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Three new species of glass sponges (Porifera: Hexactinellida) from the West Indies, and molecular phylogenetics of Euretidae and Auloplacidae (Sceptrulophora)

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Three new species and a new genus of dictyonal Hexactinellida (Hexasterophora: Sceptrulophora: Euretidae and Auloplacidae) are described from hard-bottom communities of the West Indies. The holotypes were all collected by manned submersibles operated by the Harbor Branch Oceanographic Institute between 2006 and 2011, and remained in excellent physical condition at the time of their examination and description. As a result of their relatively recent collection and ethanol storage, molecular markers established previously for the phylogenetics of glass sponges were retrievable from all three holotypes. These are the first sequences for their respective genera, *Conorete*, *Verrucocoeloidea*, and ***Dictyoplax* gen. nov.** In addition, the first sequences of the genus *Lefroyella* could be obtained. Because the only (alleged) member of the family Euretidae previously included in molecular phylogenetic studies turned out to belong to the recently resurrected family Auloplacidae (i.e. ***Dictyoplax* gen. nov.**), in the present study the phylogenetic position of Euretidae within Sceptrulophora could be inferred for the first time. Furthermore, the increased taxon sampling allowed us to conduct a first test of the monophyly of Euretidae and one of its two subfamilies, Euretinae, with molecular data. Maximum-likelihood phylogenetic analysis revealed a close relationship between Euretidae and Farreidae, but also indicated that Euretidae might be paraphyletic with respect to Farreidae. The monophyly of subfamily Euretinae, at least in its current scope, was strongly rejected by the molecular data, in line with results from other hexactinellid families with a subfamilial division. The genus *Sarostegia*, which was only recently provisionally moved to Euretidae, is here transferred to an *incertae sedis* position within the classification of Sceptrulophora, because it is clearly unrelated to the other three included euretids. Besides from that, we refrain from any changes to the classification of Euretidae until more genera of this most diverse but poorly defined sceptrulophoran family are sampled for molecular systematic studies.

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ADDITIONAL KEYWORDS: biodiversity – dictyonine – Hexasterophora – molecular phylogeny – sponges – taxonomy.

INTRODUCTION

Glass sponges (class Hexactinellida) of the West Indies–Caribbean–Gulf of Mexico region are generally considered fairly well known. The first species from this area, *Dactylocalyx pumiceus* was described by Stutchbury (1841), followed by a scattered series of single species descriptions by a variety of authors. Major additions of groups of species were made by Schmidt (1870, 1880) and Schulze (1887, 1899). Prior to the publication of *Systema Porifera* (Hooper & van Soest, 2002),

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van Soest & Stentoft (1988) assembled the first summary of the hexactinellids from the region, listing 35 species, of which only 22 were considered valid and 13 were questionable or junior synonyms; an additional six species names were listed as *incertae sedis*. A more recent tabulation was made by Rützler, van Soest & Piantoni (2009), wherein 18 hexactinellid species names are listed as presumably valid and recognizable, and one additional name is listed as unrecognizable. Unfortunately, neither of these listings is considered by us to be complete and authoritative as regards the Hexactinellida of the region. Many of the names in both lists are incorrect because of old synonymies that were missed or because of an acceptance of discreditable new synonymies proposed without supporting evidence. We provide a new authoritative summary of the hexactinellids reported from this region in Table 1, containing 50 valid species names, of which 30 are considered recognizable. The three new species described below on the basis of their morphology make a significant but minor (10%) addition to the known fauna of the region. Together with the first sequence data from *Lefroyella* Thomson, 1878, also presented here, they do, however, make an important addition to the molecular sequence catalogue of hexactinellid sponges.

Molecular phylogenetic studies (reviewed in Wörheide *et al*., 2012) have indicated that the dictyonal (i.e. with fused choanosomal megascleres) glass sponge order Hexactinosida Schrammen, 1912 does not constitute a monophyletic group, because of the phylogenetic position of Dactylocalycidae Gray, 1867 being closer to Lyssacinosida Zittel, 1877 than to other hexactinosidans. The remaining eight families of Hexactinosida are strongly supported as a clade by both morphological and molecular evidence (reviewed in Wörheide *et al*., 2012), however, forming the taxon Sceptrulophora Mehl, 1992. The group is characterized by the possession of sceptrules (a sceptre-shaped spicule type) and was only recently officially introduced to the Linnean classification of Hexactinellida, provisionally as a suborder of Hexactinosida (Dohrmann *et al*., 2011). Of the eight families, three (Craticulariidae Rauff, 1893, Cribrospongiidae Roemer, 1864, and Fieldingiidae Tabachnick & Janussen, 2004) are monogeneric and have not yet been sampled for molecular studies, whereas another three (Tretodictyidae Schulze, 1886, Aphrocallistidae Gray, 1867, and Farreidae Gray, 1872) are fairly well represented and resolved as monophyletic groups (Dohrmann *et al*., 2011, 2012). Within the framework of the taxon sampling reported in these studies, Tretodictyidae appears to be the sister group of the remaining sceptrulophorans, and Aphrocallistidae and Farreidae are most closely related. One family, Auloplacidae Schrammen, 1912, was only recently resurrected (Reiswig & Kelly, 2011) after the discovery of sceptrules in new representatives of its then only known genus, *Auloplax* Schulze, 1904 (previously in Dactylocalycidae). The most diverse and species-rich family of Sceptrulophora, Euretidae Zittel, 1877, has been thought to have an intermediate position between Tretodictyidae and a well-supported Aphrocallistidae + Farreidae clade, based on molecular evidence (Dohrmann, Collins & Wörheide, 2009; Dohrmann *et al*., 2011, 2012); however, this conclusion was based on a single specimen that we first classified as a member of a new genus of Euretidae, after preliminary investigation of its morphology. Later in-depth investigations reported here revealed that the construction of its dictyonal framework strongly suggests its placement in Auloplacidae instead. This left *Sarostegia oculata* Topsent, 1904 as the sole representative of Euretidae in the published molecular phylogenies; however, that species was only recently, and somewhat provisionally, moved back to Euretidae because its former (mis)placement in Farreidae (Reiswig, 2002a) was strongly rejected by molecular data (Dohrmann *et al*., 2011). Its exact phylogenetic position remains uncertain because of low statistical support (Dohrmann *et al*., 2011, 2012). Thus, the inclusion of three unquestionable representatives of Euretidae in the present molecular analysis allowed us to infer the phylogenetic position of that family for the first time and test its monophyly, which is of special interest because the group constitutes a 'waste-bin taxon' that is not supported by any known potential morphological autapomorphies.

MATERIAL AND METHODS

SPECIMENS

A large variety of unidentified hexactinellids were provided at the PorToL (Porifera Tree of Life) Integrative Systematics Workshop held at Florida Atlantic University, 1–10 August 2011, for species determination and for subsampling to obtain molecular sequences. The specimens originated from submersible collections of Harbor Branch Oceanographic Institute (HBOI), and were thus in excellent physical condition, and were accompanied by images and good-quality collection data. An aim of the workshop was to make additions to the Porifera Tree of Life by finding specimens that provided both good morphological and molecular data. Specimens that proved to be unassignable to known hexactinellid species, and were thus new species, and that also yielded satisfactory molecular sequences were chosen for morphological description. When the basic morphology of the three selected HBOI species had been determined, searches were made for specimens with similar morphology in the HBOI image database and other institutional

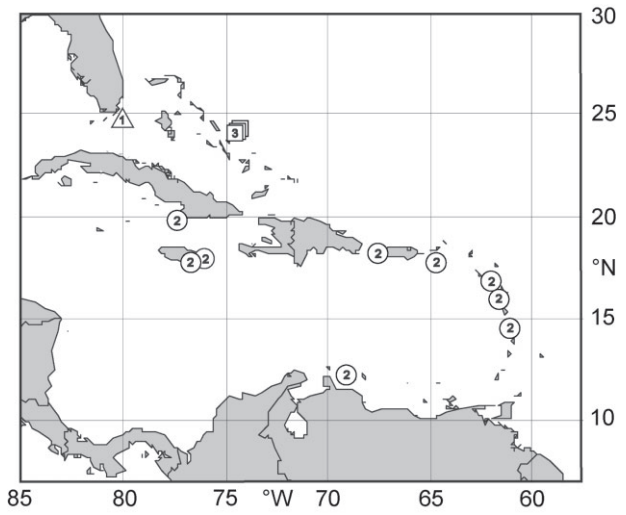

Figure 1. Map of collection sites of new hexactinellid species. 1, ***Conorete pourtalesi*** **sp. nov.** from Pourtales Terrace, Florida, USA. 2, ***Verrucocoeloidea liberatorii*** **sp. nov.** from the following sites, counter-clockwise from the lower centre: Curaçao; Martinique; Montserrat; Guadeloupe; St. Croix; Puerto Rico; Morant Ridge, Jamaica; Pedro Channel, Jamaica; Cape Cruz, Cuba. 3, ***Dictyoplax lecus*** **gen. et sp. nov.** from five closely spaced sites in the Bahamas, with overlapping symbols.

collections. After assessing their details, they were accepted as belonging to species awaiting description. The present known distribution of the three new West Indian species is shown in Figure 1.

Morphological analysis

Specimens were first digitally photographed and, where possible, small fragments of the outer surfaces were removed by forceps, dehydrated, cleared, and whole-mounted on microscope slides in Canada balsam to determine the type and position of surface-associated spicules. Larger samples of dermal surface, atrial surface, and body wall were digested in hot nitric acid (93 °C) for 2 hours. The resulting cleaned skeletal frameworks were rinsed in distilled water and either mounted with epoxy on aluminium stubs for scanning electron microscopy (SEM), or were dissected, dried, and mounted in Canada balsam on microscope slides for light microscopy (LM). Spicules in suspension were isolated from the nitric acid using several techniques. Large megascleres were picked individually from diluted acid solution under a dissecting microscope using a pipette and transferred to distilled water in embryo dishes. They were ultrasonically cleaned for 2 minutes to remove adherent clay particles, rinsed several times in distilled water, and mounted onto 9-mm square coverslips that, after drying, were epoxied to SEM stubs. Smaller spicules in acid suspension were filter-captured and post-rinsed on either 10-mm diameter ion-etched 0.22-μm pore diameter Nuclepore© polycarbonate filters for SEM or 25-mm diameter Millipore© compressed nitrocellulose fibre filters for LM. After drying, filters with spicules for SEM were attached to aluminium SEM stubs by double-sided tape; filters with spicules for LM were cleared in xylene and mounted on microscope slides in Canada balsam. All SEM stub preparations were sputter-coated with gold-palladium and viewed in either a Hitachi S-3400N or S-4800 SEM.

Measurements of spicules were made using compound or dissecting LM linked to a computer-digitizer by drawing tube (camera lucida) and SIGMA-SCAN© 3.92. The relative abundance of spicule types was estimated by categorizing individual spicules sequentially encountered in systematic scans of LM preparations – usually 100–200 spicules. Any potential bias arising from sampling location on the specimen and preparation procedure was minimized by qualitative assessment of preparations from three locations and the avoidance of spicule loss by the use of filtration techniques. Data reported in tables are given as means ± standard deviations and ranges, with the number of measurements; data reported in description text are given as minimum–mean–maximum (with the number of measurements) or simply as means. Diagnoses of families are provided only where change is required to accommodate the new described species. Restricted synonymies are given only where changes of diagnoses are made. The new specimens are deposited in the collections of the Smithsonian Institution, Washington, D.C., USA (USNM). Other institution abbreviations: HBOI, Harbor Branch Oceanographic Institute, Fort Pierce, FL, USA; HBOM, Harbor Branch Oceanographic Museum, Fort Pierce, FL, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; UWI, University of the West Indies, Mona, Jamaica.

Molecular methods and phylogenetic analysis

Near-complete nuclear *18S* and partial *28S* ribosomal DNA (rDNA), as well as mitochondrial partial *16S* rDNA and cytochrome *c* oxidase subunit I (*COI*) sequences from the holotype of *Dictyoplax lecus* gen. et sp. nov., were previously obtained and analysed by Dohrmann *et al*. (2009, 2012) under the name 'Euretidae n. gen. n. sp.'. The same name was used by Dohrmann *et al*. (2011, 2013), whereas in Wörheide *et al*. (2012: fig. 1.5) the taxon was designated as 'Gen. nov., yet-to-be described new genus of "Euretidae" '. Pieces of the same specimen were also used by Bertin *et al*. (2007) for isolation of a creatine kinase sequence (their

'hexactinellid 2', also recognized as a new species of Euretidae following our preliminary identification) and Haen, Pett & Lavrov (2014) for mitochondrial genomics (again as 'Euretidae n. gen. n. sp.').

Ribosomal DNA and *COI* sequences from the holotypes of *Conorete pourtalesi* sp. nov., *Verrucocoeloidea liberatorii* sp. nov., and a specimen of *Lefroyella decora* (HBOI 11-VII-10-1-1; collected on 11 July 2010 at Pourtales Terrace, FL, USA) were amplified using established protocols and primers (Dohrmann *et al*., 2008, 2009, 2012). The amplification of *COI*, the 3′ half of *18S*, and the 5′ half of the *28S* fragment from *V. liberatorii* sp. nov. failed, as did the amplification of *COI* from *L. decora*. Amplicons were purified by agarose gel extraction with a Qiagen Gel Extraction Kit and sent off for Sanger sequencing (for primers, see Dohrmann *et al*., 2008, 2012) to the sequencing facility of the University of Alabama, Birmingham, AL, USA.

The new sequences (GenBank accession numbers HG800594-HG800603) were manually aligned with published hexactinellid orthologues. Initial phylogenetic analyses including all available sequences confirmed that they grouped within the Sceptrulophora clade (results not shown). For the final analysis, the taxon set was thus restricted to Sceptrulophora, with *Iphiteon panicea* Bowerbank, 1869 (Dactylocalycidae) serving as the out-group for rooting purposes (see Dohrmann *et al*., 2011). After the removal of unalignable regions, alignments of the four markers were concatenated, resulting in a supermatrix of 17 taxa × 4831 bp.

Phylogenetic inference was performed in the maximum-likelihood framework using RAxML 7.2.8 (Stamatakis, 2006) under mixed substitution models: a secondary structure-specific model (S16) that takes non-independent evolution of paired sites into account (see Savill, Hoyle & Higgs, 2001) was applied to the stem-encoding regions of the nuclear rDNA markers, and independent general time-reversible (GTR) models (Lanave *et al*., 1984) were applied to *18S* loop-encoding regions, *28S* loop-encoding regions, *16S*, and *COI*. For each of the five partitions, among-site rate variation was modelled independently with a four-category discrete approximation to a gamma distribution ($+G_4$; Yang, 1994). As a proxy for clade accuracy, robustness to character resampling was used by employing rapid bootstrapping (Felsenstein, 1985; Stamatakis, Hoover & Rougemont, 2008); the number of sufficient pseudoreplicates was determined automatically with the 'autoMRE' criterion (Pattengale *et al*., 2010). RAxML was invoked with the '–f a' option, using the Pthreads-parallelized compilation. The final supermatrix and the associated structure, partition, and tree files are available at Open Data LMU (http://dx.doi.org/10.5282/ubm/data.57).

RESULTS

Morphological descriptions and systematic account

Class Hexactinellida Schmidt, 1870

Subclass Hexasterophora Schulze, 1886

Order Hexactinosida Schrammen, 1912

Suborder Sceptrulophora Mehl, 1992

Family Euretidae Zittel, 1877

Subfamily Euretinae Zittel, 1877

Genus *Conorete* Ijima, 1927

Restricted synonymy: Conorete Ijima, 1927: 165; de Laubenfels 1936: 187; Reid 1958: 18; Reiswig & Wheeler 2002: 1305, Reiswig & Kelly 2011: 45. *Eurete* (in part) Semper, 1868: 30. *Eurete (Conorete)* Reid 1958: 224.

Diagnosis: Euretidae of either simple tubular form or globular mass of branching and anastomosing tubules; unchannellized; with pinular hexactins as dermalia, macrospined pentactins, and/or pinular hexactins as atrialia. (From Reiswig & Wheeler, 2002, emended.)

Type species: Eurete erectum Schulze, 1899: 72.

Conorete pourtalesi sp. nov. (Figs 2, 3; Table 1)

Type material: Holotype: USNM 1231335, MOV '*Johnson Sea Link II*', dive 3817, 07 Aug. 2010, Alligator bioherm 1635, Pourtales Terrace, Florida, 24°42.2806′ N, 80°30.6811′ W, 198 m, 70% ethanol.

Comparative material: Conorete mucronatum (Wilson, 1904, originally *Eurete erectum mucronatum*), co-types, USNM 008488, USFS *Albatross*, stn 3358, 24 Feb. 1891, Gulf of Panama, 6°30′ N, 81°44′ W, 1015 m, four specimens, ethanol.

Diagnosis: Conorete with pinular rays of dermal hexactins styloid in form, rarely bushy; all atrialia as macrospined pentactins. Microscleres mainly oxyhexasters with discohexasters and onychohexasters as minor components.

Description: General body form of the single known specimen is clathrate–globular, an ovoid mass of branching and anastomosing tubes with overall dimensions 9.8 × 7.0 × 6.4 cm (Fig. 2A). Length of internodal components of tubes approximates tube diameter in the compact form. External tube diameter is 7.4–9.5–14.3 ± 1.4 mm (n = 24), internal diameter is 4.5–6.6–9.4 ± 1.3 mm (n = 14), and wall thickness is 1.2–1.5 mm. Tube surfaces appear fairly smooth to the naked eye, but under a dissection microscope it bears shallow pits and poorly defined ridges (Fig. 2B). Removal of tissues shows that these shallow pits are not canal

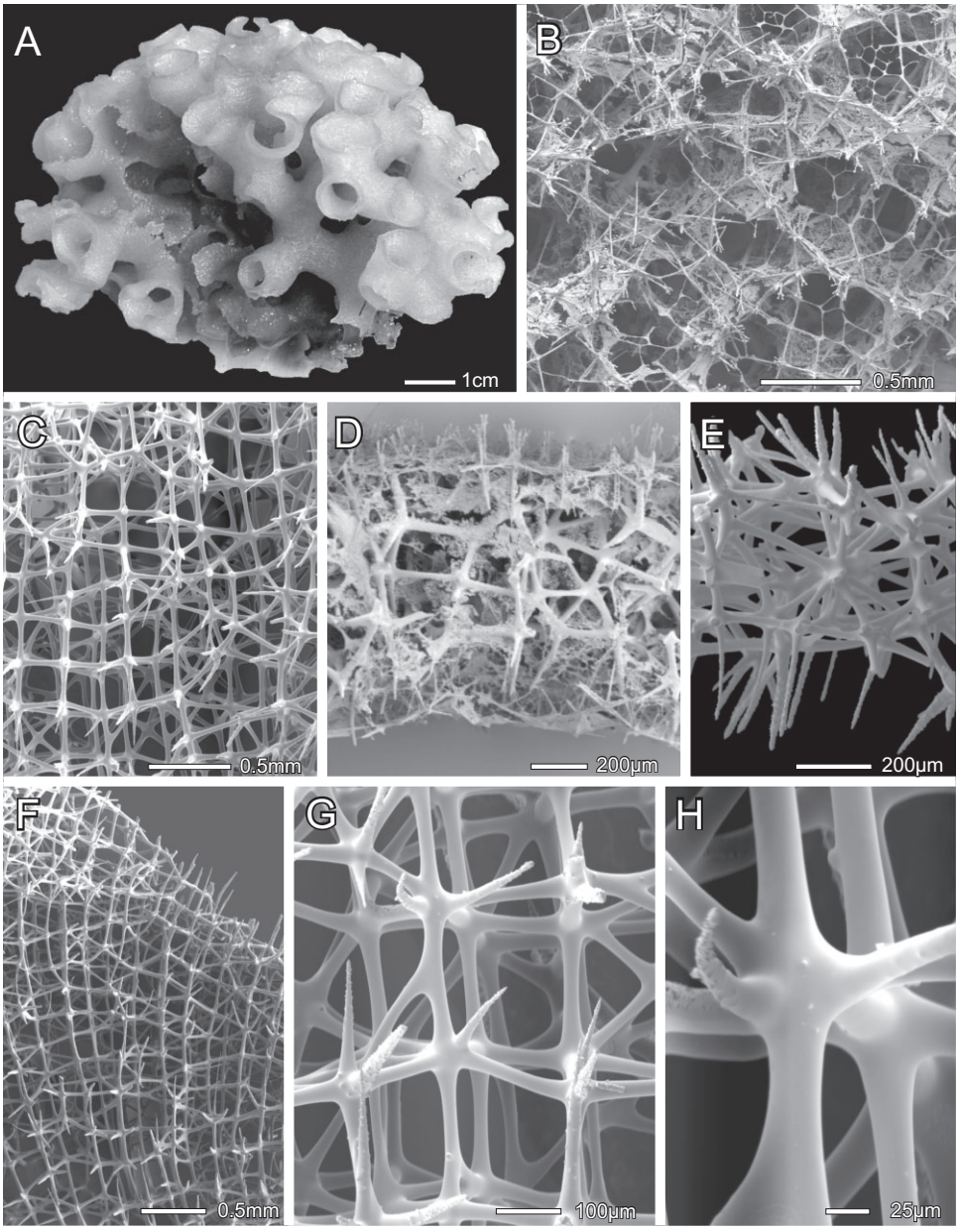

Figure 2. ***Conorete pourtalesi*** **sp. nov.**, holotype body and framework: A, deck photo of the holotype; B, dermal surface with tissues and spicules in place (SEM); C, cleaned dermal framework (SEM); D, cross section with tissues and spicules in place, dermal side up (SEM); E, cross section of cleaned framework, dermal side up (SEM); F, cleaned atrial framework, marginal direction up (SEM); G, magnified cleaned dermal framework (SEM); H, high magnification of framework node and beams with rare small spines.

apertures but merely irregularities in the surface dictyonalia (Fig. 2C, F); skeletal channels are not present. Spiculation of outer and inner surfaces of the tubes differ dramatically: outer surfaces are ornamented with projecting distal rays of hexactine dermalia, uncinate tips, and scopules, whereas the smooth inner surfaces are defined by tangential rays of pentactine atrialia (Fig. 2D). Colour, when preserved, is light brown. Symbionts consist of a dark-brown branching system of tentaculate hydrozoans with polyps opening on both inner and outer tube surfaces. The known distribution of the species is a single depth, 198 m, at a single location off southern Florida on the Pourtales Plateau (Fig. 1).

The skeletal framework (for data see Table 1) is a typical euretoid dictyonal type, of between three or four

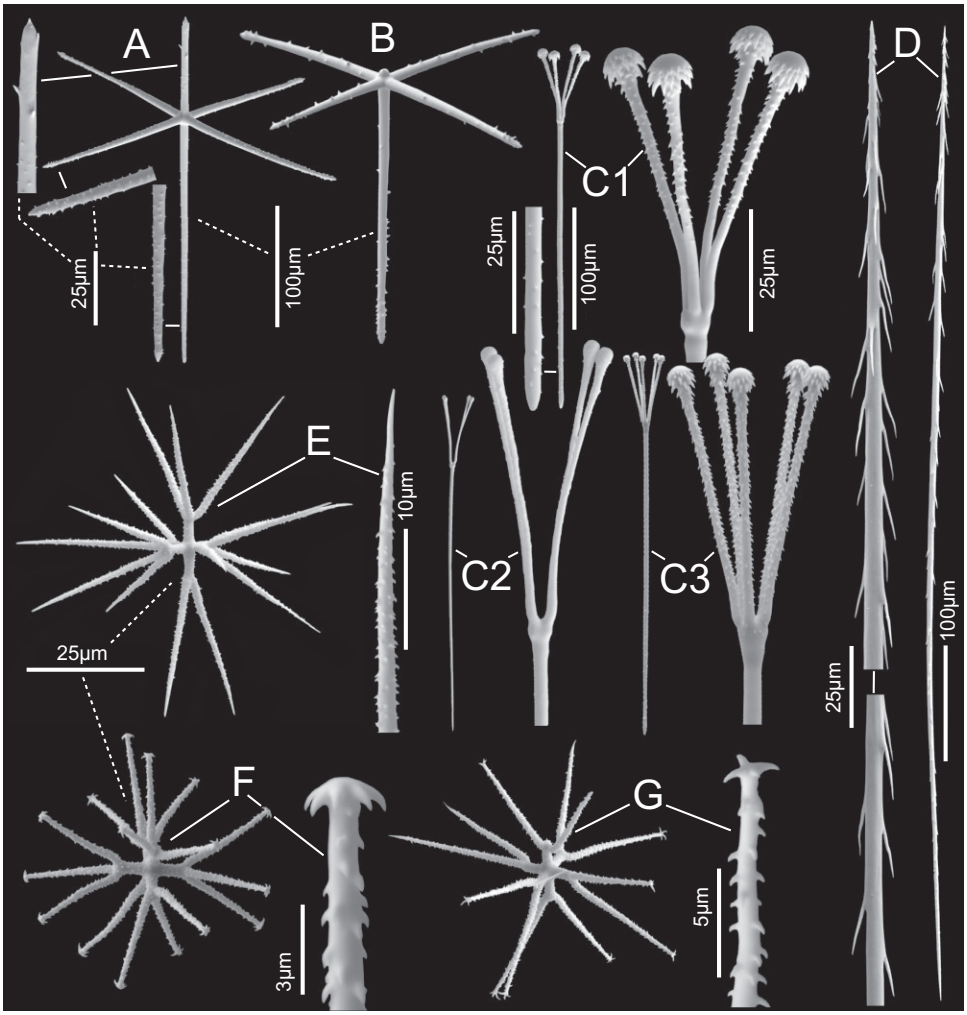

Figure 3. ***Conorete pourtalesi*** **sp. nov.**, holotype spicules (SEM): A, dermal hexactin with enlarged distal, tangential, and proximal ray ends; B, typical atrial pentactin; C1, geniculate tyloscopule, whole and magnified head and shaft tip; C2, subtyloscopule, whole and magnified head; C3, non-geniculate tyloscopule, whole and magnified head; D, uncinate, whole and enlarged anterior and middle segments; E, oxyhexaster, whole and enlarged terminal ray tip; F, discohexaster, whole and enlarged terminal ray tip; G, mixed onycho- and oxyhexaster with enlarged onychoid ray tip.

meshes in thickness (Fig. 2D–E). Longitudinal strands are present in the primary layer; they curve gently at low angles to both dermal and atrial surfaces. Irregularly arranged dictyonalia form thin patchy cortices on older areas of both surfaces. Beams are mainly smooth, with a few low spines occurring irregularly on beams or nodes (Fig. 2G–H); nodes are not swollen. Dictyonal meshes are primarily rectangular, often square. Spurs of both surfaces are long, mainly straight, rough, and sharp-pointed (Fig. 2E, G). No small oxyhexactins are appended to the framework.

Megascleres are surficial hexactins and pentactins, tylo- and subtyloscopules, and uncinates. Dermalia are mainly finely rough hexactins (Fig. 3A), with distal ray more or less differentiated by larger spines. These distal rays are occasionally bushy and pinular, in the sense of differing in form from other rays, but not in the sense of being similar to a small fir tree. Other rays are tapered and end in abruptly sharp tips. The mean dimensions of rays are: distal, 67 × 6.8 µm; tangential, 130 × 6.6 µm; and proximal, 162 × 6.7 µm. A few dermalia (< 1%) are pentactins. Atrialia are all pentactins, sparsely ornamented with macrospines and with the missing distal ray represented only by a nub (Fig. 3B). Atrialia tangential rays, 140 × 8.7 µm; atrialia proximal rays, 196 × 9.0 µm. Scopules are mostly geniculate tyloscopules, with between two and five distally spined tines ending in large caps (Fig. 3C1; 60%), common non-geniculate tyloscopules, with between three and five rough tines ending in smaller caps (Fig. 3C3; 34%), and uncommon subtyloscopules (Fig. 3C2; 6%), with three or four thin smooth tines bearing small

Table 1. List of recognizable and unrecognizable Hexactinellida species names reported from the area encompassing the West Indies, Caribbean Sea, and Gulf of Mexico, with accepted junior synonyms excluded

AMPHIDISCOSIDA RECOGNIZABLE, VALID: 5
Hyalonema kenti (Schmidt, 1880: 65, as *Asconema*)
Hyalonema schmidti Schulze, 1899: 9
Hyalonema toxeres Thomson, 1873: 248
Pheronema annae Leidy, 1868: 10
Poliopogon amadou Thomson, 1873: 29
LYSSACINOSIDA RECOGNIZABLE, VALID: 11
Asconema foliata (Fristedt, 1887: 413 as *Hyalonema*)
Calycosoma validum Schulze, 1899: 27
Euplectella jovis Schmidt, 1880: 60
Euplectella suberea Thomson, 1876: 93
Hertwigia falcifera Schmidt, 1880: 62
Heterotella pomponae Reiswig, 2000: 573
Lophocalyx oregoni Menshenina *et al*., 2007: 455
Regadrella phoenix Schmidt, 1880: 61
Rhabdopectella tintinnus Schmidt, 1880: 62
Sympagella nux Schmidt, 1870: 15
Vazella pourtalesi (Schmidt, 1870: 14 as *Holtenia*)
HEXACTINOSIDA RECOGNIZABLE, VALID: 9
Aphrocallistes beatrix Gray, 1857: 115
Claviscopulia facunda (Schmidt, 1870: 16 as *Farrea*)
Cyrtaulon sigsbeei (Schmidt, 1880: 58 as *Volvulina*)
Dactylocalyx pumiceus Stutchbury, 1841: 87
Dactylocalyx subglobosus Gray, 1867: 506
Farrea occa Bowerbank, 1862: 1118
Iphiteon panicea Bowerbank, 1869: 76
Lefroyella decora Thomson, 1877: 403
Myliusia callocyathus Gray, 1859: 439
AULOCALYCOIDA RECOGNIZABLE, VALID: 2
Cyathella lutea Schmidt, 1880: 46
Rhabdodictyum delicatum Schmidt, 1880: 46
LYCHNISCOSIDA RECOGNIZABLE, VALID: 3
Lychnocystis superstes (Schmidt, 1880: 51 as *Cystispongia*)
Neoaulocystis grayi (Bowerbank, 1869: 335 as *Myliusia*)
Scleroplegma lanterna (Schmidt, 1880: 50 as *Auloplegma*)
UNRECOGNIZABLE BUT VALID NAMES: 20
Dactylocalyx crispus Schmidt, 1870: 19
Dactylocalyx potatorum Schmidt, 1880: 53
Deanea virgultosa Bowerbank, 1875: 275
Diaretula cornu Schmidt, 1879: 45
Diaretula muretta Schmidt, 1880: 46
Farrea aculeata Bowerbank, 1875: 561
Farrea fistulata Bowerbank, 1875: 276
Farrea gassioti Bowerbank, 1875: 272
Farrea inermis Bowerbank, 1876: 536
Farrea infundibuliformis Carter, 1873: 448
Farrea laevis Bowerbank, 1875: 278
Farrea parasitica Bowerbank, 1875: 279
Farrea perarmata Bowerbank, 1876: 538
Farrea pocillum Bowerbank, 1875: 273
Farrea robusta Bowerbank, 1875: 562
Farrea spinifera Bowerbank, 1875: 558
Myliusia conica (Schmidt, 1880: 57 as *Scleroplegma*)
Myliusia seriatum (Schmidt, 1880: 57 as *Scleroplegma*)
Rhabdostauridium retortula Schmidt, 1880: 59
Scleroplegma herculeum Schmidt, 1880: 57

smooth terminal swellings. Scopules with a total length of 304 μm are very abundant on the dermal surface but are absent from the atrial surface; a few subtyloscopules occur in subatrial position between atrialia, but do not extend to the surface membrane. Uncinates (Fig 3D) are relatively small for Euretidae, with a mean length of 763 μm and a mean width of 4.7 μm, but their barbs and brackets are well developed; the anterior end is rather bushy.

Microscleres are all spherical, composed mainly of oxyhexasters (71%), accompanied by common discohexasters (26%), and rare onychohexasters (4%). Oxyhexasters with a mean diameter of 73.5 μm are robust, with between two and four sharply pointed straight terminals borne on each primary ray; all surfaces are covered with fine recurved spines (Fig. 2E). Discohexasters are similar to oxyhexasters, but are smaller and with marginally spined discs at terminal ray ends (Fig. 3F). Onychohexasters have between two and five small claws emanating perpendicularly from the distal ends of terminal rays. Individual microscleres with mixed oxy- and onycho-tips are common; terminal rays from a single primary ray often differ in form (Fig. 3G). Disco- and onychohexasters are 55.0 μm in mean diameter.

Etymology: The species name '*pourtalesi*' commemorates Louis François de Pourtalès (1824–1880), a student and close associate of Alexander Agassiz who together carried out the early explorations of the West Indian marine fauna. Pourtalès' historical importance is reflected in the name of the collection location: Pourtales Terrace.

Remarks: The new specimen with hexactine dermalia and macrospined atrialia clearly belongs to the genus *Conorete* as diagnosed in Systema Porifera (Reiswig & Wheeler, 2002). The genus presently contains three recognized species: the type species, *Conorete erectum* (Schulze, 1899), containing four subspecies, all from the tropical eastern Pacific; *Conorete mucronatum* (Wilson, 1904), from the same region; and *Conorete gordoni* Reiswig & Kelly, 2011, from the Kermadec Ridge north of New Zealand. All specimens of the first two species have columnar form, basically elongate tubular stems with lateral tubular branches in a spiral pattern. The body is usually simple, flute-like, but occasionally undergoes secondary branching without anastomoses. This contrasts with the globular form of the new species with extensive anastomoses of tubes. The body form of the third species, *C. gordoni*, remains unknown, but the small elongate tubule fragment with lateral oscula is consistent with the columnar form of the first two species, and is inconsistent with the tightly branching globular form of the new species. In spiculation all three present species have bushy pinules

of surface hexactins, whereas the new species differs in having mainly sparsely spined styloid pinules. The new species shares oxyhexasters as the major microsclere with *C. mucronatum* and *C. gordoni*, but differs from *C. mucronatum* in having some discohexasters (*C. mucronatum* has none); it differs from *C. gordoni* in having tyloscopules as the main scopule form (*C. gordoni* has mainly subtyloscopules of quite different shape). These differences justify the recognition of the new specimen as a new species, here designated *C. pourtalesi* sp. nov. This addition to the genus *Conorete* is the first member known from the Atlantic basin; it expands the distribution of the genus *Conorete*, which has previously been restricted to the eastern and western coasts of the equatorial and the southern Pacific Ocean.

Framework type, as farreoid or euretoid, has been an element of considerable interest in this genus since the description of its first species, *Conorete* (then *Eurete*) *erectum* by Schulze (1899). He noted that the terminal tube ends had a single-layered frame, like the condition in *Farrea*, and unlike the general three-dimensional non-layered framework of *Eurete*. Most later workers did not comment on the framework of *Conorete* specimens, but Wilson (1904) noted that occasional areas of one-layered frame occurred in *C. erectum tubuliferum*, and Reiswig & Kelly (2011) reported areas of one-layered farreoid framework in *C. gordoni*. In our review of *C. mucronatum* co-type fragments we did not have access to terminal tube ends, but the framework is definitely two-layered, with the second layer being a mirror image of the primary atrial layer, and completely in register with it. This is consistent with Reid's (1964) definition of an expanded farreoid framework and inconsistent with his definition of a non-layered euretoid framework; however, our detailed review of the framework of the new species shows it to be three-dimensional and non-layered, with longitudinal strands curving to both dermal and atrial surfaces, completely consistent with Reid's description of a euretoid framework. Unfortunately, we do not have undamaged terminal tube ends of this specimen to assess whether those areas are one-layered or three-dimensional. More detailed surveys of primary framework details in various members of Euretidae and Farreidae are needed to develop a better understanding of the range of framework form in the genera of these families, and how they and individual species might be related by shared patterns.

Subfamily Chonelasmatinae Schrammen, 1912

Genus *Verrucocoeloidea* Reid, 1969

Restricted synonymy: Verrucocoeloidea Reid, 1969: 485; Finks *et al*. 2011: 73.

Diagnosis: Cylindrical to funnel-shaped euretids with short lateral tubes in quincuncial, linear–longitudinal, or irregular arrangement; each lateral tube sometimes with an axillary oscule on the upper side, in addition to the terminal oscule; lateral tubes confluent with an internal system of plexiform (and spiral?) longitudinal tubes or irregular subdivisions of the atrial cavity formed by ingrowths of the atrial wall that may be only partially skeletalized; a cortex with ostia may be developed on the dermal side. Loose spicules include pentactins, hexactins, tyloscopules, strongyloscopules, uncinates, oxyhexasters, and discohexasters. (From Finks *et al*., 2011, emended.)

Type species: Verrucocoeloidea burtoni Reid, 1969.

Remarks: The original diagnosis of Reid (1969) was emended by Finks *et al*. (2011) to include a fossil species with main body form as a cylindrical tube. Finks *et al*. divided the genus into two subgenera, *Verrucocoeloidea* Reid, 1969 and *Euretella* Finks *et al*., 2011, to accommodate the recent type species, *V. burtoni*, with funnel-form body in the first, and their new cylindrical Eocene species, *Verrucocoeloidea corallina*, in the second. Here we do not deal with the subgenera diagnoses formed by Finks *et al*. (2011), as we are not involved with fossil material.

Verrucocoeloidea liberatorii sp. nov.

(Figs 4, 5; Table 2)

Type material: Holotype: USNM 1231336, MOV '*Johnson SeaLink II*', dive 3210, 11 May 2000, Seamount, off Porto Mari Baai, south-central coast, Curacao, 12°12.853′ N, 69°05.837′ W, 220 m. Paratypes: HBOM 002:00027, same data; USNM 1231337, same data; USNM 22339, Johnson-Smithsonian Deep Sea Expedition, MV *Caroline*, stn 49, 14 Feb. 1933, north of Puerto Rico, 18°14′18″ N, 67°35′30″ W, 329 m (misidentified by M.W. de Laubenfels as *Cyrtaulon sigsbeei*); USNM 00985, Caribbean Islands Expedition, 1878–1879, USFS *Blake*, stn 158, 17 Jan. 1879, off Montserrat, 16°30′ N, 62°00′ W, 271 m (misidentified by unknown as *Volvulina sigsbeei*); USNM 00986, United States Coast Survey, USFS *Blake*, stn 22, May 1880, east of Cape Cruz, Cuba, 19°48′47″ N, 77°23′00″ W, 457 m (two specimens, misidentified by O. Schmidt as *Volvulina sigsbeei*); MCZ 25428, Caribbean Islands Exploration Expedition, 1878–1879, USFS *Blake*, stn 210, 12 Feb 1879, off Martinique, 14°29′10″ N, 61°05′47″ W, 349 m (misidentified by unknown as *Volvulina sigsbeei*); MCZ 25429, Caribbean Islands Exploration Expedition, 1878–1879, USFS *Blake*, stn 166, 21 Jan 1879, off Guadeloupe, 15°55′50″ N, 61°37′05″ W, 274 m, three specimens, unidentified; MCZ 25436, Caribbean Islands Exploration Expedition, 1878–1879, USFS

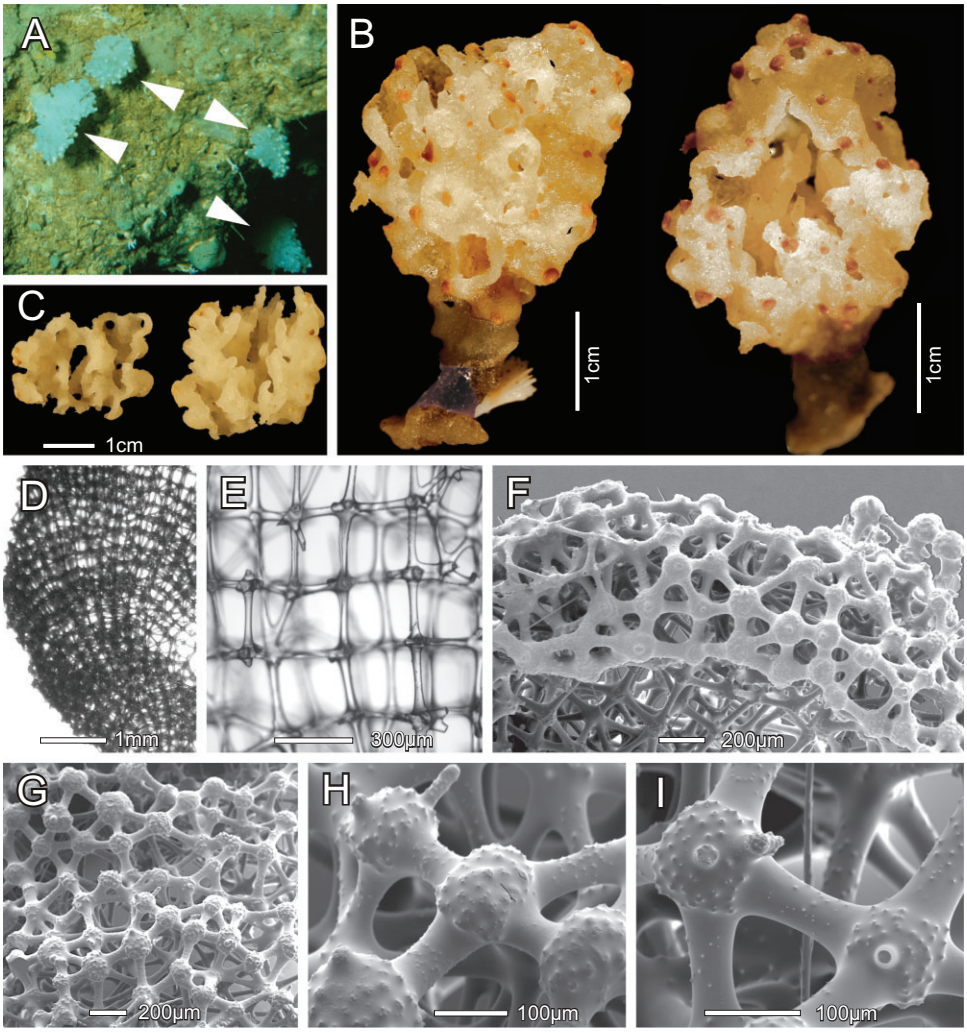

Figure 4. ***Verrucocoeloidea liberatorii*** **sp. nov.**, body and framework: A, four specimens *in situ* (arrowheads) at type locality prior to collection, including the holotype and two paratypes, 5–6 cm in height; bright reflective spots are zoanthid symbionts; B, the preserved holotype in side (left) and top (right) view, orange-brown spots are zoanthid symbionts; C, fragments of two paratypes, USNM 1231337 (left) and HBOM 002:00027 (right), opened to view the atrial surfaces with ingrowths; D, thin wall area between tubules, showing the overall regularity of the dictyonal framework, with the growth direction upwards; E, primary framework dissected from wall fragment, showing longitudinal strands, aligned transverse connecting beams, and simple unswollen nodes; F, cleaned framework of tubule margin of lateral osculum, showing external cortical surface with swollen nodes and internal atrial surface (below) with smaller nodes, note general lack of spurs (SEM); G, clean external body surface framework with swollen nodes (SEM); H, close-up of external framework showing nodes ornamented with groups of small spines and a few spurs (SEM); I, a different area with nodes ornamented with single conical evenly spaced spines (SEM). All microscopic images are taken from the holotype.

Blake, stn 139, 17 Jan 1879, off St Croix, US Virgin Islands, 17°46′45″ N, 64°48′50″ W, 399 m, unidentified; UWI GSN564, RV *Gosnold*, stn 112/88, 26 Feb. 1968, Pedro Channel, Jamaica, 17°45.8′ N, 76°45.0′ W, 1500 m (misidentified by H.M. Reiswig as *Dactylocalyx crispus*); UWI GSN062 & GSN1277B, RV *Gosnold*, stn 97/35, 18 Mar. 1967, Morant Ridge, Jamaica, 17°54.9′ N, 76°05′ W, 420 m (misidentified by H.M. Reiswig as *Dactylocalyx crispus*).

Diagnosis: Recent *Verrucocoeloidea* of plicate funnel form, with external nodes markedly swollen and spined; lateral oscula distributed without order or on longitudinal ridges. Atrial ingrowths end in simple ridges with digitate upper ends or occasionally fuse with other ridges, but not forming a secondary lining of the atrium. Loose spicules include pentactine dermalia and atrialia, tyloscopules, strongyloscopules, uncinates, oxyhexasters, and discohexasters.

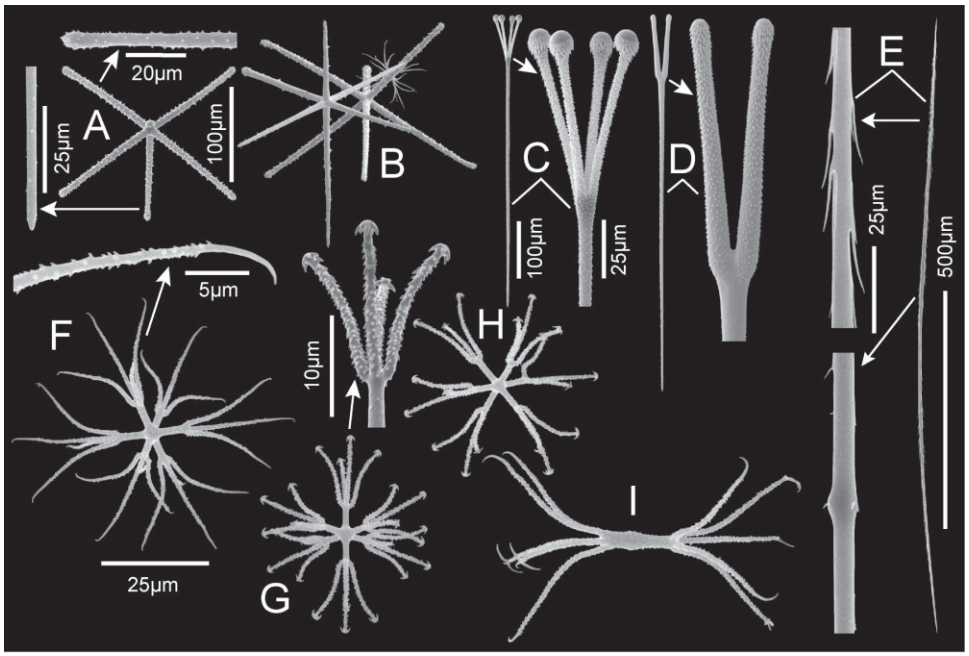

Figure 5. ***Verrucocoeloidea liberatorii*** **sp. nov.**, holotype spicules (SEM): A, dermal pentactin, whole and enlarged tangential and proximal ray ends; B, two atrial hexactins, same scale as (A); C, dermal tyloscopule, whole and enlarged head end; D, dermal subtyloscopule, whole and enlarged head end, same scales as (C); E, uncinate, whole and enlarged anterior and middle parts; F, oxyhexaster, whole and enlarged terminal ray end; G, discohexaster, whole and one enlarged ray cluster; H, onycho/discohexaster, with some terminal tips discoid and some onychoid; I, diaster, with oxyoid and onychoid ray tips; all whole microscleres at same scale as (F).

Description: Body form of all known specimens is basically consistent with that of the four specimens imaged in the type collection (Fig. 4A) and that of the holotype (Fig. 4B). The holotype is a small upright globular funnel or cup borne on a short stalk with tubular lateral extensions uniformly scattered and ending distally as small openings: the lateral oscula. The large terminal osculum is strongly plicate in shape (Fig. 4B right), as distal growth conforms to the formation of lateral tubules at its margin. Some specimens are longitudinally pleated with between two and five external ridges extending from the upper end of the stalk to the osculum, separated by deep grooves almost meeting axially. In some specimens the external tubules are restricted to the ridges, and thus occur only in longitudinal series; in others, the tubules are distributed evenly on ridges and in grooves. The holotype is 46.5 mm tall, 29.9 and 32.0 mm in greatest lateral diameters, with greatest diameters of the main osculum of 15.1 and 16.8 mm; other specimens range from 15 to 60 mm in height. Lateral tubules of the holotype are 4.0–5.5–6.5 mm (n = 23) in external diameter, 2.3–4.9–7.5 mm (n = 14) in length, and 1.1–1.9–2.9 mm (n = 28) in diameter of their distal oscula opening; external tubule diameters may be as small as 2.0 mm in other smaller specimens. Wall thickness is 0.55–0.92–1.93 mm (n = 41) where ingrowth does not occur. In many areas of the atrial surface, without a clear pattern, the inner wall is extended several millimetres into the atrium as longitudinal ridges and upright stalagmite-like digital pillars (Fig. 4B right, C), occasionally fusing, subdividing the atrial cavity, and strengthening the thin outer body wall. Both dermal and atrial surfaces are covered by a loose lattice of pentactins and occasional hexactins arranged in fairly regular quadrate meshwork. Colour of freshly collected specimens is white; after preservation, they are light orange. Symbionts of the holotype and probably all specimens include small orange to dark-brown cnidarian polyps, probably zoanthids, scattered across the external surface (Fig. 4B and strong reflective spots in Fig. 4A), which do not seem to be connected through the sponge by internal stolons, but a histological search for them has not been carried out. A large syllid polychaete occupies a pocket of the holotype atrial cavity. The species is widely distributed throughout the Greater and Lesser Antilles (Fig. 1) at depths of 271–1500 m.

The fused skeleton (Fig. 4D) consists of a thin primary framework overlain on all dermal surfaces and most of the atrial surface by irregular secondary cortex. Channellization is not present. The primary framework is euretoid in having dictyonalia linearly fused

Table 2. Framework and spicule dimensions of ***Conorete pourtalesi* sp. nov.**, holotype, USNM 1231335 (dimensions in μm)

Parameter	Mean	SD	Range	No.
Framework				
Dermal beam length	218	40	115–308	50
Dermal beam width	26.1	3.2	20.7–36.2	50
Atrial beam length	234	43	132–328	50
Atrial beam width	24.9	4.8	16.6–36.3	50
Dermal spur length	239	55	130–386	50
Atrial spur length	261	34	192–345	50
Dermal pinular hexactin				
Tangential ray length	130	19	88–170	50
Tangential ray width	6.6	1.2	5.1–10.0	50
Proximal ray length	162	47	69–232	50
Proximal ray width	6.7	1.3	3.7–10.1	50
Distal ray length	67	24	18–143	50
Distal ray width	6.8	1.3	4.4–9.9	50
Atrial pentactin				
Tangential ray length	140	18	105–176	50
Tangential ray width	8.7	1.5	4.8–12.1	50
Proximal ray length	196	48	107–282	50
Proximal ray width	9.0	1.5	6.3–12.3	50
Uncinate length	763	72	611–948	50
Width	4.7	0.8	2.8–6.5	50
Tyloscopule length	304	34	249–388	50
Head length	66.6	6.3	49.1–81.7	50
Tine length	57.3	5.8	39.4–70.2	50
Oxyhexaster diameter	73.5	7.5	47.8–87.6	50
Primary ray length	6.3	1.0	4.2–8.3	50
Secondary ray length	31.0	3.4	18.3–37.8	50
Onycho/discohexaster diameter	55.0	6.7	40.1–70.7	50
Primary ray length	5.3	1.0	2.7–8.4	50
Secondary ray length	22.6	2.7	16.7–28.4	50

to form longitudinal strands with nodes aligned and beams outlining rectangular meshes (Fig. 4E); it is between two and four dictyonalia in thickness, and is not layered. Nodes are simple, not swollen, and most surfaces are smooth, with occasional spination on both beams and nodes (see measurements in Table 2). On some internal patches of particularly thin body wall, the primary framework is not covered by an atrial cortex. The secondary cortical layers on dermal and atrial sides are composed of dictyonalia fused irregularly forming triangular to occasional polygonal meshes (Fig. 4F, G). All superficial cortical nodes are conspicuously swollen and ornamented with either small spines in groups (Fig. 4H) or evenly distributed single conical spines (Fig. 4I). Subsurface cortical nodes may be only slightly swollen, but they always exhibit spined ornamentation. Beams of the cortical layers are ornamented with simple spines scattered over their centres, but areas adjacent to nodes are smooth. Node diameter and beam thickness of the dermal cortex are greater than those of the atrial cortex, which are, in turn, greater than those of the primary layer. Spurs are uncommon and often broken on both surfaces, but where present they are short and digitate with rounded tips (Fig. 4H). No oxyhexactins are appended to the framework.

Megascleres are mostly pentactins, a few hexactins, two types of scopules, and uncinates. Dermalia are pentactins (Fig. 5A), entirely thickly spined with nearly cylindrical tangential rays ending in slightly inflated rounded tips; a small nub is present in place of the sixth distal ray. Atrialia are mostly (99%) similar pentactins and a few (1%) hexactins with short distal rays (Fig. 5B); the hexactins are often less densely spined and rays are often tapered to abruptly sharp tips. Mean lengths and widths of pentactine dermalia and atrialia are 152 × 7.2 μm for tangential rays and 125 × 7.4 μm for proximal rays. Tyloscopules, 315 μm in mean total length (Fig. 5C), are the most abundant scopule form, particularly on the dermal side; their necks are

smoothly tapered from the shaft and carry between two and six tines ending in spherical tyles with bare tops; they are entirely and densely covered with fine reclined spines. On the atrial side the tyloscopules are relatively uncommon, and those present have smaller terminal tyles. Strongylo- to subtyloscopules (Fig. 5D) are larger, with mean length 603 μm, uncommon, and occur in small patches, projecting from both dermal and atrial surfaces; their necks arise abruptly from the shaft heads and bear four stout tines ending as either simply rounded or slightly inflated tips with small bare apices. Reclined spines densely cover the head and tines, but spination on the shaft is sparse. Uncinates (Fig. 5E) are moderate in size, length 1323 μm, with well-developed brackets and barbs; a central swelling occurs in about half of these. All megasclere types have been found in all listed specimens, except strongylo/subtyloscopules, which have not been found in MCZ 25436.

Microscleres consist of oxyhexasters (91.5%), discohexasters (5.5%), hemioxyhexasters (2%), onychohexasters (1%), and oxy/onychodiasters (< 1%). Oxyhexasters, mean diameter 63.5 μm (Fig. 5F), and hemioxyhexasters are distinctive in form, being stellate and having between one and five sigmoid terminal rays curving strongly outwards; they bear fine reclined spines on all surfaces except the hooked terminal tips, and spination is less dense on primary rays. The smaller discohexasters, mean diameter 41.0 μm (Fig. 5G), are stellate, with between three and five similarly sigmoid terminals ending in discs with between four and eight strong marginal spines; reclined spines are very dense on terminals and sparse on primary rays. Onychohexasters (Fig. 5H) grade smoothly into discohexasters, and individual spicules have some terminals clearly onychoid and some clearly discoid; they are most likely to be young discohexasters that have not yet been fully developed. Diasters (Fig. 5I) occur with between three and six terminals either all bearing oxyoid tips or with some bearing onychoid tips, as illustrated. Special distributions have not been detected for any of these microsclere types. The complete set of microscleres have been found in all of the listed specimens.

Etymology: The species name, '*liberatorii*', is formed to recognize the extensive discoveries and collections of sponges and other benthic marine organisms made by Dominic Liberatore during his long career as a submersible pilot at HBOI: he and Dr Shirley Pomponi collected the holotype and two paratypes of this new species.

Remarks: The new species is unquestionably a member of the family Euretidae by virtue of its primary framework and lack of special channellization. In body form it is similar to several species of hexactinellids in the genera *Anomochone* Ijima, 1927, *Cyrtaulon* Schulze, 1866, *Calyptorete* Okada, 1925, *Dactylocalyx*, and *Verrucocoeloidea*; indeed, paratypes were often misidentified as species of the first four genera. The new form is excluded from the tretodictyid genera *Anomochone* and *Cyrtaulon* because of the lack of any indication of schizorhyses and absence of the distinctive scopule-like cyrtaulon spicule. The new form differs from the single species of *Calyptorete*, *Calyptorete ijimai* Okada, 1925, in having much smaller dermalia/atrialia, and in having oxyhexasters, swollen surface dictyonal nodes, and ingrowth of the atrial wall. The new form differs from *Dactylocalyx crispus* Schmidt, 1870 in that the type series of that species is a mixture, the main and illustrated specimen of which is identical to the tretodictyid *Cyrtaulon sigsbeei* (Schmidt, 1880) (pers. observ., H.M.R.). We compared the new specimen with the original description of *Verrucocoeloidea burtoni* Reid, 1969 and its redescription in *Systema Porifera* (Reiswig & Wheeler, 2002) and two of the co-type specimens. We consider the shared characters sufficiently strong to accept placement in the same genus. Shared characters by *V. burtoni* and the new species include body form, which is almost identical, extension of the atrial wall framework into the atrial cavity, and their formation of secondary longitudinal structures known nowhere else in Euretidae. They also share similarity of primary framework and oxyhexaster shape, among other features. The two species differ in that *V. burtoni* has all dictyonal nodes simple (not swollen), dermal epirhyses (absent in the new form), discohexasters as primary microsclere (versus oxyhexasters), and much larger uncinates (up to 3.6 mm, versus 1.8 mm). Examples of all of these differences can be found between species within other genera of Euretidae. Among all Euretidae, the genus *Verrucocoeloidea* is by far the best placement for the new form and preferable to the erection of another new monospecific genus. This previously monospecific genus has been known only from the tropical Indopacific region (Borneo); the addition of the new West Indian species expands the generic distribution and strengthens the systematic ties between the two tropical regions. The new species, *V. liberatorii* sp. nov. has been long known to one of us (H.M.R.) as a common but problematic species in many institution collections under the informal name 'the sugar candy, pillow tube down sponge'; we suggest the retention of this awkward but descriptive designation as the common name of the species.

Family Auloplacidae Schrammen, 1912

Restricted synonymy: Auloplacidae Schrammen, 1912: 191; Zittel 1915: 74; Reiswig & Kelly 2011: 136. Dactylocalycidae (in part) Gray, 1867: 505; Reiswig

2002b: 1293; Finks *et al*. 2004: 542. Tretodictyidae (in part) Schulze, 1886: 78; Ijima 1927: 112; Reid 1963: 229; Mehl 1992: 58; Finks *et al*. 2004: 501.

Diagnosis: Basiphytous Hexactinosida with rigid erect body on a short tubular stem; upper body consisting of one to several vertical plates or fans composed of either conjoined thin-walled tubes dividing acutely, and remaining tightly connected side by side, or of a network of tubes arising by the closure of marginally developing atrial grooves. Constituent tubes are open distally and by lateral oscula. Framework consists of two major recognizably different components: thin sieve area supported by coarse thick beams circumscribing large irregular polygonal meshes, and a more extensive reticular area, two or more meshes thick, with thin beams forming regular small rectangular or triangular meshes. Short longitudinal strands are present in the reticular area. Megascleres include pentactin or subhexactin surface spicules, scopules, and uncinates. Major microscleres are discohexactins, discohexasters, or oxyhexasters (emended from Reiswig & Kelly, 2011).

Type species: Auloplax auricularis Schulze, 1904.

GENUS *DICTYOPLAX* GEN. NOV.

Diagnosis: Auloplacidae with body form as a widely spread funnel attached to hard substratum by a short central stalk; a network of marginal atrial grooves or dermal ridges develop into a network of tubules by closure of the grooves atrially. The tubules are all interconnected by a branching and anastomosing lumen system, but share the common two-dimensional atrial surface of the whole specimen. Spicules consist of surficial pentactine and tyloscopule megascleres, uncinates, oxyhexasters, and their variant microscleres.

Type species: Dictyoplax lecus sp. nov.

Etymology: The genus name, '*Dictyoplax*', is formed from '*diktyon*', Gk for net, and '*plax*', Gk for plate; the gender is masculine.

Remarks: The new species described below cannot be assigned to the only recent genus of the family, *Auloplax*, because of the differences in its method of tubule formation, in its body form, and in spicules from the three known species of that genus. Erection of a new monospecific genus is thus required to enable the placement of the new species in the present Linnean classification system of the Hexactinellida. *Dictyoplax lecus* gen. et sp. nov. extends the known geographic range of family Auloplacidae to the north-west Atlantic region; the taxon was so far only known from the north-east Atlantic and New Zealand waters (Reiswig, 2002b; Reiswig & Kelly, 2011).

DICTYOPLAX LECUS GEN. ET SP. NOV.

(FIGS 6, 7, TABLE 4)

Type material: Holotype, USNM 1110010, MOV *Johnson SeaLink I*, dive 4905, 16 Nov. 2002, off Riding Rock, San Salvador, Bahamas, 24°03.5843′ N, 74°33.2534′ W, 762 m. Paratypes, USNM 1231338, MOV *Johnson SeaLink I*, dive 2306, 11 Dec. 1992, Plana Cay, Bahamas, 22°32.00′ N, 73°37.00′ W, 891 m; USNM 1231339, MOV *Johnson SeaLink I*, dive 3408, 11 Dec. 1992, west of Riding Rock, San Salvador, Bahamas, 24°03.331′ N, 74°33.254′ W, 812 m; HBOM 002:00028, MOV *Johnson SeaLink I*, dive 4507, 15 Nov. 2002, French Bay, San Salvador, Bahamas, 23°56.0048′ N, 74°30.9088′ W, 840 m; HBOM 002:00029, MOV *Johnson SeaLink I*, dive 4622, 16 Oct. 2003, Plana Cay, Bahamas, 22°33.3592′ N, 73°37.2976′ W, 785 m; USNM 1231340, MOV *Johnson SeaLink I*, dive 4623, 16 Oct. 2003, Samana Cay, Bahamas, 23°02.7928′ N, 73°45.6564′ W, 880 m.

Diagnosis: As for the genus, as it is monospecific.

Description: All known specimens have the body form of a thin-walled platter (Fig. 6A, C, E), with corrugations of both dermal and atrial surfaces easily visible in both *in situ* and deck images (Fig. 6B, D, F). All but one specimen were attached to hard substrate by a short stalk emanating from the centre of the convex (dermal) surface (Fig. 6E); *in situ* figures indicate that the exception, paratype 1, USNM 1231338, may have been attached marginally (Fig. 6A). Body diameters of paratypes before collection were 41 and 27 cm in diameter; *in situ* images of the holotype are unavailable, but at the time of the encounter, the experienced observer estimated its diameter as 30 cm and the fragment collected from it was 16.6 × 9.4 cm (Fig. 6G). Corrugations seen in images are the lateral walls of a two-dimensional system of conjoined branching and meandering tubules seen on the dermal side as a system of inflated ridges (the tubules), which circumscribe a variety of isolated irregular depressions (Fig. 6H). The tubules all share a common wall, the atrial wall of the whole specimen, and are thus never free-standing cylinders. That atrial surface is comparatively flat. Small oscula, 0.9–1.7–2.5 mm diameter (n = 53), occur through the whole wall marginally, or through the inflated upper wall of ridges on the dermal side and through the atrial wall under those ridges on the atrial side. Total thickness of the holotype is 1.9–3.5–4.7 mm (n = 15) and of paratype 1 is 0.3–2.2–4.2 mm (n = 51). Dermal ridges of the holotype (Fig. 6H) are 1.5–5.4–11.1 mm long (n = 39) and 0.8–2.5–5.2 mm wide (n = 66). Grooves of

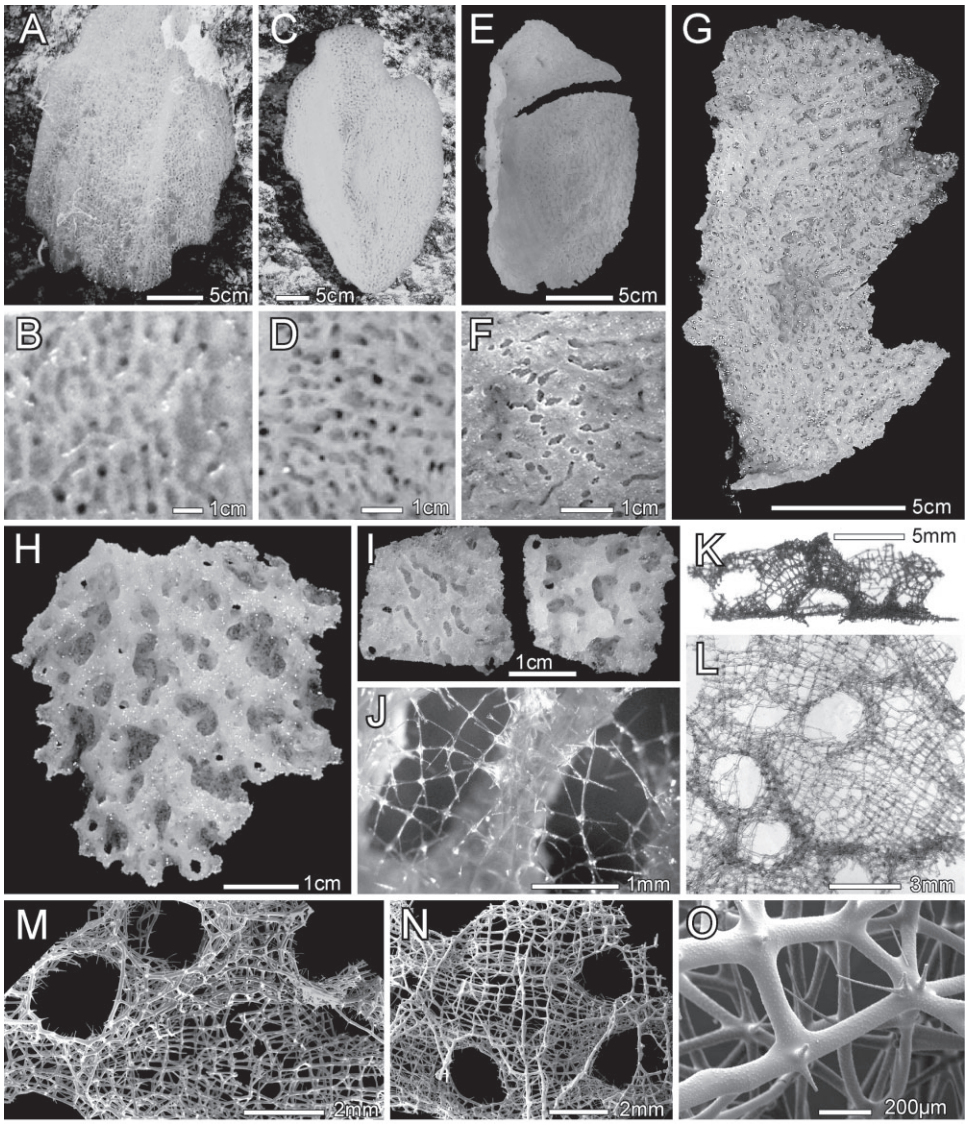

Figure 6. ***Dictyoplax lecus*** **gen. et sp. nov.**, body and framework: A, paratype 2, *in situ*; B, enlarged segment of (A); C, paratype 3, *in situ*; D, enlarged segment of (C); E, paratype 5, deck photo; F, enlarged segment of (E); G, holotype deck photo of dermal (outside) surface; H, fragment of holotype dermal surface, showing network of branching and anastomosing ridges containing system of tubes and lateral oscula; I, atrial (left) and dermal (right) surfaces of paratype 2, moist; J, atrial grooves with loose pentactin lattice in place; K, cleaned frame in cross section, atrial surface down showing tubular structure within dermal ridges; L, cleaned frame of holotype viewed from dermal side with lateral oscula opening on ridges (light microscopy); M, cleaned frame of holotype viewed from dermal side (SEM); N, cleaned frame of holotype viewed from atrial side, with thick strands; O, close-up of holotype dictyonal frame.

the atrial surface that underlie the dermal ridges are 1.4–3.6–10.2 mm long (n = 48) by 0.7–1.1–1.5 mm wide (n = 48); medially they are covered by a loose spicule lattice (Fig. 6J). The texture is hard but slightly flexible, brittle, and crumbly; color *in situ* is pale green but changes to olive green after collection on deck and preservation in ethanol. No symbionts were noted. Distribution as presently known is restricted to waters around San Salvador, Bahamas (Fig. 1).

The fused skeleton varies in thickness and complexity from marginal to medial areas of the discoid body; dimensions of elements are summarized in Table 3. Marginally, the framework consists of a two-dimensional plate with very indistinct ridges on the dermal side and grooves underlying these on the atrial side. In more medial areas the dermal ridges gradually increase in height by the formation of distinct lateral walls, and the atrial grooves thus become deeper but remain en-

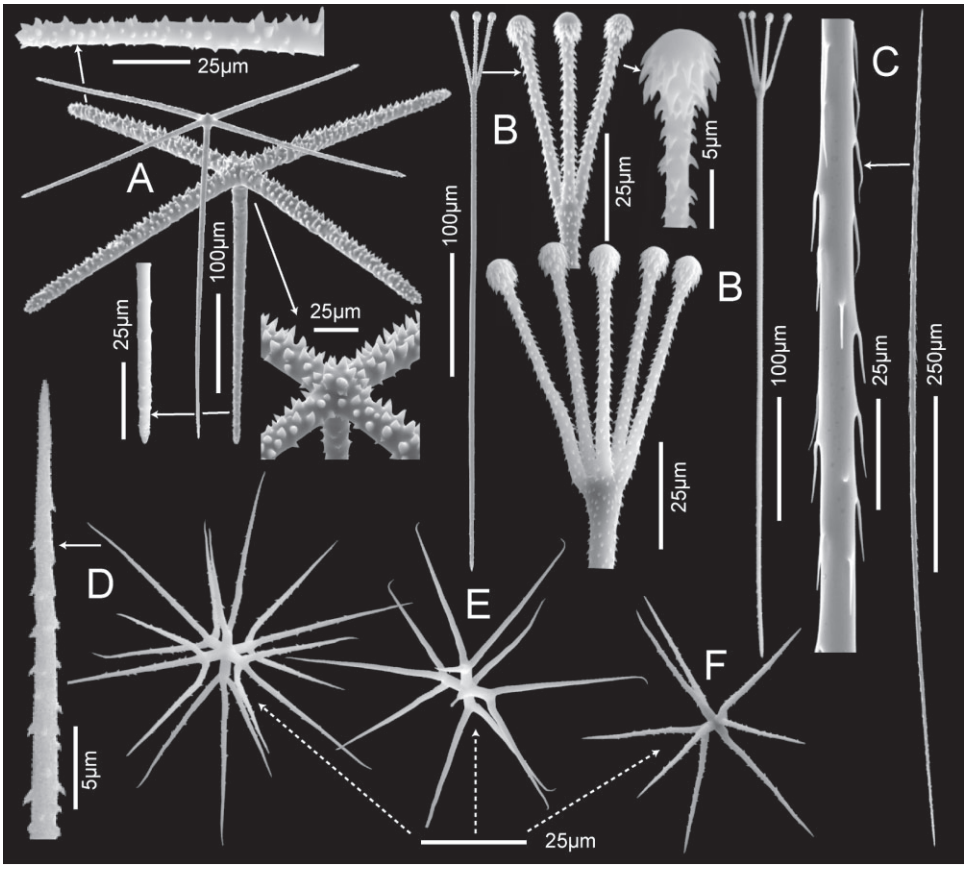

Figure 7. ***Dictyoplax lecus*** **gen. et sp. nov.**, holotype spicules (SEM): A, thick and thin whole pentactins and enlarged proximal and tangential ray ends; B, whole tyloscopules and enlarged heads and one tine tip; C, uncinate, whole and enlarged anterior segment; D, oxyhexaster and enlarged terminal ray end; E, hemioxypentaster; F, hemioxypentaster with fewer terminal rays.

tirely open. More medially, the ridges increase in height and the atrial grooves become narrower by encroachment of dictyonal walls; the grooves are now covered by a loose spicule lattice and the tubules circumscribed by them have nearly cylindrical lumina. In the most mature areas the atrial grooves become entirely covered by dictyonal lattice and the tubules within the wall are completely encased in dictyonal framework. The fused skeleton (Fig. 6K–O) of the mature stage consists of two distinct components: (1) thin sheets of somewhat regular rectangular and triangular meshes and (2) thick strands mainly developed in the atrial wall surface (Fig. 6N). The thin sheets form the primary framework of the dermal surface, as the sides and roof of the dermal ridges (Fig. 6M), the floor of the dermal pits, and the cover over the atrial grooves. Meshes have slightly longer longitudinal beams that are aligned over short distances of up to seven meshes to form poorly recognizable longitudinal strands. The sheets are between one and three meshes in thickness, and where the sheet is more than one layer in thickness, the nodes and beams of the adjacent layers are not aligned. This framework is clearly not farreoid, euretoid, nor aulocalycoid. The thick strands form borders of both dermal and atrial oscula as well as obliquely lateral strands on the atrial surface, probably forming marginal support for the atrial grooves. Dictyonal walls of the tubules are 0.16–0.44–1.13 mm (n = 8) in thickness. All nodes are regular (unswollen); nodes, beams, and spurs are finely and evenly spined (Fig. 6O). Spurs are very abundant throughout the framework; they are long, thin, and finely pointed on the regular sheet part, but shorter, thicker, and slightly swollen terminally on the thick beams. There are no small oxyhexactins appended to beams.

Megascleres consist of surficial pentactins, associated tyloscopules, and uncinates; spicule dimensions are summarized in Table 3. Pentactins (Fig. 7A) vary in thickness; the more robust forms have large conical spines densely covering the outer surfaces of tangential rays; proximal rays of the robust forms and all rays of the thin forms have a dense cover of small spines.

Table 3. Framework and spicule dimensions of ***Verrucocoeloidea liberatorii* sp. nov.**, holotype, USNM 1231336 (dimensions in μm)

Parameter	Mean	SD	Range	No.
Primary framework				
Longitudinal beam length	245	29	179–302	50
Transverse beam length	176	40	99–270	50
Beam width	25.5	3.5	19.6–34.8	50
Node diameter	79.7	9.2	55.6–96.8	50
Dermal framework				
Beam length	222	42	135–326	50
Beam width	54.0	10.9	37.4–98.0	50
Spur length	58.5	23.3	22.8–120.9	50
Node diameter	133	19	91–188	50
Atrial framework				
Beam length	197	37	122–269	50
Beam width	34.3	5.3	26.6–50.2	50
Spur length	120.0	41.0	58.9–245.5	50
Node diameter	83	21	57–201	50
Dermal/atrial pentactin				
Tangential ray length	152	26	96–220	50
Tangential ray width	7.2	1.3	5.1–11.6	50
Proximal ray length	125	27	36–176	50
Proximal ray width	7.4	1.1	5.3–10.1	50
Atrial hexactin				
Longest ray length	149	37	80–311	50
Longest ray width	7.3	2.2	3.2–13.9	50
Shortest ray length	73	24	25–157	50
Shortest ray width	6.8	1.8	2.9–10.8	50
Tyloscopule length	315	66	215–495	50
Head length	59.4	9.7	37.1–80.4	50
Tine length	50.4	8.1	29.2–66.7	50
Subtyloscopule length	603	60	489–701	50
Head length	93.6	12.9	65.9–133.8	50
Tine length	79.3	11.7	52.5–111.6	50
Uncinate length	1323	253	1021–1848	50
Width	7.4	1.5	5.2–12.0	50
Oxyhexaster diameter	63.5	6.3	47.6–77.2	50
Primary ray length	7.8	1.3	5.0–10.5	50
Secondary ray length	24.1	2.8	16.1–30.2	50
Discohexaster diameter	41.0	4.6	30.8–50.6	50
Primary ray length	7.6	1.9	4.7–11.0	50
Secondary ray length	13.1	1.9	9.8–20.4	50

These spicules form a quadrate lattice on the dermal and atrial surfaces as well as the internal lining of the tubules. Dermal and atrial pentactins have similar tangential rays, means 271 × 13.6 and 274 × 13.1 μm respectively, but differ in atrial pentactins having slightly longer proximal rays, 260 × 10.6 μm versus 311 × 11.8 μm, respectively. Tyloscopules, mean total length of 514 μm (Fig. 7B), vary considerably in the size of terminal swellings; their small heads bear between two and five straight tines that are moderately spread and covered with reclined spines. Abnormally formed heads with tines laterally offset are common. Shafts are either entirely rough or mostly smooth, but always spined at their basal ends; the shaft tip is simple and abruptly pointed without inflation. Tyloscopules are distributed as the pentactins, and usually have the entire head project above surfaces. Uncinates (Fig. 7C) are moderate in size, have a mean length of 1351 μm, with well-developed brackets, and barbs only slightly inclined from the spicule surface. They are present throughout the skeleton, oriented obliquely and radially, and project from all surfaces.

Table 4. Framework and spicule dimensions of ***Dictyoplax lecus* gen. et sp. nov.**, holotype, USNM 1110010 (dimensions in μm)

Parameter	Mean	SD	Range	No.
Framework				
Sheet beam length	387	95	220–702	77
Sheet beam width	54	11	25–79	77
Thick strand beam length	398	128	109–770	77
Thick strand beam width	97	19	60–142	77
Spur length	280	89	101–522	77
Dermal pentactin				
Tangential ray length	271	34	223–405	50
Tangential ray width	13.6	3.3	6.6–20.9	50
Proximal ray length	260	73	140–444	50
Proximal ray width	10.6	2.7	5.3–17.6	50
Atrial pentactin				
Tangential ray length	274	38	200–340	50
Tangential ray width	13.1	2.9	6.3–19.9	50
Proximal ray length	311	75	197–579	50
Proximal ray width	11.8	2.7	6.0–18.1	50
Tyloscopule length	514	121	361–872	50
Head length	63	11	42–91	50
Tine length	59	17	33–107	50
Shaft width	5.2	1.1	3.3–7.9	50
Uncinate length	1351	311	811–2128	50
Width	7.3	1.3	5.2–9.8	50
Oxyhexaster diameter	80	11	51–101	50
Primary ray length	5.1	0.9	3.5–6.7	50
Secondary ray length	35.6	5.0	25.0–45.4	50

Microscleres consist mostly of regular oxyhexasters (65%), with fewer hemioxyhexasters (19%) and irregular variants (16%); no oxyhexactins are present. Regular oxyhexasters, with mean diameter of 80 μm (Fig. 7D), have short mostly smooth primary rays of 5.1 μm in length, that carry between two and four long, straight, basally and/or distally hooked terminal rays, 35.6 μm in length, liberally covered with reclined spines. Hemioxyhexasters are similar, but one or two primary rays carry only a single terminal ray. Common irregular variants lack development of one or more primary rays, and include oxy- and hemioxypentasters (Fig. 7E), oxy- and hemioxytetrasters (Fig. 7F), oxy- and hemioxytriasters, oxydiasters and oxyspirasters. All microsclere forms are generally distributed.

Etymology: The species name, '*lecus*', is derived from '*lekos*', Gk for disc, with reference to the body form of this new species.

Remarks: The presence of a dictyonal framework and scopules mandates assignment of this species to suborder Sceptrulophora. Absence of framework channellization prevents its assignment to families Aphrocallistidae, Craticulariidae, Cribrospongiidae, or Tretodictyidae. Lack of a two-dimensional farreoid framework prevents its inclusion in Farreidae. Presence of two distinct types of framework, one with thickened beams, prohibits assignment to Euretidae and Fieldingiidae, but is consistent only with its placement in Auloplacidae. Its basic structure of branching tubular elements sharing a common wall and spiculation are also consistent with that assignment. It cannot conveniently be accepted as a member of the genus *Auloplax* because the pattern of constituent tube origin and growth differ from that known in all *Auloplax* species. In *Auloplax*, tubes branch from a basal tube, rebranch several times, but always remain joined to their last branched tube by shared common walls; the tubes may be partly free terminally but never anastomose. In the new species, the tubes never share common lateral walls but they all indirectly share a common atrial wall; the tubes divide and anastomose, forming a network of tubes not seen in any member of *Auloplax*. All three or four species of *Auloplax* [*Auloplax filholi* (Topsent, 1904) has not yet been definitely shown to be a junior synonym of *A. auricularis* Schulze, 1904] have discohexactins or discohexasters as their major microsclere, whereas the new species

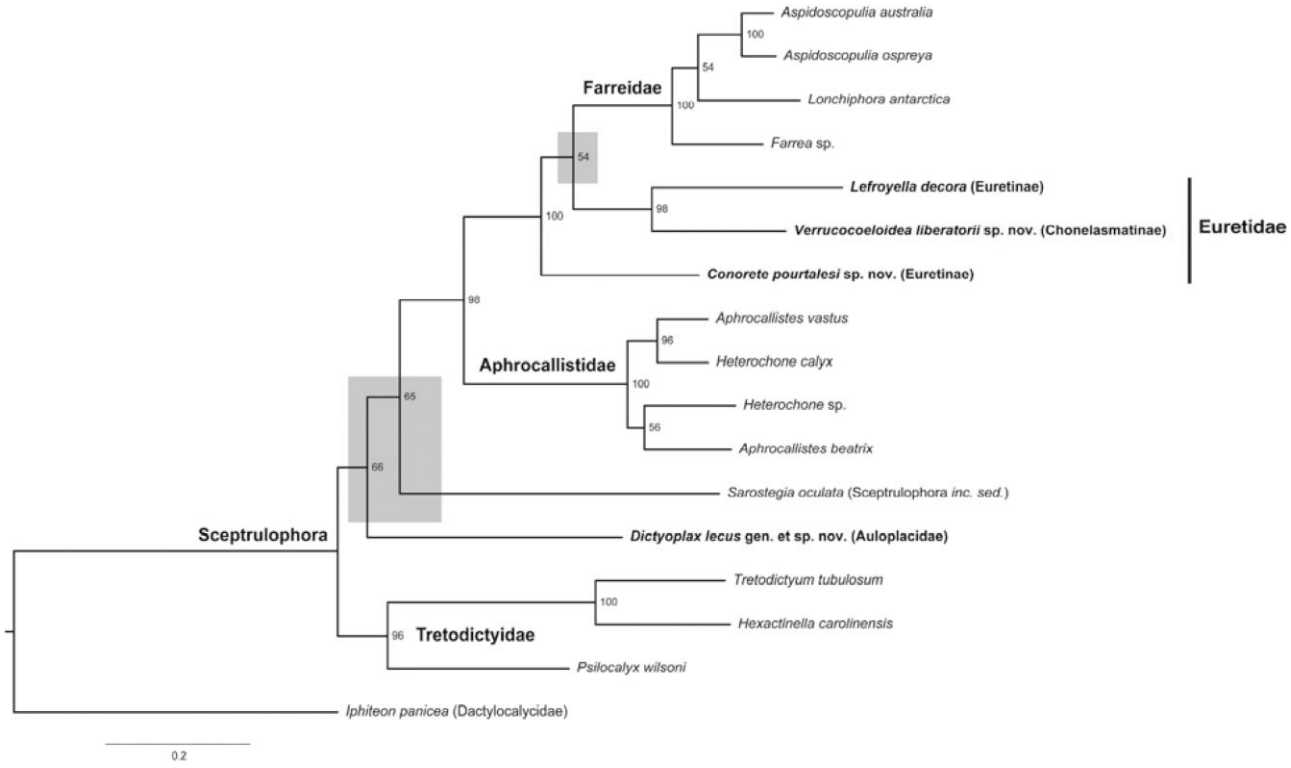

Figure 8. Maximum-likelihood phylogeny of Sceptrulophora based on concatenated nuclear *18S* and *28S* rDNA, and mitochondrial *16S* rDNA and cytochrome *c* oxidase subunit I (*COI*) sequences (1279 distinct alignment patterns, 14% gaps and completely undetermined characters). Newly sequenced/described taxa are highlighted in bold. Numbers at nodes are bootstrap proportions (based on 650 pseudoreplicates). Grey boxes indicate crucial areas of the phylogeny that could not be resolved with significant statistical support. The scale bar indicates the expected number of substitutions per site. Note: ***Dictyoplax lecus* gen. et sp. nov.** was known as 'Euretidae n. gen. n. sp.' in previous molecular phylogenetic studies.

has regular oxyhexasters instead. There is a precedent for Auloplacidae with oxy-microscleres in the form described as Auloplacidae *incertae sedis* in Reiswig & Kelly (2011). The differences in body form, constituent tube growth, and microsclere form from all *Auloplax* species mandates the erection of a new genus for the new species, proposed here as *Dictyoplax lecus* sp. nov.

Molecular phylogenetics

The molecular phylogeny obtained here (Fig. 8) is consistent with the results of Dohrmann *et al*. (2011) in showing Tretodictyidae as the sister group to the remaining sceptrulophorans, and Aphrocallistidae and Farreidae more closely related to each other than to *Sarostegia* and *Dictyoplax* (formerly known as 'Euretidae n. gen.'). The branching order of and low bootstrap support for the positions of the latter two taxa (highlighted by the lower grey box in Fig. 8) are also in line with that previous analysis. In contrast, a clade of *Sarostegia*, a genus that was provisionally transferred to Euretidae by Dohrmann *et al*. (2011), and the three newly sequenced, unquestionable euretids, is not recovered. Instead, the latter form a highly supported clade with Farreidae. For these reasons, we exclude *Sarostegia* from Euretidae in the following, regarding it as Sceptrulophora *incertae sedis*.

Verrucocoeloidea (Chonelasmatinae) and *Lefroyella* (Euretinae) appear to be very closely related, to the exclusion of *Conorete* (Euretinae). Thus, the monophyly of subfamily Euretinae – or at least a relationship of *Lefroyella* to that group of genera – is rejected by the molecular data. Likewise, the monophyly of Euretidae is not recovered because the clade of *Verrucocoeloidea* + *Lefroyella* appears more closely related to Farreidae than to *Conorete*; however, bootstrap support for the paraphyly of Euretidae is very poor (upper grey box in Fig. 8).

DISCUSSION

The discovery of three new dictyonal hexactinellids in the Caribbean region is not surprising. The earlier expeditions carried out by Agassiz and Pourtales were

not geographically exhaustive, and did not sample vertical hard substrates well. Thus the two geographically restricted species, *C. pourtalesi* sp. nov. and *D. lecus* gen. et sp. nov. were probably never sampled before. The very common and widely distributed species now known as *Verrucocoeloidea liberatorii* sp. nov. was definitely sampled in those early collections, but was not recognized as a distinct species by Schmidt because of his limited use of microscopy in specimen examination. Those specimens have borne the names of other species for over 100 years in collections around the world. It is now finally recognized as a distinct common species in the area. The discovery of a close relative of *Auloplax* is also remarkable because for more than 100 years this genus was thought to assume an isolated position within Hexactinosida. Its placement in Tretodictyidae or Dactylocalycidae has never been satisfactory (Reiswig, 2002b), and after a recent discovery of new material, including two new species, the need to classify it in a separate family finally received acceptance (Reiswig & Kelly, 2011). The description of a second genus, *Dictyoplax* gen. nov., further strengthens the validity of family Auloplacidae, and demonstrates that the full diversity of glass sponges is still incompletely known; many new surprises are likely to emerge with increasing exploration of deep waters by submersibles.

Regarding the relationship of Auloplacidae to the other families of Sceptrulophora, not much can be said at present, as the statistical support for the position of *Dictyoplax* gen. nov. in the molecular phylogeny (Fig. 8) is not significant. The same is true for the monospecific genus *Sarostegia*, which we have here decided to classify as Sceptrulophora *incertae sedis*. The alternative would have been to erect a new family for it – with the simple diagnosis 'sceptrulophorans with a euretoid framework and sceptrules in the form of sarules only'; however, we consider it premature to make such a move, because the inclusion of additional genera of Euretidae, Tretodictyidae, and of the three monogeneric families of Sceptrulophora (see above) in future molecular studies might reveal that *Sarostegia* represents just one lineage within a larger, well-supported clade that then should be classified as a new family.

The majority of sceptrulophoran families are well defined by morphological characters that can be interpreted as autapomorphies: Tretodictyidae by schizorhyses; Aphrocallistidae by cylindrical diarhyses; Farreidae by farreoid frameworks in combination with clavules; Craticulariidae and Cribrospongiidae by diplorhyses in family-specific arrangements; and Auloplacidae and Fieldingiidae by their characteristic, unique (non-euretoid) types of framework construction. In contrast, Euretidae is a 'waste-bin taxon', in which all genera (currently 18, not counting *Sarostegia*) that do not fit in any of the other well-defined families are placed. The taxon is simply characterized by euretoid frameworks without special channellization. Whereas the lack of special channellization can hardly be interpreted as apomorphic, the euretoid frameworks also characterize Tretodictyidae, Aphrocallistidae, Craticulariidae, and Cribrospongiidae, and can even be found in older parts of some large farreid specimens (e.g. Tabachnick *et al*., 2011). Thus, we propose that a euretoid framework construction is a ground-plan character of Sceptrulophora that is likely to be an autapomorphy of that group, as it is not found in other dictyonal Hexasterophora, including Dactylocalycidae, and as such its presence is not informative for differentiating family-level groups. Likewise, loose spiculation offers no clues to unite the 18 genera of Euretidae: there are no types of megascleres, scopules, or microscleres that are exclusively found in that family. Therefore, molecular data are crucial to resolve the relationships of the euretid genera.

According to our results (Fig. 8), at least a subset of the 18 genera appears closely related to Farreidae. Although clear-cut morphological synapomorphies between Farreidae and (parts of) Euretidae are hard to pin down, this result is in good agreement with the notion of taxonomists that these two families are 'close': it can sometimes even be difficult to assign specimens to one or the other family if only underwater pictures or washed-out fragments are known (see Reiswig & Kelly, 2011: 66 ff). We predict that increased taxon sampling in future molecular systematic studies will reveal that additional genera of Euretidae belong in this well-supported Euretidae + Farreidae clade. Genera that clearly group outside of this clade should be transferred to Sceptrulophora *incertae sedis* (as we have done here with *Sarostegia*) until the phylogeny of Sceptrulophora is more robustly resolved, and new clades that could be recognized as family-level taxa in the Linnean classification emerge.

Another question that needs to be addressed is whether the 'core' euretids form a monophyletic group or a paraphyletic grade along the lineage leading to Farreidae. Although the latter idea is not too far-fetched (i.e. farreids could just be viewed as derived euretids), the molecular evidence presented here is ambiguous (upper grey box in Fig. 8). This is most likely because of the limited taxon sampling, but could also be related to the fact that *COI* sequences from *Verrucocoeloidea* and *Lefroyella* are missing (see Material and methods). The closer relationship of *Lefroyella* to *Verrucocoeloidea* than to *Conorete*, however, is highly supported and implies that subfamily Euretinae is not monophyletic. On the other hand, *Lefroyella* is not a typical representative of that subfamily: it shares with *Verrucocoeloidea* a funnel-shaped body form, whereas most Euretinae are stocks of branching tubes, like

Conorete (the reason why *Lefroyella* is classified in Euretinae is that the funnel is interpreted as being composed of small branching tubes; Reiswig & Wheeler, 2002). Thus, Euretinae might still be a natural group, with only its scope in need of revision. In any case, this result is in line with previous conclusions that subfamilial divisions in Hexasterophora are largely artificial (reviewed in Wörheide *et al*., 2012). Clearly, more data are needed to resolve these issues, and for the time being we refrain from making major changes to the Linnean classification of Sceptrulophora.

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