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REVISÃO TAXONÔMICA DO GÊNERO *Plexaurella* KÖLLIKER, 1865 (CNIDARIA: ANTHOZOA: OCTOCORALLIA) BASEADA EM DADOS MORFOLÓGICOS E MOLECULARES

Recife
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Tese apresentada ao Programa de Pós-Graduação em Biologia Animal da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de Doutor em Biologia Animal.

Área de Concentração: Zoologia

Orientador: Prof. Dr. Carlos Daniel Pérez

Co-orientador: Prof. Dr. Antonio M. Solé-Cava

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Às mulheres da minha vida

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RESUMO

Octocorais são engenheiros ecossistêmicos importantes em ambientes marinhos profundos e rasos. Gorgônias são octcorais particularmente diversificados e sempre presentes em ambientes recifais ao redor do mundo. Os representantes do gênero *Plexaurella* estão entre os gêneros mais conspícuos de gorgonias em recifes do Atlântico Ocidental, no entanto, o conhecimento atual sobre a diversidade do gênero é baseado em uma série de revisões sem consultas a espécimes-tipo. Além disso, mesmo níveis de classificação taxonômica superiores (subfamílias, famílias, subordens, etc.) são atualmente incertos, uma vez que reconstruções filogenéticas não dão suporte à classificação atual de *Plexaurella* dentro da família Plexauridae e o posicionam próximo à família Gorgoniidae, também polifilética. Assim, o presente estudo revisa o gênero, baseado no exame de espécimes-tipo disponíveis e testa sua monofilia, usando marcadores moleculares mitocondriais e um nuclear (*COI+igr+mtMutS* e *28S*, respectivamente). Até o momento, até seis species eram consideradas válidas. Nossos resultados demonstram que o grupo é composto por pelo menos sete espécies válidas previamente descritas: *P. dichotoma*, *P. nutans*, *P. grisea*, *P. teres*, *P. grandiflora*, *P. regia* e *P. obesa*; e uma nova: *Plexaurella rastrera* sp. nov. A classificação atual do gênero é discutida e, baseado em reconstruções filogenéticas e distâncias genéticas, é proposta a elevação de Plexaurellinae, previamente uma subfamília de Plexauridae, ao nível de família. Embora Gorgoniidae tenha sido recuperado como polifilética, vários gêneros, incluindo *Gorgonia,* foram agrupados num clado monofilético, com o qual Plexaurellidae é relacionado.

Palavras-chave: Alcyonacea. Gorgônias. Octocorais recifais. Plexauridae. Gorgoniidae.

ABSTRACT

Octocorals are important ecosystem engineers in deep and shallow marine environments. Gorgonians are particularly diversified octocorals and ubiquitous in reef environments around the world. Representatives of the genus *Plexaurella* are amongst the most conspicuous genera of gorgonians in the western Atlantic reefs; however, current knowledge on the diversity of the genus is based on a series of revisions lacking examination of type-specimens. Furthermore, even higher classification levels (subfamilies, families, suborders, etc.) are currently uncertain, as phylogenetic reconstructions do not support the current classification of *Plexaurella* within the family Plexauridae and places it close to the polyphyletic family Gorgoniidae. Thus, this study reviews that genus based on examination of available types and test its monophyly using molecular markers, both mitochondrial and nuclear (*COI+igr+mtMutS* and *28S*, respectively). Until now, up to six species were considered valid. Results show that the group is composed by at least seven previously described species: *P. dichotoma*, *P. nutans*, *P. grisea*, *P. teres*, *P. grandiflora*, *P. regia* and *P. obesa*; and one new: *Plexaurella rastrera* sp. nov. The current classification of the genus is discussed and, based on phylogenetic reconstructions and genetic distances, is proposed the elevation of Plexaurellinae, formerly a subfamily of Plexauridae, to the family level. Although Gorgoniidae has been recovered as polyphylethic, several genera, including *Gorgonia*, were grouped within a monophyletic clade, of which Plexaurellidae is closely related.

Key words: Alcyonacea. Gorgonians. Reef octocorals. Plexauridae. Gorgoniidae.

SUMÁRIO

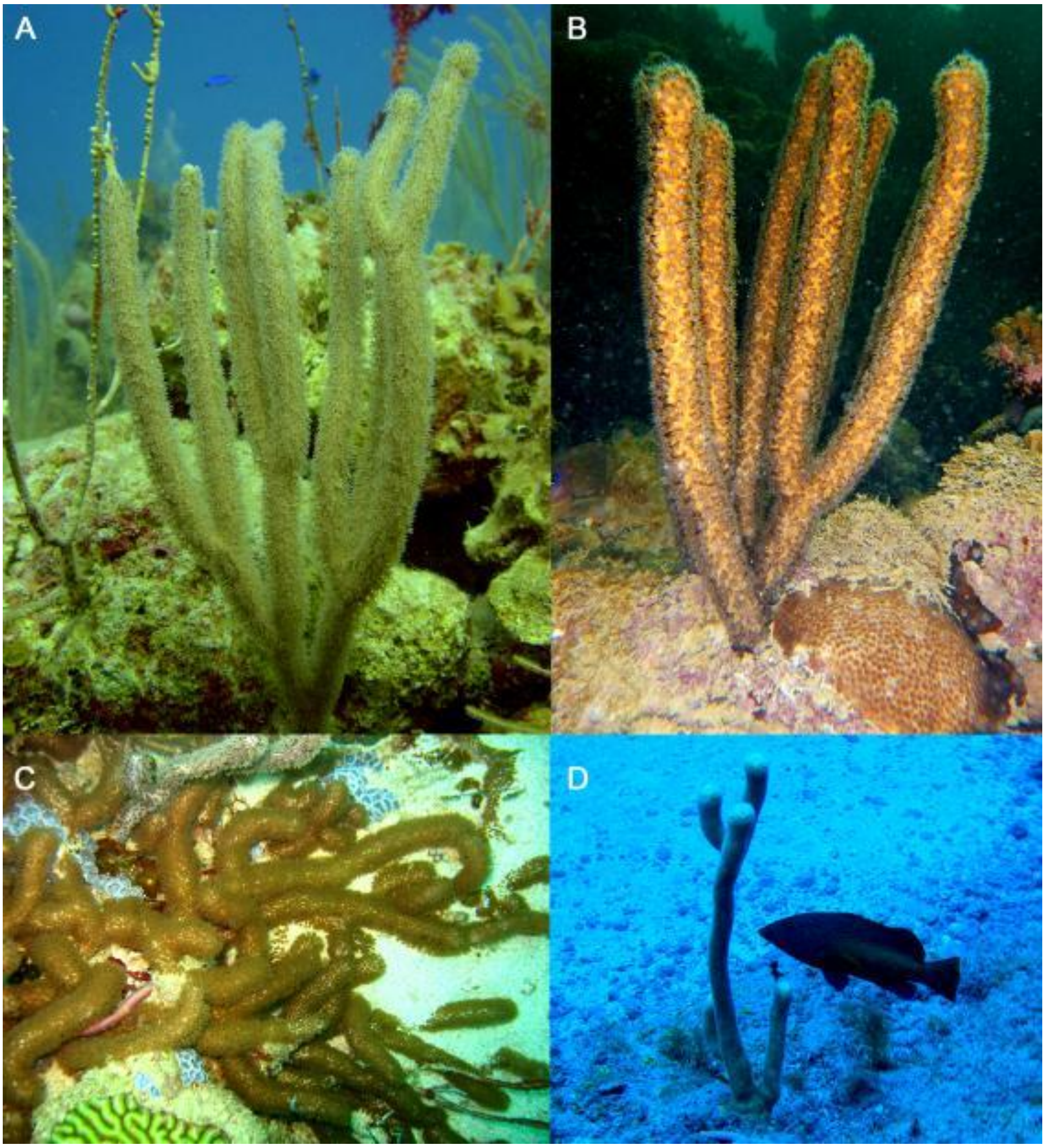
1 INTRODUÇÃO

Recifes tropicais abrigam uma diversidade de organismos maior que qualquer outro ecossistema marinho (BELLWOOD & HUGHES, 2001). Nestes ambientes, octocorais (Cnidaria: Anthozoa: Octocorallia) são engenheiros ecossistêmicos, conhecidos por construir assembleias densas, adicionando tridimensionalidade, modulando o fluxo de água e, consequentemente, agregando diversidade a esses ambientes (SÁNCHEZ et al., 1998; ROBERTS et al., 2006; MORTENSEN et al., 2010). Esses animais são particularmente diversificados em comunidades do Atlântico Ocidental e esforços recentes de mapeamento de comunidades coralineas têm mudado a forma como se entendia seus processos de dispersão e distribuição (BAKER et al., 2016; SOARES et al., 2016).

A Subclasse Octocorallia possui cerca de 3.500 espécies válidas, ocorrendo desde recifes rasos até profundidades de mais de 6.000 metros (Cairns, 2016). Os octocorais têm como autapomorfias: a presença de oito tentáculos e oito mesentérios completos em seus pólipos (McFADDEN, 2007); presença de pínulas nos tentáculos, fusionadas ou livres (ALDERSLADE e McFADDEN, 2007). As formas, tamanho, distribuição ou mesmo a presença de escleritos (microestruturas calcárias de origem ectodérmica) estão entre os principais caracteres utilizados na taxonomia do grupo (PIRES et al., 2007). Dentre os representantes mais conhecidos do grupo estão os corais azuis (Ordem Helioporacea), as canetas e penas do mar (Ordem Pennatulacea) e os corais moles e gorgônias (Ordem Alcyonacea) (BAYER, 1981; McFADDEN, 2007; WILLIAMS, 2011).

São duas as famílias de gorgônias mais diversificadas no Atlântico: Plexauridae Gray, 1859, com pelo menos 550 descritas, e Gorgoniidae Lamouroux, 1812, com cerca de 250 espécies (CORDEIRO et al., 2018). Durante muito tempo, se discutiu que gêneros pertenceriam a uma ou outra (VERRILL, 1868, 1912; BAYER, 1956, 1981), mas caracteres diagnósticos estáveis de ambas só foram estabelecidos por Bayer (1981). Essa relativa estabilidade na classificação era baseada em caracteres supostamente homólogos. Com o advento de técnicas moleculares, ambas as famílias se mostraram polifiléticas, ainda que vários grupos subfamiliares tenham sido confirmados. Gorgônias do gênero *Plexaurella* Kölliker, 1865 (Fig. 1) foram classificadas como plexaurídeos desde a criação do grupo genérico. Recentemente, porém, descobriu-se que o gênero é mais relacionado a Gorgoniidae que a Plexauridae (SÁNCHEZ et al., 2003; WIRSHING et al., 2005; McFADDEN et al., 2006).

Figura 1. Colônias de octocorais do gênero *Plexaurella* spp. A: *P. dichotoma* no Caribe (Foto: Juán A. Sánchez); B: *P. grandiflora* no sul da Bahia, Brasil (Foto: Ralf Cordeiro); C: *P. rastrera* sp. nov. em recifes de Tobago (Foto: Juán A. Sánchez); D: *P. grandiflora* em recifes do arquipélago de Trindade, Brasil (Foto: Maria Eduarda Alves).



Indivíduos do gênero *Plexaurella* estão entre espécies marinhas com alto potencial farmacológico, como antibióticos, antivirais, entre outros (ALMEIDA et al., 2014; GIONGO et al., 2016). Uma taxonomia mais clara, capaz de discriminar limites para distinção entre as espécies do grupo é essencial para embasar trabalhos de aplicação desses organismos. Além disso, por sua distribuição restrita, o gênero é um modelo ideal para o estudo da vicariância e dispersão de octocorais recifais no Atlântico Ocidental (ver BAYER, 1956).

Assim, no presente estudo, é apresentada uma revisão do gênero *Plexaurella* e, através de dados moleculares, é discutida sua relação filogenética com grupos de octocorais próximos, de modo que a classificação represente melhor a história natural do grupo.

1.2 OBJETIVOS

1.2.1 Objetivo Geral

Analisar a validade das espécies nominais do gênero *Plexaurella* Kölliker, 1865 e, através de análises moleculares, reconstruir a filogenia do gênero, estabelecendo seu posicionamento na classificação de Octocorallia.

1.2.2 Objetivos Específicos

- Analisar os tipos disponíveis das espécies nominais descritas para o gênero *Plexaurella*;
- Testar a eficácia dos marcadores moleculares mitocondrialais e nucleares para distinguir espécies do gênero *Plexaurella*;
- Propor uma hipótese filogenética para o gênero, através de caracteres moleculares.

1.3 MATERIAIS E MÉTODOS

1.3.1 Espécimes examinados

Pelo menos 400 espécimes foram examinados no presente estudo, fornecidos por diversos museus ao redor do mundo. Eles foram obtidos através de diferentes métodos de coleta ao longo dos últimos dois séculos. Todos os espécimes-tipo listados no texto foram examinados, exceto quanto mencionados. Espécimes adicionais não listados no corpo do texto foram listados numa tabela suplementar do Apêndice A (Table S1). A terminologia utilizada é baseada ou modificada de Bayer *et al.* (1983). Além das ilustrações fornecidas no texto, são incluídas outras adicionais, também no Apêndice A (37 pranchas suplementares, mencionadas como Figs. S1–S37).

1.3.2 Análises moleculares e filogenéticas

Sequências de DNA foram obtidas de espécimes coletados manualmente no Caribe e no Brasil, entre 2014 e 2016, sendo preservadas em etanol (70%–96%). Tentativas de obter sequências de espécimes-tipo foram sem sucesso. A extração de DNA dos pólipos, foi utilizado o kit DNeasy (Qiagen, Inc., Valencia, CA, USA), de acordo com protocolo do fabricante. Amplificação (PCR) dos genes mitocondriais: *mtMutS* (*msh1*), primers AnthoCorMSH (Herrera *et al*. 2010) e Mut3458R (France & Hoover 2001); *COI* + *igr1*, primers COI-LA-8398-F e COIoct-R (McFadden *et al.* 2011); e parte do gene nuclear *28s*, com primers Far e Rab (McFadden & Ofwegen 2012); seguindo protocolos de McFadden *et al*. (2006) e Cairns and Wirshing (2015). Produtos de PCR foram enviados à Macrogen (Seoul, South Korea) para purificação e sequenciamento. Todas as sequências obtidas foram alinhadas a no software online MAFFT v. 7 através do método L-INS-i (Katoh *et al*. 2017). Sequências mitocondriais e nucleares foram analizadas independemente, com ambos loci mitocondriais concatenados em uma única sequência (*barcode estendido*). O software MEGA v.7 (Kumar *et al*. 2016) foi utilizado para medir as distâncias genéticas (*p*) entre sequências e para determinar o melhor modelo de evolução nucleotídica, com o critério de Akaike (AIC) indicando o modelo GTR+G+I para ambos os conjuntos de dados. Sequências de octocorais de outras famílias também foram utilizadas nas análises como grupos externos (Table 1), incluindo *Cornularia pabloi* (McFadden & Ofwegen 2012). Análises de Máxima Verossimilhança (ML) foram rodadas na base online IQ-Tree v. 1.6.1 (Trifinopoulos *et al*. 2016), com uso de bootstrap ultra-rápido, com 1000 repetições. MrBayes v. 3 (Huelsenbeck and Ronquist 2001) foi usado para executar análises de Inferência Bayesiana (BI) em duas rodadas independents, com um *burn-in* de 25%, utilizando cinco e seis milhões de gerações para os loci nuclear e mitochondriais, respectivamente (até atingir desvio padrão de frequências <0.01). As árvores obtidas foram editadas no FigTree v.1.4.3.

1.4 ESTRUTURA DA TESE

O presente documento foi organizado em uma parte introdutória, definindo conceitos gerais da problemática abordada e objetivos do trabalho, referencial teórico e considerações finais. O texto como um todo também foi redigido em formato de artigo e incluído (com seus respectivos tópicos) ao fim do documento, como Apêndice A. O artigo trata da revisão do gênero *Plexaurella*, da reconstrução de sua história evolutiva, baseada em dados moleculares e da elevação de um grupo subfamiliar, do qual o gênero é representante monotípico, ao nível de família.

2 REFERENCIAL TEÓRICO

2.1 O GÊNERO *Plexaurella* KÖLLIKER, 1865: BREVE HISTÓRICO TAXONÔMICO

Plexaurella está entre os mais conspícuos grupos de octocorais recifais do Atlântico Ocidental, com uma distribuição disjunta na costa americana: Flórida (EUA), América Central, Antilhas e Caribe, no hemisfério norte, sem registros desde Trinidad e Tobago até o parcel de Manuel Luís, de onde ocorre em recifes costeiros e ilhas oceânicas até o Rio de Janeiro (exceto no Arquipélago de São Pedro e São Paulo) (CASTRO et al., 2010). Pelo fato de estarem sujeitos à simbiose obrigatória com zooxantelas, são dependentes de incidência direta de luz e, provavelmente por isso, jamais foram encontrados em profundidades superiores a 30 m, limitando-se aos recifes rasos (FABRICIUS & ALDERSLADE, 2001).

Atualmente, é possível encontrar mais de duas de dezenas nomes ou conceitos disponíveis para espécies deste gênero (ver Apêndice A, Tab. 2). O grupo foi proposto por Kölliker (1865), para agrupar as espécies *Plexaurella dichotoma* (Esper 1791) (=*Gorgonia dichotoma*), *Plexaurella nutans* (Duchassaing & Michelotti, 1860) (=*Eunicea nutans*) e *Plexaurella crassa* Kölliker, 1865. No entanto, mesmo após mais de 150 anos desde a proposição do gênero, nenhum estudo reuniu todos os espécimes-tipo do gênero e poucos lidaram simultaneamente com espécies brasileiras e do hemisfério norte. Um histórico dos principais estudos taxonômicos sobre o gênero é apresentado no Apêndice A – Fig. 2.

Tentativas de classificação e distinção entre espécies, baseadas em múltiplas fontes de evidências envolvendo o gênero, incluem desde caracteres morfológicos tradicionais até quimiotaxonomia e mineralogia. Na década de 80, Gerhart (1983), ao realizar um estudo de quimiotaxonomia baseado em 28 compostos terpenóides listados por Tursch et al. (1978), concluiu que *Plexaurella grisea* Kunze, 1916, *P. dichotoma* e *P. fusifera* Kunze, 1916 eram quimicamente indistinguíveis, ao passo que *P. nutans* seria mantida como uma espécie distinta.

Corroborando o trabalho de Gerhart (1983), Frenz-Ross & Kerr (2009) reafirmaram que *P. dichotoma, P. fusifera* e *P. grisea* realmente eram quimicamente indistinguíveis. Por outro lado, demonstraram que há grande variabilidade química entre indivíduos, populações e espécies de *Plexaurella*. Fenômeno que se repete em outros grupos animais marinhos e que poderia estar relacionado a microrganismos associados ou mesmo às diferenças ambientais a que estão sujeitos. Levando a crer que a proposta de uma taxonomia baseada em caracteres químicos isolados não seja o método mais adequado para distinguir entre espécies.

Baseado na variabilidade de caracteres diagnósticos, como densidade de tubérculos nos escleritos, Alcolado (1985) concluiu que *Plexaurella fusifera* Kunze, 1916 seria sinônimo de *P. dichotoma*. Sobre estas espécies, em uma chave de identificação de campo proposta por Sánchez & Wirshing (2005), é comentado que a distinção entre ambas as espécies seria baseada apenas em diferenças morfológicas externas (forma da colônia). A despeito de Sánchez & Wirshing (2005), a sinonímia proposta por Alcolado (1985) parece ter sido aceita, posteriormente [ver Castro et al. (2010, p. 793), por exemplo]. O que não é observado em trabalhos de cunho não taxonômico (Meszaros & Bigger, 1999; Olano & Bigger, 2000; Frenz-Ross et al., 2008).

Ainda sobre espécies descritas com base em aspectos externos de colônias, Castro (1989), após examinar os tipos de Verrill (1912), comentou que o número de espécies novas, suas similaridades e a pouca quantidade de exemplares indica que Verrill (1912) teria classificado apenas formas de crescimento e não espécies, propriamente ditas.

Uma ideia comum a todos os trabalhos publicados é a asserção de que a espécie-tipo do gênero, *P. dichotoma* (típica do Caribe), é uma espécie insular no Brasil. Castro et al. (2010) (última publicação que lida com o gênero), por exemplo, citam que a espécie ocorre em: “Parcel do Manuel Luís (MA), Atol das Rocas (RN) e Fernando de Noronha (PE)”. As formas de escleritos, porém, *P. dichotoma* são praticamente indistinguíveis de sua congênere costeira *P. grandiflora* (comum em recifes desde a Paraíba até o Rio de Janeiro). Observação apoiada por Castro et al. (2010), que afirmam que as ambas espécies são tão próximas, que estudos mais detalhados possivelmente estabeleceriam uma sinonímia entre elas [Castro et al. (2010, p. 793)].

Após análise do histórico confuso do gênero, é possível afirmar que eram consideradas válidas, até o momento, pelo menos cinco espécies nominais: *Plexaurella dichotoma*, *P. grisea*, *P. nutans*, *P. grandiflora* e *P. regia*. Analisando todos os trabalhos já publicados, porém, é possível dizer que a maioria deles, em algum momento, questionou a validade de todas as espécies, exceto por *P. dichotoma* e *P. regia*. Uma vez conhecidas as limitações na dispersão do grupo, sua variabilidade morfológica e a grande área geográfica em que ocorre, é compreensível que tantos nomes tenham sido propostos.

2.2 TAXONOMIA INTEGRATIVA, IMPORTÂNCIA E FILOGENIA DE *Plexaurella*

Como já mencionado, diversas propostas surgiram como possíveis ferramentas para ampliar a disponibilidade de caracteres na taxonomia de Octocorallia. Como exemplos, é possível citar a também já mencionada ‘quimiotaxonomia’ sugerida por Gerhart (1983) que utiliza metabólitos secundários como caracteres e a ‘mineralotaxonomia’ de Bayer & Macintyre (2001) que propõe o uso da composição (mineral e/ou proteica) dos eixos dos corais como caráter taxonômico. Outra proposta que visa contribuir para uma universalização da taxonomia de todos os grupos animais, no entanto, tem merecido bastante atenção nos últimos anos, a análise de códigos de barra de DNA (DNA barcode) baseada em *COI* (citocromo oxidase subunidade 1) (HERBERT et al, 2003).

Embora de uso limitado, se tomada isoladamente, a identificação de organismos através de 'DNA barcode' baseada em *COI* tem demonstrado funcionar bem com diversos grupos animais, principalmente vertebrados (HERBERT et al., 2003; WARD et al., 2005) e artrópodes (SMITH et al., 2005). A dificuldade de aplicação do ‘barcode’ para grupos de invertebrados, no entanto, ainda reside no pouco conhecimento acerca de valores de distâncias genéticas ideais para diferenciar variações intraespecíficas de divergências interespecíficas (MCFADDEN et al., 2011). Somado a isso, foi comprovado que a pouca variação de genes mitocondriais em invertebrados basais, cnidários antozoários, principalmente, limitam a utilidade do *COI* na identificação de espécies (HERBERT et al., 2003). Chen et al. (2009), por exemplo, comprovaram que o genoma mitocondrial de corais escleractínios evolui cinco vezes mais lentamente que o genoma nuclear, enquanto Hellberg (2006) chega a afirmar uma taxa de 50 a 100 vezes mais lenta que a maioria dos demais grupos animais. O que faz com que a *COI* seja pouco útil mesmo para distinguir espécies cogenéricas, se utilizada isoladamente (FUKAMI & KNOWLTON, 2005). McFadden et al. (2011), por outro lado, sugerem que, utilizando alguns marcadores mitocondriais, diferenças maiores que 1.0% entre octocorais são satisfatórias para distinguir entre espécies com segurança, ainda que diferenças menores sejam úteis em casos de forte evidência morfológica.

McFadden et al. (2011), após testarem a viabilidade do uso de marcadores *COI* e *msh1* (gene codificador de proteínas específicas de octocorais), observaram que cada um, separadamente, foi capaz de diferenciar apenas 70% das espécies. Os autores, por fim, sugerem a utilização de um ‘barcode extendido’ (*COI* + *igr1* + *msh1*), no qual *igr1* corresponde a uma região intergênica curta adjacente ao *COI*, uma vez que demonstrou eficácia na distinção de quase 99% das espécies estudadas. Ainda assim, mesmo após duas décadas com marcadores moleculares disponíveis, um único espécime de *Plexaurella nutans* teve sequências completas de loci mitocondriais (barcode) disponibilizadas (WIRSHING et al., 2005), sendo repetidamente utilizado em quase todos os trabalhos com grupos de octocorais (McFADDEN et al., 2006, 2011; AGUILAR & SÁNCHEZ, 2007; VARGAS et al., 2014).

2.3 ANÁLISE MORFOLÓGICA

Tradicionalmente, a sistemática dos octocorais é baseada no estudo de caracteres morfológicos. Seja macroscopicamente, por forma da colônia, disposição de ramos na colônia, tipos polipares presentes, etc; ou microscopicamente, através da forma, tamanho, ornamentação e cor dos escleritos (FABRICIUS e ALDERSLADE, 2001). Os primeiros são analisados com uso de paquímetro e estereomicroscópios, enquanto os últimos exigem o uso de microscópio ótico ou microscópio eletrônico de varredura (BAYER, 1961). Um glossário de termos morfológicos utilizados é dado por Bayer et al. (1983); o termo “escleroma” [Ingl. *sclerome*] foi adaptado para octocorais por Molodtsova (2013).

3 CONCLUSÕES

Análises com o 28S se mostraram pouco úteis para resolução de problemas de classificação, ainda que tenham recuperado alguns grupos em nível subfamiliar e algumas subordens. No presente estudo, foi confirmada a eficácia do uso do barcode extendido (*COI+igr+MutS*) para distinção entre espécies e em estudos de sistemática de Octocorallia. Ambas as famílias Plexauridae e Gorgoniidae se mostraram polifiléticas e *Plexaurella* foi recuperada como monofilética, ainda que de posição filogenética incerta. O gênero mostrou relação com os gorgoniidae monofiléticos (MGC - *Leptogorgia, Gorgonia, Pacifigorgia, Eugorgia* e *Pseudopterogorgia*), também incerta, já que o grupo ou cai dentro do MGC ou como grupo externo.

Plexaurelídeos apresentaram distâncias *p* intra-específicas de até 0,93% no 28S e nenhuma distância no conjunto de dados mitocondriais, mesmo com espécimes coletados em uma ampla distribuição geográfica (*P. grandiflora* do norte do Brasil e Cadeia Vitória-Trindade, e *P. nutans* da Flórida e Porto Rico). As distâncias interespecíficas dentro do gênero variaram de 0,73% a 1,17% para o locus nuclear até 0,89% para os mitocondriais, o que está de acordo com estudos prévios. As distâncias *p* para todos os taxa intimamente relacionados (MCG) foram de 6,32% a 7,49% e 5,34% a 7,1%, para os locus 28S e mitocondriais, respectivamente; 10,30% a 10,53% em comparação com os holaxônios *Muriceopsis-Pterogorgia-Pinnigorgia*; e até 27,4% quando comparado com linhagens divergentes primitivamente, como primnoídeos.

Para as seqüências 28S, apesar de *P. nutans* não mostrar diferenças intraespecíficas, *P. grandiflora* revelou uma segregação genética intrigante ao longo de sua distribuição, o que pode indicar um caso de especiação críptica, uma vez que as distâncias *p* intraespecíficas nesse locus são frequentemente pequenas.

Plexauridae (família em que *Plexaurella* era tradicionalmente incluída) e Gorgoniidae são famílias polifiléticas, porém *Plexaurella* está mais relacionada com gorgonídeos (e.g., *Gorgonia, Pacifigorgia* e *Leptogorgia*) e não com os plexaurídeos (como *Plexaura, Eunicea* e *Muricea*). A relação de Plexaurellidae com Gorgoniidae recuperada por reconstruções moleculares em nossas análises e em estudos anteriores também é apoiada por estudos morfológicos. *Plexaurella* spp. têm escleritos derivados de fusos, com tubérculos principalmente dispostos em verticilos, como na maioria dos gorgonídeos. A distinção de Plexaurellidae em relação a Gorgoniidae é reforçada pelo seu distinto eixo densamente calcificado, sua composição mineral e tamanho de escleritos.

A distinção molecular entre *Plexaurella* e táxons molecularmente próximos sustentaria a designação de uma família para a primeira ou a inclusão dela dentro de Gorgoniidae Lamouroux, 1812. Entretanto, as várias emendas que esta inclusão demandaria aumentariam muito a instabilidade da diagnose de Gorgonidae. Assim, é proposta a ressurreição do nome previamente subfamiliar (Plexaurellinae), utilizado apenas na ocasião de sua proposição, a família Plexaurellidae Verrill, 1912 new rank.

Embora Plexauridae e Gorgoniidae sejam polifiléticas, vários de seus gêneros se agrupam em clados monofiléticos. Assim, o status desses gêneros deve ser tratado com cuidado. O gênero *Plexaura* (tipo de Plexauridae) cai dentro de um forte clado monofilético junto com *Muricea, Pseudoplexaura* e *Eunicea*, e esse deve ser o ponto de partida para futuros estudos de revisão em plexaurídeos.

A diagnose de Gorgoniidae também necessita ser reavaliada, em face da crescente profusão de estudos sobre seus gêneros. Caracteres como arranjo dos eixos, mineralogia e morfologia devem ser levados em consideração no diagnóstico e descrição de espécies futuros, devido à sua importância taxonômica e à escassez de caracteres morfológicos informativos. Finalmente, sugere-se que os taxonomistas evitem emendas consecutivas de diagnose, a fim de adequar novos táxons, uma vez que essas ações tendem a fortalecer a polifilia das categorias superiores.

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APÊNDICE A – REVISION OF THE GENUS *PLEXAURELLA* KÖLLIKER, 1865 (ANTHOZOA: OCTOCORALLIA) AND ESTABLISHMENT OF THE FAMILY PLEXAURELLIDAE VERRILL, 1912 NEW RANK, INCLUDING DESCRIPTION OF A NEW SPECIES

Abstract

The current knowledge on the diversity of the genus *Plexaurella* is based on a series of dated revisions, often with no examination of types. Although being common octocorals in western Atlantic reefs, there is no consensus on an exact number of valid species within the genus. Furthermore, phylogenetic reconstructions do not support the current classification of *Plexaurella* within the family Plexauridae. Thus, this study reviews that genus based on examination of available types and assess its monophyly using molecular markers, both mitochondrial and nuclear (*COI+igr+mtMutS* and *28S*, respectively). Until now, up to six species were cosidered valid. Our results show that the group is composed by at least seven previously described species: *P. dichotoma*, *P. nutans*, *P. grisea*, *P. teres*, *P. grandiflora*, *P. regia*, and *P. obesa*; and one new: *Plexaurella rastrera* sp. nov. The current classification of the genus is discussed and, based on congruent phylogenetic reconstructions and genetic distances, we propose the elevation of the former plexaurid subfamily Plexaurellinae to family level. An illustrated key to the valid species and a list of all available names are provided. Finally, we propose the synonymy between *Pseudoplexaura crucis* and *Plexaurella tenuis* under *Pseudoplexaura tenuis* new comb.

Key words: Alcyonacea, gorgonians, reef octocoral, Plexauridae, Gorgoniidae

Introduction

Sea fans are conspicuous components in Caribbean and South American shallow reefs (Bayer, 1961; Brazeau & Lasker, 1989). *Plexaurella* Kölliker, 1865 (Fig. 1) is amongst the western Atlantic endemic genera of sea fans, found in tropical waters of the entire Caribbean and Antilles, Northeastern Gulf of Mexico, the Brazilian coast and its islands, from Bermuda to Rio de Janeiro. Representants of the genus occur in a very narrow bathymetric range, from a few centimeters to 30 m, rarely deeper (Bayer, 1961; Castro *et al.*, 2010), mainly as result of its dependence on zooxanthellae (Van-Oppen *et al.*, 2005; Frenz-Ross *et al.*, 2008).

Plexaurella species are often addressed in medical, biochemistry and correlated studies, as farmacognosy (e.g. Bashyal *et al.*, 2006; Frenz-Ross and Kerr, 2009; Giongo *et al.*, 2016). Ecological studies involving the genus are less frequent and most from the 80s and 90s (e.g. Wahle, 1983; Meszaros and Bigger, 1999; Bond *et al.*, 2005). Although several classical taxonomic papers summarize the diversity of that group (e.g. Verrill, 1912; Kunze, 1916; Bayer, 1961; Castro, 1989), there is no consensus on an exact number of valid species.

The name *Plexaurella* was first used by Valenciennes (1855) (*nomen nudum*) (Fig. 2), but attached to a specific taxonomic taxon only ten years later (Kölliker, 1865), within the family Euniceidae, along with *Eunicea* and *Plexaura* (see Kunze, 1916). At that time, Kunze (1916) listed the following species within the genus: *Plexaurella crassa* (Ellis and Solander, 1786) (=*Gorgonia crassa*), *Plexaurella dichotoma* (Esper, 1788) (=*Gorgonia dichotoma*), *Plexaurella furcata* (Lamarck, 1816) (=*Gorgonia furcata*), *Plexaurella vermiculata* (Lamarck, 1816) (=*Gorgonia vermiculata*), *Plexaurella anceps* (Duchassaing and Michelotti, 1860) (=*Eunicea anceps*) and *Plexaurella nutans* (Duchassaing and Michelotti, 1860) (=*Eunicea nutans*). In the two following centuries, several revisions (Verrill, 1907, 1912; Kunze, 1916; Kükenthal, 1919, 1924; Bayer, 1961; Castro, 1989) and surveys (Bell, 1889; Deichmann, 1936; Alcolado, 1985; Castro *et al.*, 2010) addressed the diversity of that genus (Fig. 2).

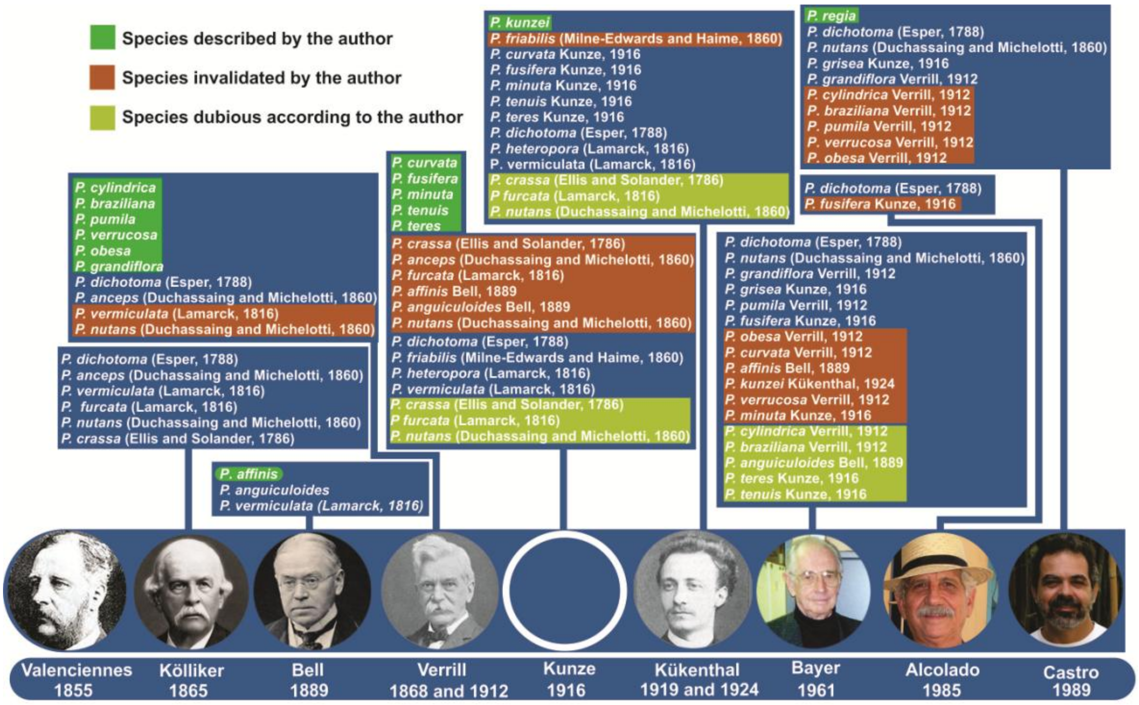
All but two revisions (Verrill, 1907; Castro, 1989) on this group were made with no examination of type specimens. Most studies are based on a small number of samples, often illustrated by a couple pairs of sclerites (e.g. Duchassaing and Michelotti, 1860; Kölliker, 1865; Kunze, 1916). Despite being insufficient, those descriptions helped scientists to identify species during more than a century. Over time, some characters proved to be inadequate to help distinguish between morphologically overlaping species. As result, synonym lists for some species are unusually long.

The basis of the current understanding of the genus was established by Bayer (1961), with few subsequent changes (Castro, 1989; Castro *et al.*, 2010) (Fig. 2). However, due to a long subjective background, currently more than 30 names and/or concepts are available for *Plexaurella* species (Cordeiro et al., 2018).

Classic papers include *Plexaurella* within the family Plexauridae Gray, 1859 (Kükenthal, 1919; Bayer, 1956), despite its densenly calcified axis. In order to accommodate this unique axis structure, Verrill (1912) proposed the subfamily

Plexaurellinae, but it was ignored in all subsequent studies (e.g. Kunze, 1916; Bayer, 1956, 1961, 1981; Castro, 1989). Recent molecular systematic assessments questioned the phylogenetic position of the genus, considering it as a sister group of gorgoniids (Sánchez *et al*., 2003; Wirshing *et al*., 2005; Cairns and Wirshing, 2015). In contrast, the diagnosis of the family Gorgoniidae Lamouroux, 1812 does not support the inclusion of *Plexaurella*, mainly because of its large four-radiate sclerites (often >0.3 mm long), and presence of three coenenchymal layers, besides the fact that Gorgoniidae itself is also polyphyletic (McFadden *et al*., 2006; Aguilar and Sánchez, 2007).

Figure 2. History of main taxonomic studies on the genus *Plexaurella* Kölliker, 1865, with species addressed by each author in the corresponding blue boxes.



Taking into account the current systematic imprecision discussed above, in this study, we provide a revision of the genus *Plexaurella*, including examination of all available types and description of a new species. Additionally, based on molecular and morphological data, we propose the resurrection of Plexaurellinae Verrill, 1912 and its elevation to Family rank.

Materials and methods

Specimens examined

At least 400 specimens were examined in this study, provided by several museums around the world. They were obtained by different collection methods throughout the last two centuries. All type specimens listed herein were examined, except when mentioned. Additional specimens not listed in the main text were included in a supplementary table (Table S1). The terminology used is based on or modified from Bayer *et al.* (1983). Besides the illustrations given herein, we provide plates for part of the material examined during this study (37 supplementary plates of sclerites, referred as Figs. S1–S37).

Molecular and phylogenetic analysis

DNA sequences were obtained from specimens manually collected in Caribbean and Brazil, between 2014 and 2016 and preserved in ethanol (70%–96%). Attempts to obtain sequences from type specimens were unsuccessful. DNeasy blood and tissue kit (Qiagen, Inc., Valencia, CA, USA) was used for DNA extraction from polyp tissues, according to manufacturer's protocol. Amplification (PCR) of the mitochondrial genes: *mtMutS* (*msh1*), primers AnthoCorMSH (Herrera *et al.* 2010) and Mut3458R (France and Hoover 2001); *COI* + *igr1*, primers COI-LA-8398-F and COIoct-R (McFadden *et al.* 2011); and part of the nuclear *28s*, primers Far and Rab (McFadden and Ofwegen 2012); followed protocols of McFadden *et al.* (2006) and Cairns and Wirshing (2015). PCR products were sent to Macrogen (Seoul, South Korea) for purification and sequencing. All sequences obtained were aligned on MAFFT v. 7 through L-INS-i method (Katoh *et al.* 2017). Mitochondrial and nuclear sequences were analysed independently, with both mitochondrial loci concatenated in a single dataset (the extended barcode) and the nuclear locus alone. MEGA v.7 (Kumar *et al.* 2016) was used to measure pairwise genetic distances (uncorrected *p*) among sequences and to determine the best model of nucleotide evolution, with the Akaike information criterion (AIC) indicating GTR+G+I for both datasets. GenBank sequences of representants of other octocoral families were also used in the analyses (Tab. 1), including *Cornularia pabloi* as outgroup, once the family Cornulariidae is considered to be the sister group of all octocorallians (McFadden and Ofwegen 2012). Maximum-likelihood (ML) analyses were run on IQ-Tree v. 1.6.1 (Trifinopoulos *et al.* 2016) using ultrafast bootstrap method, with 1000 replicates. MrBayes v. 3 (Huelsenbeck and Ronquist 2001) was used to perform Bayesian analyses (BI) in two independent runs with a burn-in of 25%, using five and six million generations for nuclear and mitochondrial loci, respectively (to reach standard deviation of split frequencies <0.01). Potential scale reduction factor (PSRF) was 1.00 for all parameters. Trees were edited on FigTree v.1.4.3.

Abbreviations

BMNH: The Natural History Museum, London; MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNRJ: Museu Nacional, Rio de Janeiro, RJ; MSNT: Museo Regionale di Scienze Naturali, Torino (temporarily closed, specimens unavailable); OBIS: Ocean Biogeographic Information System; USNM: United States National Museum (National Museum of Natural History), Washington, DC; SMF: Senckenberg Gesellschaft für Naturforschung, Frankfurt; YPM: Yale Peabody Museum of Natural History, New Haven, CT; ZMB: Zoologisches Museum, Berlin.

Results

For specimens surveyed in this study, sequencings of nuclear *28S* resulted in ~720 bp, mitochondrial *mtMutS* and *COI+igr* in ~700 bp each (concatenated alignment of 1759 sites). A total 143 specimens were used in the final analyses, but only 100 of these for the 28S dataset (Tab. 1).

Table 1. Genbank accession numbers and vouchers of octocoral taxa included in the phylogenetic analysis, according to their families. Bold: newly sequenced individuals.

Family	**Species**	***28s***	***COI+igr***	***mtMutS***
Acanthoaxiidae	*Acanthoaxis wirtzi*	JX203635	JX203816	JX203764
	Acanthogorgia breviflora	JX203636	GQ342378	GQ342464
Acrossotidae	*Acrossota amboinensis*	JX203637	GQ342379	DQ985956
Alcyonidae	*Acrophytum claviger*	JX203655	JX203823	JX203770
	Alcyonium coralloides	JX203640	GQ342380	GQ342465
	Anthomastus ritteri	JX203761	JX203824	DQ302816
	Cladiella sphaerophora	JX203653	GQ342386	GQ342471
	Discophyton rudyi	JX203659	GQ342387	DQ302808
	Eleutherobia aurea	n/a	JX203817	JX203766
	Klyxum utinomii	JX203654	GQ342392	GQ342476
	Lampophyton planiceps	JX203656	GQ342393	GQ342477
	Lobophytum pauciflorum	JX203649	GQ342394	DQ280575
	Malacacanthus capensis	JX203660	GQ342395	DQ302811
	Nephthyigorgia sp	JX203732	JX203864	JX203804
	Paraminabea aldersladei	JX203763	JX203819	JX203767
	Rhytisma fulvum	JX203728	GQ342396	GQ342478
	Sarcophyton ehrenbergi	JX203650	JX203821	DQ280516
	Sinularia querciformis	JX203652	GQ342399	FJ621469
	Thrombophyton coronatum	JX203661	GQ342400	DQ302814
Anthothelidae	*Alertigorgia* sp.	JX203662	JX203825	JX203771
	Anthothela cf. *grandiflora*	KP714021	KP714035	KP713985
	Anthothela sp.	KP714022	KP714036	KP713986
	Anthothela sp.	KP714023	KP714037	KP713987
	Erythropodium caribaeorum	JX203664	GQ342401	GQ342480
	Iciligorgia brunnea	KP714024	KP714050	KP714000
	Iciligorgia sp.	JX203665	GQ342402	GQ342481
	Solenocaulon sp	JX203668	GQ342404	GQ342483
Arulidae	*Arula petunia*	JX203670	JX203827	JX203773
Briareidae	*Briareum asbestinum*	JX203669	GQ342405	GQ342484

Table 1. Cont...

Chrysogorgiidae	*Radicipes gracilis*	n/a	HM590861	DQ297424
	Stephanogorgia faulkneri	JX203718	GQ342406	GQ342485
	Trichogorgia capensis	JX203719	JX203863	JX203798
Clavulariidae	*Azoriella bayeri*	JX203672	GQ342407	GQ342486
	Carijoa riisei	JX203673	JX203829	JX203775
	Cervera atlantica	JX203677	JN620805	JN620804
	Clavularia sp.	JX203678	JX203834	JX203778
	Inconstantia exigua	JX203690	JX203870	JX203790
	Incrustatus comauensis	JX203691	GQ342391	GQ342475
	Knopia octocontacanalis	JX203692	GQ342410	GQ342488
	Paratelesto sp.	JX203693	GQ342411	GQ342489
	Telestula sp.	JX203697	JX203846	DQ302803
Coelogorgiidae	*Coelogorgia palmosa*	JX203698	GQ342413	DQ302805
Coralliidae	*Corallium medea*	n/a	KP714040	KP713990
	Corallium rubrum	n/a	KP714041	KP713991
	Paracorallium tortuosum	n/a	KP714051	KP714001
	Paracorallium tortuosum	KP714025	KP714052	KP714002
Ellisellidae	*Ellisella* sp.	JX203702	JX203850	JX203793
	Viminella sp	JX203703	JX203852	JX203794
Gorgoniidae	*Adelogorgia phyllosclera*	n/a	KF874217.1	JN866558.1
	Eugorgia daniana	LT221083	HG917080	HG917048
	Eugorgia multifida	JX203706	GQ342417	GQ342494
	Eugorgia rubens	n/a	KF874216.1	JN866557.1
	Eunicella tricoronata	JX203707	JX203853	JX203795
	Gorgonia flabellum	JX203708	GQ342418	GQ342495
	Heterogorgia verrucosa	LT221090	HG917053	HG917013
	Leptogorgia alba	KX767434.1	KX767384.1	KX767324.1
	Leptogorgia cofrini	LT221060	HG917084	HG917037
	Leptogorgia cuspidata	KX767433	KX767380	KX767318
	Leptogorgia rigida	JX203709	GQ342420	GQ342496
	Pacifigorgia media	JX203710	GQ342421	GQ342497
	Pacifigorgia stenobrochis	n/a	HG917078	KX721194
	Pacifigorgia firma	n/a	KX351879	KX351872

Table 1. Cont...

	Pacifigorgia smithsoniana	n/a	HG917076	HG917023
	Pacifigorgia irene	LT221045	HG917070	HG917024
	Pacifigorgia cairnsi	n/a	KX767393	KX767333
	Pacifigorgia catedralensis	LT221053	HG917065	HG917019
	Pinnigorgia flava	JX203711	GQ342422	GQ342498
	Psammogorgia cf. arbuscula	n/a	HG917056	HG917043
	Pseudopterogorgia bipinnata	JX203712	GQ342423	GQ342499
	Pterogorgia anceps	JX203714	GQ342424	GQ342500
	Pterogorgia citrina	n/a	KP713966	KP687619.1
	Pterogorgia guadalupensis	n/a	KP713975.1	KP687628
	Rumphella sp.	JX203715	JX203855	JX203797
Helioporacea	*Heliopora coerulea*	JX203716	GQ342426	DQ302872
Ifalukellidae	*Ifalukella yanii*	JX203717	GQ342427	GQ342501
Isididae	*Acanella eburnea*	n/a	EF672731	EF672731
Melithaeidae	*Acabaria erythraea*	JX203720	GQ342430	GQ342503
	Acabaria sinaica	JX203721	GQ342431	GQ342504
	Clathraria rubrinodis	JX203722	GQ342432	GQ342505
	Melithaea sp.	JX203723	JX203856	JX203799
	Wrightella coccinea	n/a	JX203858	JX203801
Nepththeidae	*Eunephthya thyrsoidea*	JX124340	JX124384	JX124364
	Gersemia rubiformis	JX203648	GQ342390	GQ342474
	Paralemnalia thyrsoides	JX203727	GQ342436	GQ342509
Nidaliidae	*Chironephthya* sp.	JX203730	GQ342440	GQ342513
	Pieterfaurea khoisanianum	JX203657	GQ342437	GQ342510
Paragorgiidae	*Paragorgia alisonae*	n/a	KP714053	KP714003
	Paragorgia arborea	KP714026	KP714054	KP714004
	Paragorgia arborea	KP714027	KP714055	KP714005
	Paragorgia johnsoni	KP714028	KP714056	KP714006
	Paragorgia regalis	n/a	KP714057	KP714007
	Sibogagorgia cauliflora	n/a	KP714062	KP714012
	Sibogagorgia	n/a	KP714063	KP714013

Table 1. Cont...

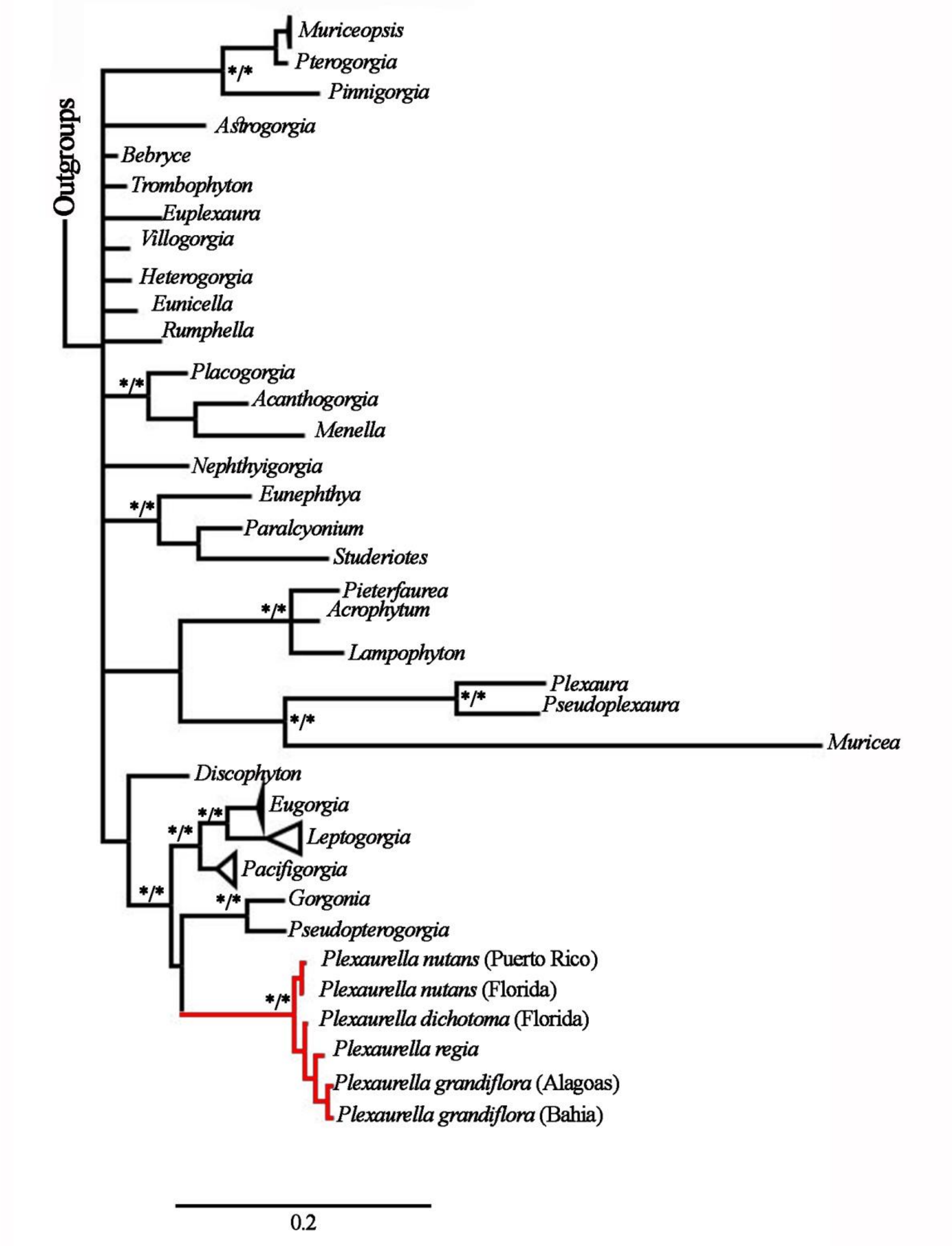
	dennisgordoni			
Paralcyoniidae	*Paralcyonium spinulosum*	JX124347	JX124389	DQ302833
	Studeriotes sp	JX124348	GQ342443	GQ342515
Pennatulidae	*Gyrophyllum sibogae*	JX203740	JX203865	DQ302869
Plexaurellidae	*P. grandiflora* (Alagoas) MNRJ (uncatalogued)	**New**	**New**	**New**
	P. dichotoma (Florida) MNRJ (uncatalogued)	**New**	**n/a**	**n/a**
	P. nutans (Puerto Rico) MNRJ (uncatalogued)	**New**	**n/a**	**n/a**
	P. grandiflora (Bahia) MNRJ (uncatalogued)	**New**	**New**	**New**
	Plexaurella nutans	JX203745.1	GQ342451	GQ342523
Plexauridae	*Astrogorgia sp.*	JX203733	JX203861	JX203805
	Bebryce sp.	JX203734	JX203862	JX203806
	Bebryce sp.	n/a	KF955033.1	KF915570.1
	Chromoplexaura markii	n/a	KX904954	KX904972
	Eunicea tourneforti	n/a	GQ342445	GQ342517
	Euplexaura sp.	n/a	GQ342446.1	GQ342518.1
	Euplexaura sp.	KF915374.1	KF955077.1	KF915617.1
	Echinomuricea sp.	n/a	KC984637.1	KC984601.1
	Menella sp.	JX203736	GQ342447	GQ342519
	Muricea atlantica	JX203747	GQ342448	GQ342520
	Muricea cf. austera	n/a	HG917058	HG917016
	Muricea fruticosa	n/a	HG917059	HG917017
	Muriceopsis flavida	JX203744.1	GQ342449	GQ342521
	Paramuricea biscaya	n/a	FJ264914.1	GQ413995.1
	Paramuricea placomus	n/a	GU563316.1	GU563312.1
	Placogorgia sp.	FJ642929.1	FJ264915.1	GU563304.1
	Plexaura kuna	JX203748	JX203866	JX203807
	Pseudoplexaura wagenaari	JX203746	GQ342452	GQ342524
	Scleracis guadalupensis	n/a	KC984590.1	KC984626.1
	Swiftia sp.	n/a	FJ264906.1	GU563302.1

Table 1. Cont...

	Swiftia sp.	n/a	FJ264904.1	GU563303.1
	Swiftia kofoidi	n/a	KX904960	KX904966
	Swiftia pacifica	n/a	KF874210.1	JN866550.1
	Swiftia simplex	n/a	KX904985	KX905008
	Villogorgia sp.	KF915551.1	KF955274.1	KF915793.1
Primnoidae	*Callogorgia formosa*	JX203749	GQ342453	GQ342525
	Thouarella grasshoffi	n/a	FJ268636	GQ868334
Protoptilidae	*Distichoptilum gracile*	JX203739	GQ342454	DQ302866
Renillidae	*Renilla* sp.	n/a	GQ342455	GQ342526
Spongiodermatidae	*Callipodium*	n/a	KP714039	KP713989
	Diodogorgia nodulifera	JX203663	JX203826	JX203772
	Diodogorgia ceratosa	n/a	KP714042	KP713992
	Homophyton verrucosum	n/a	GQ342403	GQ342482
Subergorgiidae	*Annella mollis*	n/a	KP714032	KP713982
	Rosgorgia inexpetata	KP714029	KP714061	KP714011
	Subergorgia suberosa	n/a	KP714064	KP714014
Tubiporidae	*Tubipora sp*	JX203752	GQ342458	JX203811
Virgulariidae	*Virgularia schultzei*	JX203743	GQ342459	GQ342527
Xeniidae	*Sarcothelia edmondsoni*	n/a	JX203868	JX203814
	Xenia hicksoni	JX203759	GQ342463	GQ342529
Cornulariidae	*Cornularia pabloi*	JX203699	JX203847	JX203792

Analyses with the 28S showed good resolution for some groups up to the subfamiliar level, but loselly recovering well known monophyletic subordinal clades, like the Holaxonia, mixing it with several Alcyoniina genera (Fig. 3). Both Plexauridae and Gorgoniidae were polyphyletic. *Plexaurella* was recovered as monophyletic in all analyses with the 28S, but its phylogenetic position was unresolved.

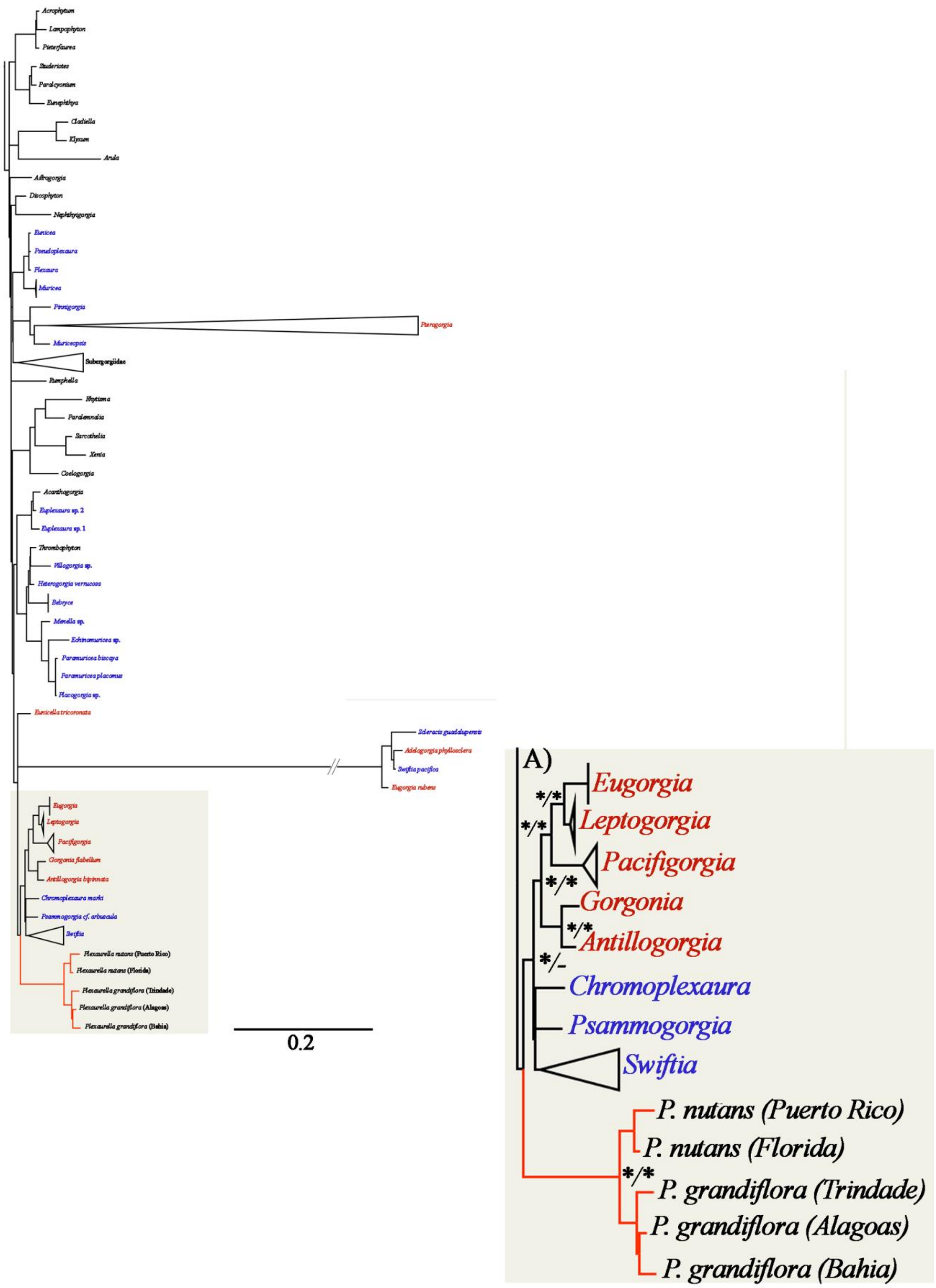
Figure 3. Phylogenetic reconstruction of octocoral families (mostly holaxonians) based on nuclear 28s locus. Topology inferred by maximum likelihood. Asterisks represent nodes with bootstrap values >95% and Bayesian probabilities of >95 in all analyses, respectively. Red branches correspond to Plexaurellidae a.



A strong monophyletic *Plexaurella* clade was also recovered in all *COI+igr+mtMutS* reconstructions (>95% of bootstrap support and posterior probabilities in ML and BI, respectively, for both datasets), although its relationship with the monophyletic gorgoniids (*Leptogorgia, Gorgonia, Pacifigorgia, Eugorgia* and *Pseudopterogorgia*) remains uncertain, as the group either falls within the MGC or as its sister lineage. Plexaurellids also fall as sister group of all the MGC-*Chromoplexaura-Psammogorgia-Swiftia* clade in most analyses with mitochondrial genes (Fig. 4). In both loci groups, the genus *Eunicella* remained unresolved, always falling within the MGC-*Plexaurella* clade, but weakly supported in all analyses.

Plexaurellids showed intraespecific p-distances up to 0.93% for 28S and no distances at all in the mitochondrial concatenated dataset, even with specimens collected in a wide geographic range (*P. grandiflora* from northern Brazil and Trindade Seamounts, and *P. nutans* from Florida and Puerto Rico). Interespecific distances within the genus ranged from 0.73% to 1.17% for the nuclear locus up to 0.89% for the mitochondrial. P-distances to all closely related taxa were from 6.32% to 7.49% and 5.34% to 7.1%, for 28S and mitochondrial loci, respectively; 10.30% to 10.53% compared with the holaxonians *Muriceopsis-Pterogorgia-Pinnigorgia*; and up to 27.4% when compared with early divergent lineages, such as primnoids.

Figure 4. Phylogenetic reconstruction of octocoral families based on concatenated mitochondrial loci *COI+igr+mMutS*. Asterisks represent nodes with bootstrap values >95% and Bayesian probabilities of >95 in all analyses, respectively. Names in red and blue are gorgoniids and plexaurids, respectively, according to the traditional classification. Red branches correspond to Plexaurellidae.



Discussion

As indicated by previous studies (e.g. McFadden *et al*. 2011), there was a complete lack of intraspecific divergence within the extended barcode (*COI+igr+MutS*), and distances between congeneric species were >0.50% in all comparisons. For the *28S* sequences, despite *P. nutans* shows no differences between specimens, *P. grandiflora* revealed an intriguing genetic segregation along its distribution range, from 0.23% (between coastal specimens) to 0.93% (when coastal are compared to insular specimens) and that may indicate a case of cryptic speciation, once intraspecific p-distances in that locus are often <0.5% (see McFadden and Ofwegen 2012). Genetic segregation along the Brazilian coast was recorded for other Brazilian reef organisms (Piccianni *et al.* 2016; Souza *et al*. 2017) and populations of the Trindade archipelago are often geneticaly isolated (Rodríguez-Rey *et al*. 2016; Teschima *et al*. 2016).

General topologies in the trees recovered were similar to other from previous studies, as follows: the Scleraxonia was largely polyphyletic, falling within at least six different clades (Cairns and Wirshing 2015); the ellisellids and pennatulaceans having a common origin (McFadden *et al*. 2006); the monophyly of the group "*Anthomastus-Paragorgiidae-Coralliidae*" (Berntson *et al*. 2001); and a mixed clade "*Holaxonia-Alcyoniina*", in which both plexaurids and gorgonids are included (Wirshing *et al*. 2005).

To date, several studies have addressed the polyphyletism within the plexaurids (Sánchez *et al*. 2003; Wirshing *et al.* 2005; McFadden *et al.* 2006; Aguilar and Sánchez 2007; Vargas *et al*. 2014) and included DNA sequences of *Plexaurella* specimens (Cairns and Wirshing 2015; Soler-Hurtado *et al*. 2017). As result, both Plexauridae (in which *Plexaurella* was included) and Gorgoniidae families are kown as polyphyletic and that *Plexaurella* is more related to the gorgonids (eg. *Gorgonia*, *Pacifigorgia* and *Leptogorgia*) rather than to most plexaurids (eg. *Plexaura*, *Eunicea* and *Muricea*). The sequences analyzed herein placed *Plexaurella* in unresolved clades, but closely related to a monophyletic gorgonid group (MGC) (formed by *Eugorgia*, *Leptogorgia*, *Pacifigorgia*, *Gorgonia* and *Antillogorgia*) and *Chromoplexaura-Psammogorgia-Swiftia*, confirming previous studies (Sanchez *et al*. 2003; Wirshing 2005; McFadden *et al*. 2006; Aguillar and Sánchez 2007; Vargas *et al*. 2014).

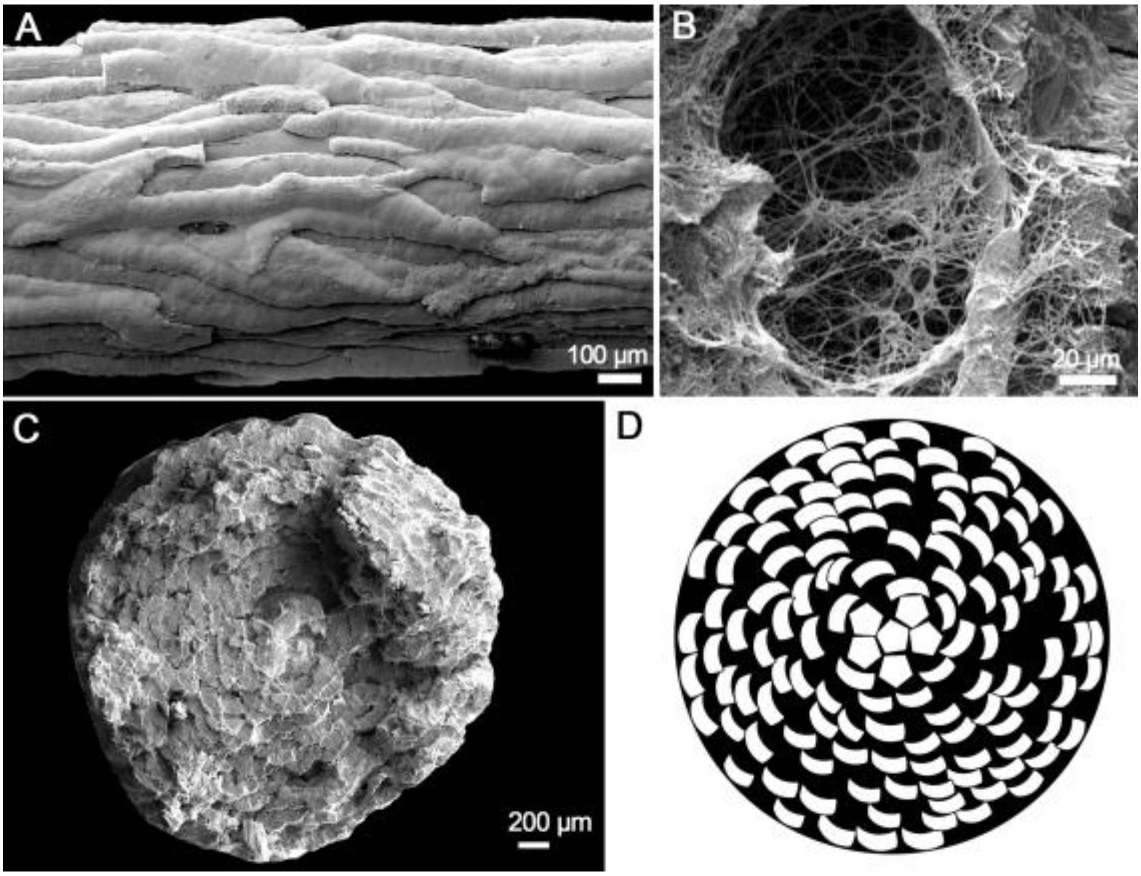
As a reflection of their polyphyly, gorgonids show diverse mineral compositions of their axes, although carbonate hydroxylapatite is only found in the MGC (Bayer and

Macintyre 2001; Wirshing *et al.* 2005; McFadden *et al.* 2006). Despite its relationship with gorgoniids, *Plexaurella* is the only monophyletic clade having axes densely calcified (Fig. 5A), with Mg-calcite, and aragonitic holdfasts, also possessing the highest rates of $MgCO_3$ (15.7 mol%) amongst the Holaxonia (Bayer and Macintyre, 2001). Whereas in most plexaurids and gorgonids the deposition of calcium carbonate is usually concentrated in the central core of the axis, in plexaurellids most of it fills the proteinaceous loculi surrounding the central core (Fig. 5C). Along with gorgonids, plexaurellids have sclerites with tubercles disposed in transverse whorls, sometimes laterally fused; in contrast, they also show a third surface layer of sclerites, and sclerites larger than those found in the MGC (<0.3 mm) (Sanchez *et al*. 2003).

Molecular distinction between *Plexaurella* and molecular closely related taxa (*p*-distances: 6.32%–7.49% and 5.34%–7.1%, for 28S and *COI+igr+msh1*, respectively) supports either the erection of a family for the former or the inclusion of it within Gorgoniidae Lamouroux, 1812. However, the various emendations that this inclusion would request would highly increase the instability of the diagnosis for gorgonids. Thus, we propose the ressurrection of the formely subfamiliar name, used only at its establishment, the family Plexaurellidae Verrill, 1912 new rank.

The families Plexauridae and Gorgoniidae, as currently known, are polyphyletic (Berntson et al. 2001; Sánchez et al. 2003; Wirshing et al. 2005; McFadden et al. 2006; Aguilar and Sánchez 2007), but several of their genera group within strong monophyletic clades (Figs. 3, 4). Thus, status of these genera must be carefuly addressed. Plexaurellids form a distinct clade, not related with the Plexaurids, and closely related to the MGC, but morphologicaly and geneticaly distinct of the latter. The genus *Plexaura* (type of Plexauridae) falls within a strong monophyletic clade along with *Muricea*, *Pseudoplexaura* and *Eunicea*, and that should be the start point for future revisionary studies on plexaurids.

Figure 5. Axis morphology in plexaurellids. A: axis of a branchlet in side-view showing longitudinal strands of Mg-Calcite; B: fibrous filaments in spaces between the strands; C: axis of a branchlet in cross-section showing loculi of Mg-Calcite; D: illustration of an axis in cross-section (white spots indicate concentration of calcareous elements).



Some representants of *Adelogorgia*, *Swiftia* and *Eugorgia* fall into a monophyletic clade along with *Scleracis guadalupensis*. Most of these taxa need special attention in further morphological and molecular assessments (Soler-Hurtado *et al*. 2017a; Breedy and Guzman 2018). We also recommend a reevaluation of the diagnosis of Gorgoniidae, in face of the crescent profusion of studies on its genera (Vargas *et al*. 2014; Soler-Hurtado *et al*. 2016, 2017a,b). Characters such as axes arrangement, mineralogy and morphology must be taken into account in future diagnosis and species descriptions, due to its taxonomic importance and the paucity of informative morphological traits (Bayer and Macintyre, 2001; Breedy and Guzman, 2014, 2018) not only for holaxonians (Pante *et al.*, 2012). Finally, we suggest taxonomists should avoid consecutive emendations of diagnosis in order to fit new taxa, once these actions tend to strength the polyphyly of higher categories.

Taxonomy

Subclass **OCTOCORALLIA** Haeckel, 1866

Order **ALCYONACEA** Lamouroux, 1812

Suborder **HOLAXONIA** Studer, 1887

Family **PLEXAURELLIDAE** Verrill, 1912 *new rank*

Plexaurellinae Verrill, 1912: 382–383 (in part: not *Euplexaura*).

Type genus: *Plexaurella* Kölliker, 1865 (by original designation, Verrill, 1912)

Diagnosis

Holaxonia with thick and porous coenenchyme, supported by sclerites mainly in form of butterflies, but also spindles, tri-radiates, four-radiates and six-radiates. Branchlets with limited flexibility. Coenenchyme divided in three distinct layers. Cortical layer usually thin and filled with six-radiate sclerites or small butterflies with very short arms. Middle layer thick, with the largest sclerites, mainly butterflies, spindles, tri-radiates, four-radiates and/or six-radiates. Axial sheath with sclerites similar to those of the middle-layer, but smaller and less ornamented, with no purple sclerites and no intrusion of middle layer sclerites. Axis with a chambered central core and loculi densely calcified, with calcium carbonate strands longitudinally placed and anastomosing between them. In cross section, concentric loculi filled with Mg-calcite. Holdfast mainly composed of aragonite. Polyps naked or with strong anthocodial armature, contractile and retractile into calyces often proeminent, but sometimes absent.

Remarks

At the time of its proposition, mostly based on generalizations of features of the genus *Plexaurella,* Verrill (1912) also included the genus *Euplexaura* and its “relatives” within the Plexaurellidae. Verrill (1912) did not list which genera he had in mind by saying “related genera”, but mentions “…in which the axis is partially calcified with strands of calcium carbonate. The coenenchyma is thick, suberous, made up of small spindles, crosses, and related forms, and everywhere permeated by tubules running in all directions, some of them terminating in external pores, rendering it very cellular”. However, *Euplexaura* has no direct evolutive relationships with *Plexaurella*, based on molecular and morphological characters. In contrast with the latter, *Euplexaura* has only two layers of coenenchyme; its surface has robust ovals or spindles, whereas *Plexaurella* has butterflies or six-radiates; moreover, *Euplexaura* has its axial layer filled with rods or spindles, never butterflies. Surface sclerites in some species of

Euplexaura (e.g. *E. boninensis* – see Ofwegen and Matsumoto, 2016) resemble those of the genus *Thesea*. *Euplexaura* falls in a loose suported clade with *Astrogorgia, Placogorgia, Acanthogorgia* and *Menella*, in analyses with nuclear 28S. With the mitochondrial loci, *Euplexaura* was also recovered as a sister-group of the plexaurids *Heterogorgia, Villogorgia, Bebryce, Menella, Echinomuricea* and *Paramuricea* (Fig. 4). Besides that, in most plexaurids, warts of spindles and four-radiate sclerites are not well organized in whorls and sclerites of surface and middle layer may be mixed in the coenenchyme. Thus, Plexaurellidae is recalled herein to group only its type genus.

The relationship of Plexaurellidae with Gorgoniidae recovered by molecular resonctructions in our analyses and in previous studies (Sánchez et al., 2003; Wirshing et al., 2005; McFadden et al., 2006; Aguillar & Sánchez, 2007) is also supported by morphological information. *Plexaurella* spp. have spindles-derived sclerites, with tubercles mostly arranged in whorls as in most gorgonids. Distinctiveness of Plexaurellidae in relation to Gorgoniidae is reinforced by its distinct densely calcified axis, its mineral composition and sclerite size.

Genus *Plexaurella* Kölliker, 1865

Plexaurella Valenciennes, 1855: 10 (*nom. nud.*).

Gorgonia. —Esper, 1788: supp. 1–2: part 14 (in part: *G. dichotoma*); 1791: P 1: 59 (in part: *G. dichotoma*).

Plexaurella Kölliker, 1865: 138. —not Wright and Studer, 1889: 140–141, pl. 33 fig. 4. (=*Menella*). —Kunze, 1916: 553–585 [in part: not *Plexaurella tenuis* (=*Pseudoplexaura tenuis* (Kunze, 1916) new comb.) (ZMB 5964)], figs. A–D1. —Verrill, 1912: 383–389. —Kükenthal, 1919: 200; 1924: 101. —not Gordon, 1925: 22–23, pl. 3 fig. 9, pl. 4 fig. 7 [=*Pseudoplexaura flagellosa* (Houttuyn, 1772)]. —not Dubrowsky, 1934: 2, figs. 1–6 [=*Pseudoplexaura porosa* (Houttuyn, 1772)]. —not Stiasny, 1935a: 28, fig. G, pl3. fig 15. [=*Pseudoplexaura porosa* (Houttuyn, 1772)]. —not Stiasny, 1935b: 238. [=*Pseudoplexaura porosa* (Houttuyn, 1772)]. —Deichmann, 1936: 94–95. —Bayer, 1956: F212. —Bayer, 1961: 167–179, figs. 50–54; 1981: 926 (key to genera). —Castro, 1989: 597.—Castro *et al.*, 2010: 790–797, fig. 12–15.

Type species**:** *Gorgonia dichotoma* Esper, 1788, by subsequent designation (Kunze, 1916: 555).

Diagnosis (emend in boldface)

Stout, dichotomously or laterally branching **Holaxonia** with thick coenenchyme and **presence and/ or** predominance of butterfly-form (four-radiate) sclerites. Cylindrical branches, usually long and straight. Polyps retracting into slitlike (ocasionally porelike) apertures often with a raised, bilabiate rim. Two rays of four-radiate sclerites usually stronger than the others. Axial sheath sclerites never purple in color. Polyps with few, small rods and rarely a strong crown (based on: Bayer, 1961, 1981; Castro *et al*., 2010; and adequated to the current phylogenetic position of the genus, based on: Wirshing *et al*., 2005; McFadden *et al*., 2006).

Remarks. Valenciennes (1855) listed *Plexaurella dichotoma* among several species with four-radiate sclerites, neither establishing the genus nor a definition for it (*nomen nudum*). The concept of *Eunicea* of Duchassaing and Michelotti (1860) was partially related to *Plexaurella*, as they included *P. nutans* and *P. anceps* within that genus.

Bayer (1981) lists *Plexaurella* within the subfamily Plexaurinae Verrill, 1912, but its inclusion is not supported by any subsequent phylogenetic reconstructions (see Sánchez et al., 2003; Wirshing et al., 2005; McFadden et al., 2006; Aguilar and Sánchez, 2007).

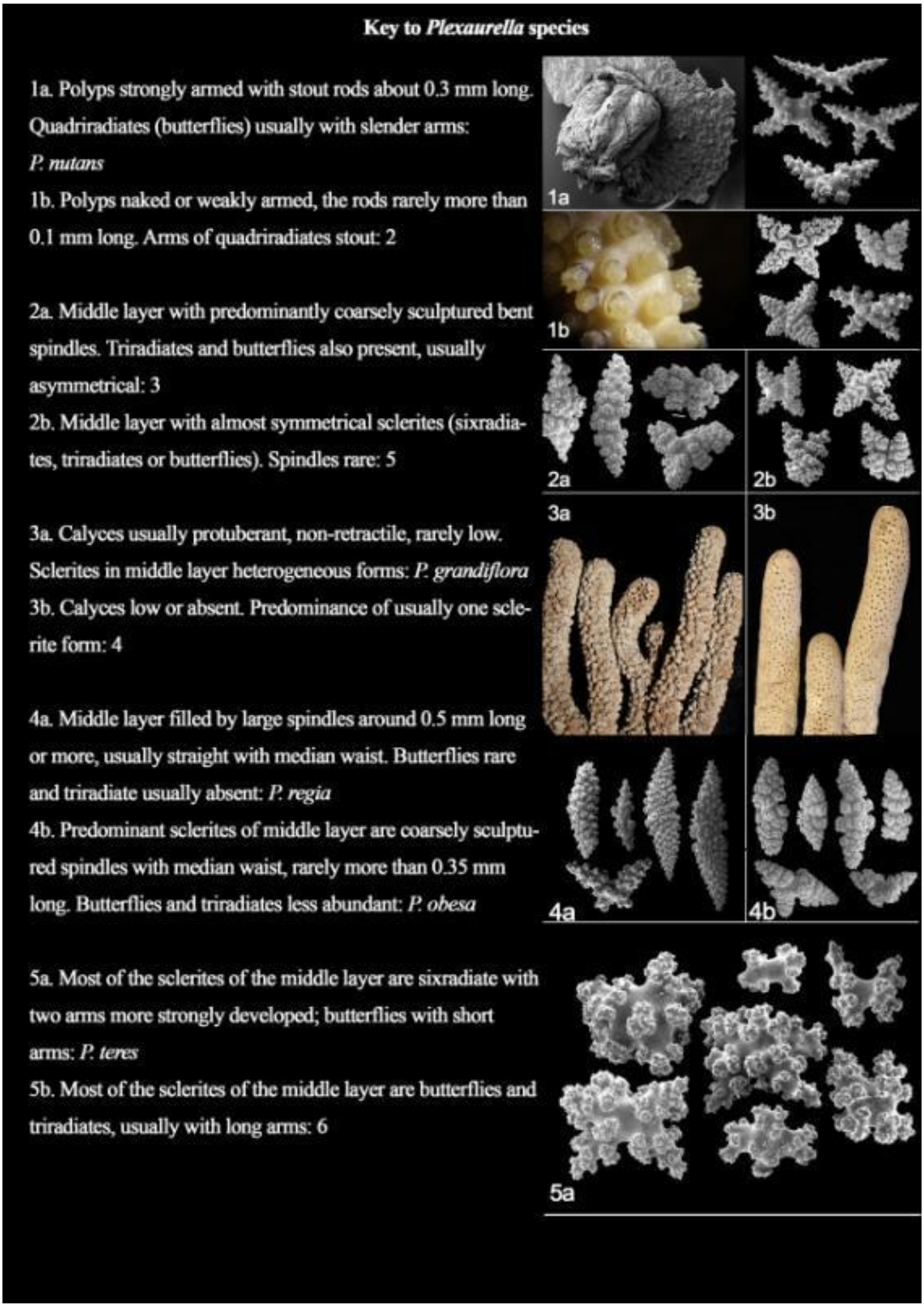
As stated by Sánchez and Wirshing (2005), the preferable way to reinforce the validity of species in this genus would be DNA sequencing of specimens, especially types. However, we failed in all attempts to obtain sequences from type specimens and it is unlikely that the remaining types have viable genetic material. Thus, an alternative way was to examinate as many specimens as possible to assess the range of variation among species. We present herein the conclusions drawn by the examination of hundreds of specimens, highlighting the wide range of sclerites variability within the genus.

Some problematic old species names remain unsolved through all revisions. For example: without examination of type specimens, Kunze (1916) suggested that both *P. crassa* (Ellis and Solander, 1786) and *P. furcata* (Lamarck, 1816) were synonyms of *P. nutans*. Bayer (1961) mentioned a similar problem with *P. vermiculata* Lamarck, 1816. In the same way, it was impossible to determinate the identity of *P. vermiculata sensu* Duchassaing and Michelotti (1860) (MSNT 236), once these specimens were unavailable. Thus, by disuse and due to the unavailability of types, species names given by Ellis and Solander (1786) (*P. crassa*) and Lamarck (1816) (*P. vermiculata*, *P. furcata*) shoud be referred to as *species inquirenda*, as these names were mostly used in museums and/or species lists (compilations) since its descriptions (Garcia-Parrado and

Alcolado, 1996; Volpi and Benvenuti, 2003). A list of concepts and names referred to *Plexaurella* is given in the Table 2.

Distribution. Tropical shallow-waters from the western Atlantic. Throughout the entire Caribbean and Antilles, also in northern Gulf of Mexico, the Atlantic coast of Central America and northern South America, and Florida and Bermuda; in Brazil, from Parcel do Manoel Luis (Maranhão State) to São João da Barra (Rio de Janeiro State), including the oceanic islands of Fernando de Noronha Archipelago, Atol das Rocas and Trindade, up to 50 m depths.

Illustrated key to *Plexaurella* species (modified from Bayer, 1961)



Key to *Plexaurella* species

1a. Polyps strongly armed with stout rods about 0.3 mm long. Quadriradiates (butterflies) usually with slender arms: *P. nutans*

1b. Polyps naked or weakly armed, the rods rarely more than 0.1 mm long. Arms of quadriradiates stout: 2

2a. Middle layer with predominantly coarsely sculptured bent spindles. Triradiates and butterflies also present, usually asymmetrical: 3

2b. Middle layer with almost symmetrical sclerites (sixradiates, triradiates or butterflies). Spindles rare: 5

3a. Calyces usually protuberant, non-retractile, rarely low. Sclerites in middle layer heterogeneous forms: *P. grandiflora*

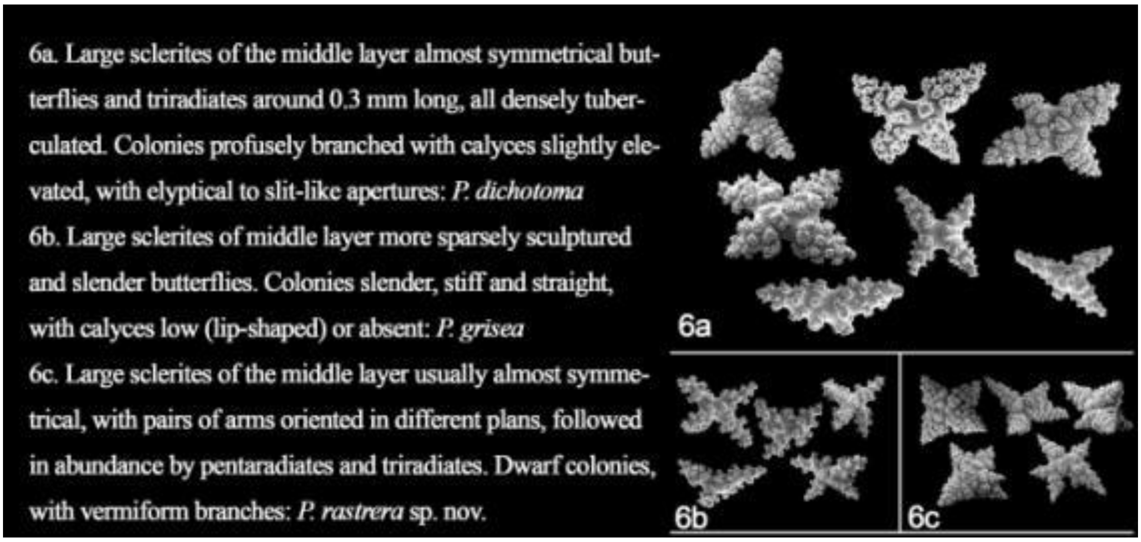
3b. Calyces low or absent. Predominance of usually one sclerite form: 4

4a. Middle layer filled by large spindles around 0.5 mm long or more, usually straight with median waist. Butterflies rare and triradiate usually absent: *P. regia*

4b. Predominant sclerites of middle layer are coarsely sculptured spindles with median waist, rarely more than 0.35 mm long. Butterflies and triradiates less abundant: *P. obesa*

5a. Most of the sclerites of the middle layer are sixradiate with two arms more strongly developed; butterflies with short arms: *P. teres*

5b. Most of the sclerites of the middle layer are butterflies and triradiates, usually with long arms: 6



6a. Large sclerites of the middle layer almost symmetrical butterflies and triradiates around 0.3 mm long, all densely tuberculated. Colonies profusely branched with calyces slightly elevated, with elyptical to slit-like apertures: *P. dichotoma*

6b. Large sclerites of middle layer more sparsely sculptured and slender butterflies. Colonies slender, stiff and straight, with calyces low (lip-shaped) or absent: *P. grisea*

6c. Large sclerites of the middle layer usually almost symmetrical, with pairs of arms oriented in different plans, followed in abundance by pentaradiates and triradiates. Dwarf colonies, with vermiform branches: *P. rastrera* sp. nov.

***Plexaurella dichotoma* (Esper, 1788)**

Figs. 1A, 6A, 7, 8, S1–4

Gorgonia dichotoma Esper, 1788: supp. 1–2: part 14; 1791: 59. —Grasshoff, 1991: 334. —Verrill, 1907: 310, pl. 36a fig. 2.

Plexaurella vermiculata. —Kölliker, 1865: 138, pl. 18 fig. 13

Plexaurella dichotoma. —Kölliker, 1865: 138, pl. 18 fig. 11, 14. —Hargitt and Rogers, 1901: 285. —Verrill, 1907: 310–311, figs. 156–157, pl. 36a figs. 1–2. —Bayer, 1961 [in part: not Verrill’s (1912) species]. —Alcolado, 1985: 1–3, fig. 1. —Sánchez and Wirshing, 2005: 514 (key), fig. 3C. —Castro *et al.*, 2010: 791–794 (in part: MNRJ 1269). —not Medeiros and Castro, 1999: 11. —not Silva and Pérez, 2002: 18. —not Almeida et al., 2005: 75.

Plexaurella fusifera. —Bayer, 1961: 179, fig. 54 e–l.

Types and type localities. *Gorgonia dichotoma*: SMF 5808 (Fig. 7A) and MCZ 67508 (slide) (Fig. 6A). Type locality: South American Islands (Caribbean, see remarks).

Material examined. USNM 1122672, Saba bank, Netherlands Antilles, 24 m (Fig. S1); USNM 7525, Kingston harbor, Jamaica, unknown depth (Fig. S2); USNM 51972, St. George's Island, Bermuda, 6.1–9.2 m; USNM 51970, St. George's Island, Bermuda, 6.1–9.2 m; USNM 1007506, Exuma Cays, White Horse, Bahamas, 10 m; USNM 50419, Key Largo, Florida; USNM 75238, 25°N, 77°W, New Providence Island, Nassau, Bahamas; USNM 51489, Bahamas; USNM 50715, 25°N, 77°W, New Providence Island, Nassau, Bahamas; USNM 50602, Longboat Key, Sarasota Bay, Florida, 10–12 m (Fig. S4); USNM 49607, Biscayne Bay, Florida; USNM 50269, Dry Tortugas, Florida; USNM 50390 and USNM 50709, Florida Keys, Dry Tortugas, Florida; USNM 51446, 22°23’33”N, 89°41’33”W, Yucatán, 15 m; USNM 52408, USNM 52410 and USNM 52411, Campeche Bank, Alacran Reef, Yucatán, 1–2 m; USNM 51359, Portland Bight, Jamaica, 20 m; USNM 51360, Port Royal Cays, Jamaica; USNM 54940 17 45 48 N, 77 00 30 W, 9–13 m, southwest of Kingston, Jamaica; USNM 51393, Cayman Islands; USNM 51394, Pigeon Island, Jamaica; USNM 54263, Discovery Bay, Jamaica; USNM 51435, 22°23’N, 89°41’W, Campeche Bank, Alacran Reef, Yucatán, 1–3 m (Bayer, 1961); USNM 50711, 21°54’49”N, 84°53’48”W, Ensenada de Cajon, Cuba (Fig. S3); USNM 34676, Jutias Cays, Cuba; USNM 34677, Santa Lucia Bay, Cuba; USNM 34678, La Esperanza, Cuba, 4 m; USNM 50420, St. Eustatius Island, Gallows Bay, Netherlands Antilles, 2 m; USNM 50697, St. Thomas Island, Virgin Islands, United States, 4 m; USNM 55091, 19°06’18”N, 69°01’00”W, Dominican Republic, 18–40 m; USNM 59166, 16°48’N, 88°05’W, Carrie Bow Cay, Belize, 4.6 m; USNM 100600, Navassa Island, Lulu Bay; USNM 50410, north of Sandy Ground, Aguilla; USNM 59044, 16°48’N, 88°05’W, Carrie Bow Cay, Belize, 20–30 m; USNM 88779, Turks And Caicos Islands, 12–13 m; USNM 88814, Turks And Caicos Islands, 1–1.5 m; USNM 91860, Eleuthera Island, Spanish Wells, Bahamas; USNM 91930, New Providence Island, Nassau, Bahamas; USNM 1150972, Bocas del Toro, Crawl Cay, 9°15”05’N, 82°07’33”W, Panamá, 7 m; USNM 1122672, 17°28’46”N, 63°13’35”W, Saba Bank, Netherlands Antilles, 24 m.

Description. Pale to dark brown, rarely white, preserved colonies, usually bushy but sometimes uniplanar, dichotomously branched up to 10th order, rarely more than 40 cm tall and straight (Fig. 1A, 8). Multiple branches sometimes arising directly from the holdfasts, probably as result of anastomosed juvenile colonies, but typically departing from an individual stem. Horny holdfasts, densely calcified, usually encrusting calcareous substrata. Terminal branches usually less than 20 cm long and from 10 to 15 mm in diameter. Morphology of branches varying depending upon the habitat, from stout and crooked to long and slender straight branches in short and long colonies, respectively (Fig. 8B–E) and sometimes laterally anastomosing (Fig. 8G). Calyces low to slightly prominent, with round or slit-like to elyptical pores, usually in number of 20 to 40 per cm^2, but sometimes up to 65 (Fig. 8F). Polyps whitish to brown in color, weakly ornamented with smooth flattened rods or completely naked, rarely longer than

0.03 mm (Figs. 7E, S1D). Cortex with small sixradiate and small butterflies, usually with one pair of arms most developed, 0.06–0.1 mm long and thick (Figs. 7D, S1C, S2B, S3C, S4E). Middle layer with butterflies, triradiates and spindles, in this order of abundance, 0.15–0.35 mm in length and 0.06–0.15 mm in arm width (Figs. 7A–B, S1A, S2A,C, S3A, S4A–C). Ornamentation varying from weakly to densely tuberculated and tubercles disposed in whorls. Buttlerflies slightly symmetrical not flattened, with one robust longer pair of arms and a robust but smaller one, both conical. Part of butterflies also tridimentionally placed, with pairs of arms oriented in different plans. Spindles rare. Axial sheath composed by butterflies, triradiates and spindles, smaller, less sculptured and more flattened than those from middle layer (Figs. 7C, S1B, S2C, S3B, S4D).

Comparisons. The predominance of usually quasi-symmetrical butterflies in middle layer with robust arms, followed by regular triradiates and spindles with a distinct median waist are the most conspicuous characters in *P. dichotoma*. *Plexaurella grisea* has more asymmetrical and flattened sclerites, slender arms, usually lacking a naked median waist and with rare regular spindles. It is different from *P. obesa* and *P. grandiflora* because these have rare or no symmetrical buttlerflies. When present, butterflies in Brazilian species have a short pair of arms or are asymmetrical and with arms laterally fused. *Plexaurella nutans* differs from *P. dichotoma* by having a fleshy texture of its coenenchyme, usually white, by having a strong anthocodial armature and slender sclerites with acute ends.

Figure 6. Slides of *Plexaurella* by Kölliker (1865), and later examinated by Verrill (1907). A: middle layer sclerites of *Gorgonia dichotoma* (=*P. dichotoma*) (MCZ 67508); B: middle layer sclerites of *Eunicea anceps* (=*P. nutans*) (MCZ 67516); C: middle layer sclerites of *Eunicea anceps* "Brazil" (=*P. grandiflora*) (MCZ 67664). Scale-bar: 0.1 mm.

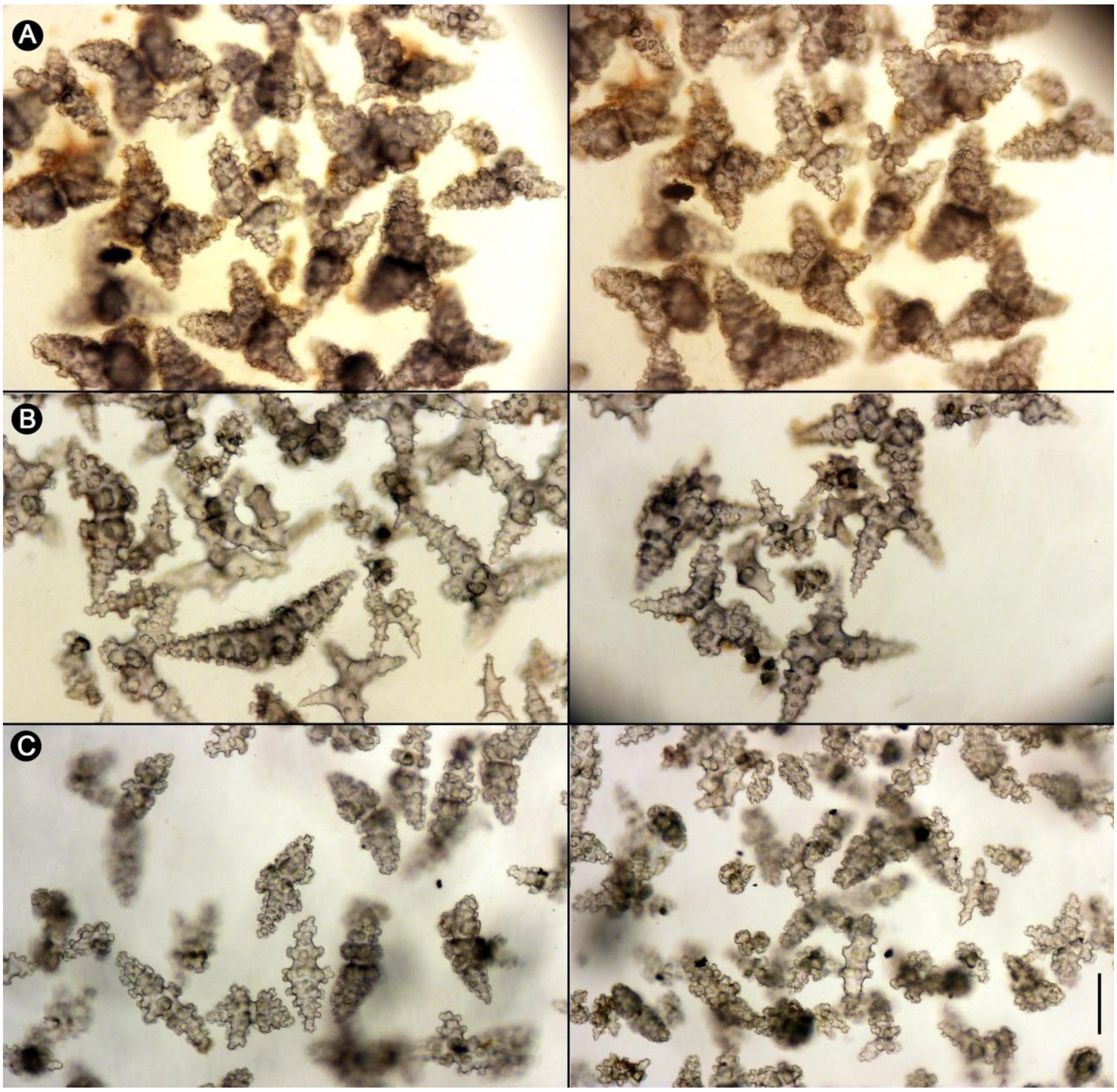
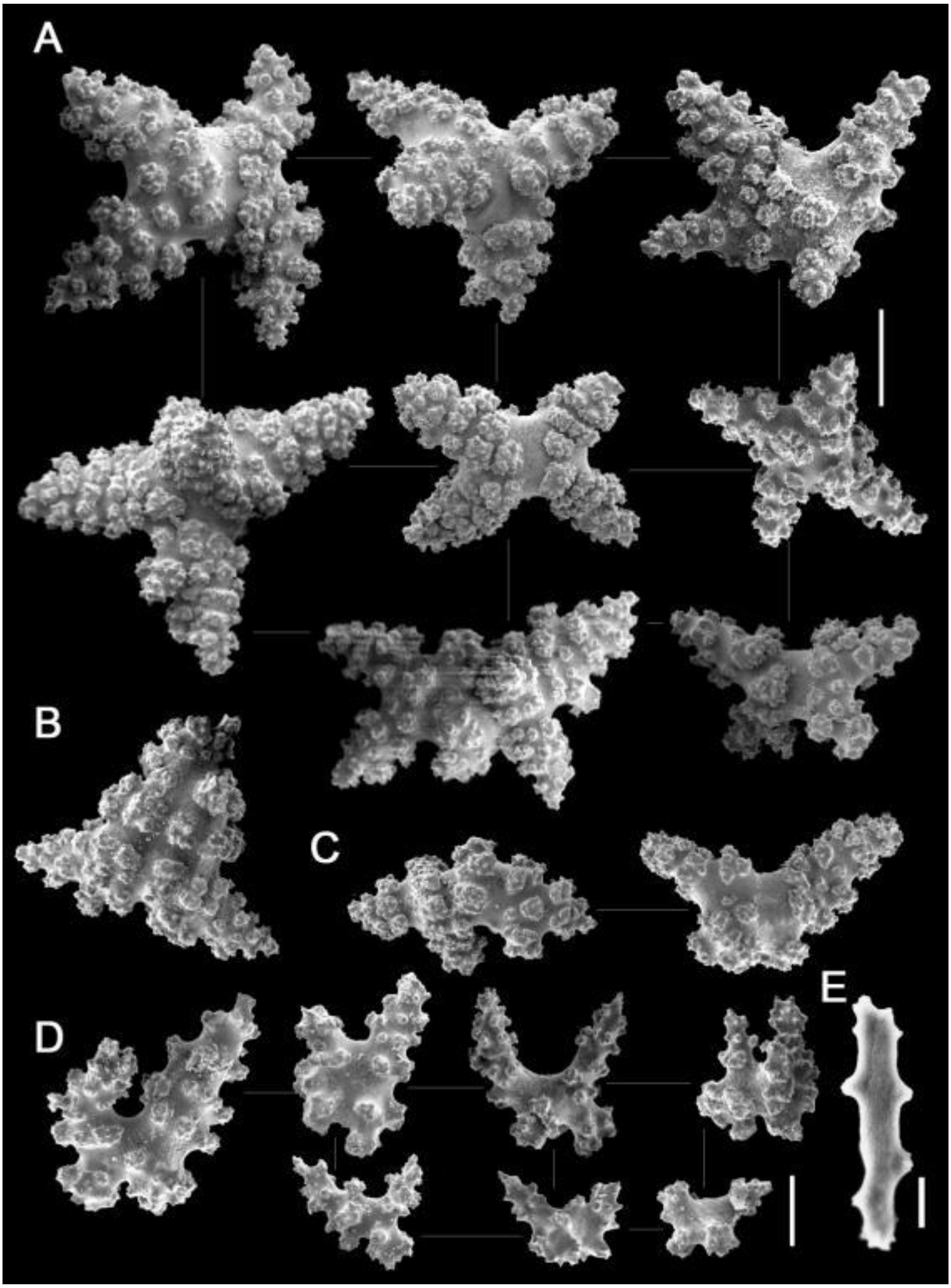


Figure 7. Sclerites of *Plexaurella dichotoma* (USNM 88779, Turks and Caicos Islands). A: butterflies from middle layer; B: triradiate from middle layer; C: irregular butterflies from axial layer; D: cortical sclerites; E: rod from body wall. Scale-bars: A–C: 0.1 mm; D: 0.05 mm; E: 0.005 mm.



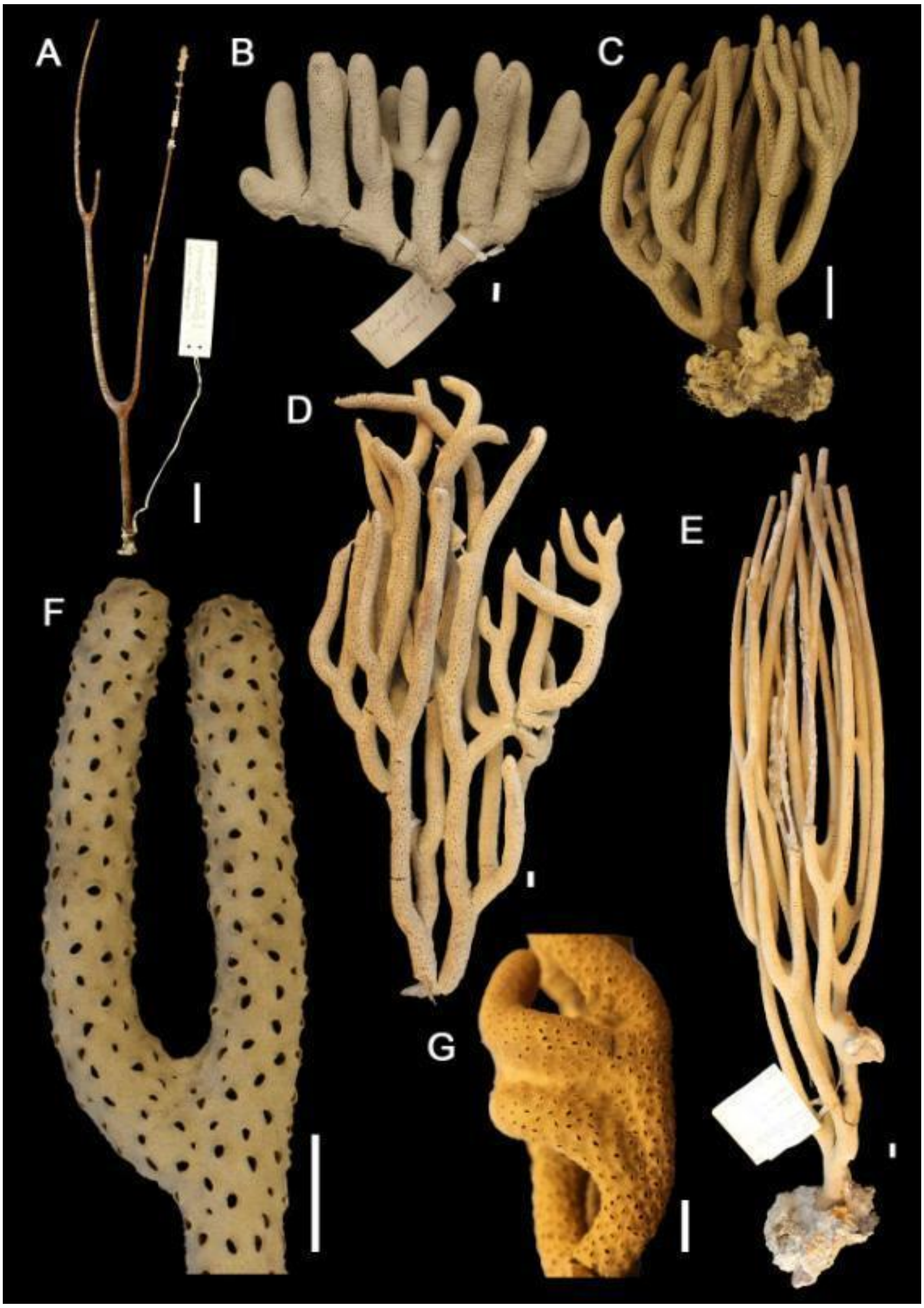
Remarks. The coenenchyme of Esper's type (SMF 5808) was completely lost (Fig. 8A), but slides of the same specimen are present in MCZ collection (MCZ 67508) [see Verrill, 1907, 310 (footnote)–311, figs. 156–157, pl. 36a, fig. 2].

Bayer (1961) marked Bermuda as the type locality of *P. dichotoma*, probably based on the illustration of the type given by Verrill (1907) in a book on coral reefs of that region. However, Esper (1791) indicates "South American islands" as the locality for *P. dichotoma*, information recalled by Castro *et al.* (2010). Sclerite morphology in Brazilian *Plexaurella* is very distinctive from Esper's type. Thus, it is likely that "South American Islands" correspond to the Caribbean. Furthermore, the occurrence of *P. dichotoma* in Brazil (Bayer, 1961; Tixier-Durivault, 1970; Castro, 1989; Castro *et al.*, 2010) is questioned herein (see remarks under *Plexaurella obesa* Verrill, 1912).

There are at least two morphotypes in *P. dichotoma*, but we could not find clear boundaries between them, due to several overlaping characters in sclerite morphology. The first morphotype (from western Caribbean, Central America and northern coast of South America) shows butterflies from middle layer similar to those from the type, with robust arms, in pairs of similar length, almost symmetrical and strongly tuberculated (Fig. 6A) (e.g. USNM 50390, USNM 88779, USNM 1122672 and USNM 91860). The second (from eastern Caribbean and Lesser Antilles) is similar to *Plexaurella grisea* Kunze, 1916, more assymmetrical, slender, weakly tuberculated and smaller butterflies (e.g. USNM 51359, USNM 51360, USNM 51393, USNM 51435, USNM 51972 and USNM 55091) (Figs. S4, S15, S21). It is expected that some species confirmation will heavy rely on molecular assessments, in case of almost indistinguishable scleromes. In fact, all of Kunze's (1916) specimens from Barbados, which he described as four different species, including *P. dichotoma*, are similar to the type of *P. grisea* (ZMB 5965). Whereas variability in sclerite thickness and tuberculation might be correlated with environmental conditions (West *et al.*, 1993; West, 1997), different patterns observed may represent genetic fixation in the populations analyzed (Prada *et al.*, 2008; Rowley *et al.*, 2015). We chose to keep both, *P. grisea* and *P. dichotoma*, separate, although they may correspond to the same species.

Distribution. Florida, Gulf of Mexico and Caribbean, up to 27 m. Morphotypes close to the holotype most common in Western and Southern Caribbean.

Figure 8. Colonies of *Plexaurella dichotoma*. A: remains of the holotype (SMF 5808, Caribbean); B: short and stout colony (USNM 14390, Nassau); C: short and profusely branched colony (USNM 50708, Florida Keys); D: colony tall, stiff and slightly crooked (USNM 50419, Florida Keys); E: stiff and straight colony (USNM 50420, Netherlands Antilles); F: detail of a branch, showing calyces morphology (USNM 100600, Navassa Island); G: detail of anastomosed branches (USNM 1125142, Venezuela). Scale-bars: A,C: 25 mm; B, D–G: 10 mm.



Plexaurella nutans (Duchassaing and Michelotti, 1860)

Figs. 6B, 9, 10, S20, S22–30

Eunicea nutans Duchassaing and Michelotti, 1860: 24, pl. 3 figs. 3–4.

Eunicea anceps Duchassaing and Michelotti, 1860: 25, pl. 3 figs. 1–2. —Verrill, 1907: 310 , pl 36a fig. 1 [in part: not Brazilian specimen, MCZ 67664 (=*P. grandiflora*)]

Plexaurella crassa. —Kölliker, 1865: 138, pl. 18 fig. 12.

Plexaurella nutans. —Kölliker, 1865: 138, pl. 18 fig. 15. —Verrill, 1907: 310 (footnote). —Bayer, 1961: 172, fig. 51, pl. 13 figs. 2a–b.

Plexaurella affinis Bell, 1889: 48, pl 3 fig. 3.

Plexaurella friabilis. —not Verrill, 1866: 186 (=*Euplexaura capensis* Verrill, 1870). —Kunze, 1916: 560, pl. 27 fig. 1.

Plexaurella fusifera Kunze, 1916: 563, figs. D–F, pl. 27 fig. 2.

Plexaurella kunzei Kükenthal, 1924: 102, fig. 73.

Types and type locality. *Eunicea nutans*: MSNT 348 (not examined) (Volpi and Benvenuti, 2003). Type locality: St. Thomas.

Eunicea anceps: MSNT 110 (not examined) (Volpi and Benvenuti, 2003), MCZ 67516 (slide from the type) (Fig. 6B). Type locality: St. Thomas.

Plexaurella affinis: ?BMNH (not examined). Type locality: West Indies.

Plexaurella fusifera: ZMB 5963 (Fig. S29= *P. nutans*). Type locality: Barbados.

Plexaurella kunzei: ZMB 5967 (Fig. 10). Type locality: St. Thomas.

Material examined. USNM 86026, 25°17’40”N, 81°48’00”W, 16 m, west of Caple Sable, Florida (Fig. S30); USNM 1237522, Curaçao, Netherlands Antilles, depth unknown (Fig. S23); USNM 1234926, 12°07’01”N, 61°32’30”W, 27 m, St. George, Grenada (Fig. S26); USNM 1122674, 17°28’13”N, 63°13’18”W, 30 m, Saba Bank, Netherlands Antilles (Fig. S25); USNM 84107, 26°46’01”N, 82°06’04”W, southwest of Marco Island, Florida, 19 m (Fig. S20); USNM 84099, USNM 84100, USNM 84101, USNM 84102, USNM 84103, USNM 84104, USNM 84105 and USNM 84106, 26°17’52”N, 82°12’37”W, southwest of Sanibel Island, Florida, 13 m; USNM 84073, USNM 84074, USNM 84075, USNM 84076 and USNM 84077, 26°17’52”N, 82°1237”W, Sanibel Island, Florida, 13 m; USNM 1214971, Red reef, Elliot Key, Florida; USNM 73487, USNM 73488 and USNM 73489, 25°45’56”N, 82°09’21”W, off Florida,19.6 m; USNM 44236, 25°40’N, 81°55’W, Cape Romano, Florida, 15 m; USNM 84108, USNM 84109 and USNM 84110, 25°17’40”N, 81°48’00”W, West of Cape Sable, Florida, 16 m; USNM 84111, USNM 84112, USNM 84115 and USNM 84116, 25°17’48”N, 81°39’48”W, West of Cape Sable, Florida, 14 m; USNM 87072 and USNM 87112, 24°36’10”N, 82°41’58”W, Florida Keys, Florida, 27 m; USNM 50130, 24°24’N, 82°55’W, Florida Keys, ?68 m; USNM 73618, Antigua and Barbuda, 11 m; USNM 84080, USNM 85981 and USNM 84082, 23°03’11”N, 82°08’27”, southwest of Naples, Florida,17 m; USNM 88786, Round Cays, Turks and Caiacos Islands, 4.6–5.5 m (Fig. S28); USNM 88797, East Of Gibbs And Round Cays, Turks and Caiacos Islands, 12.2–13.7 m; USNM 54947, 18°17’00”N, 71°03’54”W, Neiba Bay, Dominican Republic, 9–18 m; USNM 50322, Miami, Biscayne Bay, Soldier Key and Caesars Creek; USNM 55092, 18°15’30”N, 70°52’30”W, Ocoa Bay, Dominican Republic,13–24 m (Fig. S22); USNM 51361, 18°15’N, 73°30’W, Jamaica; USNM 54946, 18°03’00”N, 71°04’12”, Point Avarena, Dominican Republic, 22 m; USNM 54942, 17°37’30”N, 77°02’54”W, Portland Bight, Jamaica, 22 m; USNM 54945, 17°44’N, 71°20’W, East of Cape Beata, Dominican Republic, 17–22 m; USNM 1018059, Trinidad and Tobago, 12 m; USNM 1122675, 17°28’13”N, 63°13’18”W, Saba Bank, Netherlands Antilles, 30 m; USNM 54951, 15°15’N, 88°51’W, Mediuna reef, Honduras,18 m (Fig. S19); USNM 16848, Vaca Keys, Florida; USNM 50708, Garden Key, Dry Tortugas, Florida; USNM 73491, USNM 73492 and USNM 73494 (Fig. S24), 25°45’56”N, 82°09’21”W, Off Florida, 19.6 m; USNM 84096, USNM 84097 and USNM 84098, 25°17’48”N, 81°38’48”W, West of Cape Sable, Florida, 14 m; USNM 85980, 25°17’40”N, 81°48’00”W, West of Cape Sable, Florida, 16 m (Fig. S27); USNM 87111, 24°36’10”N, 82°41’58”W, East of Florida Keys, Florida, 27 m.

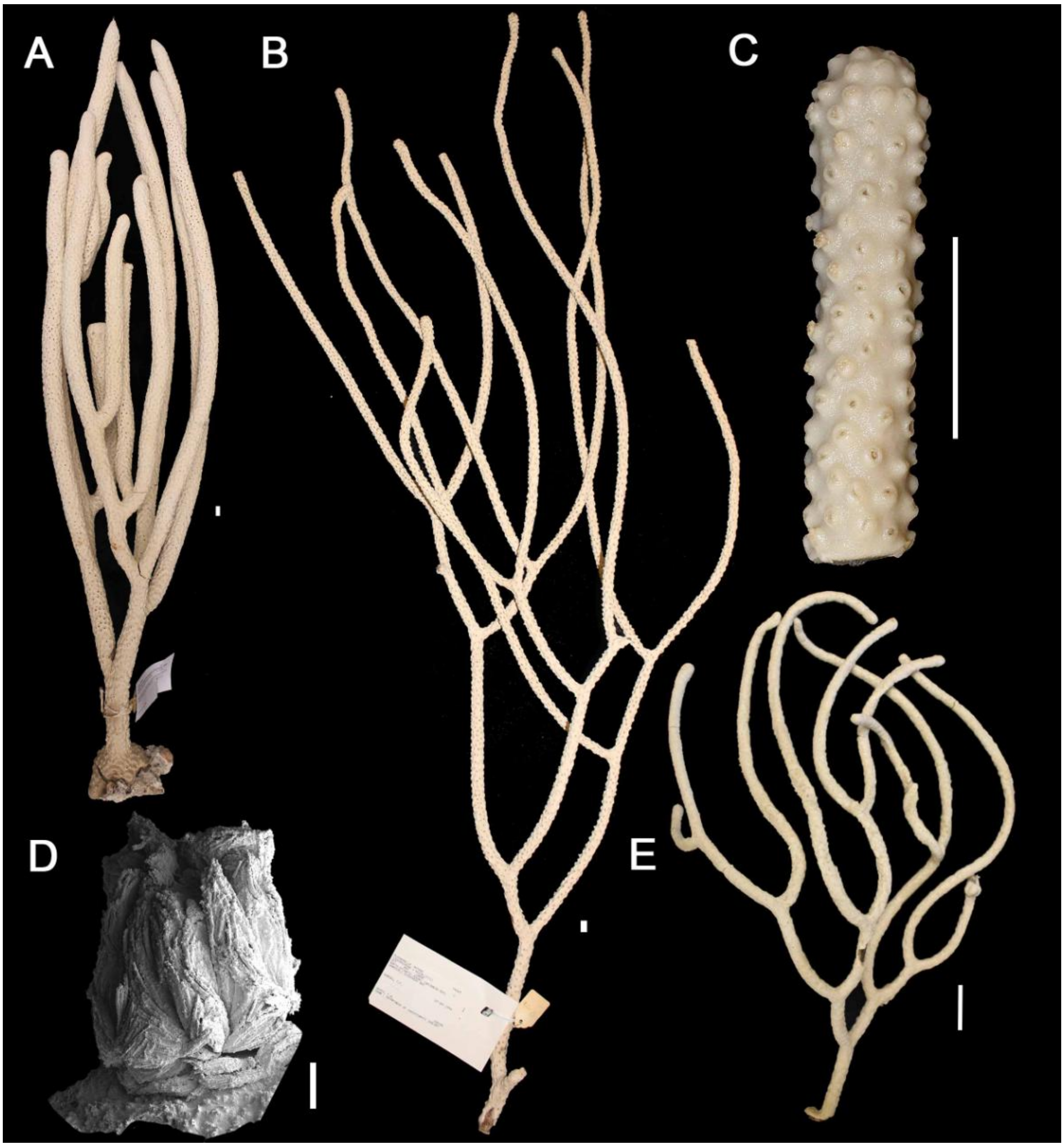
Description. White to pale brown colonies, very long (usually more than 80 cm) or short (around 50 cm long), dichotomous, both losely branched, but sometimes slightly bushy in short colonies, branching more basally (Fig. 9). Thick branches with up to 20 mm in diameter in long colonies or between 10 and 15 mm in short colonies. Terminal branches cylindrical, usually long (up to 60 cm), slender (5–8 mm thick) and flexible, with homogeneous diameter and slightly clavate tips. Calyces low, lip-shaped, longitudinally arranged in alternating rows, 5–8 polyps per cm^2 in thick branches and up to 30 polyps per cm^2 in slender branches (Fig. 9). Surface of coenenchyme smooth and with fleshy texture. Polyps strongly armed with tuberculated rods, arranged in crown and points, 0.13–0.26 mm long and 0.01–0.03 mm in width (Figs. 9D, 10A, S22C, S23C, S25C, S26E, S29B). Crown composed by 35 to 50 lines of sclerites and points basally arranged in chevron, but distally loosing this pattern, with rods longitudinally placed (see Key to species: 1a). Pinnules with small and weakly tuberculated rods, sometimes completely smooth. Polyps from terminal and/or slender branches with no evident armature. Cortex with small butterflies and sixradiate forms, 0.05–0.11 mm long and 0.01–0.05 mm wide (Figs. 10D, S22E, S23D, S24C, S25E, S26D, S27C, S28D, S29D, S30D). In older and stiff branches (basal branches), middle layer predominantly composed by moderatly tuberculated butterflies, with asymmetrical conical arms, 0.1–0.4 mm long and 0.03–0.07 mm wide; triradiates and spindles in similar proportions, with flattened appearance and sometimes bent (Fig. 6B, 10C,E,F, S22A,B, S23A,B, S24A, S25,A,B, S26A,B, S27A,B, S28A,B, 29A, S30B). Axial sheath with flattened irregular spindles, triradiates and, less frequent, butterflies, 0.8–0.18 mm long and 0.03–0.08 mm in width (Fig. 10B, S22D, S23E, S24B, S25D, S26C, S27D, S28C, S29C, S30C). Cortex in smaller colonies and/or terminal slender branches of tall colonies with the same sixradiates and butterflies, but middle layer filled predomnantly by bent spindles, followed by butterflies, rarely symmetrical, and less frequent triradiate forms, 0.15–0.3 mm long and 0.02–0.06 mm in width; other irregular forms also present; all weakly ornamented with small tubercles and very slender.

Comparisons. *Plexaurella nutans* differs from all other species in the genus mainly by having a strong anthocodial armature, slender tall colonies, smooth surface and fleshy texture of its coenenchyme.

Remarks. As *P. dichotoma*, this species was included in the genus by Kölliker (1865) and considered as valid by all subsequent authors. The fleshy/smooth characteristics are more easily observed in wet specimens. In contrast to Verrill’s (1907) conclusions, *Eunicea anceps* is a junior synonym of *P. nutans*, not *P. dichotoma*, as evidenced by slides from the type (MCZ 67516) (Fig. 6B). Although it was not possible to examinate the specimens of Wirshing et al. (2005), these authors found strong relationship between *P. nutans* and *P. fusifera*, reinforcing the synonymy between these species.

Due to its elongated nature, complete specimens are scarce in collections. Most of specimens examined are fragments or colonies completely sliced into small pieces. The tallest (yet incomplete) colony measured is 1.20 m long.

Figure 9. Colonies of *Plexaurella nutans*. A: tall and robust specimen from Florida (USNM 1214971); B: tall and slender specimen from Jamaica (USNM 54263); C: terminal branch (USNM 1122675); D: fully extended polyp (USNM 55092, Dominican Republic); E: specimen from Gulf of Mexico (USNM 84095). Scale bars: A–B: 10 mm; C, E: 25 mm; D: 0.2 mm.



The name *Plexaurella friabilis* is result of a series of consecutive indirect identifications. Lamouroux (1816) established *Plexaura friabilis*; Milne-Edwards and Haime (1857), in turn, identified one of their specimens as Lamouroux' *Plexaura friabilis*. Subsequently, Kunze (1916) presumed to have found the same species in his collection and transfered it to *Plexaurella*. However, Kükenthal (1924), after examining the specimens of his student, concluded that Kunze's *Plexaurella friabilis* was a different species and redescribed it as *Plexaurella kunzei*.

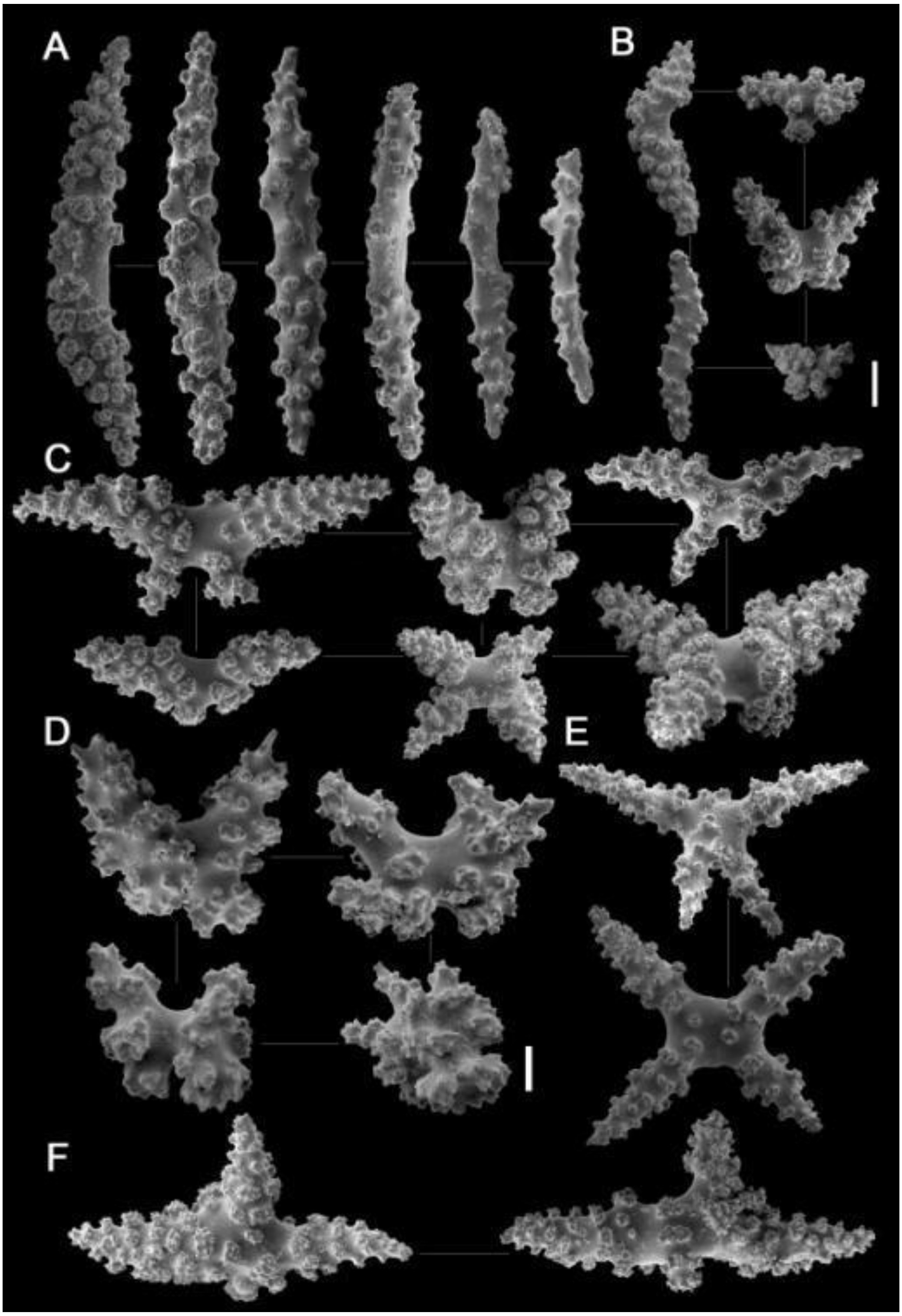
Although Kükenthal (1924) apparently solved the problem, examination of Kunze's *Plexaurella friabilis* (=*P. kunzei*) (ZMB 5967) reveals that it is actually a specimen of *P. nutans* from St. Thomas (Fig. 10).

We consider inappropriate to keep Alcolado's (1985) synonymy of *P. fusifera* with *P. dichotoma,* once we examined the type of *P. fusifera* (ZMB 5963). The specimen is white/cream-colored and shows thick terminal branches, fleshy texture, smooth surface, slender butterflies in middle layer and strong anthocodial armature (Fig. S29), all diagnostic characters of *P. nutans*, and for this reason, *P. fusifera* is considered herein as a junior synonym of *P. nutans*.

Alcolado's misperception is reasonable due to the high phenotypic plasticity in *P. nutans*. In terminal branches, specimens of *P. nutans* may lack the middle layer as well in short or very slender colonies it can show irregular sclerites. In some shorter colonies, previously identified as *P. fusifera* by Bayer (1961), sclerites are morphologically close to those from *P. dichotoma*, as mentioned by Sánchez and Wirshing, 2005.

The concept of *P. fusifera* of Alcolado (1985) is based on Bayer (1961). Actually, *P. fusifera sensu* Bayer (1961) corresponds either to young/small colonies of *P. nutans* or *P. dichotoma*. While examining specimens of *Plexaurella* deposited in NMNH collections (unpublished data), it can be noticed that Dr. Frederick Bayer ignored some colonial characters and presence of anthocodial armature in detriment of sclerite morphology. For example, some specimens of *P. nutans* were labeled by him as *P. fusifera* (USNM 54942, USNM 54947 and USNM 54951) and even *P. dichotoma* (USNM 87073).

Figure 10. Sclerites of *Plexaurella nutans* (ZMB 5967 – holotype of *P. kunzei*, from St. Thomas). A: tuberculated rods from body wall; B: irregular sclerites from axial layer; C: robust butterflies from middle layer; D: sclerites from cortical layer; E: slender butterflies from middle layer; F: triradiates from middle layer. Scale bars: A–C, E–F: 0.05 mm; D: 0.02 mm.



Plexaurella grisea Kunze, 1916

Figs. 11A–B, 12, S12–S15

Plexaurella dichotoma var. *grisea* Kunze, 1916: 573, figs. Q–R, pl. 28 fig. 6.

Plexaurella anguiculoides Bell, 1889: 48, pl. 3 fig. 4.

Plexaurella heteropora.—Kunze, 1916: 567, figs. K–M, pl. 27, fig. 4.

Plexaurella dichotoma.—Kunze, 1916: 569, figs. N–P, pl. 28 fig. 5.

Plexaurella vermiculata. —Kunze, 1916: 576–579, figs. U–W, pl. 28 fig. 7.

Plexaurella curvata Kunze, 1916: p. 582, figs. B'–E', pl. 27 fig. 9.

Plexaurella grisea. —not Bayer, 1961: 175–177, fig. 53, pl. 4 fig. 4 (=*P. teres*).

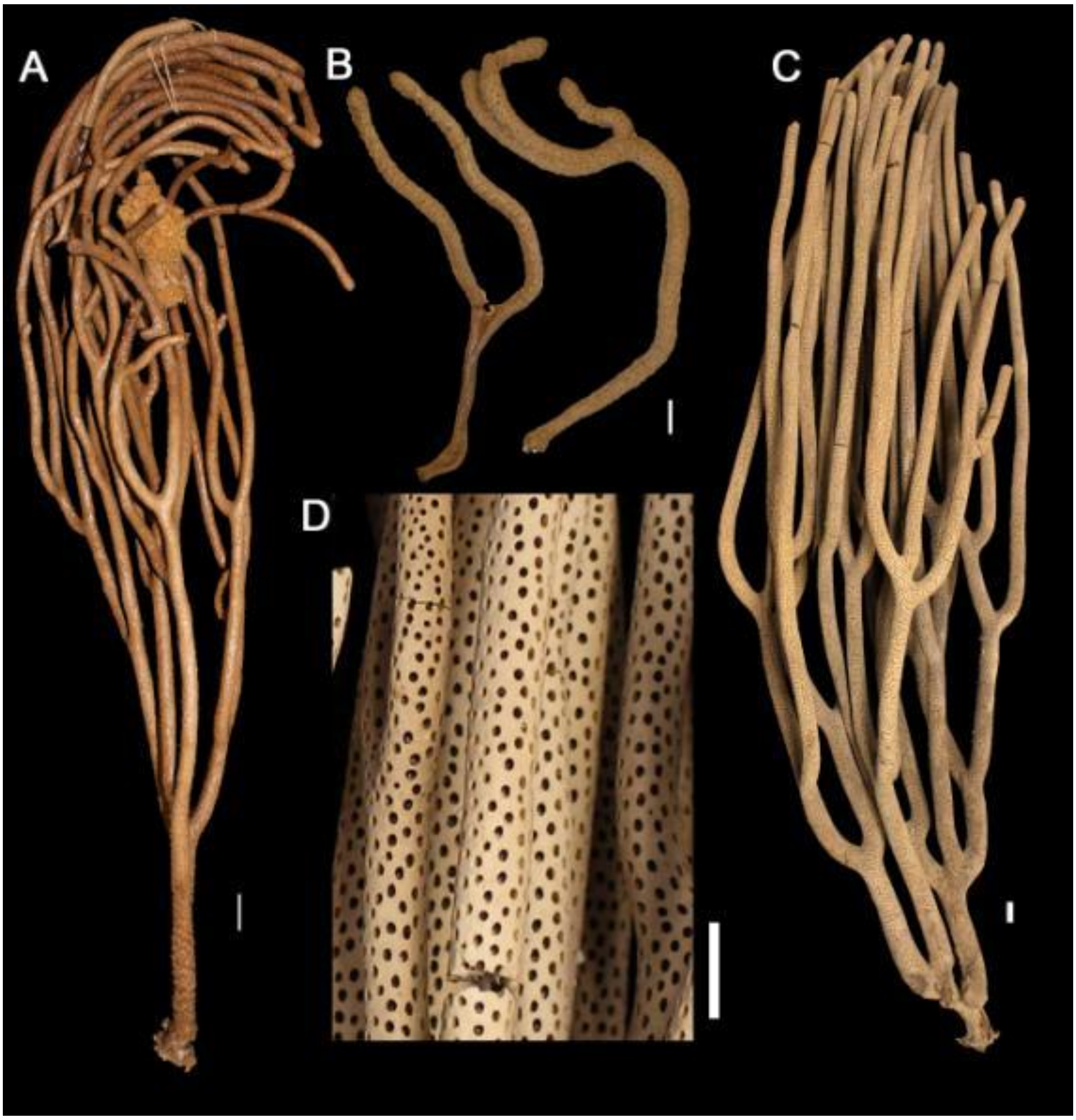
Types and type locality. *Plexaurella dichotoma* var. *grisea*: ZMB 5965. Type locality: Barbados.

Plexaurella heteropora: ZMB 5968. Type locality: Barbados.

Plexaurella curvata: ZMB 5961. Type locality: Barbados, Kingston, St. Thomas.

Material examined. ZMB 5962, ZMB 5966 and 5969, Barbados, depth unknown; USNM 7523, 17°52'00"N, 76°45'30"W, Kingston Harbor, Jamaica (Figs. 11B, S11); USNM 1248676, La Blanquilla, Venezuela (Fig. S12); USNM 54941, 17°45'30"N, 76°59'06"W, southwest of Kingston, Jamaica, 15 m; USNM 54943, 17°36'18"N, 77°02'36"W, Portland Bight, Jamaica, 24 m; USNM 54939, 17°23'36"N, 76°02'12"W, Albatross Bank, Morant Cay, Jamaica, 9–27 m; USNM 1122673, 16°56'45"N, 62°14'39"W, Saba Bank, Netherlands Antilles, 18 m; USNM 54950, 13°58'18"N, 82°03'42"W, Quita Sueno Bank, Nicaragua, 24–26 m.

Figure 11. Colonies of *Plexaurella grisea* and *P. teres*. A: colony of *P. grisea* (USNM 50711, Cuba); B: juvenile colonies of *P. grisea* (USNM 7523, Jamaica); C: colony of *P. teres* (USNM 50534, St. Kitts and Nevis); D: detail of calyces in *P. teres* (USNM 50688, Honduras). A: 2.5 cm; B–D: 10 mm.



Description. Pale do dark brown slender colonies, straight, losely branched to bushy, usually tall and stiff, but distally more flexible (Fig. 11A–B). Short colonies also flexible. Stem long, up to 20 cm, and thick up to 21 mm in diameter. Dichotomous cylindrical branches arrising most in the lower portion of the colony up to 7th order. Terminal branches up to 50 cm long with clavate tips, around 10 mm in diameter. Low lip-shaped to pore-like calyces arranged in inconspicuous alternate longitudinal rows, in number of up to 15 per cm^2. Polyps naked or weakly armed, with stout rods, 0.01–0.06 mm long and 6–11 µm wide. Cortex filled with small irregular butterflies, usually with one pair of arms more developed and tuberculated, 0.05–0.1 mm long and 0.03–0.07 mm wide (Figs. 12F, S11C, S12C, S13E, S14B, S15D, S21C). Middle layer sclerites represented mainly by irregular butterflies, rarely symmetrical, followed by trirradiates and spindles, in this order of abundance (Figs. 12A–D, S11A,B, S12A, S13A,B,C, S14A, S15A,B, S21A,B). All moderatly slender, with well spaced tubercles, 0.1–0.32 mm long, and 0.02–0.08 mm in width. Axial sheath with irregular spindles, butterflies and ocasional triradiates, 0.07–0.23 mm long and 0.03–0.08 mm wide (Figs. 12E, S11D, S12B, S13D, S14C, S15C, S21D).

Comparisons. *Plexaurella grisea* is closely related to *P. dichotoma*, by the predominance of butterflies in the middle layer, and the texture of coenenchyme. However, the latter has robust butterflies, strongly ornamented with dense warts. Colonies of *P. grisea* are indistinguishable from *P. teres*, and are distinguished by the presence or predominance of sixradiates and more asymmetrical buttlerflies in the middle layer of the latter. Additional differences from *P. teres* include: well spaced tubercles on middle layer sclerites, and more ornamented polyps in *P. grisea*. The weak anthocodial armature in *P. grisea* is more clearly observed in dry specimens, and it is not well developed as in *P. nutans*.

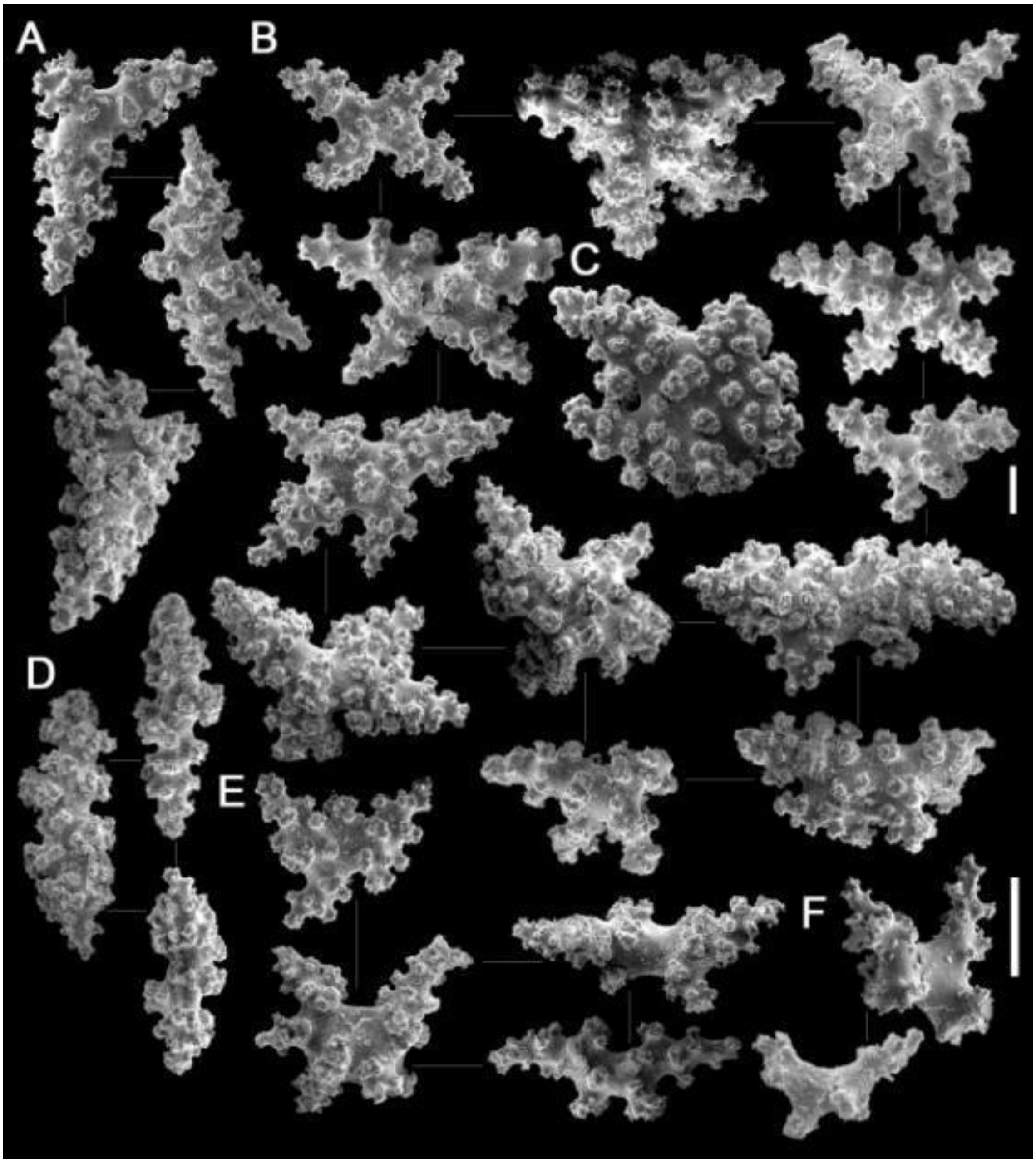
Remarks.

In contrast to Bayer's (1961) statements, it is not possible to assign specimens from Florida to Bell's *P. anguiculoides* (USNM 50535 and USNM 50536 = *P. teres*). We did not examine Bell's *P. anguiculoides*, but drawings of sclerites of the type in its original description represent forms typical of those from the holotype of *P. teres*.

Like in *P. fusifera sensu* Bayer (1961), *P. grisea sensu* Bayer (1961) does not correspond to the morphology of Kunze's (1916) types, which Bayer did not examine. Actually, *P. grisea sensu* Bayer (1961) corresponds to *Plexaurella teres* Kunze, 1916 (see Remarks under *P. teres*).

Distribution. Throughout Caribbean, from Nicaragua to Barbados, in depths up to 27 m.

Figure 12. Sclerites of *Plexaurella grisea* (ZMB 5965 – holotype of *P. dichotoma* var. *grisea*, from Barbados). A: triradiates from middle layer; B: butterflies from middle layer; C: irregular form from middle layer; D: tuberculated spindles from middle layer; E: sclerites from axial layer; F: sclerites from cortical layer. Scale bars: A–F: 0.05 mm.



Plexaurella teres Kunze, 1916

Figs. 11C–D, 13, S5–10

Plexaurella teres Kunze, 1916: 575–576, figs. S–T.

Plexaurella vermiculata. —Bell, 1889: 49, pl. 3 fig. 5.

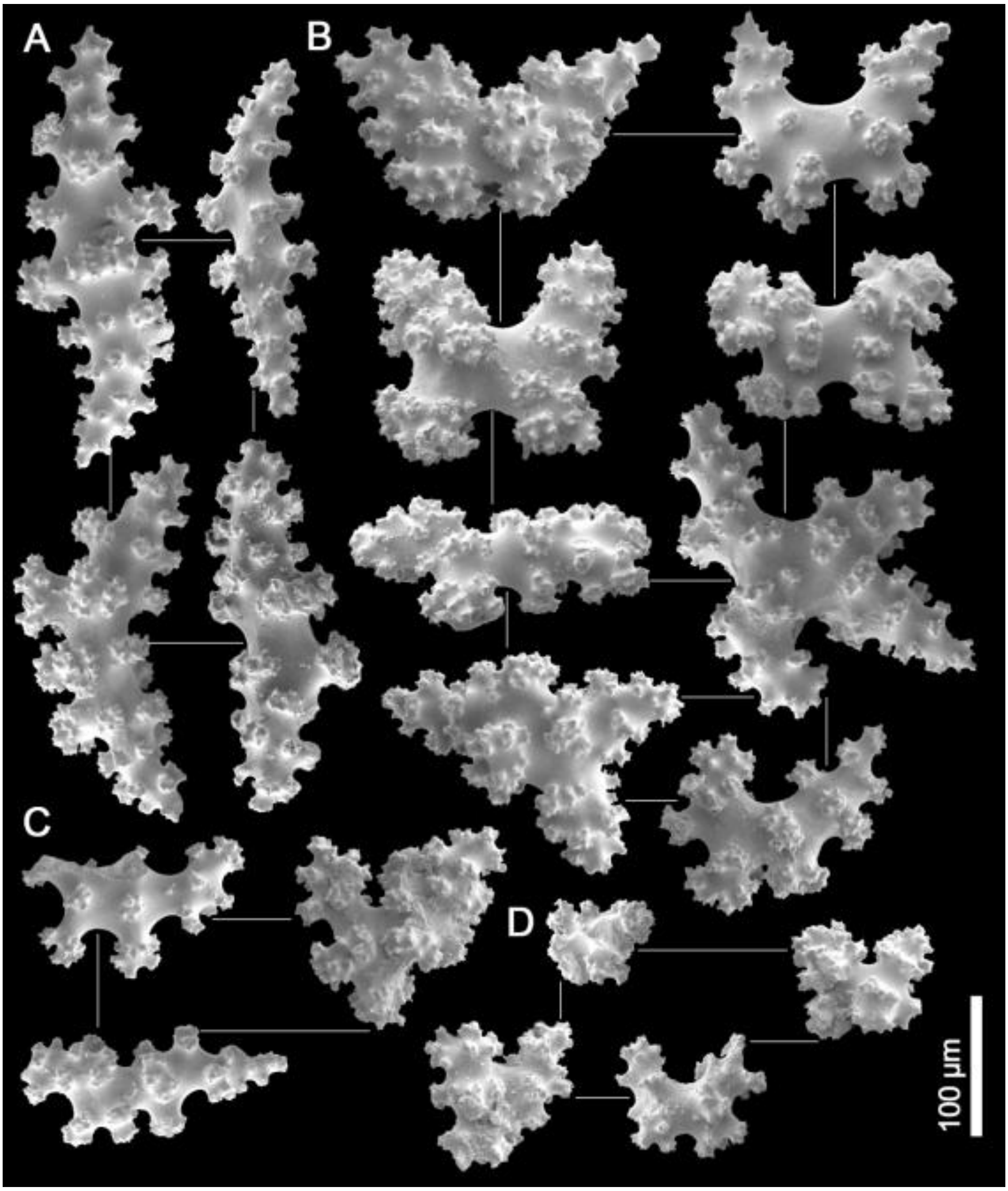
Plexaurella grisea. —Bayer, 1961: 175–177, fig. 53, pl. 4 fig. 4.

Type and type locality. *Plexaurella teres:* MCZ Alcy-103 (Fig. 13). Type locality: Florida.

Material examined. USNM 79366, 24°36’N, 76°01’W, 22–35 m, Eleuthera Island, Bahamas (Fig. S5); USNM 84093 (Fig. S6) and USNM 84095 (Fig. S9), 25°17’48”N, 81°39’48”W, West of Cape Sable, Florida, 14 m; USNM 50535, Tampa Bay, Florida; USNM 50536, Elliot key, Florida Keys, 4 m; USNM 50688, 17°25’N, 83°55’W, Swan Islands, Honduras (Fig. S8); USNM 50962, Antigua Island, Freemans Bay, English Harbor, Antigua and Barbuda (Fig. S7); USNM 50534, Windward Beach, Frigate Bay, St. Kitts and Nevis (Fig. S10); USNM 51417, Milford Bay, Trinidad and Tobago, 9–12 m.

Description. White to brown colonies, straight and bushy, stiff with flexible and slender terminal branches (Fig. 11C–D), rarely more than 60 cm tall. Terminal branches up to 40 cm long with clavate tips, around 10 mm in diameter. Stem up to 7 cm long and up to 16 mm in diameter. Dichotomous cylindrical branches arrising mainly from the lower portion of the colony, up to 5th order. Low slit-like calyces without an apparent arrangement, in number of up to 12 per cm^2 (Fig. 11D). Polyps usually naked, but showing some tentacular rods. Cortex filled with small butterflies, usually sixradiated tuberculated, capstans also present in smaller frequence, 0.06–0.09 mm long and 0.02–0.08 mm wide (Figs. 13D, S5D, S6D, S7D, S8D, S9D, S10B). Middle layer butterflies densely tuberculated with one more developed arm and median waist slightly flattened, sixradiated or not (Figs. S6A, S7A, S10A), followed in order of abundance by more scarse stout spindles 0.1–0.25 mm long and 0.04–0.13 mm in width (Figs. 13A, S5A, S6A,B, S7A, S8A, S9A,B, S10A). Symmetrical butterflies rare and triradiates usually absent (S5B, S7B, S8B). Axial sheath represented by more slender butterflies, weakly tuberculated, spindles and less tuberculated sixradiates, 0.07–0.13 mm long and 0.4–0.6 mm wide (Figs. 13C, S5C, S6C, S7C, S8C, S9C, S10C).

Figure 13. Sclerites of the holotype of *Plexaurella teres* (MCZ Alcy-103). A: spindles from middle-layer; B: butterflies from middle-layer; C: axial sclerites; D: cortical sclerites.



Comparisons. The presence/predominance of sixradiate sclerites in the middle layer is an exclusive feature in *P. teres*, distinguishing it from all other species in the genus. Butterflies of the middle layer are smaller than those in *P. grisea* and *P. dichotoma*.

Remarks. We have chosen to keep *P. teres* and *P. grisea* as separate species based on different sclerites they show, despite the fact they have very similar colonies. The unusual set of sclerites in the middle layer is a remarkable character in *P. teres*, as mentioned by Bayer (1961) (as *P. grisea*).

A number of authors included the name *P. grisea* in their manuscripts, in ecological studies (Goldberg, 1973; Jeyasuria and Lewis, 1987; Yoshioka and Yoshioka, 1989; Sánchez *et al.*, 1998), biochemistry (Gopichand and Schimidtz, 1980; Lewis *et al.*, 1992; Rueda *et al.*, 2001; Smith *et al.*, 2007) and genetics (Wirshing *et al.*, 2005). According to Wirshing *et al.* (2005), *P. grisea* has a common origin with *P. dichotoma*. However, at this time, it is uncertain to assume that the concept of *P. grisea* in these studies actually corresponds to *P. teres* or not, as their identifications are probably based on Bayer (1961).

Distribution. Throughout Caribbean, from Florida to Trinidad and Tobago, up to 14 m deep.

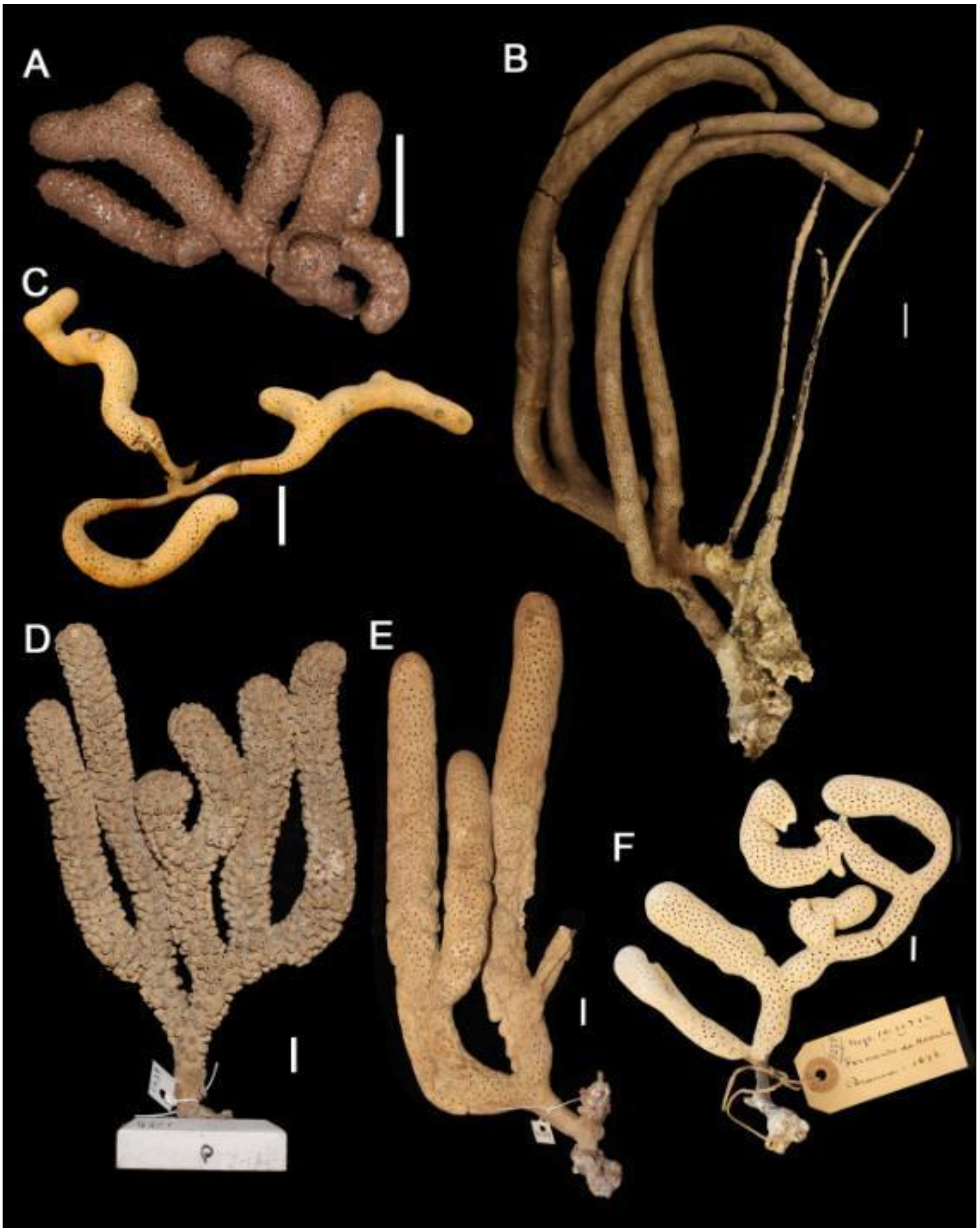
Plexaurella rastrera **sp. nov.**

Figs. 14A,C, 15, S16–18

Plexaurella dichotoma. —Bayer, 1961: 170 (in part: USNM 50745, Anguilla, north of Sandy Ground).

Types and type locality. Holotype: USNM 1018047, southwestern part of Bay, Tobago, Trinidad and Tobago, 2 m. Paratypes: USNM 73605, Des Salines, Martinique, 9 m (Fig. S18); USNM 42004, Barbados, 2–7 m (Fig. S16) USNM 50745, Sandy Ground, Anguilla (Fig. S17); USNM 1018053 and USNM 1018074, same data of the holotype; USNM 1018041, Cardinal Rock, Tobago, Trinidad and Tobago, 12 m; USNM 1018044, Little Tobago Island, Tobago, Trinidad and Tobago, 25 m; USNM 1018043, USNM 1018051 and USNM 1018052, Pirates Cove, Tobago, Trinidad and Tobago, 7–10 m.

Figure 14. Colonies of *Plexaurella rastrera* sp. nov., *P. grandiflora*, *P. regia* and *P. obesa*. A: paratype of *P. rastrera* sp. nov. (USNM 50745, Anguilla); B: paratype of *P. regia* (USNM 73399, Abrolhos); C: holotype of *P. rastrera* sp. nov. (USNM 1018047, Trinidad and Tobago); D: holotype of *P. grandiflora* (YPM 4501, Mar Grande); E: holotype of *P. obesa* (YPM 4509, Fernando de Noronha); F: specimen of *P. obesa* (USNM 5278, Fernando de Noronha). Scale bars: 10 mm.



Description. Pale to dark brown dwarf colonies, loosely branched, short, stout, stiff, crawling, dichotomous and laterally branching in all directions, not only upwards. Primary and secondary branches usually growing parallel to the substrate, rarely more than 15 cm long and around 15 cm in diameter, given a vermiform appearance to the colonies (Fig. 14A,C). Terminal branches cylindrical, up to 4th order and up to 10 cm long, with slightly clavate tips. Low calyces, with slit-like apertures, in number of up to 12 per cm^2. Slender horny holdfasts and stem, usually covered by a thin coenenchyme (usually less than a half of the diameter of terminal branches), with sparse and diminute polyp apertures and no calyces. Polyps with no ornamentation or with sparse rods in tentacles. Cortical sclerites predominantly irregular radiates and butterflies, 0.04–0.1 long and 0.02–0.07 in width (Figs. 15C, S16C, S17D, S18C). Middle layer with robust and densely tuberculated sclerites, with predominance of butterflies with symmetrical or asymmetrical arms in pairs oriented in different plans (tridimensional aspect), 0.15–0.35 mm long and 0.07–0.16 mm in width (Figs. 15A, S16A, S17A, S18A); triradiate and pentaradiate sclerites less frequent, in similar size (Fig. S17B). Axial sheath composed by slender, less tuberculated and slightly flattened butterflies (with a more developed pair of arms) and triradiates 0.15–0.25 mm long and 0.03–0.05 mm wide (Figs. 15B, S16B, 17C, 18B).

Comparisons. Some colonies of *P. dichotoma* may show similar growth forms, but the predominance of butterflies with short and robust pairs of arms oriented in diferent plans, followed in abundance by pentaradiates and triradiates are exclusive features of *P. rastrera* sp. nov. The latter always shows stout colonies with vermiform branches. In *P. dichotoma* and *P. grisea*, sclerites of the middle layer are mostly regular butterflies (slender or robust), usually lacking pentarradiates. In contrast with *P. nutans*, the new species lacks strong ornamentation in polyps and has smaller and stiffer colonies. The differences of *P. rastrera* in relation to and *P. teres* consist in the presence of sixradiates and butterflies with very short arms in the latter. Brazilian species, *P. grandiflora*, *P. robusta* and *P. regia* usually have no pentarradiates in the middle layer. The distinctiveness of *P. rastrera* is also supported by Internal Transcribed Spacer 2 sequences (ITS2) and and its respective predicted RNA secondary structures (unpublished RNA data).

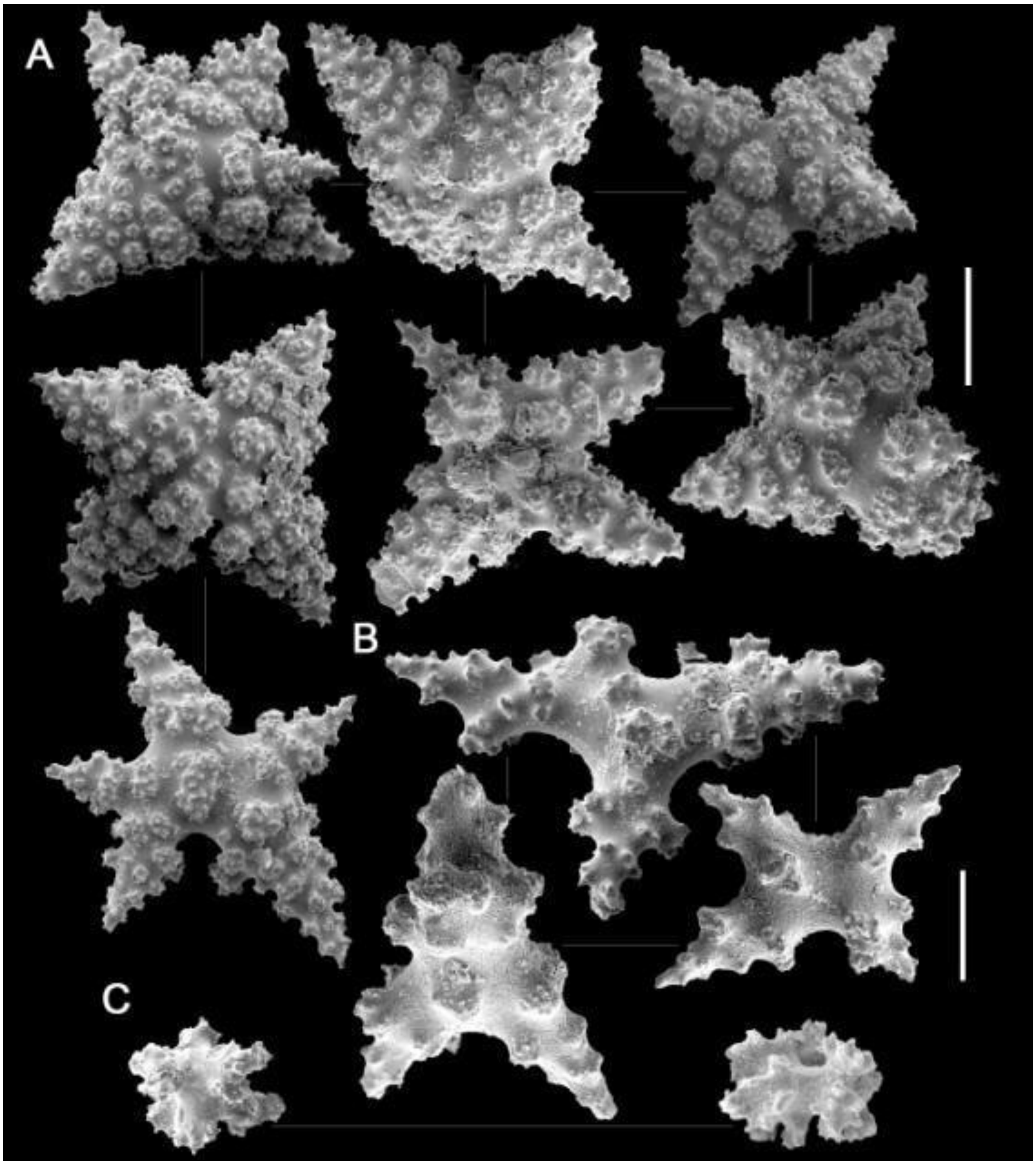
Remarks. Along with the USNM 50745, the holotype is the most complete specimen, with branches in three directions and coenenchyme damaged at the base and in one branch, lacking its tip. Most of paratypes are fragments of terminal branches.

On the field, *P. rastrera* sp. nov. attracts attention by its crawling growth form (Figs. 1C, 15A,C). Besides pentaradiate and triradiate forms, some sclerites can show more ramified arms, with a thornscale-like appearance.

Etymology. The epithet “*rastrera*” (gender fem.) is the Spanish word for “crawling”, in relation to the growth form of colonies of this species.

Distribution. Known only to Anguila and Trinidad and Tobago, up to 25 m.

Figure 15. Sclerites of *Plexaurella rastrera* sp. nov. (USNM 1018047 – holotype, from Trinidad and Tobago). A: butterflies from middle layer; B: sclerites from axial layer; C: sclerites from cortical layer. Scale bars: A: 0.1 mm; B–C: 0.05 mm.



Plexaurella grandiflora Verrill, 1912

Figs. (14D, 16, S32–37)

Plexaurella (*Pseudeunicea*) *grandiflora* Verrill, 1912: 388–389, pl. 31 fig. 6, pl. 32 fig. 10, pl. 34 fig. 1, pl. 35 figs. 3–3a. — Bayer, 1961: 173.

Plexaurella grandiflora. —Bayer, 1961: 173–175, fig. 52, pl. 5 fig. 5. —Castro, 1989: 599. —Silva and Pérez, 2002: 18. cc —Castro *et al.*, 2010: 766 fig. 1 (distribution map), 769 (key), 791 fig. 12B–C', 794–796, fig. 14.

Plexaurella anceps. —Kölliker, 1865: 138 (in part: ZMB 67664).

Plexaurella cylindrica Verrill, 1912: 384, pl. 32 fig. 7, pl. 34 fig. 4, pl. 35, figs. 4,14. — Castro, 1989: 599 (under *P. grandiflora*).

Plexaurella pumila Verrill, 1912: 386, pl. 31 fig. 5, pl. 32 fig. 8, pl. 34. fig. 2. — Bayer, 1961: 177. . —Castro, 1989: 599 (under *P. grandiflora*).

Plexaurella verrucosa Verrill, 1912: 387, pl. 31 fig. 4, pl. 32 fig. 6, pl. 34 fig. 5, pl. 35 figs. 13–13a. — Bayer, 1961: 173. — Castro, 1989: 599. —Castro, 1989: 599 (under *P. grandiflora*).

Plexaurella braziliana Verrill, 1912: 385, pl. 34 figs. 3–3a, pl. 35 figs. 12–12a, 15. — Castro, 1989: 601 (under *P. grandiflora*).

Types and type localities. *Plexaurella grandiflora*: YPM 4501. Type locality: Mar Grande, Brazil.

Plexaurella cylindrica: YPM 1597 (Fig. S36). Type locality: Abrolhos reefs.

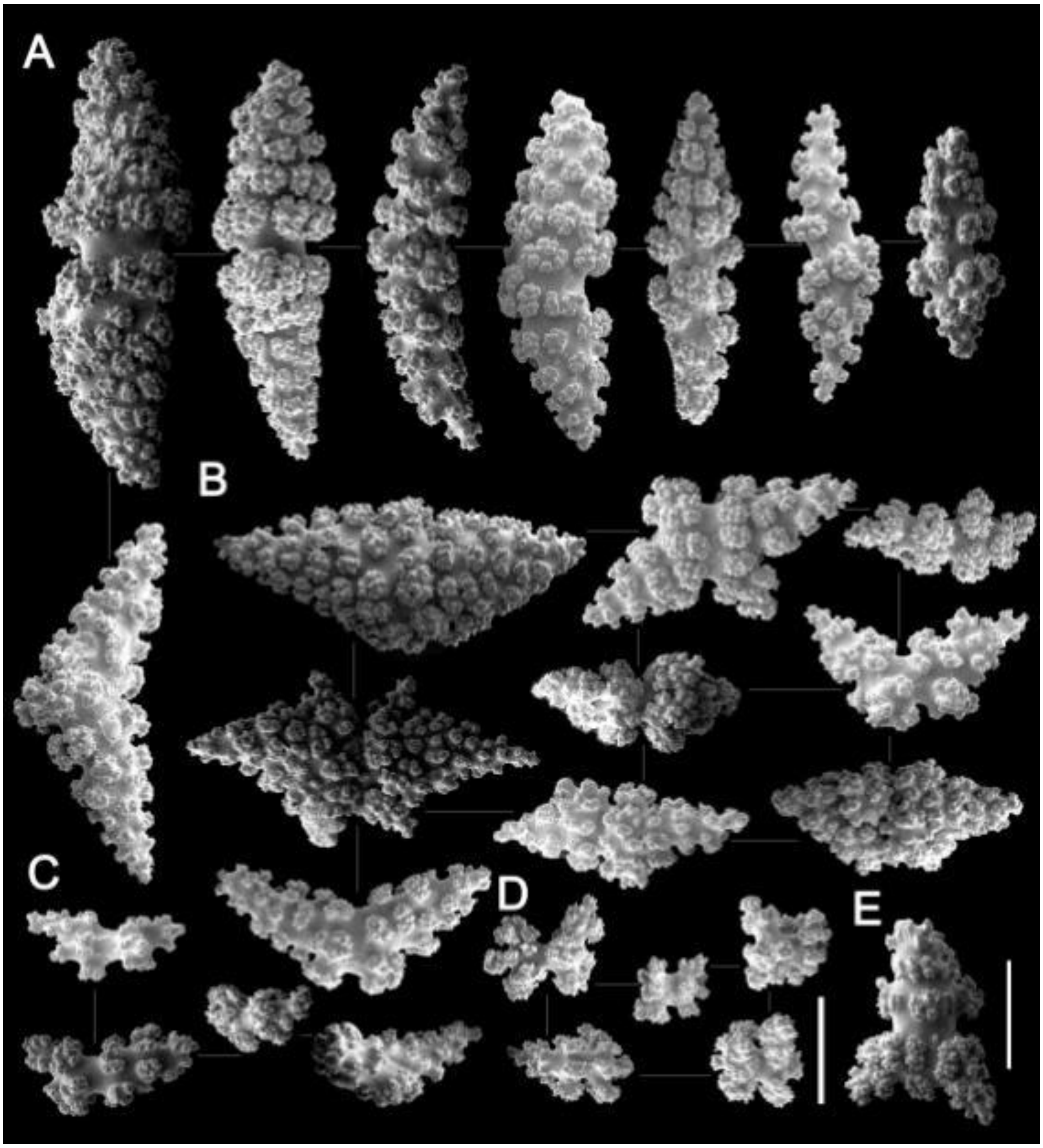
Plexaurella verrucosa: YPM 4503 (Fig. S34). Type locality: Candeias, Pernambuco, Brazil.

Plexaurella braziliana: YPM 1598 (Fig. S37). Type locality: Abrolhos reefs.

Plexaurella pumila: YPM 4502 (Fig S35). Type locality: Periperí point, Bahia, Brazil.

Material examined. MCZ 67664, South America, Brazil; MNRJ 7452, 5°1'6"S, 36°18'27"W, Guamaré, Potiguar Basin, Rio Grande do Norte, 15 m; MNRJ 446, 7°6'50"S, 34°48'35"W, Tambaú, Paraíba; MNRJ 1273, 7°0'0"S, 34°45'0"W, Paraíba; USNM 75596, Picãozinho, João Pessoa, Paraíba (Fig. S32); MNRJ 2754, 8°30'30"S, 34°59'50"W, Porto de Galinhas, Pernambuco, 30 m; MNRJ, uncatalogued, Carneiros, Pernambuco (sequenced); MNRJ, uncatalogued, Maragogi, Pernambuco (sequenced); USNM 73401, Maragogi, Alagoas state (Fig. S33); MNRJ 2752, 9°46'15"S, 35°50'15"W, Francês beach, Alagoas; MNRJ 445, 9°1'0"S, 35°13'0"W, Maragogi, Alagoas; USNM 75597 and USNM 75598, Abrolhos Islands, Bahia; USNM 75599, Sueste Island, Abrolhos; MNRJ 157, 17°20’14”S, 39°12’42”W, north of Cumuruxatiba, Bahia; MNRJ 1176, 17°58’2”S 38°42’27”W, Caravelas, Bahia; MNRJ 436, 17°57’32”S, 38°38’42”W, Parcel dos Abrolhos, 5 m; MNRJ 1182, 17°58’8”S, 38°42’36”W, Caravelas, Bahia, 5 m; MNRJ 435, 17°42’0”S, 38°58’0”W, Off Caravelas, Parcel das Paredes, Bahia; MNRJ 1397and MNRJ 1988, 13°22’27”S, 38°54’57”W, Cairu, Bahia; MNRJ 1274, 12°47’0”S, 38°27’0”W, Mapelle, Bahia; MNRJ 2199, 17°59’30”S, 39°15’25”W, Nova Viçosa, Bahia; MNRJ 2584, Caravelas, Bahia; MNRJ 2726, 17°57’40”S, 39°12’46”W, Nova Viçosa, Bahia; MNRJ 2861, Coroa Vermelha reef, Nova Viçosa, Bahia; MNRJ 4002, 12°55’0”S, 38°31’0”E, Todos os Santos bay, Bahia, 5–6 m; MNRJ 4342, 17°52’30”S 38°58’45”W, Parcel das Paredes, Bahia; MNRJ 4584, MNRJ 4585 and MNRJ4587, 17°54’15”S, 39°8’10”W, Sebastião Gomes, Parcel dos Abrolhos; MNRJ 4586, 18°1’18”S, 38°59’35”W, Popa Verde, Parcel dos Abrolhos, 16 m; USNM 73393, Guarapari, Espírito Santo, 1 m; USNM 73566, Vila Velha, Espírito Santo, 2 m; MNRJ 431, 19°57’20”S, 40°8’3”W, Aracruz, Espírito Santo; MNRJ 432 and MNRJ 441, 20°38’10”S, 40°26’21”W, Setiba beach, Guarapari, Espírito Santo; MNRJ 433 and MNRJ 437, MNRJ 635 and MNRJ 1344, 20°40’22”S, 40°29’47”W, Castanheiras beach, Guarapari, Espírito Santo, 1 m; MNRJ 438, 20°36’42”S, 40°22’41”W, Três Ilhas, Guarapari, Espírito Santo; 3 m; MNRJ 439 and MNRJ 3961, 20°38’12”S, 40°28’3”W, Três Praias, Guarapari, Espírito Santo, 2–3 m; MNRJ 442, 20°20’11”S, 40°16’40”W, Costa beach, Vila Velha, Espírito Santo, 2 m; MNRJ 639, 20°44’23”S, 40°32’12”W, Meaípe, Guarapari, Espírito Santo; MNRJ 1148, 20°54’0”S, 40°45’0”W, Piúma, Espírito Santo; MNRJ 1149, 20°51’17”S, 40°43’40”W, Cabritos island, Piúma, Espírito Santo; MNRJ 1987, 20°48’20”S, 40°36’8”W, Anchieta, Parati beach, Espírito Santo; USNM 75595, São João da Barra, Rio de Janeiro, 1.5–4 m; MNRJ 444, 21°30’0”S, 41°3’0”W, São João da Barra, Rio de Janeiro, 1 m; MNRJ uncatalogued specimen, Cabritas point, Trindade Island, depth unknown (sequenced).

Figure 16. Sclerites of *P. grandiflora* (YPM 4501 – holotype, from Mar Grande, Bahia, Brazil). A: spindles from middle layer; B: butterflies from middle layer; C: sclerites from axial layer; D: cortical sclerites; E: triradiate from middle layer. Scale bar: 0.1 mm.



Description. Colonies pale yellow to brown in color, slightly stiff, with horny holdfasts and axis (Figs. 1B,D, 14D). Dichotomous branching up to 5th order, usually in one plan and in similar diameter (cylindrical) in all orders, sometimes slightly lyrate, reaching up to 70 cm in height and rarely more than 15 cm in largest width (Fig. 14D). Axis of main stem corresponding up to 2/3 of its total diameter in cross-section. Main stem steril (polyps absent) in its basal portion, measuring up to 55 mm in height. Branches slightly elliptical in cross-section (D1:D2=1.2–1.3) and with slightly clavate tips. Calyces tall and often very prominent throughout the rest of the colonies, up to 5 mm in height, but very calyces also common in slender colonies, sometimes discreetly arranged in alternating longitudinal lines, but usually randomly distributed in numbers up to 70 per cm^2, but usually around 35. Polyps naked or weakly ornamented with small rods. Cortex with small butterflies, 70–140 µm long (Figs. 16D, S32D, S33D, S34E, S35D, S36D, S37E). Middle layer filled with spindles, tri-radiates and butterflies, in similar frequencies (Figs. 16A–B, S32B–C, S33B, S34C–D, S35A–B, S36B, S37B–C). Typical symmetrical butterflies rare. When present, similar to spindles, with a very short pair of arms, or with fused pair of arms, or even completey absent. Butterflies irregular, usually with some pair of arms more developed than others, 0.17–0.36 mm long, 0.05–0.11 mm in width and 0.03–0.08 mm in diameter of median waist (Figs. 16A, S32A, S33A, S34A, S35E, S36A, S37A). Spindles up to 0.6 mm long and 0.16 wide in specimens from deeper areas, but rare in specimens from very shallow reefs, usually with no intermediary lengths. Butterflies with 0.15–0.21 mm in length, 0.07–0.12 mm in width and 0.04–0.05 mm of median waist. Tri and quadri-radiate more common close to the axial sheet, but fewer in number and with unequal arms.

Comparisons. The sclerome in *P. grandiflora* is heterogeneous, but very distinct. In the middle layer, the common presence of spindles and robust fusiform or irregular butterflies, with a very short pair of arms, is another distinctive character from Caribbean species, as *P. dichotomai, P. grisea, P. nutans* and *P. rastrera*. *Plexaurella teres* may have butterflies with short arms, but their sixradiates are distinctive in relation to *P. grandiflora.* Common sclerites of middle layer also include tri-radiates, spindles, butterflies with fused arm pairs, which also distinguish *P. grandiflora* from *P. regia*.

Remarks. Sclerite size in gorgonians is usually correlated with depth and water motion (Grigg, 1972; West *et al.*, 1993). Indeed, specimens of *P. grandiflora* sampled in deeper environments (usually more than 5 m) showed not only longer sclerites, but also longer branches. Variability in thickness and flexibility of branches is clearly related to water movement (Grigg, 1972). Densities of different kinds of sclerites may also vary between and within specimens. Thus, predominance of a given sclerite form may be driven by its position and depth of coenenchyme layer. Verrill's (1912) types (except for *P. obesa*) are good representatives of the plastic morphological range in *P. grandiflora*. As suggested by the analyses with *28S* sequences (Fig. 3) between specimens from coastal reefs and isular environments (Trindade Archipelago), cryptic speciation between these populations of *P. grandiflora* should be further investigated.

Distribution: Brazil, from Rio Grande do Norte to Rio de Janeiro, including reefs of the Vitória-Trindade Seamount Chain, up to 30 m.

***Plexaurella regia* Castro, 1989**

Figs. 14B, 17

Plexaurella regia Castro, 1989: 599–602, figs. 2–3. —Hetzel and Castro, 1994: 92. —Medeiros and Castro, 1999: 12. —Silva & Pérez, 2002: 18. —Castro *et al.*, 2010: 796–797, figs. 1, 12D–D', 15.

Types and type locality. MNRJ 440. Type locality: Lixa reef, Abrolhos Archipelago, 4–6 m, Brazil.

Material examined. USNM 75728 and USNM 73399, same collection data of the holotype (Paratypes); USNM 73735, North of Abrolhos Islands (Paratype); MNRJ 434, 17°57'53"S, 38°40'33"W, Santa Barbara Island, Abrolhos Archipelago, 4 m (Paratype); MNRJ 1176 and MNRJ 5816, 17°58'02"S 38°42'27"W, Redonda Island, Abrolhos Archipelago; MNRJ 2748, 17°45'22"S, 39°00'37"W, Parcel das Paredes, Caravelas, Bahia; MNRJ 2751, 18°01'00"S, 39°00'00"W, Popa verde, Abrolhos bank; MNRJ 4580, MNRJ 4581 and MNRJ 4583, 17°58'55"S 38°39'06"W, Parcel dos Abrolhos; MNRJ 5562, 16°53'31"S, 39°3'17"W, Pedra do Cavalo, Itacolomis reefs, Corumbau; MNRJ 6753, 16°24.770'S, 38°59.270'W, Recife de Fora, Porto Seguro.

Description. Yellowish to dark brown colonies, tall (up to 75 cm in height), profusely laterally and basally branched upwards to 4th order, sometimes anastomosing. Branches coarsely straight, cylindrical, thick and stiff, with clavate tips (Fig. 14B). Stem short and thick, up to 60 mm in diameter. Terminal branches up to 60 cm long and 25 mm in diameter. Horny holdfasts showing calcified portions at the base. Calyces sometimes very low, but usually absent, slit-like and diminute (0.5–1 mm in diameter), not arranged in conspicuous rows, in number of up to 165 per cm^2. Polyps with few small rods (around 0.05 mm long), but not forming an anthocodial armature. Cortex filled by small butterflies and irregular forms, 0.06–0.2 mm long and 0.06–0.1 mm in width (Fig. 17D). Middle layer represented by long spindles with pointed tips, 0.15–0.7 mm long and 0.02–0.13 mm in width (Fig. 17A). Regular butterflies rare or absent (Fig. 17C). Triradiates also usually absent. When present, more common in the axial sheath, which is also composed by spindles, capstans and irregular forms 0.08–0.26 mm long and 0.02–0.08 mm in width (Fig. 17B).

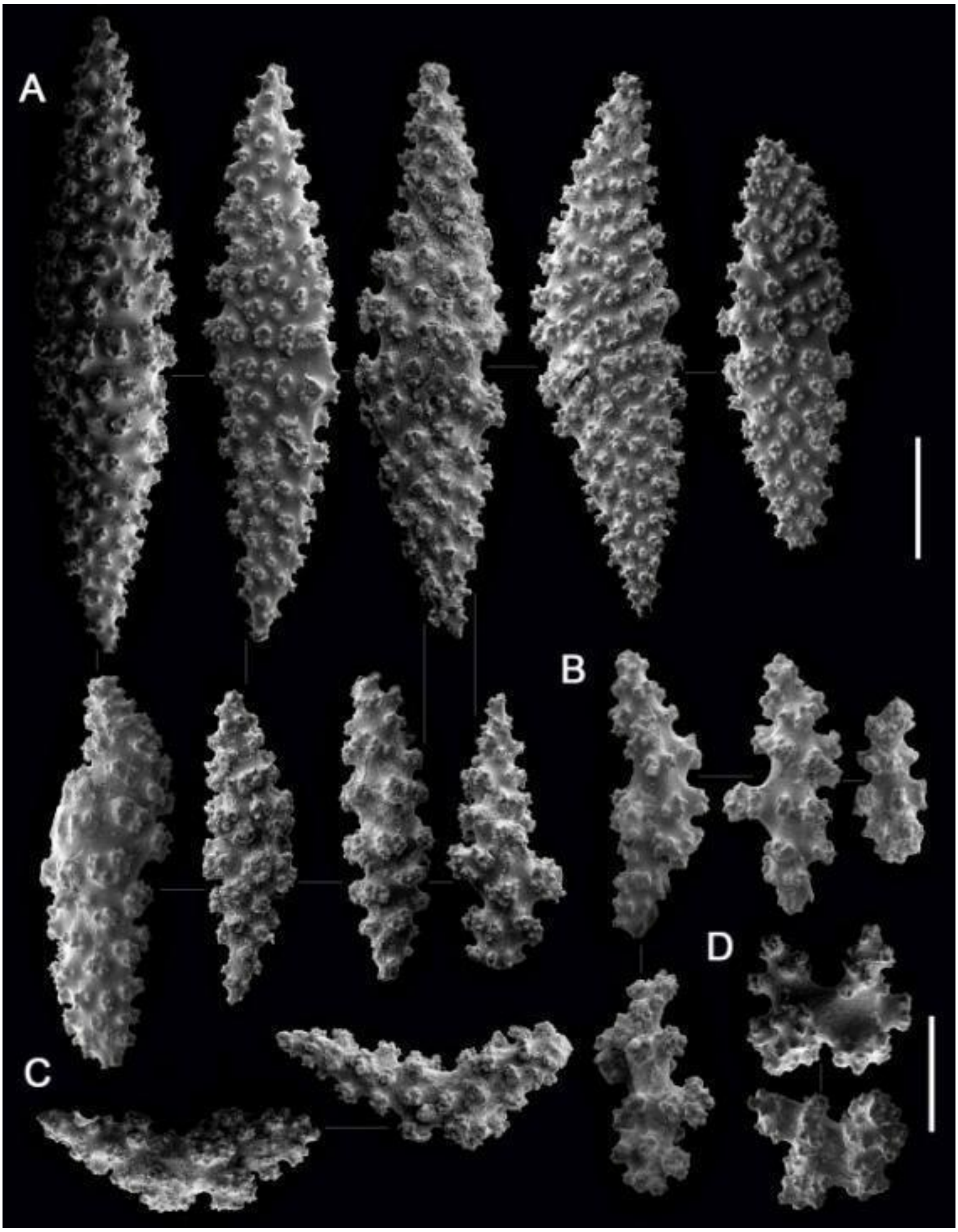
Comparisons. Colonies of *P. regia* are the most robust in the genus, with stems reaching 50 mm in diameter or more. It differs from all species by the predominance (almost exclusiveness) of very long spindles (up to 0.7 mm) in the middle layer.

Remarks. The region of the coast of Bahia shows a remarkable endemism not only in octocoral species (Castro *et al.*, 2010), but also to scleractinians and hydrocorals (Castro and Pires, 2001; Leão *et al.*, 2003). That region, along with the oceanic islands, is likely to be a source of migrant exchange for other reef areas along the Brazilian Coast (Peluso et al., 2018). Similarly, a recent study on zooxanthellae found exclusive *Symbiodinium* clades associated to scleractinians in that area (Piccianni *et al.*, 2016). Theoretically, this endemism is possible due to the northern barrier represented by the mouth of São Francisco River and by the southern barrier of Rio Doce River (Leão *et al.*, 2003). In contrast, studies with reef fishes include the entire northeastern coast of Brazil in a single biogeographic region (e.g. Floeter *et al.*, 2008), and even one study reports coral species regarded as endemic to Bahia from north Brazil (Amaral *et al.*, 2007).

Some specimens of *P. regia* (e.g. MNRJ 2748) are very slender and may be easily virtually misidentified as *P. grandiflora*.

Distribution. Probably endemic to southern Bahia; rarely collected below 10 m.

Figure 17. Sclerites of *Plexaurella regia* (USNM 75728 – paratype, from Abrolhos, Bahia, Brazil). A: spindles from middle layer; B: spindles from axial layer; C: butterflies from middle layer; D: cortical sclerites. Scale bars: A, C: 0.1 mm; B, D: 0.05 mm.



Plexaurella obesa **Verrill, 1912**

Figs. 14E,F, 18, S31

Plexaurella obesa Verrill, 1912: 383–384, pl. 31 fig. 3, pl. 32 fig. 9, pl. 34 fig. 6.

Plexaurella dichotoma. —Bayer, 1961: 171 (in part: USNM 5278). —?Tixier-Durivault, 1970: 155–156. —Medeiros and Castro, 1999: 11 (MNRJ 443, MNRJ 1534, MNRJ 1541). —Silva and Pérez, 2002: 18. —Almeida et al., 2005: 75. —Castro *et al.*, 2010: 791–794, fig 12A, 13 (MNRJ 00980 , YPM 4509, USNM 5278).

Types and type locality. YPM 4509. Type locality: Fernando de Noronha Archipelago (Fig. 14E).

Material examined. USNM 5278, Fernando de Noronha Archipelago, depth unknown (collected along with the holotype by John C. Branner, C. F. Hartt Expedition in 1876) (Fig. 14F); USNM 73400 (Fig. S31); MNRJ 1534 and MNRJ 1541, Manuel Luís Parcel, depth unknown; MNRJ 980, Fernando de Noronha Archipelago, 4–7 m; and MNRJ 443, Rocas Atoll, Outside The Atoll , 4–10 m.

Description. White to yellowish colonies, uniplanar to slightly bushy and branching, from 3rd to 7th order in short (up to 20 cm in length) and tall colonies (up to 45 cm) (Fig. 14E–F). Holdfasts horny but densely calcified. First centimeter of the stem usually naked. Coenenchyme with some wrinkled portions and rough surface in dry specimens. Shorter colonies stiff and stout and tall colonies slender and flexible. Branches in basal portions of short colonies usually cylindrical and distally elliptical with tips twice thicker than its proximal portion, 9–24 mm in diameter. In tall colonies, branches uniformly cylindrical to slightly elliptical, 7–15 mm in diameter. Polyps occurring in number of 12–20 per cm^2, but not linearly organized, retracting into slit-like pores. Number of polyps per cm^2 slightly larger in branch tips (up to 30), but tips almost sterile in colonies previously exposed to strong water flow. Calyces rare or absent. Coenenchyme without cortex in parts of the colony exposed to friction, with polyps almost absent in these areas. Polyps naked or weakly ornamented with small rods (Fig. S31C). Cortex with small butterflies and six-radiate forms 0.06–0.14 mm long (Figs. 18E, S31E). Middle layer filled with spindles, tri-radiates and butterflies, in this order of abundance. Spindles slightly curved with a naked median waist, 0.2–0.4 mm long and 0.04–0.14 mm in width (Figs. 18B, S31A). Two whorls imediate to the median waist usually composed by stronger and fused warts. Tri-radiates less frequent, with one arm more developed than the other two 0.16–0.3 mm long and 0.05–0.13 mm in width (Fig. 18A). Buttlerflies rare and usually asymmetrical, sometimes flattened and/or with supernumerary arms 0.18–0.26 mm long and 0.08–0.18 mm in width (Figs. 18C, S31B). Axial sheath composed of butterfly-like forms and rare spindles 0.15–0.3 long and 0.06–0.12 mm wide (Figs. 18D, S31D).

Comparisons. The distinction of *P. obesa* from Caribbean, such as *P. dichotoma*, species is based on the predominance of spindles in the middle layer. It differs from *P. grandiflora* because the middle layer in *P. obesa* is predominantly composed by regular spindles, always with a distinct median waist and rare butterflies, in contrast with more heterogeneous forms in variable proportions in *P. grandiflora*. Moreover, spindles in *P. obesa* are stouter and uniform, and evenly tuberculated. Some specimens of *P. obesa* may have an incomplete or even lack their cortical layer. *Plexaurella regia* have mostly straight spindles in the middle-layer and rare butterflies.

Remarks. The holotype is the only specimen showing calyces, usually very low and discrete. This specimen also possesses some very rare pink collored spindles in the cortical and middle layers, probably not homologous to axial purple sclerites in plexaurids.

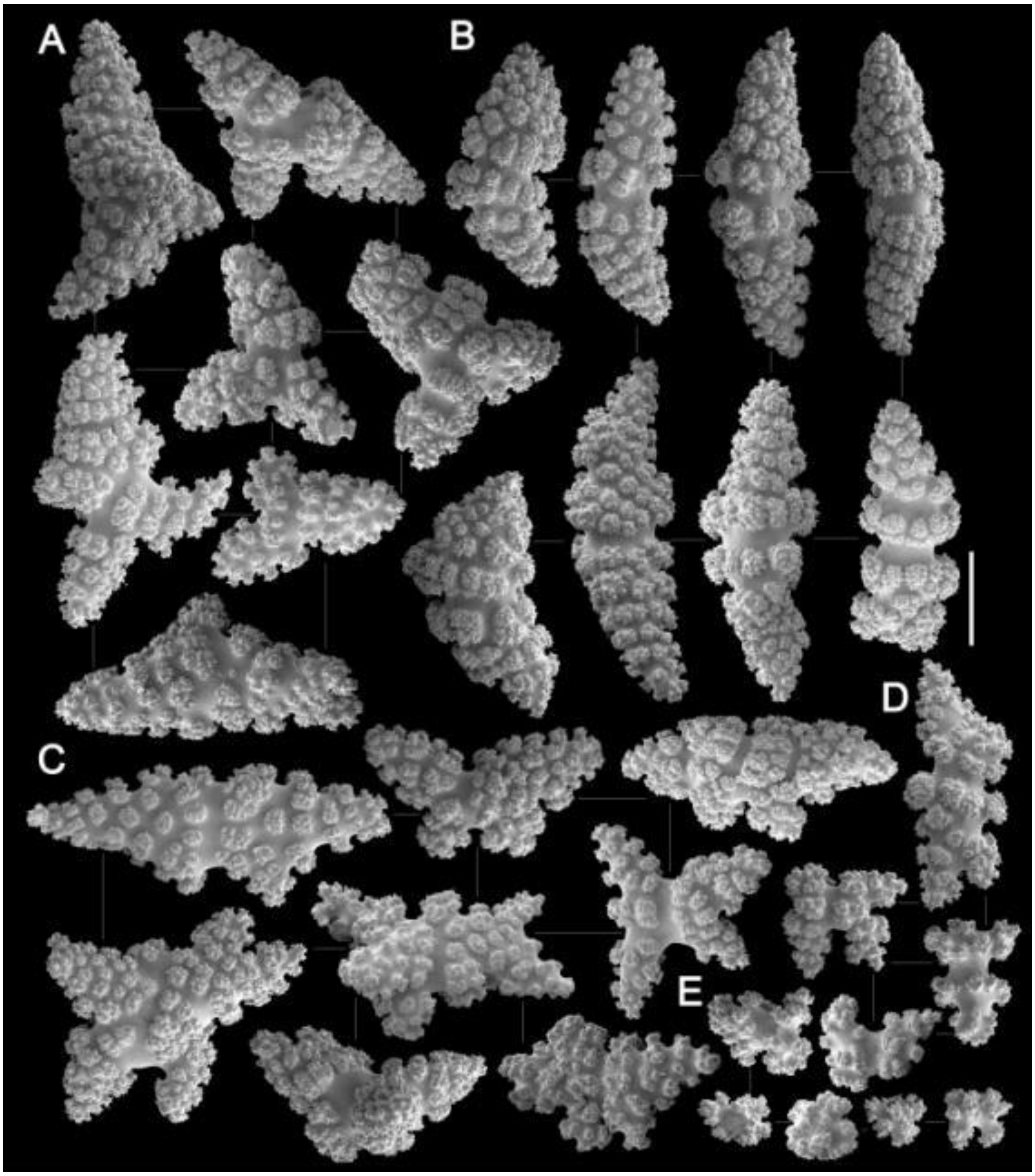
Plexaurella obesa was previously considered by Bayer (1961) and Castro *et al.* (2010) as a junior synonym of *P. dichotoma*. Besides the morphological differences between these two species, there are few biogeographical evidences supporting connectivity between reef benthic organisms between Caribbean and Southwestern Atlantic.

Even though the Rocas Atoll and Fernando de Noronha Archipelago have species more related to Caribbean populations (Lima *et al.*, 2005), most studies reinforce the hypothesis of isolation of the Brazilian shallow-water benthic fauna, driven mainly by the Amazon River barrier (Rocha, 2003; Bowen *et al.*, 2006; Nunes *et al.*, 2011; Tourinho *et al.*, 2012) and that few species can surmount this outflow (Rocha *et al.*, 2002). Additionally, studies on the coral fauna from off Amazon area show no evidence of the occurrence of *Plexaurella* in that region (Verseveldt, 1978; Cordeiro *et al.*, 2015). Thus, it is unlikely that *P. dichotoma* occurs in Brazil.

Bayer (1961) subjectively suggested a synonymy of *P. cylindrica* and *P. braziliana* with *P. obesa* (as *P. dichotoma*), hypothesis rejected herein, because the two first are synonyms of *P. grandiflora*. Also subjectively, Tixier-Durivault (1970) registered *P.*

dichotoma in Brazil, after examination of species collected by the Calypso (specimens not found).

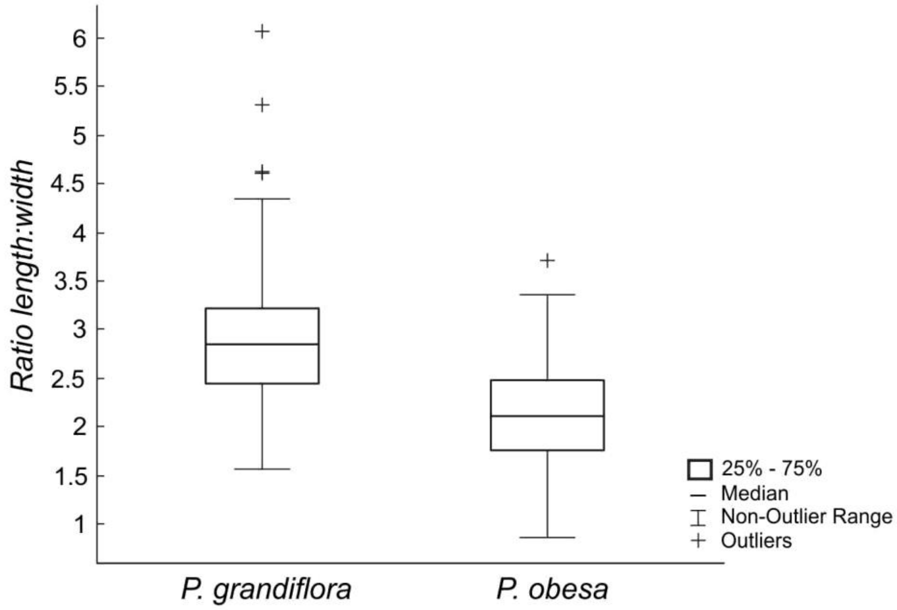
Figure 18. Sclerites of *Plexaurella obesa* (YPM 4509 – holotype, from the Fernando de Noronha Archipelago). A: triradiates from middle layer; B: tuberculated spindles from middle layer; C: butterflies from middle layer; D: sclerites from axial layer; E: cortical sclerites. Scale bar: 0.1 mm.



Castro *et al.* (2010) also commented on the possibility of synonymization of *P. obesa* (as *P. dichotoma*) and *P. grandiflora*. Indeed, whereas comparison between holotypes of *P. obesa* and *P. dichotoma* makes clear the distinction between both species, when compared with *P. grandiflora*, the distinction is less obvious. Thus, despite differences mentioned in "Comparisons" section, comparison of populations of *P. grandiflora* and *P. obesa* shows they have significantly distinct ratios between spindle lengths and widths (Fig. 19). Although it is known that sclerite size is possibly affected by depth, the analysis showed consistent sclerite shortening in sclerites of all specimens of *P. obesa*; which reinforces it as a distinct species. A second source of evidence through molecular analyses was not feasible by the time of writing this manuscript. Attempts to obtain *DNA* samples from all specimens present in both USNM and MNRJ collections were unsuccessful, due to their state of conservation. Besides that, no living colonies were found neither in the Rocas Atol, even after 30 days of divings, nor in Fernando de Noronha Archipelago.

Distribution. Manuel Luís Parcel, Fernando de Noronha Archipelago and Rocas Atoll, shallow-water.

Figure 19. Comparison of ratio of spindle lengths and widths between two Brazilian *Plexaurella* species. Mann-Whitney tests at α = 0.05 ($p<0.0001$). Spindles from middle layer of colonies of each species randomly chosen (n=134 for each species).



Final Remarks

Given the succession of subjective revisions on this genus, we attempted to summarize all the names atributed to *Plexaurella* species at some point (Tab. 2).

We also examined the holotype of *Plexaurella tenuis* Kunze, 1916 (ZMB 5964), but it has axial purple spindles, cortical leaf clubs, and none of the diagnostic characters of *Plexaurella*, placing it in the genus *Pseudoplexaura* Wright & Studer, 1889. The presence of cortical three-flanged leaf clubs around 0.1 mm long, and spindles reaching 1 mm long or more makes the specimen undistinguishable from types of *Pseudoplexaura crucis* Bayer, 1961 (Fig. 20). Based on that, we suggest synonymizing those two species under *Pseudoplexaura tenuis* (Kunze, 1916) new comb. as the valid name for this taxon, by priority order.

The drawings of *Plexaurella philippinensis* Wright and Studer, 1889 in its original description shows predominantly leaf clubs with broad lobed margins, suggesting that it belongs to the genus *Menella* Gray, 1870. Kunze (1916, p. 558) refers to this species as belonging to *Plexauroides* W&S, 1889, and that genus was subsequently considered as junior synonym of *Menella* (Bayer, 1981). Thus, provisionally, we suggest the name *Menella philippinensis* (Wright and Studer, 1889) new comb. for this taxon.

Table 2. Names or identifications assigned to the genus *Plexaurella* Kölliker, 1865 and their current synonyms.

Valid species	Synonyms	Proposed by
Plexaurella dichotoma (Esper, 1788)	*Gorgonia dichotoma* Esper, 1788	Kölliker, 1865
	Eunicea anceps Duchassaing and Michelotti, 1860	Kunze, 1916
	Plexaurella vermiculata sensu Kölliker, 1865	Herein
Plexaurella nutans (Duchassaing and Michelotti, 1860)	*Eunicea nutans* Duchassaing and Michelotti, 1860	Bayer, 1961
	Plexaurella affinis Bell, 1889	Bayer, 1961
	Plexaurella crassa sensu Kölliker, 1865	Bayer, 1961
	Plexaura friabilis sensu Kunze, 1916	Herein
	Plexaurella fusifera Kunze, 1916	Herein
	Plexaurella kunzei Kükenthal, 1924	Herein
Plexaurella grisea Kunze, 1916	*Plexaurella dichotoma* var. grisea Kunze, 1916	Bayer, 1961
	Plexaurella anguiculoides Bell, 1889	Herein
	Plexaurella curvata Kunze, 1916	Herein
	Plexaurella heteropora Kunze, 1916	Herein
	Plexaurella vermiculata sensu Kunze, 1916	Herein
Plexaurella teres Kunze, 1916	*Plexaurella vermiculata sensu* Bell, 1889	Herein
	Plexaurella grisea sensu Bayer, 1961	Herein
Plexaurella obesa Verrill, 1912	*?Plexaurella dichotoma sensu* Tixier-Durivault, 1970	Herein
	Plexaurella dichotoma sensu Castro *et al.*, 2010	Herein

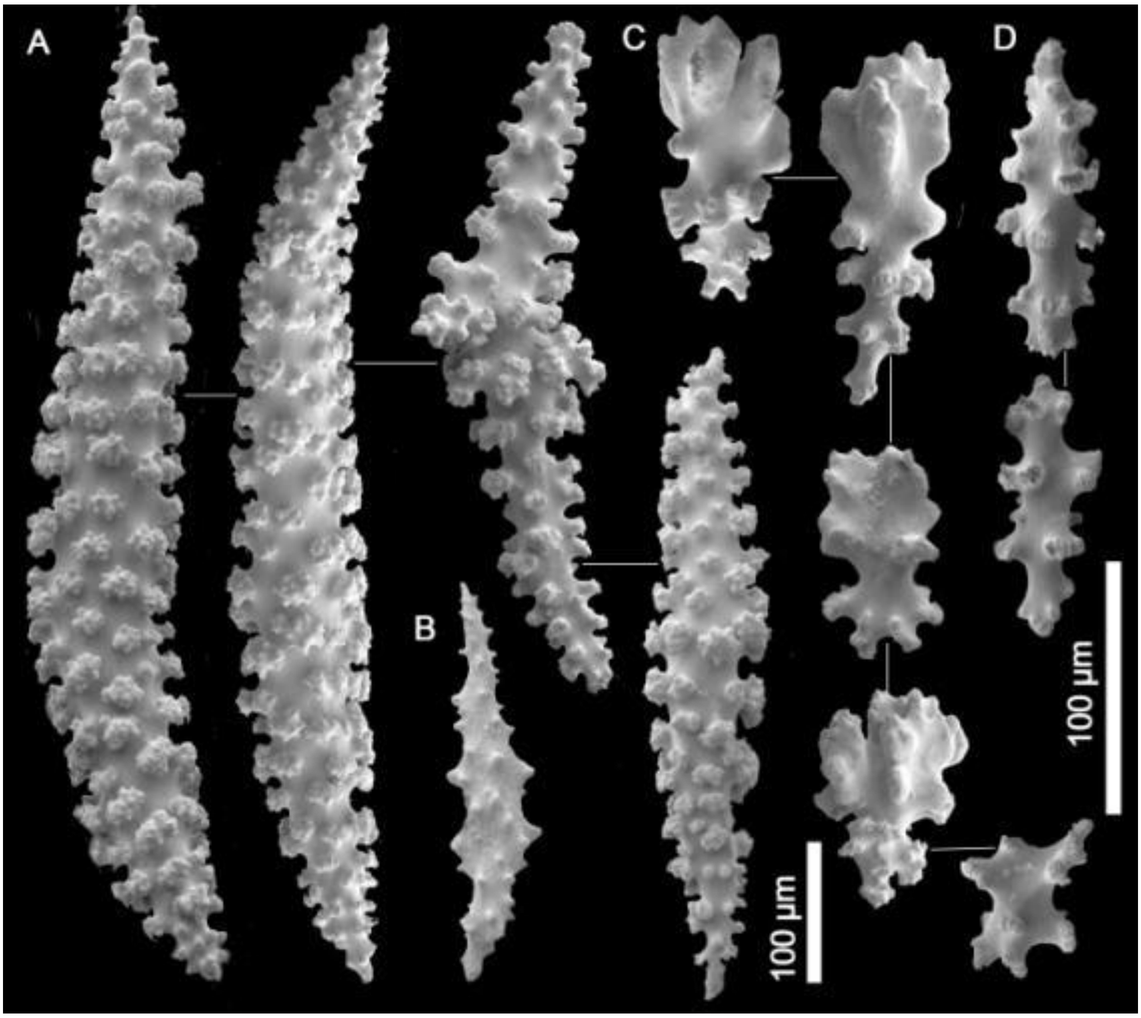
Table 2. Cont...

Plexaurella grandiflora Verrill, 1912	*Plexaurella (Pseudeunicea) grandiflora* Verrill, 1912	Bayer, 1961
	Plexaurella braziliana Verrill, 1912	Castro, 1989
	Plexaurella verrucosa Verrill, 1912	Castro, 1989
	Plexaurella cylindrica Verrill, 1912	Castro, 1989
Plexaurella rastrera sp. nov.		Herein
Plexaurella regia Castro, 1989		Castro, 1989
Species previously assigned to *Plexaurella*	**Synonyms**	**Proposed by**
Euplexaura capensis Verrill, 1870	*Plexaurella friabilis sensu* Verrill, 1866	Bayer, 1961
Pseudoplexaura crassa (Ellis and Solander, 1786)	*Gorgonia crassa* Ellis and Solander, 1786	Verrill, 1907
Pseudoplexaura porosa (Houttuyn, 1772)	*Plexaurella vermiculata* var. *porosa* Dubrowsky, 1934	Bayer, 1961
	Plexaurella dubrovskyi Stiasny, 1935a	Bayer, 1961
	Plexaurella dubrovskyi Stiasny, 1935b	Bayer, 1961
	Plexaurella van der horsti Stiasny, 1935a	Bayer, 1961
	Plexaurella vanderhorsti Stiasny, 1935b	Bayer, 1961
Pseudoplexaura flagellosa (Houttuyn, 1772)	*Plexaurella porosa* Gordon, 1925	Bayer, 1961
Pseudoplexaura tenuis (Kunze, 1916) new comb.	*Plexaurella tenuis* Kunze, 1916	Herein
Menella philippinensis (Wright and Studer, 1889) new comb.	*Plexaurella philippinensis* Wright and Studer, 1889	Herein
Uncertain		
Gorgonia crassa sensu Esper, 1791		
Gorgonia furcata Lamarck, 1816		

Table 2. Cont...

Gorgonia vermiculata Lamarck, 1816
Plexaurella vermiculata sensu Duchassaing and Michelotti, 1860

Figure 20. Sclerites of *Pseudoplexaura tenuis* (Kunze, 2016) new comb. (paratype of *Pseudoplexaura crucis* (USNM 51565), from Virgin Islands, St. John). A: spindles from the cortical layer; B: rod from body wall; C: clubs from the cortical layer; D: purple axial sclerites.



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SUPPLEMENTARY TABLE

Table S1. Specimens of *Plexaurella* spp. examined with their current identification (except types) and their collection data. Type-specimens in boldface. Museum abbreviations: MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNRJ: Museu Nacional, Rio de Janeiro; SMF: Senckenberg Gesellschaft für Naturforschung, Frankfurt; USNM: United States National Museum (National Museum of Natural History), Washington, DC; YPM: Yale Peabody Museum of Natural History, New Haven, CT; ZMB: Zoologisches Museum, Berlin.

Museum	Number	ID	Collector	Col. Date	Depth (min)	Depth (max)	Latitude	Longitude	Locality
MNRJ	157	*P. grandiflora* Verrill, 1912	P. S. Young	18.01.1980			-17.3372222	-39.2116666	5 km north of Cumuruxatiba, Bahia
MNRJ	431	*P. grandiflora* Verrill, 1912	Dept. Zoologia/IB/UFRJ	30.07.1970			-19.9555555	-40.1341666	Santa Cruz
MNRJ	432	*P. grandiflora* Verrill, 1912	T. C. A. Pires	24.09.1980			-20.6361111	-40.4391666	Setiba beach, Espírito Santo
MNRJ	433	*P. grandiflora* Verrill, 1912	P. S. Young	30.10.1980	1	1	-20.6727777	-40.4963888	Castanheiras Beach, Espírito Santo
MNRJ	**434**	***P. regia* Castro, 1989**	C. B. Castro	16.04.1981	4	4	-17.9647222	-38.6758333	Abrolhos Parcel, Chapeirão 1' Santa Bárbara Island
MNRJ	435	*P. grandiflora* Verrill, 1912	C. B. Castro	15.04.1981	3	3	-17.7	-38.9666666	Off Caravelas, Parcel das Paredes, Franja da Pedra Lixa, Bahia
MNRJ	436	*P. grandiflora* Verrill, 1912	C. B. Castro	17.04.1981	5	5	-17.9588888	-38.645	Parcel dos Abrolhos, near to the Rosalina Shipwreck
MNRJ	437	*P. grandiflora* Verrill, 1912	C. B. Castro	16.07.1981			-20.6727777	-40.4963888	Castanheiras Beach, Espírito Santo
MNRJ	438	*P. grandiflora* Verrill, 1912	C. B. Castro	17.07.1981	3	3	-20.6116666	-40.3780555	Três Ilhas, Espírito Santo
MNRJ	439	*P. grandiflora* Verrill, 1912	C. B. Castro	21.07.1981	2	2	-20.6366666	-40.4675	Três Praias, Espírito Santo

Table S1. Cont...

MNRJ	**440**	***P. regia* Castro, 1989**	C. B. Castro	15.04.1981	6	6	-17.7016666	-38.9827777	Franja da Pedra Lixa, Off Caravelas, Bahia
MNRJ	441	*P. grandiflora* Verrill, 1912	R. D. V. Thomaz	17.01.1982	1	1	-20.6361111	-40.4391666	Setiba beach, Espírito Santo
MNRJ	442	*P. grandiflora* Verrill, 1912	R. D. V. Thomaz	18.01.1982	2	2	-20.3363888	-40.2777777	Costa Beach, Espírito Santo
MNRJ	443	*P. obesa* Verrill, 1912	C. B. Castro	20.02.1982	4	4	-3.86277777	-33.805	Rocas Atoll
MNRJ	444	*P. grandiflora* Verrill, 1912	C. B. Castro	13.10.1982	1	1	-21.5	-41.05	Off Barra do Itabapoana, São João da Barra, Baixio dos Moleques, Rio de Janeiro
MNRJ	445	*P. grandiflora* Verrill, 1912	Conceição	25.08.1978			-9.01666666	-35.2166666	Maragogi, Alagoas
MNRJ	446	*P. grandiflora* Verrill, 1912	P. S. Young	06.07.1982			-7.11388888	-34.8097222	Picãozinho reef, Paraíba
MNRJ	635	*P. grandiflora* Verrill, 1912	P. S. Young	09.07.1984			-20.6727777	-40.4963888	Castanheiras Beach, Espírito Santo
MNRJ	639	*P. grandiflora* Verrill, 1912	P. S. Young	10.07.1984			-20.7397222	-40.5366667	Meaípe, Esp´rito Santo
MNRJ	980	*P. obesa* Verrill, 1912	C. B. Castro	21.06.1986	4	7	-3.87111111	-32.4361111	Fernando de Noronha, Leão beach
MNRJ	1148	*P. grandiflora* Verrill, 1912	C. B. Castro	27.04.1986			-20.9	-40.75	
MNRJ	1149	*P. grandiflora* Verrill, 1912	C. B. Castro	27.04.1986			-20.8547222	-40.7277778	Cabritos Island, Espírito Santo
MNRJ	1176	*P. regia* Castro, 1989	Celenterologia/DI/MN/UFRJ	07.10.1987			-17.9672222	-38.7075	
MNRJ	1269	*P. dichotoma* (Esper, 1791)	F. M. Bayer	08.05.1948			25.59083333	-80.1616667	Biscayne Bay, Soldier Key
MNRJ	1270	*Plexaurella fusifera* Kunze, 1916	Thomas Barrera exped.	23.05.1914			21.91222222	-84.9644444	off Cape San Antonio, Enseada de Cajon
MNRJ	1271	*Plexaurella fusifera* Kunze, 1916	Freelance	03.04.1956			17.00555556	-61.7627778	British West Indies, Antigua, English Harbor
MNRJ	1272	*P. nutans* (D & M, 1860)	R/V Oregon	13.04.1954			24.4	-82.9166667	Gulf of Mexio, 37 BR

Table S1. Cont...

MNRJ	1273	*P. grandiflora* Verrill, 1912	R. Rathbun	31.12.1876			-7	-34.75	Parahyba do Norte, Brazil
MNRJ	1274	*P. grandiflora* Verrill, 1912	R. Rathbun	31.12.1876			-12.7833333	-38.45	Mapelle
MNRJ	1300	*P. grandiflora* Verrill, 1912	C. F. Hartt Expedition	31.12.1876			-8.2	-34.9097222	Mapelle, Bahia or Candeias Reef
MNRJ	1344	*P. grandiflora* Verrill, 1912	E. S. Secco	08.10.1988			-20.6727778	-40.4963889	Praia das Castanheiras
MNRJ	1397	*P. grandiflora* Verrill, 1912	A. C. J. Marques	24.02.1989			-13.3741667	-38.9158333	Morro de São Paulo, lado esquerdo do Costão do Forte
MNRJ	1534	*P. obesa* Verrill, 1912	C. Savaget	21.07.1983			-0.87361111	-44.2166667	Parcel do Manuel Luís
MNRJ	1541	*P. obesa* Verrill, 1912	C. Savaget	21.07.1983			-0.87361111	-44.2166667	Parcel do Manuel Luís
MNRJ	1987	*P. grandiflora* Verrill, 1912	C. B. Castro	26.04.1986			-20.8055556	-40.6022222	Ubu, Praia de Parati
MNRJ	1988	*P. grandiflora* Verrill, 1912	F. B. Pitombo	19.02.1989			-13.3741667	-38.9158333	Valença, Morro de São Paulo, Costão do Forte
MNRJ	2199	*P. grandiflora* Verrill, 1912	C. B. Castro	02.10.1992			-17.9916667	-39.2569444	Recife de Nova Viçosa
MNRJ	2260	*P. grandiflora* Verrill, 1912	F. B. Pitombo	06.12.1993	22	22	-21.3	-40.4666667	Itapemerim
MNRJ	2584	*P. grandiflora* Verrill, 1912	A. L. C. D.	01.03.1994			-18.0166667	-39	Recife de Popa Verde
MNRJ	2593	*P. nutans* (D & M, 1860)	P. S. Young	01.10.1992			-17.9916667	-39.2569444	Recife de Nova Viçosa
MNRJ	2726	*P. grandiflora* Verrill, 1912	C. B. Castro [TTC-MAR (PGZ)]	01.02.1995			-17.9611111	-39.2127778	Recife de Coroa Vermelha /Nova Viçosa
MNRJ	2748	*P. regia* Castro, 1989	C. B. Castro	20.03.1995			-17.7561111	-39.0102778	Parcel das Paredes
MNRJ	2751	*P. regia* Castro, 1989	C. B. Castro	3.1993			-18.0166667	-39	Banco dos Abrolhos, Popa Verde
MNRJ	2752	*P. grandiflora* Verrill, 1912	P. S. Young	16.02.1995			-9.77083333	-35.8375	Praia do Francês
MNRJ	2754	*P. grandiflora* Verrill, 1912	P. S. Young	20.02.1995	30	30	-8.50833333	-34.9972222	Rasinho do Coiceiro, Porto de Galinhas
MNRJ	2861	*P. grandiflora* Verrill, 1912	S. M. Pinto	03.02.1996			-17.9611111	-39.2127778	Recife de Coroa Vermelha
MNRJ	3961	*P. grandiflora* Verrill, 1912	E. N. Calderon	27.06.1998	3	3	-20.6366667	-40.4675	Praia do Meio, Três Praias
MNRJ	4002	*P. grandiflora* Verrill, 1912	R. G. S. Berlinck	31.07.1999	5	6	-12.9166667	38.5166666 7	Baía de Todos os Santos, Ponta de Mont-Serrat

Table S1. Cont...

MNRJ	4342	*P. grandiflora* Verrill, 1912	C. B. Castro	20.02.2000			-17.875	-38.9791667	Pontas sul, Parcel das Paredes, Abrolhos
MNRJ	4580	*P. regia* Castro, 1989	C. B. Castro	13.12.2000			-17.9819444	-38.6516667	Parcel dos Abrolhos
MNRJ	4581	*P. regia* Castro, 1989	C. B. Castro	13.12.2000			-17.9819444	-38.6516667	Parcel dos Abrolhos
MNRJ	4582	*P. regia* Castro, 1989	C. B. Castro	13.12.2000			-17.9819444	-38.6516667	Parcel dos Abrolhos
MNRJ	4583	*P. regia* Castro, 1989	C. B. Castro	13.12.2000			-17.9819444	-38.6516667	Parcel dos Abrolhos
MNRJ	4584	*P. grandiflora* Verrill, 1912	C. B. Castro	14.12.2000			-17.9041667	-39.1361111	Sebastião Gomes, Parcel dos Abrolhos
MNRJ	4585	*P. grandiflora* Verrill, 1912	C. B. Castro	14.12.2000	0	3	-17.9041667	-39.1361111	Sebastião Gomes, Parcel dos Abrolhos
MNRJ	4586	*P. grandiflora* Verrill, 1912	C. B. Castro	14.12.2000	16	16	-18.0216667	-38.9930556	Popa Verde, Parcel dos Abrolhos
MNRJ	4587	*P. grandiflora* Verrill, 1912	C. B. Castro	14.12.2000			-17.9041667	-39.1361111	Sebastião Gomes, Parcel dos Abrolhos
MNRJ	4589	*P. grandiflora* Verrill, 1912	P. A. S. Costa	31.03.1997	100	400			Entre Regencia (ES) e Atafona (RJ)
MNRJ	4981	*P. nutans* (D & M, 1860)	P. C. Paiva	05.10.2001			9.347222222	-82.2416667	Bocas del Toro
MNRJ	5041	*P. grandiflora* Verrill, 1912	D. F. Moraes Jr.	03.11.2002			-13.3772222	-38.9136111	Morro de São Paulo, Primeira Praia
MNRJ	5562	*P. regia* Castro, 1989	B. Segal	17.11.1999			-16.8919444	-39.0547222	Pedra do Cavalo, recifes dos Itacolomis, Corumbau
MNRJ	5816	*P. regia* Castro, 1989	F. B. Pitombo	07.10.1987			-17.9672222	-38.7075	
MNRJ	6753	*P. regia* Castro, 1989	M. F. Alvarenga	22.12.2005			-16.4128333	-38.9878333	Recife de Fora, Ponto Oeste
MNRJ	6772	*P. grandiflora* Verrill, 1912	B. Segal	12.10.2005			-16.4	-38.9833333	Recife de Fora
MNRJ	8568	*P. grandiflora* Verrill, 1912	R. S. Cordeiro | C. Pérez	19.01.2015			-8.69861111	-35.0811111	Praia dos Carneiros
USNM	50130	*P. nutans* (D & M, 1860)	Oregon R/V	13/abr/54	68	68	24,40000	-82,92	Florida Keys, Loggerhead Key,

Table S1. Cont...

									South Of
USNM	50269	*P. dichotoma* (Esper, 1791)		26/abr/48					Florida Keys, Dry Tortugas, Garden Key, West Side Of Ft. Jefferson
USNM	**42004**	***P. rastrera sp. nov.***	Sloop Resolute	1918	2	7			Off Lord's Castle, East side of Barbados
USNM	50319	*P. dichotoma* (Esper, 1791)		08/mai/48					Miami, Biscayne Bay, Soldier Key & Caesars Creek
USNM	42142	*P. dichotoma* (Esper, 1791)	Fish Hawk R/V	1898					
USNM	50322	*P. nutans* (D & M, 1860)		08/mai/48					Miami, Biscayne Bay, Soldier Key & Caesars Creek
USNM	50333	*P. dichotoma* (Esper, 1791)	Freelance R/V	07/abr/56					Barbuda Island, Martello Tower, Reefs Of
USNM	50390	*P. dichotoma* (Esper, 1791)		26/abr/48					Florida Keys, Dry Tortugas, Garden Key, West Side Of Ft. Jefferson
USNM	100600	*P. dichotoma* (Esper, 1791)		18/mar/00					Navassa Island, Lulu Bay
USNM	50410	*P. dichotoma* (Esper, 1791)		19/jun/49					Sandy Ground, North Of
USNM	50419	*P. dichotoma* (Esper, 1791)		Apr 1948					Florida Keys, Key Largo, Dove Creek
USNM	50420	*P. dichotoma* (Esper, 1791)		15/jul/49	2	2			St. Eustatius Island, Gallows Bay, Southern Part Of Bay
USNM	50500	*P. verm. porosa* Dubrowsky, 1934					24,67000	-81,58	Florida Keys, Dry Tortugas
USNM	54939	*P. grisea* Kunze, 1916	Pillsbury R/V	03/jul/70	9	27	17,39330	-76,0367	Albatross Bank, Morant Cay
USNM	54940	*P. grisea* Kunze, 1916	Pillsbury R/V	05/jul/70	9	13	17,76330	-77,0083	Kingston, SW Of

Table S1. Cont...

USNM	54941	*P. grisea* Kunze, 1916	Pillsbury R/V	05/jul/70	15	15	17,75830	-76,985	Kingston, SW Of
USNM	54942	*P. nutans* (D & M, 1860)	Pillsbury R/V	05/jul/70	22	22	17,62500	-77,0483	Portland Bight
USNM	54943	*P. grisea* Kunze, 1916	Pillsbury R/V	05/jul/70	24	24	17,60500	-77,0433	Portland Bight
USNM	54945	*P. nutans* (D & M, 1860)	Pillsbury R/V	19/jul/70	17	22	17,73330	-71,3333	Cape Beata, East Of
USNM	54946	*P. nutans* (D & M, 1860)	Pillsbury R/V	19/jul/70	22	22	18,05000	-71,07	Point Avarena, South Of
USNM	54947	*P. nutans* (D & M, 1860)	Pillsbury R/V	20/jul/70	9	18	18,28330	-71,065	Neiba Bay
USNM	54950	*P. grisea* Kunze, 1916	Pillsbury R/V	29/jan/71	24	26	13,97170	-82,0617	Quita Sueno Bank, SW Of
USNM	54951	*P. nutans* (D & M, 1860)	Pillsbury R/V	01/fev/71	18	18	15,25000	-81,85	Media Luna Reef, East Of
USNM	50534	*P. teres* Kunze, 1916	Freelance R/V	12/abr/56					St. Kitts , Windward Beach, Coral Reef Opposite Frigate Bay
USNM	50535	*P. teres* Kunze, 1916		Jan 1884					Tampa Bay, Between Johns Pass And Pass-A-Grille
USNM	50536	*P. teres* Kunze, 1916		Apr 1948	4	4			Florida Keys, Elliot Key, Bache Shoal
USNM	54953	*P. grisea* Kunze, 1916	Pillsbury R/V	19/jul/71	7	8	21,36170	-70,955	Grand Turk Island, SE Of
USNM	50556	*P. dichotoma* (Esper, 1791)		1956					New Providence Island
USNM	50602	*P. dichotoma* (Esper, 1791)		24/mar/51	10	12			Sarasota Bay, Longboat Key, 3.5 Mile SW Of
USNM	50668	*P. dichotoma* (Esper, 1791)		19/jun/49					Sandy Ground, North Of
USNM	50688	*P. teres* Kunze, 1916		Feb 1887			17,41670	-83,9167	Swan Islands, Swan Island
USNM	50697	*P. dichotoma* (Esper, 1791)	Tomas Barrera Expedition	21/jul/15	4	4			St. Thomas Island, Mosquito Bay
USNM	50708	*P. nutans* (D & M, 1860)		26/abr/48					Florida Keys, Dry Tortugas, Garden Key, West Side Of Ft. Jefferson
USNM	50709	*P. dichotoma* (Esper, 1791)		26/abr/48					Florida Keys, Dry Tortugas, Garden Key, West Side Of Ft.

Table S1. Cont...

									Jefferson
USNM	50711	*P. dichotoma* (Esper, 1791)		22/mai/14			21,91360	-84,8967	Cuba
USNM	**50745**	***P. rastrera sp. nov.***		19/jun/49					Anguilla
USNM	50767	*P. dichotoma* (Esper, 1791)		1925			24,67000	-81,58	United States
USNM	55091	*P. dichotoma* (Esper, 1791)	Pillsbury R/V	16/jan/70	18	40	19,10500	-69,0167	Dominican Republic
USNM	55092	*P. nutans* (D & M, 1860)	Pillsbury R/V	20/jul/70	13	24	18,25830	-70,875	Dominican Republic
USNM	50916	*P. dichotoma* (Esper, 1791)		27/mar/55			19,22000	-96,1	Mexico
USNM	50962	*P. teres* Kunze, 1916	Freelance R/V	03/abr/56					Antigua and Barbuda
USNM	50967	*P. dichotoma* (Esper, 1791)	Freelance R/V	13/abr/56	13	13	17,47000	-63,22	Netherlands Antilles
USNM	51020	*P. nutans* (D & M, 1860)	Freelance R/V	20/abr/58					Antigua and Barbuda
USNM	59044	*P. dichotoma* (Esper, 1791)	CCRE, Belize	16/mai/75	20	30	16,80000	-88,08	Belize
USNM	51359	*P. dichotoma* (Esper, 1791)	Vidal R/V	30/mar/56	20	20			Jamaica
USNM	51360	*P. dichotoma* (Esper, 1791)		30/ago/52					Jamaica
USNM	51361	*P. nutans* (D & M, 1860)					18,25000	-77,5	Jamaica
USNM	51392	*P. dichotoma* (Esper, 1791)		23/jul/59					Jamaica
USNM	51393	*P. dichotoma* (Esper, 1791)		Dec 1944					Cayman Islands
USNM	51394	*P. dichotoma* (Esper, 1791)		02/ago/59					Jamaica
USNM	51395	*P. dichotoma* (Esper, 1791)		02/ago/59					Jamaica
USNM	51417	*P. teres* Kunze, 1916	Freelance R/V	12/abr/59	9	12			Trinidad and Tobago
USNM	51435	*P. dichotoma* (Esper, 1791)		Jul 1959	1	3	22,38000	-89,68	Mexico
USNM	51446	*P. dichotoma* (Esper, 1791)		18/mai/55	15	15	22,39250	-89,6925	Mexico
USNM	51489	*P. dichotoma* (Esper, 1791)		1903					Bahamas
USNM	51490	*P. dichotoma* (Esper, 1791)		22/mai/14			21,91360	-84,8967	Andros Island
USNM	16848	*P. nutans* (D & M, 1860)	Pillsbury R/V	19/jul/71	7	8	21,36170	-70,955	Florida Keys, Vaca Key
USNM	51725	*P. nutans* (D & M, 1860)	Pillsbury R/V	19/jul/71	7	8	21,36170	-70,955	Miami, Biscayne Bay, Soldier Key & Caesars Creek

Table S1. Cont...

USNM	51726	*P. nutans* (D & M, 1860)							Miami, Biscayne Bay, Soldier Key & Caesars Creek
USNM	51742	*P. dichotoma* (Esper, 1791)		19/jun/49					Miami, Biscayne Bay, Soldier Key & Caesars Creek, Seaward Side
USNM	51972	*P. dichotoma* (Esper, 1791)		1925			24,67000	-81,58	St. George's Island, Fort St. Catherine
USNM	51973	*P. dichotoma* (Esper, 1791)	Pillsbury R/V	16/jan/70	18	40	19,10500	-69,0167	St. George's Island, Fort St. Catherine
USNM	51975	*P. dichotoma* (Esper, 1791)	Pillsbury R/V	20/jul/70	13	24	18,25830	-70,875	Miami, Biscayne Bay, Soldier Key & Caesars Creek, Seaward Side
USNM	51986	*P. nutans* (D & M, 1860)		27/mar/55			19,22000	-96,1	Somerset Island, Southwest Reef
USNM	51987	*P. nutans* (D & M, 1860)	Freelance R/V	03/abr/56					Somerset Island, Southwest Reef
USNM	51988	*P. nutans* (D & M, 1860)	Freelance R/V	13/abr/56	13	13	17,47000	-63,22	Miami, Biscayne Bay, Soldier Key & Caesars Creek, Seaward Side
USNM	52005	*P. dichotoma* (Esper, 1791)	Freelance R/V	20/abr/58					Bermuda Island, Southampton, South Shore
USNM	59487	*P. grisea* Kunze, 1916		16/mai/75	20	30	16,80000	-88,08	South Caicos Island
USNM	44236	*P. nutans* (D & M, 1860)	Vidal R/V	30/mar/56	20	20			Cape Romano, 14 Mile West Of
USNM	52409	*P. nutans* (D & M, 1860)		30/ago/52					Campeche Bank, Alacran Reef
USNM	52410	*P. dichotoma* (Esper, 1791)					18,25000	-77,5	Campeche Bank, Alacran Reef
USNM	5264	*P. grandiflora* Verrill, 1912	Hartt Expedition	23/jul/59					Candeias, Reef, Pernambuco
USNM	5267	*P. grandiflora* Verrill, 1912	Hartt Expedition	Dec 1944					
USNM	5271	*P. grandiflora* Verrill, 1912		02/ago/59					Mar Grande

Table S1. Cont...

USNM	5273	*P. grandiflora* Verrill, 1912		02/ago/59					Mar Grande
USNM	5274	*P. grandiflora* Verrill, 1912	Freelance R/V	12/abr/59	9	12			Mar Grande
USNM	5276	*P. grandiflora* Verrill, 1912		Jul 1959	1	3	22,38000	-89,68	Mar Grande
USNM	5278	*P. obesa* Verrill, 1912		18/mai/55	15	15	22,39250	-89,6925	Fernando De Noronha Island
USNM	5280	*P. grandiflora* Verrill, 1912	Hartt Expedition	1903					Mapele
USNM	5281	*P. grandiflora* Verrill, 1912	Hartt Expedition	1876			-12,78000	-38,43	Mapele
USNM	5315	*P. grandiflora* Verrill, 1912	Hartt Expedition	1876					
USNM	5316	*P. grandiflora* Verrill, 1912	Hartt Expedition	1876					
USNM	5318	*P. grandiflora* Verrill, 1912	Hartt Expedition	1876			-12,78000	-38,43	Mapele
USNM	5319	*P. grandiflora* Verrill, 1912	Hartt Expedition	1876					Candeias, Reef
USNM	5320	*P. grandiflora* Verrill, 1912	Hartt Expedition	1876					Candeias, Reef
USNM	53578	*P. dichotoma* (Esper, 1791)	CCRE, Belize	02/mai/72	4	5	16,80000	-88,08	Carrie Bow Cay
USNM	53579	*P. dichotoma* (Esper, 1791)	CCRE, Belize	02/mai/72	4	5	16,80000	-88,08	Carrie Bow Cay
USNM	49607	*P. dichotoma* (Esper, 1791)		22/fev/48					Miami, Biscayne Bay, Soldier Key & Caesars Creek
USNM	54263	*P. dichotoma* (Esper, 1791)		23/dez/64					Discovery Bay
USNM	33742	*P. dichotoma* (Esper, 1791)		29/mai/12	5	10			Biscayne By, Off Key Biscayne
USNM	34520	*P. dichotoma* (Esper, 1791)	Tomas Barrera Expedition	14/mai/14					Santa Lucia Bay, On Reef Off Cayo Hutia
USNM	34676	*P. dichotoma* (Esper, 1791)	Tomas Barrera Expedition	12/mai/14					Jutias Cays, Between Hutia And Little Cays
USNM	34677	*P. dichotoma* (Esper, 1791)	Tomas Barrera Expedition	14/mai/14					Santa Lucia Bay, On Reef Off Cayo Hutia
USNM	34678	*P. dichotoma* (Esper, 1791)	Tomas Barrera Expedition	02/jun/14	4	4			La Esperanza, Between Anchorage And Entrance
USNM	34683	*P. dichotoma* (Esper, 1791)	Tomas Barrera Expedition	22/mai/14			21,91360	-84,8967	Ensenada De Cajon, Off Cape

Table S1. Cont...

									San Antonio
USNM	1234926	*P. nutans* (D & M, 1860)	Pillsbury R/V	03/jul/69	27	27	12,11670	-61,5417	St. George, East of
USNM	75728	*P. regia* Castro, 1989		15/abr/81	6	6			Abrolhos Islands, Paredes Reefs, Lixa Reef, Off Caravelas
USNM	88779	*P. dichotoma* (Esper, 1791)	Marsys Resolute R/V	10/jun/84	12,2	13,7			East Of Gibbs And Round Cays
USNM	88786	*P. nutans* (D & M, 1860)	Marsys Resolute R/V	10/jun/84	4,6	5,5			Round Cay, Patch Reef West Of Cay
USNM	79366	*P. teres* Kunze, 1916	Endeavor R/V	09/nov/86	22	35	24,60000	-76,02	Eleuthera Island, Off East End Point
USNM	91860	*P. dichotoma* (Esper, 1791)		Jun 1888					Eleuthera Island, Spanish Wells
USNM	73393	*P. grandiflora* Verrill, 1912		26/out/80	1	1			Guarapari, Castanheiras Beach
USNM	73399	*P. regia* Castro, 1989		15/abr/81	6	6			Abrolhos Islands, Paredes Reefs, Lixa Reef
USNM	73400	*P. obesa* Verrill, 1912		Feb 1982	4	10			Fernando De Noronha Island, Rocas Atoll, Outside The Atoll
USNM	73401	*P. grandiflora* Verrill, 1912		25/ago/78					Maragogi
USNM	73487	*P. nutans* (D & M, 1860)		29/jul/81	19,6	19,6	25,76560	-82,1558	Off Florida
USNM	73488	*P. nutans* (D & M, 1860)		28/abr/81	19,6	19,6	25,76560	-82,1558	Off Florida
USNM	73489	*P. nutans* (D & M, 1860)		08/nov/80	19,6	19,6	25,76560	-82,1558	Off Florida
USNM	73490	*P. nutans* (D & M, 1860)			19,6	19,6	25,76560	-82,1558	Off Florida
USNM	73491	*P. nutans* (D & M, 1860)			19,6	19,6	25,76560	-82,1558	Off Florida
USNM	73492	*P. nutans* (D & M, 1860)		29/jul/81	19,6	19,6	25,76560	-82,1558	Off Florida
USNM	73493	*P. nutans* (D & M, 1860)		29/jul/81	19,6	19,6	25,76560	-82,1558	Off Florida
USNM	73494	*P. nutans* (D & M, 1860)		28/abr/81	19,6	19,6	25,76560	-82,1558	Off Florida
USNM	73566	*P. grandiflora* Verrill, 1912		18/jan/82	2	2			Vila Velha, Costa Beach
USNM	85469	*P. nutans* (D & M, 1860)	SOFLA	14/dez/82	19	19	26,76690	-82,1011	Marco Island, SW Of

Table S1. Cont...

USNM	85470	*P. nutans* (D & M, 1860)	SOFLA	02/jun/83	19	19	26,76690	-82,1011	Marco Island, SW Of
USNM	85471	*P. nutans* (D & M, 1860)	SOFLA	09/dez/82	14	14	25,29670	-81,6633	Cape Sable, West Of
USNM	**73605**	***P. rastrera sp. nov.***		23/ago/85	9	9			Des Salines
USNM	73616	*P. nutans* (D & M, 1860)		21/ago/85	11	11			Antigua Island
USNM	73617	*P. nutans* (D & M, 1860)		21/ago/85	11	11			Antigua Island
USNM	73618	*P. nutans* (D & M, 1860)		21/ago/85	11	11			Antigua Island
USNM	84073	*P. nutans* (D & M, 1860)	SOFLA	05/dez/82	13	13	26,29780	-82,2103	Sanibel Island, SW Of
USNM	84074	*P. nutans* (D & M, 1860)	SOFLA	07/dez/82	13	13	26,29780	-82,2103	Sanibel Island, SW Of
USNM	84075	*P. nutans* (D & M, 1860)	SOFLA	09/dez/82	13	13	26,29780	-82,2103	Sanibel Island, SW Of
USNM	84076	*P. nutans* (D & M, 1860)	SOFLA	31/mai/83	13	13	26,29780	-82,2103	Sanibel Island, SW Of
USNM	84077	*P. nutans* (D & M, 1860)	SOFLA	31/mai/83	13	13	26,29780	-82,2103	Sanibel Island, SW Of
USNM	84078	*P. nutans* (D & M, 1860)	SOFLA	06/dez/82	17	17	26,05310	-82,1408	Naples, SW Of
USNM	84079	*P. nutans* (D & M, 1860)	SOFLA	07/dez/82	17	17	26,05310	-82,1408	Naples, SW Of
USNM	84080	*P. nutans* (D & M, 1860)	SOFLA	07/dez/82	17	17	26,05310	-82,1408	Naples, SW Of
USNM	84081	*P. nutans* (D & M, 1860)	SOFLA	01/jun/83	17	17	26,05310	-82,1408	Naples, SW Of
USNM	84082	*P. nutans* (D & M, 1860)	SOFLA	01/jun/83	17	17	26,05310	-82,1408	Naples, SW Of
USNM	84083	*P. nutans* (D & M, 1860)	SOFLA	07/dez/82	19	19	26,76690	-82,1011	Marco Island, SW Of
USNM	84084	*P. nutans* (D & M, 1860)	SOFLA	14/dez/82	19	19	26,76690	-82,1011	Marco Island, SW Of
USNM	84085	*P. nutans* (D & M, 1860)	SOFLA	14/dez/82	19	19	26,76690	-82,1011	Marco Island, SW Of
USNM	84086	*P. nutans* (D & M, 1860)	SOFLA	02/jun/83	19	19	26,76690	-82,1011	Marco Island, SW Of
USNM	84087	*P. nutans* (D & M, 1860)	SOFLA	02/jun/83	19	19	26,76690	-82,1011	Marco Island, SW Of
USNM	84088	*P. nutans* (D & M, 1860)	SOFLA	08/dez/82	16	16	25,29440	-81,8	Cape Sable, West Of
USNM	84089	*P. nutans* (D & M, 1860)	SOFLA	08/dez/82	16	16	25,29440	-81,8	Cape Sable, West Of
USNM	84090	*P. nutans* (D & M, 1860)	SOFLA	03/jun/83	16	16	25,29440	-81,8	Cape Sable, West Of
USNM	84091	*P. nutans* (D & M, 1860)	SOFLA	09/dez/82	14	14	25,29670	-81,6633	Cape Sable, West Of
USNM	84092	*P. nutans* (D & M, 1860)	SOFLA	03/jun/83	14	14	25,29670	-81,6633	Cape Sable, West Of

Table S1. Cont...

USNM	84093	*P. teres* Kunze, 1916	SOFLA	09/dez/82	14	14	25,29670	-81,6633	Cape Sable, West Of
USNM	84094	*P. nutans* (D & M, 1860)	SOFLA	09/dez/82	14	14	25,29670	-81,6633	Cape Sable, West Of
USNM	84095	*P. teres* Kunze, 1916	SOFLA	04/jun/83	14	14	25,29670	-81,6633	Cape Sable, West Of
USNM	84096	*P. nutans* (D & M, 1860)	SOFLA	04/jun/83	14	14	25,29670	-81,6633	Cape Sable, West Of
USNM	84097	*P. nutans* (D & M, 1860)	SOFLA	04/jun/83	14	14	25,29670	-81,6633	Cape Sable, West Of
USNM	84098	*P. nutans* (D & M, 1860)	SOFLA	03/jun/83	14	14	25,29670	-81,6633	Cape Sable, West Of
USNM	84099	*P. nutans* (D & M, 1860)	SOFLA	31/mai/83	13	13	26,29780	-82,2103	Sanibel Island, SW Of
USNM	84100	*P. nutans* (D & M, 1860)	SOFLA	31/mai/83	13	13	26,29780	-82,2103	Sanibel Island, SW Of
USNM	84101	*P. nutans* (D & M, 1860)	SOFLA	01/jun/83	17	17	26,05310	-82,1408	Naples, SW Of
USNM	84102	*P. nutans* (D & M, 1860)	SOFLA	06/dez/82	17	17	26,05310	-82,1408	Naples, SW Of
USNM	84103	*P. nutans* (D & M, 1860)	SOFLA	08/dez/82	17	17	26,05310	-82,1408	Naples, SW Of
USNM	84104	*P. nutans* (D & M, 1860)	SOFLA	01/jun/83	17	17	26,05310	-82,1408	Naples, SW Of
USNM	84105	*P. nutans* (D & M, 1860)	SOFLA	06/dez/82	17	17	26,05310	-82,1408	Naples, SW Of
USNM	84106	*P. nutans* (D & M, 1860)	SOFLA	06/dez/82	17	17	26,05310	-82,1408	Naples, SW Of
USNM	84107	*P. nutans* (D & M, 1860)	SOFLA	14/dez/82	19	19	26,76690	-82,1011	Marco Island, SW Of
USNM	84108	*P. nutans* (D & M, 1860)	SOFLA	08/dez/82	16	16	25,29440	-81,8	Cape Sable, West Of
USNM	84109	*P. nutans* (D & M, 1860)	SOFLA	11/dez/82	16	16	25,29440	-81,8	Cape Sable, West Of
USNM	84110	*P. nutans* (D & M, 1860)	SOFLA	03/jun/83	16	16	25,29440	-81,8	Cape Sable, West Of
USNM	84111	*P. nutans* (D & M, 1860)	SOFLA	09/dez/82	14	14	25,29670	-81,6633	Cape Sable, West Of
USNM	84112	*P. nutans* (D & M, 1860)	SOFLA	09/dez/82	14	14	25,29670	-81,6633	Cape Sable, West Of
USNM	84113	*P. nutans* (D & M, 1860)	SOFLA		14	14	25,29670	-81,6633	Cape Sable, West Of
USNM	84114	*P. nutans* (D & M, 1860)	SOFLA		14	14	25,29670	-81,6633	Cape Sable, West Of
USNM	84115	*P. nutans* (D & M, 1860)	SOFLA		14	14	25,29670	-81,6633	Cape Sable, West Of
USNM	84116	*P. nutans* (D & M, 1860)	SOFLA		14	14	25,29670	-81,6633	Cape Sable, West Of
USNM	89271	*P. dichotoma* (Esper, 1791)					24,67000	-81,58	Florida Keys, Dry Tortugas
USNM	89274	*P. dichotoma* (Esper, 1791)			10	10			St. Croix Island, Buck Island,

Table S1. Cont...

									Outside The Barrier Reef
USNM	89276	*P. nutans* (D & M, 1860)			5	10			Miami, Key Biscayne
USNM	73735	*P. regia* Castro, 1989							Abrolhos Islands, North Side Of Islands
USNM	7523	*P. dichotoma* (Esper, 1791)		Albatross R/V	393	393	17,86670	-76,7583	Kingston Harbor, South of
USNM	7524	*P. dichotoma* (Esper, 1791)		Albatross R/V	393	393	17,86670	-76,7583	Kingston Harbor, South of
USNM	7525	*P. dichotoma* (Esper, 1791)		Albatross R/V	393	393	17,86670	-76,7583	Kingston Harbor, South of
USNM	81332	*P. nutans* (D & M, 1860)							Eumedio Island, 1 Km W Of Lighthouse
USNM	87053	*P. grisea* Kunze, 1916	SOFLA	Suncoaster R/V	27	27	24,60280	-82,6994	Florida Keys, East Of
USNM	87054	*P. dichotoma* (Esper, 1791)	SOFLA	Suncoaster R/V	27	27	24,60280	-82,6994	Florida Keys, East Of
USNM	87055	*P. dichotoma* (Esper, 1791)	SOFLA	Suncoaster R/V	20	20	25,76390	-82,1017	Marco Island, SW Of
USNM	87056	*P. dichotoma* (Esper, 1791)	SOFLA	Suncoaster R/V	20	20	25,76390	-82,1017	Marco Island, SW Of
USNM	87060	*P. nutans* (D & M, 1860)	SOFLA	Suncoaster R/V	13	13	25,29220	-81,6636	Cape Sable, West Of
USNM	87061	*P. nutans* (D & M, 1860)	SOFLA	Suncoaster R/V	13	13	25,29220	-81,6636	Cape Sable, West Of
USNM	87062	*P. nutans* (D & M, 1860)	SOFLA	Suncoaster R/V	13	13	25,29220	-81,6636	Cape Sable, West Of

Table S1. Cont...

USNM	87063	*P. nutans* (D & M, 1860)	SOFLA	Suncoaster R/V	15	15	25,29030	-81,8003	Cape Sable, West Of
USNM	87064	*P. nutans* (D & M, 1860)	SOFLA	Suncoaster R/V	15	15	25,29030	-81,8003	Cape Sable, West Of
USNM	87065	*P. nutans* (D & M, 1860)	SOFLA	12/dez/84	27	27	24,60280	-82,6994	Florida Keys, East Of
USNM	87066	*P. nutans* (D & M, 1860)	SOFLA	12/dez/84	27	27	24,60280	-82,6994	Florida Keys, East Of
USNM	87067	*P. nutans* (D & M, 1860)	SOFLA	14/set/85	27	27	24,60280	-82,6994	Florida Keys, East Of
USNM	87068	*P. nutans* (D & M, 1860)	SOFLA	16/ago/84	13	13	25,29220	-81,6636	Cape Sable, West Of
USNM	87069	*P. nutans* (D & M, 1860)	SOFLA	02/mar/84	13	13	25,29220	-81,6636	Cape Sable, West Of
USNM	87070	*P. nutans* (D & M, 1860)	SOFLA	07/dez/83	16	16	26,05060	-82,1417	Naples, SW Of
USNM	87071	*P. nutans* (D & M, 1860)	SOFLA	10/mai/83	16	16	26,05060	-82,1417	Naples, SW Of
USNM	87072	*P. nutans* (D & M, 1860)	SOFLA	26/jun/85	27	27	24,60280	-82,6994	Florida Keys, East Of
USNM	87073	*P. dichotoma* (Esper, 1791)	SOFLA	26/jun/85	27	27	24,60280	-82,6994	Florida Keys, East Of
USNM	87110	*P. dichotoma* (Esper, 1791)	SOFLA	25/mar/85	27	27	24,60280	-82,6994	Florida Keys, East Of
USNM	87111	*P. nutans* (D & M, 1860)	SOFLA	25/mar/85	27	27	24,60280	-82,6994	Florida Keys, East Of
USNM	87112	*P. nutans* (D & M, 1860)	SOFLA	25/mar/85	27	27	24,60280	-82,6994	Florida Keys, East Of
USNM	97702	*P. dichotoma* (Esper, 1791)		16/set/92	17	17			Rosario Islands, Tesoro Island
USNM	97704	*P. grisea* Kunze, 1916		18/set/92	7	7			Rosario Islands, Tesoro Island
USNM	97705	*P. nutans* (D & M, 1860)		16/set/92	15	15			Rosario Islands, Tesoro Island
USNM	14376	*P. grisea* Kunze, 1916	Albatross R/V	2 May 1886			25,00000	-77	New Providence Island, Nassau
USNM	1248676	*P. grisea* Kunze, 1916		15/08/1964					La Blanquilla, lado occidental de arrecife
USNM	1214964	*P. nutans* (D & M, 1860)		19/jul/62					Florida Keys, off Elliott Key, Margot Fish Shoal
USNM	1214971	*P. nutans* (D & M, 1860)		05/jul/62					Florida Keys, Elliot Key, Margot

Table S1. Cont...

									Fish Shoal, south end of "Red Reef"
USNM	1214985	*P. dichotoma* (Esper, 1791)		1901					Florida Keys, Ragged Keys, Caesar's Creek
USNM	1214986	*P. dichotoma* (Esper, 1791)	Freelance R/V	08/abr/58	1	1			Anegada Island, Pomato Point, South Side Of Point
USNM	1214988	*P. dichotoma* (Esper, 1791)		Jan 1884					Between Johns Pass And Pass-A-Grille
USNM	1214990	*P. dichotoma* (Esper, 1791)							
USNM	1214991	*P. teres* Kunze, 1916		12/mai/12					Andros Island, Golding Key
USNM	1214992	*P. dichotoma* (Esper, 1791)		1884					Florida Keys, Key West, South Of
USNM	**1018041**	***P. rastrera* sp. nov.**		12/ago/02	12				Tobago, Cardinal Rock
USNM	**1018043**	***P. rastrera* sp. nov.**		07/ago/02	7	10			Tobago, Pirates Cove
USNM	**1018044**	***P. rastrera* sp. nov.**		14/ago/02	25				Tobago, Little Tobago Island
USNM	1018046	*P. nutans* (D & M, 1860)		17/ago/02	2				Tobago, southwestern part of Bay
USNM	**1018047**	***P. rastrera* sp. nov.**		07/ago/02	2				Tobago, southwestern part of Bay
USNM	1018050	*P. nutans* (D & M, 1860)		07/ago/02	7	10			Tobago, Pirates Cove
USNM	**1018051**	***P. rastrera* sp. nov.**		07/ago/02	7	10			Tobago, Pirates Cove
USNM	**1018052**	***P. rastrera* sp. nov.**		07/ago/02	7	10			Tobago, Pirates Cove
USNM	**1018053**	***P. rastrera* sp. nov.**		11/ago/02	12				Tobago, southwestern part of Bay
USNM	1018059	*P. nutans* (D & M, 1860)		11/ago/02	12				Tobago, southwestern part of Bay

Table S1. Cont...

USNM	1018060	*P. dichotoma* (Esper, 1791)		17/ago/02	2				Tobago, southwestern part of Bay
USNM	1018065	*P. dichotoma* (Esper, 1791)		14/ago/02	25				Tobago, Little Tobago Island
USNM	1018069	*P. grisea* Kunze, 1916		07/ago/02	4				Tobago, Pirates Cove
USNM	**1018074**	***P. rastrera sp. nov.***		17/ago/02	2				Tobago, southwestern part of Bay
USNM	1018075	*P. nutans* (D & M, 1860)		07/ago/02	7	10			Tobago, Pirates Cove
USNM	1018077	*P. nutans* (D & M, 1860)		07/ago/02	7	10			Tobago, Pirates Cove
USNM	1018078	*P. nutans* (D & M, 1860)		07/ago/02	7	10			Tobago, Pirates Cove
USNM	1017545	*P. nutans* (D & M, 1860)		07/ago/02	7	10			Tobago, Pirates Cove
USNM	1017722	*P. dichotoma* (Esper, 1791)		07/ago/02	7	10			Tobago, Pirates Cove
USNM	1211249	*P. nutans* (D & M, 1860)	Pillsbury R/V	20/jul/69	22	22	17,25830	-62,0367	West of
USNM	1007394	*P. teres* Kunze, 1916		12/jul/00	10				Exuma Cays, White Horse
USNM	1007399	*P. nutans* (D & M, 1860)		12/jul/00	15				Exuma Cays, White Horse
USNM	1007506	*P. dichotoma* (Esper, 1791)		12/jul/00	10				Exuma Cays, White Horse
USNM	1150975	*P. nutans* (D & M, 1860)		18/jul/07	5		9,32694	-82,20389	Bocas del Toro, Solarte, north side
USNM	1122672	*P. dichotoma* (Esper, 1791)		21/out/07	24		17,47950	-63,2265	Saba Bank
USNM	1122673	*P. grisea* Kunze, 1916		22/out/07	18		16,94590	-63,2442	Saba Bank
USNM	1122674	*P. nutans* (D & M, 1860)		22/out/07	30		17,47020	-63,2218	Saba Bank
USNM	1122675	*P. nutans* (D & M, 1860)		22/out/07	30		17,47020	-63,2218	Saba Bank
USNM	1145229	*P. grandiflora* Verrill, 1912		May 1958					Abrolhos Islands
USNM	1124508	*P. nutans* (D & M, 1860)		Mar 1968					La Blanquilla, south side
USNM	1125142	*P. dichotoma* (Esper, 1791)		Dec 1964					La Blanquilla, SE side
USNM	1150976	*P. nutans* (D & M, 1860)		19/jul/07	8		9,32694	-82,20389	Bocas del Toro, Solarte, north side

Table S1. Cont...

USNM	1207446	*P. nutans* (D & M, 1860)	El Torito R/V						
USNM	1207448	*P. nutans* (D & M, 1860)	Pillsbury R/V	21/mar/68	35	37	15,98670	-86,0333	Castilla Point, SW of
USNM	1207449	*P. nutans* (D & M, 1860)	Pillsbury R/V	01/fev/71	18	18	15,25000	-81,85	Media Luna Reef, East of
USNM	1241894	*P. dichotoma* (Esper, 1791)							Port Royal, reefs south of
USNM	1236119	*P. dichotoma* (Esper, 1791)		Jul 1974					Swan Islands, Swan Island
USNM	1236120	*P. nutans* (D & M, 1860)		Jul 1974					Swan Islands, Swan Island
USNM	1237805	*P. dichotoma* (Esper, 1791)							
USNM	1237807	*P. dichotoma* (Esper, 1791)							
USNM	1237814	*P. grisea* Kunze, 1916							
USNM	1150972	*P. dichotoma* (Esper, 1791)		21/jul/07	7		9,25150	-82,12578	Bocas del Toro, Crawl Cay
USNM	1150973	*P. nutans* (D & M, 1860)		20/jul/07	5	7	9,33461	-82,23606	Bocas del Toro, Carenaro
USNM	1021374	*P. nutans* (D & M, 1860)		17/ago/02	2				Tobago, south western part of bay
USNM	5261	*P. grandiflora* Verrill, 1912	Hartt Expedition	1876			-12,78000	-38,43	Mapele
USNM	5262	*P. dichotoma* (Esper, 1791)	Hartt Expedition	1876			-12,78000	-38,43	Mapele
USNM	5263	*P. grandiflora* Verrill, 1912	Hartt Expedition	1876					
USNM	5260	*P. dichotoma* (Esper, 1791)	Hartt Expedition	1876			-12,78000	-38,43	Mapele
USNM	52001	*P. dichotoma* (Esper, 1791)		25/ago/60	6,1	9,2			St. George's Island, Fort St. Catherine, Near Fort St. Catherine
USNM	52002	*P. dichotoma* (Esper, 1791)		25/ago/60	6	9			St. George's Island, Fort St. Catherine
USNM	5317	*P. dichotoma* (Esper, 1791)	Hartt Expedition	1876			-12,78000	-38,43	Mapele
USNM	52003	*P. dichotoma* (Esper, 1791)		25/ago/60	6	9			St. George's Island, Fort St. Catherine
USNM	52004	*P. dichotoma* (Esper, 1791)		03/set/60	24	27			Bermuda Island, Southampton,

Table S1. Cont...

									Off South Shore
USNM	52000	*P. dichotoma* (Esper, 1791)		25/ago/60	6,1	9,2			St. George's Island, Fort St. Catherine, Near Fort St. Catherine
USNM	88807	*P. grisea* Kunze, 1916	Marsys Resolute R/V	10/jun/84	12,2	13,7			East Of Gibbs And Round Cays
USNM	88808	*P. grisea* Kunze, 1916	Marsys Resolute R/V	Jun 1984	5,5	5,5			Round Cay, West Of
USNM	88814	*P. dichotoma* (Esper, 1791)	Marsys Resolute R/V	06/jun/84	1	1,5			Gibbs Cay, SW Of
USNM	88797	*P. nutans* (D & M, 1860)	Marsys Resolute R/V	10/jun/84	12,2	13,7			East Of Gibbs And Round Cays
USNM	5265	*P. grandiflora* Verrill, 1912	Hartt Expedition	1876					Candeias, Reef
USNM	51893	*P. dichotoma* (Esper, 1791)		10/out/60					Miami, Biscayne Bay, Soldier Key & Caesars Creek
USNM	5269	*P. grandiflora* Verrill, 1912	Hartt Expedition	1876					
USNM	52316	*P. teres* Kunze, 1916		May 1912					
USNM	5270	*P. grandiflora* Verrill, 1912	Hartt Expedition	1876					
USNM	59166	*P. dichotoma* (Esper, 1791)	CCRE, Belize	Apr 1979	4,6	4,6	16,80000	-88,08	Carrie Bow Cay, Site A Patch Reef
USNM	5266	*P. dichotoma* (Esper, 1791)	Hartt Expedition	1876					Candeias, Reef
USNM	5275	*P. grandiflora* Verrill, 1912		1876			-12,95000	-38,62	Mar Grande
USNM	51743	*P. dichotoma* (Esper, 1791)		Aug 1960					St. Croix Island, Buck Island
USNM	5272	*P. grandiflora* Verrill, 1912		1876			-12,95000	-38,62	Mar Grande
USNM	5268	*P. grandiflora* Verrill, 1912	Hartt Expedition	1876					
USNM	59486	*P. grisea* Kunze, 1916		1978	1,8	4,6			South Caicos Island
USNM	51744	*P. dichotoma* (Esper, 1791)		10/out/60					Miami, Biscayne Bay, Soldier Key & Caesars Creek
USNM	86026	*P. nutans* (D & M, 1860)	SOFLA	08/dez/82	16	16	25,29440	-81,8	Cape Sable, West Of
USNM	51970	*P. dichotoma* (Esper, 1791)		25/ago/60	6,1	9,2			St. George's Island, Fort St.

Table S1. Cont...

									Catherine, Near Fort St. Catherine
USNM	5313	*P. grandiflora* Verrill, 1912		1876			-12,95000	-38,62	Mar Grande
USNM	51971	*P. grandiflora* Verrill, 1912		25/ago/60	6,1	9,2			St. George's Island, Fort St. Catherine
USNM	5279	*P. grandiflora* Verrill, 1912	Hartt Expedition	1876			-12,78000	-38,43	Mapele
USNM	52411	*P. dichotoma* (Esper, 1791)		12/jul/60					Campeche Bank, Alacran Reef, Halfway Between Desertora And Perez Islands
USNM	5277	*P. grandiflora* Verrill, 1912		1876			-12,95000	-38,62	Mar Grande
USNM	51974	*P. dichotoma* (Esper, 1791)		25/ago/60	6,1	9,2			St. George's Island, Fort St. Catherine
USNM	5312	*P. grandiflora* Verrill, 1912		1876			-12,95000	-38,62	Mar Grande
USNM	51976	*P. dichotoma* (Esper, 1791)		07/out/60					Miami, Biscayne Bay, Soldier Key & Caesars Creek, Seaward Side
USNM	52408	*P. dichotoma* (Esper, 1791)		11/jul/60	1	2			Campeche Bank, Alacran Reef
USNM	5314	*P. grandiflora* Verrill, 1912		1876			-12,95000	-38,62	Mar Grande
USNM	75597	*P. grandiflora* Verrill, 1912		29/nov/82					Abrolhos Islands, Paredes Reefs, S Side Of Lixa Reef
USNM	75596	*P. grandiflora* Verrill, 1912		06/jul/82					Joao Pessoa, Picaozinho Reef, Tambau
USNM	75598	*P. grandiflora* Verrill, 1912		04/dez/82					Abrolhos Islands, Paredes Reefs, Vigilante, Lixa Reef
USNM	75599	*P. grandiflora* Verrill, 1912		03/dez/82					Abrolhos Islands, Sueste Island
USNM	85980	*P. nutans* (D & M, 1860)	SOFLA	08/dez/82	16	16	25,29440	-81,8	Cape Sable, West Of

Table S1. Cont...

USNM	85981	*P. nutans* (D & M, 1860)	SOFLA	01/jun/83	17	17	26,05310	-82,1408	Naples, SW Of
USNM	75595	*P. grandiflora* Verrill, 1912		13/out/82	1,5	4			Sao Joao Da Barra, Baixio Dos Moleques, Mouth Of Itabapoana River
USNM	1150974	*P. nutans* (D & M, 1860)		18/jul/07	5		9,32694	-82,20389	Bocas del Toro, Solarte, north side
USNM	75238	*P. dichotoma* (Esper, 1791)	Albatross R/V	2 May 1886			25,00000	-77	New Providence Island, Nassau
USNM	14390	*P. dichotoma* (Esper, 1791)	Albatross R/V	2 May 1886			25,00000	-77	New Providence Island, Nassau
USNM	14392	*P. dichotoma* (Esper, 1791)	Albatross R/V	2 May 1886			25,00000	-77	New Providence Island, Nassau
USNM	91930	*P. dichotoma* (Esper, 1791)	Albatross R/V	2 May 1886			25,00000	-77	New Providence Island, Nassau
USNM	1151024	*P. nutans* (D & M, 1860)		Jul 2007					Bocas del Toro
USNM	1150961	*P. nutans* (D & M, 1860)		28/jul/07	5	14	9,25150	-82,12578	Bocas del Toro, Crawl Cay
USNM	1207447	*P. nutans* (D & M, 1860)							Discovery Bay
USNM	1207451	*P. nutans* (D & M, 1860)		Nov 1964	47				Discovery Bay
USNM	1207452	*P. nutans* (D & M, 1860)		26/fev/69	38				Curacao, Piscadera Bay
USNM	1237521	*P. nutans* (D & M, 1860)		Nov 1969	47	47			Discovery Bay
USNM	1237522	*P. nutans* (D & M, 1860)		23/fev/69					Curacao, Piscadera Bay
USNM	1237800	*P. nutans* (D & M, 1860)		Nov 1969	47	47			Discovery Bay
USNM	50715	*P. dichotoma* (Esper, 1791)	Albatross R/V	2 May 1886			25,00000	-77	Bahamas
USNM	14375	*P. dichotoma* (Esper, 1791)	Albatross R/V	2 May 1886			25,00000	-77	Bahamas

Table S1. Cont...

USNM	50418	*P. dichotoma* (Esper, 1791)		05/jul/15	1	5	18,31750	-64,9142	Virgin Islands of the United States
USNM	53559	*P. grisea* Kunze, 1916	CCRE, Belize	27/abr/72	1	1,5	16,77000	-88,05	Belize
USNM	53560	*P. grisea* Kunze, 1916	CCRE, Belize	29/abr/72	1,5	1,5	16,77000	-88,05	Belize
USNM	1188440	*P. dichotoma* (Esper, 1791)	CCRE, Belize	19/abr/72	1	2	16,77000	-88,05	Belize
USNM	1158735	*P. nutans* (D & M, 1860)	CCRE, Belize	03/jul/72	23	30	17,17000	-87,93	Belize
USNM	1158721	*P. nutans* (D & M, 1860)	CCRE, Belize	03/jul/72	23	30	17,17000	-87,93	Belize
USNM	59466	*P. grisea* Kunze, 1916	CCRE, Belize	Apr 1980			16,80000	-88,08	Belize
USNM	59465	*P. grisea* Kunze, 1916	CCRE, Belize	Apr 1980			16,80000	-88,08	Belize
USNM	1234926	*P. nutans* (D & M, 1860)	Pillsbury R/V	03/jul/69	27	27	12,11670	-61,5417	Grenada
ZMB	**5961**	***P. curvata* Kunze, 1916**							Barbados
ZMB	5962	*P. dichotoma* (Esper, 1791)							
ZMB	5966	*P. dichotoma* (Esper, 1791)							
ZMB	**5964**	***P. tenuis* Kunze, 1916**							St. Thomas
ZMB	5967	*P. nutans* (D & M, 1860)							St. Thomas
ZMB	5962	*P. dichotoma* (Esper, 1791)							
YPM	**4501**	***P. grandiflora* Verrill, 1912**	Rathbun - Hartt Expedition	1876					Mar Grande, Bahia
YPM	**4503**	***P. verrucosa* Verrill, 1912**	Rathbun - Hartt Expedition						Candeias reef, Pernambuco
YPM	**4509**	***P. obesa* Verrill, 1912**	Branner - Hartt Expedition	1876					Fernando de Noronha Archipelago
ZMB	**5963**	***P. fusifera* Kunze, 1916**							Barbados
ZMB	**5965**	***P. grisea* Kunze, 1916**							Barbados
YPM	**1598**	***P. braziliana* Verrill, 1912**	Hartt - Hartt Expedition	1867					Abrolhos Archipelago, Bahia
YPM	**4502**	***P. pumila* Verrill, 1912**	Rathbun - Hartt Expedition	1876					Periperi, Bahia
YPM	**1597**	***P. cylindrica* Verrill, 1912**	Hartt - Hartt Expedition	1867					Abrolhos Archipelago, Bahia
SMF	**5808**	***G. dichotoma* Esper, 1788**							South American Islands

Table S1. Cont...

MCZ	**67508** **(slide)**	***G. dichotoma Esper, 1788***							South American Islands
MCZ	**Alcy-103**	***Plexaurella teres* Kunze, 1916**							
MCZ	67664	*P. grandiflora* Verrill, 1912							Brazil
MCZ	**67516**	***Eunicea anceps D & M, 1860***							

SUPPLEMENTARY FIGURES

FIGURE S1. Sclerites of *Plexaurella dichotoma* (USNM 1122672) from Netherlands Antilles. A: butterflies from middle layer; B: sclerites from axial layer; C: cortical sclerites; D: rods from polyp body wall.

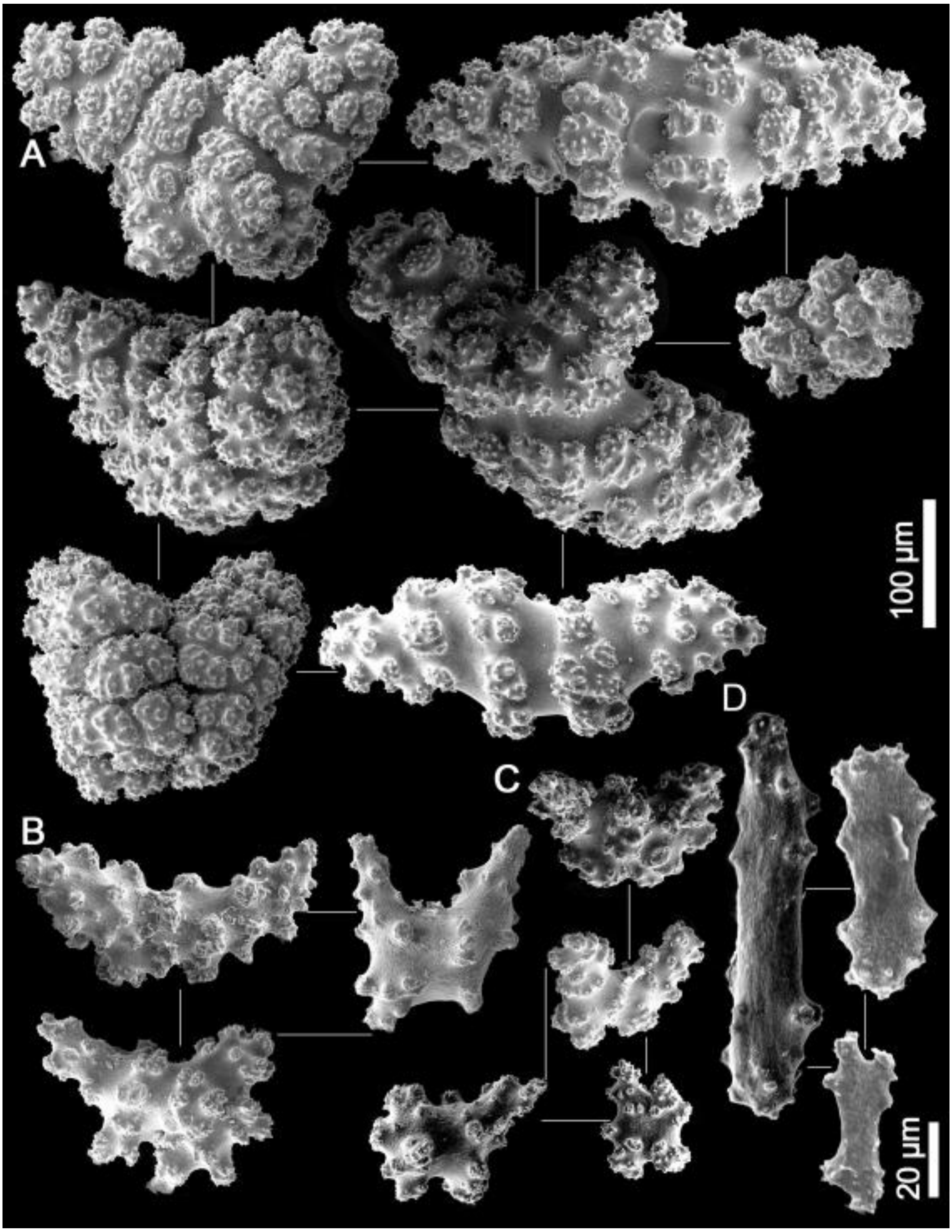

FIGURE S2. Sclerites of *Plexaurella dichotoma* (USNM 7525) from Jamaica. A: butterflies from middle layer; B: cortical sclerites; C: butterflies from axial layer; E: cortical sclerites.

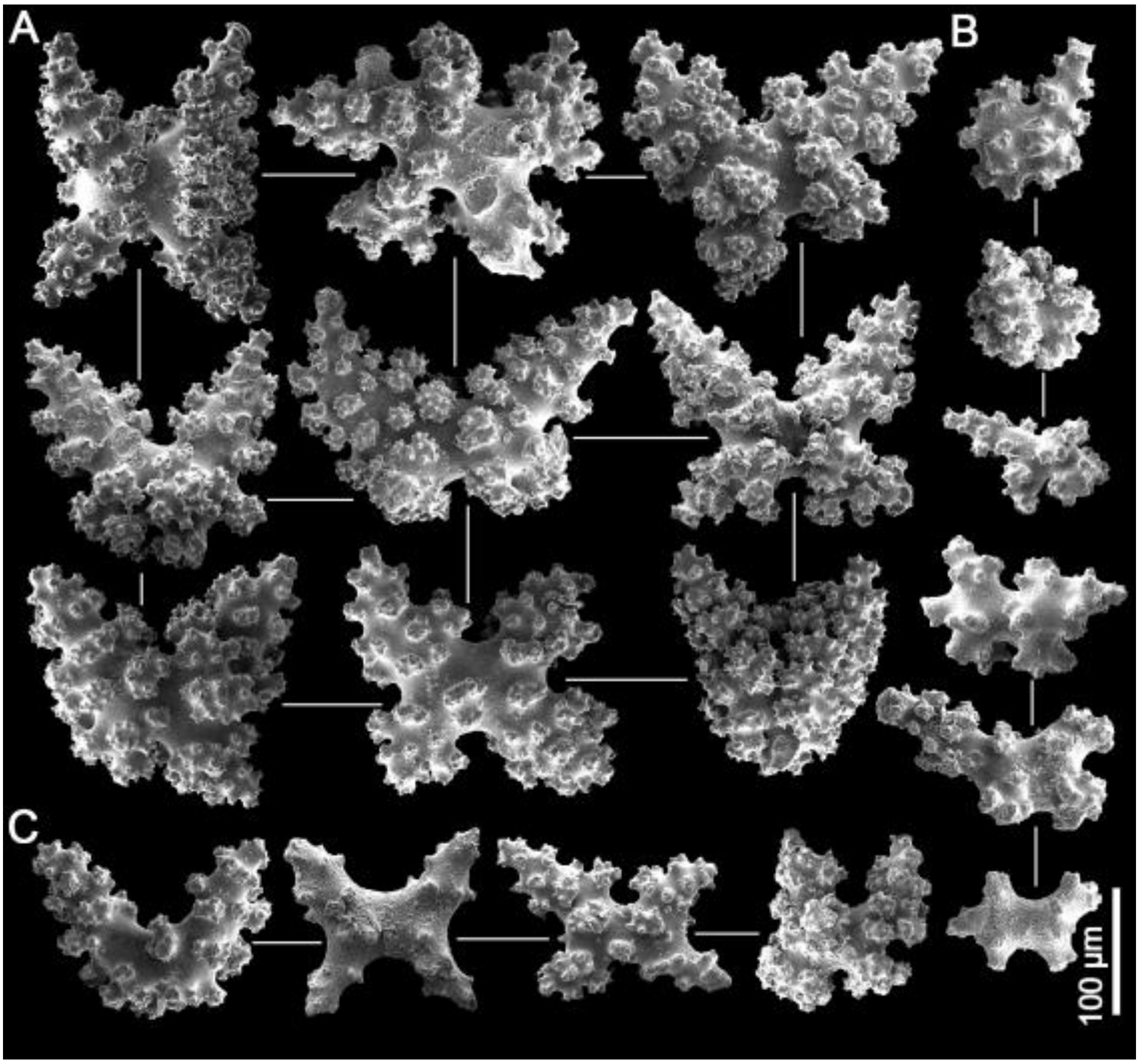

FIGURE S3. Sclerites of *Plexaurella dichotoma* (USNM 50711) from Ensenada De Cajon, Cuba. A: butterflies from middle layer; B: sclerites from axial layer; C: cortical sclerites.

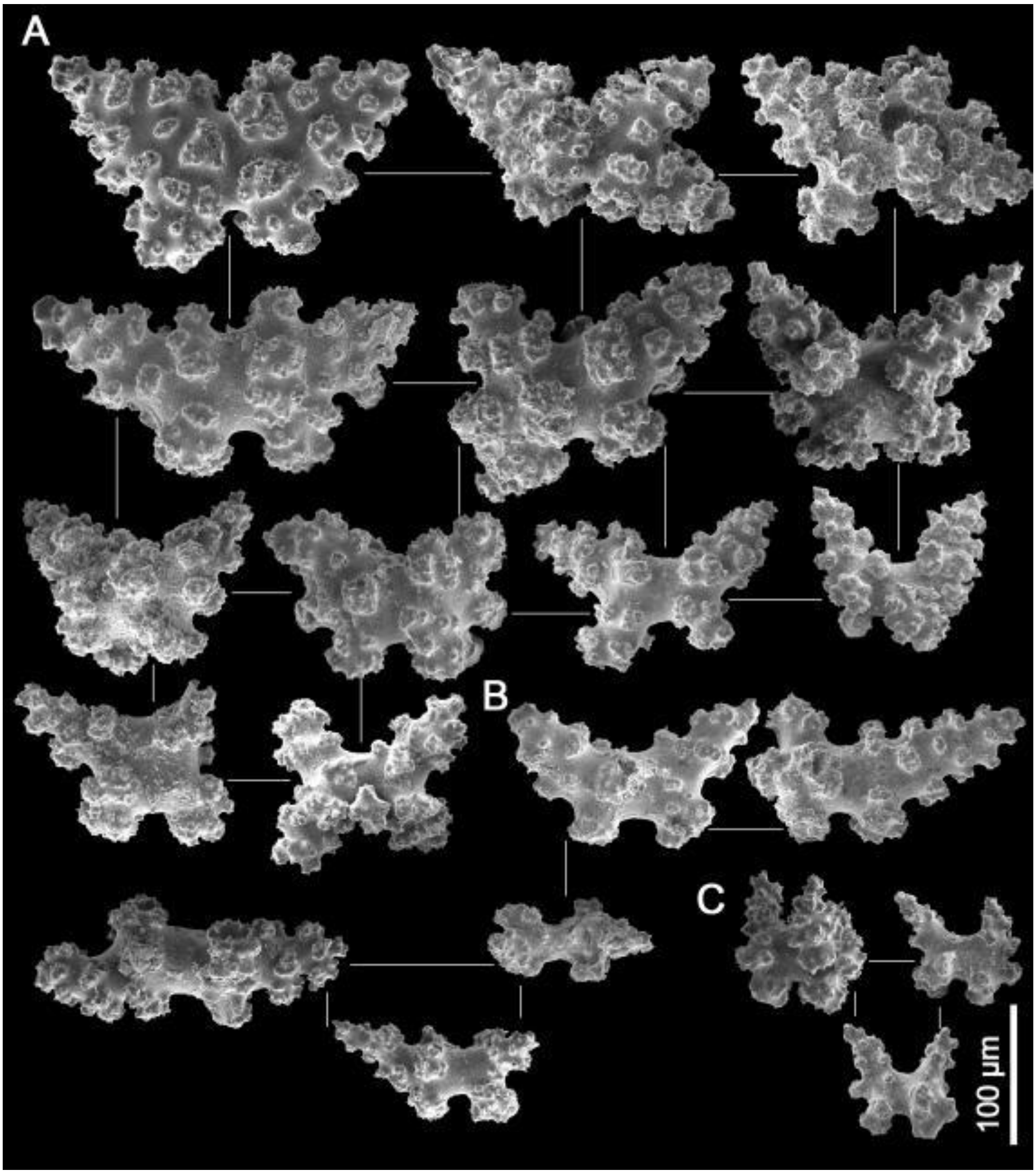

FIGURE S4. Sclerites of *Plexaurella dichotoma* (USNM 50602) from Florida. A: butterflies from middle layer; B: spindles from middle layer; C: tri-radiates from middle layer; D: irregular butterflies from axial layer; E: sclerites from cortical layer.

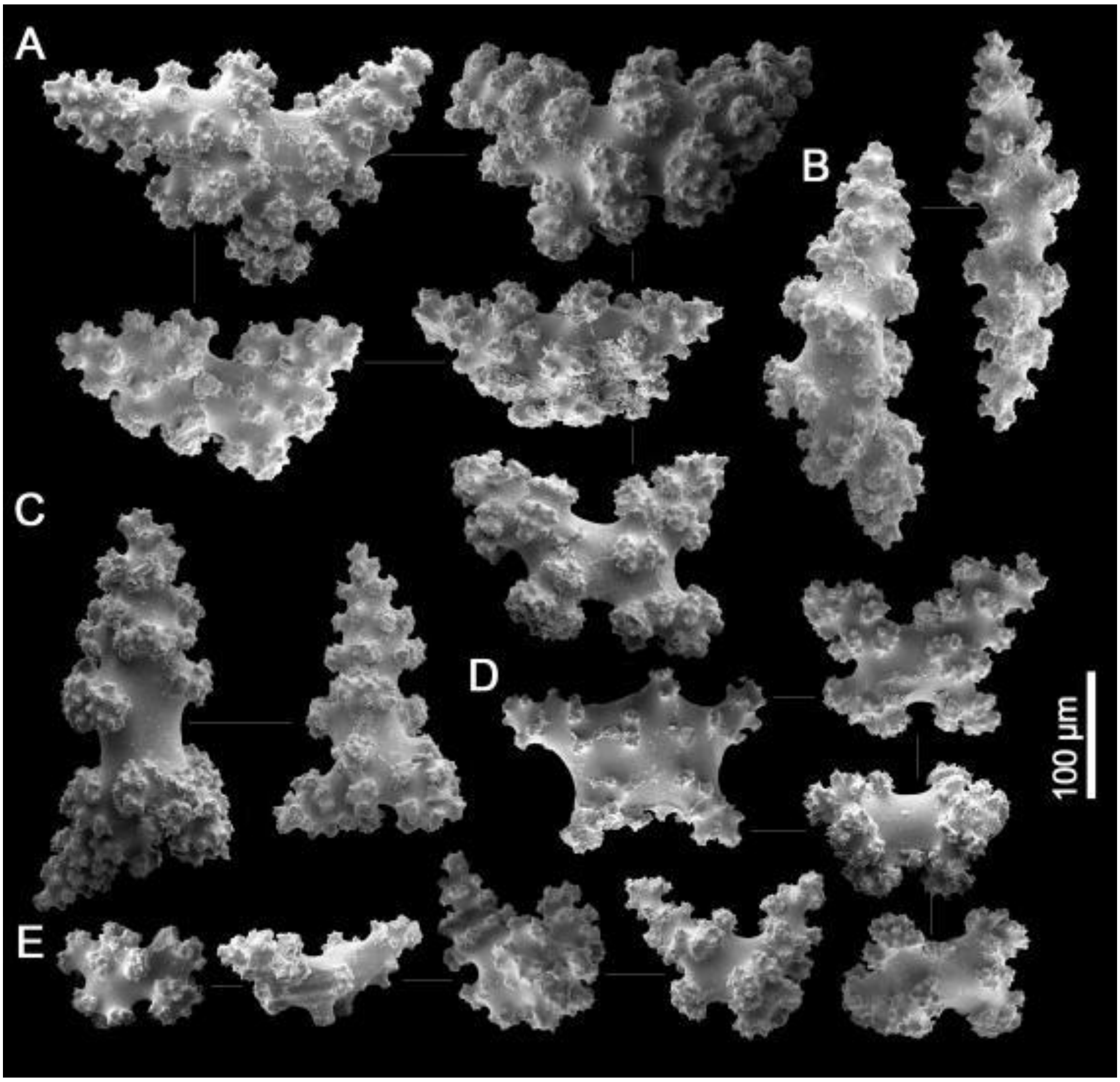

FIGURE S5. Sclerites of *Plexaurella teres* (USNM 79366) from Bahamas. A: butterflies from middle layer; B: tri-radiate from middle layer; C: sclerites from axial layer; D: cortical sclerites.

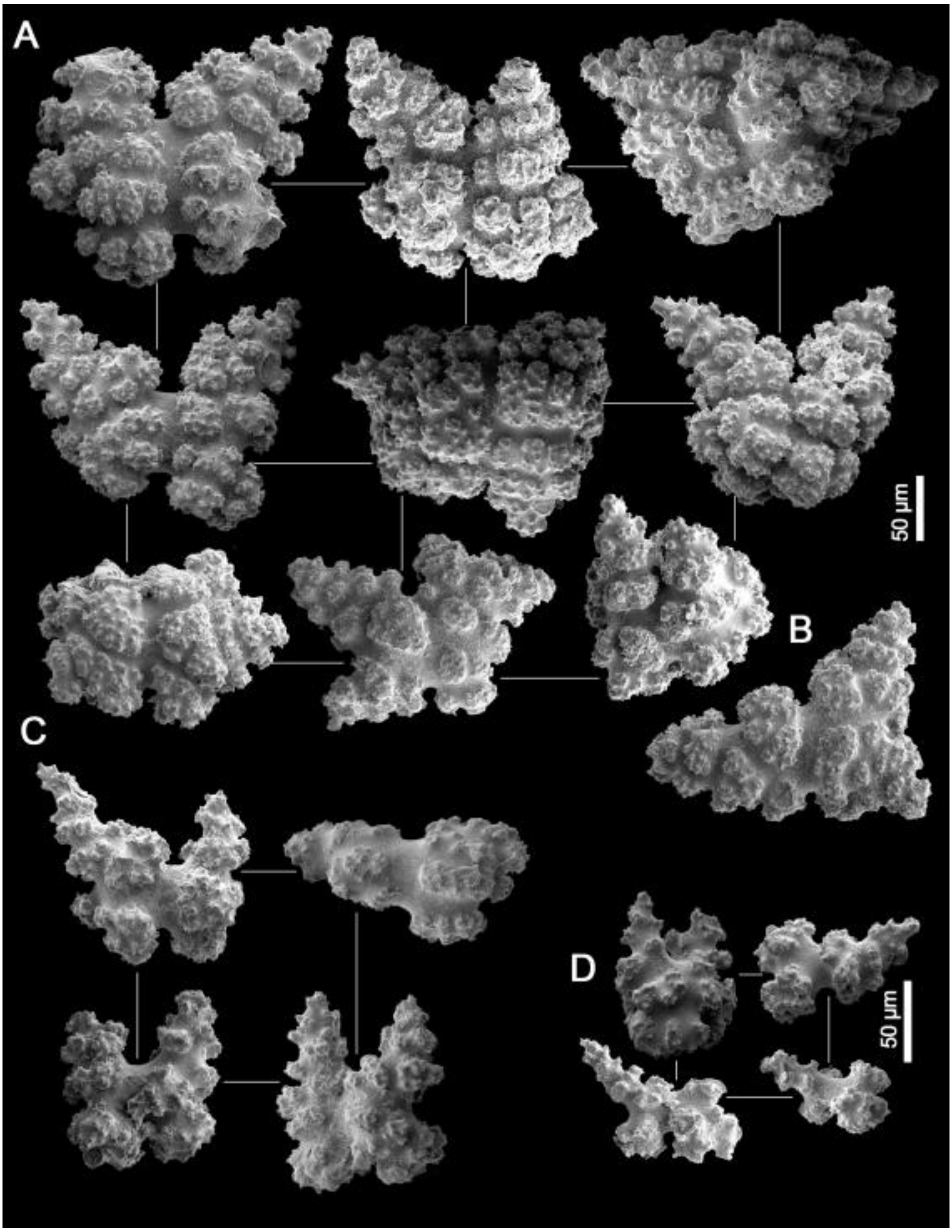

FIGURE S6. Sclerites of *Plexaurella teres* (USNM 84093) from West of Cape Sable (Gulf of Mexico, Florida). A: butterflies from middle layer; B: spindle from middle layer; C: sclerites from axial layer; D: cortical sclerites.

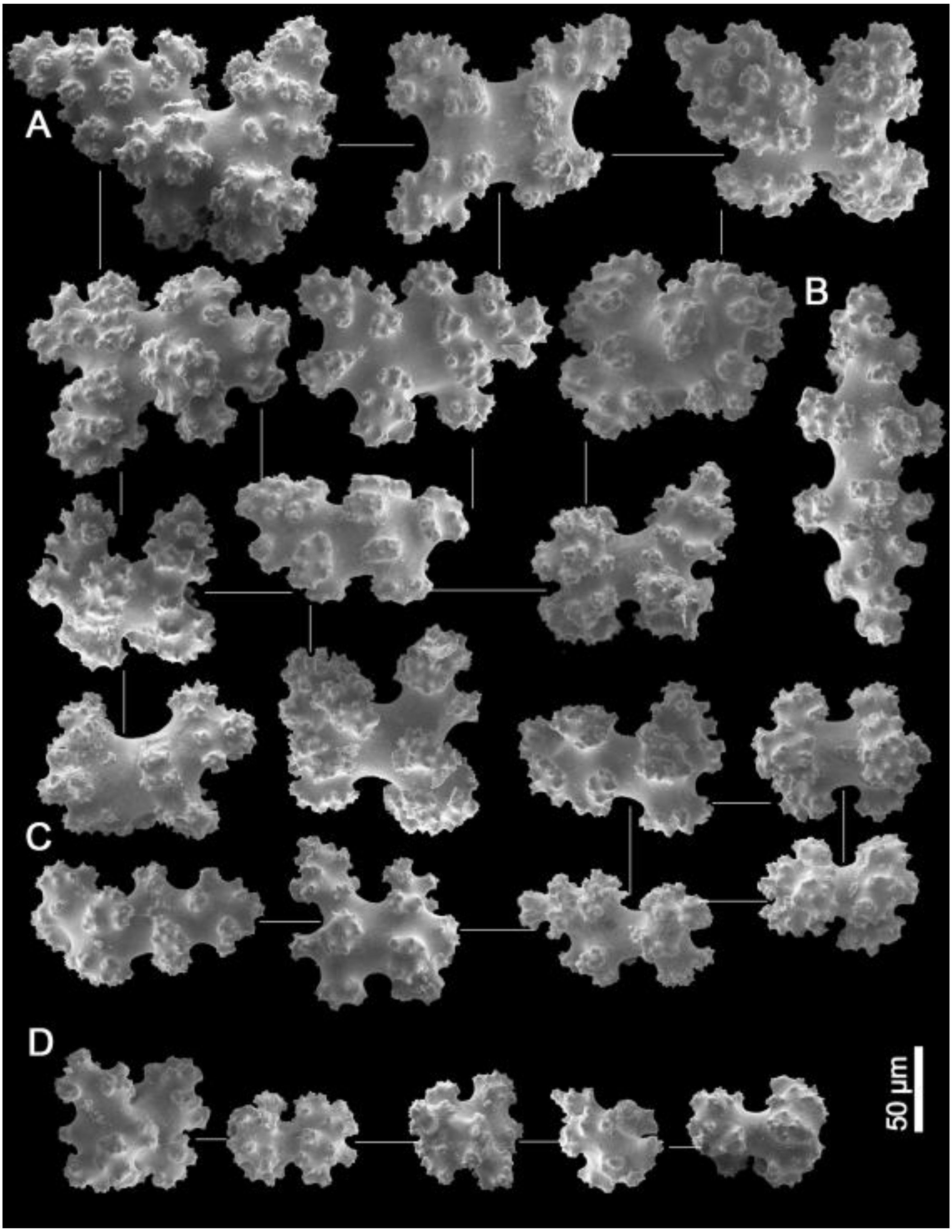

FIGURE S7**.** Sclerites of *Plexaurella teres* (USNM 50962) from Antigua and Barbuda. A: butterflies and sixradiates from middle layer; B: triradiate from middle layer; C: sclerites from axial layer; D: sclerites from cortical layer.

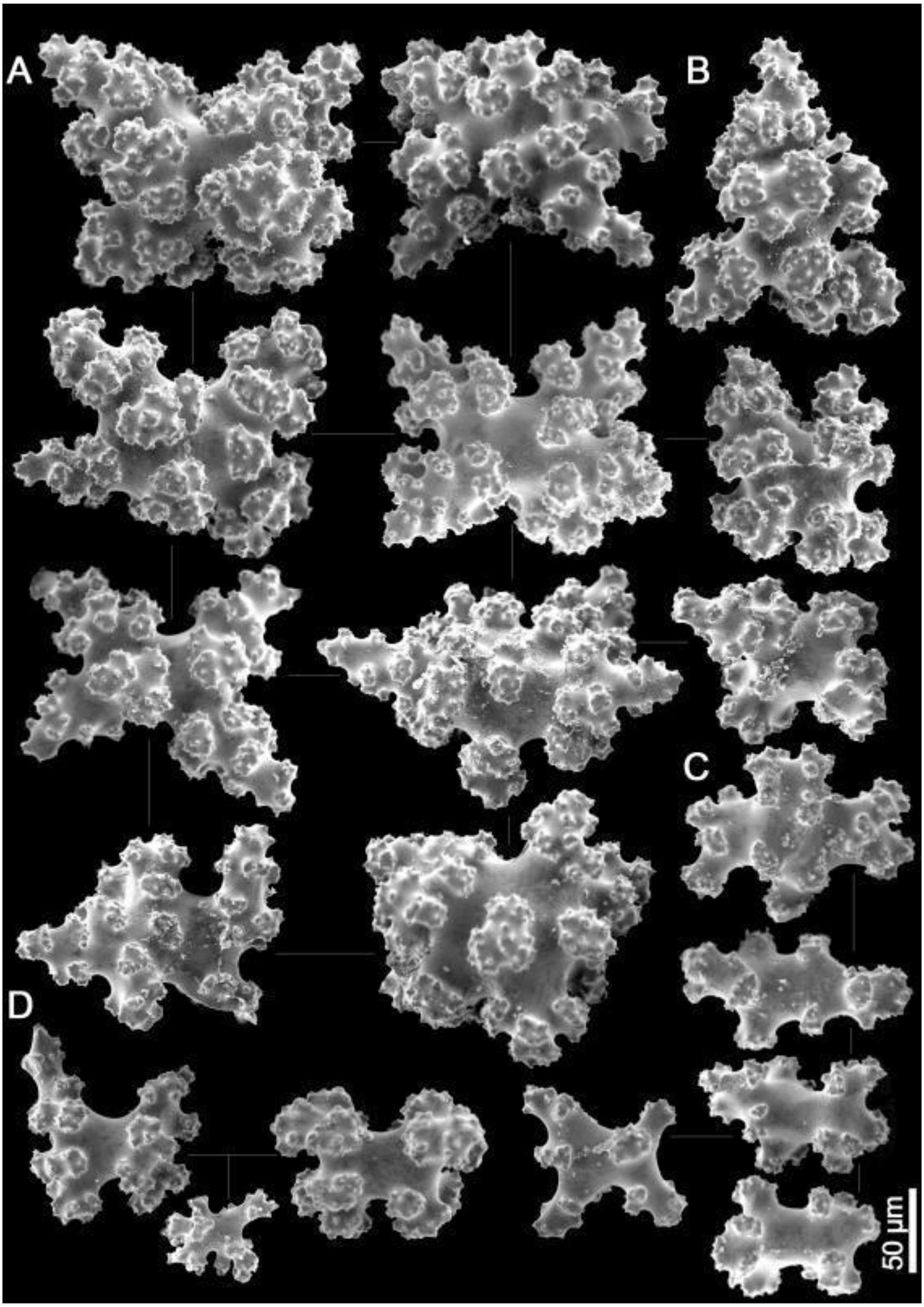

FIGURE S8. Sclerites of *Plexaurella teres* (USNM 50688) from Swan Islands, Honduras. A: butterflies from middle layer; B: tri-radiates from middle layer; C: sclerites from axial layer; D: cortical sclerites.

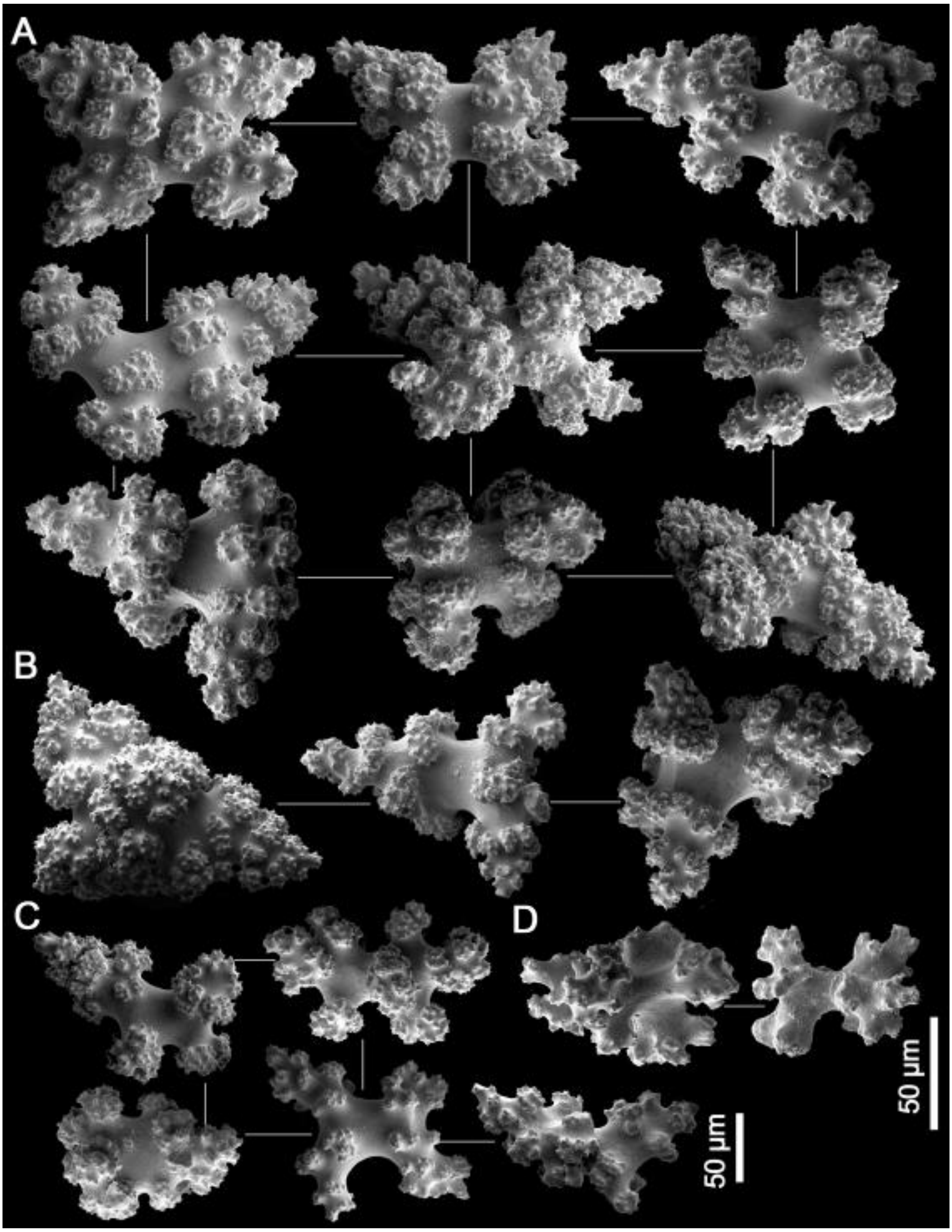

FIGURE S9. Sclerites of *Plexaurella teres* (USNM 84095) from West of Cape Sable (Gulf of Mexico, Florida). A: butterflies from middle layer; B: spindle from middle layer; C: sclerites from axial layer; D: cortical sclerites.

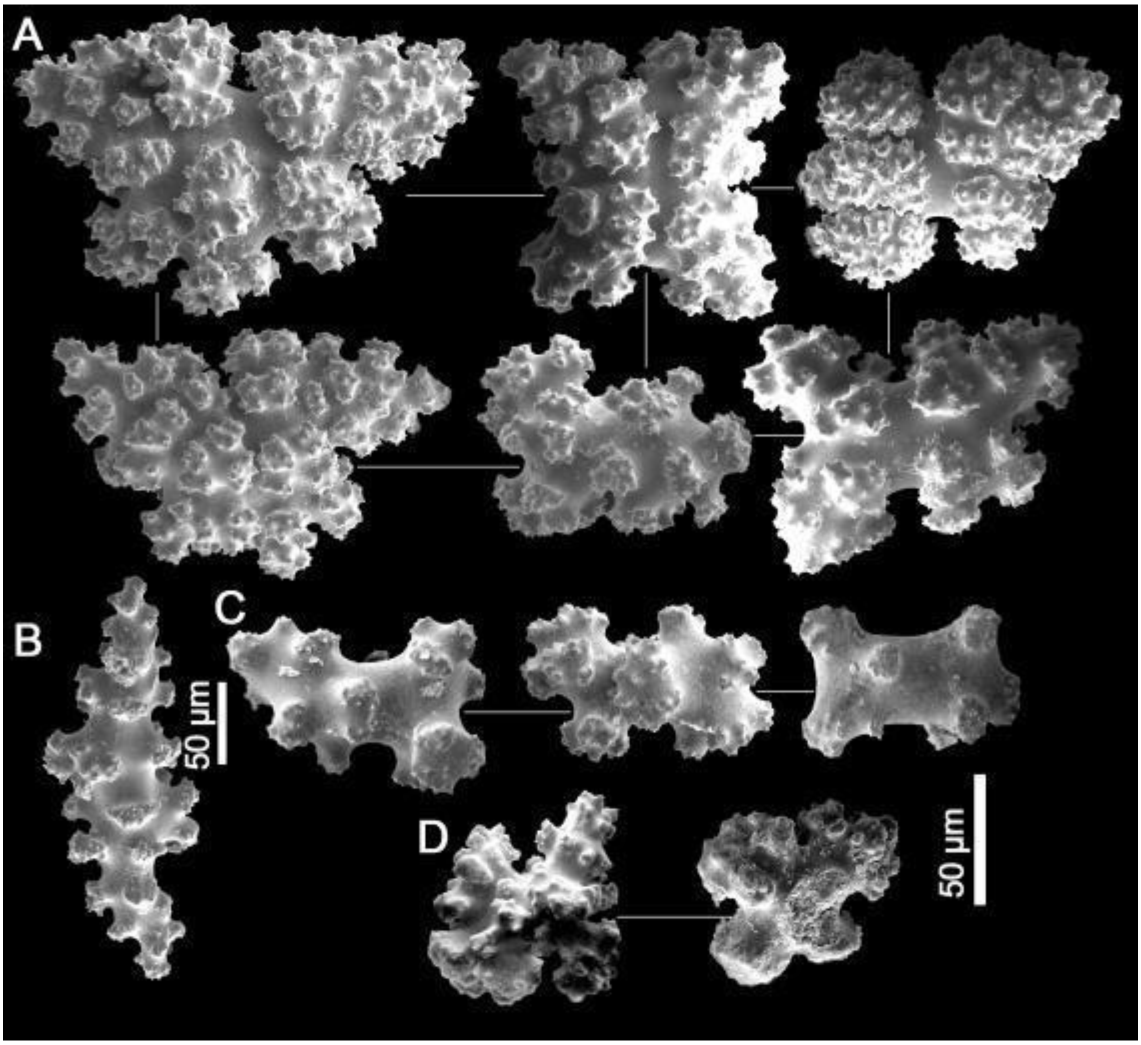

FIGURE S10. Sclerites of *Plexaurella teres* (USNM 50534) from St. Kitts and Nevis. A: butterflies from middle layer; B: cortical sclerites; C: sclerites from axial layer.

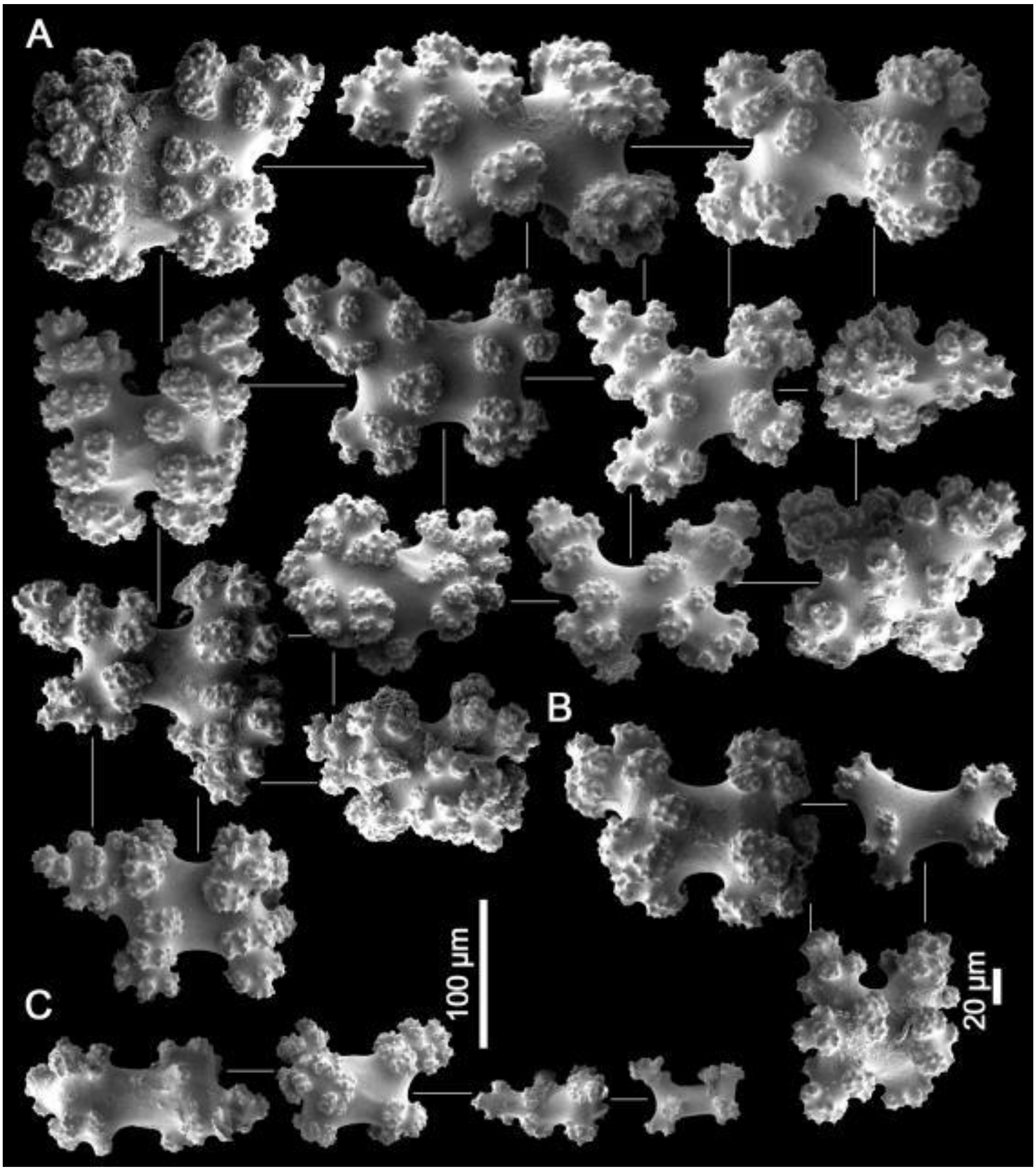

FIGURE S11. Sclerites of *Plexaurella grisea* (USNM 7523) from Jamaica. A: butterflies from middle layer; B: tri-radiates from middle layer; C: cortical sclerites; D: butterflies from axial layer.

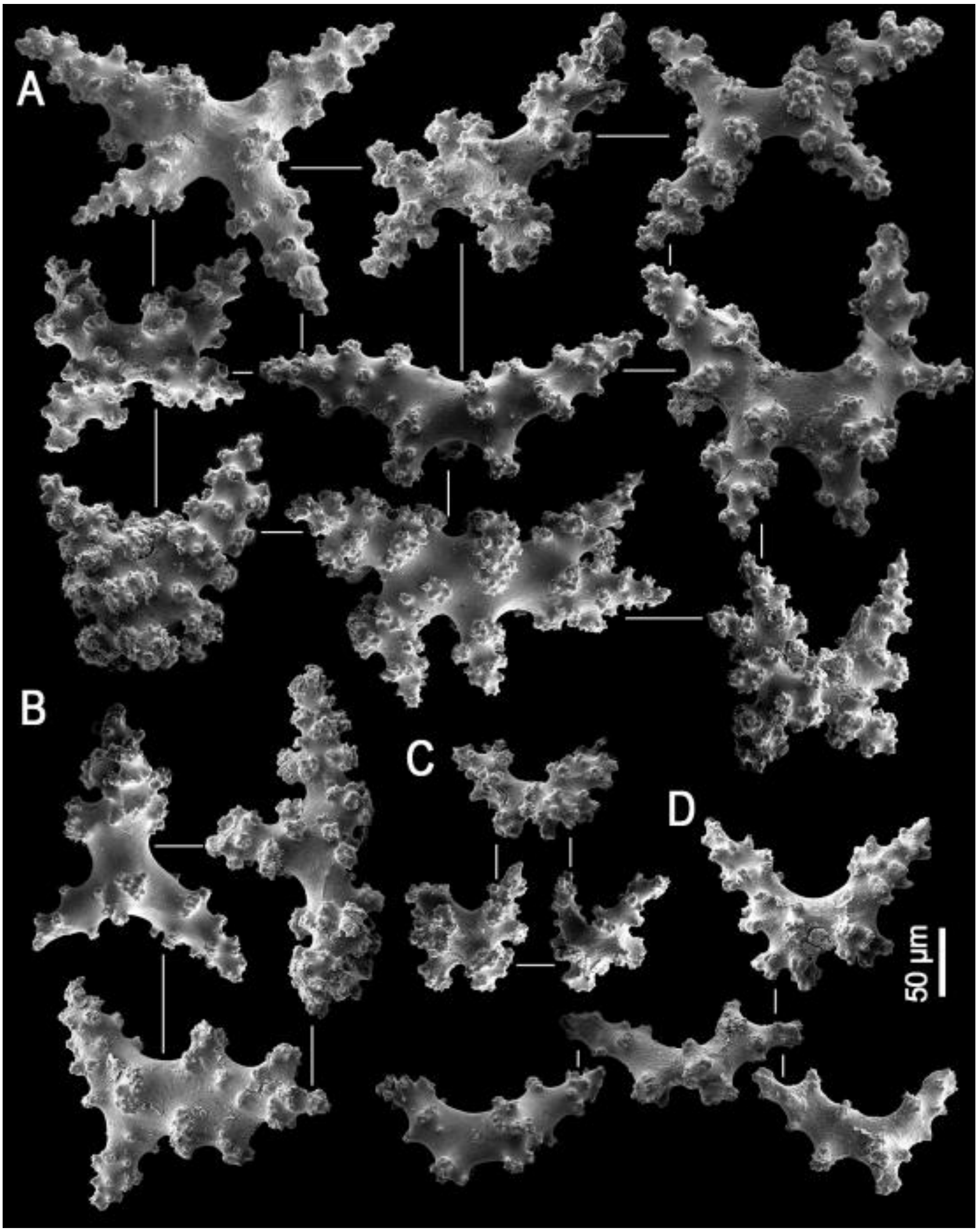

FIGURE S12. Sclerites of *Plexaurella grisea* (USNM 1248676) from Venezuela. A: butterflies from middle layer; B: axial sclerites; C: sclerite from cortex.

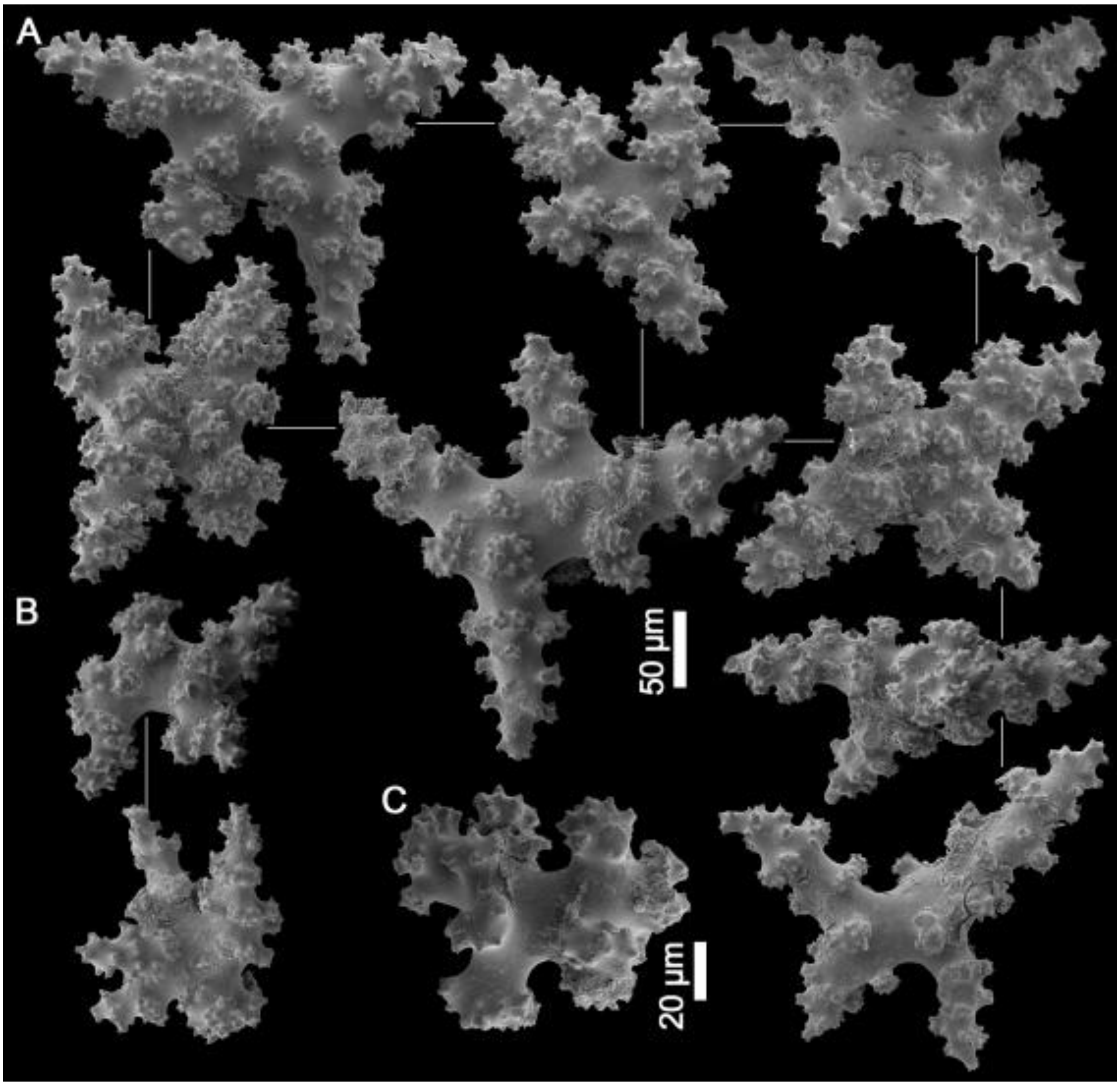

FIGURE S13. Sclerites of *Plexaurella grisea* (ZMB 5961 – holotype of *P. curvata*) (?Barbados). A: regular butterflies from middle layer, with two pair of arms equal in size; B: tuberculated spindles from middle layer; C: irregular butterflies from middle layer; D: sclerites from axial layer; E: sclerites from cortical layer.

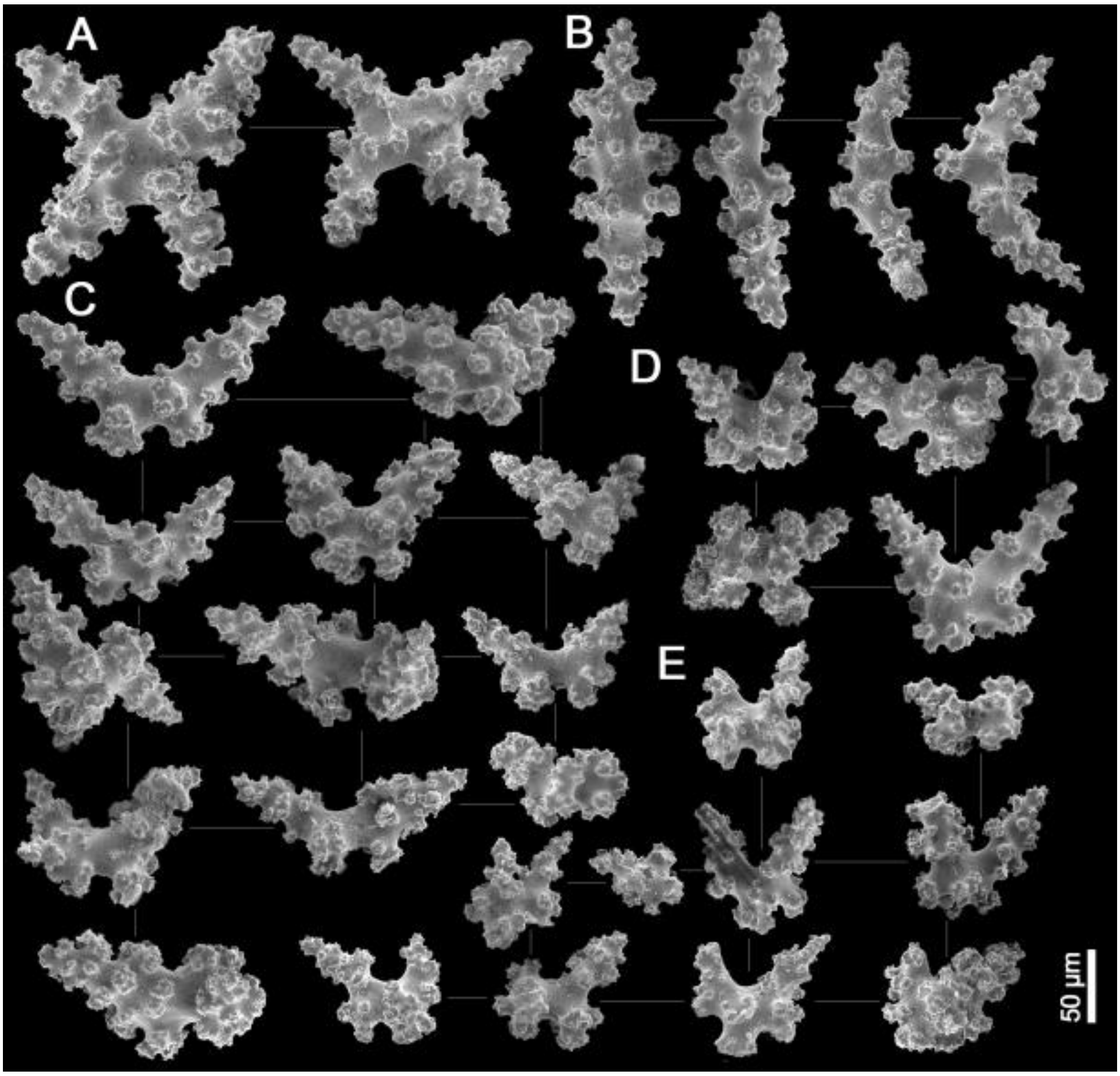

FIGURE S14. Sclerites of *Plexaurella grisea* (USNM 7524) from Jamaica. A: butterflies from middle layer; B: cortical sclerites C: sclerites from axial layer.

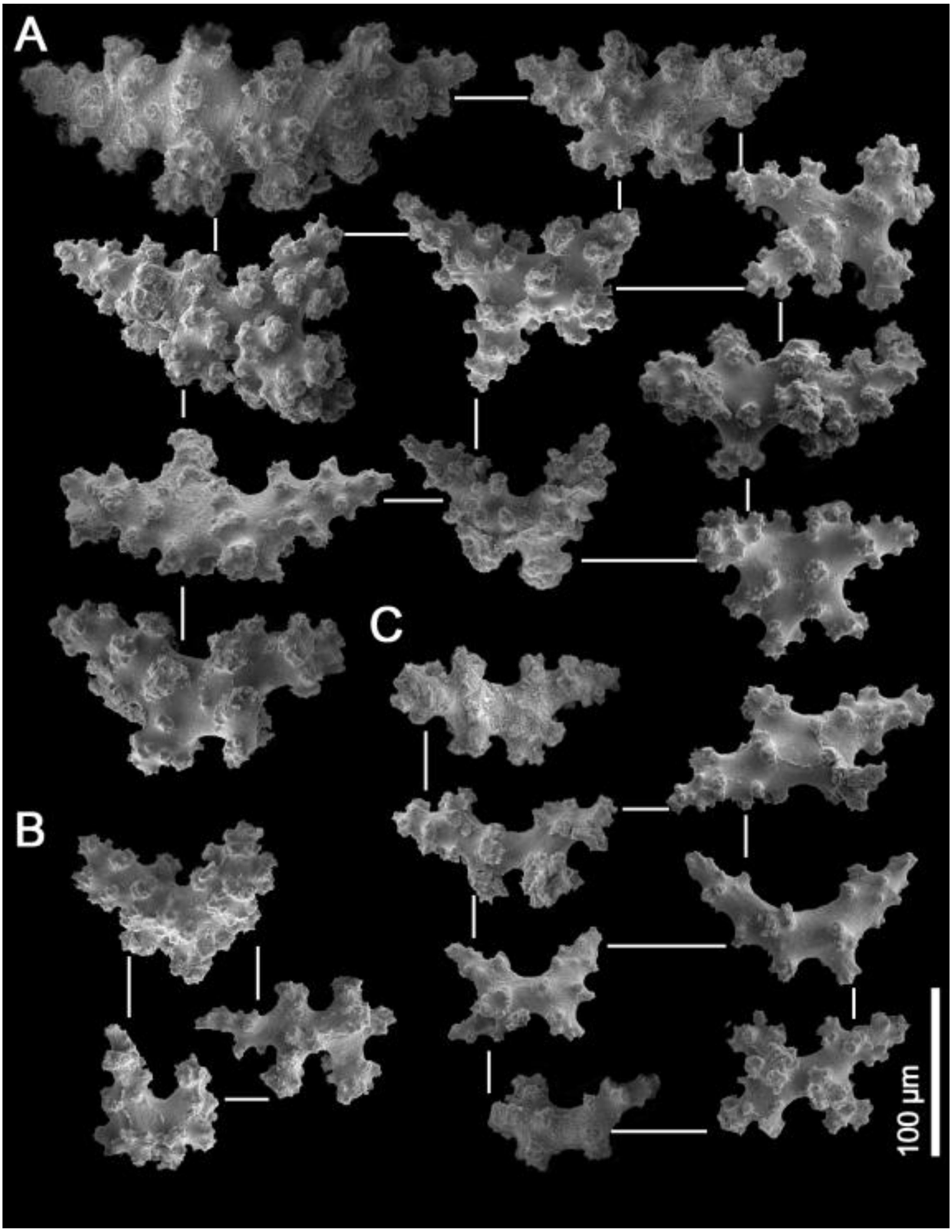

FIGURE S15. Sclerites of *Plexaurella grisea* (USNM 54940) from Jamaica. A: butterflies from middle layer; B: spindles and tri-radiates from middle layer; C: axial sclerites; D: cortical sclerites.

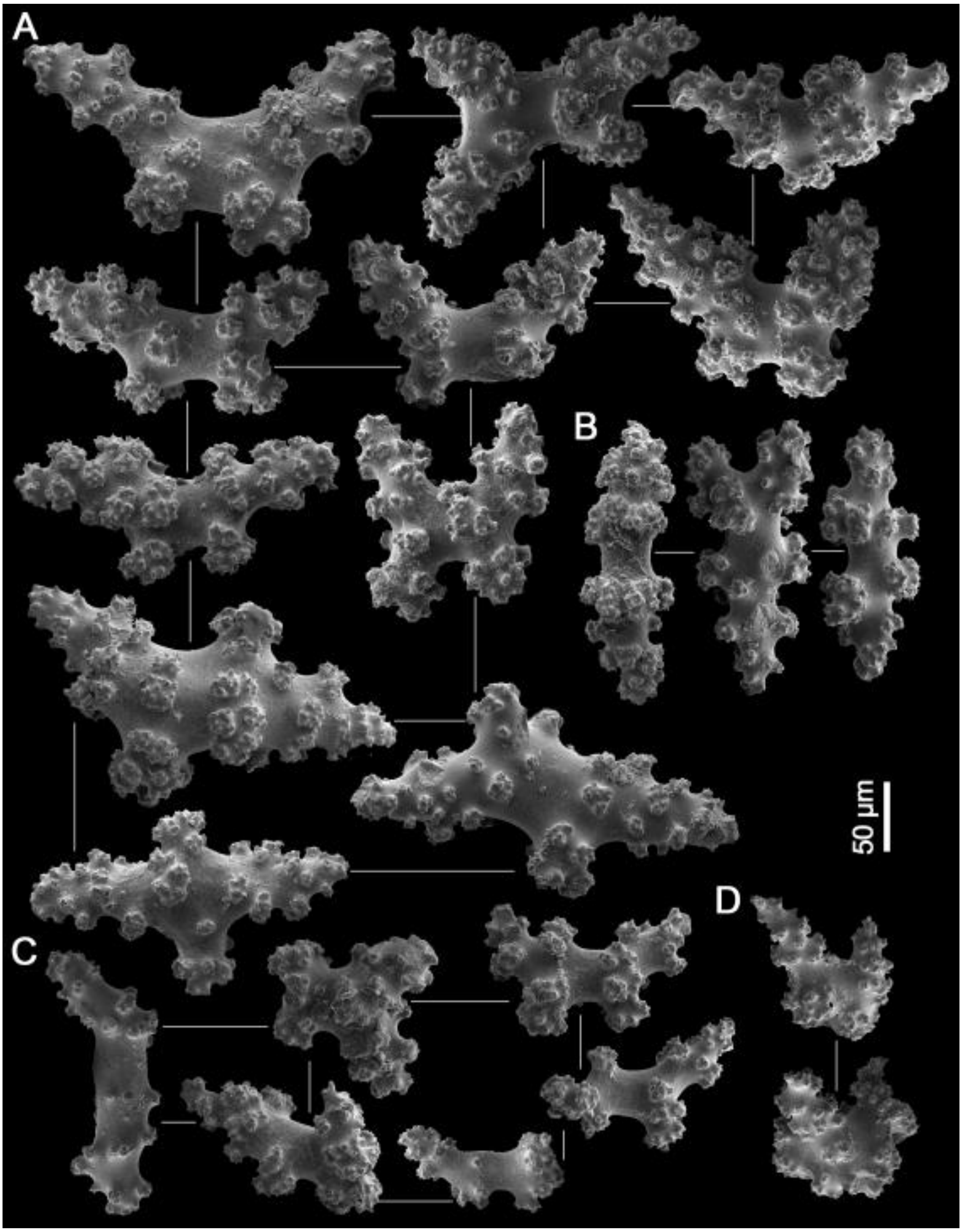

FIGURE S16. Sclerites of *Plexaurella rastrera* sp. nov. (USNM 42004) from Barbados. A: butterflies from middle layer; B: sclerites from axial layer; C: cortical sclerites.

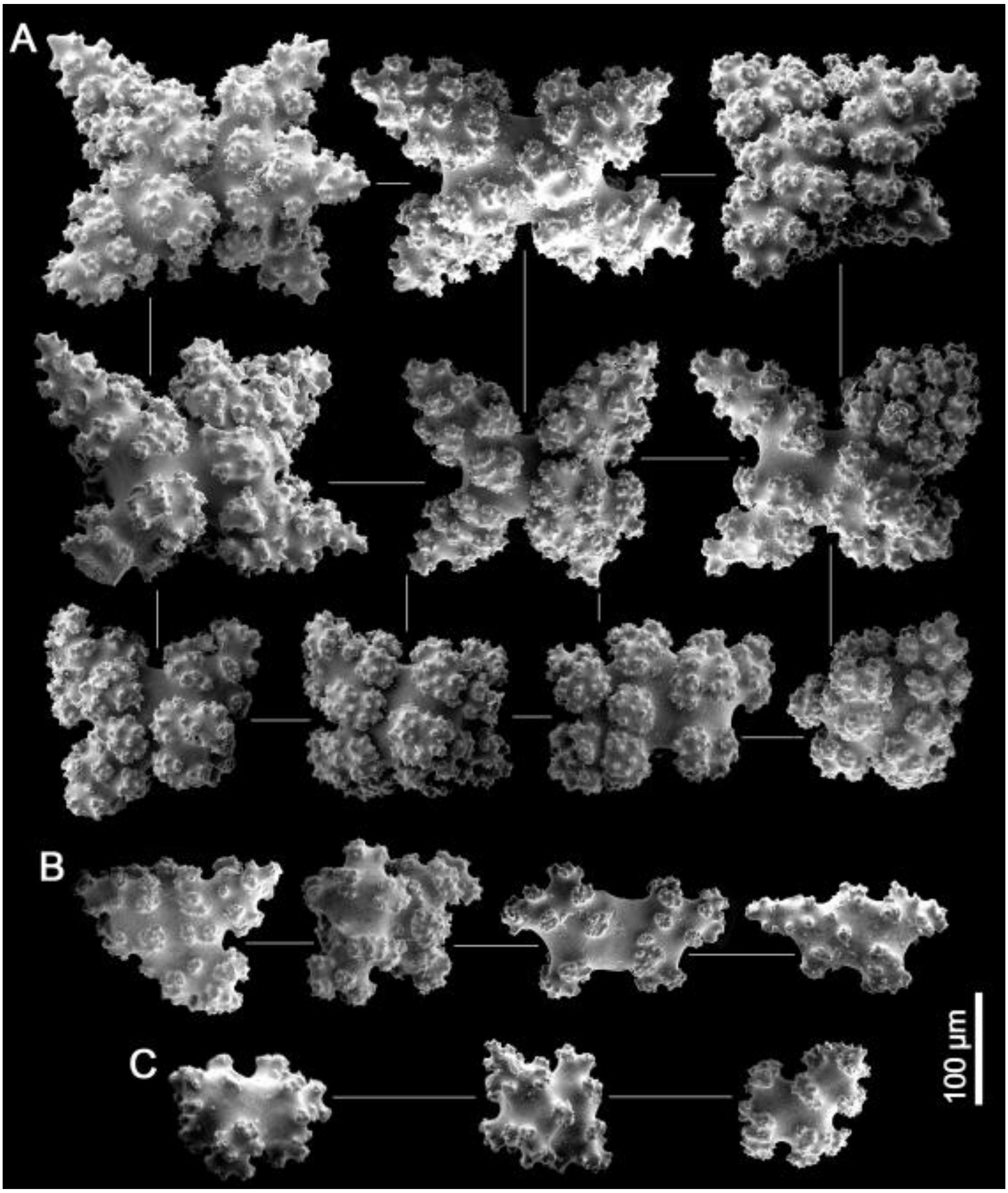

FIGURE S17. Sclerites of *Plexaurella rastrera* sp. nov. (USNM 50745) from Anguilla. A: butterflies from middle layer; B: tri-radiates from middle layer C: sclerites from axial layer; D: cortical sclerites.

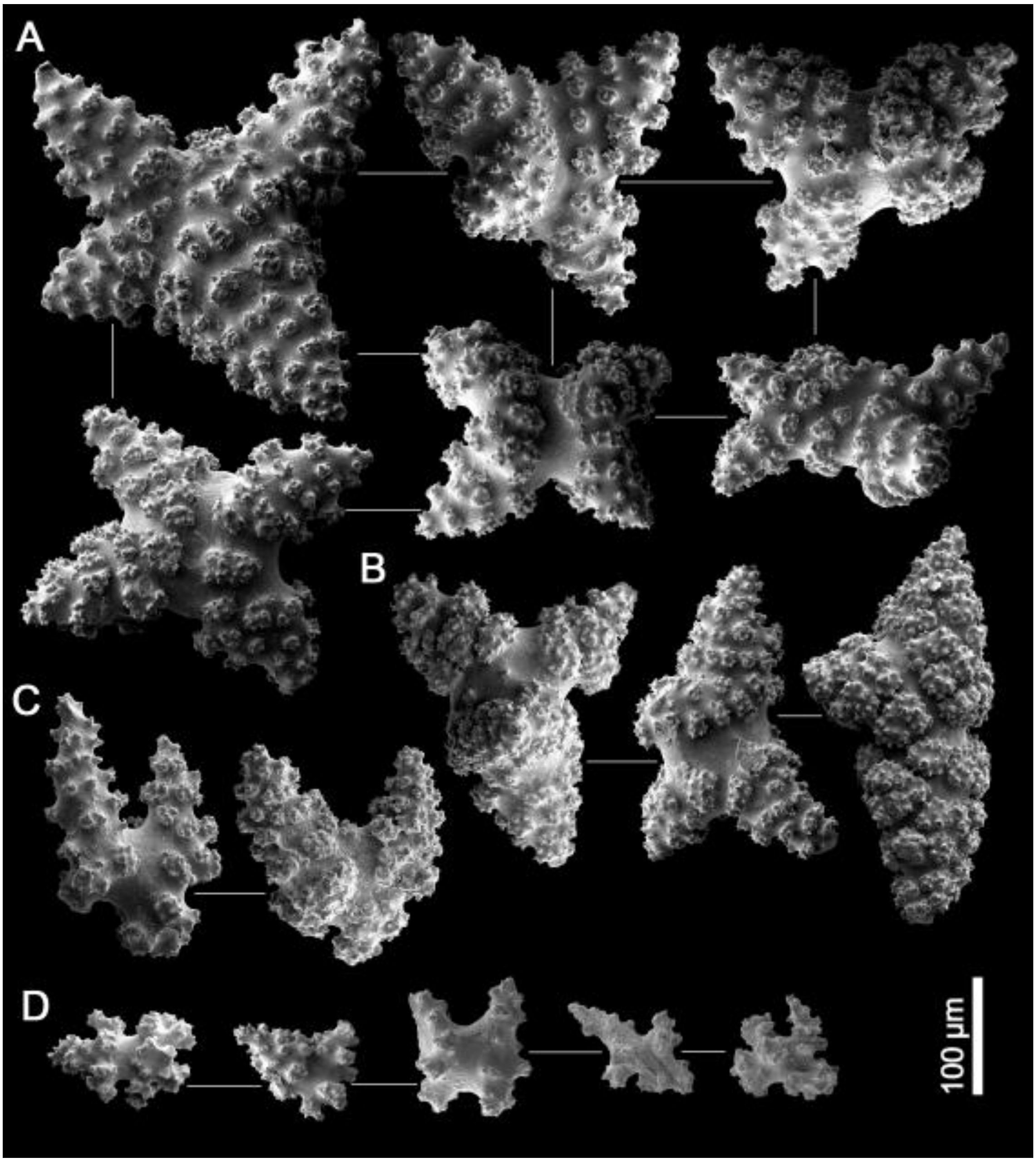

FIGURE S18. Sclerites of *Plexaurella rastrera* (USNM 73605) from Martinique. A: butterflies from middle layer; B: sclerites from axial layer; C: cortical sclerites.

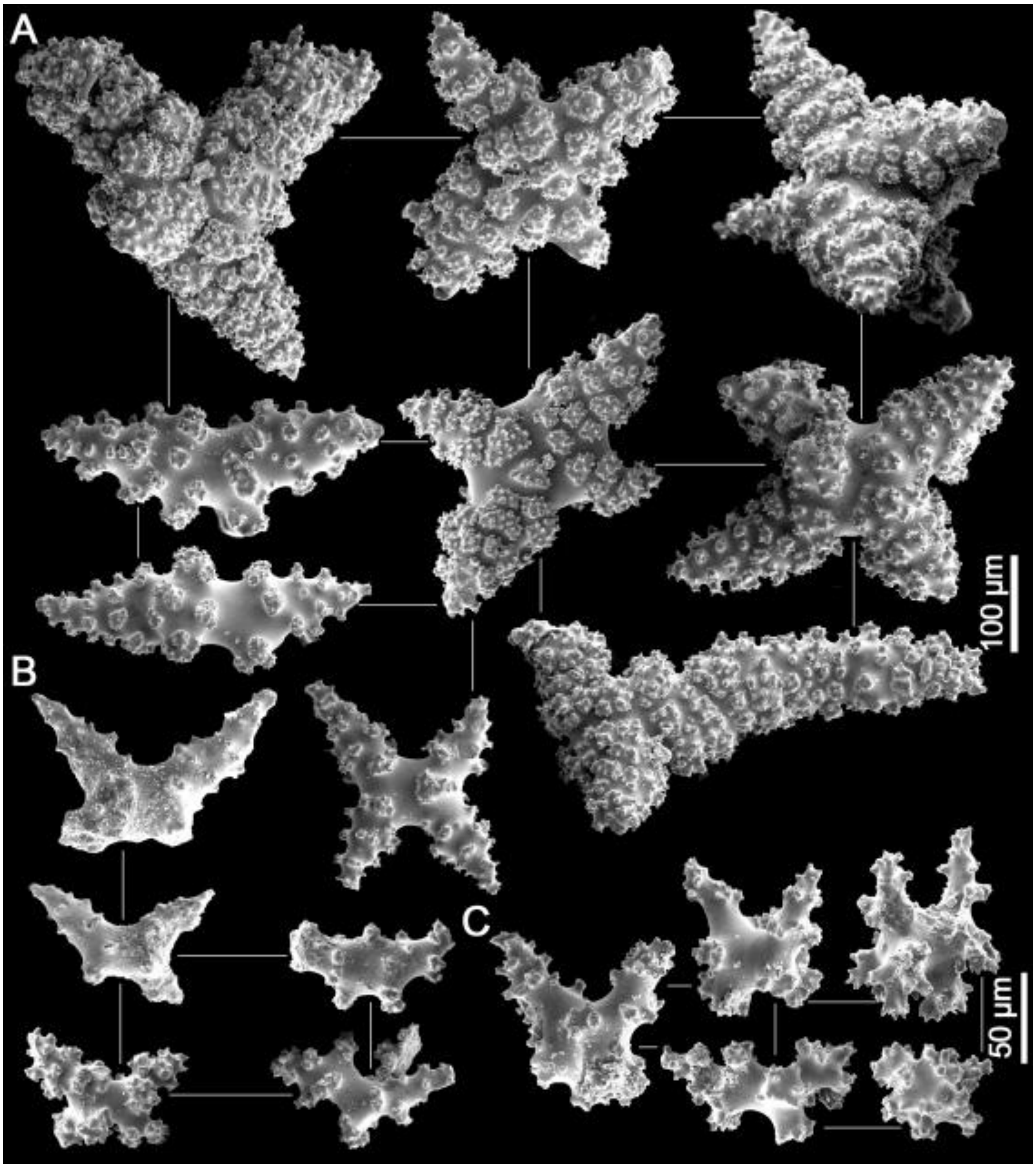

FIGURE S19. Sclerites of *Plexaurella nutans* (USNM 54951) from Honduras. A: butterflies from middle layer; B: tri-radiates from middle layer; C: spindles from middle layer; D: sclerites from axial layer; E: cortical sclerites.

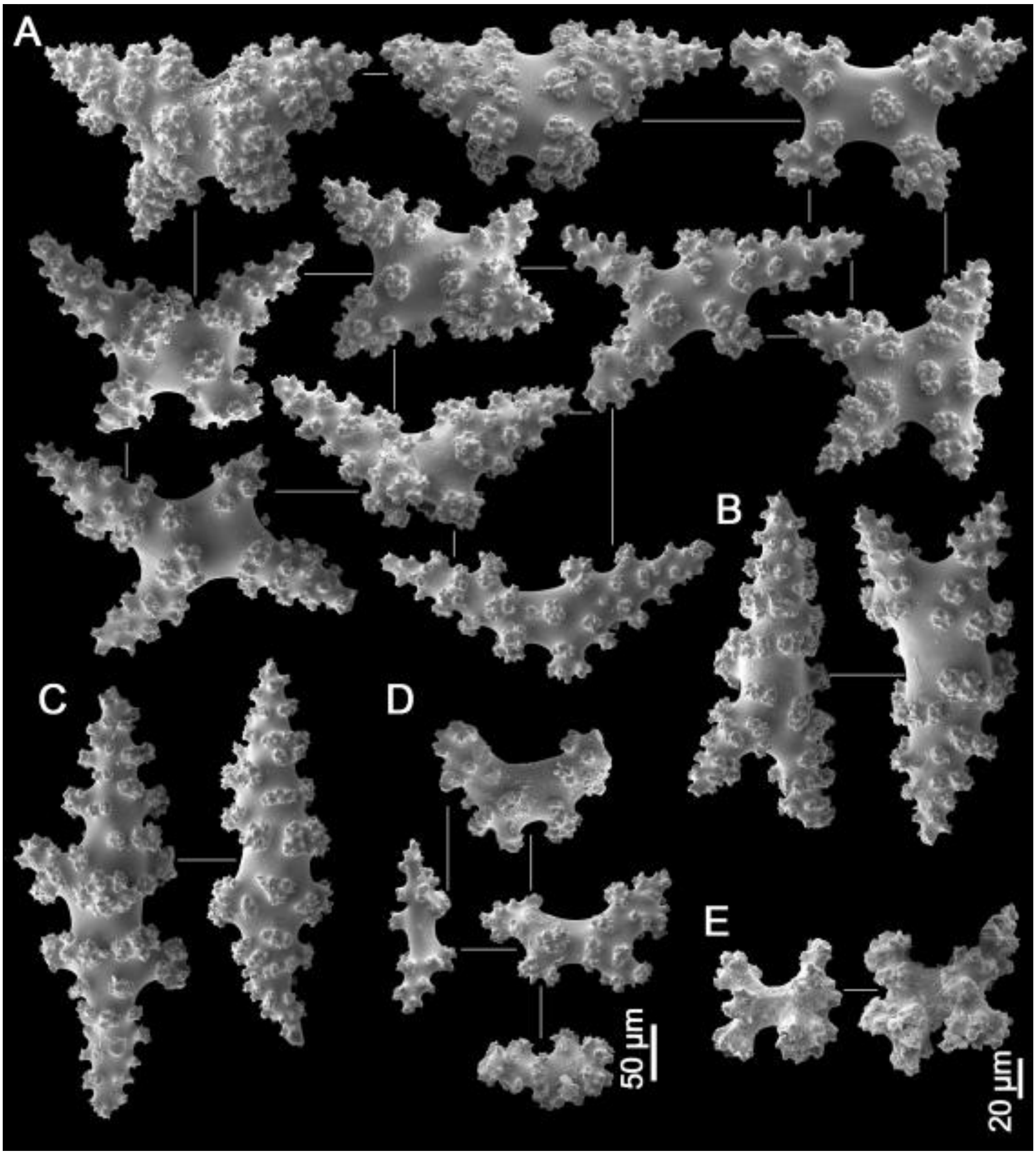

FIGURE S20. Sclerites of *Plexaurella nutans* (USNM 84107) from Florida. A: butterflies from middle layer; B: rods from polyp body wall; C: spindles from middle layer; D: sclerites from axial layer; E: cortical sclerites.

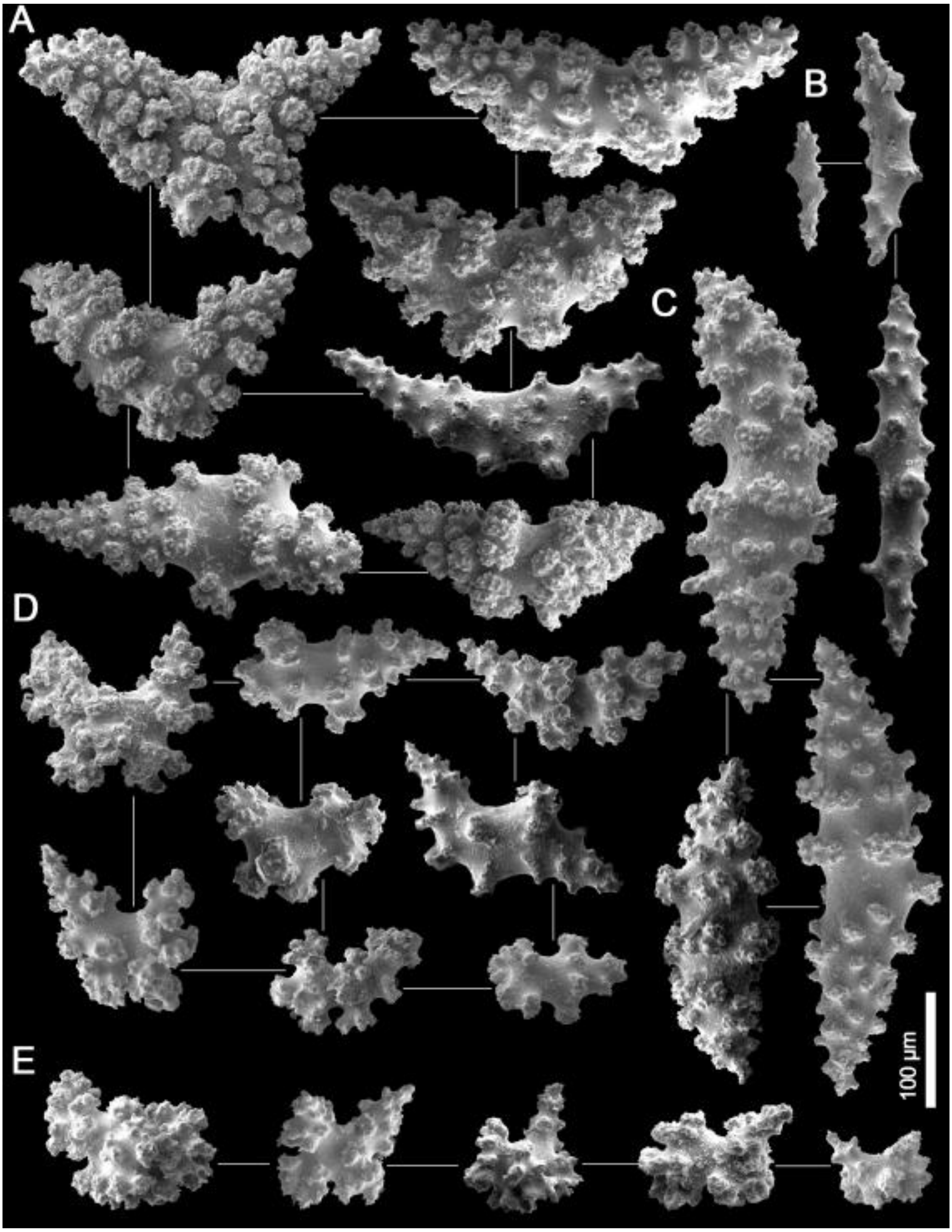

FIGURE S21. Sclerites of *Plexaurella grisea* (USNM 54953) from Turks and Caiacos Islands. A: butterflies from middle layer; B: tri-radiates from middle layer; C: cortical sclerites; D: sclerites from axial layer.

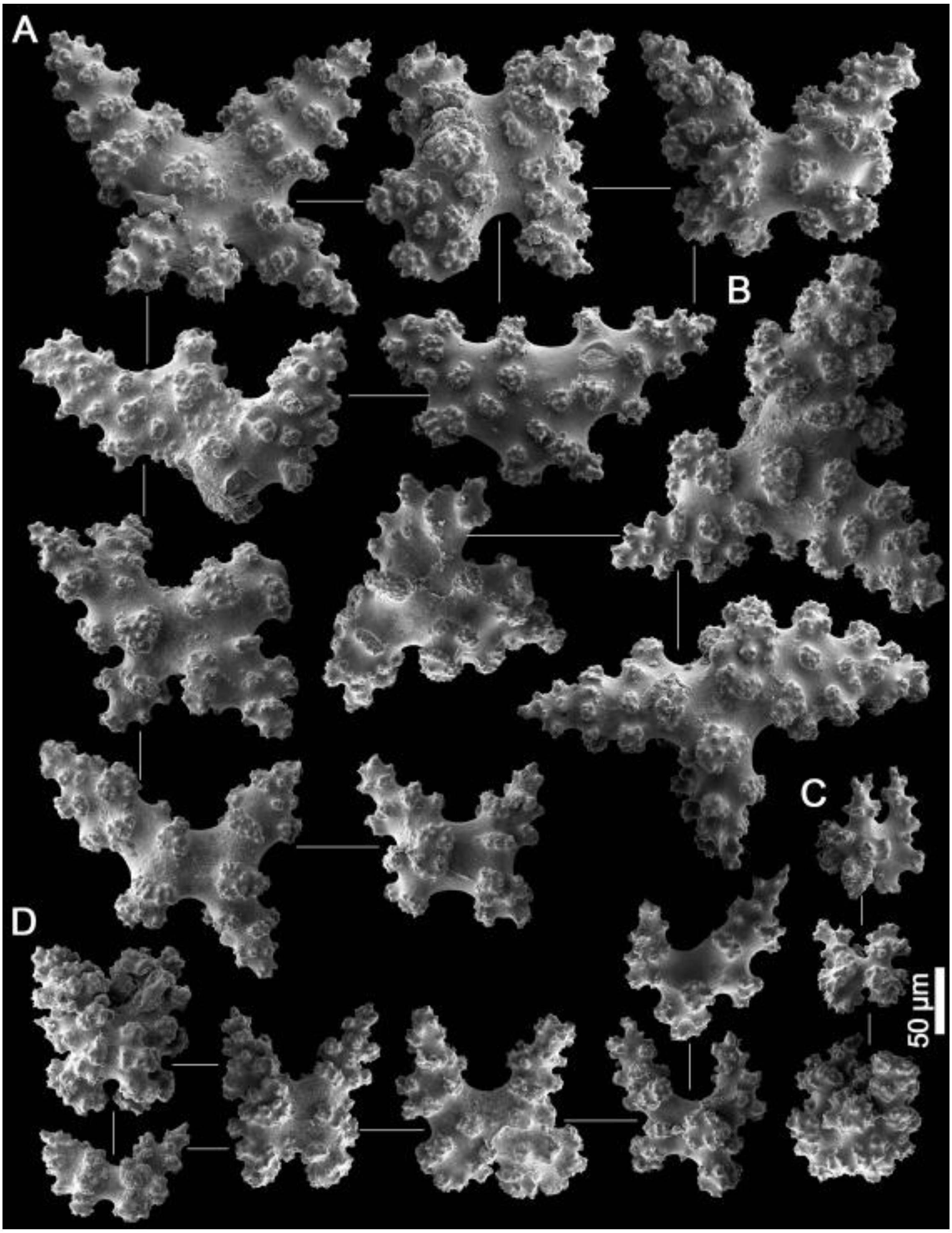

FIGURE S22. *Plexaurella nutans* (USNM 55092) from Dominican Republic. A: butterflies from middle layer; B: tri-radiates from middle layer; C: rods from polyp body wall; D: sclerites from axial layer; E: cortical sclerites.

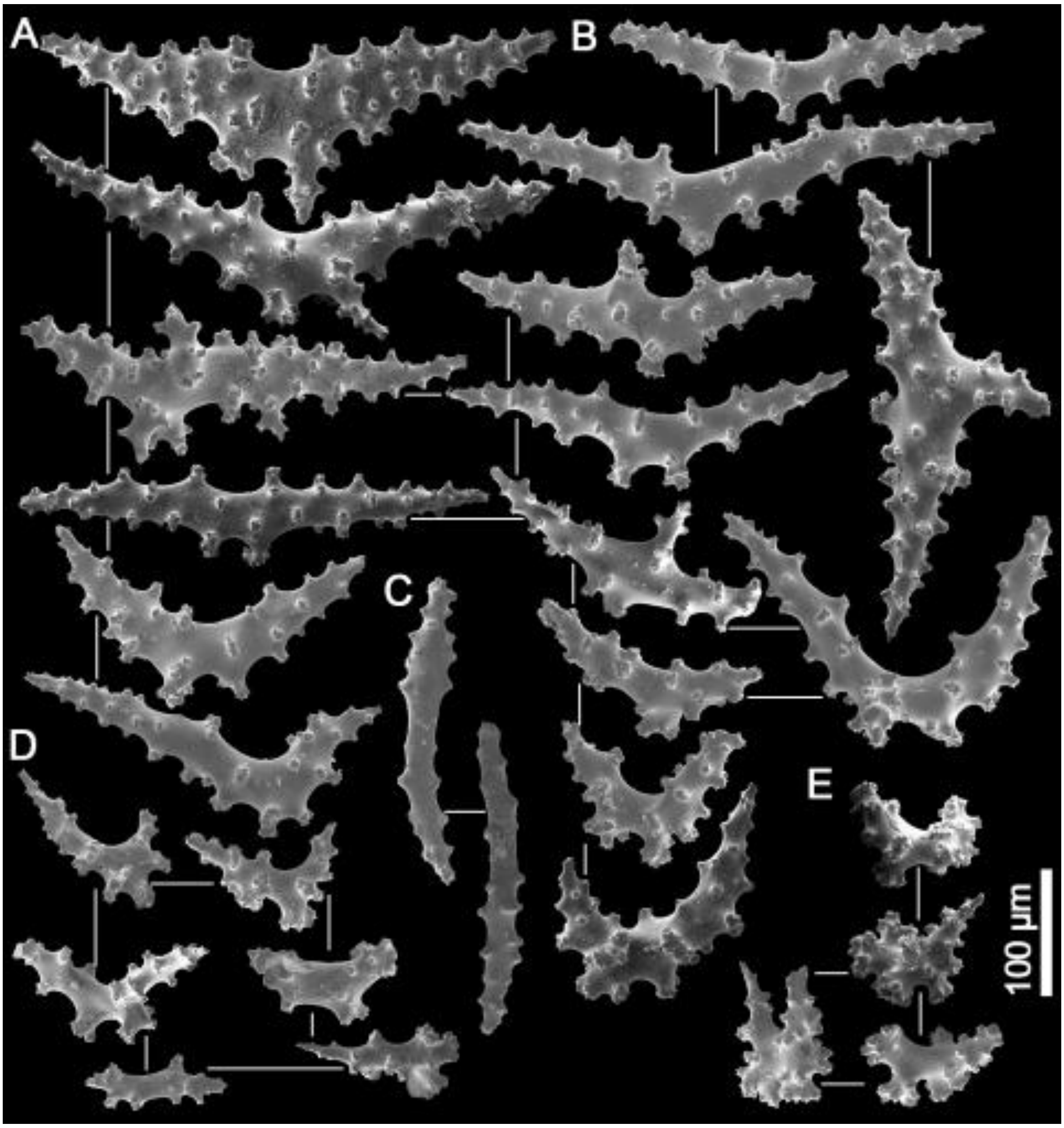

FIGURE S23. *Plexaurella nutans* (USNM 1237522) from Netherlands Antilles. A: spindles from middle layer; B: butterflies from middle layer; C: rods from polyp body wall; D: cortical sclerites; E: sclerites from axial layer.

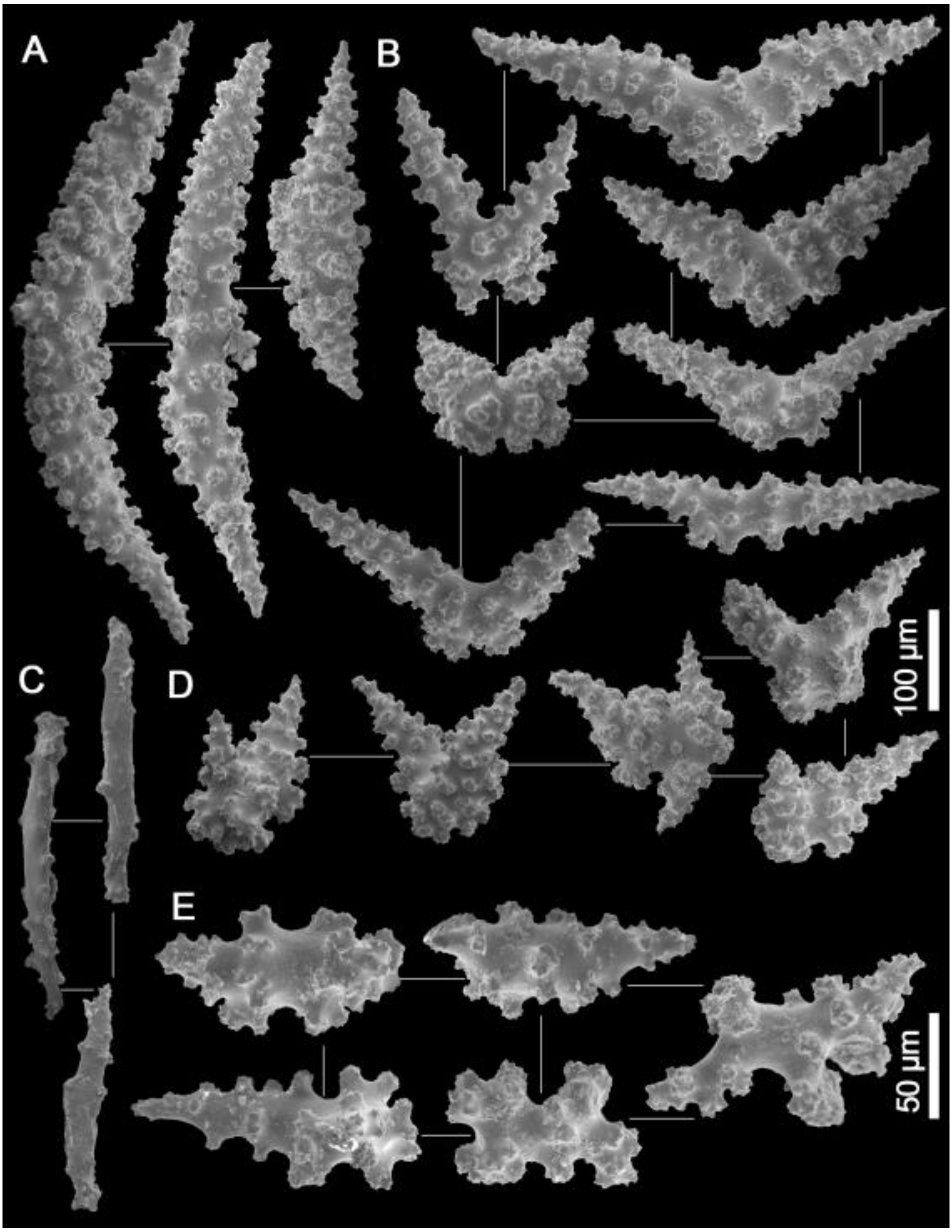

FIGURE S24. Sclerites of *Plexaurella nutans* (USNM 73494) from Florida. A: butterflies from middle layer; B: sclerites from axial layer; C: cortical sclerites.

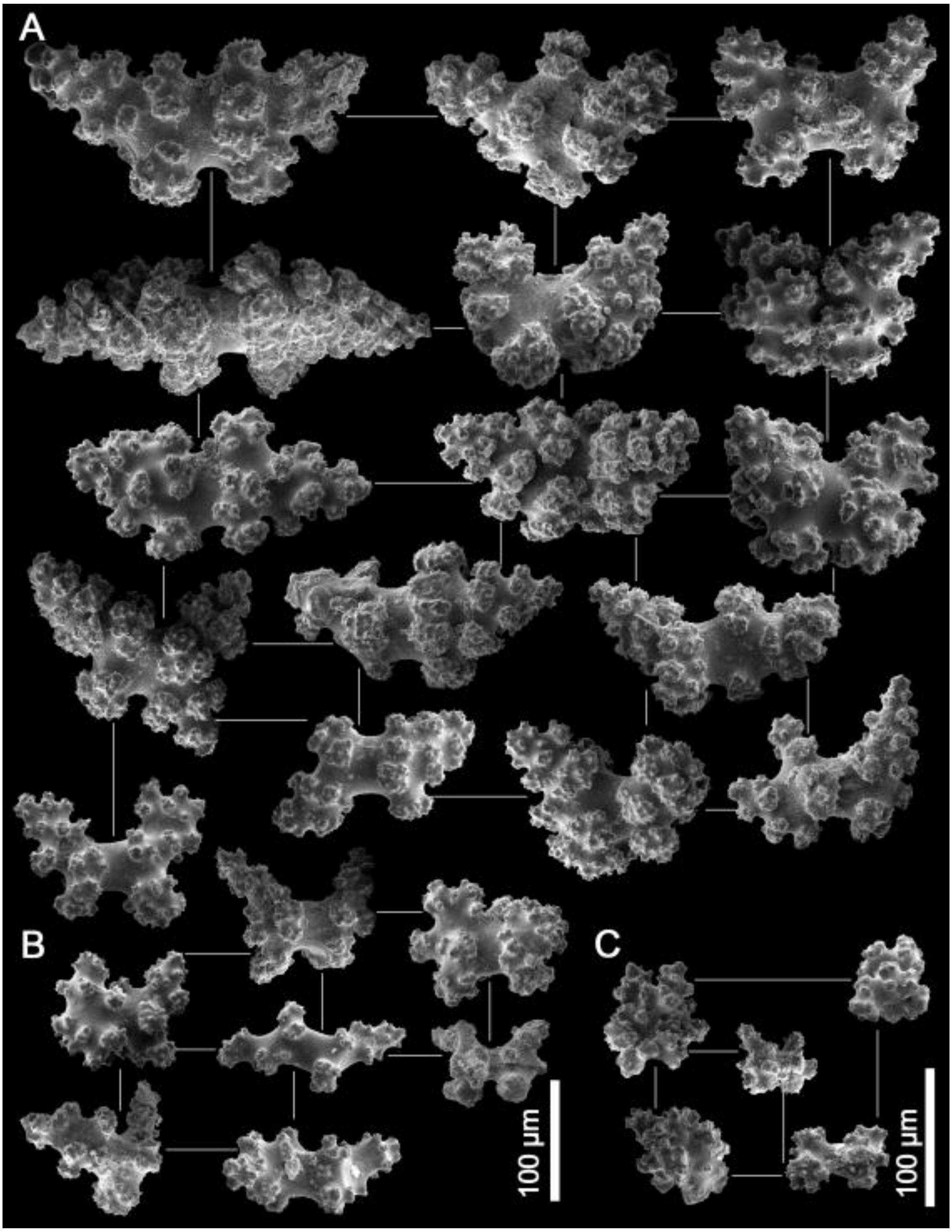

FIGURE S25. Sclerites of *Plexaurella nutans* (USNM 1122674) from Netherlands Antilles. A: butterflies from middle layer; B: tri-radiate from middle layer; C: rods from polyp body wall; D: sclerite from axial layer; E: cortical sclerites.

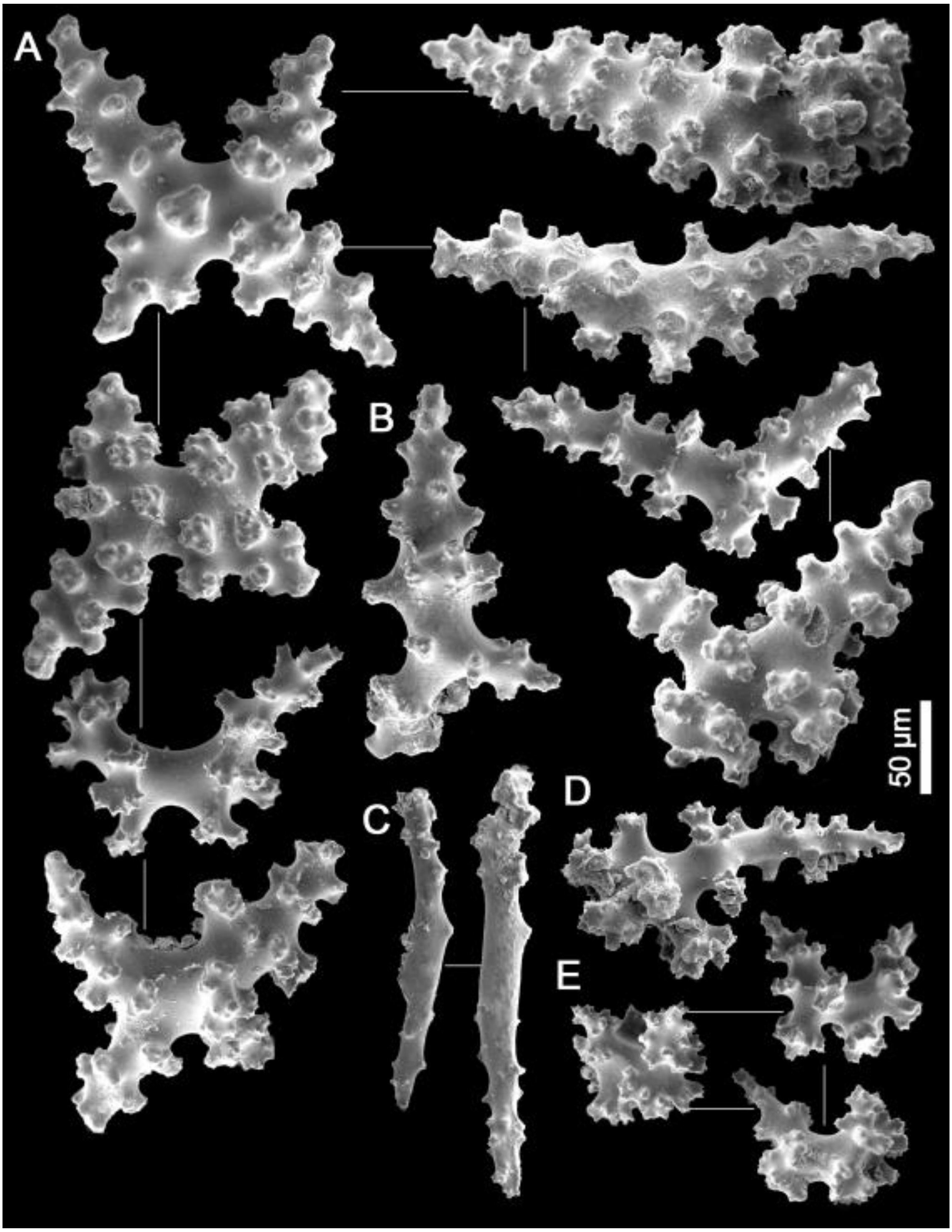

FIGURE S26. Sclerites of *Plexaurella nutans* (USNM 1234926) from Grenada. A: butterflies from middle layer; B: tri-radiate from middle layer; C: sclerites from axial layer; D: cortical sclerites; E: rods from polyp body wall.

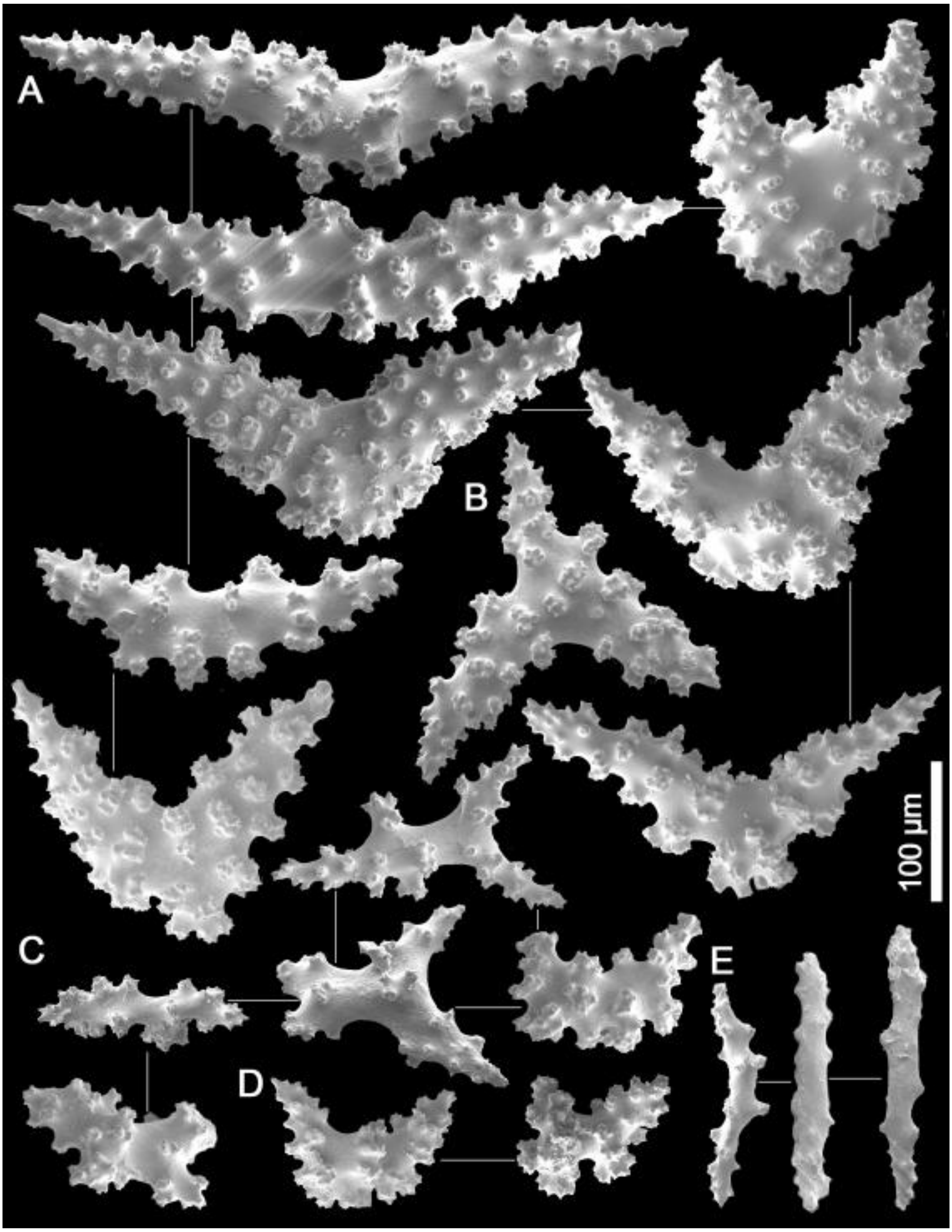

FIGURE S27. Sclerites of *Plexaurella nutans* (USNM 85980) from Florida. A: butterflies and six-radiate from middle layer; B: tri-radiates from middle layer; C: cortical sclerites; D: sclerites from axial layer.

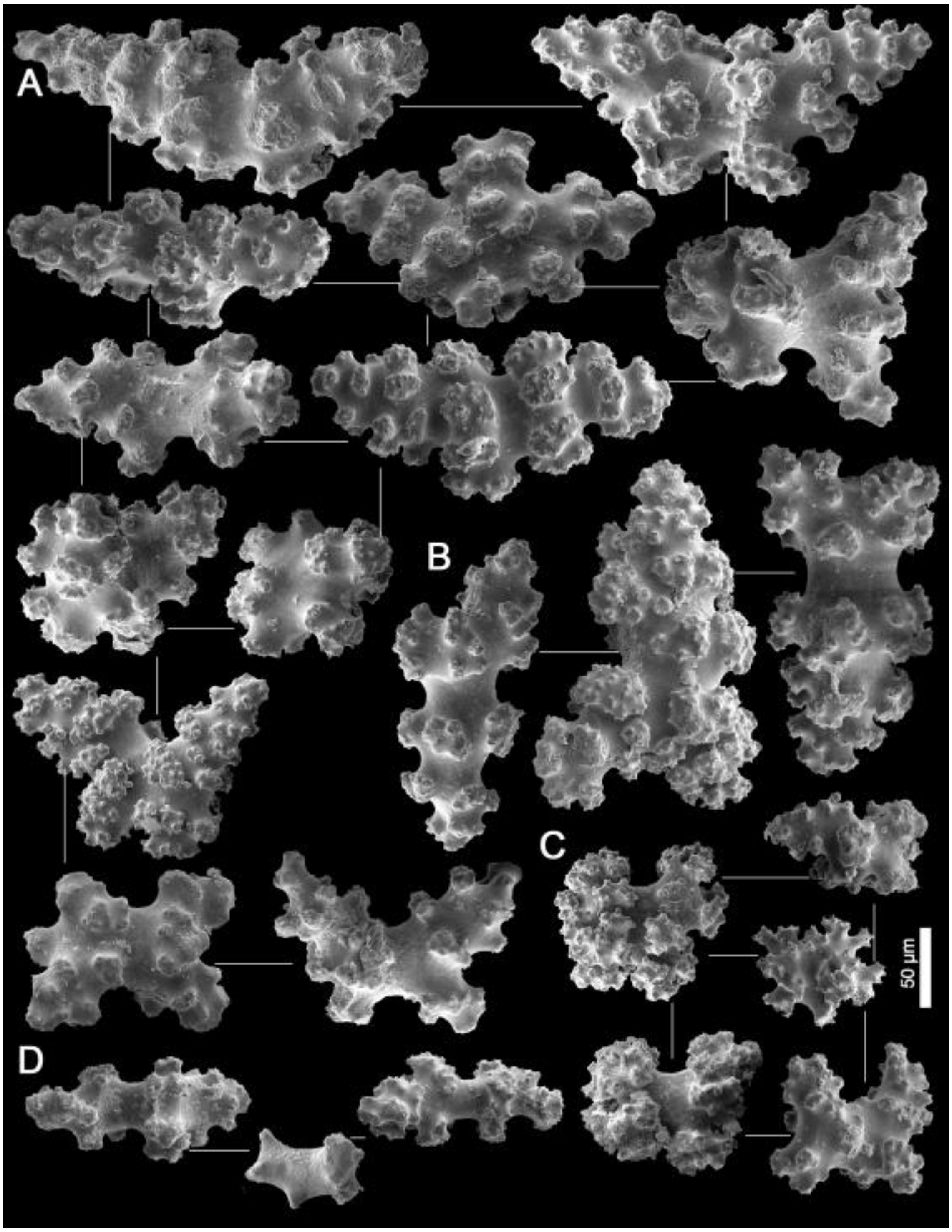

FIGURE S28. Sclerites of *Plexaurella nutans* (USNM 88786) from Turks and Caiacos. A: butterflies from middle layer; B: tri-radiate from middle layer; C: axial sclerites; D: sclerites from the cortical layer.

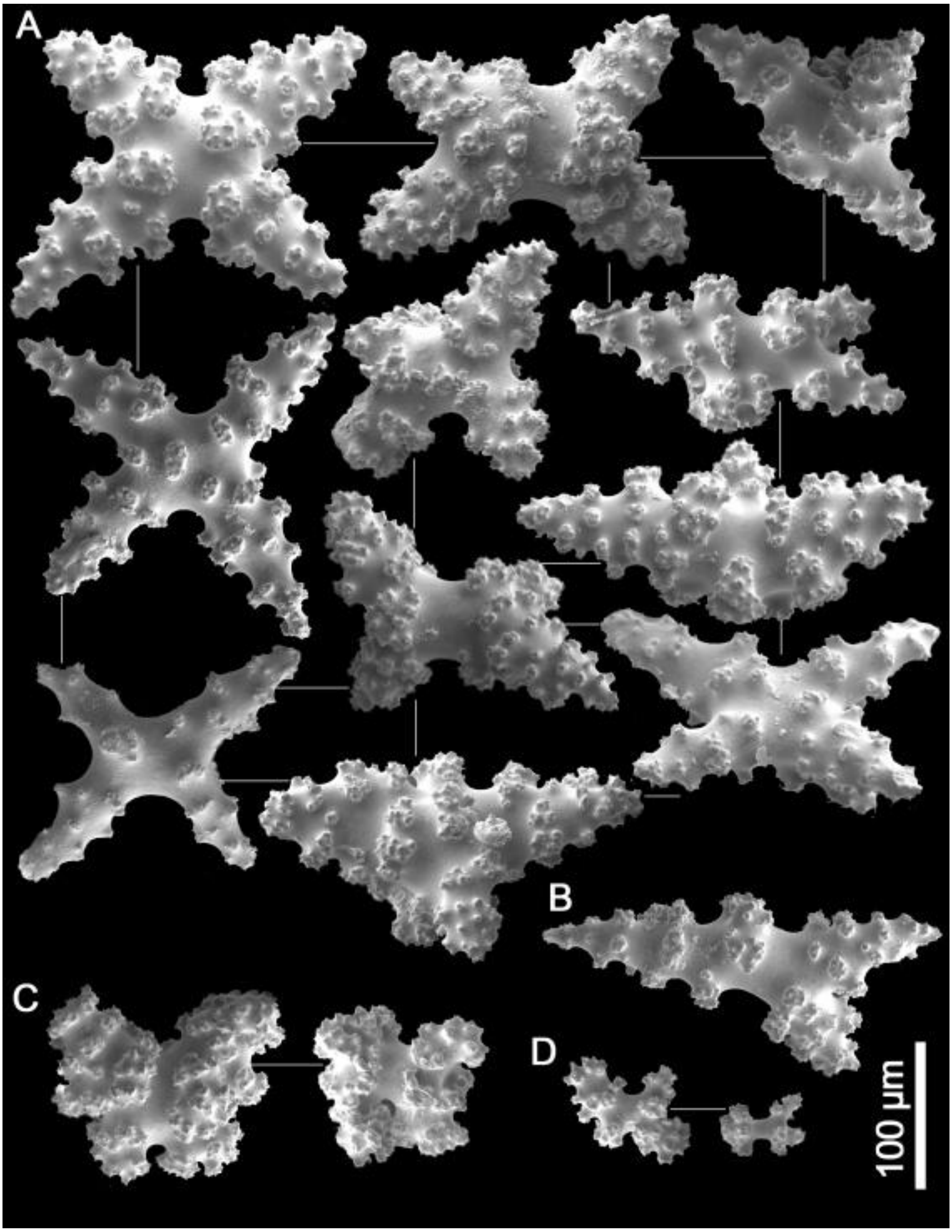

FIGURE S29. Sclerites of *Plexaurella nutans* (ZMB 5963 – holotype of *P. fusifera*) from Barbados. A: butterflies and triradiate from middle layer; B: tuberculated rods from body wall; C: irregular sclerites from axial layer; D: cortical sixradiate. Scale bars: A–C: 0.05 mm; D: 0.02 mm.

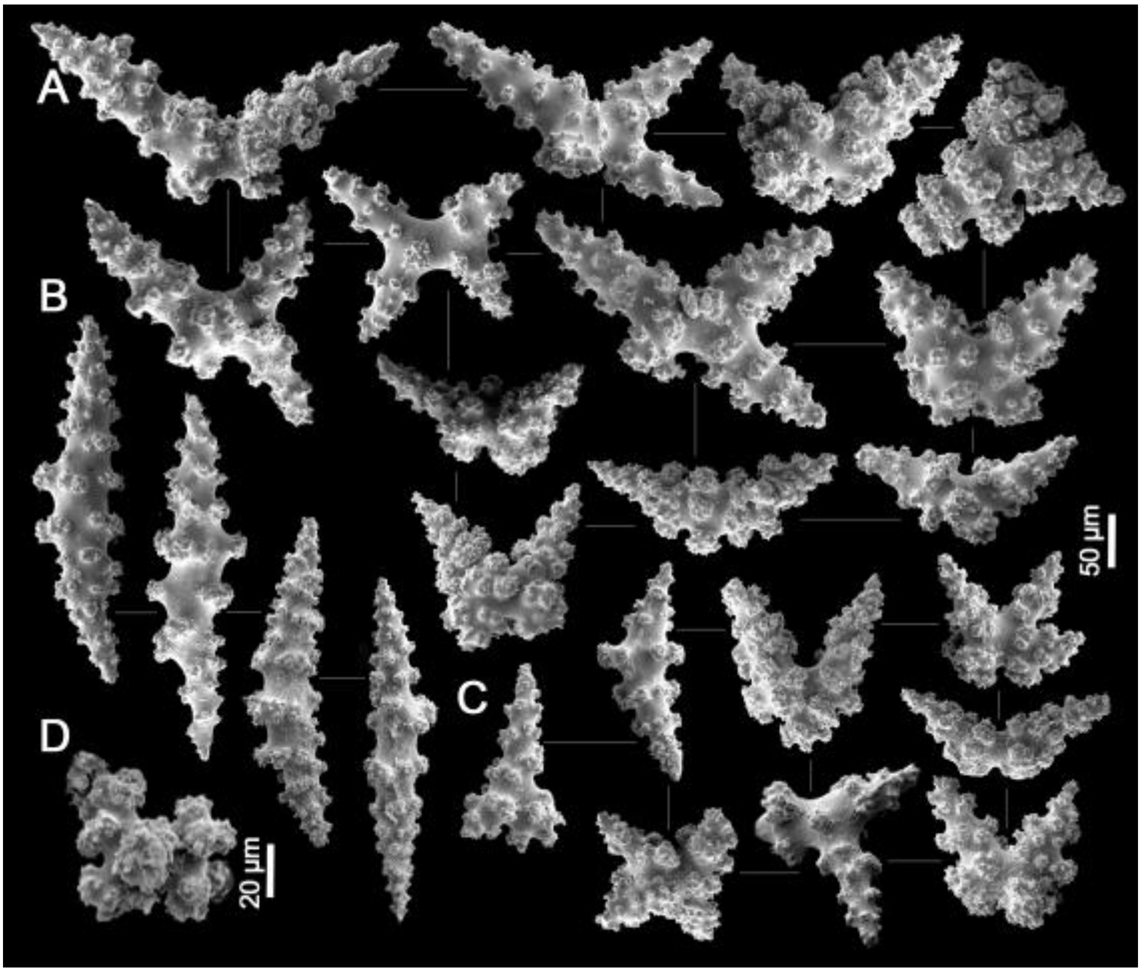

FIGURE S30. Sclerites of *Plexaurella nutans* (USNM 86026) from Florida. A: butterflies from middle layer; B: spindles from middle layer; C: irregular sclerites from axial layer; D: cortical sclerite.

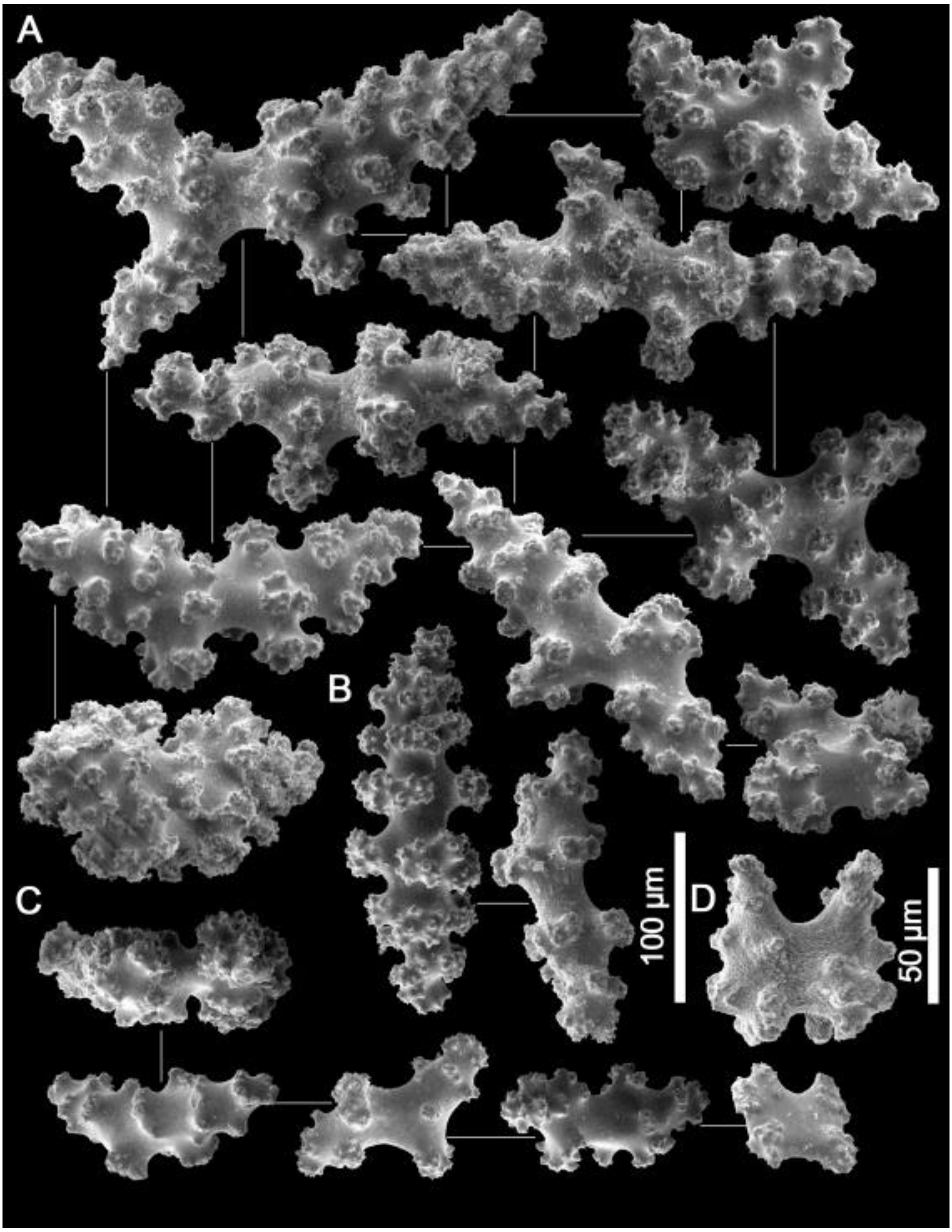

FIGURE S31. Sclerites of *Plexaurella obesa* (USNM 73400) from Fernando de Noronha, Brazil. A: spindles from middle layer; B: butterflies from middle layer; C: rod from polyp body wall; D: sclerites from axial layer; E: cortical sclerites.

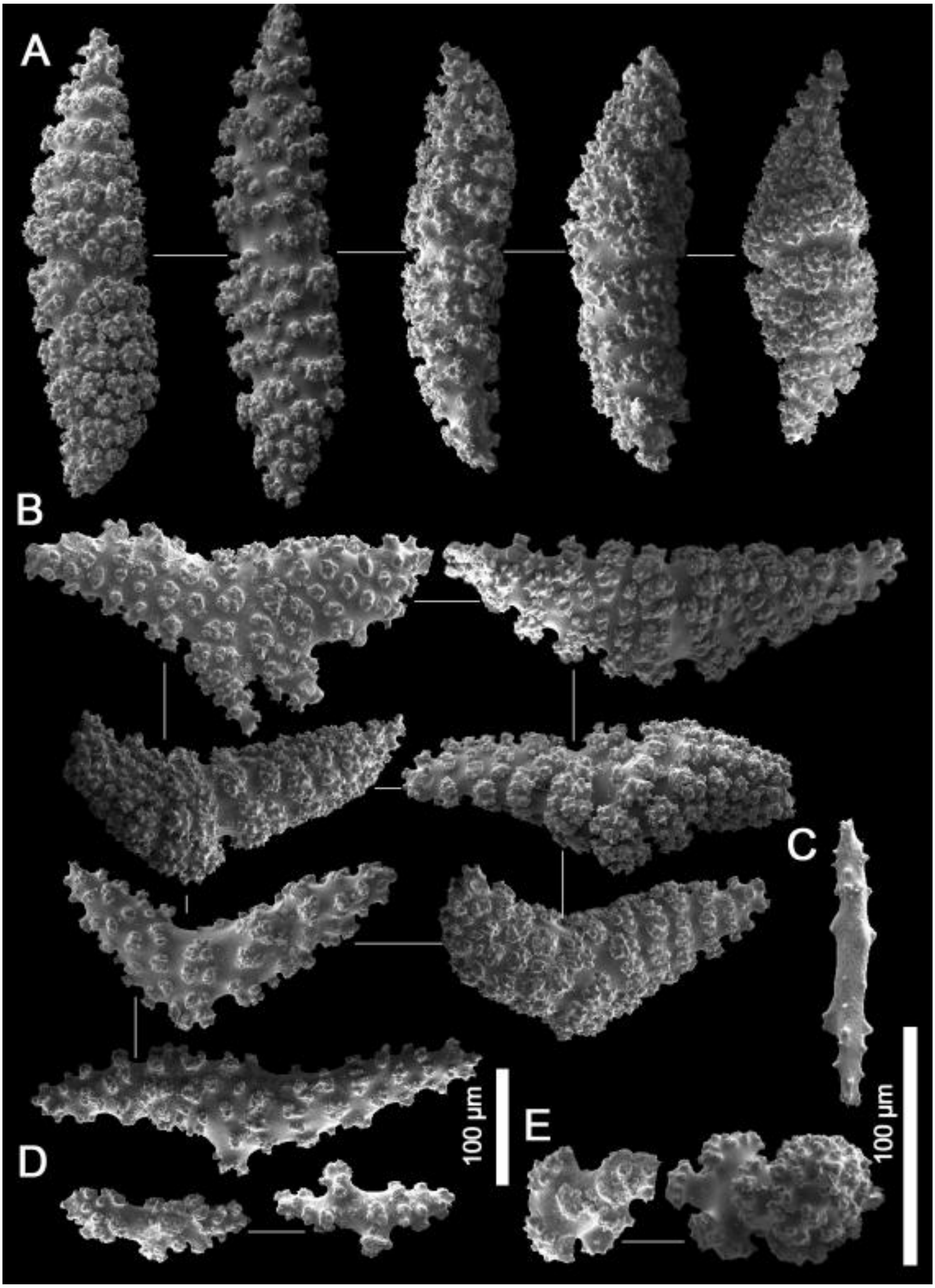

FIGURE S32. Sclerites of *Plexaurella grandiflora* (USNM 75596) from Picaozinho (Paraíba, Brazil). A: spindles from middle layer; B: butterflies from middle layer; C: tri-radiate from middle layer; D: sclerites from axial layer; E: cortical sclerites.

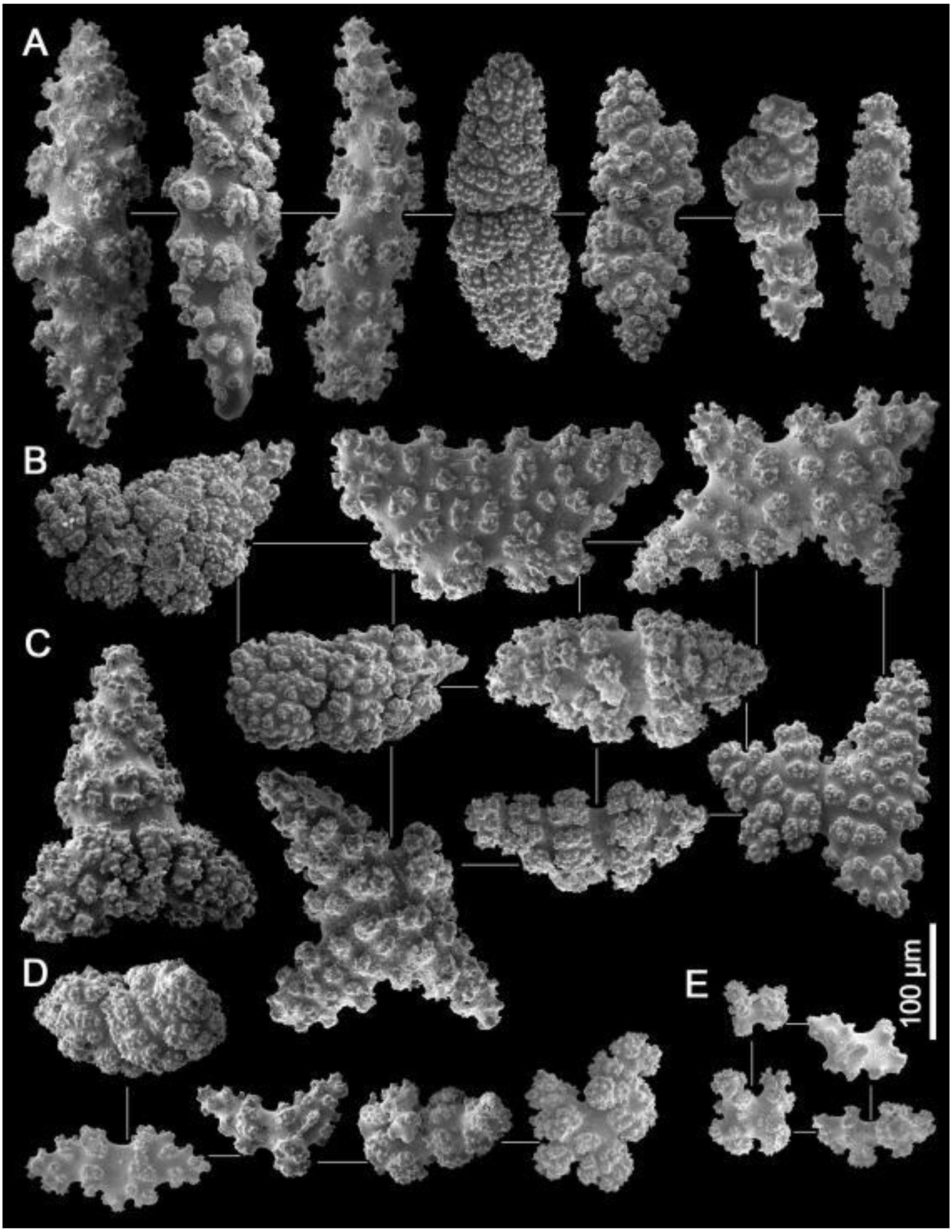

FIGURE S33. Sclerites of *Plexaurella grandiflora* (USNM 73401) from Alagoas, Brazil. A: spindles from middle layer; B: butterflies from middle layer; C: sclerites from axial layer; D: cortical sclerites.

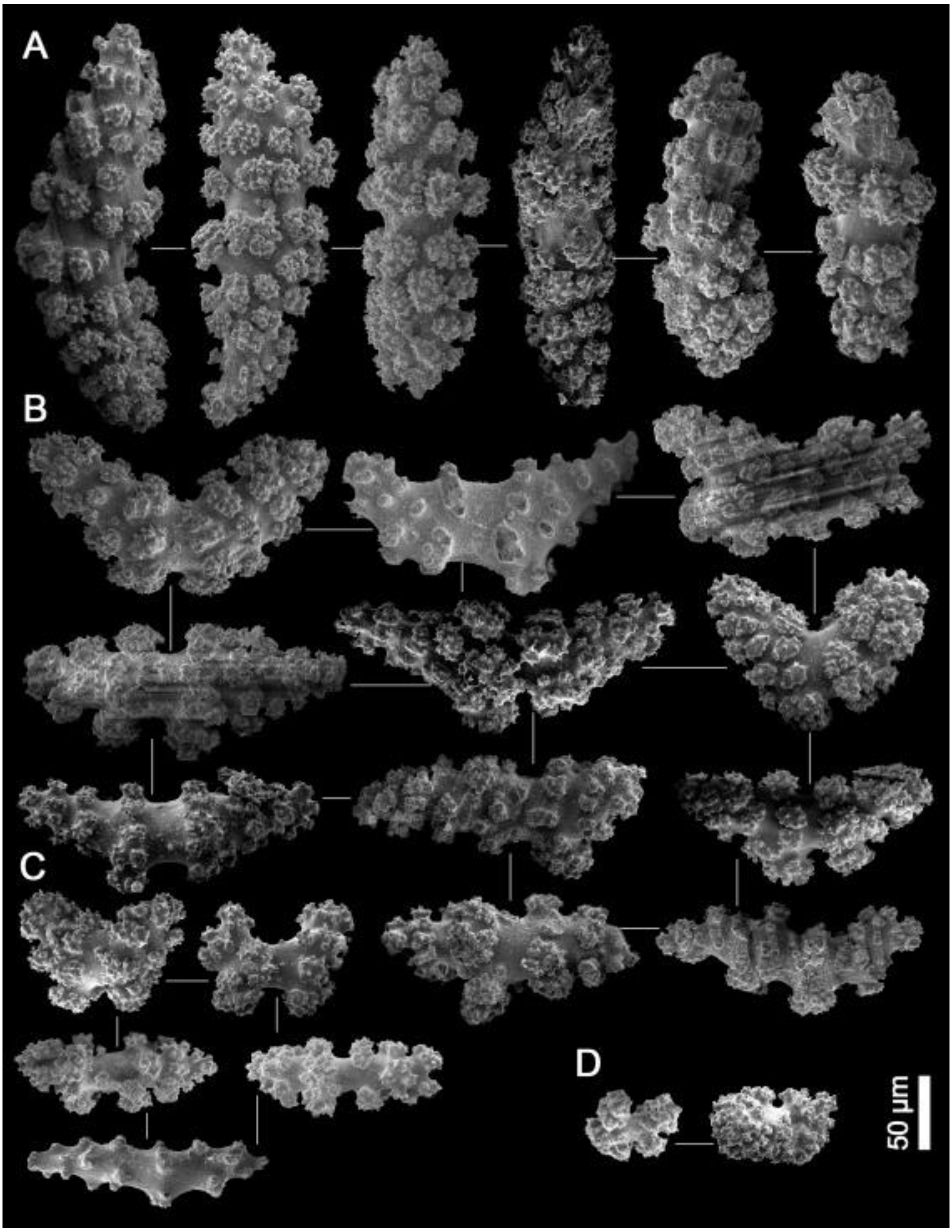

FIGURE S34. Sclerites of *Plexaurella grandiflora* (YPM 4503 – holotype of *P. verrucosa*) from Bahia, Brazil. A: spindles from middle layer; B: sclerites from axial layer; C: triradiates from middle layer; D: butterflies from middle layer; E: sclerites from cortical layer.

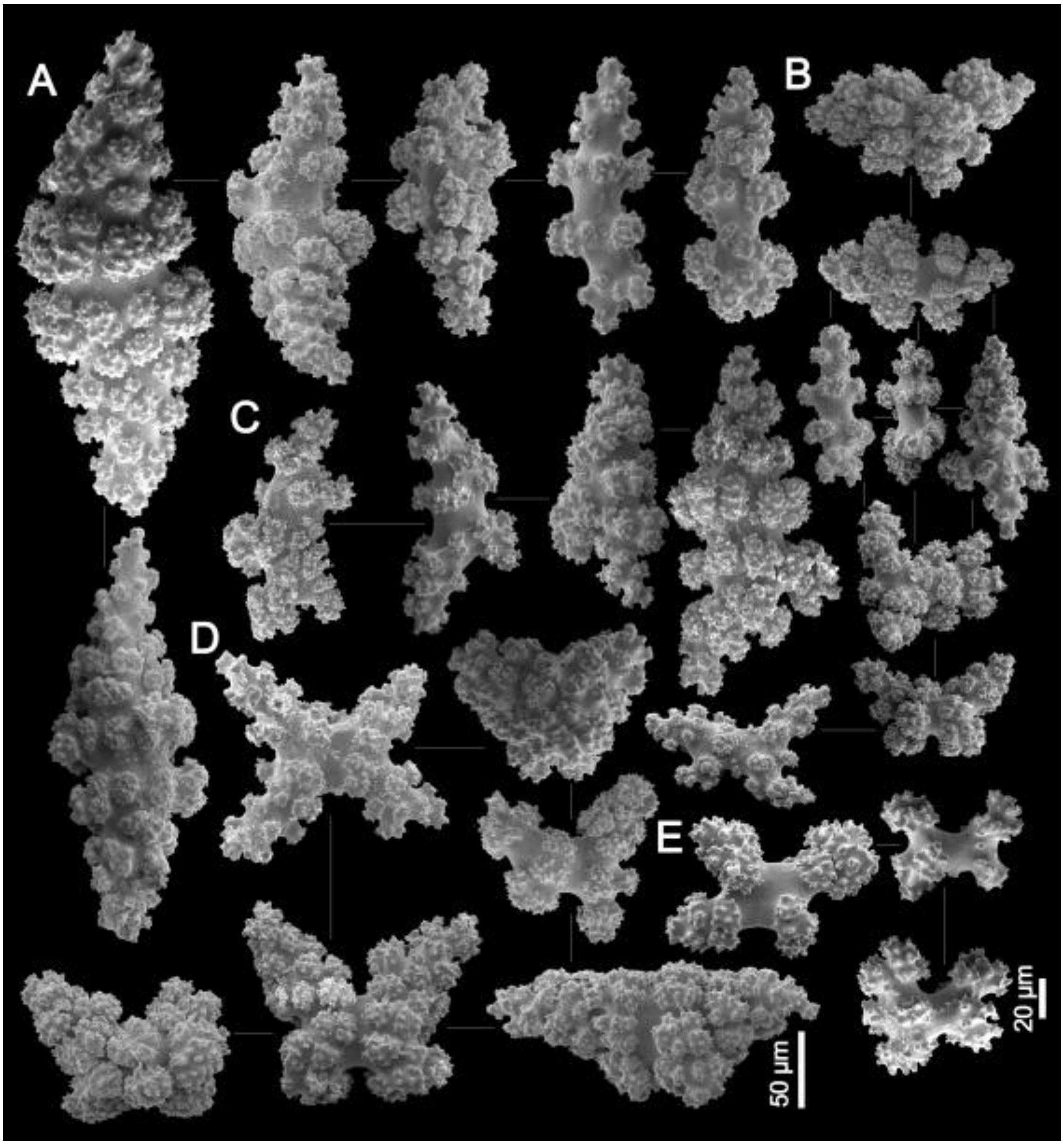

FIGURE S35. Sclerites of *Plexaurella grandiflora* (YPM 4502 – holotype of *P. pumila*) from Bahia, Brazil. A: irregular butterflies from middle layer; B: triradiates from middle layer; C: sclerites from axial layer; D: cortical sclerites; E: tuberculated spindles from middle layer.

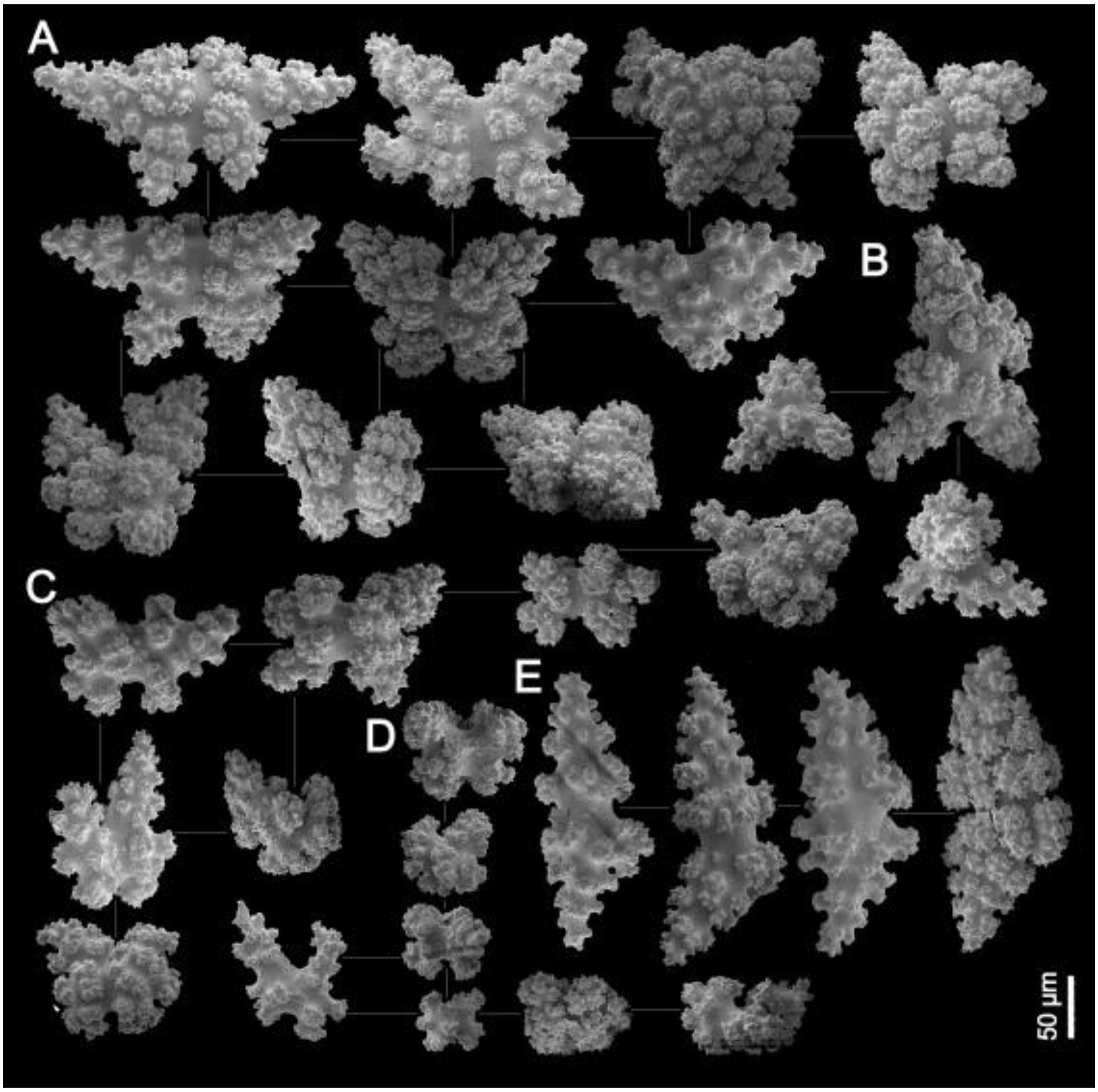

FIGURE S36. Sclerites of *Plexaurella grandiflora* (YPM 1597 – holotype of *P. cylindrica*) from Abrolhos, Brazil. A: spindles from middle layer; B: triradiates from middle layer; C: butterflies from axial layer; D: sclerites from cortical layer.

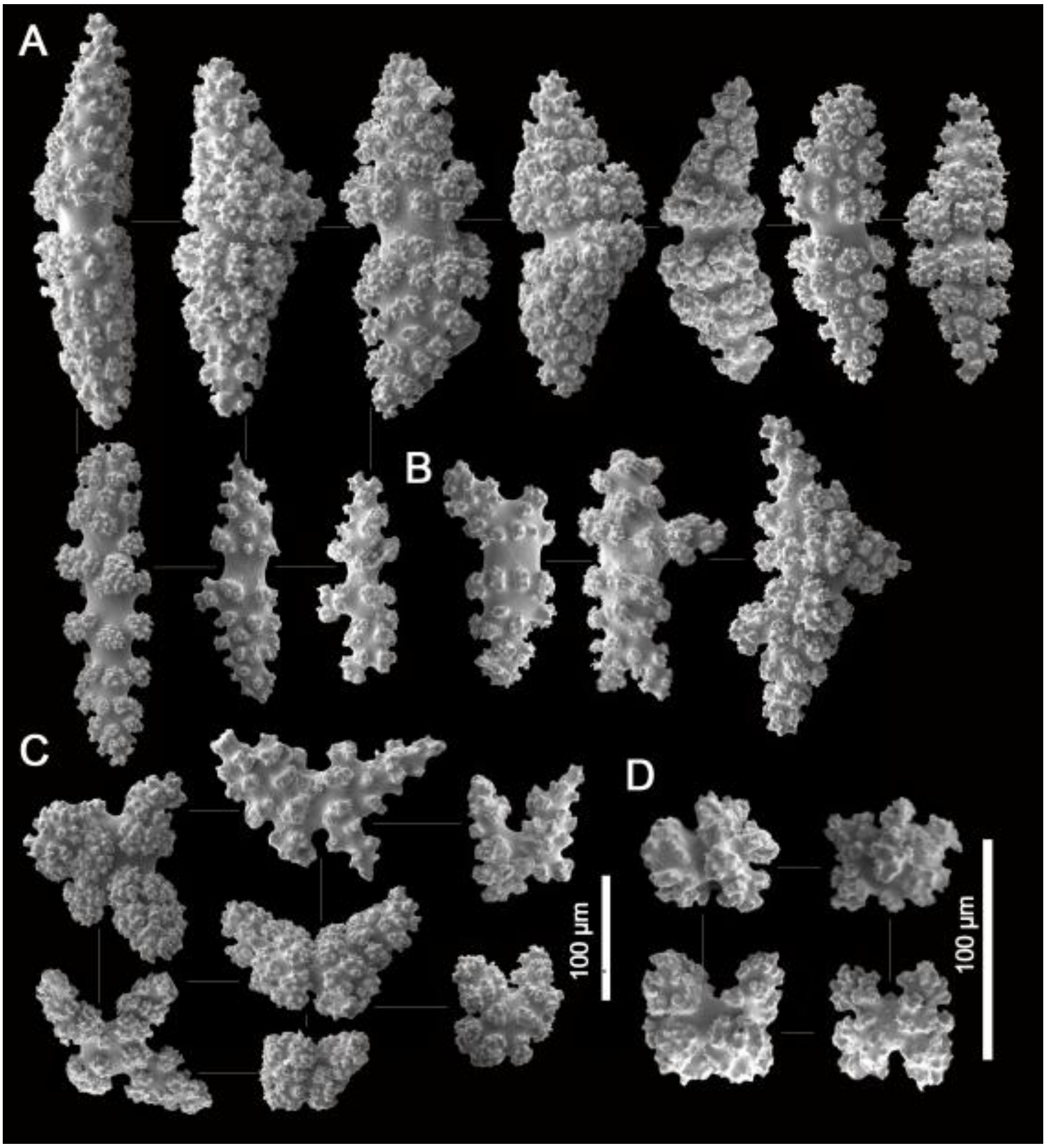

FIGURE S37. Sclerites of *Plexaurella grandiflora* (YPM 1598 – holotype of *P. braziliana*) from Abrolhos, Brazil. A: spindles from middle layer; B: butterflies from middle layer; C: triradiate from middle layer; D: sclerites from axial layer; E: cortical sclerites.