

***Hedera caerulescens* (Alcyonacea : Alcyoniidae), a new genus and species of soft coral from the temperate North Atlantic: invasive in its known range?**

I. E. Conti-Jerpe^{A,B,D} and D. W. Freshwater^C

^ADepartment of Biology & Marine Biology, University of North Carolina Wilmington, 601 South College Road, Wilmington, NC 28403, USA.

^BSwire Institute of Marine Science, School of Biological Sciences, The University of Hong Kong, Pokfulam Road, Hong Kong 999077, Hong Kong.

^CCenter for Marine Science, University of North Carolina Wilmington, 5600 Marvin K. Moss Lane, Wilmington, NC 28409, USA.

^DCorresponding author. Email: ingacontijerpe@gmail.com

Abstract. We describe a novel alcyoniid species of stoloniferous octocoral found off the coast of North Carolina, USA. Colonies have an encrusting morphology with pale to bright blue monomorphic polyps connected by spongy, sclerite-dense stolons that often form mats. Sclerites are colourless and sparsely tubercled. Sclerites of the stolons are predominantly spindles and rods with rare irregular fused forms, butterflies, and crosses. Polyps have a crown and points formation that consists of rods and spindles that can be curved or irregularly branched. Tentacles contain short flattened rods and rare crosses. Both the mitochondria-encoded COI-5P and *mtMutS* were sequenced and BLAST searches revealed no close homology with any previously sequenced species. Phylogenetic analyses of the sequence data suggested a closest relationship with species of *Alcyonium* Linnaeus, 1758 (Alcyoniidae) and *Gersemia* Marenzeller, 1877 (Nephtheidae) and supported the recognition of a new genus. This species was not previously reported in the Carolinas region despite extensive historical sampling and a recently published key to octocorals of the South Atlantic Bight. Reports and photographs from local divers suggest that this species may have been introduced in North Carolina waters ~2002–04, where it has been found on both shipwrecks and hard bottom ledges, at 13–34 m depth.

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Introduction

The anthozoan subclass Octocorallia contains a globally distributed diversity of species whose taxonomic relationships are poorly understood (Fabricius and Alderslade 2001; McFadden *et al.* 2006b, 2010; Daly *et al.* 2007). Over the past century, octocoral taxonomists have struggled to classify this group into distinct orders because there are few clear synapomorphies (Bayer 1981b; Berntson *et al.* 2001; McFadden *et al.* 2006b). The most recent morphological classification separates octocorals into three orders: Helioporacea and Pennatulacea, which have distinct morphological character states, and Alcyonacea, into which five antiquated orders (Calcaxonina, Holaxonia, Protoalcyonaria, Scleraxonia, and Stolonifera) have been subsumed in recognition of the fact that the colony morphologies used to distinguish them actually represent a continuum (Bayer 1981a; Fabricius and Alderslade 2001).

Stolonifera is still used as a loose ‘subordinal’ grouping that includes octocorals characterised as encrusting colonies of polyps connected by stolons, or extensions of the coenenchyme

that may form mats (Fabricius and Alderslade 2001; Daly *et al.* 2007). Recent molecular data, however, indicate that stoloniferous species are polyphyletic and divided among several subordinal groups and families that are scattered throughout Octocorallia (Berntson *et al.* 2001; McFadden *et al.* 2006b; McFadden and van Ofwegen 2012). Indeed, molecular data suggest that the entire current classification system for Octocorallia needs to be overhauled; however, their evolutionary relationships have yet to be fully resolved, and so researchers continue to rely on the most recent morphological classification system (Fabricius and Alderslade 2001).

The South Atlantic Bight spans the temperate Atlantic coast of the United States from south of Cape Hatteras, North Carolina, to north of Cape Canaveral, Florida (DeVictor and Morton 2010). The continental shelf in this region is characterised by sand flats peppered with segments of hard-bottom ledges and abundant shipwrecks (Boesch *et al.* 1977; Wenner *et al.* 1984). Twenty-eight species of octocorals are known to inhabit the shallow (0–200 m) waters of the South Atlantic Bight, and

they often dominate both natural and anthropogenically introduced hard substrate, increasing the complexity of these habitats and providing refuges for other organisms (Wenner *et al.* 1984; DeVicor and Morton 2010). The octocoral community of the South Atlantic Bight has been exceptionally well documented; there are several academic, federal, and state marine laboratories located in the region including the South-eastern Regional Taxonomic Center, which recently produced an exhaustive guide to octocorals of the South Atlantic Bight (DeVicor and Morton 2010).

In October 2013, we observed and photographed a bright blue, encrusting octocoral on a shallow shipwreck off the coast of North Carolina (Fig. 1). DeVicor and Morton (2010) list only one encrusting octocoral species in the region (*Scleranthelia rugosa* Pourtalès, 1867), which is not found in habitats shallower than 70 m. No local records of this species were found in the

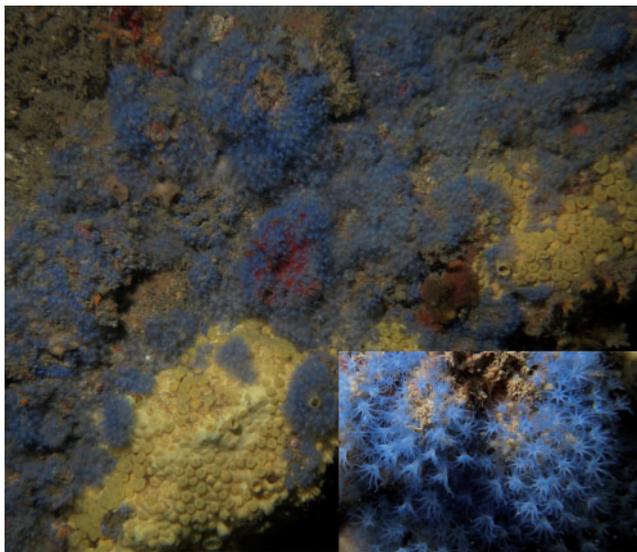


Fig. 1. *Hedera caerulea*, gen. et sp. nov., *in situ* colony growing at 13 m depth on the Alexander Ramsey shipwreck, Onslow Bay, North Carolina, October 2013.

scientific literature and interviews with recreational and scientific divers revealed that it had only recently been observed in North Carolina waters. Searches of the global taxonomic literature revealed no morphological match to the species, and BLASTn searches of sequence data generated from it revealed no close affinity to other species. These sequences were also compared with the extensive dataset of C. McFadden, and no matches were found (C. McFadden, pers. comm., August 2016). Here we describe this taxon as a new genus and species of Alcyoniidae based on morphological and DNA sequence analyses, and provide information on its currently known distribution in North Carolina waters.

Materials and methods

Specimens for morphological and molecular analyses were collected by SCUBA in October 2013, April 2014, and October 2015 from a hard-bottom ledge and concrete artificial reef structure within Onslow Bay, North Carolina (Table 1, Fig. 2). Specimens were kept alive in aquaria and tissues were sampled for morphological analysis as needed. Images of extended and retracted polyps were taken using a dissecting microscope coupled to a Leica 1.0 camera. Polyps were clipped from the colony with scissors, prepared as wet mounts, and imaged with a Nikon Labophot-2 microscope with a Moticam 1000 camera. Sclerites were isolated using a 5% sodium hypochlorite solution and imaged with a Philips XL30S FEG and a Hitachi S-4800 FEG scanning electron microscope. Morphometrics were measured from images using the software ImageJ. Sclerite terminology follows that of Bayer *et al.* (1983). The type specimen was deposited in the California Academy of Sciences invertebrate collection (CASIZ 219717).

Total genomic DNA was extracted from live polyp tentacle tissue using the DNeasy Blood & Tissue Kit (Qiagen, Valencia, CA, USA). The 5' region of COI (COI-5P) plus the adjacent intergenic spacer region (*igr*), and a portion of the octocoral-specific *mtMutS* were PCR amplified with MyTaq HS Red DNA Polymerase and buffer (Bioline USA Inc., Taunton, MA, USA) and the following primers: *igr*-COI – COII8068F (McFadden *et al.* 2004) and COIOCTr (McFadden *et al.* 2011); *mtMutS* – ND42599F (France and Hoover 2002) and mut3458R (Sánchez

Table 1. *Hedera caerulea*, sp. nov. reports from Long Bay and Onslow Bay, North Carolina

Site numbers and names relate to sites shown in Fig. 2

Site no.	Site name	Substrate type	Depth (m)	Report type and dates
1	Crahole ledge	Hard-bottom ledge	31	Observations and video, May 2014
2	Nicebottom ledge	Hard-bottom ledge	26	Observations, May 2014
3	Turd wreck	Shipwreck	25	Observations, May 2014, June 2016
4	Lady Margaret	Shipwreck	28	Observations and photo, May 2014
5	8-mile ledge	Hard-bottom ledge	18	Observations and collections, multiple dates 2002–14
6	Hyde	Shipwreck	22	Photo, September 2011
7	Aquarium ledge	Hard-bottom ledge	24	Observations and collections, multiple dates 2002–14
8	Alexander Ramsey	Shipwreck	13	Photo, October 2013; collections, April 2014
9	Papoose	Shipwreck	34	Video, March 2014
10	Indra	Shipwreck	15	Photo, July 2013
11	Alton Lennon	Shipwreck	27	Video, May 2015
12	Big 10	Hard-bottom ledge	21	Photo, May 2015
13	Titan (AR-345)	Shipwreck	20	Photo, June 2014
14	AR-345 Pipes	Concrete pipes	19	Photo, May 2015; Collection, October 2015

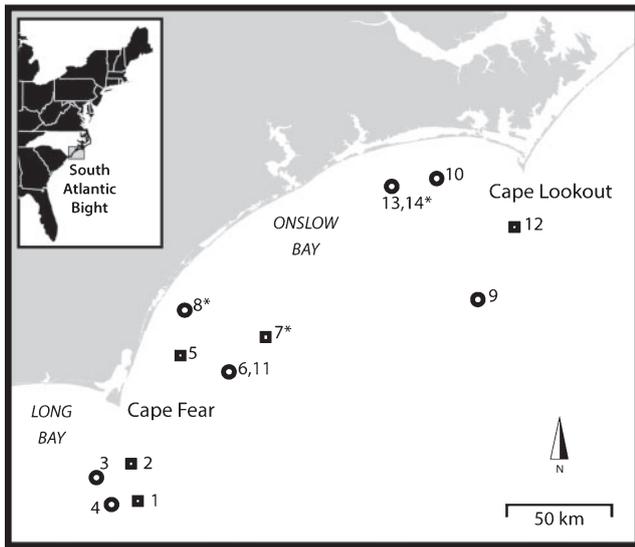


Fig. 2. Sites within Onslow Bay, North Carolina where *Hedera caerulescens* has been observed. Circles = artificial substrate; squares = natural hard-bottom substrate. Collection sites for specimens used in the morphological and molecular analyses are indicated with an asterisk. Sites: (1) Crahole ledge; (2) Nicebottom ledge; (3) Turd wreck; (4) Lady Margaret; (5) 8-mile ledge; (6) Hyde; (7) Aquarium ledge; (8) Alexander Ramsey; (9) Papoose; (10) Indra; (11) Alton Lennon; (12) Big 10; (13) Titan (AR-345); (14) AR-345 Pipes.

et al. 2003). PCR products were enzymatically cleaned with illustra ExoStar (GE Healthcare, Buckinghamshire, UK); sequence reactions carried out using BigDye v. 3 (Life Technologies, Grand Island, NY, USA) and run on an ABI 3130xl Genetic Analyzer (Life Technologies). Sequence reactions were combined and edited using Sequencher (Gene Code Corp., Ann Arbor, MI, USA) and deposited in GenBank under the accession numbers KX687904–KX687907.

Sequence alignments were built and phylogenetic analyses performed using Geneious 9.1.8 (Biomatters, Auckland, New Zealand). The newly generated COI and *mtMutS* sequences were aligned with those for 123 octocoral species available in GenBank that were part of large octocoral trees published by McFadden and van Ofwegen (2012, 2013b). The COI and *mtMutS* alignments were generated using MUSCLE (Edgar 2004) and MAFFT (Katoh *et al.* 2005), respectively.

The *igr*+COI alignment was truncated to include only the first 696 sites in the COI-coding region because of uncertainty in the homology of indel-coded sites within the *igr*. The two alignments were analysed separately and also as a combined alignment (COI-5P+*mtMutS*). Maximum likelihood (ML) and Bayesian Inference (BI) analyses were carried out using the RAxML (Stamatakis 2014) and MrBayes (Huelsenbeck and Ronquist 2001) Geneious plugins respectively. ML analyses of the separate COI-5P and *mtMutS* alignments utilised the GTR CAT I model with the data partitioned into the three codon positions and the Rapid hill-climbing algorithm. Node confidence was assessed by 500 bootstrap replications. ML analysis of the COI-5P+*mtMutS* combined alignment used the GTR CAT I model with the data partitioned by gene and codon position and the Rapid hill-climbing algorithm. Node confidence

was assessed by 1000 bootstrap replications. BI analyses utilised the GTR + gamma + invariable sites model and were performed as two simultaneous runs with four Monte Carlo Markov Chains (three heated and one cold) for 4 000 000 generations, sampling every 4000 generations, and with a burn-in of 400 000 generations.

Results

Molecular analyses

Sequences of two different specimens collected at two different sites in south-western Onslow Bay, North Carolina were identical over the entire *igr*-COI, and different at only two sites within the *mtMutS* locus. Results of separate COI and *mtMutS* ML analyses were essentially identical, and, accordingly, we have followed a total-evidence approach and presented only the combined COI-5P+*mtMutS* tree (Fig. 3; Fig. S1, available as supplementary material to this paper). This species was resolved with strong to full support as sister to a clade that included species classified within *Alcyonium* Linnaeus, 1758 and *Gersemia* Marenzeller, 1877. Stoloniferous species were polyphyletic, as were most families with multiple species represented in the analyses.

Taxonomy

Order **ALCYONACEA** Verrill

Family **ALCYONIIDAE** Lamouroux

Genus ***Hedera***, gen. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:3F1B8915-4808-471A-81E7-312A081150B8>

Type species: Hedera caerulescens, sp. nov., by original designation and monotypy.

Diagnosis

Encrusting colonial polyps connected by stolons, often continuous mats with one layer of sclerites and polyps evenly throughout. Stolon sclerites straight, lightly tubercled spindles; narrow, lightly tubercled rods; or rare irregular butterflies, crosses or fused forms. Monomorphic polyps slightly raised, mounded calyces when fully retracted. Polyps with crown and points formation of lightly tubercled spindles and rods, sometimes curved or irregularly branched on one end. Tentacle sclerites short, flattened rods and occasional crosses.

Remarks

Hedera differs from existing octocoral genera in that it has the combination of a single layer of sclerites in the stolon and low, mounded calyces that do not protrude significantly above the stolon when the polyps are retracted.

Etymology

The generic name is derived from the Latin *hedera* meaning ivy, which reflects the stoloniferous growth form with even polyp distribution exhibited by the type species.



Fig. 3. Combined COI-mtMutS maximum likelihood tree of 124 octocoral species with only the family classification shown. Inset shows details of the position of *Hedera caerulescens* within the topology, and stoloniferous species are highlighted in grey boxes. Maximum likelihood bootstrap support values are shown for branches when >70% (* = 100%). Bayesian posterior probabilities are shown when >0.80 (A = 1.00; B = 0.95–0.99; C = 0.90–0.94; D = 0.80–0.89).

Hedera caerulescens, sp. nov.

(Figs 1, 4–7)

<http://zoobank.org/urn:lsid:zoobank.org:act:FD59D077-EA05-4D21-9C3B-432E3C2BD7DB>

Material examined

Holotype. United States of America, North Carolina, Onslow Bay: AR-345, concrete artificial reef structure (34°32.141'N, 076°58.473'W), depth 19 m, 15.x.2015, coll. D. W. Freshwater and M. E. LaCroce (CASIZ 219717).

Paratypes. United States of America, North Carolina, Onslow Bay: Alexander Ramsey shipwreck (AR-370), stern section (34°10.501'N, 077°45.111'W), depth 13 m, 14.iv.2014, coll. I. E. Conti-Jerpe, M. J. Marty, and D. W. Freshwater (CASIZ 198021); 'Aquarium Ledge' (34°3.433'N, 077°24.382'W), depth 24 m, Autumn 2013, coll. M. Neill, M. Fatzinger, and P. Barrington.

Diagnosis

Encrusting octocoral with polyps evenly distributed across stolons or continuous membranes. Sclerite-rich, spongy surface of stolons crustose and grey-blue or white in colour. Anthocodiae blue in colour. Calyces slightly raised and conical in shape when polyps retracted.

Sclerites colourless, lightly tubercled. Stolon sclerites spindles (50–300 µm), rods (150–200 µm), irregular butterflies and fused forms (120–250 µm), and crosses (200–300 µm). Crown and points sclerites spindles (100–250 µm) and rods (100–500 µm), often curved or irregularly branched. Tentacle sclerites flattened rods (100–200 µm) and crosses (50–120 µm). *igt*+COI-5P and *mtMutS* DNA sequences as in GenBank Accessions KX687904 and KX687906.

Description

Holotype a colony of ~50 polyps attached to a piece of hard substrate 1.5 cm by 2.5 cm. Some polyps connected by encrusting membrane (Fig. 4), others by narrow stolons 0.5–1.0 mm in diameter, others alone. Joined polyps 0.5–1.0 mm apart (Fig. 4). All anthocodia retracted into mounding, slightly conical calyces (Fig. 4). Surface of membrane and stolons covered by dense sclerite crust, grey-white or pale blue in colour. Anthocodiae

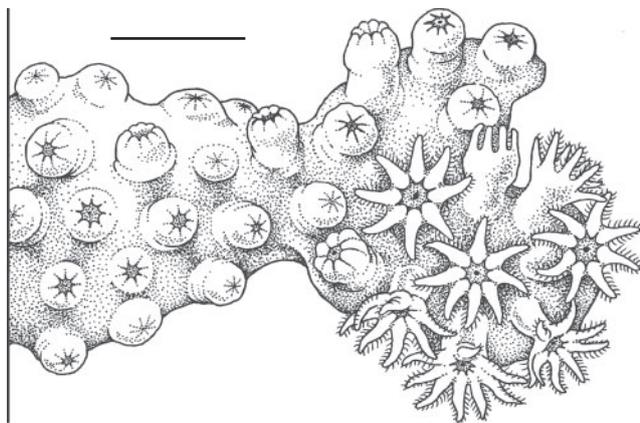


Fig. 4. *Hedera caerulescens*, gen. et sp. nov., gross colony morphology. Scale bar: 5.0 mm.

length ≤ 3.5 mm; tentacle length 1.2–2.0 mm; 8–12 pinnules on each side. When living, tentacles and oral disc pale to bright blue, while area between neck and calyx translucent blue with mesenteries and gastric cavity visible (Figs 1 and 5). Specimen pale white when preserved in ethanol.

Sclerites colourless, lightly tubercled. Stolon sclerites spindles (50–300 µm), rods (150–200 µm), irregular butterflies and fused forms (120–250 µm), and crosses (200–300 µm) (Fig. 6). Crown and points sclerites spindles (100–250 µm) and rods (100–500 µm), often curved or irregularly branched (Fig. 7). Tentacle sclerites flattened rods (100–200 µm) and crosses (50–120 µm) (Fig. 7).

DNA sequences of 5' end of COI and preceding intergenic spacer region as in GenBank accession KX687904, and DNA sequences of *mtMutS* as in GenBank accession KX687906.

Remarks

If we used morphological characters to classify *Hedera caerulescens*, it would fall within the family Clavulariidae on the basis of its stoloniferous growth form. Clavulariidae, however, is an unnatural group unified only through this colony morphology (Daly *et al.* 2007), a character state that has evolved independently multiple times (McFadden and van Ofwegen 2012). Indeed, some members of Alcyoniidae are similar to species within Clavulariidae in that they also form encrusting mats (McFadden and Hochberg 2003; Stokvis and van Ofwegen 2006). These two families were originally separated into different suborders (Alcyoniina and Stolonifera respectively) that were distinguished solely on the basis of colony morphology, but as more species were examined and described it became clear that the growth morphologies within Alcyonacea fall along a continuum that transverses suborders (Fabricius and Alderslade 2001).

Using Bayer's (1981a) key to the genera of Octocorallia, *Hedera caerulescens* keys out as a member of the monospecific genus *Trachythela* Verrill, 1922. While *H. caerulescens* shares many characteristics with *Trachythela* (membranous and spiculose

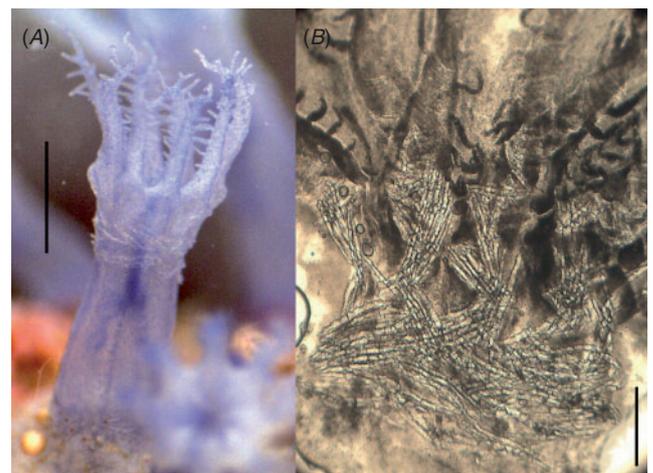


Fig. 5. *Hedera caerulescens*, gen. et sp. nov., crown and points formation: (A) exterior view of a living polyp; (B) micrograph. Scale bars: A, 0.5 mm; B, 0.2 mm.

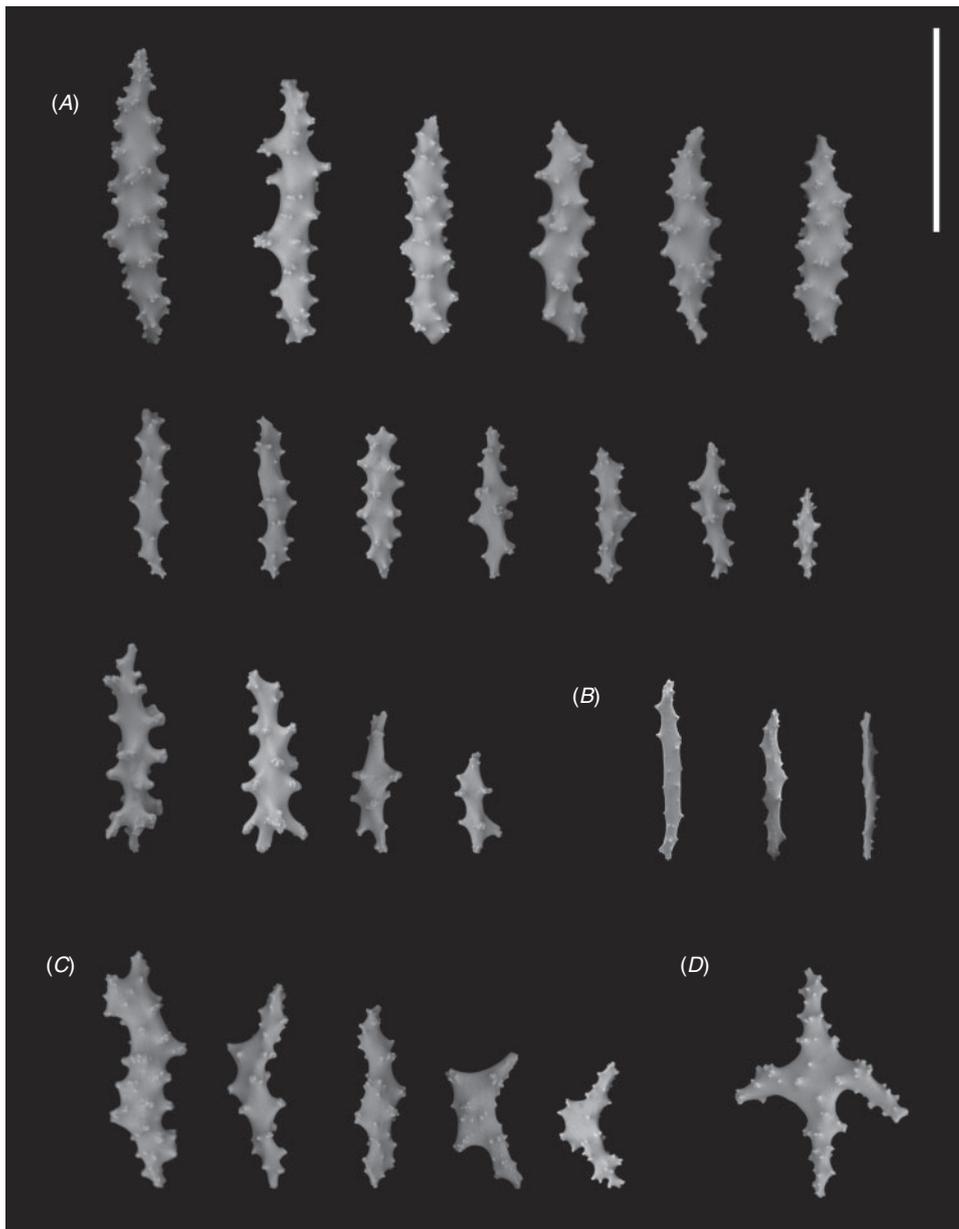


Fig. 6. *Hedera caerulescens*, gen. et sp. nov., holotype, CASIZ 219717: sclerites from stolon: (A) spindles; (B) rods; (C) irregular fused forms and butterflies; (D) crosses. Scale bar = 200 μ m.

basal crust, flattened rods and irregularly forked or branched spindles in the polyps, and a strong crown-and-points formation), they differ in that *Trachythela* has two layers of sclerites in the stolon, thorny club and double club sclerites in the lower stoloniferous layer, and spine-like projections at the top of the calyces (Verrill 1922). *H. caerulescens* and *Trachythela rudis* were also resolved in topologically distant clades in our phylogenetic analyses (Fig. 3). Furthermore, the status of *Trachythela* is ambiguous: Deichmann (1936) redesignated the type species *T. rudis* (the only species within *Trachythela*) as *Clavularia rudis* Blainville, 1830, citing that the genus had been incompletely described and the type (which had been stored in Verrill's personal collection) lost (Verrill 1922).

Some subsequent publications have therefore referred to *T. rudis* as *C. rudis* (Watling and Auster 2005; White *et al.* 2012; Quattrini *et al.* 2015).

Bayer (1981a) separated Clavulariidae into four subfamilies, two of which lacked secondary polyps: Clavulariinae, which is defined by the presence of tall, cylindrical calyces that rise prominently above the stolon, and Sarcodictyiinae, which has polyps that retract into calyces nearly flush with the stolon. Subsequently, McFadden and van Ofwegen (2012) described the genus *Inconstantia*, which includes species that fall into both of these subfamilies. Despite this, the genus *Clavularia* still retains the morphology of Clavulariinae (McFadden and Hochberg 2003), while the two genera *Incrustatus* van Ofwegen,

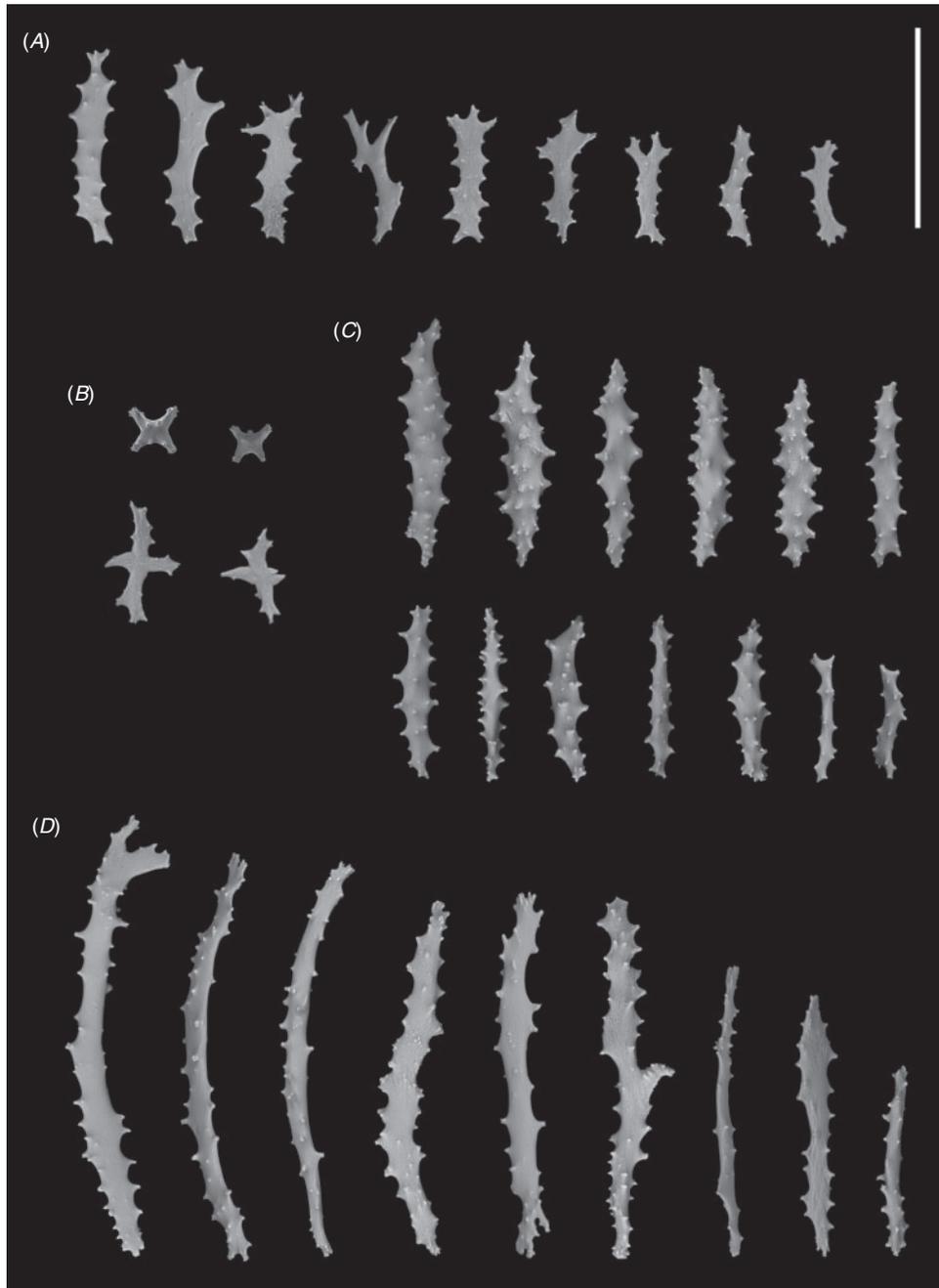


Fig. 7. *Hedera caerulescens*, gen. et sp. nov., holotype, CASIZ 219717: (A) flattened rods from tentacles; (B) crosses from tentacles; (C) spindles from crown and points; (D) rods from crown and points. Scale bar = 200 μ m.

Häussermann & Försterra, 2007 and *Cryptophyton* Williams, 2000 match Sarcodictyiinae (McFadden and van Ofwegen 2012). While *H. caerulescens* does have low calyces that protrude only slightly from the stolon (characteristic of Sarcodictyiinae), it is excluded from both *Incrustatus* and *Cryptophyton*, which both lack a crown and points formation. Indeed, *H. caerulescens* is excluded from all other genera within Clavulariidae (apart from *Trachythela*, discussed above) because these genera are defined as having axial or secondary polyps

(*Bathytelesto* Bayer, 1981, *Carijoa* F. Müller, 1867, *Paratelesto* Utinomi, 1958, *Pseudocladochonus* Versluys, 1907, *Schizophyton* Studer, 1891, *Stereotelesto* Bayer, 1981, *Telesto* Lamouroux, 1812, *Telestula* Madsen, 1944), few or no sclerites in the anthocodia (*Azoriella* Lopez Gonzalez & Gili, 2001, *Canarya* Ocaña & van Ofwegen, 2003, *Inconstantia*, *Incrustatus*, *Phenganax* Alderslade & McFadden, 2011, *Sarcodictyon* Forbes, 1847, *Stereosoma* Hickson, 1930, *Stragulum* van Ofwegen & Haddad, 2011), fused sclerites that make the

stolons or calyces ridged (*Cyathopodium* Verrill, 1868, *Rhodelinda* Bayer, 1981, *Rolandia* de Lacaze-Duthiers, 1900, *Scyphopodium* Bayer, 1981), plate or platelet sclerites (*Knopia* Alderslade & McFadden, 2007, *Moolabalia* Alderslade, 2001, *Scleranthelia* Studer, 1878, *Tesseranthelia* Bayer, 1981), or sclerites in the stolons that are flattened double cones (*Denhartogia* Ocaña & van Ofwegen, 2003).

While *Hedera caerulescens* morphologically falls into Clavulariidae, our DNA sequence analyses indicate that *H. caerulescens* is sister to a clade including species of two genera (*Alcyonium* and *Gersemia*) from different families (Alcyoniidae and Nephtheidae). The relationship between these genera has been discussed by McFadden and van Ofwegen (2013b), who argue that *Alcyonium* is paraphyletic with respect to some species of *Gersemia*, and while they fall short of reclassifying any species of *Gersemia* as *Alcyonium*, they suggest that members of each should be condensed into a single, redefined genus *Alcyonium sensu stricto* (Alcyoniidae). They restrict the previously broad definition of *Alcyonium* to include species that have a clear crown and points formation around the polyp, and different sclerites in two layers of the coenenchyme: an upper layer with radiates or clubs and a lower layer with spindles or rods. It is unclear how many of the 13 species that form a sister clade to *H. caerulescens* are united by this restricted definition. *Gersemia juliepackardae* Williams & Lundsten, 2009 lacks a distinct crown (Williams and Lundsten 2009) and *Gersemia rubiformis* Ehrenberg, 1834 has only one layer of radiates in the coenenchyme (Deichmann 1936). Additionally, while the presence of different sclerite forms in the coenenchyme is indicated in *Alcyonium digitatum* Linnaeus, 1758, *Alcyonium glomeratum* Hassall, 1843, *Alcyonium variabile* Thomson, 1921, and *Gersemia antarctica* Kükenthal, 1902, the authors fail to note whether they are found in two distinct layers (Hickson 1895; Deichmann 1936; Williams 1992). *H. caerulescens* exhibits a crown and points formation (Fig. 5), but has only one layer of sclerites in the stolon with warty spindles and irregular crosses.

Alcyoniidae was historically placed within the suborder Alcyoniina, which was defined by joined polyps embedded in a fleshy coenenchyme (Daly *et al.* 2007). Only after Alcyoniina was changed to a subordinal group did taxonomists start describing encrusting alcyoniid taxa (Bayer 1981a). *H. caerulescens* is excluded from the encrusting alcyoniid genera *Rhytisma* Alderslade, 2000 and *Discophyton* McFadden & Hochberg, 2003 because they are characterised by very large (>2 mm long) sclerites in the coenenchyme that form a 'honeycomb-like network' around the polyps, and by a lack of calyces respectively (Alderslade 2000; McFadden and Hochberg 2003). There are, additionally, several encrusting species (without lobes) currently within the genus *Alcyonium*. *H. caerulescens* fails to match these species because they do not exhibit a full crown (*Alcyonium grandiflorum* Tixier-Durivault & d'Hondt, 1974, *A. megasclerum* Stokvis & van Ofwegen, 2006, *A. profundum* Stokvis & van Ofwegen, 2006) or they present capstan sclerite forms (*Alcyonium grandis* Casas, Ramil & van Ofwegen, 1997, *A. senegalense* Verseveldt & van Ofwegen, 1992) (Verseveldt and van Ofwegen 1992; Stokvis and van Ofwegen 2006; van Ofwegen *et al.* 2007). Indeed, we would exclude *H. caerulescens* from

Alcyonium on the basis of the definition of *Alcyonium sensu stricto* proposed by McFadden and van Ofwegen (2013b). Considered together, these morphological comparisons and our molecular results necessitate the formation of a novel genus within Alcyoniidae to accommodate *H. caerulescens*.

Hedera caerulescens shares several character states with the *Alcyonium* and *Gersemia* species of its sister clade. All these species have tubercled or warty spindle sclerites, and seven (*Alcyonium bocagei* Saville-Kent, 1870, *A. coralloides* Pallas, 1766, *A. digitatum*, *A. haddoni* Wright & Studer, 1889, *A. hibernicum* Renouf, 1931, *A. palmatum* Pallas, 1766, and *A. sidereum* Verrill, 1922) contain colourless sclerites (Deichmann 1936; Verseveldt 1973; Weinberg 1977; van Soest and Weinberg 1980; Groot and Weinberg 1982; Verseveldt and Bayer 1988; Williams 1992; van Ofwegen *et al.* 2007; Williams and Lundsten 2009). *A. coralloides* and *A. haddoni* can be encrusting like *H. caerulescens*, and *A. digitatum*, *A. glomeratum*, *A. variabile*, and *Gersemia rubiformis* all have a dense layer of sclerites coating the surface of the coenenchyme similar to the spongy mat of sclerites seen in *H. caerulescens* (Hickson 1895; Verrill 1922; Deichmann 1936; Williams 1992; van Ofwegen *et al.* 2007).

We classify this novel genus within Alcyoniidae because of its close relationship with *Alcyonium* in the combined COI–mt*MutS* phylogeny and because of the morphological overlap that exists between Alcyoniidae and Clavulariidae. Current morphological concepts often fail to accurately classify octocorals, as indicated by the many polyphyletic families and genera revealed by molecular analyses (e.g. McFadden *et al.* 2010; Bilewitch *et al.* 2014). Even species classifications may be difficult, and there are multiple instances where molecular data have revealed cryptic species of octocorals that initially appear the same morphologically. Subsequent re-examination of these molecularly distinct groups has led to the identification of previously overlooked distinguishing morphological traits (Sánchez *et al.* 2003; McFadden *et al.* 2006a, 2009; McFadden and van Ofwegen 2013a). The future of the taxonomy of octocorals undoubtedly will rely on combining molecular techniques with traditional morphological approaches.

Reports of *H. caerulescens* were compiled from local divers, marine researchers, and collections staff at the North Carolina Aquarium at Fort Fisher (Table 1, Fig. 2). The first observations based on these reports occurred between 2002 and 2004, and the species has been periodically observed at a small number of sites since then. Scientific divers conducting research at a variety of hard-bottom ledge and shipwreck sites have made most of the recent observations.

Etymology

Latin for blue, *caerulescens* reflects the colour of polyps, and 'Blue Ivy' (*Hedera caerulescens*) describes both the growth form and colour of this species.

Discussion

The marine fauna of the South Atlantic Bight are relatively well studied because of the long history of academic and government marine laboratories in the region. Documentation of the octocorals present in the South Atlantic Bight began eight

decades ago (Deichmann 1936), and a complete treatment was published as recently as 2010 (DeVictor and Morton 2010). The North Carolina coast, with its many shipwrecks, is also a well-known area for recreational diving, and the brilliant blue polyps of *H. caerulescens* make it visually obvious and an excellent subject for underwater photography. It seems unlikely that this species could have remained unnoticed by both scientists and recreational divers before the recent observations.

It is impossible to conclude that *H. caerulescens* was anthropogenically introduced into the South Atlantic Bight without knowing its native range; however, it seems unlikely that its presence in the region is the result of a natural range expansion. Investigations of North Carolina's marine algal flora are revealing multiple instances of northern range expansions (Freshwater and Idol 2013; National Centers for Coastal Ocean Sciences (NCCOS) 2014), and similar findings are expected for the sessile invertebrate fauna. However, no species matching the description of *H. caerulescens* has ever been recorded from the Caribbean or other areas of the tropical Western Atlantic (Bayer 1961), and therefore its recent appearance in North Carolina waters is not the product of a northern range expansion. Similarly, no octocoral species resembling *H. caerulescens* is known from the cold temperate Western Atlantic (Watling and Auster 2005; Watling *et al.* 2011), and a southward range expansion is likewise doubtful. We expanded our search farther afield, and reviewed all clavulariid genus descriptions as well as encrusting alcyoniid descriptions globally, and failed to find a match to *H. caerulescens*.

H. caerulescens fits two of the criteria of Chapman and Carlton (1991, 1994) for invasive species: its appearance in a local region where not found previously, and having a relatively restricted distribution in the Western Atlantic compared with native octocoral species. Whether it also fits other invasive species criteria is difficult to determine because so little is known about the species. Phylogenetic analyses resolve *H. caerulescens* as the sister lineage to a clade that includes no species with a warm-temperate or tropical Western Atlantic distribution, suggesting that it fits the criteria of having an exotic evolutionary origin. Nine of the 14 current reports are from artificial substrates (shipwrecks, concrete structures), indicating that *H. caerulescens* may also fit the invasive criterion of being prevalent on, or restricted to, new or artificial environments. However, the first known sightings of *H. caerulescens* were on a natural hard-bottom ledge system, and its presence on wrecks is not unusual because sessile invertebrates dominate the wreck epibenthic community.

Octocorals are notoriously difficult to identify and categorise due to their global distribution and limited synapomorphies that are challenging to observe and interpret (microscopic sclerites of complex and varied forms). It is unsurprising that, while it seems likely that *H. caerulescens* has been recently introduced to the South Atlantic Bight, we are unable to determine its native range. Recognising, documenting, and understanding changes, anthropogenic or otherwise, to the distribution, biology, and ecology of these organisms is impossible without an improved taxonomic system based on both molecular and morphological data. As more molecular data become available, it is likely that many octocoral clades

will be revised, and this paper adds a piece to this largely incomplete puzzle.

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