Biol Invasions (2024) 26:3475–3493
https://doi.org/10.1007/s10530-024-03385-4

ORIGINAL PAPER

Intraoceanic and interoceanic dispersal of a marine invader: revealing an invasion in two ocean basins

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Received: 15 January 2024 / Accepted: 24 June 2024 / Published online: 30 July 2024

Abstract Recent collection efforts along the Brazilian coast revealed a *Haliclona* species preliminarily identified as a likely new species. However, sequencing of the 28S rRNA C-Region, a barcode marker in sponges, showed its high genetic similarity with a *Haliclona* sp. from Hawai'i (GenBank MW016137–MW016139). We applied an integrated morphological and molecular assessment, which allowed us to identify both Brazilian and Hawaiian specimens as *H.* (*Reniera*) *laubenfelsi*, a species with an Indo-Pacific distribution. We postulate this species to be exotic both in the Brazilian coast and in Hawai'i. Our evidence is based on the arrival of the species in Brazil after 2001, being first registered next to an international port. In turn, the species is distributed discontinuously in Hawai'i, being mainly restricted to sheltered bays and vicinities of ports, showing a predilection for anthropogenic substrates, which strengthen the hypothesis of its exotic origin. Recent collections in Hawai'i (2016–2018) failed to find this species in natural habitats, though it was an abundant pioneer species in Autonomous Reef Monitoring Structures. Its capacity to colonize artificial substrata may indicate either a cryptobenthic nature or an invasive potential. We highlight the need of monitoring its abundance, spatial distribution, and biotic interactions along the Brazilian coast to assess its potential environmental impacts. The full morphological description, and the molecular sequences we provided certainly will speed up the identification of this species, allowing to track its range extension.

Keywords Porifera · Non-indigenous species · Bioinvasion · Exotic species · Integrative taxonomy · Brazil · Hawai'i

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10530-024-03385-4.

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Introduction

The introduction of non-indigenous species of marine sponges is an understudied topic globally. Currently, there are at least 29 recognized marine non-indigenous sponges worldwide (Cavalcanti et al. 2020; Carlton and Eldredge 2009, 2015; Gastaldi et al. 2018; Turner 2020; Harbo et al. 2021; Samaai et al. 2022; Bertolino et al. 2022), most of them of unknown origin and vector of introduction. This number includes, besides those species listed by Cavalcanti et al. (2020), the sponge species *Batzella aurantiaca* (Lévi, 1958), *Halichondria* (*Halichondria*) *coerulea* Bergquist, 1967, *Halich.* (*Halichon.*) *melanadocia* de Laubenfels, 1936, *Haliclona* (*Halichoclona*) *vansoesti* de Weerdt, de Kluijver & Gómez, 1999, *Hymeniacidon perlevis* (Montagu, 1814), *Monanchora quadrangulata* (Lévi, 1958), *Mycale* (*Carmia*) *cecilia* de Laubenfels, 1936, *Protosuberites epiphytum* (Lamarck, 1815), *Raspailia* (*Clathriodendron*) *darwinensis* Hooper, 1991, *Suberites aurantiacus* (Duchassaing & Michelotti, 1864), *Tedania ignis* (Duchassaing & Michelotti, 1864), most of them have their origin and vector of introduction unknown. Nevertheless, these numbers are very likely underestimated as they do not account for cryptogenic and pseudoindigenous species (Carlton 2009).

The study of non-indigenous sponges is still little explored and a hard to tackle subject. The taxonomy of these organisms is often difficult, leading to a large knowledge gap of their actual distributions (*i.e.* Wallacean shortfall sensu Lomolino 2004) that hampers the detection of arrivals of alien species. Another pitfall resides in the common practice of naming new species of sponges after only a limited comparison with congeners is carried out. This is mostly justified based on the limited dispersal ability of most sponges, a consequence of the very short life span of their larvae (Maldonado 2006). This practice is more common in species-rich genera (e.g. Zea et al. 2014; Calcinai et al. 2017; Bispo et al. 2022), where taxonomic comparisons with all extant congeners is difficult to handle, and would be too time consuming. In fact, many actual dispersals may lie hidden all around the globe (pseudoindigenous species), awaiting comprehensive integrative reviews to be disclosed.

Whenever a thorough baseline of sponge species exists for a geographic region, a faster detection of exotic species is possible. For example, the invasion of *Mycale grandis* Gray, 1867 in Hawai‘i was easy to be detected because previous faunistic surveys were already available for this area (de Laubenfels 1950; Bergquist 1967). Thus, it is expected that the very conspicuous *M. grandis* would have been included in these studies, if it was there at the surveyed timeframe. However, such baseline inventories on the local biodiversity of sponges are very rare in many other areas worldwide, making early detection of exotic species almost impossible. Examples of pseudoindigenous species are usually found in these poorly known areas, where several species might be described as new and native, when they actually represent ill-known exotic species. This was the case for the calcareous sponges *Paraleucilla magna* and *Heteropia glomerosa* (Bowerbank, 1873), both exotic in the Brazilian coast, but initially thought to be native. Their exotic condition was uncovered only after integrative taxonomic assessments (Guardiola et al. 2016; Cavalcanti et al. 2020; Klautau et al. 2020). The delayed detection of introductions may compromise the evaluation of possible ecological impacts. In this sense, the regular, systematic use of coupled morphological and molecular data in species inventories could speed up the detection of introductions, as similar Molecular Operational Taxonomic Units (MOTUs) from disjunct localities can easily be detected in this way (Comtet et al. 2015; Mazzamuto et al. 2016; Rocha et al. 2019).

When studying a purportedly new species of *Haliclona* from the Brazilian coast, we discovered that our material was genetically identical to other sequences from Hawai‘i (Vicente et al. 2022a). Thus, we assessed comparatively their morphology and molecular information to answer the following questions: (1) are Brazilian and Hawaiian materials conspecific? (2) Is this a new or an already described species? (3) Is this species exotic in Hawai‘i or in Brazil?

Materials and methods

Sampling

Specimens were collected from the Costa do Descobrimento (Bahia, Brazil), São Sebastião

Channel (São Paulo, Brazil), and O'ahu (Hawai'i, USA) (Fig. 1). In Brazil, sample collections were undertaken by wading at low tide and snorkeling at tide pools, using knifes, or alternatively a small sledgehammer and chisel to remove samples from the substrate. Collection permits were issued by the Municipal Environment Secretary of Porto Seguro (#05/2019) and (#09/2020). Hawaiian specimens were collected on modified Autonomous Reef Monitoring Structures (ARMS) over two years in mesocosms at the Hawai'i Institute of Marine Biology on Moku o Lo'e (Coconut Island) in Kane'ohe Bay (O'ahu, Hawai'i) (Vicente et al. 2022a; Timmers et al. 2022). Collection permits for Hawaiian specimens were issued by the State of Hawai'i Division of Aquatic Resources SAP nos. 2018–03 and 2019–16 (covering the period of January 13, 2017, through April 10, 2019). Individuals were photographed in situ, underwater, whenever possible. Upon arrival at the beach or the field lab, specimens were subsampled, fixed in 99% ethanol, and kept at − 15 to − 18°C for subsequent molecular work. In the lab they were transferred to appropriate jars completed with 80% ethanol and deposited in either the ZUEC-POR (Museu de Zoologia da Universidade Estadual de Campinas, Brazil), the UF (Florida Museum of Natural History, USA), the BPBM (Bernice Pauahi Bishop Museum, USA), or the MNRJ (Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil) sponge collections.

Molecular phylogeny and species delimitation

Total genomic DNA was extracted through a modified phenol–chloroform protocol (Sambrook and Russell 2001), with a lysis buffer containing Tris–HCl 10 mM (pH 8.0), EDTA 50 mM, NaCl 0.1 M, 0.5% SDS and Proteinase K (20 mg/mL). We checked the concentration and quality (260/280 absorbance) of extracted DNA with a nano spectrophotometer. A fragment of the nuclear 28S rRNA gene (C-region) was amplified through PCR using the primer pair 28S–C2–fwd (GAA AAG AAC TTT GRA RAG AGA GT) and 28S–D2–rev (TCC GTG TTT CAA GAC GGG) (ca. 480bp) (Chombard et al. 1998; Erpenbeck et al. 2016). PCR amplifications were performed in 25µL reactions consisting of 22.5 µL PCR SuperMix (Invitrogen™) 0.5 µL of template DNA (up to 50 ng/uL), 0.5 µL of each primer (10 µM), supplemented with 0.5 µL of BSA (50 mg/ml). The PCR reactions were submitted to the following thermocycling profile: initial denaturation at 94 °C for 3', followed by 35 cycles of 30″ denaturation at 94°C, 30″ annealing at 50°C, 60″ elongation at 72 °C, and a final elongation at 72 °C for 5'.

The amplicons were then purified using a standard ammonium acetate-ethanol precipitation (Sambrook and Russell 2001), then both strands were sequenced using the Big Dye™ terminator v. 3.1 reaction performed on an ABI Genetic Analyzer 3500/3730 XL automated sequencer at *ACTGene Análises Moleculares* (Brazil). The electropherograms were assembled and edited using Geneious Prime 10 or 2021. Ambiguous bases were coded with IUPAC ambiguity codes. Sequences with high quality had their poriferan origin checked using the Basic Alignment Search Tool (BLAST) tool of NCBI (https://blast.ncbi.nlm.nih.gov).

The 28S rRNA C-region sequences obtained in this study (Acc. # OR229997–OR230000), the 28S rRNA sequences from Vicente et al. 2022a, b (Acc. # MW016137– MW016139) and other haplosclerid sequences available at GenBank were aligned using MAFFT v.7 (Katoh et al. 2019) online service with the FFT–NS–i algorithm. Uncorrected *p*-distance (pairwise deletion and 500 bootstrap replicates) within and among species were calculated in MEGA 7 (Kumar et al. 2016). Phylogenetic analysis was conducted using the maximum likelihood (ML) framework in RA×ML v.8.2.10 software (Stamatakis 2014) implemented in the CIPRES Science Gateway (https://www.phylo.org/portal2), using the GTRGAMMA model and 1,000 rapid bootstrap pseudoreplications (BST) to assess the confidence of the topology. Only bootstrap values above 70 are exhibited in the trees. The BLAST result of our specimens showed their close relationship with members of Clade A of Haplosclerida (Redmond et al 2013), therefore sequences from *Dasychalina melior* (KC869455) and *Amphimedon compressa* (KY825184) in Clade C were chosen as an outgroup. The Assemble Species by Automatic Partitioning—ASAP (Puillandre et al. 2021) was executed (https://bioinfo.mnhn.fr/abi/public/asap/) as a tool for molecular species delimitation, using the same fasta matrix used for phylogenetic reconstruction and based on *p*-distance.

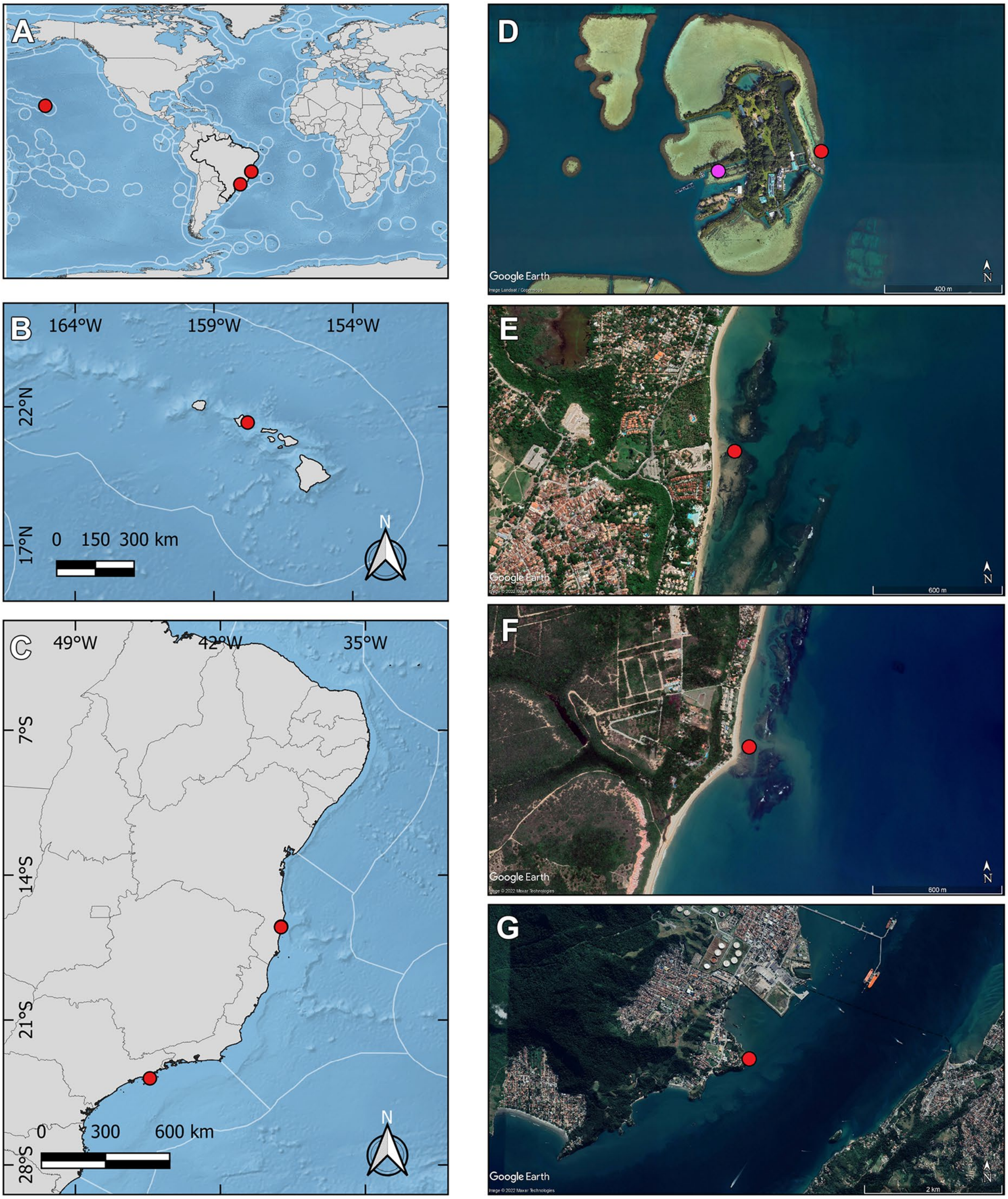

Fig. 1 Collection sites of *Haliclona* (*Reniera*) *laubenfelsi* van Soest & Hooper, 2020. **A** Map showing collection sites in Hawai‘i and Brazil; **B** Hawai‘i archipelago; **C** Brazilian coast; **D** Moku o Lo‘e (Coconut Island) in Kane’ohe Bay (O’ahu, Hawai‘i), type locality is indicated by a violet circle; **E** Detail of Pescadores Beach (Arraial D’Ajuda, Porto Seguro municipality, Bahia state); **F** Pitinga Beach (Arraial D’Ajuda, Porto Seguro municipality, Bahia state); **G** southern corner of Araça Bay (São Sebastião Channel, São Sebastião municipality, São Paulo state). Ecoregions are delimited by white lines

Morphological identification

Taxonomic identification was achieved by the usual procedures for sponges as outlined in Hajdu et al. (2011), including the preparation of thick anatomical sections and dissociated spicules. Data gathered in this way was contrasted to that available in the specialized literature, as compiled in de Voogd et al. (2023). Type material of *Toxadocia violacea* de Laubenfels, 1950 [=*Haliclona* (*Gellius*) *laubenfelsi*] was obtained on loan from the USNM (Smithsonian Institution, Washington DC). Spicule measurements were made from Light Microscopy (LM) for each type of spicule. In the main text the measurements correspond to the total of spicules measured in all the specimens examined and are expressed in micrometers as minimum–*mean*–maximum for length × width.

Results

Our morphological and molecular analyses of the 28S rRNA gene indicate conspecificity of Brazilian (Southwestern Atlantic) and Hawaiian samples (Central Pacific Ocean). The latter were identified as *Haliclona* sp. in Genbank (Acc. # MW016137–MW016139). We thus compared the morphology of our specimens with the species of *Haliclona* from the Central Pacific and the Atlantic, resulting in their identification as *Haliclona* (*Gellius*) *laubenfelsi* van Soest & Hooper, 2020 by the presence of toxas and oxeas of similar shape to that observed in our material. This identification was confirmed through comparison with type material. We propose the transfer of this species to the subgenus *Haliclona* (*Reniera*) based on its skeletal architecture (see below in Discussion).

Molecular phylogeny and species delimitation

The aligned dataset included 25 terminals and 580bp after trimming. *Haliclona* (*Reniera*) *laubenfelsi* is positioned within Clade A of Haplosclerida (Redmond et al. 2013). Our specimens clustered in a highly supported clade (84 BST), being sister (94 BST) with an unidentified *Haliclona* from the Caribbean. Other closely related species are *Haliclona* (*Reniera*) *tubifera* (George & Wilson, 1919) and *Haliclona* (*Gellius*) *toxia* (Topsent, 1897) (Fig. 2). The genetic distance within sequences of *H. (Re.) laubenfelsi* ranged from 0 to 0.6%. There was no correlation between geographic and genetic distances, as some sequences from Bahia and São Paulo (MNRJ 23911 and MNRJ 22807) were more similar to Hawaiian samples than to other samples from the same localities (MNRJ 23723 and ZUEC-POR 23), respectively (0.2–0.6% in *p*-distance, see in Table S1).

Haliclona (*Reniera*) *laubenfelsi* sequences showed a genetic divergence greater than 3.8% to *Haliclona* sp. and greater than 21% and 19% in *p*-distance to *H.* (*G.*) *toxia* and *H.* (*Re.*) *tubifera*, respectively, values that considerably exceed the observed intraspecific genetic divergence in *H.* (*Re.*) *laubenfelsi*, of up to 0.6% in *p*-distance (Table S1). ASAP results recovered two partitions with the same asap-score of 4.00: Partition 1 and Partition 2 recovered 14 and 10 putative species, respectively. The barcode gap for each Partition was ~3% in Partition 1 and ~19% in Partition 2, which resulted in the union of *Chalinula molitba* (de Laubenfels, 1949), *Calyx nicaeensis* (Risso, 1827), *Neopetrosia rosariensis* (Zea & Rützler, 1983) and *Neopetrosia subtriangularis* (Duchassaing, 1850) in the same MOTU in Partition 2. Nevertheless, in both Partitions the ASAP analyses retrieved all the sequences of *H.* (*Re.*) *laubenfelsi* from Brazil and Hawai'i in the same MOTU.

Systematics

Class Demospongiae Sollas, 1885
Order Haplosclerida Topsent, 1928
Family Chalinidae Gray, 1867
Genus *Haliclona* Grant, 1841
Subgenus *Haliclona* (*Reniera*) Schmidt, 1862
Haliclona (Reniera) laubenfelsi van Soest & Hooper, 2020
(Figs. 3, 4, 5).

Haliclona enamela sensu de Laubenfels (1939) [Non *Haliclona enamela* de Laubenfels, 1930]—de Laubenfels (1939): 1.
Toxadocia violacea de Laubenfels, 1950—de Laubenfels (1950): 16, Fig. 9; de Laubenfels (1951): 259; de Laubenfels (1954): 338; de Laubenfels (1957): 247; Bergquist (1965): 154,

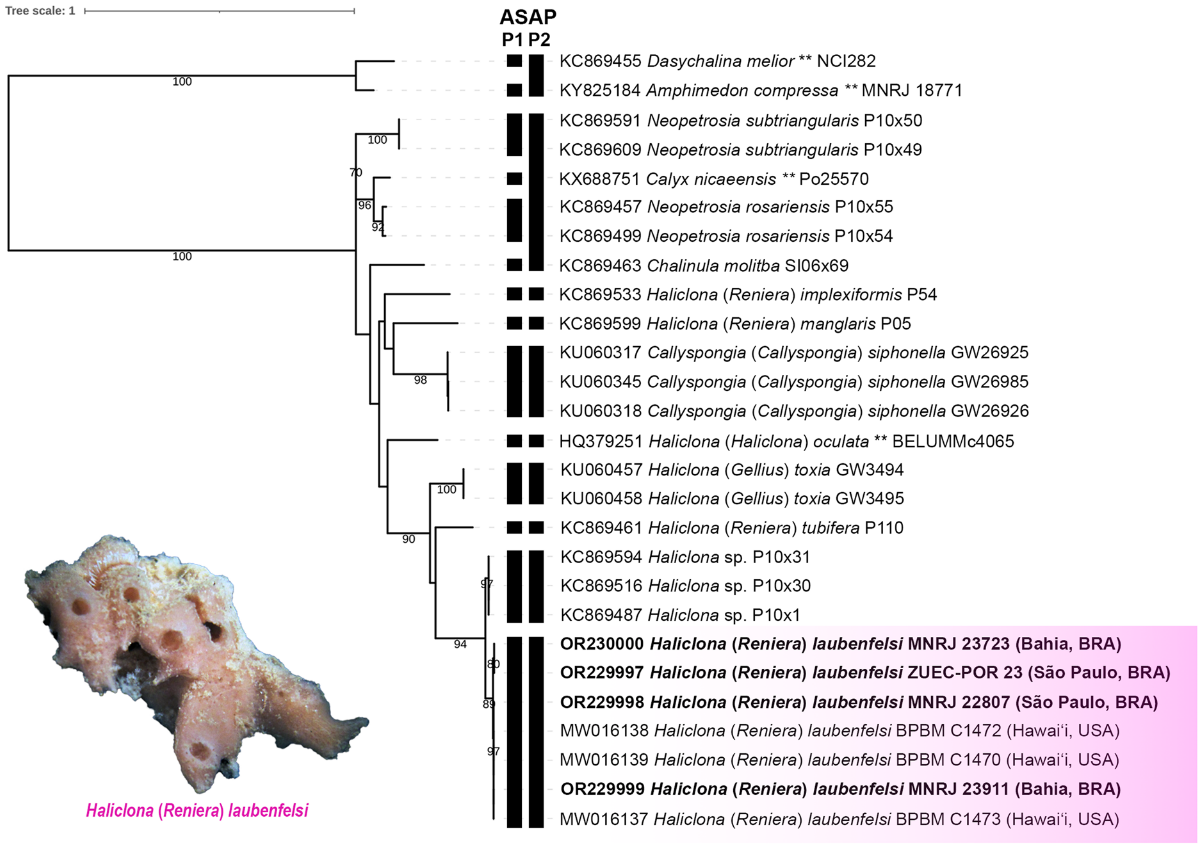

Fig. 2 Maximum likelihood phylogeny of selected Clade A Haplosclerida based on partial 28S rDNA (C-Region), including *Haliclona* (*Reniera*) *laubenfelsi* van Soest & Hooper, 2020 from Brazil and Hawai'i. OTUs in bold highlight original sequences. Bootstrap values > 70 are shown on the branches. Haplosclerida Clade C sequences KC869455 and KY825184 were used as outgroups. Black vertical bars indicate Assemble Species by Automatic Partitioning (ASAP) putative species, P1 = Partition 1, P2 = Partition 2

Fig. 17; ? Vacelet and Vasseur (1971): 113, Fig. 74; Bigger et al. 1983: 240.

Haliclona (*Gellius*) *violacea* van Soest et al., — van Soest et al. (2011): 31, Fig. 14.

Haliclona (*Gellius*) *laubenfelsi* van Soest & Hooper, 2020—van Soest et al. (2020): 66.

? *Kaneohea poni* de Laubenfels, 1950—Bergquist (1967): 159; Bergquist (1977): 65.

Material examined

Holotype: USNM 22752, Moku o Lo'e (Coconut Island, Kāne'ohe Bay, O'ahu Island, Hawai'i, USA), 1m depth, coll. M. W. de Laubenfels, 3rd November 1947.

USA (Hawai'i): on Autonomous Reef Monitoring Structure (ARMS) inside mesocosms at the Hawai 'i Institute of Marine Biology (HIMB) in Moku o Lo'e (Coconut Island) (21.4334, − 157.7868; Kāne'ohe Bay, O'ahu Island), coll. Jan Vicente: BPBM C1473 and BPBM C1474, 16th March 2018; BPBM C1471/ UF 3956, 7th June 2017; BPBM C1470, 19th December 2016; BPBM C1472, 19th April 2017.

Brazil (São Paulo State): MNRJ 22807, Araçá Bay entrance (− 23.8195, − 45.405; São Sebastião municipality), depth not recorded, coll. G. Dias, 1st October 2012. ZUEC-POR 23, Araçá Bay entrance (São Sebastião municipality), depth not recorded, coll. F. Dutra, 1st January 2013, subsampled under MNRJ 22759.

Brazil (Bahia State): MNRJ 20478, Praia da Pitinga (− 16.51333, − 39.07333; Arraial D'Ajuda, Porto Seguro municipality), intertidal, coll. E. Hajdu and A. Fioravanso, 23rd March 2019. MNRJ 23620

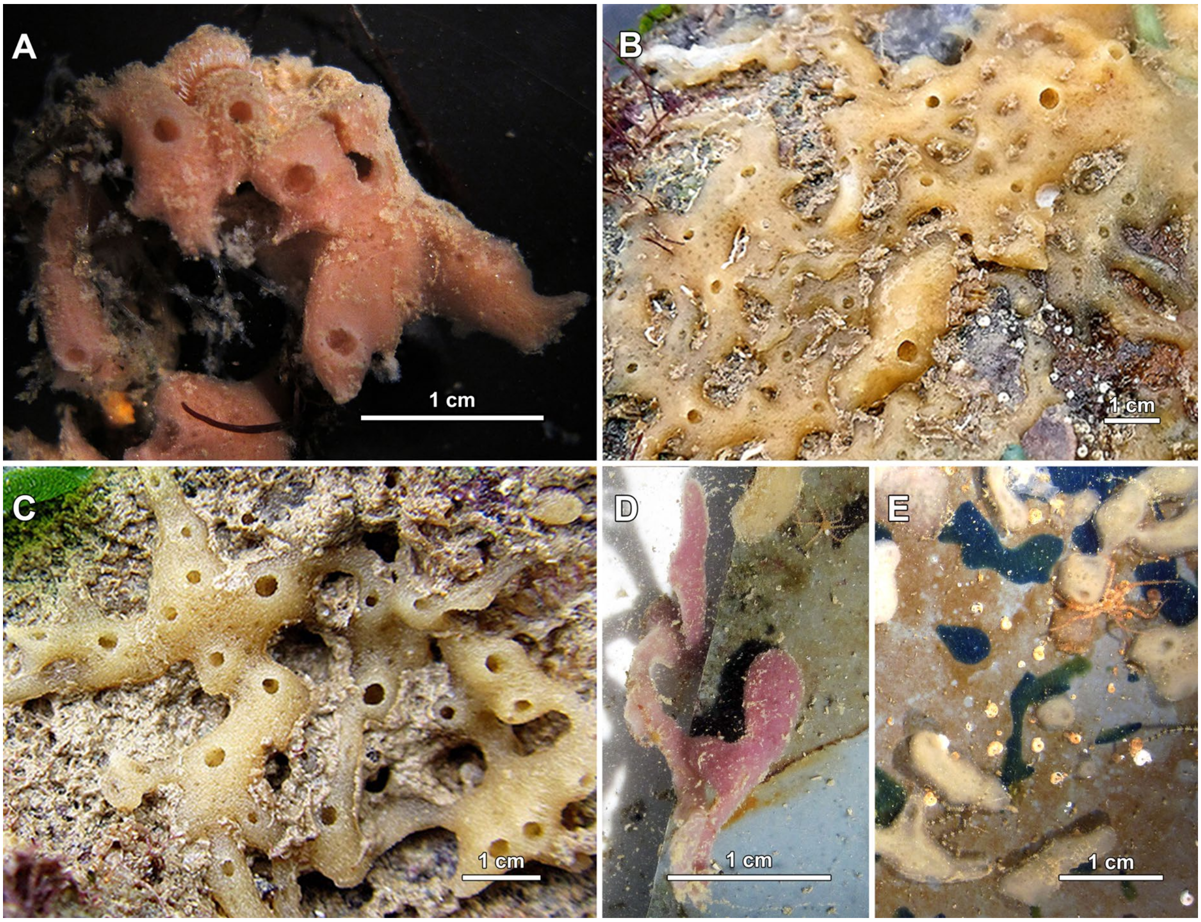

Fig. 3 Morphological variability of *Haliclona* (*Reniera*) *laubenfelsi* van Soest & Hooper, 2020 alive. **A**–**C** Material from Brazil. **D**–**E** Material from Hawai'i Archipelago. **A** MNRJ 22807 from São Paulo. **B** MNRJ 20478 from Bahia. **C** MNRJ 23723 from Bahia. **D** BPBM C1471 or UF 3956 from O'ahu. **E** BPBM C1470 from O'ahu. Photographs: **A** M. Borges, **B**–**C** E. Hajdu, **D**–**E** J. Vicente

and MNRJ 23723, Praia da Pitinga (−16.51333, −39.07333; Arraial D'Ajuda, Porto Seguro municipality), intertidal, coll. L. Bettcher, J.C.C. Fernandez and E. Hajdu, 22nd August 2021. MNRJ 23911 Praia dos Pescadores (−16.4881, −39.0666; Arraial D'Ajuda, Porto Seguro municipality), intertidal, coll. A. Bispo, A. Lage and D. Rezende, 5th November 2021.

Description

Encrusting digitate morphology expanding both laterally as mounds, 0.3–1.0 cm thick, and vertically with irregular, slender, digitiform projections, 1.0–5.0 mm in diameter (Fig. 3). Long thin branches stem from encrusting mounds. Oscula circular to oval, 0.5–4.0 mm in diameter, flush with the surface or apical on short digitate projections, aligned or more randomly distributed. Surface is smooth. Consistency is soft and fragile. Color in situ varies between dull beige, pinkish beige, pink, purple, but always beige in ethanol.

Skeleton

Ectosome a delicate, slightly regular, unispicular, isodictyal reticulation, forming three- to four-sided meshes, or confused (Fig. 4c, e, g). Choanosome of the same structure (Fig. 4a, b, d, f). Dark pigments dispersed throughout the skeleton. Spongin scarce

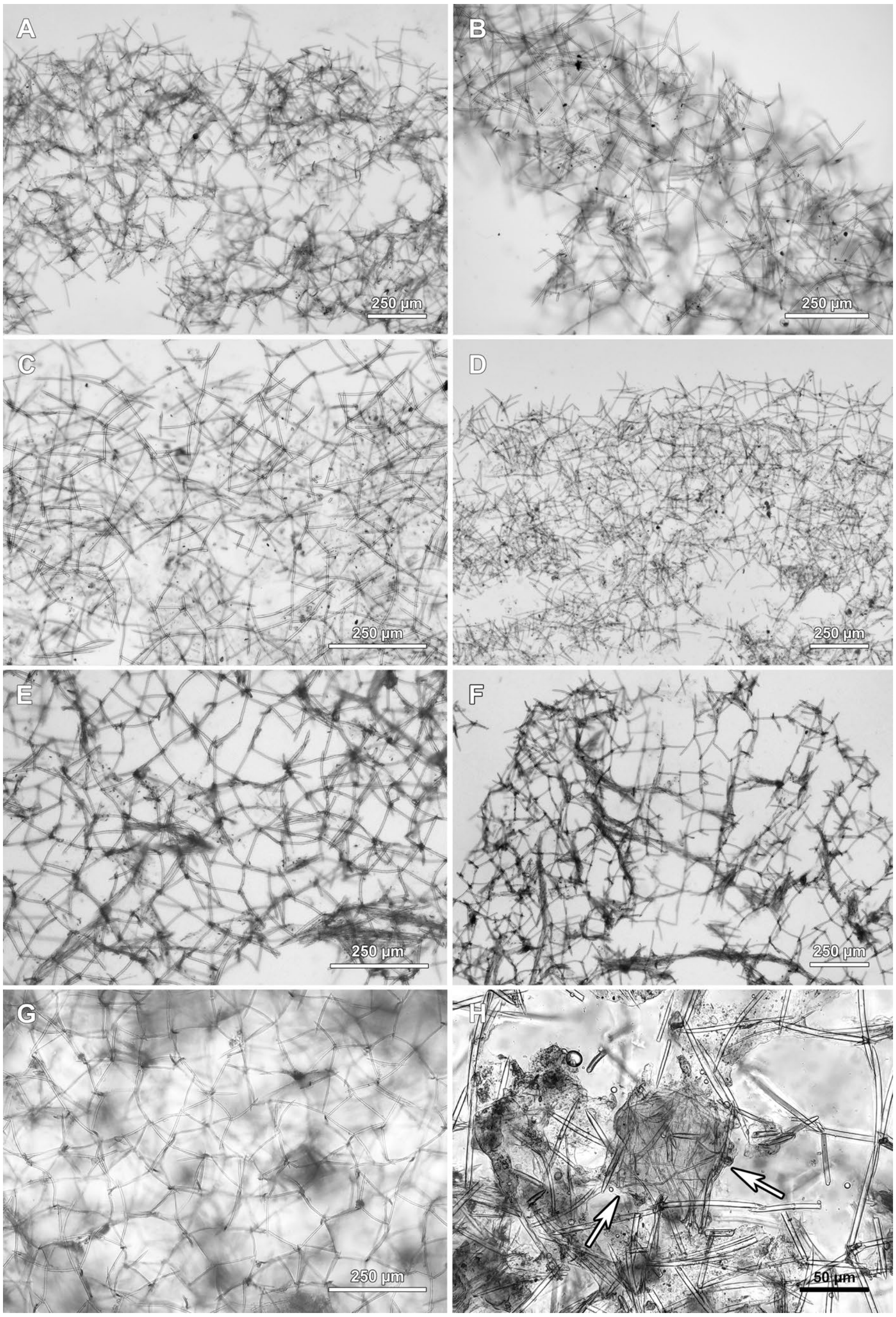

Fig. 4 *Haliclona* (*Reniera*) *laubenfelsi* van Soest & Hooper, 2020, variability of skeletal architecture. **A**, **C**, **E**, **G** ectosome. **B**, **D**, **F**, **H** choanosome. **A**–**B** Holotype, USNM 22752 from O'ahu. **C**–**D** BPBM C1473 from O'ahu. **E**–**F** MNRJ 22807 from São Paulo. **G**–**H** MNRJ 20478 from Bahia, arrows indicate the presence of embryos in **H**

to abundant. The holotype and the specimens from the mesocosm tanks in Hawai'i have very scarce spongin, creating a looser/confused reticulation (Fig. 4a–d). Specimens from São Paulo are more spicule-reinforced, including development of pauci- to multispicular tracts in MNRJ 22807 (Fig. 4e, f). Specimens from Bahia are more spongin-reinforced (Fig. 4g, h). Embryos present in MNRJ 20478, 62–*85.1*–113 µm in diameter, contain small oxeote spicules (Fig. 4h).

Spicules

Oxeas (Fig. 5a, b, c), mainly hastate, abruptly tapering to a sharp point, some modified to styles or strongyles, most slightly curved, 64–*111.7*–141 × 2.0–*4.6*–7.4 µm

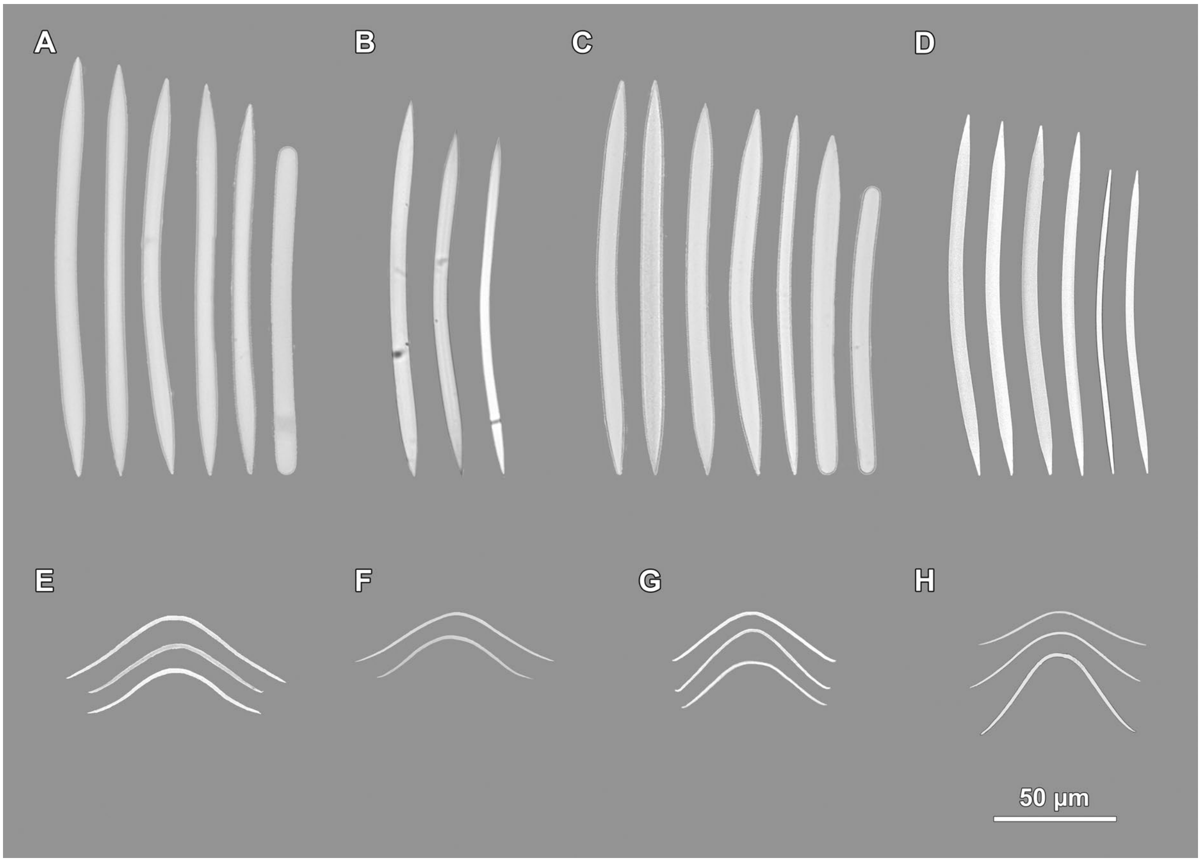

Fig. 5 *Haliclona* (*Reniera*) *laubenfelsi* van Soest & Hooper, 2020, variability of spicules. **A**–**D** oxeas. **E**–**H** toxas. **A**, **E** Holotype, USNM 22752 from O'ahu. **B**, **F** BPBM C1470 from O'ahu. **C**, **G** MNRJ 22807 from São Paulo. **D**, **H** MNRJ 20478 from Bahia

(Table 1). Toxas (Fig. 5d, e, f), in a single, deeply curved category, 32–*51.6*–71 µm long (Table 1). Only a single toxa was found in ZUEC-POR 23, ca. 50 × 1.0 µm. Small oxeote spicules < 2.0µm thick are understood as immature oxeas and were found in most specimens in variable amounts. Oxeote spicules measured directly from embryos in MNRJ 20478, 37–*48*–55 µm long (n = 10).

Ecology and distribution

Haliclona (*Re.*) *laubenfelsi* is rare along the Brazilian coast, found in rocky shores close to the port of São Sebastião (São Paulo state), or in crevices and overhangs in areas protected from direct sunlight (sciophilous) of intertidal sandstone reefs fringing the city of Porto Seguro (Bahia state). Despite intense collecting on several reefs spread over 30km in southern Bahia (Bettcher et al. 2023), only four specimens were found in a single reef. In Hawai'i, our specimens recruited onto Autonomous Reef Monitoring Structures (ARMS) placed in mesocosm tanks supplied with unfiltered flow-through seawater from Kāne'ohe Bay. ARMS mimic a cryptic low light reef environment which attracts a high diversity of cryptobenthic sponge species (Vicente et al. 2022a).

This species is known from the Central Pacific (Hawai'i as *Toxadocia violacea*; de Laubenfels 1950), the East Pacific (Clipperton Atoll as *H.* (*Gellius*) *violacea*; van Soest et al. 2011), the West Pacific (Palau as *T. violacea*; Bergquist 1965), and the western Indian Ocean (Madagascar as *T. violacea*; Vacelet and Vasseur 1971). However, we consider this latter record as doubtful, given the black color of the specimen, much unlike the purplish, pinkish or beige hues of *H.* (*Re.*)

Table 1 Summary of external morphology, skeletal architecture and spicule measurements of *Haliclona* (*Reniera*) *laubenfelsi* van Soest & Hooper, 2020 from Brazil and Hawai‘i. Spicule dimensions were based on the measurements of 30 + spicules per specimen, except when indicated, and expressed as minimum–*mean*–maximum for length × width

Voucher	Locality	Shape and color	Skeleton	Oxeas (µm)	Toxas (µm)
USNM 22752 (Holotype)	Hawai‘i, EUA	Encrusting-digitate, violet (sensu de Laubenfels 1950)	Isotropic, unispicular, scarce spongin	96–*125.6*–141 × 2.2–*5.1*–7.0	33–*55.8*–74
BPBM C1470	Hawai‘i, EUA	Encrusting mound with distal branch, light pink	No skeletal preparation made	76–*107.9*–122 × 2.5–*4.1*–6.1	45–*59*–64 (n = 10)
BPBM C1471	Hawai‘i, EUA	Encrusting-branched, pinkish beige to pink	Isotropic, unispicular; scarce spongin	81–*107.9*–120 × 2.3–*3.8*–5.6	51 × 3 (n = 1)
BPBM C1472	Hawai‘i, EUA	Encrusting mound, beige	No skeletal preparation made	111–*123.0*–135 × 4.1–*5.9*–7.4	55–*59.7*–66 (n = 10)
BPBM C1473	Hawai‘i, EUA	Encrusting mounds, laterally ramified, beige	Isodictyal to isotropic, unispicular; scarce spongin	94–*110.8*–125 × 2.4–*3.6*–4.8	46–*56.2*–69 (n = 10)
BPBM C1474	Hawai‘i, EUA	Encrusting mounds, laterally ramified, beige	Isotropic, unispicular; scarce spongin	100–*114.4*–122 × 2.3–*4.6*–6.8	42–*59.9*–71 (n = 10)
ZUEC-POR 23	São Paulo, BR	Encrusting mounds, laterally ramified, anastomosed, color alive unknown	Isodictyal to isotropic, unispicular; scarce spongin	82–*105.1*–118 × 2.5–*5.7*–7.3	50 (n = 1)
MNRJ 22807	São Paulo, BR	Encrusting mounds, laterally ramified, pink to beige	Isodictyal, unispicular, with some pauci- to multispicular tracts; scarce spongin	92–*116.3*–130 × 2.4–*5.9*–7.4	44–*52.4*–66 (n = 10)
MNRJ 20478	Bahia, BR	Encrusting mounds, laterally ramified, anastomosed, beige	Isodictyal to isotropic, unispicular; moderate spongin	67–*104.2*–120 × 2.2–*4.0*–5.6	32–*48.7*–68
MNRJ 23620	Bahia, BR	Encrusting mounds, laterally ramified, beige	Isodictyal to isotropic, unispicular; moderate spongin	90–*109.4*–120 × 2.2–*4.5*–6.3	38–*50*–62
MNRJ 23723	Bahia, BR	Encrusting mounds, laterally ramified, beige	Isodictyal to isotropic, unispicular; moderate spongin	64–*100.0*–118 × 2.4–*4.2*–5.6	37–*46.5*–59
MNRJ 23911	Bahia, BR	Encrusting mounds, laterally ramified, beige	Isodictyal to isotropic, unispicular; moderate spongin	75–*108.1*–123 × 2.0–*3.9*–5.3	48–*52.4*–66 (n = 12)

Italic represents the mean value for each spicule type

laubenfelsi. A map of the currently known distribution of *H.* (*Re.*) *laubenfelsi* and a timeline of its records are presented in Fig. 6. Type locality: Moku o Lo‘e (Coconut Island, Kāne‘ohe Bay, O‘ahu Island, Hawai‘i, USA). The type locality is a man-modified structure within the lagoon (de Laubenfels 1950).

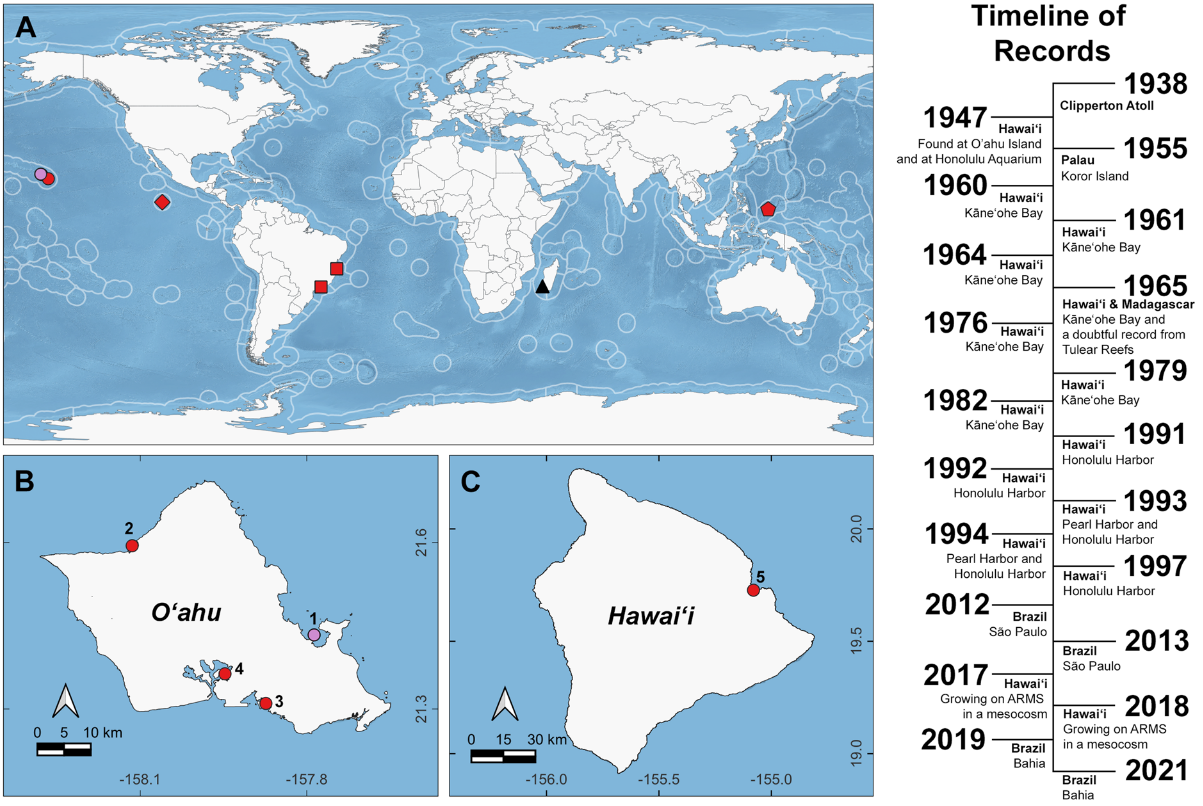

Fig. 6 Geographic distribution of *Haliclona* (*Reniera*) *laubenfelsi* van Soest & Hooper, 2020 and Timeline Chart with the records of the species globally. Global (**A**) and small-scale distribution of *H.* (*Re.*) *laubenfelsi* at O‘ahu (**B**) and at Hawai‘i (**C**) islands. Type locality is indicated by a violet circle. Black triangle indicates the doubtful record from Madagascar. Legends: violet and red circles = Hawai‘i Archipelago, red diamond = Clipperton Atoll, red pentagon = Palau, black triangle = Madagascar, red squares Brazil, 1 = Kāne‘ohe Bay, 2 = Waialua Bay, 3 = Honolulu Harbor, 4 = Pearl Harbor, 5 = Hilo. References used for timeline: Bergquist (1965), Coles (1997, 1999a, 2002), de Laubenfels (1950, 1951, 1954, 1957), Vacelet and Vasseur (1971), van Soest et al. (2011)

Discussion

Taxonomy

Haliclona (*Reniera*) *laubenfelsi* was originally described as *Toxadocia violacea* by de Laubenfels (1950) from Hawai‘i. Subsequent records were made for Micronesia (Bergquist 1965), Madagascar (Vacelet and Vasseur 1971) and Clipperton Atoll (van Soest et al. 2011). The record from Madagascar is considered doubtful given the black colour of the specimen which deviates from the typical coloration of *H.* (*Re.*) *laubenfelsi*. De Weerdt (2002) synonymized *Toxadocia* with *Haliclona (Reniera)*, but van Soest et al. (2011), in reporting *violacea* from Clipperton Atoll, preferred to classify it in *H. (Gellius)* instead. Curiously, this species was first collected in 1938 at Clipperton Atoll, but its presence there remained hidden until 2011 on a misidentification as *H. enamela* (de Laubenfels 1939; van Soest et al. 2011). Van Soest and Hooper (2020) noted the synonymy between *H. (G.) violacea* (de Laubenfels 1950) and *H.* (*H.*) *violacea* (Keller, 1883), and proposed to rename the junior synonym as *H.* (*G.*) *laubenfelsi*. In opposition to van Soest et al. (2011), we propose the assignment of this species to *H.* (*Reniera*), as the reticulation of small-sized oxeas (< 200 µm) is mainly isodictyal, suggesting a better allocation in the latter subgenus than in *H.* (*Gellius*), according to the *Systema Porifera* definitions (de Weerdt 2002).

Our specimens conform to the type material of *Haliclona* (*Reniera*) *laubenfelsi* in habit, skeleton, and shape and dimensions of the spicules. Morphological variability lies mainly in the color and in the skeletal architecture. Whereas the holotype was described to be vivid violet colored in life, the remaining specimens from Brazil and Hawai‘i are beige or pink. This color variability might be related to light exposure (Bergquist and Warne 1980; Fromont 1993; Cavalcanti et al. 2007; Calcinai et al. 2017), with specimens in sciophilous conditions showing a beige color and those who experienced increased light exposure showing pinkish hues. We could also observe that specimens from Hawai‘i (including the holotype) have less spongin content in their skeleton, creating a looser and more confused reticulation than that observed in specimens from Brazil, where the skeleton tends to be more regular and isodictyal. In addition, a specimen from Brazil also exhibits a few loose, pauci- to multispicular reinforcing tracts in its skeleton. Nevertheless, this is within this species' known intraspecific variability, as similar pauci—to multispicular tracts were also observed in conspecific Palau materials (Bergquist 1965). Similar variability on spongin and spicule density has been previously observed in other chalinid species (Jones 1987).

Another toxa-bearing species in the Pacific is *H.* (*Gellius*) *toxia* (Topsent 1897). Both species can develop similar shape, share the same spiculation and skeletal architecture, and may have a similar color (Topsent 1897; Desqueyroux-Faúndez 1981; Pulitzer-Finali 1993). Desqueyroux-Faúndez (1981) reported an isodictyal, seemingly mostly unispicular reticulation, with occasional 3–5 spicule-thick tracts in her Indonesian material of *toxia* (as *Toxadocia toxius*) which fits smoothly in *H. (Reniera)* as did *H. (Re.) laubenfelsi*. The only small apparent difference between both species lies in the dimensions of the oxeas, which are slightly longer in *H.* (*G.*) *toxia* (145–180 µm), while the longest oxea already reported for *H.* (*Re.*) *laubenfelsi* was 158 µm (Bergquist 1965). Nevertheless, usual common upper limits for the oxeas in *H.* (*Re.*) *laubenfelsi* are close to 130–140 µm (de Laubenfels 1950; this study). In addition, two Genbank sequences (Acc. # KU060457 and KU060458) (Erpenbeck et al. 2016) identified as *H.* (*Gellius*) *toxia*, from the Red Sea, nested in a close relationship with *H. (Re.) laubenfelsi* (Fig. 1), but their genetic divergence (*p*-distance 21–23%) and ASAP analysis indicate non-conspecificity. However, it is highly desirable to sequence topotypical materials of *H.* (*G.*) *toxia*, whose type locality is in Indonesia, in order to attest more confidently that both species are not synonymous.

Two other Hawaiian sponge species were assigned by Bergquist (1967, 1977) to the synonymy of *H.* (*Re.*) *laubenfelsi*: *Kaneohea poni* de Laubenfels, 1950 [currently *Phoriospongia poni* (de Laubenfels, 1950)] and *Neoadocia mokuoloe* de Laubenfels, 1950 [currently *Haliclona* (*Halichoclona*) *mokuoloe* (de Laubenfels, 1950)]. However, except for mentioning that type material was revised, no argumentation was provided in these papers that could support such a decision. These three species share similar colour, isodictyal skeleton, oxeas of the same size and the presence of raphidiform spicules. However, *N. mokuoloe* was revised in the *Systema Porifera* (de Weerdt 2002: 863), when the raphidiform spicules were not observed, and the species was allocated in *H.* (*Halichoclona*). This species is being redescribed based on Hawaiian material and there is genetical and morphological evidence that it is distinct from *H.* (*Re.*) *laubenfelsi* (Jan Vicente, in prep.).

On the other hand, at first glance, the lack of toxas and presence of sand incorporated in the skeleton of *K. poni* might distinguish this species from *H.* (*Re.*) *laubenfelsi*. Nevertheless, the presence of oxeas modified to styles or strongyles were also observed in Brazilian materials of *H.* (*Re.*) *laubenfelsi* and the rarity of toxas in some specimens (like ZUEC-POR 23) render both species similar in spiculation as well. The presence of sand in the choanosome of *Kaneohea poni* allowed a tentative allocation of this species in *Phoriospongia* (van Soest 2002: 524), presuming that oxeas were not endogenous. These inconsistencies, despite some evidence that *K. poni* could indeed be a junior synonym of *H.* (*Re.*) *laubenfelsi*, require previous reexamination of type material and collection of fresh specimens to establish this synonymy confidently. Thus, it is only tentatively that we follow the suggestions by Bergquist (1967, 1977).

The introduction of *H.* (*Re.*) *laubenfelsi* in Brazil and Hawai ‘i

In the present work, specimens of *H.* (*Re.*) *laubenfelsi* from Brazil and Hawai‘i are accurately identified using an integrative approach including morphological (oxeas, toxas and the skeleton architecture) and genetic data (high similarity of their 28S rDNA C-region sequences). This represents the first record of this species in the Atlantic Ocean. According to our data, it is not possible to recover the origin of this species, which hampers the recognition of where it was subsequently introduced in the Indo-Pacific. However, according to the nine criteria proposed by Chapman and Carlton (1994) to recognize alien species, we can infer that *H.* (*Re.*) *laubenfelsi* is exotic both in Brazil—where it is undergoing a process of local and regional dispersion—and in Hawai'i.

The species was absent in previous inventories carried out between 1997 and 2001 on the coast of São Paulo (Brazil) (Custódio and Hajdu 2011; Bispo et al. in prep.), which indicates that it arrived later at this location (Criterion 1—Previously Unknown in Local Region). Although its distribution in Brazil is confined to natural environments (rocky shores and sandstone reefs), the species was first collected there close to a large Brazilian port at São Sebastião (São Paulo State), suggesting fouling on vessels or marine structures as a possible vector of its introduction (Criterion 3—Human mechanisms of Introduction), likewise described for the scleractinean corals *Tubastraea* spp., the octocoral *Stragulum bicolor* van Ofwegen and Haddad 2011, and the ascidians *Pyura gangelion* (Savigny, 1816) and *Sidneioides peregrinus* Kremer et al. 2011 (Kremer et al. 2011; van Ofwegen and Haddad 2011; Capel et al. 2019; Skinner et al. 2019), also reported for the Brazilian coast.

The abundance of *H.* (*Re.*) *laubenfelsi* along the Brazilian coast still seems to be quite low. The species was first found in Brazil in 2012–2013 (São Paulo, two individuals), and then in 2019 (Bahia, one individual) and lastly in 2021 (Bahia, three individuals). Despite a significant sampling effort aiming at a faunistic inventory of the area in 2019 (Bettcher et al. 2023), the species was found only in one location, while in 2021 it was observed in two locations (Criterion 2—Post-introduction Range Expansion). Embryos were observed in one of the specimens collected in 2021, which indicates that sexual reproduction is playing a role in the establishment of the species there. It is unlikely that the species dispersed naturally or by rafting from São Paulo (São Sebastião, 23 °S) to Bahia (Porto Seguro, 16 °S)—1300 km apart—as the Brazilian current, main current system acting in the region, flows southwards (Stramma and England 1999) in opposite route of the hypothetical species dispersion. The lack of a port in Porto Seguro also weakens fouling on ship hulls as a vector for the arrival of the species there. On the other hand, it is possible that an independent arrival occurred in the port of Ilhéus, only 200 km north of Porto Se-guro, followed by a local expansion southwards, where the species found several intertidal reefs naturally disturbed by coastal run-off, salinity and water temperature fluctuations, air exposure during low tides, etc. (Leão et al. 2016). Such a disturbed habitat may facilitate the establishment of exotic species (Altman and Whitlatch 2007; Bugnot et al. 2016).

There is also strong evidence that *H.* (*Re.*) *laubenfelsi* is exotic (pseudoindigenous) in Hawai'i according to the Chapman and Carlton (1994) criteria. The Hawaiian archipelago was once characterized as being the centre of maritime traffic and biological invasions in the Pacific Ocean (Carlton 1987; Coles et al. 1999b; Coles 2006; Concepcion et al. 2010) and there are many native Indo-Pacific species that were later introduced there, such as *Mycale* (*M.*) *grandis* (Coles et al. 2007). The same is true for other benthic invertebrates, as the octocoral *Carijoa riisei* (Grigg 2003). The most comprehensive surveys (Carlton and Eldredge 2009, 2015; Pons et al. 2017) indicated that from the 141 sponge species reported for Hawai'i, 63 are considered invasive or cryptogenic. In addition, a large proportion of the biota in Kāne'ohe Bay is recognized as non-indigenous (Coles et al. 2002) (Criterion 4—Association with Known Introductions).

Although the original description of *H.* (*Re.*) *laubenfelsi* mentions the presence of this species on dead corals along Kāne'ohe Bay, its type specimen was collected in 1947 on man-made structures of Hawaii Institute of Marine Biology at O'ahu (Hawai'i) (de Laubenfels 1950). We observed that this species has great affinity for artificial substrates, such as the concrete walls of an aquarium tank in Honolulu (de Laubenfels 1954) or the PVC plates of ARMS where they were collected in 2016–2018 at Kāne'ohe Bay (Vicente et al. 2022a) (Criterion 5—Association with Artificial or Altered Environments). A temporal study of the cryptic sponge community in Kāne'ohe Bay consistently found *H.* (*Re.*) *laubenfelsi* on mesocosm ARMS, but absent on reef ARMS during a two year monitoring period. Another recent effort to describe sponge fauna from Kāne'ohe Bay failed in finding *H.* (*Re.*) *laubenfelsi* in natural habitats as well (Pons et al. 2017) and the last record of this species in natural habitats of Kāne'ohe Bay was made in 1982, about 40 years ago (Bigger et al. 1983). Vicente et al. (2022b) attribute community differences between mesocosm and reef ARMS to different stages of ecological succession where sponges in mesocosm ARMS resemble early colonizers, and those on reef environments resemble the climax community of the reef. The ease of colonizing artificial environments, such as ARMS in mesocosms, may indicate that the species is cryptobenthic or that it has invasive potential. The hypothesis of a strict cryptobenthic habit is weakened as previous reports describe it as a photophilic species abundant on the upper reef (Bigger et al. 1983).

Similarly to many other invasions on Hawai'i, *H.* (*Re.*) *laubenfelsi* is mainly restricted to sheltered sites and harbor vicinities at O'ahu Island, like Kāne'ohe Bay (de Laubenfels 1950; Coles et al. 2002), Pearl Harbor (Coles et al. 1997) and Honolulu Harbor (Coles et al. 1999a). This indicates that this species is not widespread along the archipelago (Criterion 6—Discontinuos or Restricted Regional Distribution) and that it has a great affinity with areas associated with exotic species, like harbors (Criterion 3—Human mechanisms of Introduction). Exceptions for this pattern are the single records at Waialua Bay (O'ahu Island) (de Laubenfels 1957) and at Hilo (Hawai'i Island) (de Laubenfels 1950), which might represent a local expansion after an initial event of introduction in Kāne'ohe Bay, or even independent arrivals of this species in the archipelago.

The species has a postulated distribution including the Pacific, Indian and Atlantic oceans, but with disjunct records (Criterion 7—Disjunct Global Distribution). This is in marked contrast to the expected low dispersal ability of most sponges, a consequence of their short-lived larvae (Maldonado 2006). For example, in *Haliclona* (*Gellius*) *amboinensis* (Lévi, 1961) and *H.* (*Soestella*) *xena* de Weerdt, 1986, larval settlements can occur in approximately 2 h after larval release into the water column (Wapstra and van Soest 1987; Nada et al. 2020). In *H.* (*Rhizoniera*) *indistincta* (Bowerbank, 1866), the larval settlement may take longer (at least 25h, Stephens et al. 2013). This timeframe is still considered a short time, insufficient for transoceanic dispersal, except if juvenile sponges have attached to any sort of floating substrate. Thus, sponges and associated larvae have "difficulty" carrying out long-distance dispersion or withstanding survival in ballast water (Carlton and Geller 1993) (Criterion 8—Insufficient Life History Adaptations for Global Dispersal). Rafting could have played a role in the spread of *H.* (*Re.*) *laubenfelsi* within the Indo-Pacific, and this might explain the long-range dispersal of the sponge *Terpios hoshinota* in the Indo-Pacific (Chow et al. 2022) and of the red algae *Chondrus retortus* K.Matsumoto & S.Shimada, 2013 from Japan to Hawaii (Kittle et al. 2023). However, it is impossible to explain the introduction of *H.* (*Re.*) *laubenfelsi* in the Atlantic through natural passive dispersal mechanisms, such as rafting on biological or artificial substrata or even on pumice. For instance, the longest known dispersion by rafting in anthropogenic debris reached about 7000km following the Great Japan Earthquake in 2011, and it was restricted to the Pacific Ocean (Carlton et al. 2017; Elvin et al. 2018). Furthermore, rafting on pumice is a phenomenon mainly restricted to areas of high volcanic activity, like the Southwest Pacific and the Iceland shelf (Bryan et al. 2012; Larsen et al. 2014). However, ocean currents make it unlikely that volcanic pumice originating in the SW Pacific will reach the Atlantic.

Therefore, we hypothesize that *H.* (*Re.*) *laubenfelsi* has an Indo-Pacific origin and was ship-mediated introduced to Hawai'i. This archipelago stands out as the major receiver area of introduced species coming from several points of the Pacific. Main donors are the Northwest Pacific, French Polynesia, the Mariana Islands, and the Central Indo-Pacific (Carlton 1987). The presence of this species in Palau, more than 7000km apart from Hawai'i, strengthens this hypothesis. On the other hand, introduction in the Atlantic could have occurred either from Hawai'i or elsewhere in the Indo-Pacific also via ship hull. The routes of introduction of this species should be tested in future studies with wider geographic sampling and using microsatellite markers or next-generation sequencing (Rius et al. 2015; Cristescu 2016; Cavalcanti et al. 2020; Cóndor-Luján et al. 2021).

The Brazilian coast is facing a plethora of new arrivals of exotic species (Teixeira and Creed 2020; Soares et al. 2022) that is to some extent comparable to what Hawai'i faced during the World War II. These arrivals are modifying the community structure of several benthic ecosystems, like coralline reefs and rocky shores (Carvalho-Junior et al. 2023; Lolis et al. 2023). Despite that, only four alien or cryptogenic sponge species have been recognized in Brazil so far, all of them pertaining to the Calcarea (Cavalcanti et al. 2020; Klautau et al. 2020), contrasting with the 56 cryptogenic and seven exotic sponges already reported from Hawai'i (Pons et al. 2017). The number of exotic non-indigenous sponge species in Brazil is also discrepant from the number of exotic species of other benthic taxa, like corals (van Ofwegen and Haddad 2011; Mantelatto et al. 2018; Carpinelli et al. 2020; Menezes et al. 2021; Dutra et al. 2023), ascidians (Kremer et al. 2011; Rocha et al. 2019; Skinner et al. 2019) and bryozoans (Farrapeira et al. 2011; Miranda et al. 2018; López-Gappa et al. 2010), which suggests that the number of alien sponge species is underestimated.

The Wallacean shortfall and the challenging taxonomy of Porifera are certainly key factors limiting the recognition of exotic sponge species everywhere. Such pitfalls are easily overcome using an integrative taxonomic framework, as was the case of *H. perlevis*, *P. magna*, *H. glomerosa* and now *H.* (*Re.*) *laubenfelsi*. Otherwise, if the present assessment had been based only on morphological data *H.* (*Re.*) *laubenfelsi* would have been described as a new species native to the Brazilian coast, and its exotic nature both in Brazil and Hawai'i would remain hidden for more years or decades, a classic example of pseudoindigenous species. Thus, we strongly recommend the integration of morphological and molecular analyses in the taxonomy of Porifera, especially on speciose genera with a meagre set of taxonomically informative morphological features, such as *Haliclona*.

While *Haliclona* (*Re.*) *laubenfelsi* appears to be in the beginning of an expansion process along the Brazilian coast, it is still lacking a robust assessment of its possible invasiveness and efforts should be made to fill this gap, as already done for other sponge species (Pérez et al. 2006; Coles et al. 2007; Ávila and Carballo 2009; Henkel and Janussen 2011; Rossi et al. 2015; Turicchia et al. 2018). We strongly recommend monitoring its abundance, reproductive biology, spatial distribution, and biotic interactions at the sites where this species occurs both in Brazil and Hawai'i. Such studies are essential to delineate strategies to cope with this and other alien sponge species. Still, the species now counts with a comprehensive description showing its phenotypic plasticity, and DNA sequences can be generated from newly collected samples of similar morphology, enhancing traceability during *H.* (*Re.*) *laubenfelsi*'s spread process.

Acknowledgements Drs. Cristiana Castello Branco, Júlio C.C. Fernandez, Camille V. Leal, Marianela Gastaldi and Sula Salani, M.Sc. Aline G. Fioravanso and Dora M.B. Leite, undergrads Clara M.R. Goulart, Daniela S. França, Dafinny R. Batista, Dhara Avelino-Alves and Pedro H.B. Clerier are warmly thanked for their help with field and lab work. We are thankful to the Curatorial staff from studied collections: Dr. Michela Borges (ZUEC) for providing access to samples from São Paulo state; Dr. Allen Collins and Abigail Reft (USNM) for providing access to the type material of *H. laubenfelsi*; Dr. Gustav Paulay (FLMNH), Amanda Bemis (FLMNH) and Holly Bolick (BPBM) for helping us obtaining voucher museum specimens of Hawaiian material. We are thankful to the editor, Dr James T. Carlton, and two anonymous reviewers for all the comments and suggestions made, allowing a significant improvement of the text. Drs. Jean Vacelet and Alexander Ereskovsky (Station Marine d'Endoume, Aix-Marseille Université) are thanked for helping us interpret the embryos present in MNRJ 20478. Dr. Robert J. Toonen is thanked for providing lab space for molecular and taxonomic work at the Hawai'i Institute of Marine Biology. This is HIMB 1963 and SOEST 11828 contribution numbers.

Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by A Bispo, Larissa Bettcher, Eduardo Hajdu, Jan Vicente and Emily Rutskoswki. The first draft of the manuscript was written by Larissa Bettcher and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Funding for the work in Brazil was provided by CAPES and CNPq fellowships (Postdoctoral Fellowship #152552/2022-7 to AB), Research Productivity fellowship #310914/2021-3 to UP, and #308303/2017-2 to EH) and grants of the programs EntreMares (CAPES, #88887.469843/2019-00), Universal (CNPq, #425839/2016-8 to EH), Cientista do Nosso Estado (FAPERJ, #E-26/202.624/2019, #E-26/200.534/2023, both to EH) and Projeto Temático (FAPESP #2019/17721-9 to Prof. Dr. R.G.S. Berlinck). Funding for the work in Hawai'i was provided by an NSF Postdoctoral Research Fellowship in Biology (#1612307), NSF awards OA#1416889 and OCE# 2048457, and by the National Oceanic and Atmospheric Administration's Ocean Acidification Program (#60046834).

Data availability All data generated or analyzed during this study are included in this published article and its Supplementary Information files. The sequences of *Haliclona* (*Reniera*) *laubenfelsi* generated and analysed during the current study are

available in the GenBank repository under accession numbers: OR229997–OR230000; MW016137–MW016139.

Declarations

Competing interest The authors have no relevant financial or non-financial interests to disclose.

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