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Expanded distribution and a new genus for rock-inhabiting sea pens (Cnidaria, Anthozoa, Octocorallia, Pennatuloidea)

UPASANA GANGULY[1]* & SCOTT C. FRANCE[2]
[1]*Department of Biology, University of Louisiana at Lafayette, Louisiana, USA 70504*
[2] *scott.france@louisiana.edu;* *https://orcid.org/0000-0002-2114-5968*
**Corresponding author:* *upasana.ganguly05@gmail.com;* *https://orcid.org/0000-0002-0128-6835*

Abstract

Sea pens (Superfamily Pennatuloidea) are a specialized group of octocorals that evolved to live embedded in a soft-sedimented seafloor using their peduncles as anchors. Rock-inhabiting sea pens ("rock pens") were first described in 2011; their peduncle is modified into a suction cup-like structure that allows them to attach onto the surface of hard substrates, an adaptation previously unknown in sea pens. There are currently four species that have been identified as rock pens based on their peduncular morphology: three of these are in the genus *Anthoptilum* (Anthoptilidae), and one in the genus *Calibelemnon* (Scleroptilidae). Herein, we explore the geographic distribution and depth ranges of rock pens using observations from remotely operated vehicles and investigate the evolutionary origins of the rock pens. We present a phylogenomic study of sea pens, based on DNA sequences from hundreds of ultraconserved elements (UCE) and compare these trees to those constructed using mitochondrial gene regions. Our results show that the ancestral sea pen had a typical elongated peduncle. The adaptation to attach onto hard, rocky substrates using the special suction cup-like peduncle evolved along a single derived lineage that is sister to a lineage comprising the genus *Anthoptilum*. We propose all known rock pen species be grouped into a single new genus, described herein, in the family Anthoptilidae, to reflect the phylogenetic history.

Key words: rock pens, Anthoptilidae, phylogenetics, deep sea, Ultra-conserved Elements (UCE), mitogenome

1 Introduction

Octocorals are colonial, sessile marine invertebrates that are morphologically highly diverse. Among them, the sea pens are a specialized group that is sufficiently distinct to have been formerly classified in their own Order (Pennatulacea), though they are now recognized as the Superfamily Pennatuloidea (Mcfadden *et al.*, 2022). Sea pens comprise a single primary polyp, or the oozooid, that forms the main structure or the central axis and gives rise to secondary polyps on the distal part of that axis (the rachis) (Kükenthal & Schulze, 1915). The secondary polyps arise directly from tissue of the rachis or from secondary leaf or lobe-like structures that extend from the rachis. The basal part of the primary polyp forms an inflatable, muscular, elongated structure called the peduncle, with which the colony anchors itself into soft sediments (Williams, 1990, 1995, 2011).

In 2011, Williams and Alderslade (2011) described three new species of sea pens with the peduncle modified into a suction-cup like structure that allows them to attach to hard-rock substrata. These sea pens have been referred to as rock-inhabiting sea pens, or rock pens. At the time of the 2011 publication, rock pens were known from only 9 specimens. Of these, 3 were identified as *Anthoptilum lithophilum*, four as *Anthoptilum gowlettholmesae*, and one as *Calibelemnon francei*. The ninth specimen remains unidentified. The authors also designated another sea pen from the Indian Ocean, *Anthoptilum decipiens* Thompson & Henderson, 1906, as a rock pen based on its written description. There are no published records of rock-inhabiting sea pens since Williams and Alderslade (2011). Thus, our current knowledge suggests there are four species of rock pens[1]: three in the genus *Anthoptilum*, Family Anthoptilidae, and one in genus *Calibelemnon*, family Scleroptilidae. *Calibelemnon francei* is the only rock pen

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[1] While this paper was in manuscript review, a description of a fifth species of rock pen, *Anthoptilum gnome*, from Japan, was published by Kushida *et al.* (2024)

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known from the Atlantic Ocean; all the *Anthoptilum* rock pens were collected from Pacific Ocean and Indian Ocean. However, in recent years, many rock pen colonies have been observed *in situ* during deep-sea expeditions in both the Pacific and Atlantic Oceans and several additional collections have been made.

The aims of this study were to:

1. provide a more complete understanding of geographical distribution and depth range of rock pens based on *in situ* observations from remotely operated vehicle (ROV) video.
2. investigate the evolutionary history of the rock pens using molecular phylogenetics to determine the number of times this novel trait evolved among Pennatuloidea.

2 Methods

The NOAA Ship *Okeanos Explorer* deploys remotely operated vehicles (ROVs) to record high-definition video from the unexplored and under-explored deep sea, capturing high-quality observations from under-sampled habitats (Kennedy *et al.*, 2019). Annotated videos are available via the Ocean Networks Canada annotation platform SeaTube (Kennedy *et al.*, 2019). We used SeaTube to view, search and analyse videos from 216 dives from 16 expeditions from 2015 to 2023 from observations of rock pen colonies. Metadata associated with these observations, such as location and depth, were extracted and plotted using R-studio.

Several rock pen colonies have been collected since the 2011 study. We acquired tissue samples from 17 rock pen colonies including type specimens of three of the four described species. (Table 1). To place the rock pens into evolutionary context of all sea pens, we sampled tissues from across all known families of sea pens for genetic analyses. Most sea pen tissue samples used in this study were acquired from the collections of Smithsonian Institution's National Museum of Natural History (NMNH), California Academy of Sciences (CAS) and Harvard University's Museum of Comparative Zoology (MCZ). These include the type specimens of the rock pen species and the rock pen colonies collected during the NOAA Ship *Okeanos Explorer* expeditions, *E/V Nautilus* NA137 expedition and the two rock pen colonies collected by SCF during the *R/V Falkor* Deep Coral Diversity at Emperor Seamount Chain 2019 expedition.

Genomic DNA was extracted from tissue samples following a modified CTAB-chloroform protocol (France *et al.*, 1996). The 5' end of the mitochondrial protein-coding gene *mtMutS* was amplified by polymerase chain reactions using primers ND4L2475F (Brugler & France, 2008), ND42599F (France & Hoover, 2002), Mut3010F, CO3bam5657F (Brugler & France, 2008) and Mut3458R (Sánchez *et al.*, 2003). Positive PCR products were cleaned using Exonuclease I (Fermentas) and FastAP Thermosensitive Alkaline Phosphatase (Fermentas) (Werle *et al.*, 1994) and sent to Eurofins Genomics for Sanger sequencing. Sequences from both directions of the amplicon were cleaned and edited on Geneious Prime and then the *mtMutS* regions were aligned using MUSCLE (Edgar, 2004) on the same software. A sequence (GenBank accession number DQ302864) from an ellisellid species, the sister taxon to Pennatuloidea, was downloaded from GenBank and used as an outgroup for this dataset.

We obtained a broader survey of the genome for a subset of the samples using a UCE bait capture method (Faircloth, 2016). Genomic DNA was quantified using the Invitrogen Qubit™ dsDNA BR assay kit on an Invitrogen Qubit™ 4 Fluorometer, and 1000ng of DNA from each specimen was sent to Arbor Biosciences for processing. UCE baits designed specific to octocorals ("octo-V2 bait set" Erickson *et al.*, 2021) were used to generate the data. The bait set currently has 30,000 baits around 3000 loci. Fragments were sequenced on an Illumina NovaSeq 6000 platform.

For analysis of UCE data, the FASTQ files were processed using PHYLUCE workflow (Faircloth, 2016) running on the Louisiana Optical Network Interface (LONI) High Performance Computing cluster. PHYLUCE is an open-source Python package developed for cleaning, assembling and aligning data collected from UCE experiments. Steps in the workflow included removing the adapters from the raw untrimmed reads using Illumiprocessor (Faircloth, 2016); assembling the cleaned reads using Spades (Bankevich *et al.*, 2012); extracting the UCE loci and aligning and trimming them using MAFFT (Katoh & Standley, 2013) and GBlocks (Talavera & Castresana, 2007) respectively. The aligned data were viewed and checked on Geneious Prime version 2022.2.2 prior to downstream phylogenetic analyses.

Phylogenetic analyses were done separately for the *mtMutS* sequences and the UCE dataset. Both Maximum Likelihood (ML) (Steel & Penny, 2000) and Bayesian Inference (BI) trees (Alfaro & Holder, 2006) were built for the two datasets. For the *mtMutS* data, the ML and BI trees were constructed using RAxML and MrBayes on

CIPRES (Miller *et al.*, 2011) after selecting for correct models of evolution (GTR+I+G in both cases). The UCE dataset was analysed on ExaBayes (Aberer *et al.*, 2014) for BI trees, on RAxML for ML trees, and on ASTRAL (Mirarab *et al.*, 2014) for species tree. All the tree files were viewed on FigTree.

Rock pen sample ANN1141 was selected for sequencing the whole mitogenome. Total genomic DNA was sent to Novogene Corporation Inc. for library preparation and sequencing on Illumina NovaSeq (150 PE). Adapters were trimmed from the reads using Geneious Prime version 2022.2.2 and subsequently assembled on LONI using NOVOPlasty 4.3.1 (Dierckxsens *et al.*, 2017). Sequences of protein-coding genes from *Anthoptilum grandiflorum* (GenBank accession number NC044086) were used as seed sequences on NOVOPlasty. The mitogenome (GenBank accession number PP960129) was annotated in Geneious Prime using reference sequences downloaded from GenBank.

2.1 Abbreviations of museum collections

CAS	California Academy of Sciences
MCZ	Harvard University's Museum of Comparative Zoology
USNM	Smithsonian Institution's National Museum of Natural History

3 Results

3.1 Distribution of rock pens

On most ROV dives where we encountered rock pens, we observed individual colonies in a single frame of view and only 1 to 2 colonies across the entire dive (Fig. 1). However, there were two dives when rock pens were observed in very high density (thousands of colonies); both dives were in the central Pacific Ocean. The first instance was during NOAA Ship *Okeanos Explorer* EX1504L4, Dive 2 on the southwest slope of the island Ni'ihau. On this dive, a field of rock pens was observed at an average depth of 417 m, over a distance of ≈51 m. Another smaller field of rock pens was observed during NOAA Ship *Okeanos Explorer* EX1606 Dive 11 on Wake Atoll at depth of ≈472 m, along a distance of ≈21 m and spanning a depth range of ≈22.5 m (Fig. 2). Typically rock pens are observed in a frequency of 1 or 2 colonies per dive. On EX1606 Dive 11, as the ROV climbed the slope below the field, rock pen occurrences increased significantly. This gradually led to the dense field of rock pens, and a higher-than-normal abundance of rock pens further continued for some distance after the field as the ROV continued its ascent.

In our dataset, the two fields of rock pens have been denoted by single data points for each dive, representing the thousands of rock pens observed in these two areas. Additionally, two data points have been used to represent the high abundance of rock pens leading up to the field and continuing after the field during EX1606 Dive 11 (Supplemental Table 1 has the start and end points of the fields listed). Thus, we have 217 events of rock pen observations; 208 of these are new records of rock pen colonies. We have *in situ* imagery of 204 of 208 observations from our review of ROV videos; the remaining 4 come from museum collections that lacked *in situ* imagery. 14 new physical collections of rock pen colonies have been added to the collections since 2011. Our new observations come from both the Pacific (n=199) and the Atlantic (n=16) Oceans (Fig. 3). We did not have access to any expedition video from the Indian Ocean or polar regions.

The vertical distribution of rock pen observations extended from 368 m to deeper than 3500 m (Fig. 4). More specifically, rock pens were observed from 368 m to 2445 m in the Pacific Ocean and between 1060 m to 2000 m in the Atlantic Ocean. In 2021 we found 4 colonies at depth greater than 3780 m on Asterina Seamount in the North Atlantic (*Okeanos Explorer* EX2104, dive 18), with the deepest observed rock pen colony being recorded at 3788.6 m.

3.2 Phylogenetic analysis

The UCE data set included representatives from 14 of the 16 currently described sea pen families. Similar topologies were recovered in concatenated ML, 75p ML, 50p ML, concatenated Bayesian, 75p Bayesian, 50p BI and species trees. For the purposes of this project on the rock pens, here we show the 75p BI tree (Fig. 5); we will discuss details of phylogenetic relationships among other sea pen taxa in a later publication.

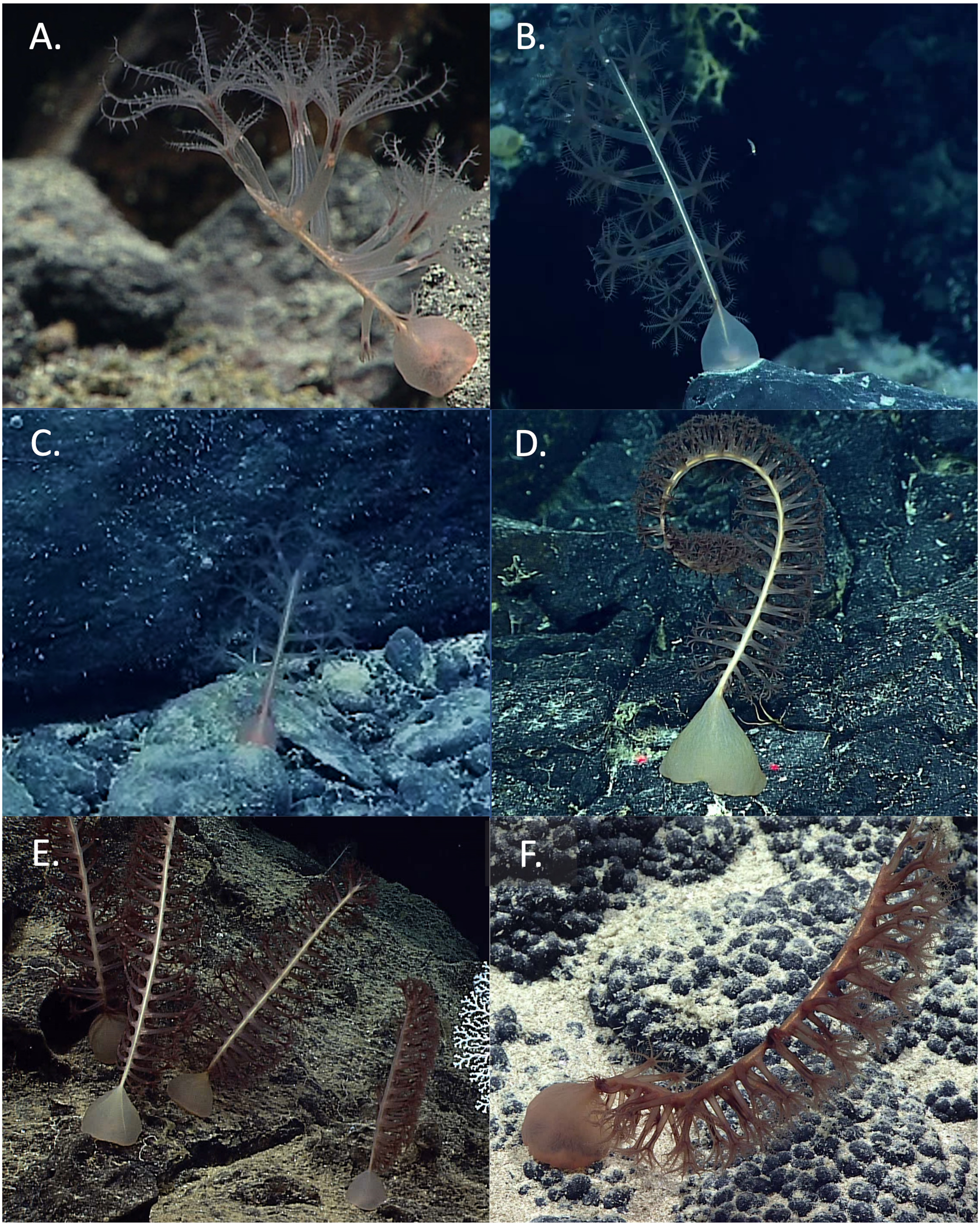

FIGURE 1. Images of rock pen colonies from various depths and locations. A. EX1605L3 Dive 15, Central North Pacific, 1872.6 m depth; B. EX2107 Dive 05, Western North Atlantic, 1392 m depth; C. EX2104 Dive 18, Western North Atlantic, 3788.5 m depth, one of the deepest observed colonies to date; D. EX1605L1 Dive 01, Eastern North Pacific, 595.8 m depth; E. EX1504L4 Dive 02, Central North Pacific, 418.9 m depth; F. EX1706 Dive 13, Central North Pacific, 1515.1 m depth. Images courtesy of NOAA Ocean Exploration.

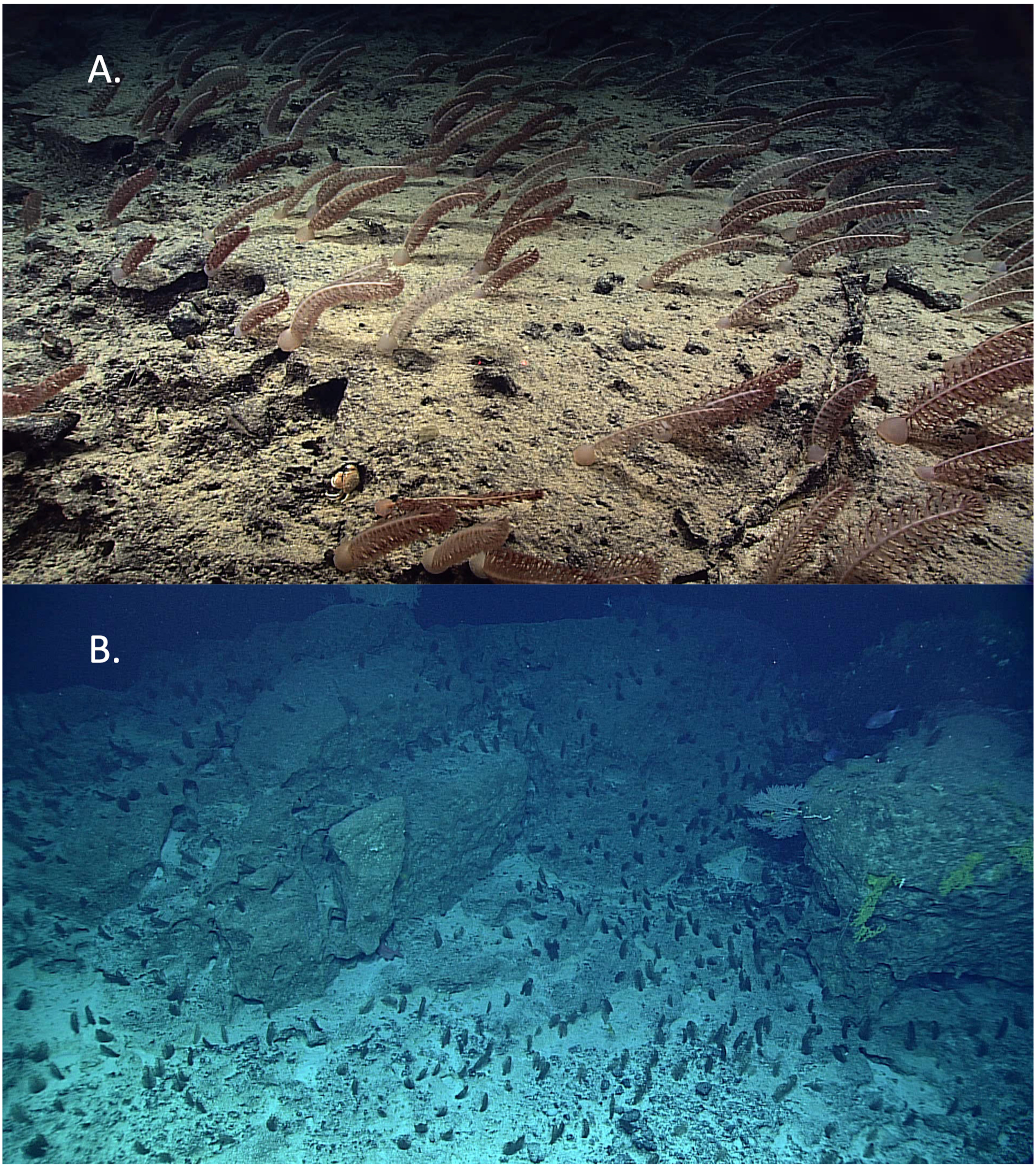

FIGURE 2. Images of rock pen fields observed during NOAA Ship *Okeanos Explorer* expedition in the Pacific Ocean. A. Rock pen field observed during EX1504L4 Dive 02; B. Rock pen filed observed during EX1606 Dive 11. Images courtesy of NOAA Ocean Exploration.

All our phylogenies recovered the rock pens to a single monophyletic clade. The rock pen clade is sister to a clade of typical, sediment-dwelling *Anthoptilum* species, namely *Anthoptilum grandiflorum* (Verrill, 1879) and *Anthoptilum murrayi* Kölliker, 1880). For example, on the 75p BI tree (Fig. 5), rock pens cluster with members of the family Anthoptilidae on a monophyletic clade (A) with high support (PP=1). Clade A is sister to a clade (B) comprising a mixture of taxa from 3 families, including a typical sediment-dwelling *Calibelemnon* Nutting, 1908 (family Scleroptilidae), *i.e.* not a rock pen. Within clade A, the rock pens form a well-supported sub-clade (PP=1) (A1) sister to non-rock pen *Anthoptilum* specimens (A2). The rock pen *Calibelemnon francei* (family Scleroptilidae) is also placed within clade A1. The rock pen clade includes the sequences of the holotype of *Calibelemnon francei* and the paratypes of *Anthoptilum gowlettholmesae* and *Anthoptilum lithophilum*.

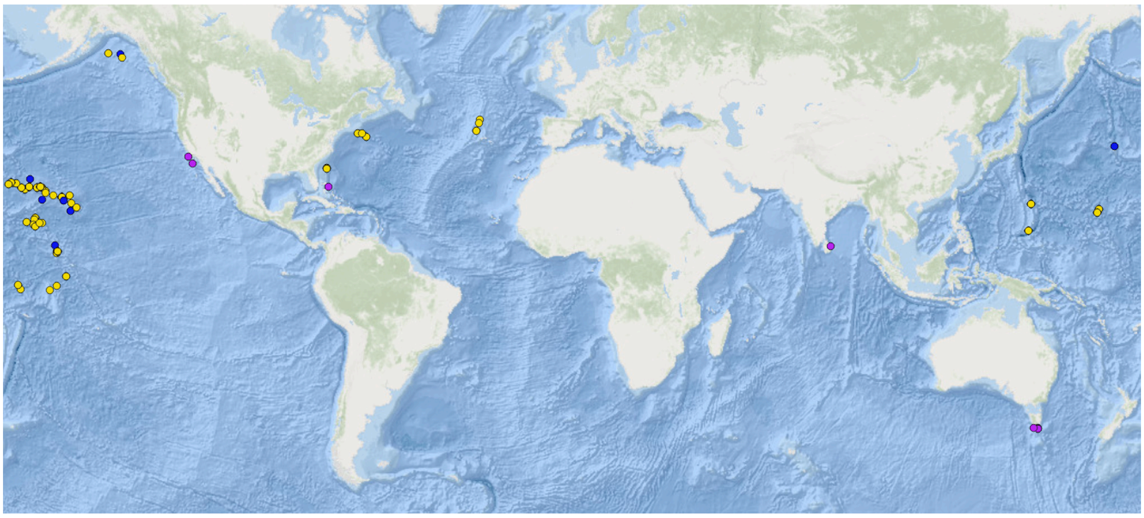

FIGURE 3. Map displaying the locations of rock pens observed (and collected) by ROV. Symbol colours represent the type of observation: purple for the specimens included in Williams and Alderslade (2011), yellow for visual-only, and blue for collected samples.

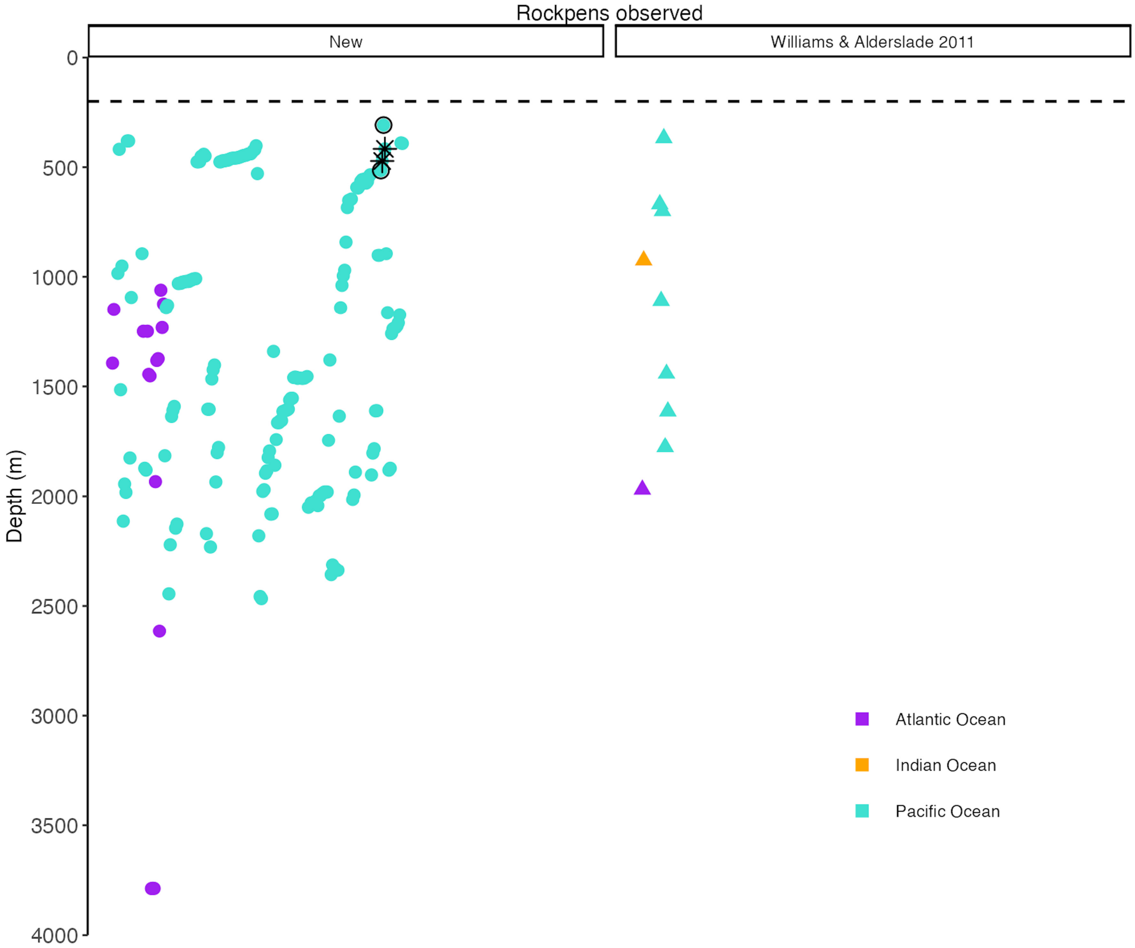

FIGURE 4. Plot showing the depth range of rock pens observed (and collected) by ROV, colour-coded by ocean. Rock pens originally reported by Williams and Alderslade (2011) have been indicated by triangles. The two rock pen fields observed at depths 417m and 472m during the NOAA Ship *Okeanos Explorer* expeditions EX1505L4 Dive 02 and EX1606 Dive 11, respectively, in the Pacific Ocean have been denoted by the * symbols. The high-density occurrences of rock pens leading up to the field in EX1606 Dive11 and away from it have been pointed out by circled dots.

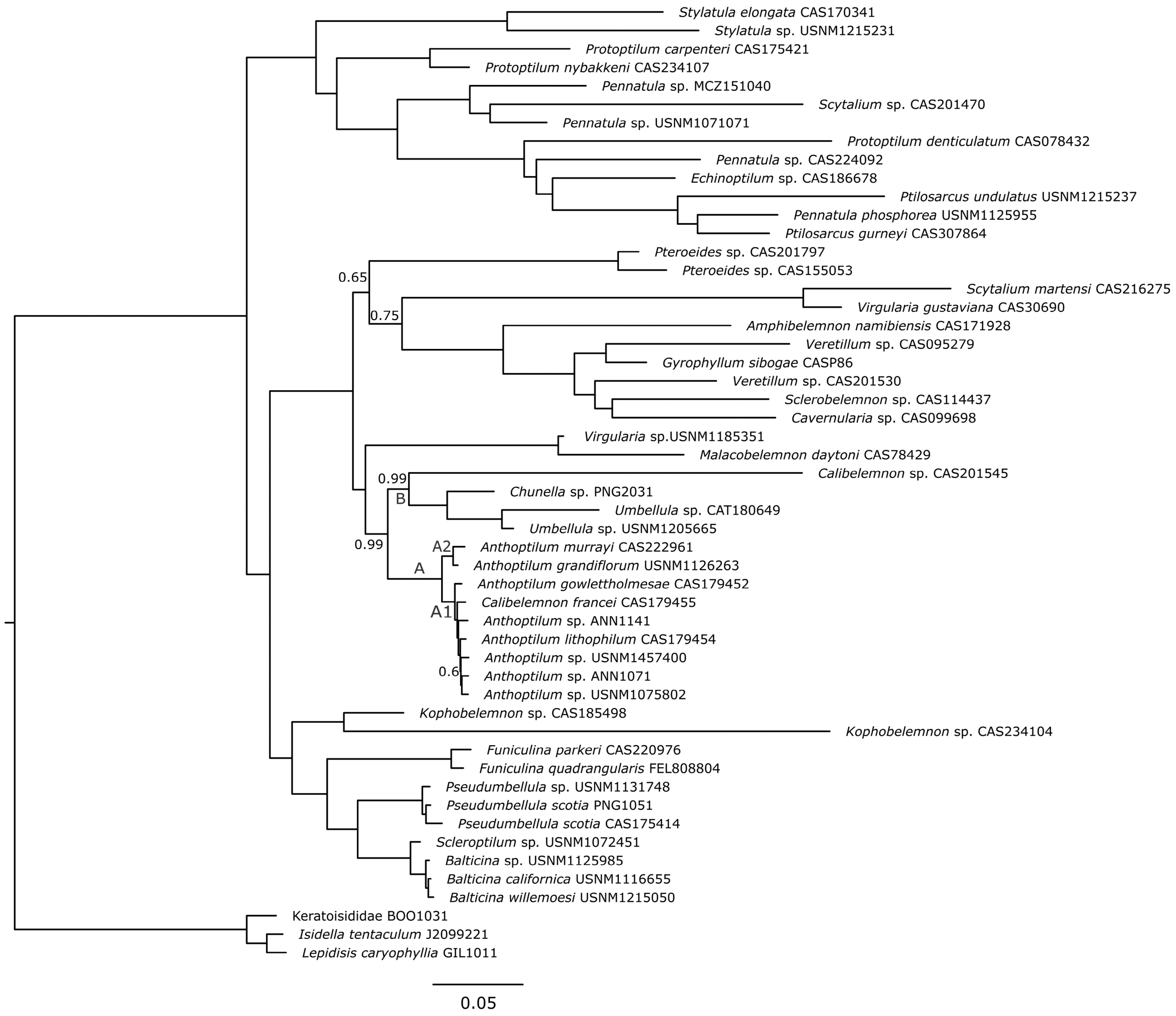

FIGURE 5. Bayesian Inference tree of sea pens based on 75p UCE data set. This tree shows that all the rock pens cluster to form a well-supported monophyletic clade with high support sister to the non-rock pen *Anthoptilum* taxa. Posterior probability (PP) values are indicated at the nodes. PP=1 at all nodes unless indicated otherwise. The names of the taxa on the tree represent identifications based on the most recent phylogenies.

Our findings from the *mtMutS* data with respect to rock pens are congruent with the results of the UCE analyses (Fig. 6). This dataset has sequences from a greater number of rock pen samples than the UCE dataset and includes sequences from the paratype of *Anthoptilum gowlettholmesae* and holotypes of the other two species. As with the UCE trees, rock pens consistently form monophyletic clades in both ML and BI phylogenies. In Fig 6, within clade A, the rock pen clade (A1) is sister to *Anthoptilum grandiflorum* and *Anthoptilum murray* (PP=0.99). *Calibelemnon francei* groups in the same clade as the other *Anthoptilum* rock pen specimens. Clade A is sister to clade B (PP=0.96), which includes a sediment-dwelling non-rock pen *Calibelemnon* sp., representatives of genus *Umbellula* and *Chunella* sp.

Hogan *et al.* (2019) reported *Anthoptilum grandiflorum* to have a different mitochondrial gene order (Octocoral gene order B) compared to other sea pens. Our PCR results for *mtMutS* support that *Anthoptilum murrayi* and all the rock pens may have Octocoral gene order B, *e.g.* primers spanning genes *cox*3 to *mtMutS* are required for amplification. To further verify, we sequenced the whole mitochondrial genome for ANN1141 and confirmed that this rock pen has the same gene complement and arrangement as Octocoral gene order B (Fig.7). PCR results for the non-rock pen *Calibelemnon* sp. sample support presence of Octocoral gene order A in this taxon as *NAD4L* is upstream of *mtMutS*.

Our phylogenetic results support the separation of rock pens into a new genus to distinguish them from their sister taxon, *Anthoptilum*, which have the sediment-dwelling habitus typical of sea pens.

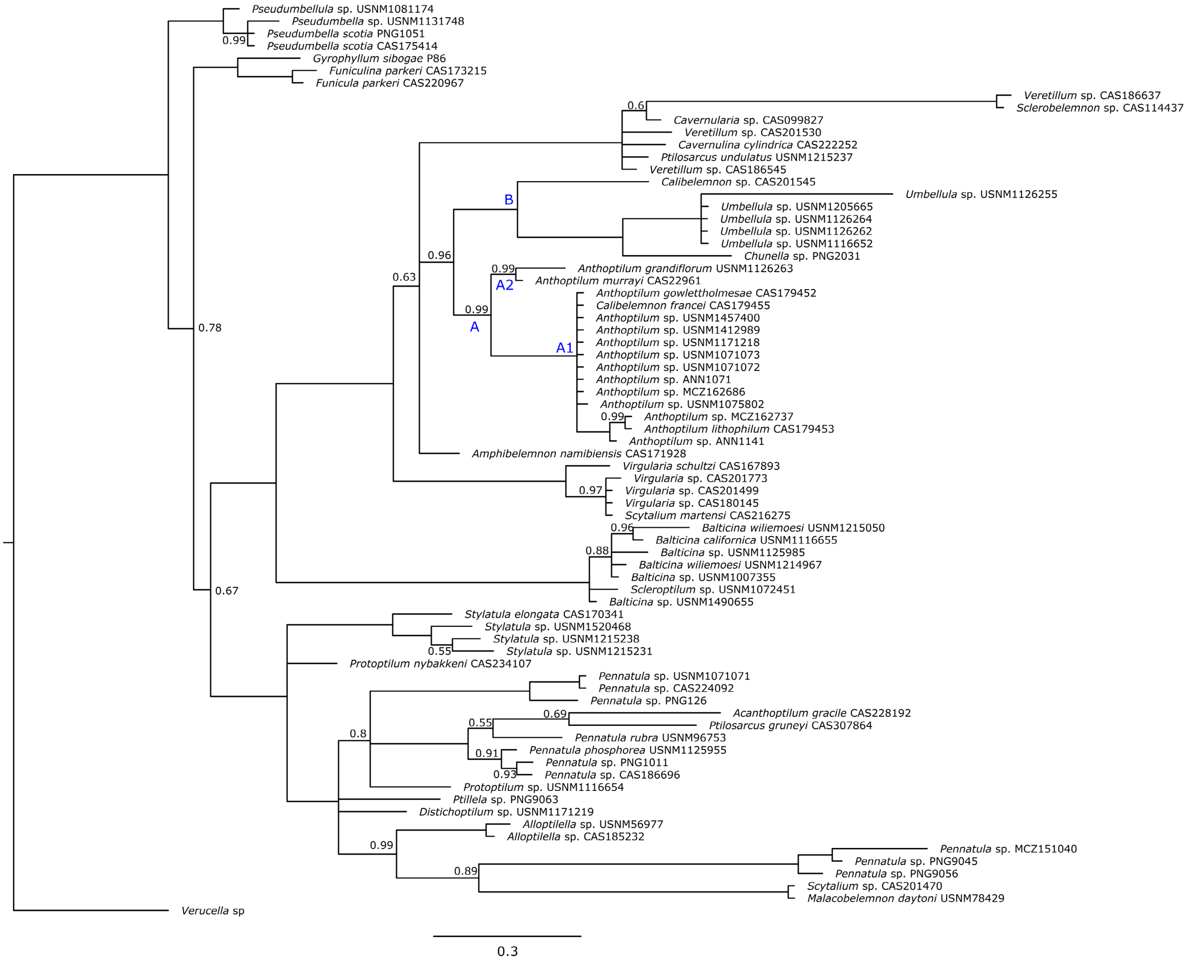

FIGURE 6. Bayesian Inference tree of sea pens based on *mtMutS* gene region. The tree shows monophyly of the rock pens (A1) and their relative position with respect to non-rock pen sea pens. Posterior probability (PP) values are indicated at the nodes. PP=1 at all nodes unless indicated otherwise. The names of the taxa on the tree represent the latest IDs based on the most recent phylogenies.

3.3 Taxonomy

Phylum Cnidaria

Subphylum Anthozoa

Class Octocorallia

Order Scleralcyonacea

Superfamily Pennatuloidea

Family Anthoptilidae

Genus *Lithoptilum* gen. nov.

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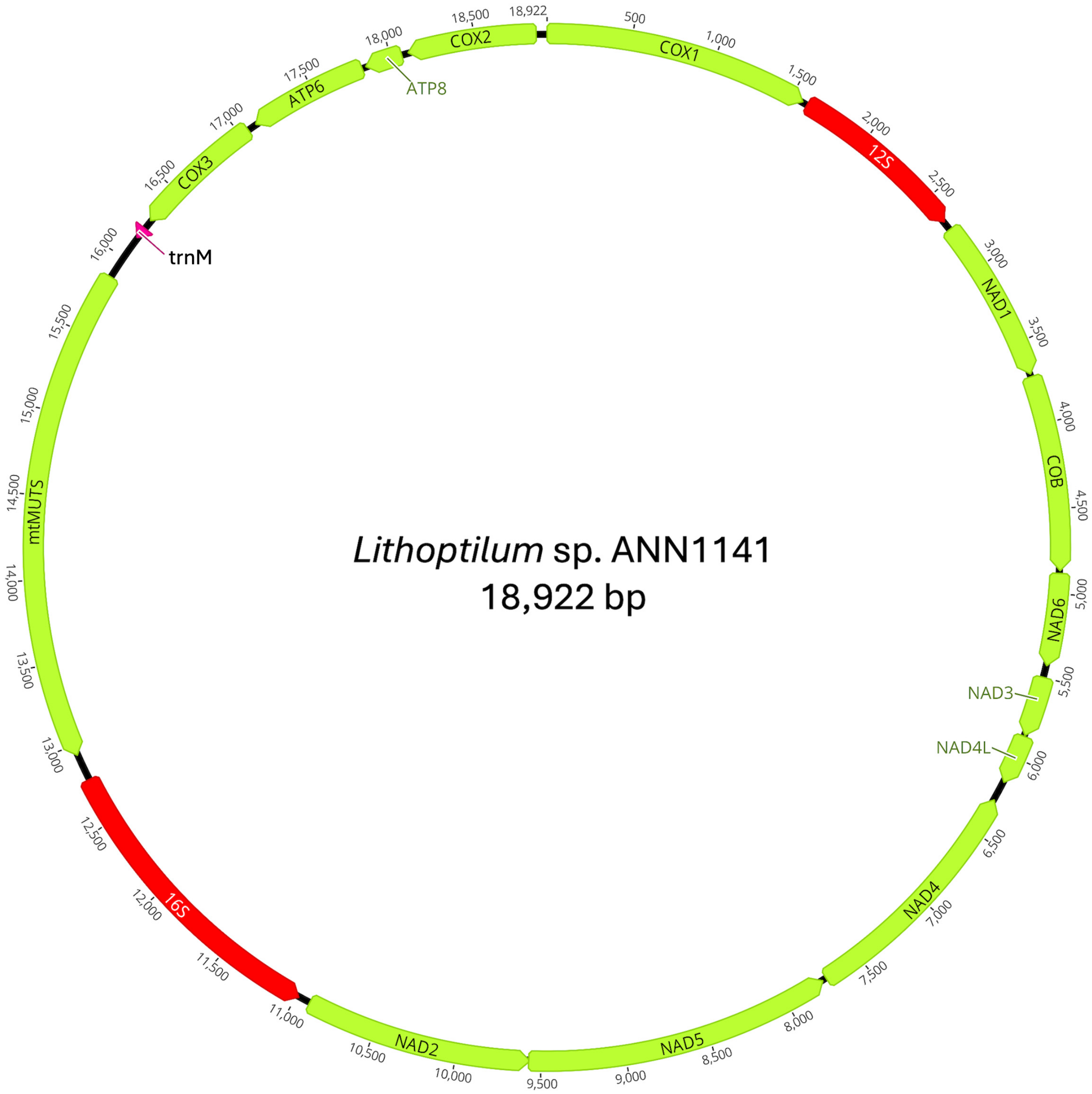

FIGURE 7. Annotated mitogenome of rock pen sample ANN1141 (GenBank accession number PP960129) collected on Annei Seamount on the Emperor Seamount Chain in 2019. This mitogenome shows the same gene arrangement as that of the octocoral mitochondrial gene order B (Hogan *et al.*, 2019). Protein-coding genes are shown in green boxes, rRNA genes in red and trnM in pink. The genes from *cox1* to *nad4L* are on the same strand and transcribed clockwise, while the remaining genes are on the opposite strand. The black lines between genes are proportional in length to the intergenic regions.

3.3.1 Diagnosis

The peduncle is an enlarged distinct bulbous structure; in *in-situ* colonies the peduncle is loosely attached to the surface of a hard substratum. In a collected specimen, the base of the peduncle is a widened and folded structure with a terminal knob. In phylogenetic trees of sea pens, members of this genus form a monophyletic clade sister to *Anthoptilum* spp., *Anthoptilum grandiflorum* and *Anthoptilum murrayi*.

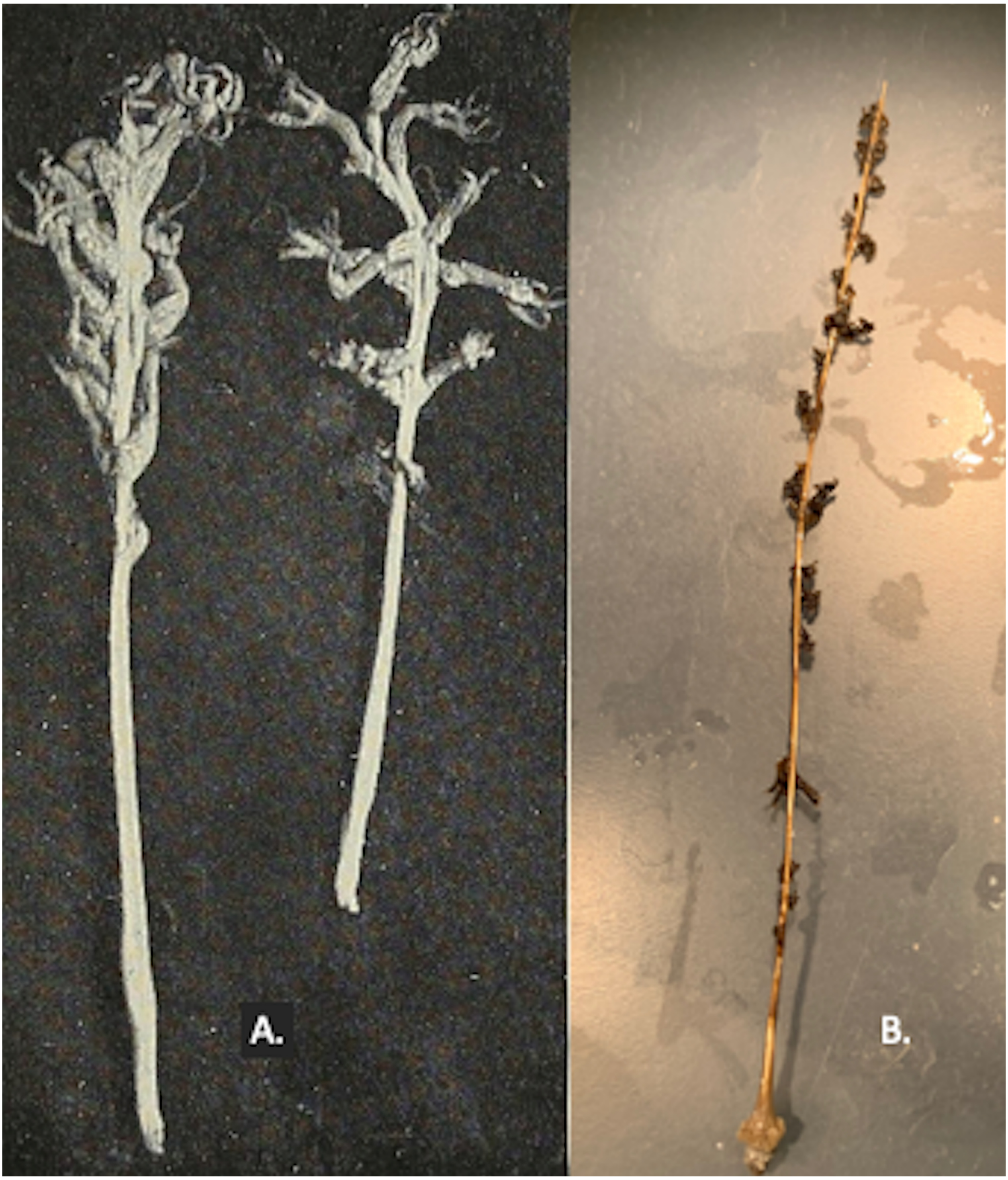

FIGURE 8. A comparison of the peduncle of two sea pens. A. an image from Nutting,1908 of the type specimen for the genus *Calibelemnon*, *Calibelemnon symmetricum* Nutting,1908 showing an elongated peduncle, typical of soft-sediment dwelling sea pens. B. the type specimen for *Calibelemnon francei* (CAS179455) showing the bulbous and folded peduncle characteristic of rock pens.

3.3.2 Type Species

Anthoptilum lithophilum Williams & Alderslade, 2011, is designated as the type species.

3.3.3 Nominal Species

There are currently 5 species[2] that should be included in *Lithoptilum* gen. nov.—*Lithoptilum decipiens* (Thomas & Henderson, 1906), comb. nov, *Lithoptilum gowlettholmesae* (Williams & Alderslade, 2011), comb. nov., *Lithoptilum lithophilum* (Williams & Alderslade, 2011), comb. nov., *Lithoptilum gnome* (Kushida et al, 2024), comb. nov., and *Lithoptilum francei* (Williams & Alderslade, 2011), comb. nov.

3.4 Etymology

The name of the new genus is derived from a combination of the Greek words "litho" meaning stone and "ptil" meaning a feather. The name is a reflection of the habitat utilization by these sea pens. Gender of this taxon name is neutral.

4 Discussion

The expanded development and deployment of tools that allow for visual surveys of the deep ocean has increased our knowledge of communities inhabiting hard-bottom seafloors, such as seamounts, ridges, and canyons, that historically have been difficult to sample using trawls and dredges. These technologies led to the discovery of rock-inhabiting sea pens (Williams & Alderslade, 2011). Our review of videos captured by deep-diving ROVs exploring the central North Pacific and western North Atlantic revealed rock pen colonies to be sparsely distributed in their habitat; on the ROV dives where they are observed, typically only one or two colonies are seen. However, on two occasions, both in the central Pacific Ocean, very high density of rock pens—numbering in the thousands of colonies—were observed, at depths around 450 m. No such field of rock pens have been observed in deeper parts of the ocean.

Rock pens are found to inhabit a broad depth range (Fig. 4) and are geographically widespread (Fig. 3). In 2011, Williams and Alderslade reported only a single rock pen colony from the Atlantic but we have found rock pens across multiple expeditions and locations in the Atlantic (Fig. 3, 4). Presently, rock pens appear to be more abundant in the Pacific than in the Atlantic Ocean, however, more data is necessary to confirm this. Including the description of *Anthoptilum decipiens* from the Indian Ocean (Thomson *et al.*, 1906) makes the rock pens circumglobal in distribution.

Current taxonomy classifies the rock pens in two different families, Anthoptilidae and Scleroptilidae (Williams & Alderslade, 2011). However, in our phylogenetic trees based on a multilocus dataset and single mitochondrial-marker dataset, all rock pens form a monophyletic clade within a larger clade that represents the family Anthoptilidae. This necessitates the removal of *Calibelemnon francei* from the family Scleroptilidae and genus *Calibelemnon*. This action is further supported by the fact that the type specimen for the genus *Calibelemnon*, *C. symmetricum* Nutting, 1908, is a colony with an elongated peduncle typical of soft sediment-dwelling sea pens (Nutting, 1908) (Fig. 8). This would render the genus *Calibelemnon* to be homogeneous with respect to the elongated peduncle. Together, our results suggest that the modification of the peduncle to attach onto hard rocky substrates evolved only once among the sea pens. These analyses, in turn, support the erection of a new genus, *Lithoptilum* gen. nov., to house the rock pens; this genus is a sister taxon of *Anthoptilum* in the family Anthoptilidae, Superfamily Pennatuloidea.

Our analysis of the mitochondrial gene order shows that rock pens have the same gene order as reported in *Anthoptilum grandiflorum* (Hogan *et al.*, 2019) i.e., Octocoral gene order B. In *Anthoptilum murrayi*, as well, the *cox3* gene is upstream of *mtMutS* as is in Octocoral gene order B. This is interesting in that the arrangement differs from all other sea pens but matches that of bamboo corals (Family Keratoisididae) (Brugler & France, 2008). Among the seven species currently described in the family Anthoptilidae, our data supports that six have the same gene order. We were unable to test the mitochondrial gene arrangement in *Anthoptilum malayense* due to unavailability of tissue samples.

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[2] While this paper was in manuscript review, Kushida *et al.* (2024) published a description of a fifth species of rockpen, *Anthoptilum gnome*, from Japan. This species has the modified peduncle and Octocoral gene order B characteristic of *Lithoptilum*.

This is the first comprehensive study looking at the distribution and evolutionary history of the rock pens. We have utilized data collected during several deep-sea expeditions from the last 11 years to expand our knowledge of range utilization by rock pens both geographically and bathymetrically. The samples collected during these expeditions contribute significantly to the establishment of phylogenetic relationships among the rock pens and other sea pen taxa. However, large parts of the world's oceans still remain unexplored and under studied; explorations in such areas can potentially reveal more about evolutionary history of such organisms.

TABLE 1. Taxon ID, sample numbers, GenBank accession numbers, UCE sequence data generated, and location and depth of sea pen samples sequenced for this study. The museum specimens with updated identifications based on the most recent phylogenies have been indicated by an asterisk. The taxon IDs for the rock pen specimens have not been updated to the new genus.

Taxon ID	Specimen ID	Family	GenBank accession number	UCE	Depth (m)	Latitude	Longitude
Anthoptilidae							
Anthoptilum gowlettholmsae	CAS179452	Anthoptilidae	PP960139	Y	1109	-44.42	147.44
Anthoptilum lithophilum	USNM1171218	Anthoptilidae	PP960133		1826	22.17	-167.04
Anthoptilum lithophilum	CAS179453	Anthoptilidae	PP960137		699	32.27	-119.67
Anthoptilum lithophilum	CAS179454	Anthoptilidae	Only UCE	Y	700	34.06	-121.05
Anthoptilum murrayi	CAS222961	Anthoptilidae	PP960140	Y	1116	60.102	-179.47
Anthoptilum sp. *	USNM1071072	Anthoptilidae	PP960132		381	18.71	-158.27
Anthoptilum sp. *	USNM1071073	Anthoptilidae	PP960131		381	18.71	-158.27
Anthoptilum sp. *	USNM1075802	Anthoptilidae	PP960147	Y	1094	56.3	-142.47
Anthoptilum grandiflorum *	USNM1126263	Anthoptilidae	PP960141	Y	920	49.55	-127.35
Anthoptilum sp.	USNM1412989	Anthoptilidae	PP960130		418.9	21.81	-160.29
Anthoptilum sp.	USNM1457400	Anthoptilidae	PP960134	Y	1515.2	14.06	-169.32
Anthoptilum sp.	ANN1071	Anthoptilidae	OQ927988	Y	1982	36.69	171.61
Anthoptilum sp.	ANN1141	Anthoptilidae	OQ927989 PP960129 (mitogenome)	Y	1944	36.69	171.61
Anthoptilum sp.	MCZ162686	Anthoptilidae	PP960136		951.39	6.41	-162.48
Anthoptilum sp.	MCZ162737	Anthoptilidae	PP960138		2113.83	8.24	-162.94
Balticinidae							
Balticina californica *	USNM1116655	Balticinidae	PP929821	Y	1291–1410	49.74	-127.82
Balticina sp. *	USNM1007355	Balticinidae	PP960142		93	54.03	-164.38
Balticina sp. *	USNM1125985	Balticinidae	PP929826	Y	1165–1196	49.05	-127.04
Balticina sp. *	USNM1490655	Balticinidae	PP929823		1518.9	34.78	-75.35
Balticina willemoesi *	USNM1214967	Balticinidae	PP929825		1041	43.57	-125
Balticina willemoesi *	USNM1215050	Balticinidae	PP929820	Y	1204	42.13	-124.95
Chunellidae							
Chunella sp.	PNG2031	Chunellidae	PP929828	Y	676-720	-5.33	145.85
Echinoptilidae							
Echinoptilum sp.	CAS186678	Echinoptilidae	Only UCE	Y	183-188	14.02	120.32
Funiculinidae							

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TABLE 1. (Continued)

Taxon ID	**Specimen ID**	**Family**	**GenBank accession number**	**UCE**	**Depth (m)**	**Latitude**	**Longitude**
Funiculina parkeri	CAS173215	Funiculinidae	PP929851				
Funiculina parkeri	CAS220976	Funiculinidae	PP929852	Y	963.27	37.99	-123.5
Funiculina quadrangularis	FEL808-804	Funiculinidae	Only UCE	Y	833-950	27.35	91.08
Gyrophyllidae							
Gyrophyllum sibogae	P86	Gyrophyllidae	PP929850	Y			
Kophobelemnidae							
Kophobelemnon sp.	CAS185498	Kophobelemnidae	Only UCE	Y	721-761	13.6	120.65
Kophobelemnon sp.	CAS234104	Kophobelemnidae	Only UCE	Y	1885.11	36.67	-122.4
Malacobelemnon daytoni	CAS78429	Kophobelemnidae	PP929806	Y	12	-62.23	-58.66
Sclerobelemnon sp.	CAS114437	Kophobelemnidae	PP929808	Y	0-20.4	-11.18	151.86
Pennatulidae							
Alloptilella sp. *	USNM56977	Pennatulidae	PP929842		348–466	13.28	-61.09
Alloptilella sp. *	CAS185232	Pennatulidae	PP929843		636-664	13.61	120.72
Pennatula phosphorea	USNM1125955	Pennatulidae	PP929853	Y	2009–2036	49.02	-127.34
Pennatula sp.	CAS224092	Pennatulidae	PP929840	Y	144	7.27	134.52
Pennatula rubra	USNM96753	Pennatulidae	PP960144		101–128	5.33	4.75
Pennatula sp.	PNG9056	Pennatulidae	PP929819		760-823	-5.59	153.46
Pennatula sp.	USNM1071071	Pennatulidae	PP929841	Y	406.6	19.8	-156.63
Pennatula sp.	MCZ151040	Pennatulidae	PP929817	Y	1955.2	25.55	-164.2
Pennatula sp.	PNG126	Pennatulidae	PP929839		382-389	-4.08	151.93
Pennatula sp.	PNG9045	Pennatulidae	PP929818		613-660	-3.96	153.71
Pennatula sp.	CAS186696	Pennatulidae	PP929854		180	7.28	134.53
Pennatula sp.	PNG1011	Pennatulidae	PP929855		400-656	-3.81	144.65
Ptilella sp. *	PNG9063	Pennatulidae	PP929844		995-1050	-3.95	153.81
Pteroides sp.	CAS155053	Pennatulidae	Only UCE	Y			
Pteroides sp.	CAS201797	Pennatulidae	Only UCE	Y	0-20	13.7	120.88
Ptilosarcus gurneyi	CAS307864	Pennatulidae	PP960145	Y	12	57.01	-135.25
Ptilosarcus undulatus	USNM1215237	Pennatulidae	PP960148	Y	34.5–50.7	13.16	-87.69
Protoptilidae							
Distichoptilum sp.	USNM1171219	Protoptilidae	PP929862		1901	25.66	-168.84
Protoptilum carpenteri	CAS175421	Protoptilidae	Only UCE	Y	1665	44.22	-53.14
Protoptilum denticulatum	CAS78432	Protoptilidae	Only UCE	Y			
Protoptilum nybakenni	CAS234107	Protoptilidae	PP929860	Y			
Protoptilum sp. *	USNM1116654	Protoptilidae	PP960143		928–952	49.68	-127.74
Pseudumbellulidae							
Pseudumbellula sp. *	USNM1131748	Pseudumbellulidae	PP929847	Y	1478–1574	27.17	-91.17
Pseudumbellula sp. *	USNM1081174	Pseudumbellulidae	PP929846		4656	53.07	-161.19

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TABLE 1. (Continued)

Taxon ID	**Specimen ID**	**Family**	**GenBank accession number**	**UCE**	**Depth (m)**	**Latitude**	**Longitude**
Pseudumbellula scotia *	CAS175414	Pseudumbellulidae	PP929848	Y	371.7-408.4	-61.67	-58.85
Pseudumbellula scotia *	PNG1051	Pseudumbellulidae	PP929849	Y	361-750	-3.88	144.68
Scleroptilidae							
Calibelemnon francei	CAS179455	Scleroptilidae	PP960135	Y	1969	25.67	-76.77
Calibelemnon sp.	CAS201545	Scleroptilidae	PP929827	Y	62.4	26.51	127.88
Scleroptilum sp.	USNM1072451	Scleroptilidae	Only UCE	Y	1807	25.7	-171.45
Umbellulidae							
Umbellula sp.	USNM1116652	Umbellulidae	PP929833		839–1068	49.56	-127.5
Umbellula sp.	USNM1126255	Umbellulidae	PP929805		526–569	49.26	-127.08
Umbellula sp.	USNM1126262	Umbellulidae	PP929832		1804–1827	49.34	-127.53
Umbellula sp.	USNM1126264	Umbellulidae	PP929831		823–1028	49.51	-127.41
Umbellula sp.	USNM1205665	Umbellulidae	PP929830	Y	1215	47.58	-125.23
Umbellula sp.	CAT180649	Umbellulidae	Only UCE	Y	324-410	-60.49	-45.14
Veretillidae							
Ambhibelemnon namibiensis	CAS171928	Veretillidae	PP929834	Y	130-128		
Cavernularia sp.	CAS099827	Veretillidae	PP929837		18		
Cavernularia sp.	CAS099698	Veretillidae	Only UCE	Y	18	-9.51	147.28
Cavernulina cylindrica	CAS222252	Veretillidae	PP929836		30		
Veretillum sp.	CAS186545	Veretillidae	PP929838			13.69	120.89
Veretillum sp.	CAS201530	Veretillidae	PP929835	Y	0-20.1	13.7	120.88
Veretillum sp.	CAS095279	Veretillidae	Only UCE	Y	20.4		
Veretillum sp.	CAS186637	Veretillidae	PP929809		31	13.63	120.947
Virgulariidae							
Acanthoptilum gracile	CAS228192	Virgulariidae	PP960149		88.8	37.13	-122.5
Scytalium martensi	CAS216275	Virgulariidae	PP960146	Y	3-24.9	9.17	123.25
Scytalium sp.	CAS201470	Virgulariidae	PP929807	Y	0-9.1	13.7	120.88
Stylatula elongata	CAS170341	Virgulariidae	PP929856	Y	5	37.86	-122.42
Stylatula sp.	USNM1215231	Virgulariidae	PP929859	Y	31.5	13.07	-87.83
Stylatula sp.	USNM1215238	Virgulariidae	PP929858		104	13.34	-90
Stylatula sp.	USNM1520468	Virgulariidae	PP929857		1670	36.54	-74.26
Virgularia guataviana	CAS30690	Virgulariidae	Only UCE	Y			
Virgularia schultzei	CAS167893	Virgulariidae	PP929812		31		
Virgularia sp.	CAS180145	Virgulariidae	PP929815		13.7	13.76	121.38
Virgularia sp.	CAS201499	Virgulariidae	PP929816		0-9.1	13.69	120.9
Virgularia sp.	CAS201773	Virgulariidae	PP929813			13.66	120.9
Virgularia sp.	USNM1185351	Virgulariidae	Only UCE	Y	0–30	-62.21	-58.93

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TABLE 1. (Continued)

Taxon ID	Specimen ID	Family	GenBank accession number	UCE	Depth (m)	Latitude	Longitude
Verucellidae							
Verucella sp.	NTM-C014982	Verucellidae	DQ302864				
Keratoisididae							
Isidella tentaculum	USNM1659764	Keratoisididae	Only UCE	Y	1349	51.3	-177.02
Lepidisis caryophyllia	YPMIZ044549	Keratoisididae	Only UCE	Y	2152	40.6	-67.52
undescribed species	YPMIZ107123	Keratoisididae	Only UCE	Y	1302	23.78	-75.13

5 Conflict of Interest

The authors declare no conflict of interest.

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Supplementary Material. The following supporting information can be downloaded at the DOI landing page of this paper:

SUPPLEMENTAL TABLE1: Table listing the observations of rock pens from deep-sea expeditions from 2015 to 2023 and associated metadata.