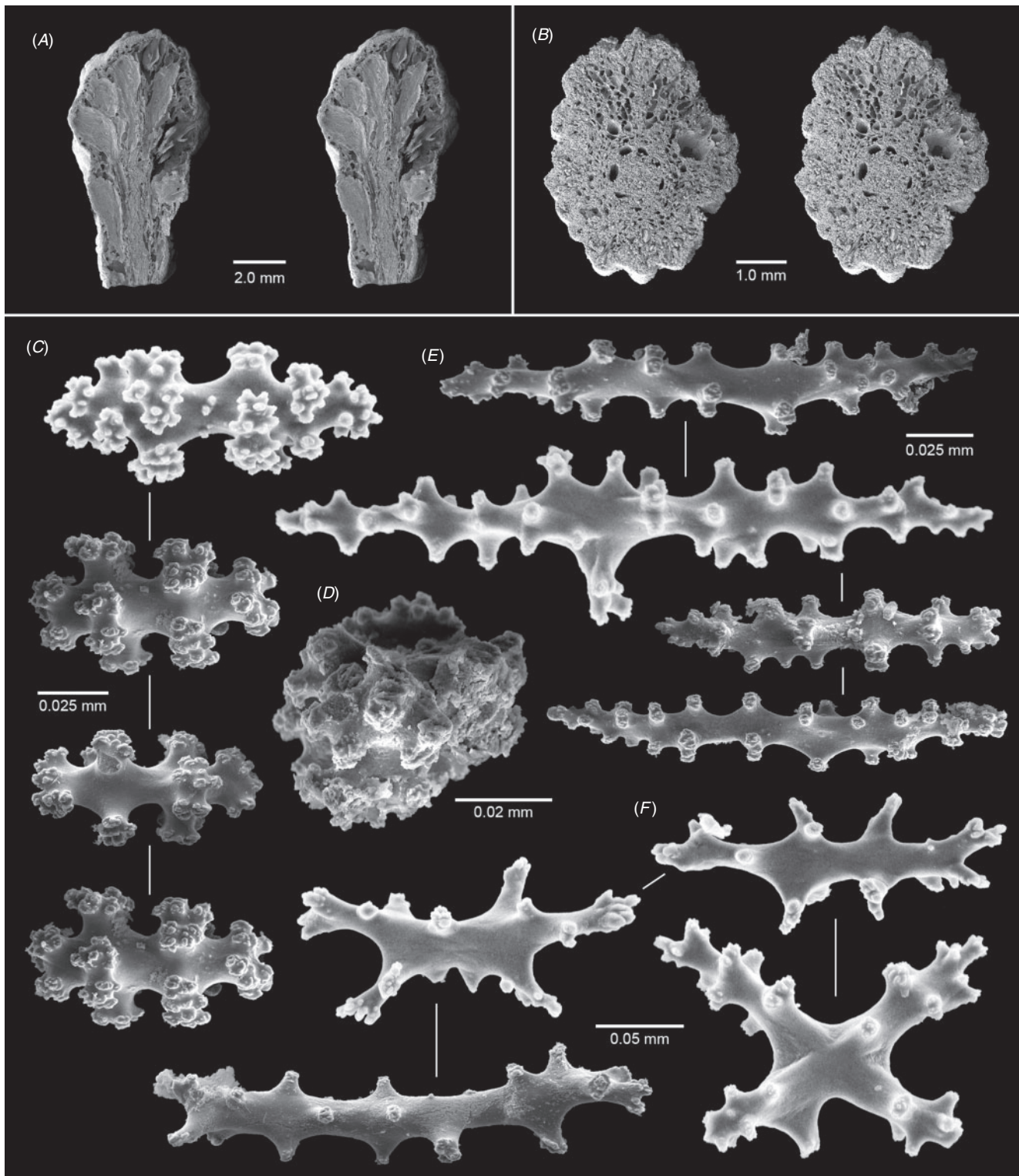
Fig. 10.   (*A*, *B*, *F*) *Tripalea clavaria*, USNM 43421 (see above), (*C*–*E*) USNM 84390, Mar de Plata, depth unknown. (*A*) Stereo longitudinal view of distal branch showing several polyps and a longitudinal canal; (*B*) stereo view of branch cross section showing single ring canal system, medulla and cortex; (*C*) girdled spindles from outer cortex; (*D*) tuberculate spheroid from outer cortex; (*E*) spiny spindles from inner cortex; (*F*) medullar rods.
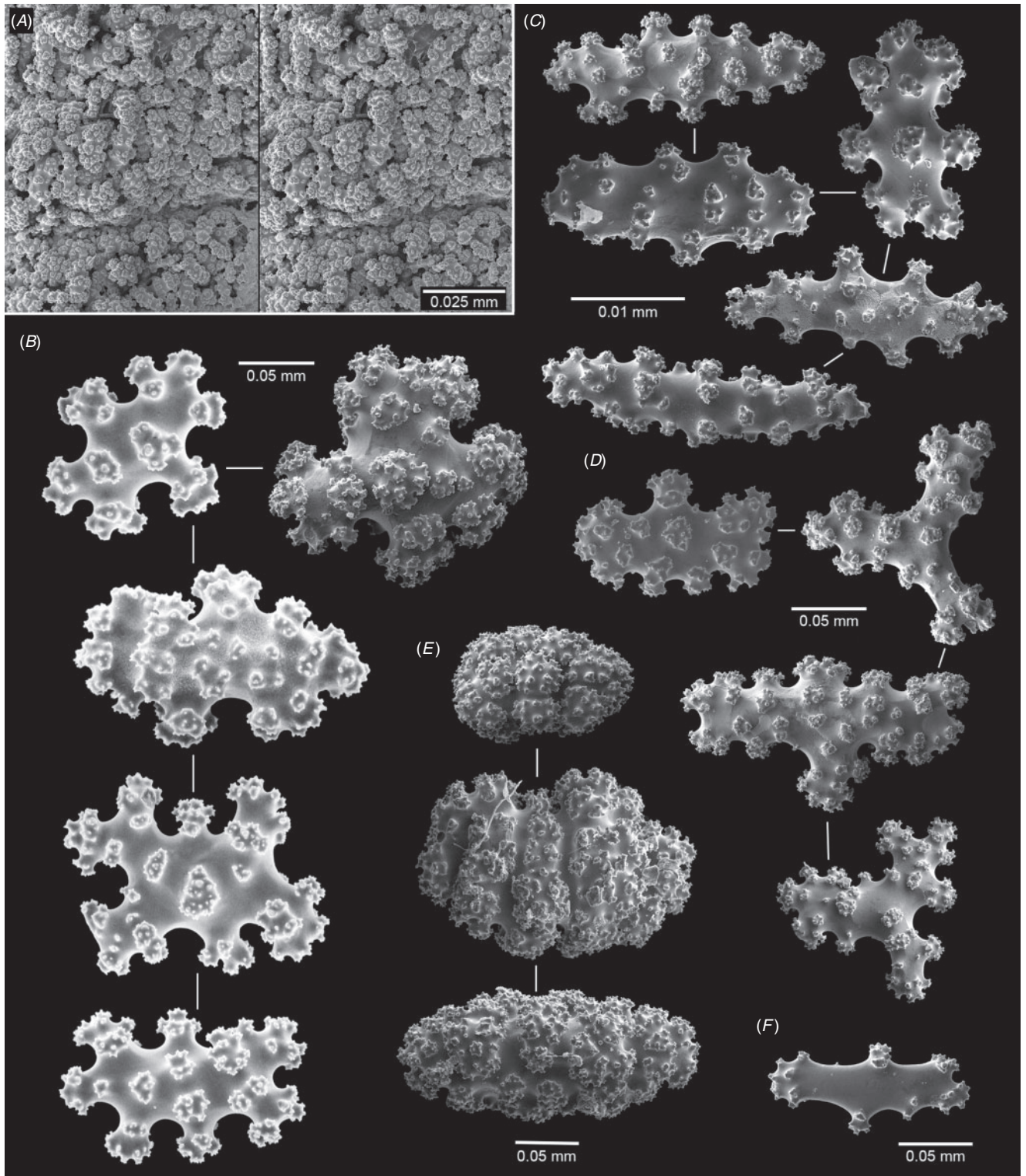
Fig. 11. (*A*, *C–F*) *Callipodium rubens*, USNM 50523 (see above), (*B*) *Callipodium pacificum*, YPM 588, syntype. (*A*) Stereo view of girdled tuberculate spindles from cortex; (*B*) 7- to 8-radiates from cortex; (*C*) tuberculate girdled spindles; (*D*) branched spindles from cortex; (*E*) ovals from cortex; (*F*) medullar rod?

Description of type species

Colonies unbranched and up to 26 cm in length, with an encrusting base, a basal branch diameter up to 8 mm, and a terminal clavate branch tip up to 12 mm in diameter (Fig. 5C, F). Calyces flush with branch surface. Colony and sclerites white. Outermost cortex composed of small (0.038–0.056 mm in diameter) tuberculate spheroids (Fig. 10D) and short (0.069–0.120 mm in length) girdled or belted spindles (Fig. 10C). The inner cortex, which is thick and spongy (Fig. 10A), consists of slender spiny spindles (Fig. 10E) 0.15–0.26 mm in length, with an L : D ratio of up to 5.5. Relatively small medullar region composed of densely packed, longitudinally arranged rods 0.14–0.22 mm in length and often bifurcate at their tips (Fig. 10F). Only one ring of longitudinal boundary canals present (Figs 3E, 10B), located between medulla and cortex, composed of relatively few (8–10) large (up to 0.35 mm in diameter) tubes that are circular to elliptical in cross section. Smaller (0.12 mm diameter) longitudinal canals occur throughout the cortex but are not arranged in rings (Fig. 3E).

Remarks

Tripalea is distinctive among the subergorgiids in having only one longitudinal ring canal system, clavate branches, and spiny spindles in its inner cortex (Table 2).

Useful descriptions, comments and/or illustrations of the type species can be found in: Studer (1878), Kükenthal (1919) and Bayer (1961).

Other species

The genus is monotypic.

Distribution

East coast of South America from southernmost Brazil (Rio Grande do Sul) to 40°S off Argentina, 20–55 m.

Genus *Callipodium* Verrill, 1869

(Figs 5B, E, 11A–F)

Sympodium: Verrill, 1866: 329 (in part: *S. pacificum*).
Callipodium Verrill, 1869: 455; Wright & Studer, 1889: xvi; Bayer, 1956: F196; 1981: 945.
Anthopodium Verrill, 1872: 434 (type species: *A. rubens* Verrill, 1872 by monotypy); Wright & Studer, 1889: xv; Bayer, 1961: 78, 79; 1981: 909, 945.
Type species: *Sympodium pacifica* Verrill, 1866 by original designation.

Diagnosis

Colonies encrusting (Fig. 5B, E), forming a mat or a reticulate stoloniferous expansion. Sclerite complement consists of short girdled spindles (Fig. 11A, C), branched spindles (Fig. 11D), ovals (Fig. 11E), and 7- and 8-radiates (Fig. 11B). Medullar or basement layer (Bayer 1961) may be present. Ring canals absent.

Description of type species

Colonies usually encrust rocks and dead shells, forming a continuous thin mat (up to 8 cm in width) or a stoloniferous expansion, which is sometimes reticulate. Colonies and sclerites bright red, purplish-red or orange. Calyces often project from the surface as much as 0.10 mm, sometimes

unilinearly arranged on stoloniferous colonies. Uppermost layer of cortex composed of small (0.07–0.16 mm in diameter) 7- or 8-radiates, below which are short (0.13–0.32 mm in length), straight (Fig. 11C) and branched girdled spindles, as well as ovals up to 0.29 mm in length, with an L : D ratio of ~1.6. Medulla and ringed solenial canals not detectable.

Remarks

Callipodium is unique among the spongiodermid genera in having an encrusting growth form, branched spindles, and lacking longitudinal ring canals (Table 2).

Useful descriptions, comments and/or illustrations of the type species only can be found in Verrill (1869). *Callipodium pacificum* is known from the eastern Pacific from the Pearl Islands to Peru at intertidal depths.

Useful references to *Anthopodium rubens* can be found in: Verrill (1872), Deichmann (1936) and Bayer (1961). It is known from off North Carolina and Texas, at 9–92 m (Cairns and Bayer 2009). Bayer (1961) described a 'basement' or medullar zone for this species sometimes composed of fused rods.

Verrill (1872: 434) stated that *Anthopodium* and *Callipodium* had 'very different spicula' and thus kept them as separate genera. Oddly, Kükenthal (1924) did not mention either genus. In Bayer's (1956) classification, *Callipodium* is included but *Anthopodium* not even mentioned as a junior synonym. Then five years later Bayer (1961) treated *Anthopodium rubens* and stated that 'the spicules of *Anthopodium* bear a closer resemblance to those of *Callipodium* than Verrill indicated, although they are not identical'. Finally, in his classification of key to the genera, Bayer (1981) included in his key *Anthopodium* (but not *Callipodium*) but in his summary classification (Bayer 1981: 945) listed: '*Callipodium* (=*Anthopodium*?)'. Finally, unexplainably *Anthopodium rubens* was not included in the revision of DeVictor and Morton (2010). Thus, the treatment of these two encrusting genera is quite inconsistent and sometimes contradictory. Nonetheless, *Anthopodium rubens* has the same sclerite complement (Fig. 11A, C–F) as *Callipodium pacificum* and thus we suggest accepting the synonymy of these two genera.

Other species

Callipodium aureum Verrill, 1869: Pacific Panama, depth not stated.

Callipodium rubens (Verrill, 1872): off North Carolina and Texas, at 9–14 m.

Callipodium australe Verrill, 1876: Bluff Harbour, New Zealand, depth not stated.

Distribution

North Carolina, northern Gulf of Mexico, eastern Pacific from Pearl Islands Panama to Peru, New Zealand, 0–92 m.

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