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Integrative taxonomy of introduced Haplosclerida and four new species from Hawai‘i

JAN VICENTE[1*], EMILY RUTKOWSKI[1], DENNIS V. LAVROV[2], GABRIELLE MARTINEAU[1], MOLLY TIMMERS[1,3] & ROBERT J. TOONEN[1]

[1]*Hawai‘i Institute of Marine Biology, School of Ocean and Earth Science and Technology, University of Hawai‘i at Mānoa, Kāne‘ohe, HI, 96744, USA.*
Emily Rukowski: ecrutkow@hawaii.edu; https://orcid.org/0009-0008-9526-1241
Gabrielle Martineau: dlavrov@iastate.edu; https://orcid.org/0000-0003-3980-4631
Robert J. Toonen: rjtoonen@gmail.com; https://orcid.org/0000-0001-6339-4340
[2]*Department of Ecology, Evolution, and Organismal Biology, Iowa State University, 343A Bessey, IA, 50011-1020, USA.*
Dennis V. Lavrov: dlavrov@iastate.edu; https://orcid.org/0000-0002-2745-1704
[3]*Pristine Seas, National Geographic Society, Washington, DC 20036, USA.*
Molly A. Timmers: mtimmers@ngs.org; https://orcid.org/0000-0003-0545-8443
Corresponding author. janv@hawaii.edu; https://orcid.org/0000-0003-4741-0261

Abstract

Haplosclerid sponges (Porifera: Demospongiae: Heteroscleromorpha), and particularly the family Chalinidae, are notoriously difficult to identify through taxonomic methods alone. Here we use an integrative approach to confirm the identification and report both polymorphic characters and different morphotypes exhibited from a recruitment stage that complicate identification of introduced haplosclerid species *Haliclona* (*Soestella*) *caerulea* and *Gelliodes conulosa* **sp. nov.** in Hawai‘i. Using these same methods, we also describe three new species *Haliclona* (*Gellius*) *pahua* **sp. nov.**, *Haliclona* (*Reniera*) *kahoe* **sp. nov.**, *Haliclona* (*Rhizoniera*) *loe* **sp. nov.** from our collections in Kāne‘ohe Bay. Using a combination of mitochondrial and ribosomal RNA sequences, we compile a phylogeny that is consistent with previous molecular work but is at odds with the morphological characters used to classify species belonging to Chalinidae and Niphatidae families within Haplosclerida. Although shared morphological traits were distributed across taxa throughout the tree, both mitochondrial and ribosomal RNA sequences were diagnostic, with an average of at least 3 % sequence divergence among species and their closest relative. This study highlights both the use of standardized Autonomous Reef Monitoring Structures (ARMS) to access the hidden diversity of haplosclerid sponges, and the potential for competition between these introduced and newly described and potentially endemic species.

Key words: phylogeny, sponge cryptofauna, exotic species, polymorphism

Introduction

Integrating sequence data with classical taxonomy when establishing a baseline of biodiversity is invaluable. Molecular data can delineate species boundaries (Galitz *et al.* 2023), populations within species (Cóndor-Luján *et al.* 2021; Wörheide *et al.* 2002), reveal cryptic speciation among individuals with conserved morphological characters (Concepcion *et al.* 2008) and improve the detection of introduced species (Geller *et al.* 1997; Morais & Reichard 2018). Integrated molecular and morphological data provide molecular databases with more accurate taxonomic classifications (Deck *et al.* 2017; Ratnasingham & Hebert 2007), which are essential when applying metabarcoding techniques, such as environmental DNA, to biodiversity monitoring and invasive species detection (de Santana *et al.* 2021). And yet, there have been limited efforts to integrate both into biodiversity studies, in part due to the deficiency of the taxonomic workforce (Hopkins & Freckleton 2002; Sangster & Luksenburg 2015). As a result, availability of sequencing data has greatly outpaced the rate at which species belonging to taxonomically challenging phyla are described (Thines *et al.* 2018) resulting in broad taxonomic assignments for operational taxonomic units, which in many studies are classified only at the phylum level (Leray & Knowlton 2015; Nichols & Marko 2019; Stat *et al.* 2017).

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Sponges (phylum Porifera) are a prime example of such challenging phyla where taxonomic orders show a wide range of diagnostic characters from many to only a few (Hooper & van Soest 2002). In particular, the order Haplosclerida, the third most specious order within the class Demospongiae, (de Voogd *et al.* 2023) is notoriously difficult to identify due to the lack of distinct and diagnostic morphological characters, the plasticity of characters among conspecifics, and family polyphyly (Redmond *et al.* 2011; van Soest & Hooper 2002). However, integrative approaches using DNA sequencing with morphological characters have aided in overcoming this hurdle. For example, three different morphotypes of *Neopetrosia proxima* that shared similar external morphological features (consistency and color) and spicule composition but varied in skeletal composition and reproduction were deemed conspecific until COI and 28S rRNA sequencing determined them to be heterospecific (Vicente *et al.* 2019).

Supplementing traditional taxonomy with molecular phylogeny has revealed a remarkable richness of haplosclerid sponges from shallow coral reef habitats in Hawai‘i. Previous sponge collection efforts mainly relying on traditional taxonomic approaches documented only 12 haplosclerid species throughout the Hawaiian Archipelago (de Laubenfels 1950, 1951). But recent surveys integrating taxonomy with molecular phylogeny, targeting cryptobenthic and surface-dwelling sponges showed haplosclerid richness in Hawai‘i to be grossly underestimated, with at least 30 confirmed species in Kāne‘ohe Bay alone (Bertolino *et al.* 2023; Pons *et al.* 2017; Vicente *et al.* 2022b). Many haplosclerid species, particularly in the Chalinidae family, in Hawai‘i show little variation in morphological characters that necessitate molecular data for their classification (Vicente *et al.* 2022b).

The most specious genera among the Chalinidae from shallow benthic reef communities of Hawai‘i are *Haliclona* spp. (6 described). They are efficient colonizers during pioneering stages of ecological succession but exhibit rapid turnover and become less abundant during climax stages of community development (Vicente *et al.* 2022a). Members of this genus along with other haplosclerids have also historically been a group of concern in Hawai‘i due to species introductions from the Caribbean (*Haliclona* (*Soestella*) *caerulea*), West Indo-Pacific (*Haliclona* (*Reniera*) *laubenfelsi,* Bettcher *et al.* 2024), and Indonesia (putative *Gelliodes wilsoni*), which are now common residents in confined lagoonal habitats of the archipelago (Eldredge & Smith 2001). Morphological variation among individuals and locations leads to uncertainty about whether these introduced species are polymorphic or there are multiple species present. The true diversity of this group remains elusive, because a genetic repository anchored to vouchered specimens that would serve as resource for accurate classification is missing.

Haplosclerid sponges are important but challenging members of benthic reef communities, due to their ecological relevance and diversity, vast geographical distribution, and conserved taxonomic characters. Thus, we integrate morphological characterization with molecular phylogeny based on mitochondrial and rRNA sequences to evaluate the morphological diversity of introduced sponges *H.* (*Soestella*) *caerulea*, and provide morphological evidence to erect the new name *Gelliodes conulosa* which was previously known as *Gelliodes wilsoni* and has historically been an alien species of Hawaiian harbors and bays for the past 3 decades (Carballo *et al.* 2013; Coles 2006; Coles *et al.* 2002; Eldredge & Smith 2001; Pons *et al.* 2017; Vicente *et al.* 2022b). We confirm the identity of these species, and report polymorphic characters and variable morphotypes from different recruiting stages rather than multiple species. We then use the same approach to describe three new *Haliclona* spp. from our Kāne‘ohe Bay collections. Our integrative approach will aid future biodiversity studies in providing voucher validated sequences for successful identification of these challenging sponges, and define boundaries of potentially endemic and introduced sponge species throughout the Eastern Indo-Pacific.

Materials and Methods

Sample collection

Sponges were photographed *in situ* and collected from a variety of habitats including: Autonomous Reef Monitoring Structures (ARMS), floating docks, pier pilings, marine mammal pens, and shallow (0.3 to 3 m) natural reef environments in Kāne‘ohe Bay, Ke‘ehi Harbor and Shark’s Cove on the island of O‘ahu, Hawai‘i (Fig. 1). Collections from ARMS were conducted monthly throughout a 2-year sampling period (July 2016 through June 2018) following methods in (Timmers *et al.* 2020) and Vicente *et al.* (2021). Sponge species were mapped using the ggmap v.3.0.901 package (Kahle & Wickham 2013) in R v.4.3.2 (R Core Team 2023). Field observations of morphology, color, consistency, surface, and oscules for each specimen were recorded. Samples were preserved in 95% ethanol and when enough material was available, were also fixed in 4% paraformaldehyde (PFA) for 24

hrs and then transferred to 70% ethanol. Type and other specimens were deposited in the Florida Museum of Natural History (catalogue numbers beginning with acronym UF) in Florida, USA, and the Bernice Pauahi Bishop Museum (catalogue numbers beginning with acronym BPBM) in O'ahu, USA. Samples from Kāne'ohe Bay were collected under special activities collection permits SAP2018-03 and SAP2019-06 (covering the period of January 13, 2017, through April 10, 2019) issued by the State of Hawai'i Division of Aquatic Resources. Samples from Pūpūkea Marine Life Conservation District were collected under permit SAP2023-20 (covering the period of March 11, 2022, through March 10, 2023). Samples from Kewalo and Ke'ehi harbors were collected by the Division of Aquatic Resources Aquatic Invasive Species team who do not require special activities permits.

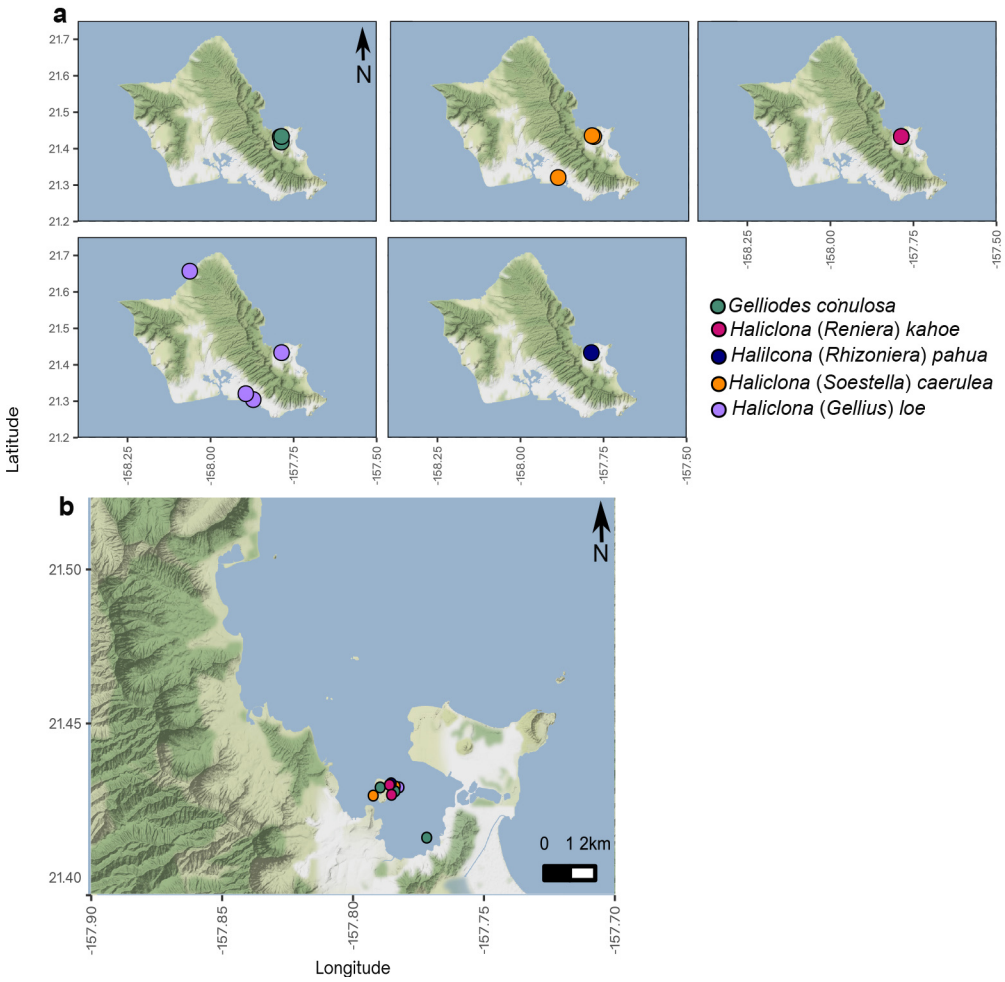

FIGURE 1. Collection sites of sponge species on a, the windward side (Kāne'ohe Bay) and South shore (Ke'ehi Harbor) of O'ahu. Zoomed in location of sponges collected in b, South Kāne'ohe Bay including Moku o Lo'e.

DNA extraction, sequencing, and assembly

Subsamples of sponge tissue (30 mg) were removed from type material preserved in 95% ethanol and were processed for DNA extraction. Two different approaches were utilized for DNA extraction and downstream analysis. First, we followed protocols in Vicente *et al.* (2021) for DNA extractions, polymerase chain reactions (PCR) for amplifying partial fragments of both 28S rRNA and COI genes and for Sanger sequencing. Forward and reverse reads were assembled, trimmed, and edited by eye using Geneious 10 (Kearse *et al.* 2012). Sequences were checked for contamination using the online BLAST server (Altschul *et al.* 1990) and results that showed at least 85% sequence identity to sponges were used for subsequent analysis. All assembled chromatograms resulted in >90% high quality base pair reads with a mean Phred quality score $\geq$ 40. Second, total DNA from holotypes of *Haliclona* (*Gellius*) *loe* BPBM C1523, *Haliclona* (*Reniera*) *kahoe* BPBM C1539, *Haliclona* (*Rhizoniera*) *pahua* BPBM C1518, vouchers BPBM C1519, BPBM C1510 for *Haliclona* (*Soestella*) *caerulea* and *Gelliodes conulosa* respectively were extracted

with a phenol-chloroform method modified from Saghai-Maroof *et al.* (1984) and used directly for library preparation with the Illumina True-Seq PCR free kit and low-coverage of whole genome sequencing on Illumina NovaSeq 6000 at the Iowa State University DNA facility. A detailed protocol for mitochondrial and ribosomal genome sequences for these samples can be found in Lavrov *et al.* (2024).

Phylogenetic analysis

Haplosclerida sequences within GenBank closely resembling (>90% sequence identity) new sequences in our study were selected for the phylogenetic analysis. These only included sequences from species associated with voucher specimens associated with a peer reviewed publication authored or coauthored by taxonomists. ClustalW with default parameters was used for aligning partial and complete 28S rRNA and COI sequences. Alignments consisted of 300 bp of the 28S and 480 bp of the COI gene sequence. RaxML (Stamatakis 2006) included Geneious 10 was used for maximum likelihood (ML) analysis with the GTR+GAMMA model of nucleotide substitution, 100 starting maximum parsimony trees, and 1,000 bootstrap replicates. Resulting bootstrap values of >50 from the ML posterior probabilities are shown on the tree. Phylogenetic trees were rooted on *Ephydatia fluviatilis* OX175335.1 and ON000190.1 for 28S and COI, respectively.

Sequences of holotypes and other specimens for each species were deposited to GenBank under accession numbers: MW016123, MT452542, MT586742, MW016124, MW059074, MW143255, MW016168, MW059064, MW059059, MW016133, MT586743, MW016360, MW016153, MW016155, MW016154, MW059075, MW016154. All accession numbers pertaining to each species are also available in Table S1.

Sectioning and spicule preparation

Sponge pieces (3–5 mm^3) containing both ectosomal and choanosomal tissue fixed in either 4% PFA or 95% ethanol were transferred to 70% ethanol. Sponge pieces were dehydrated in an alcohol series of 35%, 50% and 70%, 100% and embedded in paraffin. Sections >100 μm thick were cut perpendicular to the surface through the ectosome and choanosome with a microtome. In specimens where the ectosome was specialized, tangential sections across the sponge surface were made at 100 μm thickness. Small pieces were also boiled in nitric acid for 1–2 min or until solution turned clear. Spicules were let to settle, and the acid was discarded. Spicules were then rinsed two times with distilled water to remove the acid; water was then changed to 95% ethanol for storage. Spicules were suspended and a few drops were observed under light microscopy, photographed, and measured using ImageJ (Abràmofff *et al.* 2005) http://imagej.nih.gov/ij/). Fifty oxeas and if present ten sigmas per species were measured [lengths and widths, expressed herein as minimum–mean [±1 standard deviation (SD)]–maximum length / width in μm (n)]. A few drops of the spicule suspension were added to a stub, air dried and imaged under a Hitachi S-4800 FESEM Scanning Electron Microscope (SEM) at the Biological Electron Microscope Facility at the University of Hawai‘i Mānoa.

Summarizing morphological characters of congeneric comparative material

Sponge species found throughout the Hawaiian Archipelago are shared with the Central Indo-Pacific (Australia, Philippines, the Mariana Archipelago), Temperate Australasia (New Zealand), Temperate Northern Pacific (Japan), the Eastern Mexican Pacific, Caribbean, Mediterranean and the Northeast Atlantic (Bergquist 1967; Carballo *et al.* 2013; de Laubenfels 1950; van Soest *et al.* 2021). We used the World Porifera database to include a summary of morphological characters for 51 *Haliclona* spp. closely resembling the new species in this study. These species were selected from geographic locations with shared species with the Hawaiian Archipelago. Species from the Temperate Atlantic, Black Sea, Arctic or Southern Ocean were considered improbable species due to geographic barriers and temperate climates. Species from these ecoregions were therefore disregarded as comparative material.

Systematics

Class Demospongiae Sollas 1885

Order Haplosclerida Topsent 1928

Family Chalinidae Gray 1867

Haliclona Grant 1841

Definition. Chalinidae with secondary lines unispicular and one spicule long (Bispo *et al.* 2022; de Weerdt 2002).

Haliclona (*Gellius*) (Gray, 1867)

Subgenus *Gellius*

Definition. Chalinidae with a choanosomal skeleton consisting of a rather confused, subhalichondroid reticulation of pauci- to multispicular primary lines, irregularly connected by unispicular secondary lines. Ectosomal skeleton, if present, either a regular, tangential, unispicular, isotropic reticulation, or consisting of irregularly strewn, tangentially orientated spicules. Microscleres if present, sigmas and toxas (modified from de Weerdt 2002).

Remarks. The definition of Gellius from de Weerdt (2002) does not include presence of microscleres but it was published as a "key to subgenera of *Haliclona*" by de Weerdt (2002). As such, the statement "microscleres if present, sigmas and toxas" have been added to the original definition.

Haliclona (*Gellius*) *loe* sp. nov. (Fig. 2–3, Table 1)

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Haliclona sp. JV 11 in Vicente *et al.*, 2022a, 2022b

Holotype and type locality. BPBM C1523-Mammal pens at Moku o Loʻe (Coconut Island), Kāneʻohe Bay, Oʻahu, (21.4324 °N, -157.7908 °W); 0.5 m, coll. Jan Vicente, 2016-12-16. **Paratypes.** BPBM C1549, BPBM C1533; ARMS in mesocosms at the Hawaiʻi Institute of Marine Biology (HIMB) in Moku o Loʻe (Coconut Island), Kāneʻohe Bay, Oʻahu, (21.4335 °N, -157.7864 °W); 0.3 m coll. Jan Vicente, 2018-03-16, 2018-03-16, and 2018-06-11 respectively. BPBP C1534-Keʻehi harbor, Oʻahu (21.3208 °N, -157.8940 °W); 2 m, coll. Jan Vicente, 2018-5-15. BPBM C1673-Kewalo Marina, Oʻahu (21.2937 °N, -157.8566 °W); 3 m, coll. Jan Vicente, 2018-5-25. BPBM C1672- Pūpūkea Marine Life Conservation District, Oʻahu (21.6534, -158.0626); 10 m, coll. Jan Vicente, 2022-09-03. Additional information from other vouchers can be found in Table S1.

Diagnosis. A thickly encrusting or cushion shaped *Haliclona* (*Gellius*), with light yellow, bright yellow, brownish pink exterior and interior**,** uneven punctate surface, firm but crumbly consistency, undefined ectosome but with a unispicular to paucispicular confused choanosomal skeleton that becomes more unispicular and isodictyal closer to the surface, spicules are oxeas (138–253 x 1– 9 μm) and small sigmas (7–12.0 x 0.3–1.1 μm).

Description (Fig. 2): Thick (1–2 cm) cushion-shaped encrustation that spreads laterally (16 cm). Surface can be hispid, uneven, bumpy and punctate. Oscula are volcano shaped measuring between 2–6 mm in diameter and rise 0.5 cm from the base of the sponge surface. Consistency is firm but crumbly and breaks easily when compressed. Color in life of the sponge surface varies between light brownish pink in small recruits to faint yellow and bright yellow in larger specimens, sponge interior is brownish pink. Exudes dark brown pigments when preserved in ethanol and the remaining color of the specimen is grey. Embryos measuring 500 μm in diameter were abundant in the choanosome of the holotype BPBM C1523 (Fig. 2b).

Skeleton (Fig. 3a–e): Ectosome is not specialized. The choanosome is confused, isotropic, consisting of

unispicular to paucispicular (1–2 spicule thick) lines occasionally in isodictyal reticulation but also halichondroid. Reticulation is more confused deep in the choanosome and becomes somewhat anisotropic closer to the ectosome. At the surface, more organized, unispicular to paucispicular lines are connected irregularly by unispicular secondary lines which occasionally break the surface by a single oxea (100–140 µm from the surface). 4–10 spicules meet at the nodes forming triangular (90–100 µm in diameter), pentagonal, and hexagonal meshes (up to 240 µm in diameter). A network of canals (cavernous system) is observed in the choanosome. Spongin is present at the nodes and throughout the skeleton giving the choanosome a light brown pigmentation.

Spicules (Fig. 3f-h; Table 1): Oxeas straight and curved at the center with acerate tips 138–179–253 x 1–5– 9 µm (Fig. 3f–g). Oxeas with blunt tips are rare. Sigmas are C-shaped, very abundant throughout the sponge tissue, and are in a single size category 8.7–9.9–12.0 x 0.3–0.6–1.1 µm (Fig. 2h).

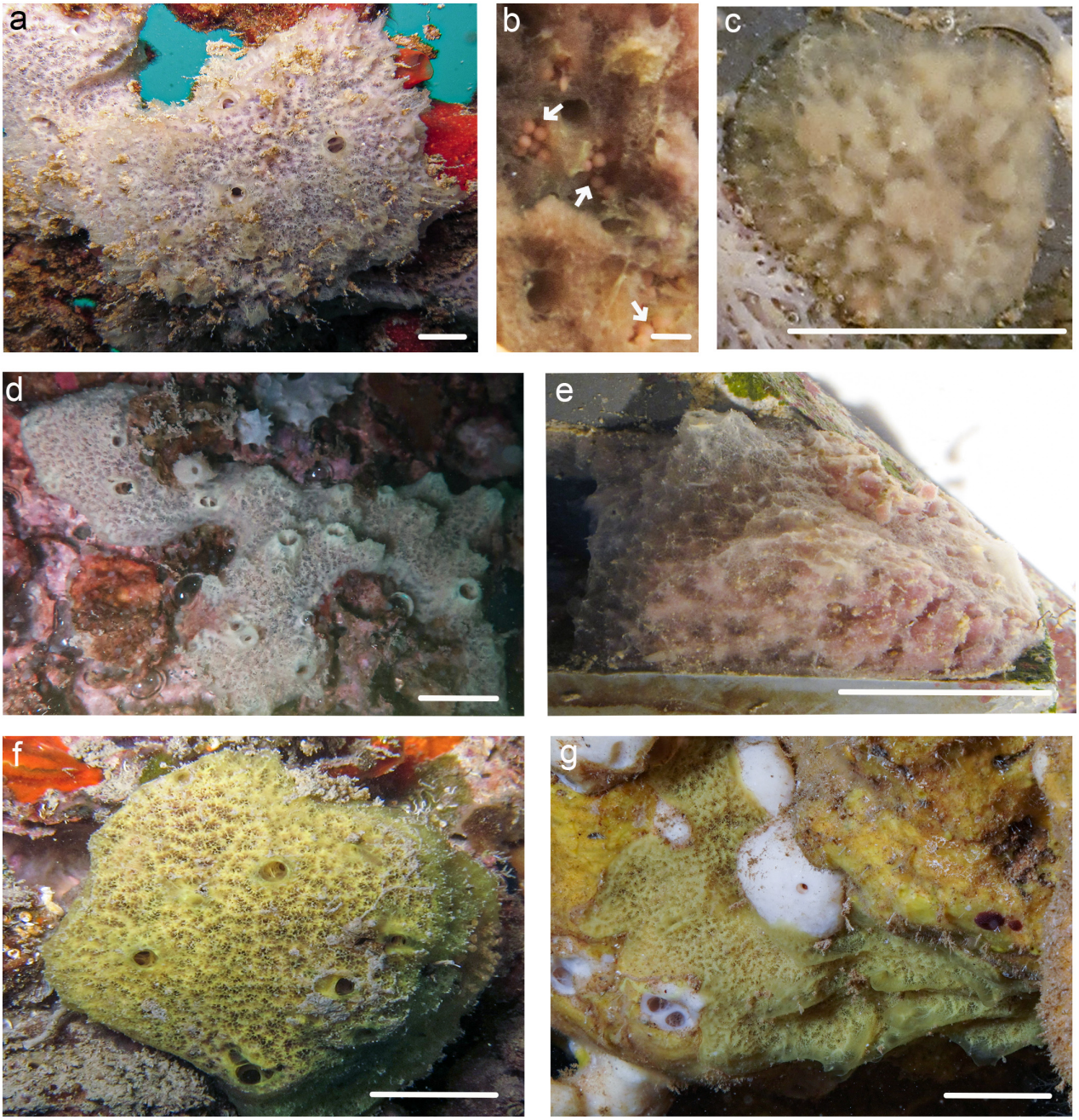

FIGURE 2. In situ growth variations of *Haliclona* (*Gellius*) *loe* **sp. nov.** a. holotype BPBM C1523 in situ; b. Embryos in the mesohyl of holotype BPBM C1523 indicated by white arrows. c. Six-month recruit of paratype BPBM 1533. d. paratype BPBP C1534. e. One year recruit of paratype BPBM C1549. f. paratype BPBM C1673. g. paratype BPBM C1672. Scale bars: a, 1 cm; b, 0.5 cm; c-g, 1 cm.

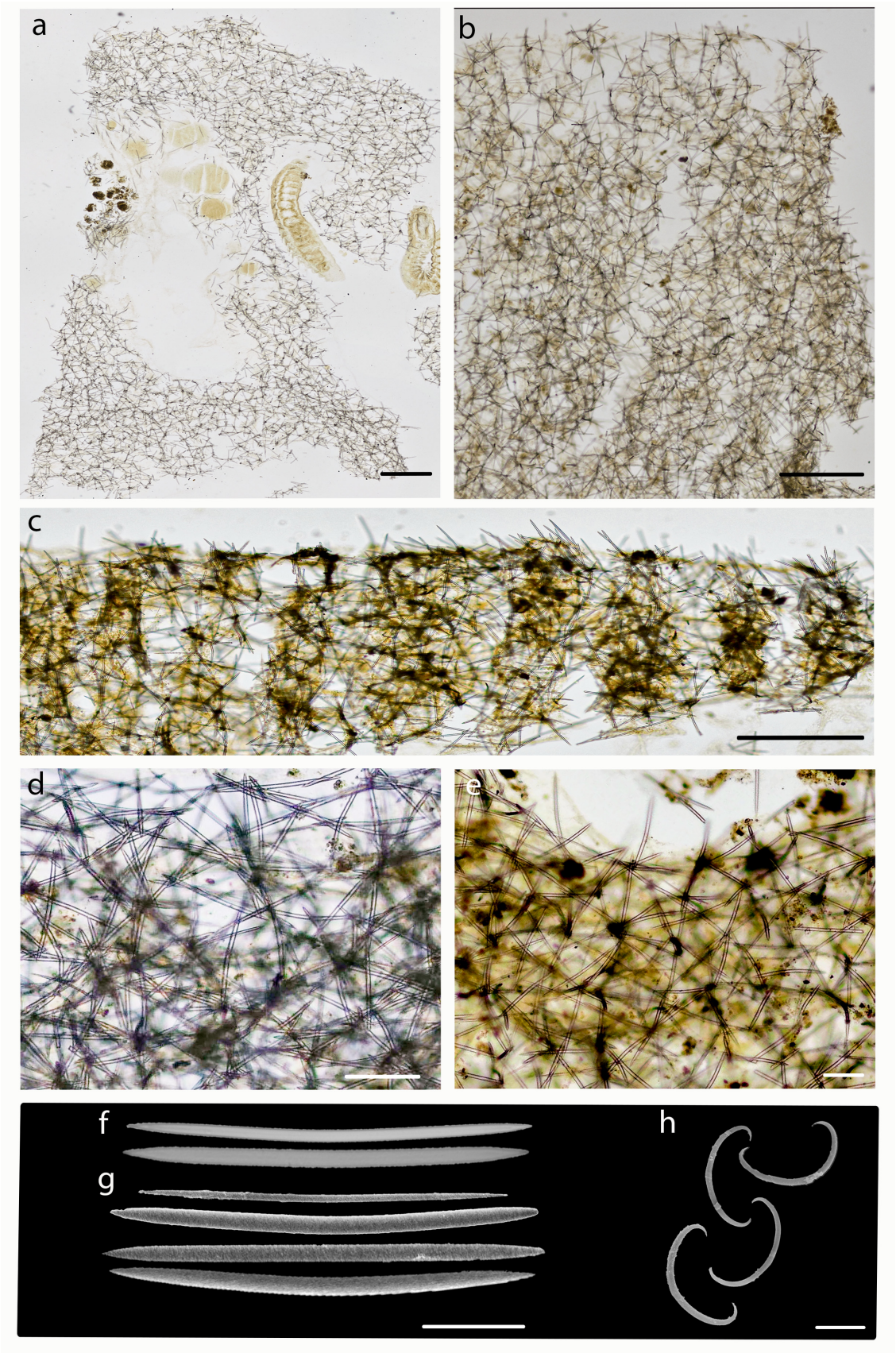

FIGURE 3. Skeletal architecture of *Haliclona* (*Gellius*) *loe* **sp. nov.** Perpendicular section through the ectosome and choanosome in a, holotype BPBM C1523; b, paratype BPBM C1549; c, paratype BPBM C1673; close up of the choanosome in d–e paratype BPBP C1534. Light microscopy images in f, oxeas of paratype BPBM 1533 SEM images in g, oxeas and h, sigmas of holotype BPBM C1523. Scale bars: a–b, 500 µm; c, 250 µm; d–e, 100 µm; f–g, 50 µm; h, 5 µm.

Habitat and ecology. Specimens were collected inside lava tubes on Oahu's North shore, on shaded pilings in Keʻehi Harbor on the south shore, and on nets that used to confine mammals at HIMB. Specimens were also collected inside mesocosm ARMS. Absence of these species on reef ARMS, where the surrounding sponge community is at a climax stage of succession, suggests that *Haliclona* (*Gellius*) *loe* **sp. nov.** is an early colonizer during pioneering stages of ecological succession (Sup. Fig. S3 in Vicente *et al.*, 2022a). Presence of embryos within the holotype indicates viviparous reproduction.

Distribution (Fig. 1). Moku o Loʻe (Coconut Island), Kāneʻohe Bay and Keʻehi harbor on the island of Oʻahu, Hawaiʻi.

TABLE 1. Spicule measurements of oxeas and sigmas for *Haliclona* (*Gellius*) *loe* **sp. nov.** . Measurements are expressed as minimum–mean (±1 standard deviation)–maximum. N=50 for oxeas and N=10 for sigmas.

Voucher	Oxeas		Sigmas	
	Length (μm)	**Width (μm)**	**Length (μm)**	**Width (μm)**
BPBM C1523 (h)	158.0–(191.3±11.6)–216.4	2.2–(5.4±1.6)–8.2	8.9–(10.2±0.7)–11.5	0.4–(0.7±0.2)–1.1
BPBM C1533 (p)	138.3–(174.3±14.3)–201.5	1.1–(4.0±1.2)–6.7	8.7–(9.7±0.5)–10.6	0.5–(0.6±0.1)–0.8
BPBM C1524 (p)	142.5–(165.1±11.8)–224.5	2.3–(4.2±0.7)–5.4	8.8–(9.5±0.4)–10.0	0.4–(0.6±0.1)–0.8
BPBM C1534 (p)	148.8–(185.2±11.9)–207.2	4.6–(6.3±1.0)–9.2	9.5–(10±0.4)–10.5	0.3–(0.5±0.1)–0.7
BPBM C1673 (p)	140.1-(205.0±19.4)-253.0	5.0-(6.0±0.7)-8.2	10.0-(11.0±0.7)-12.0	0.5-(0.6±0.1)-0.8

Etymology. The given name honors the moʻolelo (historical accounts from native Hawaiians) of how Moku O Loʻe was named. Loʻe was the sister of three brothers who kept honesty within the family. We use the feminine *loe* following the feminine gender of *Haliclona* and Article 31.2 of the International Code for Zoological Nomenclature (http://www.iczn.org/, accessed on October 16, 2023).

Taxonomic remarks. Variability of the skeleton morphology in *Haliclona* (*Gellius*) *loe* between unispicular to paucispicular or from halichondroid, isodictyal, to anisotropic at the sponge surface matches the definitions for either, *H.* (*Gellius*), *H.* (*Halichoclona*) or *H*. (*Soestella*) (de Weerdt, 2002). All replicates of *H.* (*Gellius*) *loe* lack a specialized ectosome as well as the presence of subectosomal or choanosomal spaces which are characteristic of *H.* (*Halichoclona*). Likewise, paucispicular lines do not form circular meshes anywhere throughout the choanosome or ectosome, which is diagnostic of *H*. (*Soestella*). The closest fitting definition remaining considering all characters of the new species including the presence of sigmas as microscleres is that of *H*. (*Gellius*).

The spicule composition of 80% of *H.* (*Gellius*) spp. (61 species) consist of sigmas and oxeas. *Haliclona* (*Gellius*) *loe* stands out from most of these species by the smaller length of sigmas (8.7–11.5 μm in length). The only species having sigma dimensions similar to *Haliclona* (*Gellius*) *loe* **sp. nov.** are *Haliclona* (*Gellius*) *amboinensis* (Lévi 1961) (9–17 μm in length), *Haliclona* (*Gellius*) *microsigma* (Babic 1922) (8–10 μm in length) and *Haliclona* (*Gellius*) *patbergquistae* van Soest *et al.* 2020 (11–14 μm in length) (Table S2). These species are set apart from *H.* (*Gellius*) lo*e* by their larger sized oxeas (*H*. (*Gellius*) *microsigma* (200–240 x 5–10 μm), *H*. (*Gellius*) *patbergquistae* (305–343 x 12 μm), *H*. (*Gellius*) *amboinensis* (175–230 x 7–14 μm)). Other matching *H*. (*Gellius*) spp. possibilities possibilities with small sigmas are *Haliclona* (*Gellius*) *concreta* Bispo *et al.*, 2022 (5–8 μm in length), *Haliclona* (*Gellius*) *dubia* (Babic, 1922) (12–16 μm in length), *Haliclona* (*Gellius*) *rava* (Stephens 1912) (8 μm in length), *Haliclona* (*Gellius*) *regia* (Brøndsted 1924) (10–18 μm in length), *Haliclona* (*Gellius*) *tenerrima* (6–10 μm in length) Burton 1954. However, these small-sigma-bearing sponges are distinguishable from the new species in that they all have toxas in their spicule composition. Among sigma bearing *Haliclona* spp. of unknown subgenera are *Haliclona aperta* (Sara 1960) (34–43 μm in length) from the Mediterranean, *Haliclona libera* (15 μm in length) and *Haliclona uwaensis* (Hoshino 1981) (10–22 μm in length) from Japan, and *Haliclona sabulosa* Bergquist & Warne 1980 (34–43 μm in length) from New Zealand. All can be discarded as possible matches by the size of their sigmas which exceeds the length of sigmas of the new species.

Haliclona (*Reniera*) Schmidt 1862

Subgenus *Reniera*

Definition. Chalinidae with a choanosomal skeleton consisting of a delicate, regular, unispicular, isotropic reticulation. Ectosomal skeleton if present, also a tangential, unispicular, isotropic, very regular, and continuous reticulation. Spongin always present at the nodes of the reticulation, but never abundant. Oxeas frequently blunt pointed or strongylote. Microscleres, if present, toxas and sigmas. Sponges commonly soft and fragile (de Weerdt 2002).

Haliclona (*Reniera*) *kahoe* sp. nov.

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(Fig. 4–5, Table 2)

Haliclona sp. JV 1; Vicente *et al.*, 2022b, Vicente *et a*l., 2022a: Sup. Fig. S7

Holotype and type locality. BPBM C1539-ARMS on reef at Moku o Loʻe (Coconut Island), Pūpūkea, Kāneʻohe Bay, Oʻahu (21.4335 °N, -157.7863 °W); 0.3 m, coll. Jan Vicente, 2018-03-16. **Paratypes.** BPBM C1570, BPBM C1540, BPBM C1538- ARMS on reef at Moku o Loʻe (Coconut Island), Kāneʻohe Bay, Oʻahu (21.4335 °N, -157.7863 °W); 3 m, coll. Jan Vicente, 2017-11-21, 2018-03-16, 2018-06-11, respectively. BPBM C1553, BPBM C1554, BPBM C1552, BPBM C1551, and BPBM C1537-ARMS in mesocosms at the Hawaiʻi Institute of Marine Biology (HIMB), Moku o Loʻe (Coconut Island), Kāneʻohe Bay, Oʻahu (21.4334 °N, -157.7868 °W); 0.3 m, coll. Jan Vicente, 2016-12-19, 2017-02-13, 2017-08-01, 2018-01-19, 2018-03-16, and 2018-06-11 respectively. Additional vouchers with metadata can be found in Table S1.

Diagnosis. A soft, thin to thickly encrusting *Haliclona* (*Reniera*) displaying a variety of irregular, and regular cushion shaped growth morphologies with apical oscula that are mainly light brown in color. The skeleton is exclusively composed of oxeas (154–197 x 1– 9 µm) arranged mainly in unispicular, isotropic, isodictyal, reticulation throughout the choanosome and ectosome.

Description (Fig. 4): Thin to thickly encrusting with erect regular to irregular oscular lobes. Individuals spread laterally measuring 1–4 cm in length, width of ≤1 cm and a thickness up to 0.5 cm. Oscula measure 1–3 mm in diameter and may rise 0.5 cm in height. Some colonies have multiple oscular lobes stemming from one base. The base is thinly encrusting, spreading laterally. Base's surface is smooth, even, and occasionally irregular with few microscopic pores. In some specimens multiple, long, thin anastomosing branches project outward from the base. Oscula may spread laterally across branches. Superficial canals are slightly pronounced along the base of some individuals but are rarely present. Consistency is soft, delicate, compressible, and easily torn. Color in live specimens ranges from light brown, light purple to greyish yellow. A gradient from dull yellow to purple can be observed concurrently on the same individual.

Skeleton (Fig. 5a–h): Ectosome is ill defined in some specimens but when present, is composed of an isotropic unispicular, isodictyal reticulation of oxeas. Rectangular (80–120 µm in diameter) or quadrangular meshes (up to 150 µm in diameter) are composed of 5–10 oxeas which meet at the nodes with very little spongin. The lack of spongin gives the ectosome a translucent appearance. Choanosome in some specimens is less organized and consists of an isotropic to subisotropic reticulation forming meshes similar in size and shape to those found in the ectosome. Few discernable unispicular ascending primary tracts (spaced 100–150 µm apart) are visible in some individuals but are not connected by a regular frequency of secondary tracts (Fig. 5b). Spongin and small auxiliary oxeas is scattered sporadically throughout the choanosome.

Spicules (Fig. 5i-j); Table 2): Oxeas are straight or slightly curved with acerate tips measuring 154–162–197 x 1–4.5– 9 µm (Fig. 5i-j) Oxeas with both round and acerate ends are rare.

Taxonomic remarks. The delicate unispicular, isotropic to subisotropic reticulation of oxeas in both the choanosome and ectosome of *Haliclona* (*Reniera*) *kahoe* agrees with both *H.* (*Reniera)* (Schmidt, 1862) and *H.* (*Halichoclona*) de Weerdt, 2002. Yet, the soft consistency, compressibility, and the lack of subectosomal or choanosomal spaces is more similar to those of *H*. (*Reniera)* than of *H*. (*Halichoclona*). The skeleton lacks a ladder-

like morphology with primary lines connected irregularly (characteristic of *H.* (*Rhizoniera*) Griessinger 1971 or regularly (characteristic of *H.* (*Haliclona*) de Weerdt, 2002) by unispicular secondary lines. Skeleton reticulation is also not subhalichondroid with multispicular lines as defined for *H.* (*Gellius*) Gray 1867 nor does it tend to form rounded meshes in the ectosome by paucispicular lines as defined for *H.* (*Soestella*) de Weerdt, 2002. Although, *H.* (*Reniera)* is the most appropriate classification for this species, the ectosomal skeleton when present is not "very regular" nor does the presence of spongin conform to its definition. Spongin is not only present at the nodes of spicules that build the skeletal framework but is also abundant throughout the choanosome.

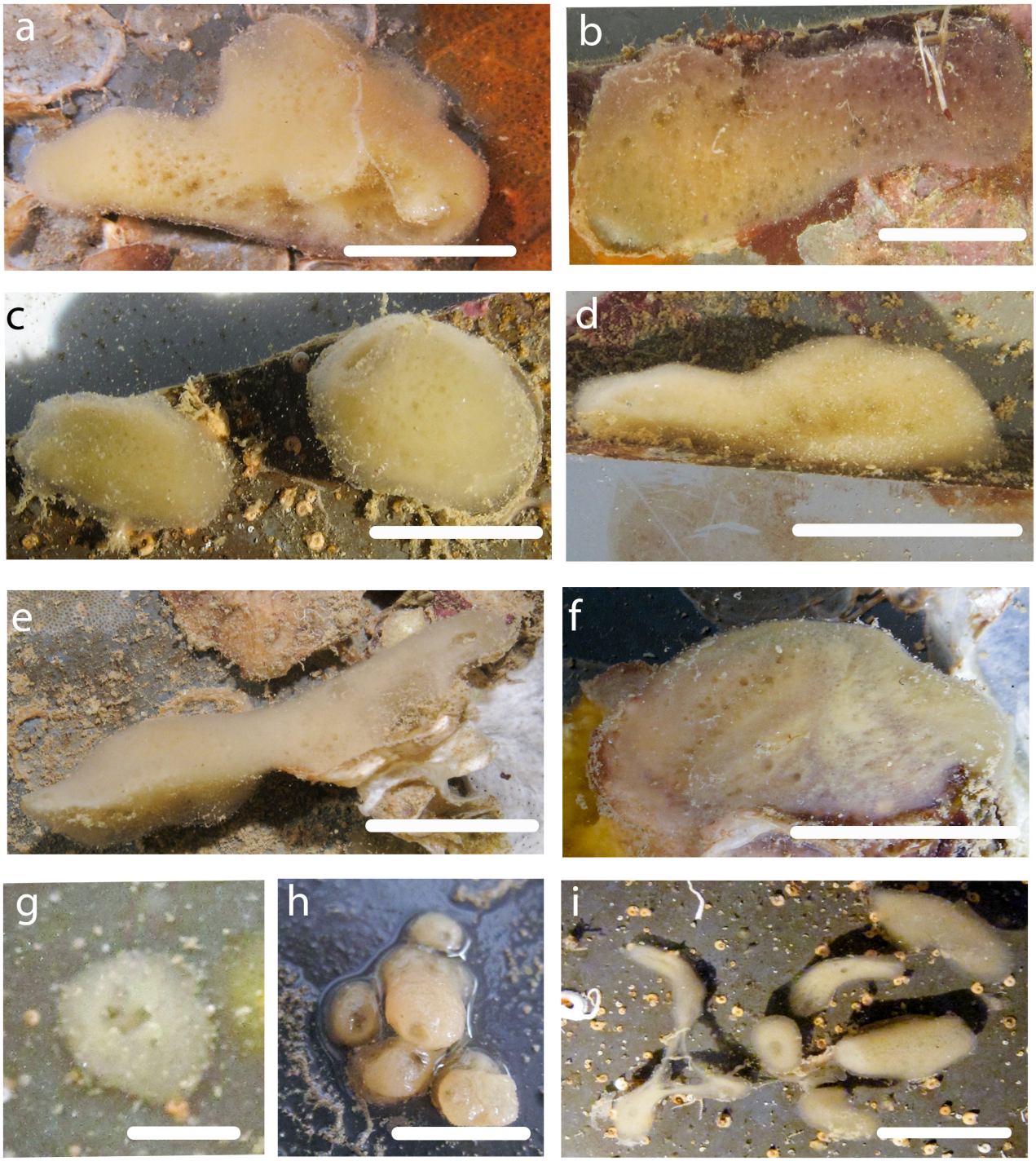

FIGURE 4. In situ growth variations of *Haliclona* (*Reniera*) *kahoe* **sp. nov.** a, holotype BPBM C1539; b, paratype BPBM C1538; c, paratype BPBM C1551; d, paratype BPBM C1537; e, paratype BPBM C1540; f, paratype BPBM C1570; g, paratype BPBM C1554; h, BPBM C1553; i, paratype BPBM C1552. Scale bars: a-f, 1 cm; g, 0.5 cm; h-i, 1 cm.

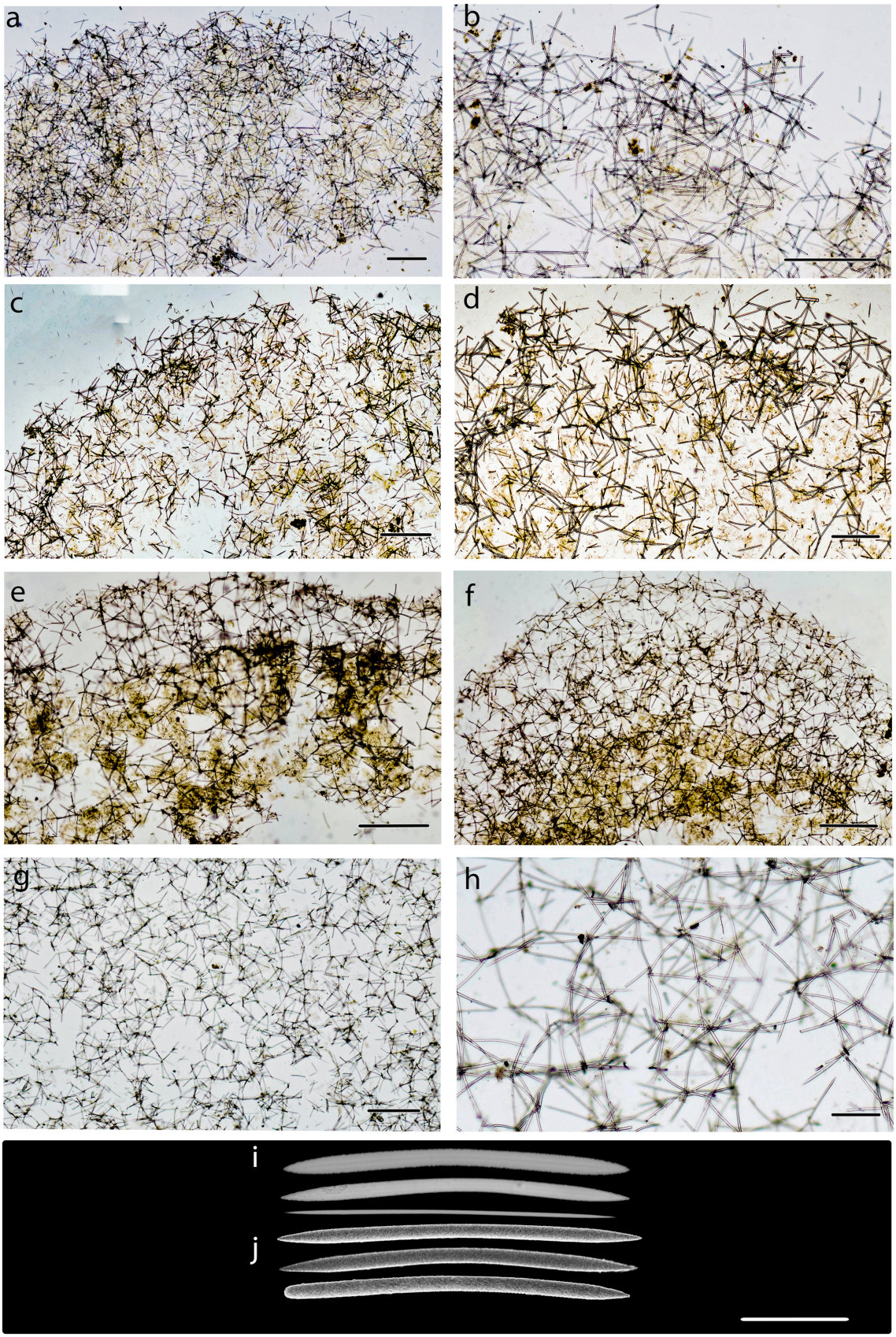

FIGURE 5. Skeletal architecture of *Haliclona* (*Reniera*) *kahoe* **sp. nov.** Perpendicular section through the ectosome and choanosome in a-b, holotype BPBM C1539; c-d, paratype BPBM C1537; e-f, paratype BPBM C1551. Tangential section of the ectosome in g-h, paratype BPBM C1537. Light microscopy images of i, first oxea from holotype, second oxea from BPBM C1538 and third from BPBM C1540. SEM images of oxeas from holotype j. Scale bars: a, c, e, f, 500 μm; b, d, g, 300 μm; h, 100 μm; i–j 50 μm.

TABLE 2. Spicule measurements of oxeas for *Haliclona* (*Reniera*) *kahoe* holotype (h) and paratypes (p). Measurements are expressed as minimum–mean (±1 standard deviation)–maximum. N=50.

Voucher	Length (µm)	Width (µm)
BPBM C1539 (h)	153.9–(174.9±9.5)–197.4	2.5–(5.7±1.4)–8.6
BPBM C1538 (p)	125.9–(165.8±16.5)–197.3	1.1–(5.0±1.7)–8.2
BPBM C1537 (p)	137.0–(155.6±10.5)–185.3	2.5–(4.5±0.8)–5.9
BPBM C1551 (p)	111.8–(150.8±16.2)–186.0	1.1–(3.9±1.4)–7.1

There are 23 *Haliclona* (unknown subgenera) spp., two *Haliclona* (*Haliclona*) spp., three *Haliclona* (*Reniera*) spp. and one *Haliclona* (*Rhizoniera*) spp. sharing a thin to thick, irregularly encrusting morphology, similar color patterns and spicule composition to *H.* (*Reniera*) *kahoe* (Table S2). However, these species can be discarded as possible matches by 1. the presence of smaller oxeas (as in *H. carteri* Burton 1954 (40 x 8 µm), *H. hydroida* Tanita & Hoshino 1989 (120 –145 x 7–14 µm), *H. innominata* (Kirkpatrick 1900) (108 x 2.5 µm), *H. isodictyalis* Bergquist 1961 (130 x 7 µm), *H. macropora* (Thiele 1905) (118–125 × 4–5.2–8 µm), *H. minima* (Lendenfeld 1887) (67 x 3 µm), *H. nitens* Desqueyroux-Faúndez 1990 (100–118 × 1.6–4 µm), *H. offerospicula* Hoshino 1981 (75–82–90 x 2–2.8–3 µm), *H. rectangularis* (Ridley & Dendy 1886) (88 x 9 µm), *H. reversa* (Kirk 1911) (100 x 5 µm), *H. tenuis* Hoshino, 1981(83–100 x 5–8 µm), *H. translucida* Desqueyroux-Faúndez, 1990 (94–116 x 6–7 µm), *H. venustina* (Bergquist, 1961) (100 x 4 µm), *H*. (*Haliclona*) *tonggumiensis* Kang *et al.*, 2013 (60–110 x 1– 5 µm), *H*. (*Reniera*) *cinerea* (Grant 1826) (76–113 x 5–10 µm), *H*. (*Reniera*) *clathrata* (Dendy 1895) (107 x 6 µm), *H.* (*Rhizoniera*) e*namela* de Laubenfels 1930) 2. larger oxeas (as in *H. densaspicula* Hoshino, 1981(187–250 x 3–15 µm), *H. maxima* Bergquist & Warne, 1980 (274–417 µm), *H.* (*Haliclona*) *ieoensis* Kim *et al.* 2017 (160–230 × 2.5–12.5 µm), 3. Firm or hard consistency (as in *H. glabra* Bergquist, 1961, *H. rapanui* (Desqueyroux-Faúndez, 1990), *H. sataensis* Hoshino, 1981) and 4. Presence of multispicular tracts throughout the skeleton (as in *H. madagascarensis* Vacelet *et al.* 1976, and *H. tenacior* Bergquist, 1961) Other clearly distinguishable characters setting *H.* (*Reniera*) *kahoe* apart from the remaining species are the absence of a conulose surface (characteristic of *Haliclona lentus* Hoshino, 1981), rough oxeas with an uneven surface (diagnostic of *Haliclona scabritia* Tanita & Hoshino, 1989 and the absence of a "very regular" continuous ectosome (as observed in *Haliclona* (*Reniera*) *venusta* (Bowerbank 1875). Of the *H*. (*Halichoclona*) spp., *H.* (*Halichoclona*) *mokuoloea* (de Laubenfels, 1950) from Kāneʻohe Bay shares similar consistency and an isodictyal reticulation of oxeas within the skeletal framework. Nevertheless, *H.* (*Halichoclona*) *mokuoloea* is set apart by the yellow, reddish color, smaller oxeas (120–135 x 6 µm) and massive growth morphology.

Habitat and ecology. All specimens were common in confined cryptic environments of Autonomous Reef Monitoring Structures (ARMS). Specimens were collected from ARMS deployed on the patch reef slope adjacent to Moku o Loʻe (Coconut Island), and ARMS inside mesocosms supplied with unfiltered flow through seawater at the Hawaiʻi Institute of Marine Biology (HIMB) in Moku o Loʻe (Coconut Island). Time series observations show quick growth and abundance of *Haliclona* (*Reniera*) *kahoe* throughout pioneering and climax stages of succession (Sup. Fig. S3, Sup. Fig. S7 in Vicente *et al.*, 2022a).

Distribution. Moku o Loʻe (Coconut Island), Kāneʻohe Bay on the island of Oʻahu, Hawaiʻi.

Etymology. The given name is based on Loʻe's faithful brother Kahoe, who was a farmer that regularly provided crops he had grown to his brother Pahu. We use the feminine *kahoe* following the feminine gender of *Haliclona* and Article 31.2 of the International Code for Zoological Nomenclature (http://www.iczn.org/, accessed on October 16, 2023).

Subgenus (*Rhizoniera*) Griessenger, 1971

Definition. Chalinidae with an anisotropic, ladder-like choanosomal skeleton consisting of uni- to multispicular primary lines, connected by irregular unispicular secondary lines. Ectosomal skeleton usually absent; if present, consisting only of some vaguely strewn tangentially oriented oxeas. Spongin moderate to absent. Megascleres usually slender oxeas with acerated points. No microscleres (Muricy *et al.* 2015).

***Haliclona* (*Rhizoniera*) *pahua* sp. nov.**
LSIDurn:lsid:zoobank.org:act:9FFF3BF0-9722-44AA-9B71-2656F5198E68
(Fig. 6, Table 3)

Haplosclerida sp. JV8; Vicente *et al.* 2022a, 2022b

Holotype. BPBM C1518-ARMS in mesocosms at the Hawai'i Institute of Marine Biology (HIMB), Moku o Lo'e (Coconut Island), Kāne'ohe Bay, O'ahu (21.4334 °N, -157.7868 °W); 0.3 m, coll. Jan Vicente, 2017-08-01. **Paratypes.** BPBM C1517, BPBM C1531, ARMS in mesocosms at the Hawai'i Institute of Marine Biology (HIMB), Moku o Lo'e (Coconut Island), Kāne'ohe Bay, O'ahu (21.4334 °N, -157.7868 °W); 3 m, coll. Jan Vicente, 2017-09-27 and 2018-03-16 respectively.

Diagnosis. A soft, compressible solitary mound shaped *Haliclona* (*Rhizoniera*) with apical oscula, light brown in color, that has a skeleton exclusively composed of oxeas (75–151 x 3–5 μm) arranged in unispicular, anisotropic, ascending ladder-like reticulation and the absence of an ectosome.

Description (Fig. 6a–c). Thickly encrusting solitary, circular, mounds less than 1 cm in height and diameter. Surface is smooth but slightly hispid and somewhat punctate. Oscula are circular, 0.5–1 mm wide, and are flush with the surface. There is one osculum per sponge individual. Color of live specimens varies from light to darker shades of brown. Same color pattern is observed in the interior and exterior of the sponge. Consistency is compressible with delicate elasticity. Embryos measuring 150–165 μm in diameter were spotted deep in the choanosome of BPBM C1518 (Fig 6d).

Skeleton (Fig. 6d–f): Ectosome is not specialized. Choanosome is unispicular, mainly anisotropic where primary lines are connected irregularly by secondary lines (120–130 μm in length). There is some disorganization in areas of the choanosome where the skeleton is subisotropic with isodictyal reticulation. Continuous connection of primary and secondary lines results in an ascending ladder like pattern, of triangular (80–100 μm) or polygonal (140–160 μm) meshes (μm) visible from deep in the choanosome. Secondary lines are absent at the sponge surface resulting in a hispid projection of a single, or a bundle of up to three oxeas. Choanosomal spaces (220–370 μm in diameter) are present but rare. Scarce amounts of spongin is present throughout the choanosome and at the nodes. Small auxiliary oxeas are abundant.

Spicules (Fig. 6g; Table 3): Oxeas straight and curved at the center with hastate tips 75–129–151 x 3–4.1–5 μm.

Habitat and ecology. Specimens were collected from ARMS inside mesocosms supplied with unfiltered flow through seawater at the Hawai'i Institute of Marine Biology (HIMB) in Moku o Lo'e (Coconut Island). During the same period specimens were absent from ARMS on a reef surrounded by a climax sponge community throughout a 2-year monitoring period (Sup. Fig. S3 in Vicente *et al.*, 2022a). Presence of embryos supports viviparous reproduction in this species.

Taxonomic remarks. The unispicular, anisotropic, choanosomal skeleton of the new species conforms to some of the characters defined for *H.* (*Reniera*), *H.* (*Haliclona*) and *H.* (*Rhizoniera*). Nevertheless, the connection of primary and secondary lines in the new species is irregular, discarding *H.* (*Haliclona*) as an ideal match, since species in this subgenus have a very regular, ladder like reticulation. Species belonging to *H.* (*Reniera*) have a more isotropic organization of oxeas rather than anisotropic and reticulation is also very regular. Therefore, all characters of the new species are preferably supported by the definition of *H.* (*Rhizoniera*) which includes species with an anisotropic, ladder-like choanosomal organization of oxeas, with primary lines connected irregularly by secondary lines and the usual absence of the ectosome.

There are currently no *H.* (*Rhizoniera*) spp. reported for the Northern or Central Pacific but the thick encrusting, morphology of the new species with oxeas measuring 75–151 x 3–5 μm match other congenerics. These include *H.* (*Rhizoniera*) *australis* (Lendenfeld 1888) from Eastern Australia, *H.* (*Rhizoniera*) *curacaoensis* (van Soest 1980) from the Caribbean, *H.* (*Rhiz.*) *enamela* de Laubenfels, 1930 from the Eastern Pacific, *H.* (*Rhizoniera*) *fugidia* Muricy *et al.*, 2015 from Brazil, *H.* (*Rhizoniera*) *manglarensi* and *H.* (*Rhizoniera*) *zanabriai* (Bispo *et al.*, 2022) from Peru, and *H.* (*Rhizoniera*) *viscosa* (Topsent 1888) from the Northeast Atlantic (Table S2). Conversely, none of these species grow in the shape of a solitary mound with a single apical oscula, making this a diagnostic character for the new species.

Within unknown subgenera of *Haliclona* there are ~ 30 species worldwide which share oxea lengths between 75–151 μm or an average length of oxeas between 125–130 μm. Most of these species can be discarded as possible

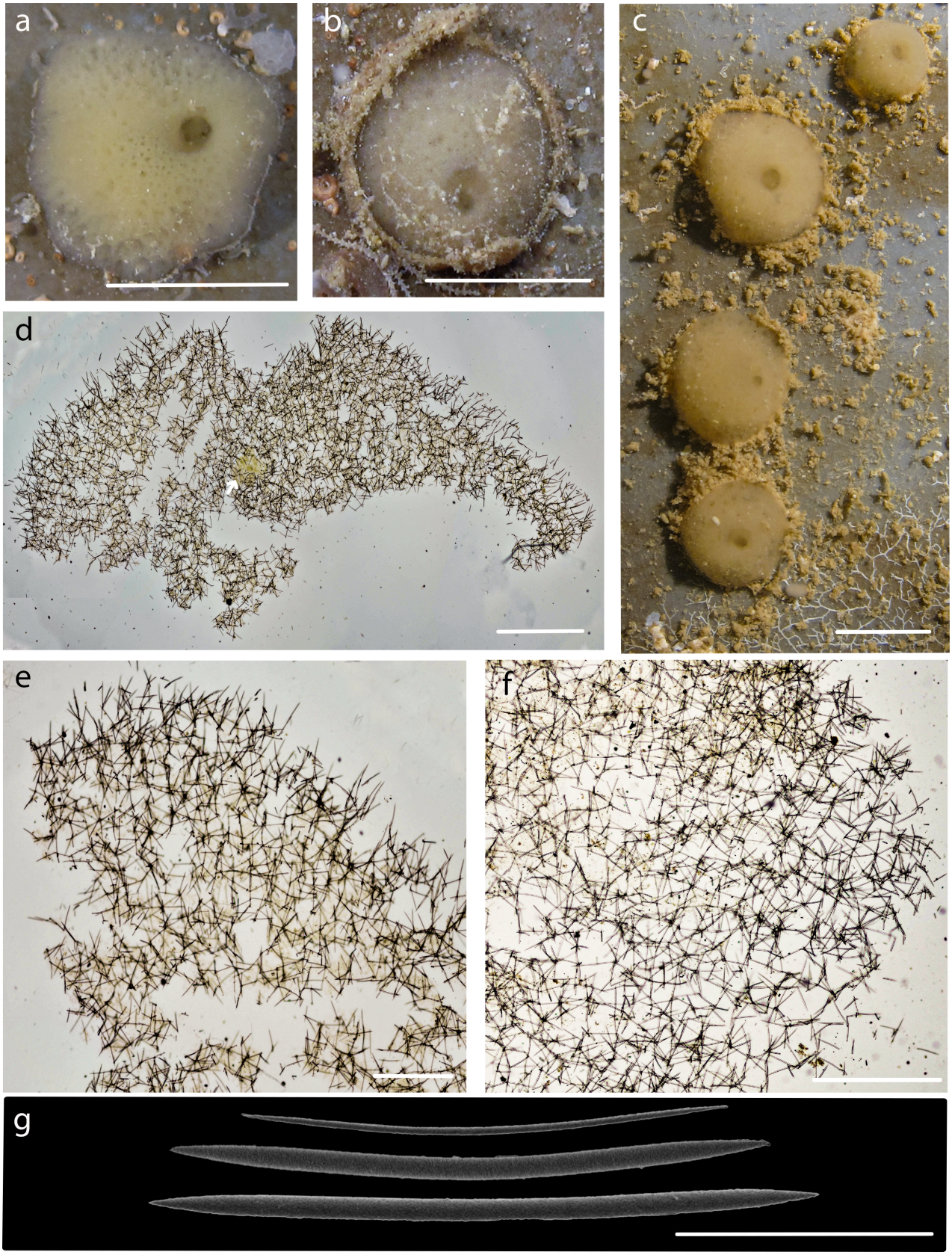

FIGURE 6. *Haliclona* (*Rhizoniera*) *pahua* **sp. nov.** a, holotype BPBM C1518 (in situ); b, paratype BPBM C1531 (in situ); c, paratype BPBM C1517 (in situ). d-e, perpendicular section through the ectosome and choanosome in holotype BPBM C1518 and in f, paratype BPBM C1531. SEM images of oxeas in g, holotype BPBM C1518. Multiple eggs or embryos in the choanosome are indicated by white arrow in (d). Scale bars: a-c, 0.5 cm; d, 1 mm; e-f, 500 µm; g, 50 µm.

matches, based on their massive, branching, growth forms or mismatching color and the presence of multispiculated fibers. Among species sharing similar spicule lengths, growth morphology and color of unknown subgenera of *Haliclona* spp. are *H. isodictyalis* Bergquist, 1961 and *H. sasajimensis* Hoshino, 1981. The new species still differs from these in the presence of the anisotropic ladder like arrangement of the choanosome which is absent in both species.

Distribution (Fig. 2). Moku o Loʻe (Coconut Island), Kāneʻohe Bay on the island of Oʻahu, Hawaiʻi.

Etymology. The given name is based on Loʻe and Kahoe's brother Pahu a selfish fisherman who was reluctant to share his catch even though his brother provided him with crops. We use the feminine *pahua* following the feminine gender of *Haliclona* and Article 31.2 of the International Code for Zoological Nomenclature (http://www.iczn.org/, accessed on October 16, 2023).

TABLE 3. Spicule measurements of oxeas for *Haliclona* (*Rhizoniera*) *pahua* holotype (h) and paratypes (p). Measurements are expressed as minimum–mean (±1 standard deviation)–maximum. N=30.

Voucher	Length (µm)	Width (µm)
BPBM C1518 (h)	75–(126.6±13.3)–146.9	3.2–(4.3±0.4)–4.9
BPBM C1531 (p)	108.1–(129.4±9.1)–150.5	2.5–(3.9±0.5)–4.8
BPBM C1517 (p)	86.8–(129.6±12.7)–143.5	3.5–(4.1±0.4)–4.9

Subgenus *Haliclona* (*Soestella*) de Weerdt 2000

Haliclona (*Soestella*) *caerulea* (Hechtel 1965)

(Table 4; Fig. 7–8)

Synonyms and References

Sigmadocia caerulea—Hechtel, 1965: 30, Fig 5, plate III; Zea, 1987: 69, Fig 16.
Sigmadocia coerulea (misspelling)-Van Soest, 1980: 21, Fig 7, Plate II Fig 4
Haliclona caerulea—Cruz-Barraza & Carballo, 2008: 750, Figs 6, 7D; Hajdu, E., Peixinho, S. & Fernandez, 2011: 180; (Bispo *et al.* 2016): 5, Table 2 Pérez *et al*., 2017: Fig 6
Haliclona (*Soestella*) *caerulea*, de Weerdt, 2000: 29, Figs 3F, 16A-E; Bispo, 2019: 104, Fig 35–37; Pons *et al.*, 2017: 42, Fig 20; Vicente *et al.*, 2020: 111, Fig 1; Vicente *et al.*, 2022b Table S4–S5; Ugalde *et al.*, 2021: 37, Fig 29
Haplosclerida sp. 11 -Vicente et al; 2022b: Table S4–S5; Vicente *et al*., 2022a: Suppl. Table S1–2
Haplosclerida sp. 12 -Vicente et al; 2022b: Fig 4, Table S4–S5; Vicente *et al*., 2022a: Suppl. Table S1–2
Additional synonyms are listed in de Weerdt, 2000

Type locality. Rasta's wreck, Jamaica (17°56′30″N, 76°50′0″W).

Material examined. BPBM C1519 -Mammal pens, Moku o Loʻe (Coconut Island), Kāneʻohe Bay, Oʻahu, (21.43243 °N, -157.79078 °W); 0.5 m, coll. Jan Vicente, 2017-05-29. BPBM C1541, BPBM C1543, BPBM C1544, BPBM C1542 ARMS on reef at Moku o Loʻe (Coconut Island), Kāneʻohe Bay, Oʻahu (21.4335 °N, -157.7863 °W); 3 m, coll. Jan Vicente on 2018-03-16, 2018-06-11, 2018-06-11, 2018-06-11, 2018-06-11 respectively. BPBM C1638—ARMS in mesocosms at the Hawaiʻi Institute of Marine Biology (HIMB), Moku o Loʻe (Coconut Island), Kāneʻohe Bay, Oʻahu (21.4334 °N, -157.7868 °W); 0.3 m, coll. Jan Vicente, 2020-08-13. BPBM C1520—Keʻehi harbor, Oʻahu (21.3208 °N, -157.894 °W); 2 m, coll. Jan Vicente, 2018-5-15. BPBM C1545—Sunken City, Kāneʻohe Bay, Oʻahu, (21.4357 °N, -157.7923 °W); 2 m, coll. Jan Vicente, 2017-5-25. Jan Vicente, 2018-03-16.

Description (Fig. 7). Thickly encrusting, cushion shaped mounds. Consistency may vary from fragile, compressible, firm to hard and difficult to cut when associated with the coralline macroalgae *Jania adhaerens*. Surface is punctate and can vary from smooth to very rough in specimens associated with *J. adhaerens*. Oscula were not visible in recruits growing on ARMS but were visible as fused tubular projections in larger individuals measuring 2 to 8 mm in diameter and up to 1 cm in height. Color varies from different shades of light blue, turquoise, light purple (in specimens associated with *J. adhaerens*), white or cream. White speckled blotchy pattern is visible on surface of some individuals. Embryos measuring 350–400 µm with developing oxeas were spotted deep in the choanosome of BPBM-C1545 (Fig. 7b).

Skeleton (Fig. 8a–h). Ectosome in recruits growing on ARMS and associated specimen with *J. adhaerens* show unispicular, isodictyal, reticulation. In larger individuals the ectosome consists of dense, multispicular circular meshes (400–600 µm). The choanosome is disorganized in small recruits but can also form unispicular to paucispicular reticulation of circular meshes (100–150 µm) in larger individuals. Subectosomal and choanosomal spaces (200–750 µm) are present in larger individuals. Sponging was scarcely present throughout the choanosome.

Spicules (Fig. 8i–j; Table 4). Oxeas are straight and slightly bent mostly with hastate tips 93.5–175.5–210 x 1.2–6.5–11.5 µm (Fig. 8i). Sigmas are C-shaped, very abundant throughout the sponge tissue in a single size category 16.9–19.3–23.1 x 0.7–1.3–2 µm (Fig. 8j).

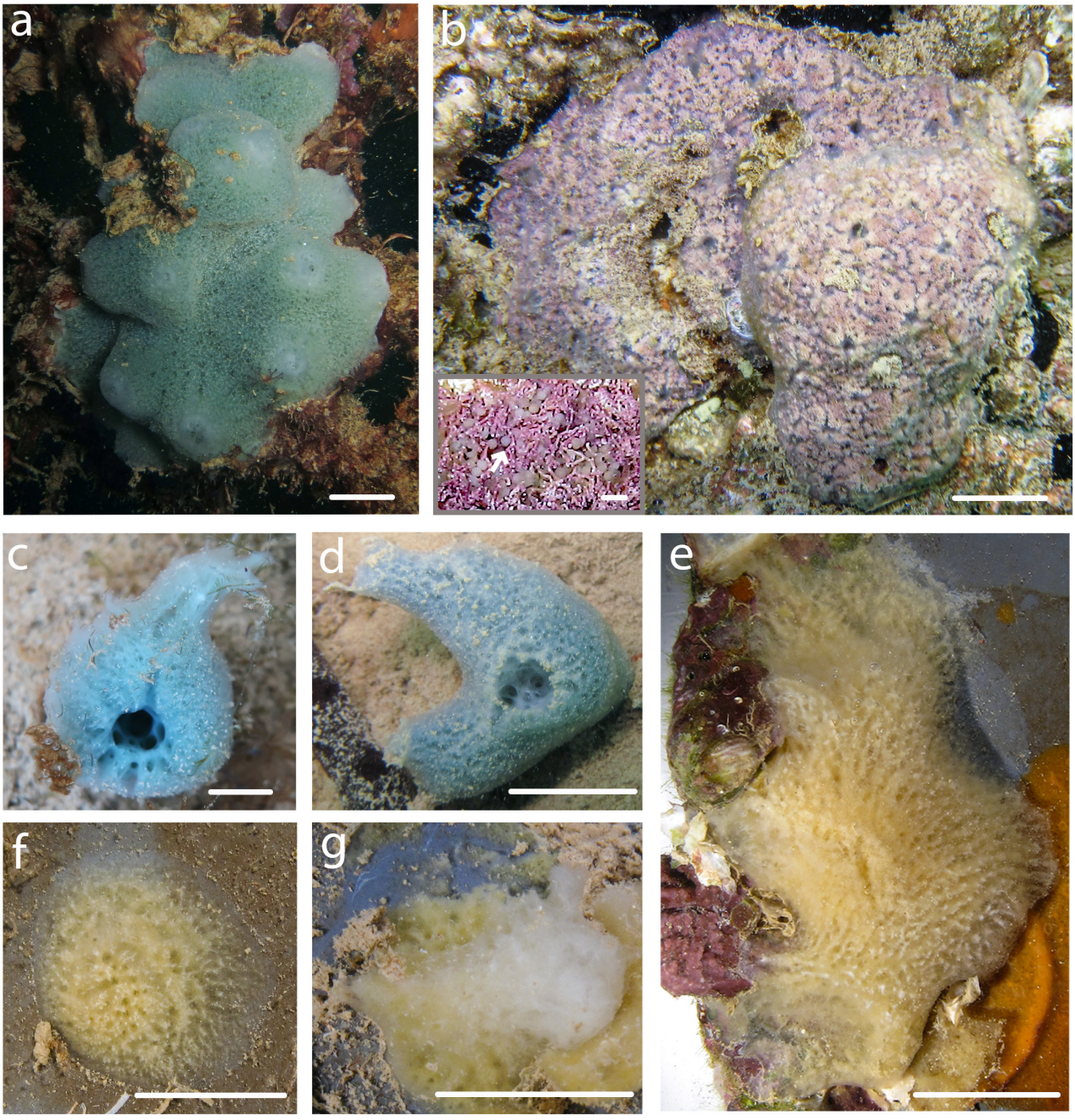

FIGURE 7. In situ growth variations of *Haliclona* (*Soestella*) *caerulea.* a, specimen BPBM C1519; b, specimen BPBM-C1545 associated with *Jania adhaerens* and with embryos zoomed in subpanel within b; c–g, specimens BPBM C1638, BPBM C1520, BPBM C1544, BPBM C1543, and BPBM C1541 respectively. Scale bar: a–g, 1 cm; subpanel in b, 1 mm.

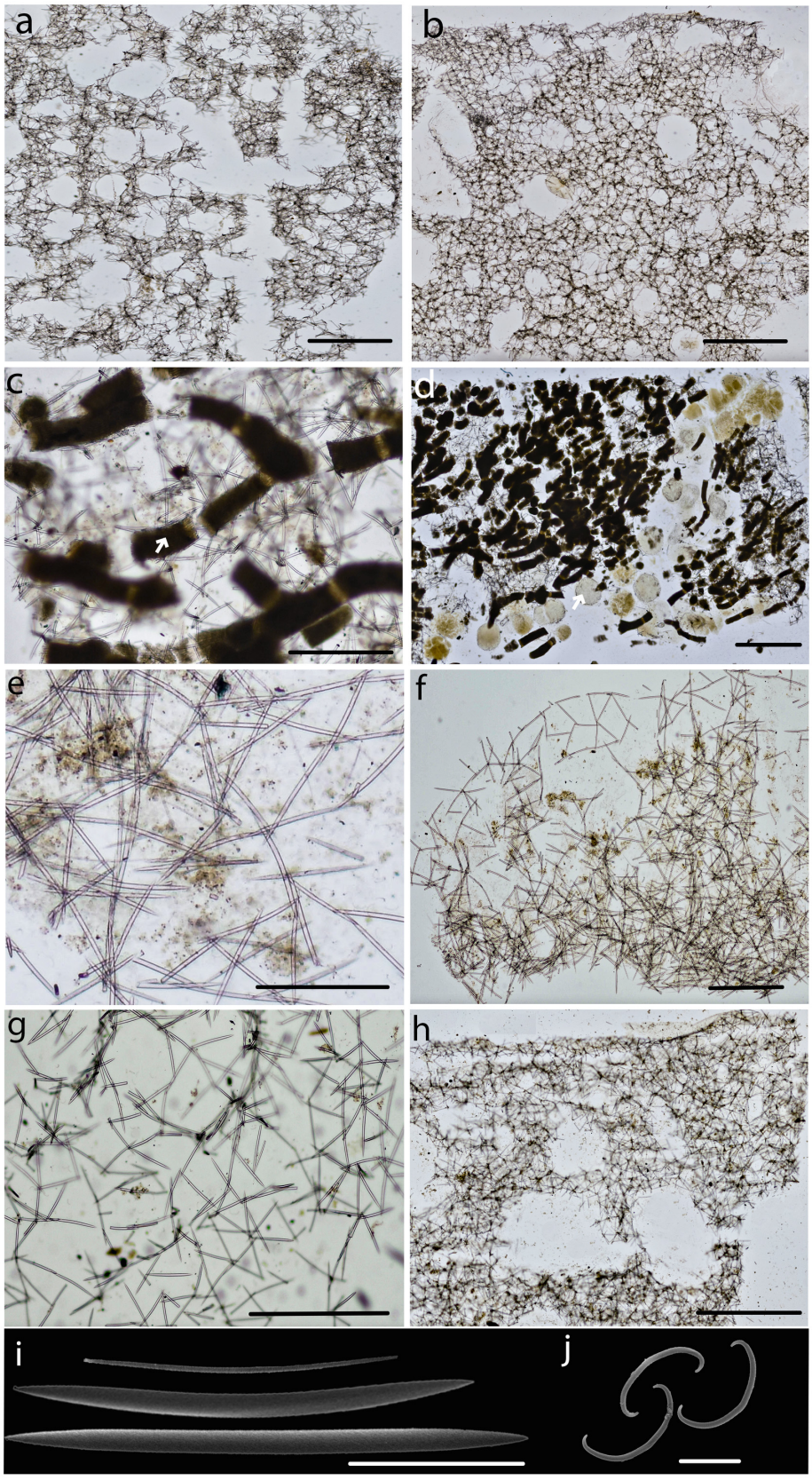

FIGURE 8. Skeletal architecture of *Haliclona* (*Soestella*) *caerulea*. a-b, specimen BPBM C1519; c-d, specimen BPBM-C1545 associated with *Jania adhaerens* and with embryos (indicated by white arrows); e-f, specimen BPBM C1543; g-h, specimen BPBM C1544. a, c, e, g, show tangential sections of the ectosome. b, d, f, h, show perpendicular sections through the ectosome and choanosome. SEM images of i, oxeas and j, sigmas of specimen BPBM C1519. Scale bars: a–b, 1 mm, c, 500 µm, d, 1 mm, e, 200 µm, f, 500 µm, g, 500 µm, h, 1 mm, i, 50 µm, j, 10 µm.

TABLE 4. Spicule measurements of oxeas and sigmas for specimens of *Haliclona* (*Soestella*) *caerulea*. Measurements are expressed as minimum–mean (±1 standard deviation)–maximum. N=50 for oxeas and N=10 for sigmas. Measurements for the holotype were provided from Hechtel (1965)

Voucher	Oxeas		Sigmas	
	Length (µm)	Width (µm)	Length (µm)	Width (µm)
BPBM C1519	104.2–(176±19.9) –196	1.9–(7.1±2.3)–9.3	16.9–(20±1.5)–22.1	1.2–(1.5±0.2)–2.0
BPBM C1520	135.6–(168.9±12.2)–189.0	2.7–(5.4±1.1)–7.7	17.2–(19.2±1.5)–22.0	0.7–(1.0±0.3)–1.6
BPBM C1545	131.2–(166.9±15.4)–198.9	2.2–(6.6±2.4)–10.9	15.1–(18.7±1.6)–20.2	1.0–(1.2±0.2)–1.4
BPBM C1543	144.0–(171.9±10.4)–194.2	3.4–(5.1±0.6)–6.0	15.2–(18.0±1.8)–21.3	0.9–(1.1±0.2)–1.5
BPBM C1541	128.0–(167.9±10.5)–185.7	1.8–(5.2±1.0)–6.5	17.0–(20.0±1.3)–22.0	0.9–(1.1±0.1)–1.4
BPBM C1544	93.5–(191.3±17.2)–209.7	1.2–(7.9±1.3)–9.2	16.2–(18.2±1.9)–22.6	0.7–(1.0±0.2)–1.2
BPBM C1542	126.0–(188.6±11.6)–206.0	1.7–(8.2±1.9)–11.5	18.5–(19.7±0.9)–21.0	0.8–(0.9±0.1)–1.1
BPBM C1638	125.2–(172.8±11.6)–194.8	1.8–(6.3±1.1)–8.1	17.2–(20.4±1.6)–23.1	1.0–(1.3±0.3)–1.9
MNRJ 22768*	136–154.9–176	4–6.6–9	14–16.9–20	None provided
YPM 5047 (h)	143–200	None provided	17–23	None provided

***** Specimen from Northeastern Brazil corresponding to 28S sequence (acc. No. MZ366950) (Bispo *et al.*, 2019).

Habitat and Ecology. All specimens were collected on artificial structures including ARMS, pilings, and derelict nets. Long term monitoring of the cryptic sponge community using ARMS showed appearance of *H.* (*Soestella*) *caerulea* only on reef ARMS after 18 months (Sup. Fig. S3 in Vicente *et al.*, 2022a), suggesting that this species is present during climax stages of ecological succession. A predation study using native Hawaiian Tiger cowries (*Cypraea tigris*) revealed *H.* (*Soestella*) *caerulea* to be a preferred prey item which lacks chemical defenses against fish or mollusks (Vicente *et al.*, 2020). Embryos present in specimen BPBM-C1545 associated with *J. adhaerens* supports viviparous reproduction in this species.

Distribution. North and Southern Gulf of Mexico (Mexico) (Rützler, K.; van Soest, R. W. M.; Piantoni 2009; Ugalde *et al.* 2021), Caribbean (Cuba, Jamaica (Hechtel, 1965), Puerto Rico (Van Soest, 1980), Martinique (de Weerdt, 2000), Curaçao (Van Soest, 1980), Venezuela (Díaz, H.; Bevilacqua, M.; Bone 1985), Colombia (David-Colón, J.D.; Marin-Casas 2020), Panama, Mexico), Atlantic (Eastern Brazil) (Hajdu *et al.*, 2011), Eastern Indo-Pacific (Hawai‘i) Pons *et al.*, 2017; Knapp *et al.*, 2015; Eldredge *et al.*, 2001, Central Pacific (Palmyra) (Knapp *et al.* 2011)

Taxonomic remarks. Introduced in the last 20 years, this species has now been reported in lagoonal habitats of the main and Northwestern Hawaiian Islands (Eldredge *et al.*, 2001). Previous descriptions of *H.* (*Soestella*) *caerulea* from Moku o Lo‘e were made from sponges fouling on artificial floating docks (Pons *et al.*, 2017) and from sponges growing on dead coral. Here the sponge is observed as a common species of the sponge cryptofauna inside ARMS and a potential invasive within the coral reef cryptobiota of Kāne‘ohe Bay. Dimensions of oxeas and sigmas in Hawaiian specimens fit the size categories of the holotype and paratypes from the Caribbean (oxeas: 117–200 x 3–5 µm/sigmas: 13–28 µm) (Hechtel, 1965). These are also similar to specimens previously collected in Hawai‘i (oxeas:147–220 x 3.7–10 µm/sigmas:15–25 µm) (Pons *et al.*, 2017). Morphological plasticity between cryptobenthic individuals, and those found on more exposed habitats includes variations in external color (white, blue, light brown and pink) and consistency (hard, soft, brittle) which were similarly observed by Bispo *et al.*, (2019) and in individuals associated with *J. adhaerens* by Enríquez *et al.*, (2009). Differences were also observed in the skeleton structure between small recruits having a confused choanosome and a unispicular ectosome with isodictyal reticulation, and larger individuals having paucispicular circular meshes.

Family Niphatidae Van Soest, 1980

Genus *Gelliodes* Ridley 1884

***Gelliodes conulosa* sp. nov.**
LSIDurn:lsid:zoobank.org:act:5E90EDDF-F3BF-4F98-8334-F4ADCD17EF1E

Gelliodes wilsoni—Pons *et al.*, 2017: 46, Fig 22; Vicente *et al.*, 2020: 111, Fig 1; Vicente et al; 2022b: Fig 4, Table S4-S5; Vicente *et al.*, 2022a: Suppl. Table S1-2

Comparative material

Gellius varius var. fibrosus—Wilson, 1925: 388, Fig 3, Plate 40
Gelliodes fibrosa—de Laubenfels, 1935:329, Fig 2, Plate 1; see additional synonyms in Carballo *et al.* (2013).
Gelliodes wilsoni Carballo, Aguilar-Camacho, Knapp & Bell, 2013
For additional species see Table S3

Holotype and type locatlity. BPBM C1510-Mammal pens, Moku o Loʻe (Coconut Island), Kāneʻohe Bay, Oʻahu, (21.43243 °N, -157.79078 °W); 0.5 m, coll. Jan Vicente, 2016-11-18.

Paratypes. BPBM C1636-Yacht club, Kāneʻohe Bay, Oʻahu, (21.4182°N, -157.7719 °W); 2 m, coll. Jan Vicente, 2020-09-18. BPBM C1637, BPBM C1512, BPBM C1513, BPBM C1514 (p)—ARMS on reef at Moku o Loʻe (Coconut Island), Kāneʻohe Bay, Oʻahu (21.4335 °N, -157.7863 °W); 0.3 m, coll. Jan Vicente on 2016-12-19, 2017-06-07, 2017-08-01, and 2018-01-19 respectively. Additional vouchers with metadata can be found in Table S1.

Diagnosis. A tough, elastic, compressible irregular mound shaped *Gelliodes* with a conulose surface, light to dark bluish grey to almost black color provided by pigmented cells, that has a skeleton consisting of an irregular network of fibers forming meshes (230–780 µm) that run paratangentially through the ectosome or rise from the choanosome pushing the ectosome upwards, spicules consist of oxeas (124–152–186 x 2.5–5.3–8.1 µm) embedded within fibers or that are auxiliar and an abundance of randomly distributed sigmas (10–14.2–22 x 0.5–1.0–1.7µm).

Description (Fig. 9). Thickly encrusting to irregular massive mounds (10 x 5 x 2 cm). Consistency is compressible, tough, elastic, and difficult to tear. Surface is conulose (horny), from projecting fibers underlying the sponge surface. Tangential surface fibers can be seen in small recruits growing on ARMS. Distance between the points of superficial cones varies between 1.5–3 mm. Superficial cones are between 1–2.3 mm long. Oscula are abundant, slightly elevated but also flush along the sponge surface measuring 0.1–0.5 cm in diameter and spread unevenly. A thin dermal membrane surrounds oscular openings. Exterior color of live and preserved specimens in ethanol varies from light to dark bluish grey to almost black from pigmented cells on the sponge surface. Color of the choanosomal tissue is usually lighter in color than the sponge surface. Exudes light yellow pigments in ethanol but the color of the specimen remains the same as in situ.

Skeleton (Figure 10a–e). In some specimens, the ectosome is distinguished from the choanosome by the appearance of a dark layer of pigmented cells (7–13 µm in diameter) that are densely packed within the first 300 µm of the sponge surface across the choanosome. Abundance of pigmented cells dissipates deep throughout the choanosome where they are less abundant. The ectosome is composed of an irregular organization of fibers (90–125 µm in diameter) which run tangentially through the sponge surface. Circular to elliptical meshes (230–780 µm) are also present throughout the ectosome. The choanosome is similar in composition to the ectosome and is also composed of an irregular arrangement of multispiculated fibers (28–120 µm in diameter) with auxiliary oxeas and sigmas surrounding the choanosomal meshes. Fibers pushing the sponge surface outward can be seen forming cones (250 µm in height and 100 µm thick). Echinating paucispicular (2–3 oxeas) tracts are also observed along the sponge surface. Circular and elliptical subectosomal (300–400 µm in diameter) and choanosomal spaces (200–650 µm in diameter) are abundant through the sponge body.

Spicules (Fig10f–g; Table 5). Oxeas are straight and slightly bent mostly with hastate tips 124–152–186 x 2.5–5.3–8.1 µm (Fig. 10f) can be auxiliary or embedded within fibers. Sigmas are C-shaped, with an abundant but random distribution throughout the sponge tissue in a single size category 10–14.2–22 x 0.5–1.0–1.7µm (Fig. 10g).

Habitat and Ecology. Specimens were collected on derelict nets, coral rubble, and ARMS. Successional observations of *G. wilsoni* shows the appearance of pioneering recruits exclusively on reef ARMS only after four months (Sup. Fig. S3 in Vicente *et al.*, 2022a). Predation studies with the gastropod *Cypraea tigris* revealed *G. wilsoni* to be a preferred species that lacks chemical defenses against spongivorous fish and mollusks (Vicente *et al.*, 2020).

Taxonomic remarks. The original description for Hawaiian specimens were erected as *Gelliodes wilsoni* by Carballo *et al.*, (2013) and argued to be a conspecific with *Gellius varius fibrosus* Wilson (1925), which was historically transferred to *Gelliodes fibrosa* by de Laubenfels (1935). *Gelliodes fibrosa* was already used as a name by Dendy (1905) to describe a different species. Therefore, *G. wilsoni* was proposed by Carballo and colleagues (2013) to refer to the material originally described by Wilson (1925) and de Laubenfels (1935) from the Philippines which dissolved the homonym *G. fibrosa* for both heterospecifics. Carballo and colleagues (2013) determined that *G. wilsoni* from Mexico, Hawai'i and Palmyra were conspecific with *G. varius fibrosus* Wilson (1925), and *G. fibrosa* de Laubenfels (1935) based on similar spicule composition and fiber dimensions. However, comparisons of in situ images between *G. wilsoni* by Carballo *et al.*, (2013) with images (in spirit) of the type of *G. varius fibrosus*

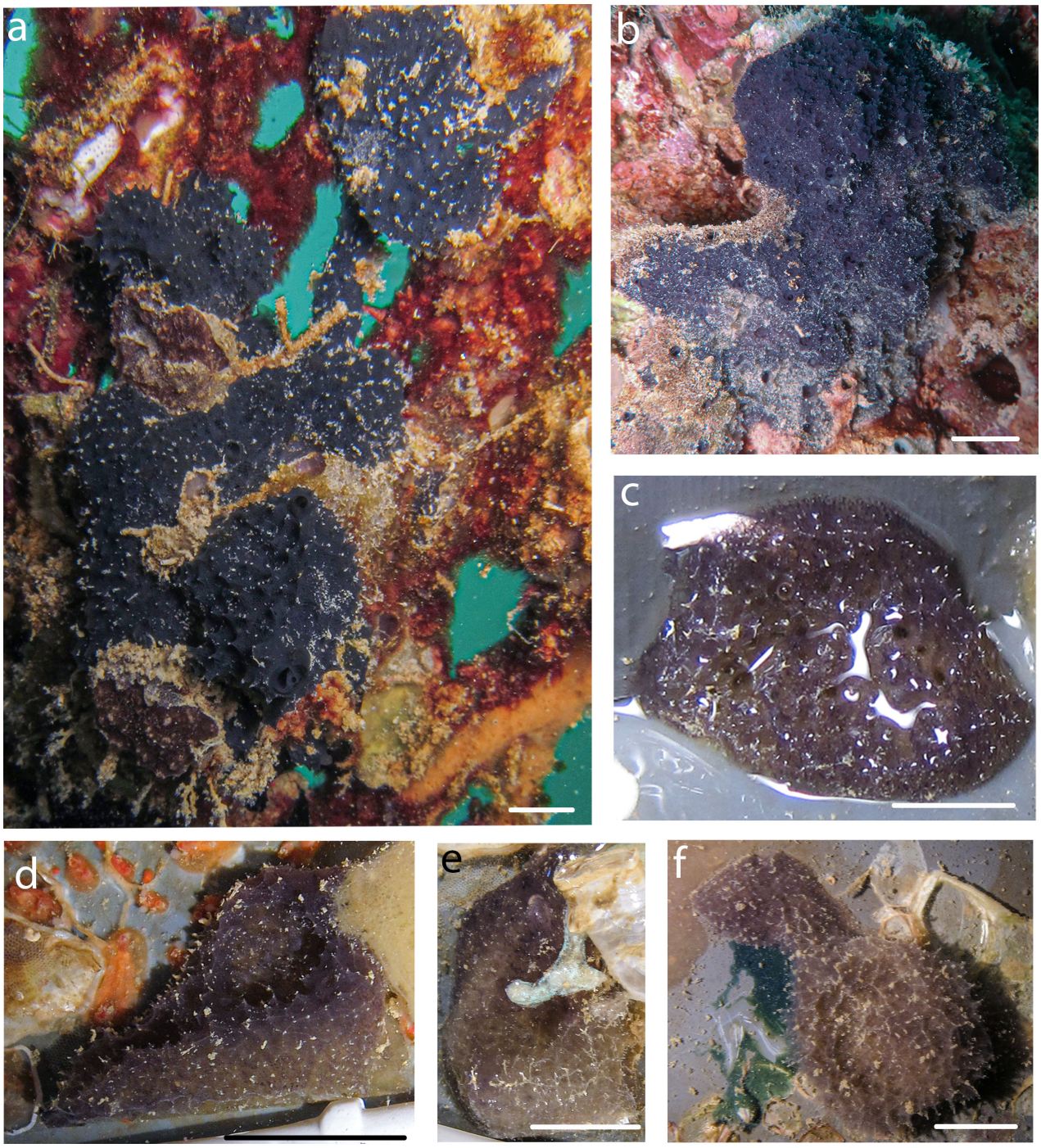

FIGURE 9. In situ growth variations of *Gelliodes conulosa*. a, holotype specimen BPBM C1510; b, specimen BPBM C1636; c, specimen BPBM C1637; d, specimen BPBM C1512; e, specimen BPBM C1513; f, specimen BPBM C1514. Scale bars: a-b, 1 cm, c, 5 cm, d-f, 1 cm.

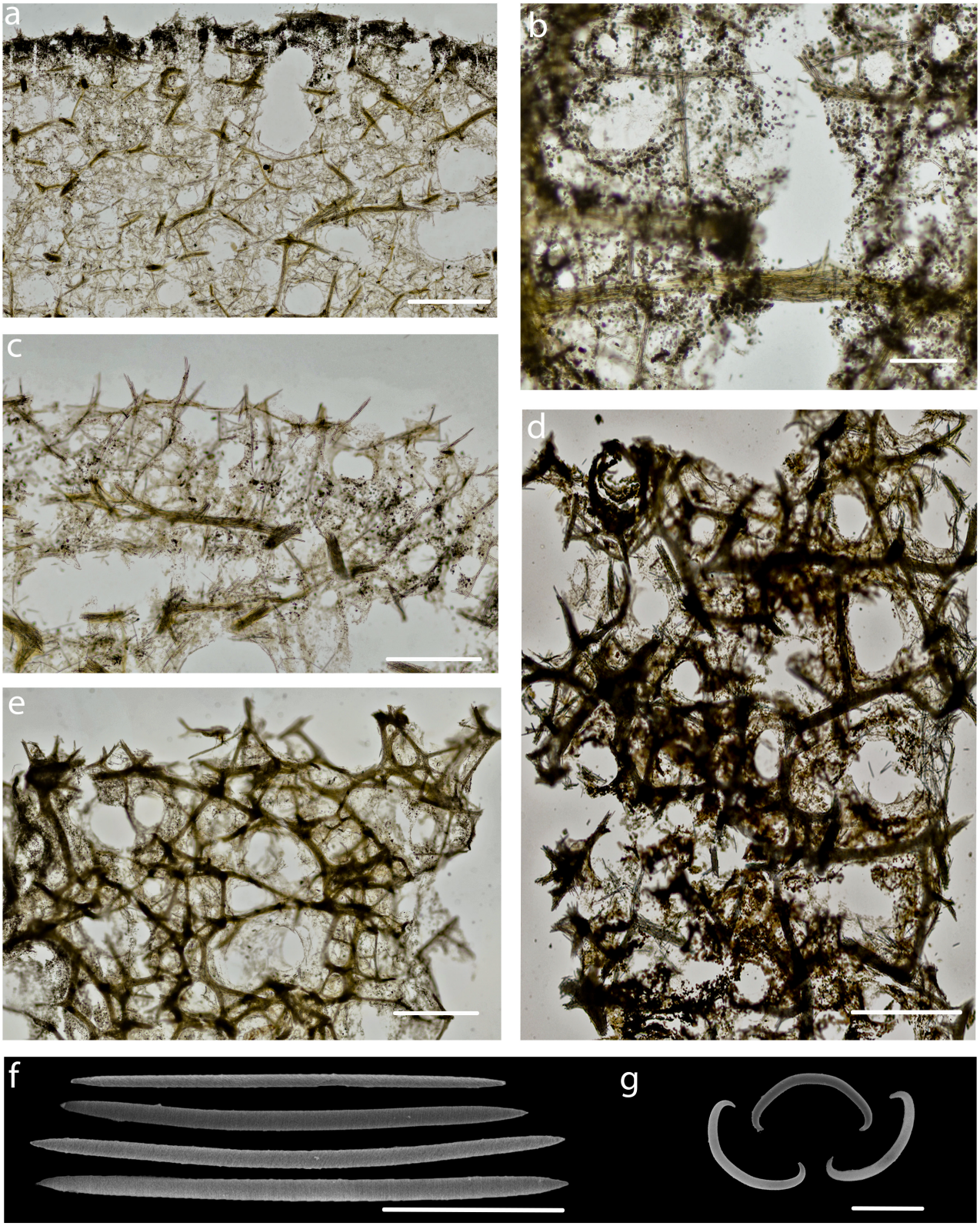

FIGURE 10. Skeletal architecture of *Gelliodes conulosa*, a-c, holotype specimen BPBM C1510. d-e, specimen BPBM C1636. a, c, d show perpendicular sections through the ectosome and choanosome. Pigmented cells are concentration throughout the sponge tissue surface. b, e shows tangential sections of the ectosome. SEM images of oxeas in f and sigmas in g, of specimen BPBM C1510. Scale bar: a, 1 mm; b, 200 µm, c, 500um, d-e, 1 mm, f, 50 µm, g, 10 µm.

Wilson (1925) (de Voogd *et al.*, 2023) revealed conspicuous morphological disparities to confirm heterospecificity. For example, the type material has oxea measurements of 220 x 14 μm which exceed the size limits of Hawaiian specimens. The morphology of the type also has an erect, cylindrical, branching, anastomising morphology with a rather even surface; oscula are numerous, evenly distributed and flush with the surface (Table S3). In contrast the specimens in Carballo *et al.*, (2013) and this study consist of thickly encrusting mounds, with a conulose surface, and elevated oscula. The material by de Laubenfels (1935) more closely resemble the description of specimens collected by Carballo *et al.* (2013) and those in this study with oxeas measuring 150–190 x 4–6 and fibers 60–160 μm in diameter. The exterior blue grey color and lighter toned grey color of the interior of de Laubenfels' Puerto Galera specimen preserved in alcohol also match the Hawaiian specimens. However, de Laubenfels also adds the description of a cavernous endosome, tangential oxeas, and no mention of a conulose surface from echinating fibers. The Hawaiian paratypes do not have tangentially oriented oxeas but rather echinating fibers which give them a conspicuous conulose appearance in all Hawaiian paratypes. Compared to the other 32 *Gelliodes* spp. there are six species with similar sizes of oxeas and sigmas as *G. conulosa* (Table S3). These can be excluded as conspecifics by differences in color and texture. For example, *Gelliodes callista* De Laubenfels 1954 is pinkish orange. *Gelliodes obtusa* Hentschel, 1912 is grey with brownish tinges. *Gelliodes petrosioides* Dendy, 1905 is pale yellowish grey and has a stony composition. *Gelliodes porosa* Thiele, 1903 is brown, smooth and cylindrical. *Gelliodes spinosella* Thiele, 1899 is a soft bodied sponge with lighter colored pigments. Other species baring sigmas and oxeas without reported measurements include *Gelliodes truncata* (Kieschnick 1896), *Gelliodes licheniformis* (Lamarck 1814), and *Gelliodes fibrosa* (Dendy 1905). However, *G. truncata* is a soft brown branching sponge, *G. licheniformis* is described as a loosely smooth sponge from the Atlantic Ocean and *G. fibrosa* is also described as a soft sponge; all of which do not match the description for *G. conulosa*.

Dimensions of fibers in Hawaiian specimens described in this study fit those previously reported by Carballo and colleagues (2013) (70–145 μm). However, the diameter of circular meshes more closely resemble those reported by Pons *et al.*, 2017 (600 μm) and are much wider than those reported by Carballo and colleagues (2013). Localization of pigmented cell within the sponge surface and presence of numerous auxiliary oxeas and sigmas in the present material is also added as diagnostic characters for this species.

Based on these novel findings we propose the new name *Gelliodes conulosa* for the specimens described in this study and those previously analyzed by Pons *et al.* (2017). We also, propose that *Gelliodes wilsoni* be kept as the name for the species described by Wilson, 1925. *Gelliodes conulosa* is considered an introduced species in Hawai'i and is confined to lagoonal habitats throughout the main Hawaiian Islands (Eldredge *et al.*, 2001). At the moment the origin of this species remains cryptogenic.

Distribution. Eastern Indo-Pacific (Hawai'i) (Pons *et al.*, 2017; Eldredge *et al.*, 2001).

Etymology. The given name is based on the distinct conulose surface of the sponge. We use the feminine *conulosa* following the feminine gender of *Gelliodes* and Article 31.2 of the International Code for Zoological Nomenclature (http://www.iczn.org/, accessed on October 16, 2023).

Phylogenetic analysis

Partial sequences of nuclear and mitochondrial genes revealed similar tree topologies, placing haplosclerid species described in this study in either clades A or B as presented in Redmond *et al.* (2011). For example, close relatives of *Haliclona* (*Reniera*) *kahoe* included sequences belonging to the genera *Cladocroce*, and *Haliclona* in Clade A. The closest relative being the introduced Hawaiian species *Cladocroce* sp. 1 with a 67.87%/94.2% (28S/COI) sequence identity. Replicates of *H.* (*Reniera*) *kahoe* exhibiting light purple (BPBM C1538) and light brown (BPBM C1554) morphotypes had identical 28S sequences, supporting in situ color variations as a plastic character among conspecifics (Fig. 4 and Fig. 11a).

Haliclona (*Soestella*) *caerulea* is supported in clade B with 28S and COI sequences 98.7% / 94.1% identical to the Australian species *Amphimedon queenslandica* respectively (Fig. 11). Conspecificity between *Haliclona* (*Soestella*) *caerulea* vouchers showing morphological plasticity was confirmed by identical spicule composition and identical 28S sequences among six specimens (BPBM C1519, BPBM C1541, BPBM C1542, BPBM C1543, BPBM C1544, BPBM C1545) and identical COI sequences between two specimens (BPBM C1544 and C1519) (Fig. 7 and Fig. 11). Molecular phylogeny also confirmed the association status of *H.* (*Soestella*) *caerulea* with *Jania adhaerens* and in situ color variations as polymorphic characters of *H.* (*Soestella*) *caerulea*. Identical 28S sequences

between voucher MRJ 22768 from Brazil also confirmed geographic expansion of *H.* (*Soestella*) *caerulea* between the Tropical Atlantic and the Eastern Indo-Pacific. Voucher MRJ 22768 from Brazil also shares similar skeleton morphology and spicule composition as *H.* (*Soestella*) *caerulea* samples in our study (Bispo *et al.*, 2019) (Figure 11; Table 5).

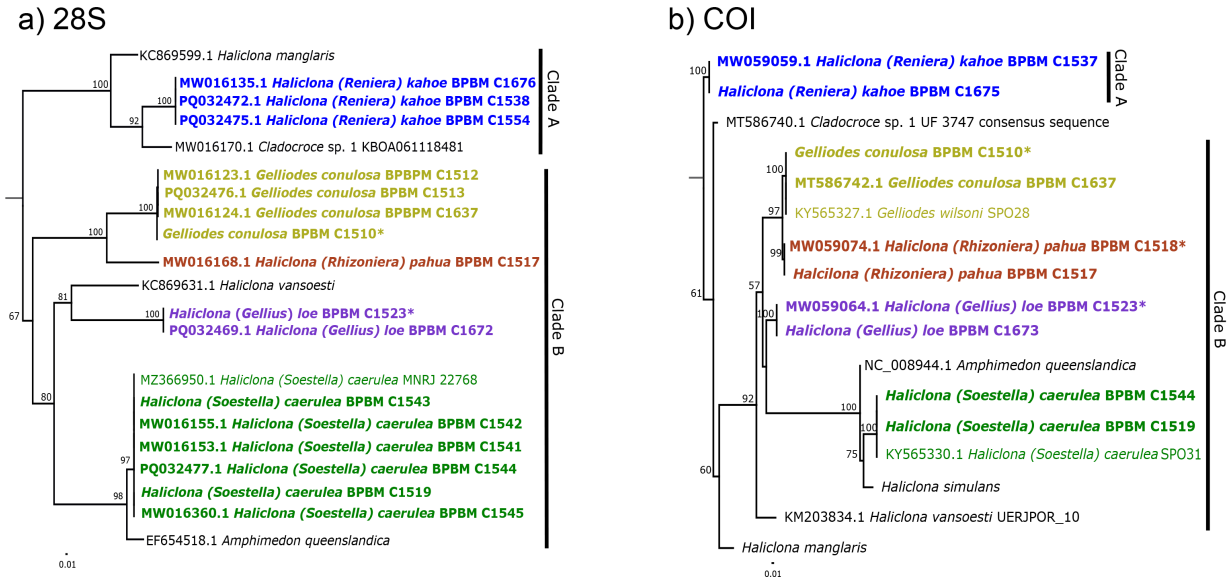

FIGURE 11. Maximum likelihood topology generated from partial sequences spanning the a, D1 region of the 28S rRNA gene and b, Folmer (5') region of the COI gene, from Haplosclerida generated in this study (bold) or downloaded from GenBank. Clades A and B were assigned by Redmond *et al.*, 2011. Numerical values at nodes show RAxML bootstrap values. Bootstrap values less than 50% have been omitted from the trees. Phylogenetic trees were rooted on *Ephydatia fluviatilis* OX175335.1 and ON000190.1 for 28S and COI, respectively.

TABLE 5. Spicule measurements of *oxeas* and *sigmas* for holotype (h) and paratype (p) specimens of *Gelliodes conulos*. Measurements are expressed as minimum–mean (±1 standard deviation)–maximum. N=50 for oxeas and N=10 for sigmas.

Voucher	Oxeas		Sigmas	
	length	width	length	width
BPBM C1510 (h)	133.1–(146.5±6.4)–168	2.5–(5.3±1.4)–8.1	14.0–(18.2±2.4)–22.0	0.8– (1.2±0.3) –1.7
BPBM C1636 (p)	131.4–(143.2±6.3)–159.4	4.0–(6.2±0.9)–7.8	10.8–(12.7±1.2)–14.56	0.9–(1.0±0.1)–1.1
BPBM C1512 (p)	141.1–(167.3±8.0)–181.1	3.3–(4.5±0.6)–6.1	10.0–(12.0±1.4)–14.5	0.5– (0.8±0.1) –1.0
BPBM C1513 (p)	124.0–(147.0±8.4)–164.0	3.2–(4.6±0.6)–6.0	11.0– (14.0±1.5)–15.8	0.9– (1.1±0.1) –1.4
BPBM C1514 (p)	138.0–(156.1±9.3)–186.2	4.0–(6.0±1.0)–8.1	11.0–(14.0±2.0)–17.1	0.8– (1.1±0.1) –1.4
G. wilsoni Acapulco Bay*	120.0–(149.8±14.0)–185.0	2.5–(3.5±1.5)–7.5	7.5–(16.9±5.1) –25.0	None provided
G. wilsoni La Paz*	130.0–(148.6±11.0)–175.0	2.5–(3.1±1.0)–5.0	12.5–(18.0±3.2)–25.0	None provided
G. wilsoni Kāne'ohe Bay*	125.0–(160.8±12.1)–180.8	2.0–(3.8±1.4)–7.5	10.0–(16.7±3.0)–25.0	None provided
G. wilsoni Palmyra*	110.0–(133.4±10.2)–160	1.7–(3.2±1.1)–6.0	12.5–(17.6±3.2)–25.7	None provided

*Specimens and values adapted from Table 1in Carballo *et al.* (2013) (n=58 measurements).

Both phylogenies also supported *Haliclona* (*Gellius*) *loe* **sp. nov.**, *Haliclona* (*Rhizoniera*) *pahua* **sp. nov.** and *Gelliodes conulosa* **sp. nov.** in Clade B. *Gelliodes conulosa* **sp. nov.** and *H.* (*Rhizoniera.*) *pahua* **sp. nov.** were the closest relatives with 88.0%/97.9% (28S/COI) sequence identity with *H.* (*Gellius*) *loe*. The combination of spicule composition, identical 28S sequences among four *G. conulosa* specimens (BPBM C1510, BPBM C1636, BPBM C1514, BPBM C1637) and two identical COI sequences from specimens BPBM C1510, BPBM C1637 confirmed conspecifity between sponges exhibiting lighter tones of grey in the sciophilous ARMS environment (Fig. 9c–f) and darker pigmented individuals in more exposed habitats (Fig. 9a–b). COI sequences of *Gelliodes conulosa* were also identical to *Gelliodes wilsoni* voucher SPO28 from Kāne'ohe Bay (Pons *et al.*, 2017).

Among *H.* (*Rhizoniera*) *pahua,* PCR and 28S Sanger sequencing only worked for voucher BPBM C1517 while two identical COI sequences for vouchers BPBM C1517 and BPBM C1518 were retrieved for specimens exhibiting similar morphological characters. *Haliclona* (*Gellius*) *loe* formed a separate subclade within Clade B from *G. conulosa* and *H.* (*Rhiz.*) *pahua* with an 85.6%/90.1% (28S/COI) identity to *Haliclona vansoesti*. 28S sequences for the holotype BPBM C1523 exhibiting a light, yellowish purple in situ color were 100% identical to voucher BPBM C1672 exhibiting a bright yellow phenotype. The same was true between COI sequences of the holotype with voucher BPBM C1673 which was also bright yellow. Conspecificity between *H.* (*Rhiz*.) *pahua* vouchers were confirmed by both systematics and phylogenetics.

Discussion

In this study we used a combination of traditional taxonomic and molecular phylogenetic approaches to confirm the recruitment of two introduced haplosclerid species within the cryptic spaces of ARMS and to describe three new species *Haliclona* (*Gellius*) *pahua* **sp. nov.**, *Haliclona* (*Reniera*) *kahoe* **sp. nov.**, *Haliclona* (*Rhizoniera*) *loe* **sp. nov.** from our collections in Kāneʻohe Bay. Here, we document the recruitment of known introduced sponges within the cryptic spaces of ARMS (mimicking coral reef interstices) and evaluate the morphological variability seen among these alien sponge species in differing habitats around the island of Oʻahu, Hawaiʻi. We produce genetic sequences from vouchered morphological samples to confirm species boundaries of *Haliclona* (*Soestella*) *caerulea* and show that specimens exhibiting morphological variability from alien species *H*. (*Soestella*) *caerulea* and *Gelliodes conulosa* are plastic rather than multiple species. For example, *H*. (*Soestella*) *caerulea* exhibited a wide variety of color morphs between mature individuals and recruits. These ranged from blue, turquoise, and pink in mature individuals and in associated states with *Jania adhaerens*. In contrast, recruits in ARMS exhibited paler colors such as white and beige color patterns. The texture and consistency of associated *H.* (*Soestella*) *caerulea* individuals with *J. adhaerens* were also noticeably tougher to cut than non-associated individuals. Similar to *H*. (*Soestella*) *caerulea,* recruits in *G. conulosa* were also different in consistency and color patterns to mature individuals, which were softer and with lighter colored pigments. However, genetic sequences of each morphotype were 100% identical to each other which confirmed intraspecific plasticity between morphotypes (Figure 11).

Using mitochondrial and ribosomal gene sequences, we find polyphyletic relationships among haplosclerid sponges within Niphatidae and Chalinidae families. Similar to previous molecular phylogenetic studies showing species within these families were polyphyletic (Erpenbeck *et al.*, 2007; Redmond *et al.*, 2011), neither mitochondrial nor ribosomal tree topologies here matched the shared morphological features used for classification of Niphatidae or Chalinidae or any of the subgenera within *Haliclona* spp., such as spicule composition, length, presence/absence of multispicular fibers or differences in skeletal arrangements. Despite polymorphism of these taxonomic characters, sequences were unique and diagnostic for each species, and showed more than 3 % divergence from their closest match for both loci.

The majority of previous *Haliclona* spp. records in Hawaiʻi include species with broad geographic distribution, and three introduced species. For example, *H.* (*Gellius*) *laubenfelsi* extends from the Western Indian Ocean, through the Tropical Northwestern, Eastern Indo-Pacific and over to the Atlantic (Bettcher *et al.*, 2024). *Haliclona flabellodigitata* Burton, 1954 spans the Great Barrier Reef and Hawaiʻi (de Laubenfels (1957). *Haliclona* (*Reniera*) *aquaeductus* (Schmidt, 1862) and *H*. (*Reniera*) *cinerea* (Grant, 1826) originally described from the Northeastern Atlantic and *H.* (*Soestella*)) *caerulea* from the Caribbean are all considered introduced species to Hawaiʻi. In contrast, *H. mokuoloea* described in 1950s is the only haplosclerid considered endemic to Hawaiʻi because this species has not been found outside Kāneʻohe Bay in nearly 75 years.

We add three new species to this list with the descriptions herein, and the molecular barcoding tools to evaluate their distribution. While newly described from the Hawaiian archipelago, determining the endemicity of the described species in this study remains a challenge for several reasons. The artificial surface and cryptic habitats of ARMS provide recruitment of species that are difficult to encounter on reef habitats. In a recent survey comparing diversity of haplosclerid species between ARMS and cryptic natural reef habitats, 15 species were found only on ARMS, six were shared between habitat types and eight species were found exclusively in reef habitats (Vicente *et al.*, 2021). Of the new species described here, *H. (Reniera) kahoe* and *H.* (*Rhizoniera*) *pahua* have only been collected on ARMS whereas *H.* (*Gellius*) *loe* has been found on both ARMS and natural reef surfaces from lava tubes on the north shore

of O‘ahu (voucher BPBM C1672). Further, Kāne‘ohe Bay is a hotspot for non-indigenous species introductions, with at least 10 sponge introductions from the Indo-Pacific and the Caribbean (Bergquist 1977; Coles 2006; Coles *et al.* 2002). To date, all documented introductions are from emergent species that are easily recognizable on the reef surface. The small and encrusting *H. (Reniera) kahoe* and *H.* (*Rhizoniera*) *pahua* specifically inhabit cryptic spaces that have been understudied historically. Collecting sponge species from natural spaces within the reef matrix is extremely challenging, both technically and in terms of permitting, which could explain why these species were missed in previous surveys of sponge diversity (Bergquist 1977; de Laubenfels 1951, 1954, 1957; Pons *et al.* 2017). Such gaps in our knowledge make it difficult to quantify diversity and distinguish whether these newly described congeners are introduced or endemic species.

Our integrative systematic approach was particularly useful in distinguishing individuals of *H. (Reniera) kahoe* exhibiting similar solitary mound growth morphologies to *H.* (*Rhizoniera*) *pahua* since these species share almost exact *in situ* growth, color patterns and consistency (Fig. 4c and Fig. 6c). However, *H. (Reniera) kahoe* and *H.* (*Rhizoniera*) *pahua* were unmistakably, genetically distinct with mitochondrial and ribosomal sequences showing <84% identity between them. Broader efforts are needed to begin to resolve the geographic distribution of benthic reef sponges throughout the Indo-Pacific, and to address the question of whether newly discovered species are recently introduced, broadly distributed but under studied, or undiscovered endemics. Certainly, continued use of standardized sampling modules such as ARMS throughout the tropical Pacific and Caribbean will shed light on the global distribution of species inhabiting the reef matrix, which would otherwise be difficult to sample or study.

In addition to discovering potentially new endemic sponge species, our study provides the first evidence of competition for space between endemic and introduced sponges. *Haliclona* (*Soestella*) *caerulea* and *Gelliodes conulosa* were both discovered in the matrix inside ARMS units (Vicente *et al.*, 2022), directly competing for space with the new species described here. While the ecological role of these newly described sponges remains to be determined, this observed competition implies that there could be an impact of these introduced sponges on native species and coral reef ecosystems. For example, temporal observations showed some pioneering species belonging to Calcarea and Haplosclerida (including *H. (Reniera) kahoe*) in Kāne‘ohe Bay to be short lived (Vicente *et al.*, 2022a). Based on their time series of observations, Vicente *et al.* (2022a) ypothesized that particulate organic carbon (POC) derived from dead sponge tissue could serve as an important food source for detritovores which fuels higher trophic levels throughout early successional stages of habitat development. Although rare, growth of *G. conulosa* showed recruitment during early stages of habitat development which continued throughout the 2-year monitoring period. Continued growth and longer-lived presence of *G. conulosa* reduces the available space for pioneering species to settle, and would reduce their capacity to return POC as food to the ecosystem through successional stages. Despite persistent growth of *G. conulosa* on artificial structures, future recruitment studies need to be conducted on natural reef surfaces to confirm whether *G. conulosa* follows similar recruitment and growth rates on calcified structures that threatens native sponges by limiting their recruitment during early pioneering stages.

Haplosclerid sponges are notoriously difficult to identify based on traditional taxonomy alone. Long term monitoring of the benthic reef community in Kāne‘ohe Bay revealed that sponges belonging to the order Haplosclerida are highly diverse and widely underexplored (Timmers *et al.*, 2020; Vicente *et al.*, 2021). Here we show that an integrative approach with molecular phylogeny and traditional taxonomy proves successful, both to identify morphologically variable species as single taxa and to differentiate cryptic species with similar morphology. We use this approach to confirm the identification of some of the most common introduced sponges in the state, and then describe three new species for the Hawaiian Archipelago from those same surveys. Together with the production of barcodes anchored to morphological descriptions of vouchered specimens, this work advances our understanding of invasive species origination and sponge diversity in Hawai‘i. These results will be of particular relevance to the re-evaluation of historical collections identified as *Gelliodes fibrosa* sensu de Laubenfels (1935) or of samples previously identified as *G. wilsoni* (Carballo *et al.*, 2013) throughout the Pacific which will help resolve the distribution of this species. Our dataset will enrich genetic databases with accurate taxonomic information to improve detection of native and endemic sponge species through metabarcoding techniques such as eDNA and processing of future ARMS samples from across the Indo-Pacific. We advocate for the continued use and processing of ARMS installations across the Pacific to gain a better understanding on the diversity and geographic range of small benthic species such as these that are easily overlooked or impossible to sample from deep within the living reef matrix. Such continued work will advance our understanding of coral reef biodiversity and endemism in relation to other island archipelagos throughout the Pacific.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper, also available from here: https://github.com/vicentejan/vicenteetal2024zootaxa/blob/main/Supplemental%20material.pdf

Table S1. Museum voucher and Genbank accession numbers for each species, holotype and paratype specimens. FMNH refers to the Florida Museum of Natural History and BPBM to Bernice Pauahi Bishop Museum. *Refers to the holotype specimen

Table S2. Summary of morphological data of known *Haliclona* spp. sharing similar characters to new species described in this study from the Pacific Ocean, Indian Ocean, Arabian Sea, Adaman Sea, Gulf of Aden, Atlantic Ocean, Caribbean Sea, Mediterranean Sea, Adriatic Sea and Aegean Sea.

Table S3. Summary of morphological data of known Gelliodes spp. sharing similar characters to Gelliodes conulosa