Sea anemones (Cnidaria: Actiniaria) of the Faroe Islands: A preliminary list and biogeographic context

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Abstract

We have identified 20 species of sea anemones (order Actiniaria) from BIOFAR material, eight of them new records for the Faroe Islands. This brings the total number of anemone species known thus far from the Faroes to 30. The Faroes shares six (or possibly only five) of those 30 species with Norway, Iceland, and the Shetland Islands, probably 10 (but possibly 11) with Norway and Iceland, two with Norway and the Shetlands, three with only Norway, three with only Iceland, and one with only the Shetlands. The other five species are known from elsewhere in the North Atlantic. They came from 69 of the 1,331 stations sampled in the BIOFAR program. Of the 20 species we identified, 10 were found at only one BIOFAR station, and no more than three were collected at any one site. Additional specimens, comprising perhaps 10 species from 66 more stations, await identification. Taxonomic issues impede clearly synthesizing the sea anemone biogeography of the Faroe Islands.

Introduction

We have identified 20 species of sea anemones *sensu strictu* (order Actiniaria) collected at 69 BIOFAR stations; eight are new records for the Faroe Islands (Table 1). We anticipate enlarging this inventory by no more than 10 species from material left to be identified that was collected at an additional 66 stations; many of the remaining specimens are likely to be unidentifiable to species because they are damaged or poorly preserved. In the only previous explicit study of this fauna, Carlgren (1930) recorded 11 species of actiniarians in addition to two species of zoanthids; we found seven of those anemones. Deep-water records for the Faroes are included in Danielssen's (1890) monograph, Carlgren's (1905) note dealing mainly with the fiords of northern Norway, and Carlgren's (1921, 1942) compendia from the Danish Ingolf Expedition. The most recent report on Faroes anemones is that of den Hartog (1986).

In this contribution, we present a preliminary biogeographic analysis of the Faroese actiniarian fauna, which is about equally similar to those of Norway and Iceland, but richer than that of the Shetland Islands. Taxonomic confusion and impreci-

Table 1. *Species of Actiniaria identified from the BIOFAR Programme. New records for the Faroe Islands are indicated in bold. Depth is given as a range for species collected at more than one site. Asterisks indicate stations from which multiple species were collected. Depths, sediment types, and their abbreviations from Nørrevang et al. (1994): c = coarse; C = cobbles and stones; f = fine; F = fines (clay and silt); G = gravel; hb = hard bottom; M = mud (fines with organic material); S = sand; sb = soft bottom; SH = bivalve shells; Shg = shell gravel.*

Species	Stations	Depth (m)	Sediment types
***Acthelmis intestinalis* (Fabricii, 1780)**	502*	890	F, G, sb
***Actinauge richardi* (Marion, 1882)**	693	290	fS
***Allantactis parasitica* Danielssen, 1890**	149, 169, 563, 755, 9012	252-1030	C, F, sb
Amphianthus margaritaceus (Danielssen, 1890)	328, 536*	400-435	hb
Bathyphellia margaritacea (Danielssen, 1890)	720, 750*, 769	600-700	C, F, fS, G, M, S
Bolocera tuediae (Johnston, 1832)	027, 049, 233, 486, 602, 649, 691	225-380	C, cC, F, G, hb, S
***Cactosoma abyssorum* Danielssen, 1890**	728*	640	cG
***Edwardsia andresi* Danielssen, 1890**	728*	640	cG
Edwardsia danica Carlgren, 1921	9018*	503	cS
Edwardsia tuberculata Düben and Koren, 1847	9018*	503	cS
***Halcampoides abyssorum* Danielssen, 1890**	294, 420, 425, 501, 705, 729, 730*, 731, 750*	597-1096	C, G, F, fC, fS, M, S, sb
Hormathia digitata (Müller, 1776)	381, 467, 524*, 779	402-421	C, G, F, M, S
Liponema multicornis (Verrill, 1880)	492	900	fS
***Monactis vestita* (Gravier, 1918)**	477, 505, 516, 524*, 525*, 1807	350-1150	C, F, G, S
Parasicyonis sarsii Carlgren, 1921	453	400	C, S
Phelliactis hertwigi Simon, 1892	536*	435	
Phelliactis robusta Carlgren, 1928	525*	1006	G
***Scolanthus ingolfi* (Carlgren, 1921)**	082, 267, 502*, 730*	890-949	C, G, F, S, sB
Stomphia coccinea (Müller, 1776)	120, 500, 540, 597*, 717, 767	100-714	C, cC, F, fG, G, Sh
Urticina eques (Linnaeus, 1761)	003, 371, 455, 597*, 1015, 1018, 1025, 1223, 1232, 1416, 1517, 1574, 1575, 1577, 1581, 1587, 1595, 1638, 1662, 1674, 1675, 1796	5-103	C, Sh, Shg

sion confound the interpretation of the biogeography of several species found in the Faroe Islands. In a later publication, as we resolve some of the ambiguities, we will provide taxonomic details for the species in the BIOFAR collection.

Materials and methods

Specimens were examined whole for information on gross anatomy. To obtain histological information, longitudinal and cross-sectional serial sections were made from selected specimens following established protocols (e.g., White *et al*., 1999). We identified the types of cnidae and their sizes from key regions on the body of selected specimens. Small amounts of macerated tissue were examined at 1,000x using differential interference microscopy; length and width of undischarged cnidae were measured using ScanPro measurement software (Jandel Scientific Software) and a Summa Sketch digitizing tablet (Summagraphics).

Collection data, including depth and bottom type, are from Nørrevang *et al.* (1994).

We searched the biological component (Fautin, 2003) of the website "Biogeoinformatics of Hexacorals" (Fautin and Buddemeier, 2003) for occurrence records of sea anemones from the Faroe Islands, Iceland, Norway, and the Shetland Islands. Virtually all taxonomic literature concerning sea anemones and much of the ecological literature is now searchable through that site. To be certain we found all locality records for a species, we used three search strategies, and then double-checked those records with their literature sources. On a map display of sea anemone occurrences (search sequence "Distributional data"/"Locality on map"/"World map") focused in on the N Atlantic, we clicked each spot displayed for the Faroes, Iceland, Norway, and the Shetlands to find the name of the species recorded as occurring there. We searched for anemone records within the EEZ of the Faroes, Iceland, and Norway (search sequence "Distributional data"/"Locality by name"/"EEZ name"). And we searched for anemone records by the names Faroe Islands, Iceland, Norway, and Shetland Islands (search sequence "Distributional data"/"Locality by name"/"Place name"). The first two strategies found records in the database that were georeferenced (contained latitude and longitude); the last found records that contained a verbal description of the locality that included the name of the country. Some records were found in all searches, but those that were not georeferenced were found only in the last, and those that contained no verbal locality description were found only in the first two. We include in our tally all species found within the EEZ of the Faroes, Iceland, and Norway; since the EEZ extends to 200 nautical miles offshore, we include some records rather remote from land that might not be attributed to the country in a visual search. Because the Shetland Islands does not have sovereign status, it has no EEZ; searching on "Shetland" by name also brings up records for the South Shetland Islands, which we ignored.

Results

Actiniarians were collected in 135 of the 1,331 stations of BIOFAR programmes (Tables 1 and 2), most using a detritus sledge or a heavy triangular sampler. The 20 species we have thus far identified came from 69 of those stations: 10 were found at only one station, the other 10 at 2-22 stations (Table 1). No more than three ac-

Table 2. *Stations from which actiniarian specimens not yet identified to species were collected; station data as for Table 1. Sediment types not identified by Nørrevang et al. (1994) abbreviated as follows: B = boulders; Ct = concrete. "Identifying information" includes family or other higher taxonomic assignment, or ecological information that may be relevant to identification.*

Station	Depth (m)	Sediment type	Identifying information	Station	Depth (m)	Sediment type	Identifying information
65	322		on gastropod shell	723	1015	F, fG	
192	107			724	191	Shs, C	Edwardsiidae
227	1098	S, G	Athenaria	727	500	C, G	Endomyaria
304	1061	F, G, C	on gastropod shell	730	949	F, G, C	
			containing hermit	737	850	FG	
			crab	748	498	M, cG	
320	133	C, G		773	705	M, F, C	
400	242	FG, cC		776	200	C, Shg	
452	416			781	80	Shs	
453	400	S, C	Actinostolidae	1023	5		
458	675	G, fC	Hormathiidae	1140	2		on aggregated
470	335	Hb	Hormathiidae				worm tube
477	1150	F, S, C	Hormathiidae	1142	0	B	
483	405	G	Hormathiidae	1175	0	Hb	juvenile
493	800	Sb, F, fsH		1184	2	Ct	
494	703	Sb, fs, C	Boloceroididae	1228	5	Hb	
496	515	FShs, G		1229	15	B	
500	714	G, cC		1395	10		
501	804	Sb, fC	Edwardsiidae	1413	10	B	
503	513	hb, G, C	Hormathiidae	1519	5	Hb	
515	700	S, G	on dead *Lophelia*	1521	15	Hb, B	
520	405	FG, C		1522	10	Hb	
522	514	F, fS, fC		1588	15	Hb	
528	250			1606	74	Hb	
529	260			1612	31	Hb	
543	139	C, Shs		1637	20	B, C	
548	100	G, Shs, cC		1642	10	B, C, Shg	
564	1500	Sb		1705	90	Shg	
584	105			1740	76	Hb	
599	240		Acontiaria	1746	41	Hb	
604	260	cC		1750	65	Shg	
605	100	MS		1789	60	Shg, Shs	
607	70	S		1790	56	S	on flat piece of shell
609	90	M, S, Sh		1801	55	B	
615	950			1810	35	Hb	
646	600	G, C		1814	92	Shg, Shs	
721	810	F, fS		1834	100	Shg, Shs	Acontiaria

tiniarian species were collected at any one site (Table 3). Typically more than one individual of a species is represented in material from a single site, but quantitative comparisons are impossible because of the diversity of collecting gear used.

Table 3. *BIOFAR stations at which multiple species of Actiniaria were collected. Unidentified specimens lack the diagnostic attributes of the identified species with which they co-occur. The two unidentified species at Sta. 304 differ in external morphology and habit: one has a low, wide column with an expanded pedal disc attached to a gastropod shell, the other has a stout, cylindrical column equal in diameter along its length. The unidentified specimen at Sta. 730 has a distinct pedal disc, placing it in the suprafamilal group Thenaria; a specimen of* H. abyssorum *or* S. ingolfi *has a rounded proximal end rather than a distinct pedal disc and thus belongs to the suprafamilial group Athenaria.*

Station	Depth (m)	Species	Species	Species
304	1061	UnID	UnID on gastropod shell	
477	1150	*M. vestita*	Hormathiidae	
500	714	*S. coccinea*	UnID	
501	804	*H. abyssorum*	Edwardsiidae	
502	890	*A. intestinalis*	*S. ingolfi*	
524	702	*M. vestita*	*H. digitata*	
525	1006	*M. vestita*	*P. robusta*	
536	435	*P. hertwigi*	*A. margaritacea*	
597	100	*S. coccinea*	*U. eques*	
728	640	*E. andresi*	*C. abyssorum*	
730	949	*H. abyssorum*	*S. ingolfi*	UnID Thenaria
750	600	*H. abyssorum*	*B. margaritacea*	
9018	530	*E. danica*	*E. tuberculata*	

Eight of the species we identified have not previously been recorded from the Faroes (Tables 1, 4). Their reported distributions, according to summaries in Fautin (2003), are highly varied. *Acthelmis intestinalis* has been recorded from Greenland and the Shetland Islands. *Actinauge richardi* and *Edwardsia andresi* are widespread in the N Atlantic. *Allantactis parasitica* is circumboreal. *Cactosoma abyssorum* has been recorded only from high latitudes off Norway. *Halcampoides abyssorum* is recorded from the Antarctic as well as off Norway. *Monactis vestita* has been recorded in mid-latitudes of the Pacific as well as the Atlantic. *Scolanthus ingolfi* was previously known from a single locality between Iceland and Greenland.

In summary, 30 species of actiniarians are currently known from the Faroe Islands (Table 4). The status of a 31st species is uncertain: Danielssen (1890) described *Kodiodes pedunculata* from near the Faroe Islands, but it has not been mentioned in the literature since, and Carlgren's (1949) catalog does not include it.

In Table 4, we document occurrence of the 30 species also in Norway, Iceland, and the nearest archipelago of comparable size, the Shetland Islands. Five species are found in all four places and another probably is, but there is uncertainty about the species to which the name refers, so it may actually occur only in Norway and Iceland, other than the Faroes. Aside from that one, 10 species are known from Norway and Iceland, in addition to the Faroes, but not the Shetlands (the records of *Bathyphellia margaritacea* in Icelandic waters are from within the EEZ quite far northeast of the is-

Table 4. *Occurrence of actiniarians known from the Faroe Islands in Norway, Iceland, and the Shetland Islands based on specimens we examined ("BIOFAR") and from the literature, with source for the information and name used in the publication. Asterisks indicate ambiguity in name use. The Faroes records for* Liponema multicornis *and* Phelliactis hertwigi *were from Thor Expedition station 99; Carlgren's (1921, page 144) placing the station "In the neighbourhood of Bear Island" is incorrect (Ole Tendal, pers. comm.).*

Valid name	Faroes	Norway	Iceland	Shetland Islands
Acthelmis intestinalis (Fabricii, 1780)	BIOFAR			Pennant, 1812 [as *Actinia truncata*]
Actinauge richardi (Marion, 1882)	BIOFAR	Carlgren, 1942		Carlgren, 1942
Actinia equina (Linnaeus, 1758)	Carlgren, 1930	Carlgren, 1921; Jaworski, 1938		Carlgren, 1921
Allantactis parasitica Danielssen, 1890	BIOFAR	Danielssen, 1890; Riemann-Zürneck, 1994	Carlgren, 1939; 1942	
Amphianthus margaritaceus (Danielssen, 1890)	BIOFAR; Carlgren, 1942	Danielssen, 1890 [as *Korenia margaritacea*]	Carlgren, 1942	
Bathyphellia margaritacea (Danielssen, 1890)	BIOFAR; Carlgren, 1942	Danielssen, 1890 [as *Phellia margaritacea*]; Riemann-Zurneck, 1997	Carlgren, 1942	
Bolocera tuediae (Johnston, 1832)	BIOFAR; Carlgren, 1921; 1930; den Hartog, 1986	Carlgren, 1921; Gravier, 1922	Carlgren, 1939	Norman, 1869 [as *Bulocera tuediae*]
Cactosoma abyssorum Danielssen, 1890	BIOFAR	Danielssen, 1890		
Cribrinopsis similis Carlgren 1921	Carlgren, 1921; 1930	Carlgren, 1921	Carlgren, 1921; 1939	
Daontesia praelonga (Carlgren, 1928)	Carlgren, 1942		Carlgren, 1942	
Edwardsia andresi Danielssen, 1890	BIOFAR	Danielssen, 1890; Carlgren, 1905; 1921; Daly, 2002	Carlgren, 1939	
Edwardsia danica Carlgren, 1921	BIOFAR; Carlgren, 1930			
Edwardsia tuberculata Düben and Koren, 1847	BIOFAR; Carlgren, 1930	Carlgren, 1921; Daly, 2002	Carlgren, 1921; 1939	
Halcampoides abyssorum Danielssen, 1890	BIOFAR	Danielssen, 1890 [as *H. abyssorum* and *Fenja mirabilis*]		
Halcampoides purpurea (Studer, 1879)	Carlgren, 1921	Carlgren, 1921	Carlgren, 1921; 1939	

Valid name	Faroes	Norway	Iceland	Shetland Islands
Hormaigitata (Müller, 1776)	BIOFAR; Carlgren, 1930; 1942	Gravier, 1922 [as *Chondractinia digitata*], Carlgren, 1942	Carlgren, 1939; 1942	*Pennant, 1812 [as *Actinia crassicornis*]; Norman, 1869 [as *Tealia digitata*]; Haddon, 1889 [as *Hormathia margaritae*]
Hormathia nodosa (Fabricii, 1780)	Carlgren, 1930	Carlgren, 1942	Carlgren, 1939; 1942	
Kadosactis rosea Danielssen, 1890	Danielssen, 1890	Danielssen, 1890; Carlgren, 1942	Carlgren, 1942	
Liponema multicornis (Verrill, 1880)	BIOFAR; Carlgren, 1921 [as *Bolocera multicornis*]			
Metridium senile (Linnaeus, 1761)	Carlgren, 1905; 1930 [as *M. dianthus*]; 1942 [as *M. s. dianthus*]	Carlgren, 1905 [as *M. dianthus*]; 1942 [as *M. s. dianthus*]	Carlgren, 1939; 1942	Norman, 1869 [as *Actinoloba dianthus*]
Monactis vestita (Gravier, 1918)	BIOFAR			
Parasicyonis sarsii Carlgren, 1921	BIOFAR; Carlgren, 1921	Carlgren, 1921	Carlgren, 1921; 1939	
Phelliactis hertwigi Simon, 1892	BIOFAR; Carlgren, 1942		Carlgren, 1942	
Phelliactis robusta Carlgren, 1928	BIOFAR; Carlgren, 1942		Carlgren, 1942; Doumenc, 1975	
Pycnanthus laevis Carlgren, 1921	Carlgren, 1921			
Sagartia troglodytes (Price in Johnston, 1847)	Carlgren, 1930, 1942	Carlgren, 1942	Carlgren, 1939; 1942	Norman, 1869
Sagartiogeton laceratus (Dalyell, 1848)	den Hartog, 1986	Carlgren, 1942		
Scolanthus ingolfi (Carlgren, 1921)	BIOFAR			
Stomphia coccinea (Müller, 1776)	BIOFAR; Carlgren, 1930; den Hartog, 1986	Carlgren, 1921	Carlgren, 1939; 1942	*Norman, 1869 [as *Stomphia churchiae*]
Urticina eques (Gosse, 1860)	BIOFAR; Carlgren, 1930 [as *U. (Tealia) felina coriacea*]; den Hartog, 1986	Carlgren, 1893 [as *U. crassicornis*]; 1905 [as *Tealia* (*Madoniactis*) *lofotensis*]; 1921 [as *U. f. lofotensis, U. f. crassicornis,* and *U. f. tuberculata*]	Verrill, 1869 [as *U. crassicornis*]; Carlgren, 1921 [as *U. f. crassicornis*)]; 1939 [as *Tealia felina*]	Pennant, 1812 [as *Actinia crassicornis*]; Norman, 1869 [as *Bulocera eques*]; *Norman, 1869 [as *Stomphia churchiae*]

land Carlgren, 1942). Two species are shared with Norway and the Shetlands but not Iceland, and none occurs in the three island groups but not Norway. Three Faroese species are shared exclusively with Norway, three with Iceland, and one with the Shetlands. The five species found in the Faroes but not in Norway, Iceland, or the Shetlands are all known from elsewhere in the N Atlantic, and some more widely (Fautin, 2003).

Discussion

We found seven of the 11 species recorded in the only previous publication on Faroe sea anemones, that of Carlgren (1930). One of those seven, *Urticina* (*Tealia*) *felina coriacea*, which we identify as *U. eques*, was the most commonly obtained species, collected at 22 shallow stations. Two of the four species in Carlgren's list that we have not found, *Actinia equina* and *Metridium dianthus* (now considered *M. senile*), also are typical of shallow water. We infer, because no other anemones we have identified came from diving depths, that the shallow sampling by BIOFAR may have been biased – anemones of the genus *Urticina* are large and conspicuous, whereas the other two may not be. The site diversity of the deep-sea BIOFAR anemones is typical: no more than two species of anemones were reported from any *Challenger* station, for example (Hertwig, 1882; 1888, summarized by Fautin, 2003).

The diversity of Actiniaria in the Faroe Islands appears to be greater than that of the Shetland Islands and about equal to that of Iceland (Carlgren, 1939; Fautin, 2003), but more than twice as many species have been reported from Norway (Fautin, 2003). Part of this difference may be attributable to collecting effort: the shallow-water sea anemones of both the Faroes and Iceland remain largely unknown. However, given the relative length of the Norwegian coast, it is likely to have a larger biota. It is premature to attempt to analyze the biogeographical affinities of the Faroese actiniarian fauna because of the small number of samples of most species in the Faroes and limited distributional knowledge of them elsewhere.

In addition, problems of taxonomy obscure a clear biogeographic interpretation of the fauna of the Faroe Islands and the biogeographic patterns of particular species. Some of the species found in the Faroes have been reported from elsewhere under a different name (Table 4). We have addressed this problem in part by reporting published records under the current valid names. However, in some instances it is impossible to determine which species was meant. For example, Norman (1869) reported *Stomphia churchiae* from the Shetland Islands, a name that has been applied to both *S. coccinea* and *Urticina eques*, but since Norman also reported the latter as *Bulocera eques*, we infer his record refers to the former. Pennant's (1812) record of *Actinia crassicornis* in the Shetlands cannot be so easily resolved: the name has been applied to two Faroes species, *Hormathia digitata*, which has been recorded from the Shetlands by others, and *U. felina*, which has not. Carlgren's (1921) citation of *Halcampoides purpurea* may refer to specimens of *H. abyssorum* because he consid-

ered them to be synonyms. Riemann-Zürneck (1993) distinguished between the two based on cnidom and morphology. We identified *H. abyssorum* from the BIOFAR samples, and found no specimens we could attribute to *H. purpurea*. However, specimens that are unambiguously members of *H. purpurea* are known from depths shallower than those sampled during the BIOFAR program, so we cannot rule out the possibility that both *H. abyssorum* and *H. purpurea* occur in the Faroe Islands.

Based on published records, *M. senile* is distributed through much of the northern hemisphere (Fautin, 2003). Populations of *M. senile* from the NW Atlantic, NE Atlantic, and NW Pacific oceans differ genetically (Bucklin and Hedgecock, 1982; Bucklin, 1985), so Fautin *et al.* (1990) recommended recognizing each as a subspecies. Disentangling occurrence records for *Metridium senile* in the NE Atlantic is complicated by the historical use of varietal names. What has in some publications been known as *M. s. dianthus* was considered in others as a distinct species, *M. dianthus*, which Carlgren (1930) reported from the Faroe Islands. Agreeing with Stephenson (1935), Carlgren (1942) later considered *M. dianthus* a variety of *M. senile.* Therefore, we consider Carlgren's (1930) record of *M. dianthus* in the Faroes as *M. senile*.

Urticina, which includes ecologically important species in both the N Atlantic and the N Pacific, has a more confused taxonomic history. More than 20 species names have been used (Fautin, 2003), most associated with the generic name *Tealia*, a junior synonym of *Urticina* (Manuel, 1981; den Hartog, 1986). Although six species are known from the N Pacific (Hauswaldt and Pearson, 1999), supposedly only two occur in European waters (e.g. Manuel, 1981, Cornelius *et al*., 1995). Manuel (1981) regarded *U. tuberculata* as a junior synonym of *U. felina*, and considered the specimens from the NE Atlantic that Carlgren (1921) identified as *T. felina coriacea* to be *U. felina*. den Hartog (1986) identified specimens of *Urticina* from the Faroe Islands as the other species recognized by Manuel (1981), *U. eques*, a species described from Britain that he considered synonymous with at least the NE Atlantic members of *U. lofotensis*. We identified the most abundant anemones in the BIOFAR collection as *U. eques* (Gosse, 1860); we infer this is the species Carlgren (1930) recorded as *U. (T.) felina coriacea*. We suspect, however, from the variability we encountered, that more than one species may be represented. For NE Pacific species, Hand (1955) discarded the epithet *felina*, elevating the five varieties of *Tealia* (= *U.*) *felina* (Linnaeus, 1761) to species as *U. crassicornis* (Müller, 1776), *U. coriacea* (Cuvier, 1798), *U. lofotensis* (Danielssen, 1890), and *U. tuberculata* (Cocks, 1851). All except *U. tuberculata* are known from the NW Pacific and the NW Atlantic; *U. tuberculata* is known only from southern Sweden, southern Norway, and Denmark (Carlgren, 1921). Resolving the circumscription of *Urticina* species will require consideration of specimens from a variety of localities, depths, and habitats.

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