

A taxonomic survey of the shallow-water (<150 m) black corals (Cnidaria: Antipatharia) of the Hawaiian Islands

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The shallow-water (<150 m) antipatharian fauna of the Hawaiian Archipelago is described and illustrated based on a systematic examination of skeletal spine morphology, polyp morphology, colony branching pattern and *in situ* photographs. A total of 172 black coral specimens were examined, including all available type material of species previously reported from shallow waters off Hawai'i. The examined specimens were assigned to three families (Antipathidae, Aphanipathidae, and Myriopathidae), six genera (*Antipathes*, *Cirripathes*, *Stichopathes*, *Aphanipathes*, *Acanthopathes*, and *Myriopathes*), and eight species: *Antipathes griggi* Opresko, 2009, *Antipathes grandis* Verrill, 1928, *Cirripathes* cf. *anguina* (Dana, 1846), *Stichopathes echinulata* Brook, 1889, *Stichopathes?* sp., *Aphanipathes verticillata mauiensis* Opresko et al., 2012, *Acanthopathes undulata* (Van Pesch, 1914), and *Myriopathes* cf. *ulex* (Ellis and Solander, 1786). The biogeographical distribution of Hawaiian shallow-water black corals is presented and discussed.

Keywords: Anthozoa, Hawai'i, precious coral, scanning electron microscopy, taxonomy

Introduction

The taxonomic study of Hawaiian antipatharians began in 1928 when Verrill described *Antipathes grandis* and *Antipathes irregularis*. However, only the *A. grandis* nomen remains valid, because *A. irregularis* has since been identified as a gorgonian coral (Grigg and Opresko, 1977). In 1958, large aggregations of *A. grandis* and a second antipatharian species (see below) were discovered off Maui at depths between 30 and 90 m, a discovery that led to the establishment of a local black coral fishery (reviewed by Grigg, 2001). In 1961, this second antipatharian species was tentatively identified as *Antipathes dichotoma* Pallas, 1766 (Bayer, 1961), a species originally described from the Mediterranean (Opresko, 2003a). In 1977, Grigg and Opresko published a taxonomic survey of Hawaiian black corals based on colony branching pattern that included species descriptions of 14 species found in 30–570 m. Since the study of Grigg and Opresko (1977), skeletal spine morphology has become an increasingly important character in antipatharian taxonomy (Opresko, 1972, 2001, 2002, 2003b, 2004, 2005a, 2006; and references therein), because this character is thought to be largely independent of environmental factors, as compared to other more plastic morphological characters (Lapian et al., 2007; Wagner et al., 2010). In particular, the high-resolution imaging of scanning electron microscopy (SEM) has aided in the use of skeletal spine morphology as a taxonomic character for antipatharians by allowing visualization of minute spine features that may be diagnostic of individual species,

genera and families (Opresko, 1972, 1998, 2001, 2002, 2003b, 2004, 2005a, 2006; Lapian et al., 2007; Wagner et al., 2010; Bo et al., 2012). As a result of this advance, type specimens of numerous antipatharian species have recently been reexamined and redescribed (Grange, 1988; Opresko and Genin, 1990; Opresko and Cairns, 1994; Opresko and Baron-Szabo, 2001; Opresko, 2003a; Molodtsova and Pasternak, 2005; Opresko and Sanchez, 2005; Ocaña et al., 2006; Bo and Opresko, 2015), including two species from Hawaiian waters (Opresko, 2009; Wagner et al., 2010).

Unlike many other parts of the world, antipatharian populations have been well documented in Hawai'i (see Wagner et al., 2012b). This is in large part due to a black coral fishery that has operated in Hawai'i since the late 1950's (reviewed by Grigg, 2001), and has led to many black coral surveys. However, many previous surveys in Hawai'i did not identify black corals to species level, in large part due to the absence of detailed taxonomic studies until recently, as well as difficulties in differentiating species *in situ* or from video data alone (Opresko, 2009; Wagner et al., 2010; Opresko et al., 2012). The purpose of this study was to provide a taxonomic guide to the shallow-water black corals of the Hawaiian Islands using (1) skeletal spine morphology, (2) polyp morphology, (3) branching pattern, and (4) *in situ* photographs. For this purpose, type material of species previously reported from Hawai'i were reexamined where available, and compared to recently collected specimens from Hawaiian waters. This study was mostly limited to those species found at depths shallower than the top of the thermocline in the Main Hawaiian Islands (~120 m; Kahng and Kelley, 2007), because of the scarcity of specimens available from deeper waters. Additionally, this depth also represents the lower limit for several Hawaiian antipatharians, and thus serves as a logical cutoff point for this study.

Materials and Methods

A total of 172 antipatharian samples were examined as part of this study, and included museum specimens deposited at (1) the Bernice P. Bishop Museum in Honolulu, Hawai'i (BPBM), (2) the National Museum of Natural History, Smithsonian Institution in Washington, D.C. (USNM), (3) the Museum of Comparative Zoology in Cambridge, Massachusetts (MCZ), and (4) specimens recently collected using conventional SCUBA, mixed-gas technical diving and the Hawai'i Undersea Research Laboratory (HURL) manned submersibles *Pisces IV* and *V* (Table 1). Museum samples ranged from whole colonies to colony fragments of various sizes, and included type material of *Antipathes grandis*, *A. griggi*, *Stichopathes echinulata*, *Aphanipathes verticillata*, and *Acanthopathes undulata* (Table 1). For recently collected specimens, entire colonies were photographed *in situ*, and 5–10 tissue samples were clipped from each colony and preserved in 10% formaldehyde in seawater. Morphometric measurements of polyps and spines were made from photographs of preserved specimens as described by Wagner et al. (2010). Additionally, samples were prepared for SEM analysis of skeletal spines, and viewed under a S-4800 Hitachi Field Emission SEM (Hitachi High-Technologies

Corporation, Tokyo, Japan) at the University of Hawai'i at Mānoa (Wagner et al., 2010). Literature records of Hawaiian black corals were reviewed with the purpose of synonymizing different names that have previously been used for the same species. In cases where species assignments could not be verified from literature records alone, authors were contacted and species identifications were made using previously collected specimens, *in situ* photographs or collection information provided by authors.

Results and Discussion

Based on the overall morphology of colonies, polyps and skeletal spines, the 172 examined samples belong to three families (Antipathidae, Aphanipathidae, and Myriopathidae), six genera (*Antipathes*, *Cirripathes*, *Stichopathes*, *Aphanipathes*, *Acanthopathes*, and *Myriopathes*), and eight species (Tables 1, 2). Five species were identified by directly comparing Hawaiian specimens to type material, and included (1) *Antipathes griggi* Opresko, 2009, (2) *Antipathes grandis*, Verrill, 1928, (3) *Stichopathes echinulata* Brook, 1889, (4) *Aphanipathes verticillata mauiensis* Opresko et al., 2012, and (5) *Acanthopathes undulata* (Van Pesch, 1914) (Table 2). Additionally, specimens that are consistent with the descriptions of *Cirripathes anguina* (Dana, 1846), and *Myriopathes ulex* (Ellis and Solander, 1786) were identified. However, because the type material of both *C. anguina* and *M. ulex* is lost and the original descriptions are very brief, Hawaiian specimens cannot be conclusively assigned to these species until neotypes are designated and a thorough taxonomic study is undertaken. Finally, the examined material included an undescribed wire coral species, which is tentatively assigned to the genus *Stichopathes*. The diagnostic characters of the Hawaiian species identified as part of this study are highlighted in Figures 1–8 and Table 2, and discussed in the systematic section and taxonomic key below.

Systematics

Family Antipathidae Ehrenberg, 1834

The Antipathidae is characterized by polyps that (1) are usually larger than 1 cm in transverse diameter (range = 1–3 mm), (2) are not elongated in the transverse plane, (3) possess 10 mesenteries (six primary and four secondary), and (4) have sagittal tentacles (the two tentacles that are perpendicular to the branch bearing the polyp) that are substantially longer than its lateral tentacles (the four tentacles that are nearly parallel to the branch bearing the polyp) when fully expanded (Opresko, 2005b; Opresko and Sanchez, 2005; Bo, 2008; Moon and Song, 2008a). However, this latter feature is frequently lost during the preservation process. The Antipathidae has historically been considered a taxonomic dumping ground, and is the oldest and most speciose antipatharian family (Daly et al., 2007; Bo, 2008). Consequently, colony and skeletal spine morphology are very heterogeneous within this family. Several taxa that formally belonged to the Antipathidae have been transferred to new families (Opresko, 2001, 2002, 2003b, 2004, 2005a, 2006); however, the family is

TABLE 1 | Antipatharian samples examined as part of this study.

Species	Family	Sample number	Date (month/day/year)	Collector	Depth (m)	Locality	Latitude	Longitude
<i>Antipathes grandis</i>	Antipathidae	BPBM 102	–	–	–	Maui	–	–
<i>Antipathes grandis</i>	Antipathidae	F-027	12/8/2007	HURL P4-200	92	Maui	20.942	–156.759
<i>Antipathes grandis</i>	Antipathidae	F-030	12/8/2007	HURL P4-200	97	Maui	20.943	–156.758
<i>Antipathes grandis</i>	Antipathidae	F-031	12/8/2007	HURL P4-200	96	Maui	20.943	–156.758
<i>Antipathes grandis</i>	Antipathidae	F-032	12/8/2007	HURL P4-200	96	Maui	20.943	–156.758
<i>Antipathes grandis</i>	Antipathidae	F-033	12/8/2007	HURL P4-200	91	Maui	20.943	–156.758
<i>Antipathes grandis</i>	Antipathidae	F-035	12/11/2007	HURL P4-202	62	Kaua'i	21.856	–159.433
<i>Antipathes grandis</i>	Antipathidae	F-046	4/3/2008	HURL P4-204	95	Maui	20.936	–156.767
<i>Antipathes grandis</i>	Antipathidae	F-047	4/3/2008	HURL P4-204	95	Maui	20.936	–156.768
<i>Antipathes grandis</i>	Antipathidae	F-049	4/3/2008	HURL P4-204	96	Maui	20.936	–156.768
<i>Antipathes grandis</i>	Antipathidae	F-051	4/3/2008	HURL P4-204	96	Maui	20.936	–156.770
<i>Antipathes grandis</i>	Antipathidae	F-058	4/4/2008	HURL P4-205	95	Maui	20.951	–156.753
<i>Antipathes grandis</i>	Antipathidae	F-059	4/4/2008	HURL P4-205	88	Maui	–	–
<i>Antipathes grandis</i>	Antipathidae	F-060	4/4/2008	HURL P4-205	91	Maui	20.951	–156.753
<i>Antipathes grandis</i>	Antipathidae	F-061	4/4/2008	HURL P4-205	90	Maui	20.951	–156.753
<i>Antipathes grandis</i>	Antipathidae	F-067	4/5/2008	HURL P4-206	91	Maui	20.942	–156.757
<i>Antipathes grandis</i>	Antipathidae	F-068	4/5/2008	HURL P4-206	96	Maui	20.943	–156.758
<i>Antipathes grandis</i>	Antipathidae	F-070	4/5/2008	HURL P4-206	90	Maui	20.943	–156.756
<i>Antipathes grandis</i>	Antipathidae	F-071	4/5/2008	HURL P4-206	94	Maui	20.942	–156.757
<i>Antipathes grandis</i>	Antipathidae	F-072	4/5/2008	HURL P4-206	102	Maui	20.943	–156.757
<i>Antipathes grandis</i>	Antipathidae	F-197	4/4/2008	HURL P4-206	90	Maui	20.951	–156.753
<i>Antipathes grandis</i>	Antipathidae	F-199	5/28/2008	T. Montgomery	52	Maui	20.879	–156.747
<i>Antipathes grandis</i>	Antipathidae	F-200	5/28/2008	T. Montgomery	52	Maui	20.879	–156.746
<i>Antipathes grandis</i>	Antipathidae	F-201	5/28/2008	T. Montgomery	52	Maui	20.879	–156.747
<i>Antipathes grandis</i>	Antipathidae	F-204	5/28/2008	T. Montgomery	54	Maui	20.879	–156.747
<i>Antipathes grandis</i>	Antipathidae	F-205	5/29/2008	T. Montgomery	58	Maui	20.884	–156.724
<i>Antipathes grandis</i>	Antipathidae	F-249	10/31/2009	D. Wagner	28	Kaua'i	21.928	–159.661
<i>Antipathes grandis</i>	Antipathidae	F-365	2/22/2009	HURL P5-716	100	Maui	20.941	–156.761
<i>Antipathes grandis</i>	Antipathidae	F-442	4/7/2009	HURL P5-739	127	Maui	20.941	–156.761
<i>Antipathes grandis</i>	Antipathidae	F-445	4/7/2009	HURL P5-739	102	Maui	20.941	–156.761
<i>Antipathes grandis</i>	Antipathidae	F-446	4/7/2009	HURL P5-739	102	Maui	20.941	–156.761
<i>Antipathes grandis</i>	Antipathidae	USNM 99812	7/16/1902	R/V Albatross	48-91	Hawai'i	19.783	–155.074
<i>Antipathes griggi</i>	Antipathidae	USNM 52436	July 1961	H. Hall	45	Maui	–	–
<i>Antipathes griggi</i>	Antipathidae	F-019	7/17/2007	T. Montgomery	37	Ni'ihau	22.030	–160.102
<i>Antipathes griggi</i>	Antipathidae	F-028	12/8/2007	HURL P4-200	95	Maui	20.943	–156.761
<i>Antipathes griggi</i>	Antipathidae	F-029	12/8/2007	HURL P4-200	93	Maui	20.943	–156.761
<i>Antipathes griggi</i>	Antipathidae	F-034	12/11/2007	HURL P4-202	62	Kaua'i	21.856	–159.433
<i>Antipathes griggi</i>	Antipathidae	F-036	12/11/2007	HURL P4-202	62	Kaua'i	21.856	–159.433
<i>Antipathes griggi</i>	Antipathidae	F-037	12/11/2007	HURL P4-202	62	Kaua'i	21.856	–159.433
<i>Antipathes griggi</i>	Antipathidae	F-038	12/11/2007	HURL P4-202	62	Kaua'i	21.856	–159.433
<i>Antipathes griggi</i>	Antipathidae	F-039	12/11/2007	HURL P4-202	62	Kaua'i	21.856	–159.433
<i>Antipathes griggi</i>	Antipathidae	F-040	12/11/2007	HURL P4-202	62	Kaua'i	21.856	–159.433
<i>Antipathes griggi</i>	Antipathidae	F-041	12/11/2007	HURL P4-202	62	Kaua'i	21.856	–159.433
<i>Antipathes griggi</i>	Antipathidae	F-042	12/11/2007	HURL P4-202	62	Kaua'i	21.856	–159.433
<i>Antipathes griggi</i>	Antipathidae	F-053	4/4/2008	HURL P4-205	90	Maui	20.952	–156.749
<i>Antipathes griggi</i>	Antipathidae	F-055	4/4/2008	HURL P4-205	99	Maui	20.950	–156.753
<i>Antipathes griggi</i>	Antipathidae	F-352	2/4/2009	D. Wagner	30	Kaua'i	21.889	–159.583
<i>Antipathes griggi</i>	Antipathidae	F-448	4/7/2009	HURL P5-739	93	Maui	20.942	–156.759
<i>Antipathes griggi</i>	Antipathidae	F-526	6/13/2009	T. Montgomery	58	Kaua'i	22.173	–159.755

(Continued)

TABLE 1 | Continued

Species	Family	Sample number	Date (month/day/year)	Collector	Depth (m)	Locality	Latitude	Longitude
<i>Antipathes griggi</i>	Antipathidae	F-530	6/15/2009	T. Montgomery	52	Kaua'i	21.857	-159.433
<i>Antipathes griggi</i>	Antipathidae	F-561	8/1/2009	D. Wagner	35	Maui	20.885	-156.730
<i>Antipathes griggi</i>	Antipathidae	F-571	8/1/2009	D. Wagner	56	Maui	20.777	-156.620
<i>Antipathes griggi</i>	Antipathidae	F-589	8/15/2009	D. Wagner	58	Laysan	25.726	-171.824
<i>Antipathes griggi</i>	Antipathidae	F-606	8/27/2009	D. Wagner	70	Laysan	25.711	-171.810
<i>Antipathes griggi</i>	Antipathidae	F-610	8/30/2009	D. Wagner	58	Necker	23.634	-164.742
<i>Antipathes griggi</i>	Antipathidae	F-611	8/30/2009	D. Wagner	58	Necker	23.634	-164.741
<i>Antipathes griggi</i>	Antipathidae	F-072b	8/28/2008	D. Wagner	23	O'ahu	21.593	-158.111
<i>Antipathes griggi</i>	Antipathidae	F-029b	11/22/2006	D. Wagner	10	O'ahu	21.260	-157.709
<i>Antipathes griggi</i>	Antipathidae	6-1-13-AM	6/1/2013	D. Wagner	76	Johnston	16.662	-169.571
<i>Antipathes griggi</i>	Antipathidae	9-19-2011	9/19/2011	D. Wagner	40	FFS	23.849	-166.368
<i>Antipathes griggi</i>	Antipathidae	9-15-2011	9/16/2011	D. Wagner	38	Lisianski	25.956	-174.091
<i>Antipathes griggi</i>	Antipathidae	9-19-2012	9/19/2012	D. Wagner	55	Lisianski	26.081	-174.160
<i>Antipathes griggi</i>	Antipathidae	9-18-2014	9/18/2014	D. Wagner	85	Pearl and Hermes	27.740	-175.962
<i>Cirripathes cf. anguina</i>	Antipathidae	F-045	1/1/2006	D. Wagner	30	O'ahu	21.280	-157.860
<i>Cirripathes cf. anguina</i>	Antipathidae	F-212	10/29/2008	D. Wagner	10	O'ahu	21.260	-157.709
<i>Cirripathes cf. anguina</i>	Antipathidae	F-213	10/29/2008	D. Wagner	10	O'ahu	21.260	-157.709
<i>Cirripathes cf. anguina</i>	Antipathidae	F-250	10/31/2008	D. Wagner	24	Kaua'i	21.928	-159.661
<i>Cirripathes cf. anguina</i>	Antipathidae	F-252	11/6/2008	D. Wagner	10	O'ahu	21.282	-157.678
<i>Cirripathes cf. anguina</i>	Antipathidae	F-353	2/4/2009	D. Wagner	30	Kaua'i	21.889	-159.583
<i>Cirripathes cf. anguina</i>	Antipathidae	F-354	2/4/2009	D. Wagner	30	Kaua'i	21.889	-159.583
<i>Cirripathes cf. anguina</i>	Antipathidae	F-403	3/4/2009	D. Wagner	23	Kaua'i	21.887	-159.602
<i>Cirripathes cf. anguina</i>	Antipathidae	F-404	3/4/2009	D. Wagner	23	Kaua'i	21.887	-159.602
<i>Cirripathes cf. anguina</i>	Antipathidae	F-405	3/4/2009	D. Wagner	23	Kaua'i	21.887	-159.602
<i>Cirripathes cf. anguina</i>	Antipathidae	F-410	3/4/2009	D. Wagner	30	Kaua'i	21.889	-159.583
<i>Cirripathes cf. anguina</i>	Antipathidae	F-483	5/4/2009	D. Wagner	30	Kaua'i	21.889	-159.583
<i>Cirripathes cf. anguina</i>	Antipathidae	F-484	5/4/2009	D. Wagner	30	Kaua'i	21.889	-159.583
<i>Cirripathes cf. anguina</i>	Antipathidae	F-490	5/4/2009	D. Wagner	15	Kaua'i	21.881	-159.492
<i>Cirripathes cf. anguina</i>	Antipathidae	F-523	6/2/2009	D. Wagner	12	Kaua'i	21.907	-159.629
<i>Cirripathes cf. anguina</i>	Antipathidae	F-524	6/2/2009	D. Wagner	12	Kaua'i	21.907	-159.629
<i>Cirripathes cf. anguina</i>	Antipathidae	F-525	6/2/2009	D. Wagner	12	Kaua'i	21.907	-159.629
<i>Cirripathes cf. anguina</i>	Antipathidae	F-569	8/1/2009	D. Wagner	35	Maui	20.885	-156.730
<i>Cirripathes cf. anguina</i>	Antipathidae	F-583	8/1/2009	D. Wagner	56	Maui	20.777	-156.620
<i>Cirripathes cf. anguina</i>	Antipathidae	F-619	9/5/2009	D. Wagner	82	Ni'ihau	22.018	160.102
<i>Cirripathes cf. anguina</i>	Antipathidae	F-620	9/5/2009	D. Wagner	82	Ni'ihau	22.018	160.102
<i>Cirripathes cf. anguina</i>	Antipathidae	F-621	9/5/2009	D. Wagner	82	Ni'ihau	22.018	160.102
<i>Cirripathes cf. anguina</i>	Antipathidae	F-622	9/5/2009	D. Wagner	82	Ni'ihau	22.018	160.102
<i>Cirripathes cf. anguina</i>	Antipathidae	F-636	7/2/2010	D. Wagner	10	O'ahu	21.260	-157.709
<i>Cirripathes cf. anguina</i>	Antipathidae	BPBM 361	8/1961	-	11	Hawai'i	-	-
<i>Cirripathes cf. anguina</i>	Antipathidae	USNM 91845	7/18/1902	-	44-152	Hawai'i	-	-
<i>Cirripathes cf. anguina</i>	Antipathidae	USNM 99918	-	R.A. Kinzie	9	-	-	-
<i>Cirripathes cf. anguina</i>	Antipathidae	F-235a	4/24/2010	D. Wagner	43	Palmyra	5.864	-162.137
<i>Cirripathes cf. anguina</i>	Antipathidae	F-269a	8/17/2010	D. Wagner	30	FFS	23.635	-166.186
<i>Cirripathes cf. anguina</i>	Antipathidae	F-166a	8/14/2009	D. Wagner	59	Laysan	25.710	-171.806
<i>Cirripathes cf. anguina</i>	Antipathidae	F-209b	9/4/2009	D. Wagner	27	Ni'ihau	22.022	-160.097
<i>Cirripathes cf. anguina</i>	Antipathidae	5-30-13-AM	5/30/2013	D. Wagner	46	Johnston	16.789	-169.476
<i>Cirripathes cf. anguina</i>	Antipathidae	9-19-2011	9/19/2011	D. Wagner	38	FFS	23.848	-166.368
<i>Stichopathes echinulata</i>	Antipathidae	USNM 100371	-	R/V Challenger	-	Mauritius	-	-
<i>Stichopathes echinulata</i>	Antipathidae	F-001	10/23/2006	HURL P4-173	129	Maui	-	-

(Continued)

TABLE 1 | Continued

Species	Family	Sample number	Date (month/day/year)	Collector	Depth (m)	Locality	Latitude	Longitude
<i>Stichopathes echinulata</i>	Antipathidae	F-362	2/22/2009	HURL P5-716	130	Maui	20.941	-156.761
<i>Stichopathes echinulata</i>	Antipathidae	F-441	4/6/2009	HURL P5-738	129	Maui	20.735	-156.655
<i>Stichopathes echinulata</i>	Antipathidae	USNM 99705	10/23/1970	R/V Cromwell	108-198	Hawai'i	19.772	-156.109
<i>Stichopathes echinulata</i>	Antipathidae	USNM 99817	10/27/1967	R/V Cromwell	183	Lāna'i	20.751	-156.843
<i>Stichopathes echinulata</i>	Antipathidae	P4-221-0010	11/20/2009	HURL P4-221	120	Maui	-	-
<i>Stichopathes echinulata</i>	Antipathidae	P4-223-0040	11/23/2009	HURL P4-223	160	Maui	-	-
<i>Stichopathes echinulata</i>	Antipathidae	F-073a	12/11/2007	HURL P4-202	172	Kaua'i	21.853	-159.434
<i>Stichopathes</i> sp. (white morphotype)	Antipathidae	P4-226-9	12/1/2009	HURL P4-226	332	Ni'ihau	21.817	-160.071
<i>Stichopathes?</i> sp.	Antipathidae	F-211	10/29/2008	D. Wagner	10	O'ahu	21.260	-157.709
<i>Stichopathes?</i> sp.	Antipathidae	F-251	10/31/2008	D. Wagner	27	Kaua'i	21.928	-158.339
<i>Stichopathes?</i> sp.	Antipathidae	F-399	3/4/2009	D. Wagner	23	Kaua'i	21.887	-159.602
<i>Stichopathes?</i> sp.	Antipathidae	F-400	3/4/2009	D. Wagner	23	Kaua'i	21.887	-159.602
<i>Stichopathes?</i> sp.	Antipathidae	F-408	3/4/2009	D. Wagner	30	Kaua'i	21.889	-159.583
<i>Stichopathes?</i> sp.	Antipathidae	F-409	3/4/2009	D. Wagner	30	Kaua'i	21.889	-159.583
<i>Stichopathes?</i> sp.	Antipathidae	F-488	5/4/2009	D. Wagner	15	Kaua'i	21.881	-159.492
<i>Stichopathes?</i> sp.	Antipathidae	F-489	5/4/2009	D. Wagner	15	Kaua'i	21.881	-159.492
<i>Stichopathes?</i> sp.	Antipathidae	F-570	8/1/2009	D. Wagner	35	Maui	20.885	-156.730
<i>Stichopathes?</i> sp.	Antipathidae	F-608	8/30/2009	D. Wagner	58	Necker	23.634	-164.742
<i>Stichopathes?</i> sp.	Antipathidae	F-618	8/30/2009	D. Wagner	58	Necker	23.634	-164.741
<i>Stichopathes?</i> sp.	Antipathidae	F-637	7/2/2010	D. Wagner	10	O'ahu	21.260	-157.709
<i>Stichopathes?</i> sp.	Antipathidae	F-213b	9/4/2009	D. Wagner	27	Ni'ihau	22.022	-160.097
<i>Stichopathes?</i> sp.	Antipathidae	5-31-13-AM	5/31/2013	D. Wagner	61	Johnston	16.770	-169.522
<i>Stichopathes?</i> sp.	Antipathidae	9-19-2011	9/19/2011	D. Wagner	40	FFS	23.849	-166.368
<i>Acanthopathes undulata</i>	Aphanipathidae	USNM 100409	-	R/V Siboga	113	Indonesia	-	-
<i>Acanthopathes undulata</i>	Aphanipathidae	P4-223-0041	11/23/2009	HURL P4-223	160	Maui	-	-
<i>Acanthopathes undulata</i>	Aphanipathidae	USNM 99801	7/11/1902	R/V Albatross	130-269	Hawai'i	20.008	-155.879
<i>Acanthopathes undulata</i>	Aphanipathidae	USNM 77103	5/16/1902	R/V Albatross	144-238	Laysan	25.865	-171.786
<i>Acanthopathes undulata</i>	Aphanipathidae	USNM 99581	12/6/1968	T.A. Clarke	30-37	O'ahu	-	-
<i>Acanthopathes undulata</i>	Aphanipathidae	USNM 99584	10/23/1970	R/V Cromwell	108-198	Hawai'i	19.784	-156.108
<i>Acanthopathes undulata</i>	Aphanipathidae	USNM 99807	10/30/1976	R/V Cromwell	165	-	-	-
<i>Acanthopathes undulata</i>	Aphanipathidae	P4-226-2	12/1/2009	HURL P4-226	263	Ni'ihau	21.824	-160.069
<i>Acanthopathes undulata</i>	Aphanipathidae	BPBM 966	3/7/1983	HURL M83-151	259	O'ahu	-	-
<i>A. verticillata verticillata</i>	Aphanipathidae	MCZ 68	-	R/V Siboga	-	Mauritius	-	-
<i>A. verticillata verticillata</i>	Aphanipathidae	USNM 99727	11/14/1981	R.F. Bolland	79	Okinawa	26.500	127.848
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1150095	4/7/2009	HURL P5-739	88	Maui	20.941	-156.761
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1127632	4/3/2008	HURL P4-204	96	Maui	20.937	-156.765
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1127629	4/3/2008	HURL P4-204	113	Maui	20.953	-156.736
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1127635	4/4/2008	HURL P4-205	101	Maui	20.951	-156.769
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1127630	4/4/2008	HURL P4-205	111	Maui	20.950	-156.753
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1127631	4/4/2008	HURL P4-205	99	Maui	20.951	-156.752
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1128318	4/5/2008	HURL P4-206	93	Maui	20.942	-156.759
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1128319	4/5/2008	HURL P4-206	103	Maui	20.941	-156.760
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1128320	4/5/2008	HURL P4-206	114	Maui	20.943	-156.758
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1157500	2/22/2009	HURL P5-716	88	Maui	20.941	-156.761
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1157501	2/22/2009	HURL P5-716	114	Maui	20.940	-156.761
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1157502	2/22/2009	HURL P5-716	113	Maui	20.941	-156.761
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1157503	2/22/2009	HURL P5-716	126	Maui	20.940	-156.761
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1157504	2/22/2009	HURL P5-716	130	Maui	20.941	-156.761
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1150087	4/7/2009	HURL P5-739	127	Maui	20.941	-156.761

(Continued)

TABLE 1 | Continued

Species	Family	Sample number	Date (month/day/year)	Collector	Depth (m)	Locality	Latitude	Longitude
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1150092	4/7/2009	HURL P5-739	91	Maui	20.942	-156.759
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1150093	4/7/2009	HURL P5-739	92	Maui	20.941	-156.761
<i>A. verticillata mauiensis</i>	Aphanipathidae	USNM 1150094	4/7/2009	HURL P5-739	121	Maui	20.942	-156.759
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-066	4/5/2008	HURL P4-206	96	Maui	20.943	-156.758
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-596	8/17/2009	D. Wagner	61	Pearl and Hermes	27.762	-175.983
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-597	8/17/2009	D. Wagner	61	Pearl and Hermes	27.762	-175.983
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-598	8/17/2009	D. Wagner	61	Pearl and Hermes	27.762	-175.983
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-599	8/17/2009	D. Wagner	61	Pearl and Hermes	27.762	-175.983
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-600	8/17/2009	D. Wagner	61	Pearl and Hermes	27.762	-175.983
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-601	8/17/2009	D. Wagner	61	Pearl and Hermes	27.762	-175.983
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-602	8/17/2009	D. Wagner	61	Pearl and Hermes	27.762	-175.983
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-603	8/17/2009	D. Wagner	61	Pearl and Hermes	27.762	-175.983
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-604	8/25/2009	D. Wagner	70	Pearl and Hermes	27.764	-175.986
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-605	8/25/2009	D. Wagner	70	Pearl and Hermes	27.764	-175.986
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-617	8/30/2009	D. Wagner	58	Necker	23.634	-164.741
<i>Myriopathes cf. ulex</i>	Myriopathidae	F-002a	9/11/2004	HURL P5-570	58	Maui	20.879	-156.759
<i>Myriopathes cf. ulex</i>	Myriopathidae	USNM 99827	9/29/1970	R/V Cromwell	326	O'ahu	21.298	-157.538
<i>Myriopathes cf. ulex</i>	Myriopathidae	USNM 99928	–	–	41	–	–	–
<i>Myriopathes cf. ulex</i>	Myriopathidae	USNM 1010727	9/12/2002	HURL P4-049	170	Brooks	24.005	-166.676
<i>Myriopathes cf. ulex</i>	Myriopathidae	USNM 1010729	9/12/2002	HURL P4-049	255	Brooks	24.004	-166.674
<i>Myriopathes cf. ulex</i>	Myriopathidae	5-31-13-AM	5/31/2013	D. Wagner	61	Johnston	16.770	-169.522
<i>Myriopathes cf. ulex</i>	Myriopathidae	9-11-2014	9/11/2014	D. Wagner	88	FFS	23.631	-166.185
<i>Myriopathes cf. ulex</i>	Myriopathidae	USNM 1092637	7/11/1902	R/V Albatross	130–269	Hawai'i	20.008	-155.879

Samples listed in bold represent holotypes. BPBM, Bernice P. Bishop Museum; F, Personal collection of D. Wagner; USNM, National Museum of Natural History; MCZ, Museum of Comparative Zoology at Harvard University; HURL, Hawai'i Undersea Research Laboratory submersible dive; –, data not available.

still not monophyletic and in need of future taxonomic revisions (Daly et al., 2007).

Genus *Antipathes* Pallas, 1766

Antipathes is the oldest antipatharian genus and is distinguished by colonies that are all branched, with branching patterns varying from fan-shaped to bushy (Opresko, 1972; Opresko and Sanchez, 2005). Like the Antipathidae, *Antipathes* is also considered a taxonomic dumping ground that is morphologically heterogeneous (Opresko and Baron-Szabo, 2001; Daly et al., 2007; Bo, 2008; Moon and Song, 2008a). Even though many species have been removed from *Antipathes* and added to new genera (Opresko and Cairns, 1994; Opresko, 2001, 2002, 2003b, 2004, 2006), the genus still groups together many uncertain species and is in need of revision (Bo, 2008).

Antipathes griggi Opresko, 2009

Antipathes dichotoma: (Bayer, 1961, p. 8); *Antipathes grandis*: (Grigg, 1964, pp. 1–74, Figures 2–4, 7, 9, 11–13, 17, 22, 24); *Antipathes grandis*: (Grigg, 1965, pp. 244–260, Figures 1, 3, 5–10); *Antipathes dichotoma*: (Grigg, 1974, pp. 235–240); *Antipathes dichotoma*: (Grigg, 1976, pp. 1–48, Figures 1, 4, 15); *Antipathes dichotoma*: (Grigg and Opresko, 1977, pp. 242–261, Figures 9, 10); *Antipathes dichotoma*: (Grigg, 1984, pp. 57–74); *Antipathes dichotoma*: (Grigg, 1993, pp. 50–60,

Figure 5); *Antipathes dichotoma*: (Pyle and Chave, 1994, p. 92); *Antipathes dichotoma*: (Montgomery and Crow, 1998, pp. 103–108); *Antipathes dichotoma*: (Montgomery, 2002, pp. 157–164); *Antipathes dichotoma*: (Grigg, 2001, pp. 291–299, Figures 2, 3); *Antipathes dichotoma*: (Grigg, 2002, p. 13); *Antipathes dichotoma*: (Grigg et al., 2002, p. 79, Figures 6, 7); *Antipathes* sp.: (Opresko, 2003a, p. 491); *Antipathes dichotoma*: (Grigg, 2003, pp. 121–122); *Antipathes dichotoma*: (Grigg, 2004, pp. 1–6); *Antipathes dichotoma*: (Greenfield and Randall, 2004, p. 513); *Antipathes dichotoma*: (Boland and Parrish, 2005, pp. 411–420); *Antipathes dichotoma*: (Kahng and Grigg, 2005, pp. 556–562); *Antipathes* sp.: (Fenner, 2005, pp. 96, 99, 3 unnumbered figure on pp. 96 and 99); *Antipathes* sp.: (Hoover, 2006, p. 69, unnumbered figure on p. 69); *Antipathes dichotoma*: (Roark et al., 2006, pp. 1–14); *Antipathes dichotoma*: (Parrish and Baco, 2007, pp. 159, 170); *Antipathes cf. dichotoma*: (Parrish and Baco, 2007, p. 185); *Antipathes cf. curvata*: (Parrish and Baco, 2007, pp. 159, 162, 164, 170, 173, 185, Figure 4.5 right); *Antipathes dichotoma*: (Kahng and Kelley, 2007, pp. 684, 686); *Antipathes cf. curvata*: (Baco, 2007, p. 112); *Antipathes griggi*: (Opresko, 2009, pp. 277–291, Figures 1a,b, 2a–f, 3a–d, 4a–f); *Antipathes griggi*: (Wagner et al., 2010, pp. 271–290, Figures 9e–h); *Antipathes griggi*: (Grigg, 2010, pp. 1–9); *Antipathes griggi*: (Wagner et al., 2011a, pp. 249–255, Figure 2); *Antipathes griggi*: (Wagner et al., 2011b, pp. 1323–1328, Figures 2a,b); *Antipathes griggi*: (Wagner et al., 2011c, pp.

TABLE 2 | Morphometric comparison of Hawaiian antipatharian species examined as part of this study.

	<i>Antipathes griggsi</i> Opreško, 2009	<i>Antipathes grandis</i> Verrill, 1928	<i>Cirripathes cf. anguina</i> (Dana, 1846)	<i>Stichopathes echinulata</i> Brook, 1889	<i>Stichopathes</i> sp.	<i>Aphanipathes verticillata mauiensis</i> Opreško et al., 2012	<i>Acanthopathes undulata</i> (Van Pesch, 1914)	<i>Myriopathes cf. ulex</i> (Ellis and Solander, 1786)
COLONY								
Branching pattern	Bushy	Bushy	Unbranched	Unbranched	Unbranched	Bushy	Fan-shaped	Fan-shaped
Max. height (m)	3	3	2	1	5	1	0.5	3
Terminal branch diameter with tissue at midpoint (mm)	0.87 (0.46–1.66)	0.52 (0.31–0.79)	2.78 (1.39–6.12)	1.00 (0.74–1.22)	3.21 (1.74–5.55)	0.90 (0.60–1.23)	0.67 (0.55–0.91)	0.36 (0.24–0.64)
POLYPS								
Transverse diameter (mm)	1.12 (0.58–1.75)	0.84 (0.35–1.42)	2.03 (0.67–4.45)	0.98 (0.51–1.35)	1.82 (0.82–3.98)	1.35 (0.72–1.81)	0.87 (0.50–1.15)	0.56 (0.32–0.92)
Polyp spacing (mm)	1.43 (0.57–2.83)	1.12 (0.47–1.78)	2.39 (0.92–4.76)	1.33 (0.81–1.93)	1.82 (1.02–3.44)	1.71 (0.89–2.76)	1.26 (1.01–1.58)	0.84 (0.31–1.71)
Density (polyps/cm)	7 (5–10)	9 (6–14)	4 (3–7)*	8 (6–10)	6 (4–8)	6 (5–8)	8 (7–8)	12 (8–15)
SPINES								
Forks or apical knobs present	Yes	No	Yes	No	Yes	No	No	Yes (on main stem)****
Secondary spines present	Yes	No	No	No	Yes	No	No	No
Polypar spine height (µm)	181 (105–382)	87 (49–168)	213 (110–380)**	139 (81–190)	352 (199–785)	163 (90–266)	249 (85–460)***	122 (76–196)
Abpolypar spine height (µm)	127 (68–243)	62 (31–110)	213 (110–380)**	89 (54–147)	212 (95–442)	115 (54–201)	204 (113–329)	92 (51–172)
Spine spacing (µm)	379 (209–654)	280 (131–469)	524 (167–1806)	367 (187–670)	666 (276–1246)	324 (200–507)	234 (155–361)	177 (70–366)
HABITAT								
Depth range (m)	10–110	27–127	9–82	129–183	10–58	88–130	30–263	41–326

Unless otherwise noted, listed values represent means and ranges (in parentheses). *, polyp density measured on one side of corallum only; **, there is no distinction between polypar and abpolypar spines in *C. cf. anguina*; ***, polypar spine measurements of *A. undulata* include both hypostomal and circumpolypar spines; ****, forked spines are only present on the main stem and thicker branches of *M. ulex*.

211–225, Figures 1c,d, 4a); *Antipathes griggi*: (Opresko et al., 2012, pp. 24, 36–38, Figures 8e–h); *Antipathes griggi*: (Wagner et al., 2012a, pp. 795–806, Figures 2a–j); *Antipathes griggi*: (Wagner et al., 2012b, pp. 67–132, Figure 2.1a); *Antipathes griggi*: (Wagner et al., 2013, pp. 341–345, Figure 2 right); *Antipathes griggi*: (Brugler et al., 2013, pp. 312–361, Figures 2–5); *Antipathes griggi*: (Wagner et al., 2014, pp. 4, 8).

The Hawaiian species *Antipathes griggi* (Figure 1) was previously identified as *A. dichotoma* (Bayer, 1961), a species originally described from off Marseilles in the Mediterranean (Pallas, 1766; Opresko, 2003a). Subsequent comparisons between specimens from Hawai'i and the Mediterranean revealed considerable morphological differences (Opresko, 2003a). As a result, the Hawaiian "*A. dichotoma*" was assigned the new name of *Antipathes griggi* (Opresko, 2009). Surveys for *A. griggi* have been particularly frequent in Hawai'i, because it is the main species targeted by the Hawaiian black coral fishery (Grigg, 1993, 2001, 2004; Parrish and Baco, 2007). Opresko (2009) presented

a detailed taxonomic description of *A. griggi*, and the main diagnostic features are briefly summarized here.

A. griggi colonies can reach heights of up to 3 m, and are extensively branched with eight or more orders of branching (Figures 1E,F). Branches are arranged irregularly on all sides of the corallum on the lower part of the colony, and become more planar on the highest order branches (Figures 1E,F). Terminal branches reach up to 10 cm in length without becoming branched. Spines are conical, some have bifurcations toward their apex, and are covered with elongated tubercles over the biggest portion of their surface (Figure 1I). At midpoint, the terminal branches usually measure 0.4–1.7 mm in diameter with tissue, and contain polypar spines that are on average 181 μm tall (range = 105–382 μm), and abpolypar spines that are on average 127 μm tall (range = 68–243 μm). Smaller secondary spines, up to 40 μm tall, are present on some portions of the corallum, especially on thicker branches (Figure 1D). On branchlets and smaller

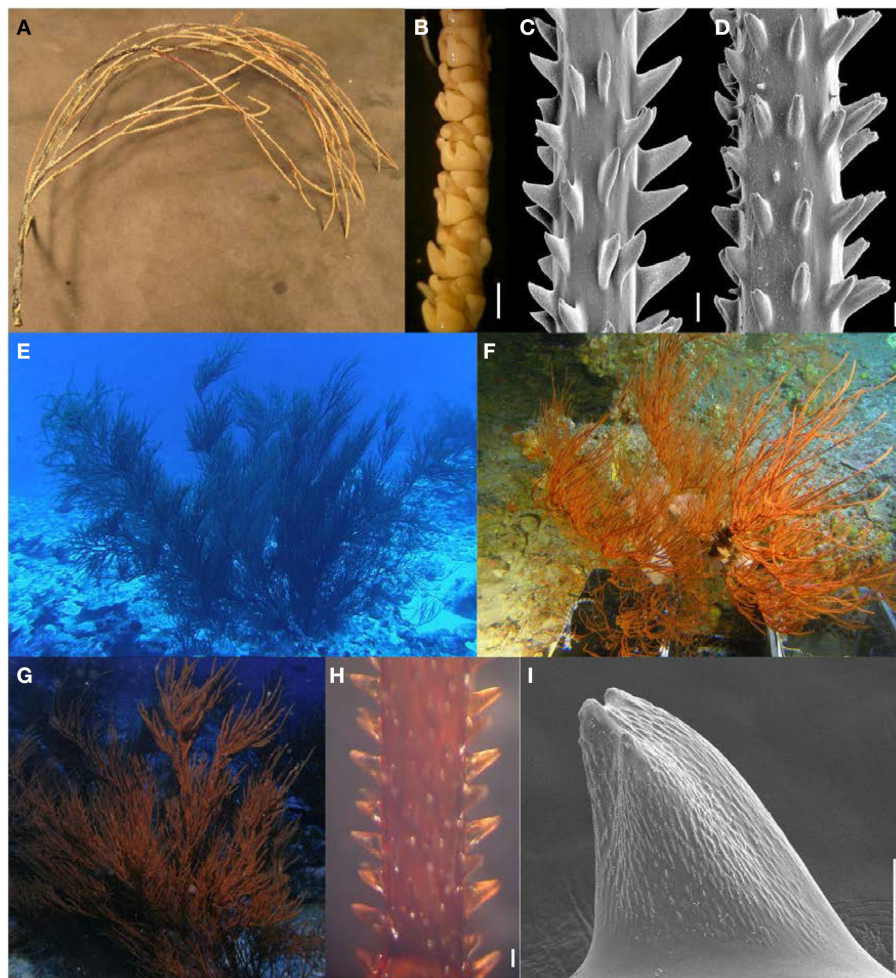


FIGURE 1 | (A–D) *Antipathes griggi* holotype (USNM 52436) showing (A) entire specimen, (B) polyps on terminal branch under light microscopy (scale bar = 1 mm), and (C,D) skeletal spines on terminal branch under SEM (scale bars = 100 μm). (E–G) *A. griggi*

colonies *in situ*; (H) skeletal spines under light microscopy (scale bar = 100 μm); (I) close-up of polypar spine under SEM (scale bar = 50 μm). (Photos courtesy of E,G Tony Montgomery, and F HURL).

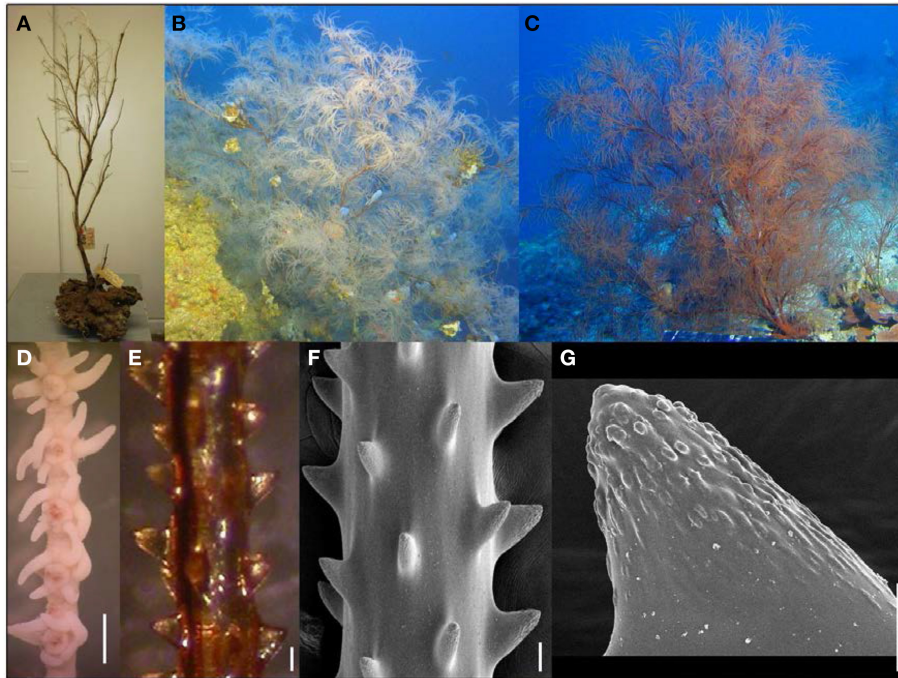


FIGURE 2 | (A) *Antipathes grandis* holotype (BPBM 102); **(B,C)** colonies of *A. grandis* *in situ*; **(D)** preserved polyps on terminal branch under light microscopy (scale bar = 1 mm); **(E)** skeletal spines on terminal branch under

light microscopy (scale bar = 100 μ m); **(F)** skeletal spines on terminal branch under SEM (scale bar = 100 μ m); **(G)** close-up of polypar spine under SEM (scale bar = 25 μ m). **(B,C)** Photos courtesy of HURL).

branches, spines are arranged in axial rows, with adjacent rows offset in a spiral pattern around the corallum (**Figures 1C,D**). Polyps average 1.12 mm in transverse diameter (range = 0.58–1.75 mm), and are typically spaced 1.43 mm apart (range = 0.57–2.83 mm), resulting in 7 polyps per cm (range = 5–10). The tissues of living colonies are colored brown to bright red (**Figures 1E,F**).

To date, specimens identified as *A. griggi* have only been reported from the Hawaiian Archipelago from Hawai'i Island to Pearl and Hermes Atoll at depths ranging between 10 and 110 m (**Table 1**; Opresko, 2009; Wagner et al., 2011a), as well as from Johnston Atoll at 76 m (Wagner et al., 2014). However, colonies with similar morphologies, identified as *A. dichotoma*, have also been reported from other locations in the Indo-West Pacific including the Philippines, Indonesia, Palau, China and Guam (Van Pesch, 1914; Grigg, 1975; Zhou and Zou, 1984, 1992; Zou and Zhou, 1984; Paulay et al., 2003; Rogers et al., 2007; Qi et al., 2009). These locations are all outside the range of *A. dichotoma*, which is only known from the Mediterranean and East Atlantic (Opresko, 2003a; Bo, 2008). Like the previous misidentification of *A. dichotoma* from Hawai'i (see above), these misidentified *A. dichotoma* records may also be *A. griggi*. However, detailed taxonomic investigations of specimens from the Indo-West Pacific will have to be undertaken to confirm this. Currently, there are no museum specimens of *A. griggi* that were collected outside of Hawai'i or Johnston Atoll.

Antipathes grandis Verrill, 1928

Antipathes grandis: (Verrill, 1928, pp. 7, 9, Figures 1i–m, pl. IIc); *Antipathes grandis*: (Grigg, 1974, pp. 235–240); *Antipathes grandis*: (Grigg, 1976, pp. 1–48); *Antipathes grandis*: (Grigg and Opresko, 1977, pp. 242–261, Figures 1, 11); *Antipathes grandis*: (Grigg, 1984, pp. 57–74); *Antipathes grandis*: (Grigg, 1993, pp. 50–60); *Antipathes grandis*: (Grigg, 2001, pp. 291–299); *Antipathes grandis*: (Grigg, 2002, p. 13); *Antipathes grandis*: (Grigg, 2003, pp. 121–122); *Antipathes grandis*: (Grigg, 2004, pp. 1–6); *Antipathes grandis*: (Fenner, 2005, p. 100, 2 unnumbered figure on p. 100); *Antipathes grandis*: (Boland and Parrish, 2005, pp. 411–420); *Antipathes grandis*: (Kahng and Grigg, 2005, pp. 556–562); *Antipathes grandis*: (Parrish and Baco, 2007, pp. 159, 162, 164, 170, 185, Figure 4.5 left); *Antipathes grandis*: (Baco, 2007, p. 112); *Antipathes grandis*: (Kahng and Kelley, 2007, pp. 684, 686); *Antipathes grandis*: (Wagner et al., 2010, pp. 271–290, Figures 2–7, 8a,b, 9a–d, 10); *Antipathes grandis*: (Grigg, 2010, pp. 1–9); *Antipathes grandis*: (Wagner et al., 2011b, pp. 1323–1328, Figure 2c); *Antipathes grandis*: (Wagner et al., 2012a, pp. 795–806); *Antipathes grandis*: (Wagner et al., 2012b, pp. 67–132); *Antipathes grandis*: (Brugler et al., 2013, pp. 312–361, Figures 2, 3, 5).

Like its sympatric congener *Antipathes griggi*, *A. grandis* (**Figure 2**) is also commercially harvested in Hawai'i to supply the precious coral jewelry industry (reviewed by Grigg, 2001). *A. grandis* was the first antipatharian species described from Hawaiian waters (Verrill, 1928). A detailed taxonomic

redescription of *A. grandis* is presented by Wagner et al. (2010), and briefly summarized here. Colonies can reach massive heights of over 3 m, and are extensively branched. Branches are long, distally-directed, and disposed irregularly on all sides of the corallum (Figures 2A–C). Terminal branchlets reach lengths of up to 10 cm without becoming subbranched and typically measure 0.5 mm in diameter with tissue at their midpoint (range = 0.31–0.79 mm). The spines on terminal branches are conical and never bifurcated toward their apex, and covered with circular to elongated oval-shaped tubercles over the distal half of their surface (Figures 2F,G). Polypar spines are slightly larger (range = 49–168 μm) than abpolypar spines (range = 31–110 μm) and both tend to be inclined distally (Figures 2E,F). There are no secondary spines present on any parts of the corallum. On branchlets and smaller branches spines are arranged in axial rows, with adjacent rows offset in a spiral pattern around the corallum (Figures 2E,F). On average, polyps are 0.84 mm in transverse diameter (range = 0.35–1.42 mm) and spaced 1.12 mm apart (range = 0.47–1.78 mm), resulting in 9 polyps per cm (range = 6–14). The color of living colonies ranges between red, pale-red and white (Figures 2B,C).

A. grandis was originally described from off Maui (Verrill, 1928), and subsequently reported throughout the Main Hawaiian Islands from Hawai'i to Ni'ihau at depths between 27 and 127 m (Wagner et al., 2010). Additionally, there are two reports of this species from China (Zhou and Zou, 1984; Zou and Zhou, 1984), however, these records cannot be confirmed until specimens from that locality are examined. Furthermore, a morphologically similar species, identified as *Antipathes* sp., has been reported from Indonesia (Lapian et al., 2007; Tazioli et al., 2007).

Genus *Cirripathes* (Blainville, 1834)

The genus *Cirripathes* was originally established to differentiate antipatharian taxa with unbranched colonies from those with branched ones (Blainville, 1834). Later, Brook (1889) created *Stichopathes*, another genus with unbranched colonies, and used polyp arrangement as the diagnostic feature to differentiate between *Cirripathes* and *Stichopathes*. Polyps are arranged irregularly on all sides of the corallum in *Cirripathes*, whereas polyps are positioned in a single row on one side of the corallum in *Stichopathes* (Brook, 1889; Bo and Opresko, 2015). More recently, a third genus, *Pseudocirripathes*, has been established for yet another group of antipathids with unbranched colonies (Bo et al., 2009). Like *Cirripathes*, *Pseudocirripathes* also has polyps arranged irregularly on all sides of the corallum, but differs by having spines with distinct tubercles that are arranged in verticils, and tentacles that cannot completely contract (Bo et al., 2009). As a result, *Cirripathes* is now characterized by (1) unbranched colonies, (2) polyps that are arranged irregularly on all sides of the corallum, and (3) spines that are not arranged in verticils (Brook, 1889; Silberfeld, 1909; Summers, 1910; Van Pesch, 1914; Zou and Zhou, 1982, 1984; Echeverria, 2002; Moon and Song, 2008a; Bo et al., 2009).

Cirripathes cf. anguina (Dana, 1846)

Cirripathes sp.: (Davis and Cohen, 1968, pp. 749–761, Figures 1(top)–2); *Cirripathes anguina*: (Grigg and Opresko, 1977, pp.

242–261, Figure 4); *Cirripathes anguina*: (Grigg, 1993, p. 50); *Antipathes anguina*: (Grigg, 1993, p. 56); *Cirripathes anguina*: (Montgomery and Crow, 1998, pp. 103–108); *Cirripathes* sp.: (Coles et al., 1998, p. 24); *Cirripathes anguina*: (Greenfield and Randall, 2004, pp. 513–514, Figure 55); *Cirripathes* sp.: (Maragos et al., 2004, p. 230); *Cirripathes anguina*: (Fenner, 2005, p. 97, unnumbered figure on p. 97); *Cirripathes anguina*: (Hoover, 2006, p. 71, Figures a,b); *Cirripathes anguina*: (Parrish and Baco, 2007, pp. 159, 185); *Cirripathes* sp.: (Wagner et al., 2010, pp. 270–291, Figure 10); *Cirripathes cf. anguina*: (Wagner et al., 2011b: pp. 1323–1328, Figure 2d); *Cirripathes cf. anguina*: (Wagner et al., 2011c: pp. 211–225, Figures 1E,G); *Cirripathes anguina* TMKO-111/-113/-114: (Brugler et al., 2013, pp. 312–361, Figures 2–5); *Cirripathes cf. anguina*: (Wagner et al., 2014, p. 4).

Davis and Cohen (1968) published the first account of *Cirripathes cf. anguina* from Hawai'i (Figure 3) as part of a description of the associated fauna of this wire coral: a gobiid fish and a palaemonid shrimp. Later descriptions of this species also highlighted these characteristic faunal associates of the wire coral (Greenfield and Randall, 2004; Fenner, 2005; Hoover, 2006). Based on previous literature accounts and specimens examined as part of this study (Table 1), the following features characterize *C. cf. anguina*. Colonies are unbranched and can reach vertical heights of 2 m or more. The corallum is usually straight in small colonies, and becomes irregularly sinusoidal in larger colonies (Figures 3B–E). The corallum diameter is generally 1.4–6.1 mm at midheight. Polyps are of variable size, ranging from 0.65 to 4.45 mm in transverse diameter, and are arranged irregularly on all sides of the corallum (Figures 3B–F). The spacing between adjoining polyps varies between 0.92 and 4.76 mm. The color of coenenchyme is typically brown with yellow or green tentacles, but the coloration of tentacles varies between yellow, green, red, white and pink (Figures 3B–E). Skeletal spines are conical in shape, some of which have bifurcations toward the apex, and are covered with circular to elongated oval-shaped tubercles over the distal half of their surface (Figure 3H). Spines are generally 110–380 μm tall, and arranged in regular rows, with adjoining rows offset in a spiral pattern around the corallum (Figures 3G,H). Within a row, spines spacing is highly variable and ranges between 167 and 1806 μm .

This Hawaiian wire coral species has previously been identified as *Cirripathes anguina* Dana, 1846 (Grigg and Opresko, 1977), a species originally described from the reefs off Vanua Lebu Island in Fiji (Dana, 1846). The description of *C. anguina* is rather brief and highlights yellowish tentacles that are brownish-gray at their base, and spines that are laterally compressed and sub-acute, features that are also evident in the Hawaiian specimens examined as part of this study (Figure 3). Unfortunately, the type material of *C. anguina* is lost, and therefore no further comparisons can be made until a neotype is designated. Pending such a taxonomic revision, the name *Cirripathes cf. anguina* is used to refer to the Hawaiian wire coral described here (Figure 3).

Specimens examined as part of this study were collected throughout the Hawaiian Islands including the islands of Maui, O'ahu, Kaua'i, Ni'ihau, French Frigate Shoals, Necker, and Laysan

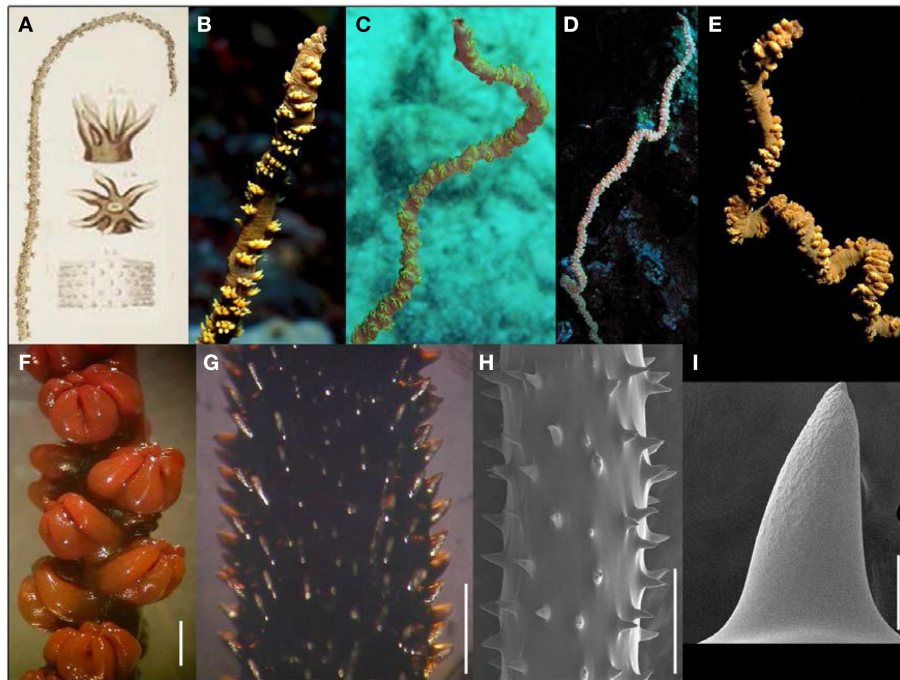


FIGURE 3 | (A) Plate accompanying Dana's (1846) original description of *Cirrhipathes anguina*, a species for which the type material is now lost. **(B–E)** *In situ* photographs of *Cirrhipathes* cf. *anguina* colonies from Hawaiian waters; **(F)** preserved polyps of Hawaiian species under light microscopy

(scale bar = 1 mm); **(G)** spines of Hawaiian species under light microscopy (scale bar = 1 mm); **(H,I)** spines of Hawaiian species under scanning electron microscopy (scale bars: **H** = 1 mm; **I** = 50 μ m). **(B–E)** Photos courtesy of Jim Maragos).

at depths between 9 and 82 m, as well as off Johnston Atoll at 47 m and off Palmyra Atoll at 43 m (Table 1). *C. anguina* has previously been reported throughout the Indo-West Pacific at depths ranging between 2 and 158 m (Dana, 1846; Gray, 1857; Brook, 1889; Cooper, 1903, 1909; Van Pesch, 1914; Pax, 1932; Tsuda et al., 1977; Humes, 1979; Bruce, 1982; Zou and Zhou, 1982, 1984; Heard, 1986; Okiyama and Tsukamoto, 1989; Montgomery and Crow, 1998; Okuno, 1998; Jones et al., 2000; Paulay et al., 2003; Greenfield and Randall, 2004; Parrish and Baco, 2007; Rogers et al., 2007; Bo, 2008; Moon and Song, 2008a). However, a thorough taxonomic survey will be needed to determine whether these Indo-West Pacific records correspond to the same Hawaiian species described here.

Genus *Stichopathes* Brook, 1889

Like *Cirrhipathes*, the genus *Stichopathes* is characterized by unbranched colonies (see above). Brook (1889) established polyp arrangement as the main diagnostic feature to distinguish between these two unbranched genera. Polyps are arranged irregularly on all sides of the corallum in *Cirrhipathes* (see above), whereas *Stichopathes* colonies have polyps that are arranged in a single row on one side of the corallum. However, the validity of these two genera has been questioned by several authors (Van Pesch, 1914; Pax, 1918; Pasternak, 1977; Bo, 2008; Bo et al., 2012). *Pseudocirrhipathes*, a third genus with unbranched colonies, was recently established for colonies with polyps that are arranged irregularly on all sides of the corallum, and spines

that are positioned in verticills (Bo et al., 2009; see above). Further taxonomic revisions among unbranched antipathids are, however, needed (Van Pesch, 1914; Pax, 1918; Pasternak, 1977; Bo, 2008). Pending such revisions, polyp arrangement is the only character that distinguishes *Stichopathes* from the other two unbranched antipatharian genera *Cirrhipathes* and *Pseudocirrhipathes* (Blainville, 1834; Brook, 1889; Bo et al., 2009, 2012; Bo and Opresko, 2015).

Stichopathes echinulata Brook, 1889

Stichopathes echinulata: (Brook, 1889, pp. 92, Pl. XII Figure 9); *Stichopathes* cf. *echinulata*: (Grigg and Opresko, 1977, pp. 242–261); *Stichopathes* cf. *echinulata*: (Wagner et al., 2011b, p. 1325); *Stichopathes echinulata*: (Wagner et al., 2011c, pp. 211–225, Figures 1h, 2b).

Stichopathes echinulata was originally described from off Mauritius (Brook, 1889). The original species description is rather brief, but emphasizes spines that are short, triangular and distally inclined, and arranged in regular rows, with nine or 10 rows visible in one aspect (Brook, 1889). Based on comparisons with the original description of *S. echinulata* (Brook, 1889; Grigg and Opresko, 1977) reported a morphologically similar species from Hawaiian waters (Figure 4). At the time, Grigg and Opresko (1977) did not have *S. echinulata* type material available for comparison, and because the original species description is rather brief (Brook, 1889), they did not conclusively assign the Hawaiian species to *S. echinulata*. As part of this study, a

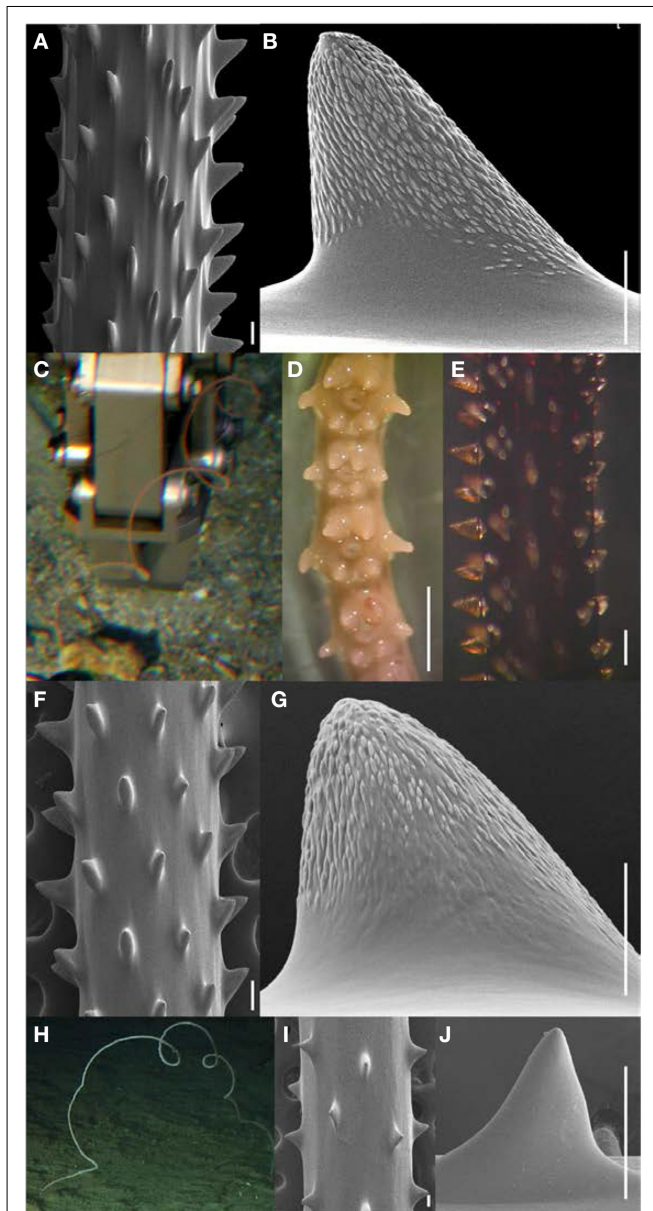


FIGURE 4 | (A,B) Skeletal spines of *Stichopathes echinulata* holotype (USNM 100371) under SEM (scale bars = 100 μm). **(C–G)** Hawaiian *S. echinulata* colonies c. *in situ*; **(D)** preserved polyps under light microscopy (scale bar = 1 mm); **(E)** skeletal spines under light microscopy (scale bar = 200 μm); **(F)** skeletal spines under SEM (scale bars = 100 μm); and **(G)** close-up of polypar spine under SEM (scale bar = 50 μm). **(H–J)** Hawaiian *Stichopathes* sp. with white tissues **(H)** *in situ*; **(I,J)** Skeletal spines under SEM (scale bars = 100 μm). **(C,H)** Photos courtesy of HURL.

small fragment of the *S. echinulata* holotype (USNM 100371) was examined under SEM (**Figures 4A,B**). The shape, size and arrangement of the spines of the holotype is very similar to the Hawaiian species examined here (**Figures 4E–G**). Consequently, the Hawaiian specimens are assigned to *S. echinulata*, and used to emend the description of the species as follows. Colonies are up to 1 m in height or more and coiled distally forming

multiple spirals. At midheight, colonies typically measure 0.74–1.22 mm in diameter with tissue. Polyps are arranged in a single row on one side of the corallum, and spaced 0.81–1.93 mm apart, resulting in 6–10 polyps per cm (**Figure 4D**). Skeletal spines are arranged in regular rows, with adjoining rows offset in a spiral pattern around the corallum. Within a row, spines are typically spaced 187–670 μm apart. Spines are conical, inclined distally, never bifurcated toward their apex, and covered with oval-shaped tubercles over the biggest portion of their surface (**Figures 4B,G**). Polypar spines are generally 81–190 μm tall and abpolypar spines are typically 54–147 μm tall. The coloration of living colonies was only noted for a few samples that were recently collected for this study (**Table 1**), but were all light-brown. Colonies with similar overall morphologies but with white tissues have also been reported from Hawaiian waters (**Figure 4H**; Chave and Malahoff, 1998). Only a single colony with white tissues was examined as part of this study (**Table 1**; **Figure 4H**). However, its skeletal spines are substantially different from *S. echinulata*, in that its spines are more triangular, and only covered by faint tubercles toward the very tip of spines (**Figures 4I,J**), whereas *S. echinulata* has distinct tubercles on the biggest portion of its spines (**Figures 4B,G**). Furthermore, the skeletal spines of the white morphotype are smaller than *S. echinulata*, with polypar spines ranging between 99 and 142 μm and abpolypar spines varying between 42 and 137 μm . Unfortunately only a single specimen of the white morphotype was available for comparison, however, the substantial morphological differences in spine shape, indicate that it is a different species (**Figures 4I,J**).

S. echinulata was originally described from Mauritius (Brook, 1889), but subsequently reported from East Africa (Summers, 1910), the Seychelles (Cooper, 1909), and Madagascar (Humes, 1967). All Hawaiian specimens examined as part of this study were collected from the Main Hawaiian Islands off Hawai'i, Lāna'i, Maui and Kaua'i in 108–198 m (**Table 1**).

Stichopathes? sp.

Unbranched species: (Grigg, 1964, p. 10); *Stichopathes* sp.: (Montgomery and Crow, 1998, pp. 103–108); *Stichopathes* cf. *echinulata*: (Fenner, 2005, p. 98, unnumbered figure on p. 98); *Stichopathes* cf. *echinulata*: (Hoover, 2006, p. 71, unnumbered figure on bottom of p. 71); *Stichopathes* sp.: (Wagner et al., 2011c, pp. 211–225, Figure 11); *Stichopathes* clade D?: (Bo et al., 2012, pp. 1–13, Figures 3m,p, 5a–n); *Stichopathes?* sp.: (Wagner et al., 2014, pp. 3–4).

Within depths accessible through regular SCUBA diving (<40 m), two unbranched black corals can be found in Hawaiian waters in areas with high current flow and reduced light intensity: one with green or yellow polyps that are arranged irregularly on all sides of the corallum (*Cirrhopathes* cf. *anguina*; see above), and another with brown polyps that are arranged in a single row on one side of the corallum (**Figure 5**). The latter represents an unnamed species that has been assigned to the genus *Stichopathes* based on the arrangement of its polyps, which are always positioned in a single row on one side of the corallum (Montgomery and Crow, 1998; Fenner,

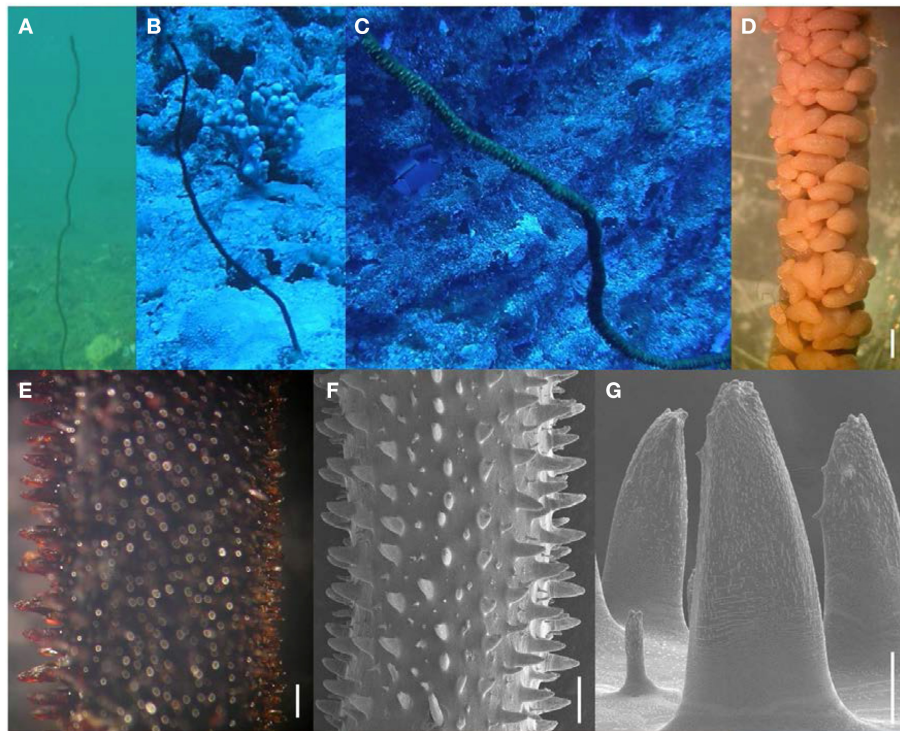


FIGURE 5 | *Stichopathes?* sp. (A–C) *in situ*; (D) preserved polyps under light microscopy (scale bar = 1 mm); (E) skeletal spines under light microscopy (scale bar = 500 μ m); (F) skeletal spines under SEM (scale bar = 500 μ m); and (G) close-up of polypar spines under SEM (scale bar = 100 μ m).

2005; Hoover, 2006). However, the skeletal spines of this Hawaiian wire coral are very different from other *Stichopathes* spp., which never have bifurcations or apical knobs toward their apex (Brook, 1889; Schultze, 1903; Roule, 1905; Thomson, 1905; Cooper, 1909; Summers, 1910; Van Pesch, 1914; Goenaga, 1977; Opresko and Genin, 1990; Opresko and Sanchez, 2005; Moon and Song, 2008a). In contrast, apical bifurcations are common on most of the spines of this Hawaiian wire coral species (Figures 5E–G). Therefore, the assignment to the genus *Stichopathes* is very questionable, and this Hawaiian wire coral may therefore represent both an undescribed genus and species. Colonies of this species are unbranched and can attain extreme lengths of up to 5 m (Grigg, 1964). The corallum of small colonies is relatively straight, and becomes more irregularly sinusoidal or spiraled in large colonies (Figures 5A–C). At midheight, colonies generally measure 1.74–5.55 mm in diameter with tissue. Polyps are arranged in a single row on one side of the corallum and are crowded together tightly (Figure 5D). On average, polyps measure 1.82 mm in transverse diameter (range = 0.82–3.98 mm) and are spaced 1.82 mm apart (range = 1.02–3.44 mm), resulting in 6 polyps per cm (range = 4–8). Skeletal spines are covered by elongated tubercles over the largest portion of their surface and are usually bifurcated toward their apex (Figures 5F,G). Polypar spines are distinctly larger on the polypar side, where they range between 199 and 785 μ m in height, whereas abpolypar spines vary between 95 and 442 μ m in height. Smaller, secondary spines (<100 μ m) are present throughout the

corallum (Figure 5G). The color of living colonies is greenish brown (Figures 5A–C).

Specimens examined as part of this study were collected throughout the Hawaiian Islands from Maui to French Frigate Shoals at depths ranging between 10 and 58 m, as well as from Johnston Atoll at 61 m (Table 1). Based on the morphology of spines and polyps, a very similar species, referred to as *Stichopathes* clade D, is known from Indonesia (Bo et al., 2012), but specimens from that locality will have to be examined to confirm those records.

Family Aphanipathidae Opresko, 2004

The Aphanipathidae is characterized by polyps with 10 mesenteries (six primary and four secondary), that are 0.5–1.3 mm in transverse diameter, and have short sagittal and lateral tentacles (shorted than the polyp diameter) that are nearly of the same length when fully expanded (Opresko, 2004; Opresko and Sanchez, 2005; Daly et al., 2007; Bo, 2008). Furthermore, the skeletal spines of the Aphanipathidae often penetrate through the soft tissues, are typically adorned with conical tubercles, and do not possess bifurcations toward their apex like many members of the Antipathidae (Opresko, 2004; Opresko and Sanchez, 2005; Daly et al., 2007; Bo, 2008). The family Aphanipathidae is divided into the two subfamilies Aphanipathinae and Acanthopathinae based on the relative sizes of skeletal spines in the area underneath a polyp (Opresko, 2004). The name of the family Aphanipathidae is derived

from the Greek root *aphano* meaning invisible, in reference to its inconspicuous polyps which are often obscured through elongated spines that penetrate through the coenenchyme (Brook, 1889).

Subfamily Aphanipathinae Opresko, 2004

The subfamily Aphanipathinae is distinguished by having skeletal spines of consistently similar heights on the side of the corallum bearing the polyps (Opresko, 2004). In contrast, the subfamily Acanthopathinae (see below) has members whose skeletal spines are reduced in size in the areas directly below the oral opening (the hypostomal spines), and then give way to elongated spines in the areas underneath the outer edges of polyps (the circumpolypar spines). Spines of intermediate length are present between polyps in the Acanthopathinae (Opresko, 2004).

Genus *Aphanipathes* Brook, 1889

The genus *Aphanipathes* is characterized by colonies that are irregularly branched like a bush or broom, and skeletal spines that penetrate through the coenenchyme (Brook, 1889; Pax, 1932; Opresko and Baron-Szabo, 2001; Opresko, 2004).

Aphanipathes verticillata mauiensis Opresko et al., 2012

Undescribed Aphanipathidae: (Wagner et al., 2010, p. 274, Figure 10); *Aphanipathes* sp.: (Wagner et al., 2011b, p. 1325); *Aphanipathes verticillata*: (Wagner et al., 2011c, pp. 211–225, Figures 1j, 2c); *Aphanipathes verticillata*: (Wagner et al., 2012a, pp. 799, 804); *Aphanipathes verticillata mauiensis*: (Opresko et al., 2012, pp. 24–39, Figures 1b, 4a–d, 5a–d, 8a–d); *Aphanipathes verticillata mauiensis*: (Brugler et al., 2013, pp. 312–361, Figures 1–5).

During black coral surveys conducted off West Maui in 2008–2009, numerous specimens superficially resembling *Antipathes griggi* were collected (Opresko et al., 2012). Upon closer examination of the skeletal spines, these specimens proved to be morphologically very different from *A. griggi*, and similar to *Aphanipathes verticillata* Brook, 1889, a species never before reported from the Hawaiian Islands. Subsequent comparisons of the *A. verticillata* holotype to Hawaiian specimens revealed various morphological similarities, although the Hawaiian form is considered a distinct subspecies (*A. verticillata mauiensis*) due to unique features of its skeletal spines (Opresko et al., 2012). In particular, the tubercles on the skeletal spines of *A. verticillata mauiensis* occur in lower densities than on the holotype of this species, which has been assigned to the new subspecies *A. verticillata verticillata* Opresko et al., 2012. A detailed taxonomic description of *A. verticillata mauiensis* is presented by Opresko et al. (2012), and briefly summarized here. Colonies are up to 1 m in height or more, with up to 10 orders of branching. The branches are generally pointed straight upwards or slightly curved (Figures 6D–F). On terminal branchlets, polypar spines are typically 90–266 μm tall and abpolypar spines generally 54–201 μm in height. Skeletal spines are arranged in verticils with spines in the same row typically spaced 200–507 μm apart (Figures 6H–J). Spines are covered with distinct conical tubercles over the largest portion of their surface of both

polypar and abpolypar spines. Polyps are on average 1.35 mm in transverse diameter (range = 0.72–1.81 mm), arranged on a single side of the corallum on terminal branches, and spaced 0.89–2.76 mm apart, resulting in 6 polyps per cm (range = 5–8) (Figure 6G).

A. verticillata was originally described from off Mauritius (Brook, 1889). Later, two other *A. verticillata* specimens were collected off Okinawa at a depth of 79 m (Table 1). All Hawaiian specimens examined as part of this study were collected at depths between 88 and 130 m in the the Au'au Channel, located between the islands of Maui and Lāna'i (Table 1).

Subfamily Acanthopathinae Opresko, 2004

The subfamily Acanthopathinae is characterized by skeletal spines of different heights in the areas underneath polyps. Hypostomal spines are reduced in size, whereas circumpolypar spines are substantially elongated. Spines of intermediate length are present between polyps in the Acanthopathinae (Opresko, 2004). The name of this subfamily is derived from the Greek root *acantho* meaning spiny, in reference to the enlarged size of its circumpolypar spines (Opresko, 2004).

Genus *Acanthopathes* Opresko, 2004

The genus *Acanthopathes* is characterized by colonies that are branched in a single plane like a fan, and spines that are either greatly reduced or absent in the areas directly below the oral cone (Opresko, 2004).

Acanthopathes undulata (Van Pesch, 1914)

Aphanipathes undulata: (Van Pesch, 1914, pp. 87–89, Figures 74–76, Pl. VIII Figure 8); *Antipathes undulata*: (Grigg and Opresko, 1977, pp. 242–261, Figure 5); *Acanthopathes undulata*: (Opresko, 2004, p. 232); *Acanthopathes undulata*: (Eldredge, 2006, p. 65); *Acanthopathes undulata*: (Parrish and Baco, 2007, p. 186); *Acanthopathes undulata*: (Wagner et al., 2011b, p. 1325).

Grigg and Opresko (1977) were the first to identify *Antipathes undulata* (Van Pesch, 1914) from the Hawaiian Archipelago (Figure 7). In 2004, Opresko reassigned *A. undulata* to the newly established antipatharian family Aphanipathidae and the new genus *Acanthopathes*, resulting in the new name *Acanthopathes undulata*. Van Pesch's (1914) original description of this species emphasized (1) colonies that are fan-shaped and planar, (2) spines that are distally inclined, needle-like, covered with minute tubercles toward the distal half, generally 375–450 μm tall, spaced 150–225 μm apart, and penetrated through the tissues of the polyps, and (3) polyps that are arranged on one side of the colony and spaced 1.1 mm apart. These features are all consistent with the Hawaiian specimens examined here (Figure 7). Additionally, a fragment of the holotype was examined under SEM (USNM 100409), and its spines are also very similar to the Hawaiian specimens in terms of shape, arrangement and size (Figures 7D,J,K). Furthermore, this comparison also highlights the differences in relative sizes of the skeletal spines on the side of the branch bearing the polyp, being greatly reduced underneath the oral cone,

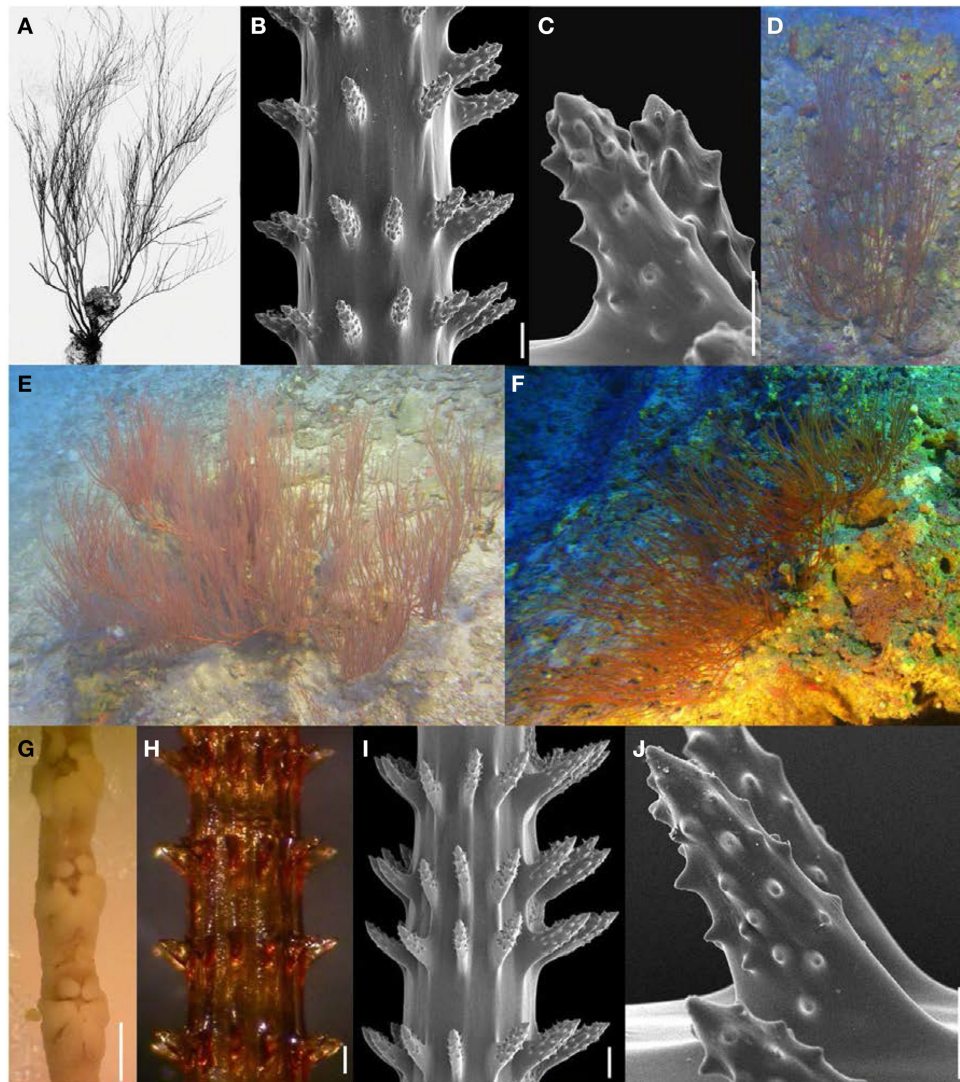


FIGURE 6 | (A–C) *Aphanipathes verticillata verticillata* holotype (MCZ 68) showing (A) entire specimen, (B,C) skeletal spines under SEM (scale bars: (B) = 100; μm ; C = 50 μm). (D–J) *A. verticillata mauiensis* specimens showing (D–F) colonies *in situ*, (G) preserved polyps on terminal branch

under light microscopy (scale bar = 1 mm), (H) skeletal spines on terminal branch under light microscopy (scale bar = 100 μm), (I) skeletal spines on terminal branch under SEM (scale bar = 100 μm), and (J) close-up of polypar spine under SEM (scale bar = 50 μm). (D–F) Photos courtesy of HURL).

and enlarged toward the outer edges of polyps (Figures 7I,J). Collectively, the comparison of *A. undulata* type material to Hawaiian specimens corroborates previous identifications of this species from Hawaiian waters (Grigg and Opresko, 1977; Chave and Malahoff, 1998; Eldredge, 2006; Parrish and Baco, 2007). Additionally, this comparison revealed several characteristic features of the species, which have previously not been described. Colonies are fan-shaped, typically smaller than 50 cm in height, and are extensively branched giving the appearance of a net (Figures 7E–H). Polyps are arranged on a single side of fan-shaped colonies, are typically 0.87 mm in transverse diameter (range = 0.50–1.15 mm) and spaced 1.26 mm apart (range = 1.01–1.58 mm), resulting in 8 polyps per cm (range = 7–8) (Figures 7C,I). The spines are needle-like in shape and penetrate

through the soft tissues, except for the area underlying the oral cone (Figures 7C,I). On the side of the fan not bearing the polyps, spines are uniform in height and average 204 μm (range = 113–329 μm). In contrast, the side of the colony bearing polyps contains skeletal spines of varying lengths (Figure 7J). The tallest spines are located in the area underneath the outer edges of polyps and reach heights of 270–459 μm , whereas the shortest spines are situated in the area underneath the oral cone and reach heights of 85–257 μm . Skeletal spines are smooth or gently adorned with fine papillae toward the distal portion of the spine (Figures 7D,K). Spines are arranged in regular rows with adjoining rows being offset in a spiral pattern around the corallum (Figure 7J). Within a row, spine spacing is typically variable and ranges between 155 and 361 μm . The color of living

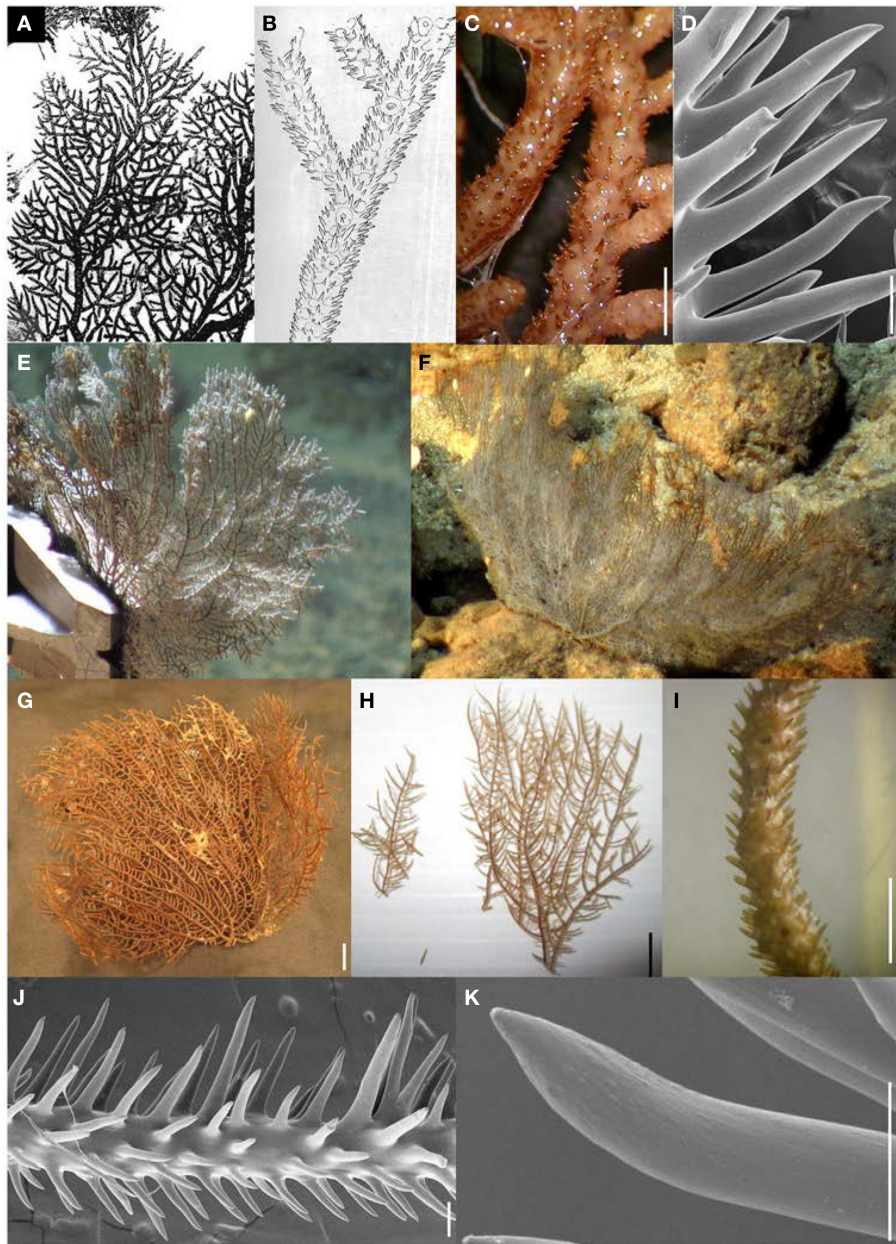


FIGURE 7 | (A,B) Plates accompanying the original description of *Acanthopathes undulata* (Van Pesch, 1914); **(C)** spines of schizoholotype (USNM 100409) under light microscopy (scale bar = 1 mm); **(D)** spines of schizoholotype under SEM (scale bar = 100 μ m); **(E,F)** *in situ* photographs of colonies from Hawaiian waters;

(G,H) specimens from Hawai'i (scale bars = 1 cm); **(I)** spines and polyps on terminal branch under light microscopy (scale bar = 1 mm); **(J)** spines on terminal branch under SEM (scale bar = 100 μ m); **(K)** close-up of spine under SEM (scale bar = 30 μ m). **(E,F)** Photos courtesy of HURL.

colonies is grayish-white, and is influenced by the skeletal spines that penetrate through tissues and give colonies a brownish hint (Figures 7E,F).

Acanthopathes undulata was originally described from specimens collected at 113 m in the Solor Strait off Indonesia (Van Pesch, 1914), and later reported from Hawai'i (Grigg and Opresko, 1977; Chave and Malahoff, 1998; Eldredge, 2006; Parrish and Baco, 2007) and the Mariana Islands (Paulay et al.,

2003). All Hawaiian specimens examined as part of this study were collected throughout the Hawaiian Islands from Hawai'i to Laysan at depths ranging between 30 and 269 m (Table 1).

Family Myriopathidae Opresko, 2001

The Myriopathidae are characterized by polyps with 10 mesenteries (six primary and four secondary), that are 0.5–1.0 mm in transverse diameter and possess short tentacles

with rounded tips. The skeletal spines of the Myriopathidae are usually blade-like or needle-like on smaller branches, and frequently forked or antler-like on the main stem and larger branches (Opresko, 2001; Opresko and Sanchez, 2005; Daly et al., 2007; Bo, 2008; Moon and Song, 2008b). The name of the Myriopathidae is derived from the Greek word *myriophylla* meaning many branches, in reference to the extensive branching of colonies within this family.

Genus *Myriopathes* Opresko, 2001

The genus *Myriopathes* contains colonies, whose highest order branches are pinnulated, i.e., they contain ramifications that are arranged symmetrically in a plane like a fern. Furthermore, *Myriopathes* pinnules are themselves always branched giving rise to secondary and tertiary subpinnules (Opresko, 2001; Moon and Song, 2008b).

Myriopathes cf. *ulex* (Ellis and Solander, 1786)

Antipathella sp.: (Grigg, 1964, pp. 11, 14, Figure 5); *Antipathes ulex*: (Grigg and Opresko, 1977, p. 244); *Antipathes ulex*: (Grigg, 1993, pp. 50, 56); *Antipathes ulex*: (Montgomery and Crow, 1998, pp. 103–108); *Antipathes ulex*: (Chave and Malahoff, 1998, p. 40, Figure 93); *Myriopathes ulex*: (Opresko, 2001, pp. 349, 351–352); *Antipathes ulex*: (Montgomery, 2002, pp. 157–164); *Myriopathes ulex*: (Fenner, 2005, p. 101, 2 unnumbered figure on p. 101); *Antipathes ulex*: (Boland and Parrish, 2005, pp. 411–420); *Myriopathes ulex*: (Eldredge, 2006, p. 65); *Myriopathes ulex*: (Hoover, 2006, p. 70, unnumbered figure on p. 70); *Myriopathes ulex*: (Parrish and Baco, 2007, pp. 162–163, 170, 186); *Myriopathes ulex*: (Kahng and Kelley, 2007, p. 684); *Myriopathes ulex*: (Bo, 2008, unnumbered figure in app. 1); *Antipathes ulex*: (Grigg, 2010, p. 3); *Myriopathes ulex*: (Wagner et al., 2011a, pp. 249–255, Figure 3); *Myriopathes ulex*: (Wagner et al., 2011b, p. 1325); *Myriopathes ulex*: (Wagner et al., 2011c, pp. 212, 214); *Myriopathes ulex*: (Wagner et al., 2012a, p.796); *Myriopathes ulex*: (Wagner et al., 2012a, pp. 67–132, Figure 2.1b); *Myriopathes ulex*: (Wagner et al., 2013, pp. 341–342, Figure 1 left); *Myriopathes ulex*: (Wagner et al., 2014, pp. 4, 8).

Along with *Antipathes griggsi* and *A. grandis*, *Myriopathes* cf. *ulex* (Figure 8) is the third antipatharian species that has been targeted by the Hawaiian black coral fishery (Grigg, 1993, 2010; Wagner et al., 2011a). However, in comparison to *A. griggsi* and *A. grandis*, harvesting of *M. cf. ulex* is much less frequent, because the species is quite rare in the 40–75 m depth zone where black coral harvesting takes place in Hawai'i (Grigg, 2001, 2002; Boland and Parrish, 2005). Grigg (1964) presented the first published account of *M. cf. ulex* from Hawai'i (as *Antipathella* sp.). Since then, brief descriptions of this Hawaiian species were presented by Chave and Malahoff (1998), Fenner (2005) and Hoover (2006). The main distinguishing features of this species, are its large (up to 3 m), fan-shaped colonies that consist of small feather-like branchlets or pinnules (Figures 8A–C). This characteristic branching pattern gives rise to the common name of this species: feathery black coral. Polyps are on average 0.56 mm in transverse diameter (range = 0.32–0.92 mm), and generally spaced 0.84 mm apart (range = 0.31–1.71) resulting in 12 polyps per cm (range 8–15). On the highest order branches,

spines are blade- to needle-like in shape and inclined distally (Figures 8F–H), with polypar spines generally 122 μ m in height (range = 76–196 μ m), and abpolypar spines typically 92 μ m in height (range = 51–172 μ m). Spines are smooth or covered with faint papillae, and are arranged in regular rows on the highest order branches, with spines in the same row typically spaced 177 μ m apart (range = 70–366 μ m). On the main stem and thicker branches, many spines are forked at their apex.

Grigg and Opresko (1977) were the first to identify *Antipathes ulex* Ellis and Solander, 1786 from Hawaiian waters. In 2001, Opresko reassigned *A. ulex* to the newly established antipatharian family Myriopathidae and the new genus *Myriopathes*, resulting in the name *Myriopathes ulex* (Opresko, 2001; Eldredge, 2006). The original species description is rather brief and highlighted short skeletal spines and numerous epibionts including barnacles, which Ellis and Solander (1786) incorrectly identified as the ovaries of the black coral. The two plates accompanying the species description show a planar and pinnulated branching pattern (Figures 8A,B), features that are also characteristic of the Hawaiian specimens examined here (Figures 8C–E). Unfortunately, the type material of *M. ulex* has been lost (Opresko, 2001), and therefore no further comparisons can be made until a neotype is designated. Pending such taxonomic revisions, the name *Myriopathes* cf. *ulex* is used to refer to the Hawaiian specimens examined here, which were collected throughout the Hawaiian Archipelago from Hawai'i Island to Pearl and Hermes Atoll at depths between 41 and 326 m, as well as off Johnston Atoll at 61 m (Table 1). *Myriopathes ulex* was originally described from Indonesia (Ellis and Solander, 1786), but subsequently reported throughout the Indo-West Pacific at depths ranging between 25 and 364 m (Blainville, 1834; Gray, 1857; Brook, 1889; Van Pesch, 1914; Grigg and Opresko, 1977; Colin and Arneson, 1995; Chave and Malahoff, 1998; Parrish and Baco, 2007; Rogers et al., 2007; Bo, 2008; Moon and Song, 2008b). However, a thorough taxonomic investigation is needed to verify whether all of these records correspond to the same species that is present in Hawaiian waters.

Species Key of Hawaiian Shallow-Water Antipatharians

- | | |
|--|--|
| 1a. Colonies unbranched (wire like)..... | 2 |
| 1b. Colonies branched | 4 |
| 2a. Polyps in multiple rows..... | <i>Cirripathes</i> cf. <i>anguina</i> |
| 2b. Polyps in a single row | 3 |
| 3a. Polyps ~1 mm in diameter with adjacent polyps separated by a well defined interpolypar space | <i>Stichopathes echinulata</i> |
| 3b. Polyps ~1.85 mm in diameter with adjacent polyps crowded together tightly | <i>Stichopathes?</i> sp. |
| 4a. Colonies bushy | 5 |
| 4b. Colonies fan-shaped | 7 |
| 5a. Spines arranged in verticils around thinner branches..... | <i>Aphanipathes verticillata mauiensis</i> |

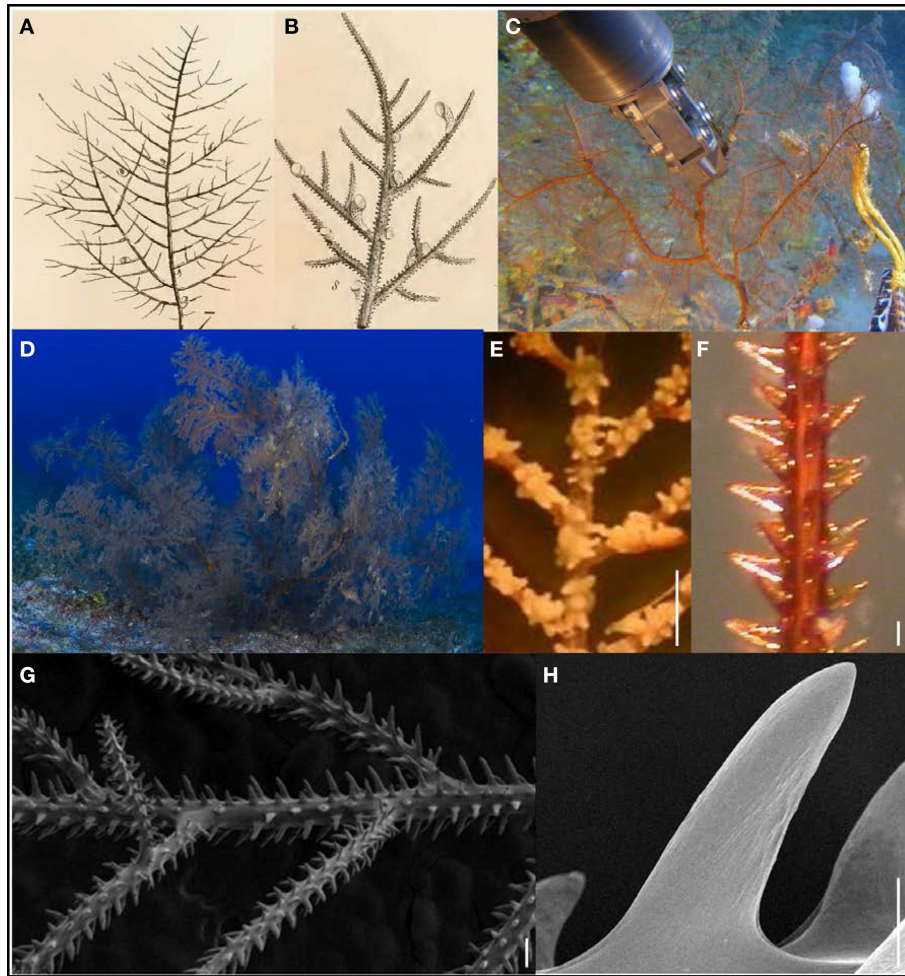


FIGURE 8 | (A,B) Plates accompanying the original description of *Myriopathes ulex* (Ellis and Solander, 1786), a species for which the type material is now lost. **(C,D)** *In situ* photographs of colonies from Hawaiian waters; **(E)** preserved polyps of Hawaiian species under light microscopy

(scale bar = 1 mm); **(F)** spines on terminal branch under light microscopy (scale bar = 100 μ m); **(G)** spines on terminal branch under SEM (scale bar = 200 μ m); **(H)** close-up of polypar spine under SEM (scale bar = 50 μ m). (Photos courtesy of **C** HURL, and **D** Greg McFall).

- 5b. Spines not arranged in verticils around thinner branches..... 6
- 6a. Some spines with bifurcation on apex and secondary spines ($\leq 40 \mu\text{m}$ tall) present on thicker branches..... *Antipathes griggi*
- 6b. Spines without bifurcations on apex, and no secondary spines present on any parts of the corallum.....*Antipathes grandis*
- 7a. Colonies small (<0.5 m) and densely reticulated giving the appearance of a net.....*Acanthopathes undulata*
- 7b. Colonies large (<3 m) with highest order branches forming symmetric pinnules like a fern.....*Myriopathes cf. ulex*

previously grouped due to taxonomic constraints in ecological surveys. As a result, potential ecological differences amongst various antipatharian species have not been identified, which is critical information for the management of the Hawaiian black coral fishery. At least three different species with different habitat preferences have been targeted by the Hawaiian black coral fishery (*Antipathes griggi*, *A. grandis*, and *Myriopathes cf. ulex*); however, the fishery has historically been managed as a single stock, in large part due to difficulties in identifying the targeted species. In addition to fishery management applications, the combined use of various morphological characters may help in future systematic studies among the Antipatharia, a taxonomic order that has been notoriously problematic.

Conclusion

The use of traditional taxonomic characters, including branching pattern, polyp and skeletal spine morphology, provides a comprehensive basis for the classification of the shallow-water Hawaiian black coral fauna, an assemblage that has been

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Conflict of Interest Statement: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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