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First shallow record of *Bathyphysa conifera* (Studer, 1878) (Siphonophora, Cystonectae), a live specimen in the Strait of Gibraltar. Worldwide species distribution review

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Abstract

The rarely observed cystonect siphonophore *Bathyphysa conifera* was recorded for the first time in shallow depth water (- 16 m) as a live specimen, at the entrance to the Mediterranean Sea by SCUBA divers. It is a delicate oceanic species, with earlier records coming mostly from deep water, where it readily adheres to deep sea fishing cables and nets, causing painful stings to fishermen. Deep water sightings from ROVs include in the North Atlantic, off Angola, the Gulf of Mexico, and Monterey Canyon. The present specimen was swimming actively by contracting and expanding its stem, in a yo-yo movement. A review of all reliable records for this species worldwide has been carried out to gain a better knowledge of the present known distribution of this species, both geographical and bathymetric. *Bathyphysa conifera* may possibly represent an important component of the food web and be perhaps also a competitor to fish in the regions it inhabits.

Keywords: Mediterranean Sea; bathymetric distribution; gelatinous zooplankton; jellyfish.

Introduction

The cystonect family Rhizophysidae comprises four species in two genera: *Rhizophysa eysenhardtii* Gegenbaur, 1859, *R. filiformis* (Forskål, 1775), *Bathyphysa conifera* (Studer, 1878) and *B. sibogae* Lens & van Riemsdijk, 1908. In *Rhizophysa* species, there are no ptera, or wings, on the gastrozooids, and the pneumatophore contains large hypocystic villi in the posterior half (Pagès & Gili, 1992, figs 2-3), which arise from the gas gland. These villi fill the gastrovascular space around the pneumatosaccus (Chun, 1897, fig. 17). In *Bathyphysa* species, younger gastrozooids have ptera, which are used to aid locomotion (Munro *et al*., 2018; Robison, 1995; Youngbluth pers. comm.). There is also a lamella extending from the posterior side of each young gastrozooid, which holds it out so that the distal end faces posteriorly (Dunn & Wagner, 2006). *Bathyphysa* species also have hypocystic villi in the pneumatophore, but in this genus the villi are smaller and do not obscure the pneumatosaccus (Biggs & Harbison, 1976; Mackie *et al*., 1987).

Bathyphysa conifera is readily identified underwater by the absence of tentilla (side branches) on its tentacles, which arise from more mature gastrozooids on the siphosome. Except for apolemiids, no other cystonect or physonect siphonophore lacks tentilla on the tentacles. The tentilla of all non-apolemiid physonects comprise a complex nematocyst battery including a cnidoband of stinging nematocysts, typically of two types, which may or may not be coiled (Damián-Serrano *et al*., 2020; Mapstone, 2014). Such complex structures do not occur on *B. conifera*, even though other rhizophysid cystonects, including *Bathyphysa sibogae* and both species of *Rhizophysa*, display side branches on their tentacles, bearing pads of mostly isorhizas. These nematocysts of cystonects cannot penetrate the hard exoskeletons of planktonic copepods (Purcell, 1984; Damián-Serrano *et al*., 2020).

In the past, almost all specimens were caught attached to plumb lines of deep-sea fishing vessels or wires of cable-laying ships (Studer 1878, Fewkes 1886, 1889). Subsequent specimens were caught on wires or found in the trawl nets of expeditionary vessels (Bedot, 1893; Lens & van Riemsdijk 1908). In most of these cases many of the zooids had been lost by the time the specimens reached the surface. However, one long and untwisted, but probably incomplete, specimen was described by Fewkes in 1889 (Fewkes, 1889). Shortly afterwards an intact specimen of *B. conifera* was collected in Indonesian waters, illustrated by Lens and van Riemsdijk (1908, pl. XIX, as *Pterophysa grandis*), and reproduced by Totton (1965, pl.

VI, fig. 1). A second figure of a live *B. conifera* colony taken by Rob Sherlock has been published by Pugh (2019, fig. 34C).

Materials and Methods

A live specimen of *Bathyphysa conifera* (Fig. 1 and video in Suppl. Material) was observed on the 6th of May 2012 off Tarifa Island, Strait of Gibraltar, at the entrance of the Mediterranean Sea (35.9996° N, -5.6091° W, Fig. 2A, Table 1) by SCUBA divers expert in marine flora and fauna identification. High-definition underwater pictures and a short film of the colony were taken during the encounter. The imaging allowed the identification of the species by the authors (based on the characters given in Pugh, 2019). The observation has been included in the Biological Reference Collections (CBR) at the Institut de Ciències del Mar (ICM-CSIC, Barcelona, Spain) under the catalogue number ICMCBR000380 (Guerrero *et al*., 2020).

Moreover, a review of all reliable records for *B. conifera* worldwide has been prepared to summarize the geographic and vertical distribution of this species (see Table 1 and Fig. 2B). Each record in the published literature from 1878 to the present, the GBIF database and notations from official websites of marine research institutions (JAMSTEC and MBARI) have been carefully examined and confirmed. The data of this review have been published and are available in Guerrero & Mapstone (2020).

Results

The present specimen was easily identified as *Bathyphysa conifera* from the pictures and short film taken by the SCUBA divers, based on the absence of tentilla (side branches) on its tentacles (Pugh, 2019). As noted above, the three other species in the family Rhizophysidae (*Rhizophysa eysenhardti, R. filiformis* and *B. sibogae*) all have tentilla arising from their tentacles. The live colony was actively swimming by contracting and expanding its stem at 14-16 m depth (see video in Suppl. Material). The length of this specimen varied from approximately 0.5 to 1.5 m, depending on the degree of contraction of the anterior siphosomal stem. As described by one of the divers "at first sight the colony appeared to be a plastic bag sinking slowly through the water column, then suddenly the inert mass changed direction and began moving upwards like a yo-yo". On close inspection, a distinctive pneumatophore, and a posterior siphosome bearing mature gastrozooids with tentacles were recognized (Fig. 1 A-B). Long, thin tentacles from the posterior part of the siphosome hung downward, presumably to capture prey; but most tentacles had contracted before the video and still shots were taken.

Based on up-to-the-present records, *B. conifera* is considered a rarely observed species. All reliable deep-water samples and chance discoveries over the last two hundred years are shown in Table 1 and Fig. 2B. This species is generally distributed from warm temperate to tropical latitudes. Latitudinal records for *B. conifera* in the Atlantic range from 46.7614° N to -24.4012° S. All but one of Studer's (1878) original specimens came from the Atlantic, and further specimens were described from this ocean by

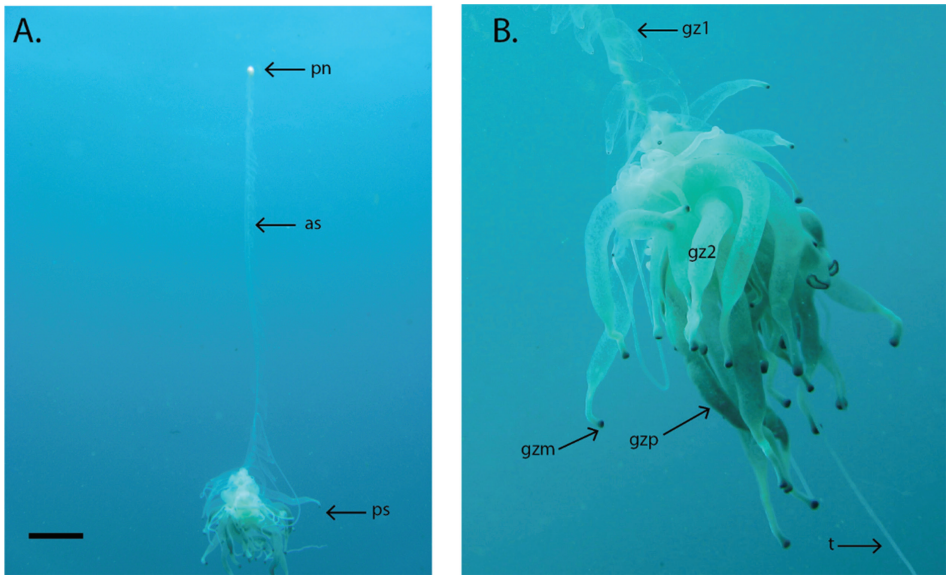

Fig. 1: Underwater pictures of *Bathyphysa conifera* observed on the 6th of May 2012 off Tarifa Island, Strait of Gibraltar, at the entrance of the Mediterranean Sea (35.9996° N, -5.6091° W). A: whole specimen; B: detail of posterior part of A. as – anterior siphosome; gz1 – young gastrozooid (no tentacle yet); gz2 mature gastrozooid (with tentacle); gzm – mouth of gastrozooid; gzp – pigmented mature gastrozooid; pn – pneumatophore; ps – posterior siphosome; t – tentacle (from mature gastrozooid). Scale Bar 10 cm.

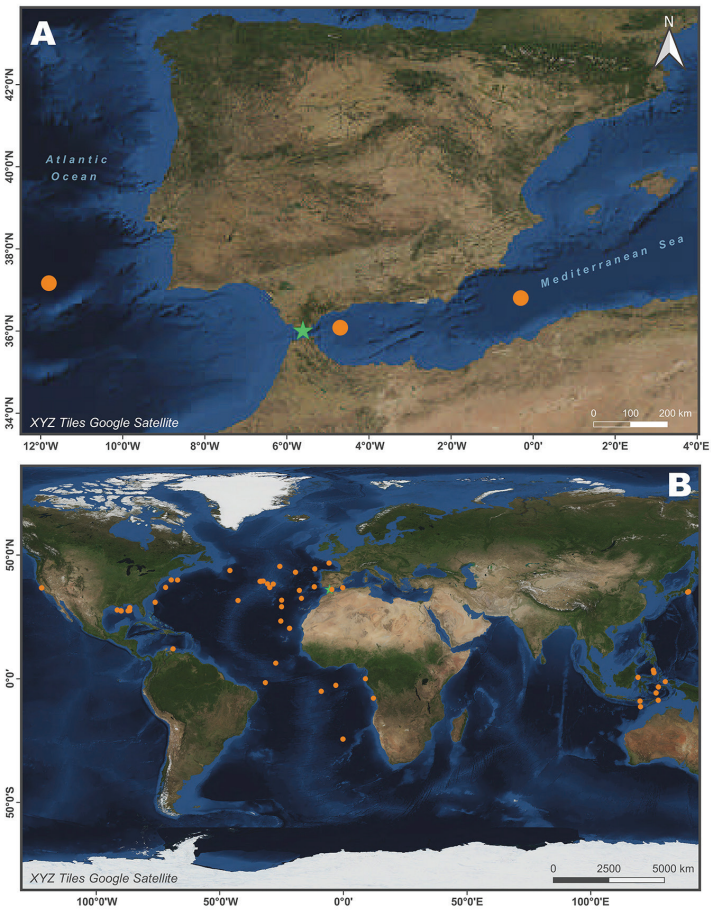

Fig. 2: A) Location of the present found *Bathyphysa conifera* specimen (green star) in the Strait of Gibraltar, and the three closest records from the literature (orange dots). B) Locations of all reliable records for *B. conifera* worldwide (see Table 1).

Fewkes from the western North Atlantic and Gulf of Mexico (Fewkes, 1886; 1889), and by Bedot from the Azores (Bedot, 1893). Leloup described nine specimens from the North Atlantic and two from the Western Mediterranean in two different expeditions (Leloup, 1936; 1955a and see Table 1). Totton (1965) reported Atlantic specimens twisted around the grappling wire of the cable-ship 'Monarch'.

Other seas have been less well sampled, and only a single record was reported from the eastern Indian Ocean in deep water south of the island of Sumba in the Indonesian Lesser Sunda Islands Archipelago. That *B. conifera* specimen was collected by Studer (1878) on the slopes of the Java Trench, close to one of the five deepest ocean basins (7290m, Stewart & Jamieson, 2019). Other specimens of *B. conifera* were collected north of this location in Indonesian seas (the Banda Sea, Celebes Sea and nearby sites) during the Siboga Expedition (1899-1900) (Table 1, Fig. 2B).

The advent of explorations with underwater vehicles in the Atlantic and Pacific oceans established that *B. conifera* is distributed worldwide (Table 1). Colonies from Monterey Bay are pictured in the MBARI Deep Sea Guide, video footage was taken in the Gulf of Mexico and off Angola, and specimens were collected by net tows in the Gulf of Mexico and by a submersible in Curaçao in the Caribbean (Table 1).

The review of the depth ranges where *B. conifera* occurred show 31 records from bathypelagic depths (1000 to 4000 m), 14 records from mesopelagic depths (200 to 1000 m), only 6 records, including the present work, from epipelagic depths (surface to 200 m) and 5 records from abyssopelagic depths (4000 to 6000 m). This review confirms the present record as the shallowest (- 16 m) for *B. conifera* so far. However, we highlight that the available information from the records, including the present one, indicates that *B. conifera* stays close to the bottom, either in deep or shallow depths.

Discussion

Morphological features of the recorded shallow water colony resemble those exhibited by other *Bathyphysa conifera* specimens. The young gastrozooids are translucent, while the older more mature gastrozooids further down the siphosome have black pigment around the

Table 1. Review of all reliable records for *Bathyphysa conifera* worldwide conducted to summarize the geographic and vertical distribution of this species. Lat., latitude; Lon, longitude. The data of the review is published and available in GBIF (Guerrero & Mapstone, 2020).

Species (cited as)	Lat	Lon	Geographic area	Depth (m)	Year	Reference	Observations
Bathyphysa conifera	35.9996	-5.6091	Gibraltar Strait	16	2012	Present paper	SCUBA diving
Bathyphysa abyssorum	43.7480	-45.9353	North Atlantic	1820-3239	1875	Studer, 1878	On a grapnel rope from cable laying ship 'Faraday'
Rhizophysa conifera	35.7151	-17.8347	North Atlantic	2877	1874	Studer, 1878	On plumb-line from His Prussian Majesty's corvette 'Gazelle' world voyage
Rhizophysa conifera	23.3148	-25.3512	North Atlantic	2743	1874	Studer, 1878	As above
Rhizophysa conifera	-5.0681	-8.9674	Equatorial Atlantic	1463	1874	Studer, 1878	As above
Rhizophysa conifera	-24.4012	-0.2005	Tropical Atlantic Ocean	3658	1874	Studer, 1878	As above
Rhizophysa conifera	-11.3009	120.1518	Eastern Indian Ocean	3658	1875	Studer, 1878	As above
Pterophysa grandis	36.9205	-71.9182	Eastern US coast	3841	1884	Fewkes, 1886	Collected by USFC Albatross in region of Gulf Stream
Bathyphysa conifera	39.9000	-67.0917	Georges Bank, South of	3316	1885	GBIF Secretariat, 2019	United States Fish Commission. Id by Nishiyama, Eric, Federal University of ABC (UFABC)
Pterophysa grandis	28.7473	-86.4344	Gulf of Mexico	415	1885	Fewkes, 1889	Collected by USFC Albatross in region of Gulf Stream
Pterophysa grandis	30.8974	-76.1513	Gulf Stream	3316	1885	Fewkes, 1889	As above
Bathyphysa grimaldii	39.4768	-32.4809	N Atlantic, near the Azores	2000	1888	Bedot, 1893	Scientific results of yacht voyage by Prince Albert 1st of Monaco
Bathyphysa grimaldii	39.4423	-33.3851	N Atlantic, near the Azores	1557	1888	Bedot, 1893	As above
Bathyphysa grimaldii	39.2996	-33.5392	N Atlantic, near the Azores	1384	1888	Bedot, 1893	As above
Bathyphysa grimaldii	39.3782	-33.7267	N Atlantic, near the Azores	1372	1888	Bedot, 1893	As above
Bathyphysa grimaldii	38.3740	-30.7147	N Atlantic, near the Azores	1294	1888	Bedot, 1893	As above
Pterophysa grandis	-9.0509	119.9518	Savu Basin, south of Flores Is	959	1899	Lens & van Riemsdijk, 1908	Siboga expedition. Deep Sea Trawl
Pterophysa grandis	-3.3344	127.3851	Manipa-strait, Indonesia	1536-0	1899	Lens & van Riemsdijk, 1908	Siboga expedition. Deep Sea Trawl
Pterophysa grandis	-8.7176	127.3018	Flores Sea, Indonesia	828	1899	Lens & van Riemsdijk, 1908	Siboga expedition. Deep Sea Trawl

Continued

Table 1 continued

Species (cited as)	Lat	Lon	Geographic area	Depth (m)	Year	Reference	Observations
Pterophysa studeri	3.4511	125.3185	Celebes Sea, Indonesia	2053	1899	Lens & van Riemsdijk, 1908	Siboga expedition. On cable
Pterophysa grandis	0.5766	119.1416	Makassar Strait, Indonesia	1301	1899	Lens & van Riemsdijk, 1908	Siboga expedition. Deep Sea Trawl
Pterophysa grandis	2.4500	125.5833	West of Halmahera, Indonesia	1327	1899	Lens & van Riemsdijk, 1908	Siboga expedition. On cable
Pterophysa grandis	-1.1750	130.1500	West of Sorong, Indonesia	1798	1899	Lens & van Riemsdijk, 1908	Siboga expedition. On cable
Pterophysa grandis	-5.7450	126.4550	Banda Sea, Indonesia	4391	1899	Lens & van Riemsdijk, 1908	Siboga expedition. On cable
Bathyphysa conifera	31.7649	-25.0014	West of the Canary Islands	0-3000	1904	Leloup, 1936	Prince Albert 1st of Monaco Scientific Expedition
Bathyphysa conifera	31.6396	-42.6349	SW of the Azores	2000	1905	Leloup, 1936	As above
Bathyphysa conifera	43.0569	-19.4100	Off Galicia, Spain	0-5940	1909	Leloup, 1936	As above
Bathyphysa conifera	46.7614	-5.8349	West of the Bay of Biscay	3910	1910	Leloup, 1936	As above
Bathyphysa conifera	44.4071	-11.6016	Off Galicia, Spain	0-1900	1910	Leloup, 1936	As above
Bathyphysa conifera	37.1652	-11.8013	East of the Azores	0-4750	1910	Leloup, 1936	As above
Bathyphysa conifera	36.8029	-0.3012	S Balearic Basin, Mediterranean Sea	0-2590	1910	Leloup, 1936	As above
Bathyphysa conifera	32.5067	-17.0013	Near Madeira	0-2380	1911	Leloup, 1936	As above
Bathyphysa conifera	38.2760	-28.3850	Azores, south of Pico Island	0-1200	1912	Leloup, 1936	As above
Bathyphysa japonica	35.1814	139.5856	Sagami Bay, Japan	80	1940	Kawamura, 1954	Pugh (2019, p.72) concludes this species is a junior synonym of *B.conifera*. Collected off Arasaki
Bathyphysa conifera	-0.0014	8.8996	African coast, South Atlantic	390-400	1949	Leloup, 1955a	Belgian Oceanographic Expedition to S. Atlantic African coast. First record of a colony from off Gabon
Bathyphysa conifera	36.0820	-4.7013	Just east of Strait of Gibraltar, Mediterranean	900-0	1910	Leloup, 1955b	'Michael Sars' North Atlantic Deep-Sea Expedition
Bathyphysa conifera	29.1149	-25.0347	West of the Canaries	370	1910	Leloup, 1955b	As above
Bathyphysa conifera	36.8815	-29.7849	Just SW of the Azores	100	1910	Leloup, 1955b	As above
Bathyphysa conifera	45.4318	-25.7519	Just E of Mid-Atlantic Ridge	2000	1910	Leloup, 1955b	As above

Continued

Table 1 continued

Species (cited as)	Lat	Lon	Geographic area	Depth (m)	Year	Reference	Observations
Bathyphysa conifera	-1.5850	-31.5844	Atlantic Ocean	914-2743	1948	Totton, 1965	On grappling wire of cable-ship 'Monarch'
Bathyphysa conifera	-2.6681	-3.0840	Atlantic Ocean	4489	1948	Totton, 1965	As above
Bathyphysa conifera	20.4149	-21.7845	Atlantic Ocean	4189	1948	Totton, 1965	As above
Bathyphysa conifera	6.3149	-27.3844	Atlantic Ocean	1097	1948	Totton, 1965	As above
Bathyphysa conifera	39.9363	-69.6383	Veatch Canyon, NW Atlantic	168	1987	Janssen *et al*., 1989	Observed during Johnson-Sea-Link dive 2148
Bathyphysa conifera	36.6969	-122.0335	Monterey Bay	500	1989-1994	Robison, 1995	MBARI's ROV Ventana
Bathyphysa conifera	35.0043	139.2251	Sagami Bay	306	2000	JAMSTEC, 2020	BISMAL website; two videos taken by Shinkai
Bathyphysa conifera	27.7972	-91.5176	Gulf of Mexico, Bush Hill site	550	2003	Young & Youngbluth (pers. comm.)	JSL I dive 4650
Bathyphysa conifera	36.7041	-122.0529	Monterey Bay	186	2007	MBARI, 2016	Deep Sea Guide, consulted 25 April 2020
Bathyphysa conifera	36.7472	-122.0996	Monterey Bay	346	2008	MBARI, 2016	Deep Sea Guide, consulted 25 April 2020
Bathyphysa conifera	36.7012	-122.0444	Monterey Bay	542	2009	MBARI, 2016	Deep Sea Guide, consulted 25 April 2020
Bathyphysa conifera	36.7011	-122.0447	Monterey Bay	539	2010	MBARI, 2016	Deep Sea Guide, consulted 25 April 2020
Bathyphysa conifera	12.0832	-68.8991	west of Curaçao substation	184	2011	GBIF Secretariat, 2019	Colins et al, 2011
Bathyphysa conifera	27.5880	-86.4754	Gulf of Mexico, northern	600-1001	2011	Youngbluth (pers.comm.)	MOCNESS 10 net, NOVA Southeastern University (Tracey Sutton's Lab)
Bathyphysa conifera	27.4941	-87.1111	Gulf of Mexico, northern	200-600	2011	Youngbluth (pers.comm.)	MOCNESS 10 net, NOVA Southeastern University (Tracey Sutton's Lab)
Bathyphysa conifera	27.4752	-89.9397	Gulf of Mexico, northern	999-1099	2011	Youngbluth (pers.comm.)	MOCNESS 10 net, NOVA Southeastern University (Tracey Sutton's Lab)
Bathyphysa conifera	27.4379	-89.8792	Gulf of Mexico, northern	195-601	2011	Youngbluth (pers.comm.)	MOCNESS 10 net, NOVA Southeastern University (Tracey Sutton's Lab)
Bathyphysa conifera	27.4649	-89.8993	Gulf of Mexico, northern	601-800	2011	Youngbluth (pers.comm.)	MOCNESS 10 net, NOVA Southeastern University (Tracey Sutton's Lab)
Bathyphysa conifera	-7.8683	12.1422	S Atlantic, off Angola	1325	2015	Jones & Pugh, 2018	Oceaneering Millennium ROV

mouth (Fig. 1B) and some black pigment in the column. These patterns also resemble pigmentation in the larger Angolan specimen at the end of the YouTube video (link in Jones & Pugh, 2018) as the ROV was retreating. In the original gastrozooid figure by Studer (1878, Pl. 1, figs 1, 4) there are also yellow and black pigments near the mouth. However, the light purple pigment near the mouth observed by Pugh (2019) was not apparent, perhaps due to different lighting conditions.

The relatively short length of the observed *B. conifera* (1.5 m when expanded) and the absence of any cone-shaped gonodendra on the posterior siphosome suggest that it was a young individual (gonodendra are shown as yellow in the MBARI 2016 Deep Sea Guide). Other observed and/or captured specimens are known to be much longer and to bear many more gastrozooids with tentacles, and, typically, gonodendra. In the Flores Sea (Indonesia) at 959 m depth, Lens & van Riemsdijk (1908, pl. 19, fig. 146, some lengths omitted) collected a complete individual 3.773 m long that bore immature gastrozooids in the anterior region and many mature gastrozooids (with tentacles), and associated gonodendra in the posterior region (see Table 1). A large specimen recorded by video from 1800 m depth in the Gulf of Mexico was at least 1.8 - 2 m long when extended (Young & Youngbluth pers. comm.), and a further specimen from ca. 500 m depth in Monterey Bay had an estimated length of 2 m (Robison, 1995). The posterior region of the present specimen was small relative to that of the larger individuals described above. Only ca. 3 extended tentacles could be discerned, whereas in the Gulf of Mexico video ca. 14 extended tentacles were evident, and in the large specimen from Angola ca. 26 extended tentacles were identifiable (Jones & Pugh, 2018, Fig. 1). The latter specimen was not apparently extending and contracting the anterior region significantly, in contrast to the present specimen and that from the Gulf of Mexico. The Angolan specimen appeared similar to that illustrated and described by Robison (1995) from Monterey Bay. Robison concluded that this colony, at 500 m depth, could detect ROV lights at low levels, which elicited an escape reaction in which the "exceptionally elastic" anterior stem exhibited "a series of pounding contractions and relaxations of the upper stem that had the effect of driving the animal downwards" away from the ROV lights.

The depths reported in Table 1 for *B. conifera* specimens collected or observed before the advent of ROVs (Janssen *et al.,* 1989) are necessarily less reliable, because determining the exact depth of specimens captured on a dredge rope or a cable with a trap deployed on the seabed is difficult (Fewkes, 1886, p.928). Attachment likely occurs close to bottom depth, including from deep-water trawl nets because the latter were only opened once they had reached considerable depths to increase the chance of capture from the bathypelagic realm (Bedot, 1893; Leloup, 1936; 1955b). Totton (1965) noted that the cable-laying ship 'Monarch' that collected the *B. conifera* specimens was working only between 914 m and 4,489 m depths. In addition, more recent observations of *B. conifera* from ROVs and submersibles indicate that this species prefers to stay close to the bottom, as discussed below, lending further support to the accuracy of the depths given in Table 1.

Although most observations of *B. conifera* have been of apparently isolated individuals, video footage exists showing several individuals drifting near the seafloor during a single ROV dive (Youngbluth, pers. comm.). Thus, this species may not be as rare as worldwide records suggest (Fig. 2B), since it seems to mostly inhabit the bathypelagic zone, which is only infrequently sampled by ROVs and notoriously difficult to sample by standard nets, leading to apparent rarity (Lindsay & Pagès, 2010; Martell *et al*., 2018). The authors wish to highlight that, based on the available information from the records, *B. conifera* seems to stay close to the bottom throughout its depth range (which is primarily in deep water) and it may be a bentho-pelagic feeder. *Bathyphysa conifera* appears to exhibit benthic-boundary layer coupling, as also shown by rhodaliid siphonophores (Angel, 1990). Cystonects are known to be important predators of larval fish (Purcell, 1984), and *B. conifera* in particular has been recorded capturing myctophid fish in Monterey Bay (Robison, 1995; MBARI, 2016). This species might represent an important component of the food web and maybe also a competitor to fish in these regions. The biomass of demersal fish is greatest at the benthic boundary layer between 800 and 1500 m depths (Mauchline & Gordon, 1991), and this group includes many myctophid specimens collected in demersal trawls (Braga *et al*., 2014). Video records from the Gulf of Maine revealed that *B. conifera* drags its tentacles through the epibenthic fluff layer (Youngbluth pers. comm.) and may ingest components of this interface community. Such a feeding tactic is employed by undescribed large red cydippid ctenophores (Youngbluth pers. comm.), and the trachymedusan *B. pedunculata,* which had copepods, crustacean exoskeletons, foraminiferans, and sediment particles in the stomachs of five examined individuals (Smith *et al*., 2020). We hypothesise that *B. conifera* might be an opportunistic feeder, ingesting components of the epibenthic fluff layer when fish prey are unavailable, but further investigations are needed to verify this suggestion.

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Supplementary data

The following supplementary information is available on line for the article:

Video 1. Underwater film of *Bathyphysa conifera* actively swimming by contracting and expanding its stem, observed on the 6th of May 2012 off Tarifa Island, Strait of Gibraltar, at the entrance of the Mediterranean Sea (35.9996° N, -5.6091° W), at 14-16 m depth.