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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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 is used to aid locomotion (Munro et al., 2018; Robison, 1995; Youngbluth pers. comm.). *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 rhizophyid 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.
Materials and Methods

A live specimen of Bathypsysa 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 Bathypsysa 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 eysenhardtii, 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
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* | 35.996 | -5.609 | Gibraltar Strait              | 16        | 2012 | Present paper                      | SCUBA diving                                     |
| *Bathyphysa abysorum* | 43.740 | -45.353 | North Atlantic               | 1820-3239| 1875 | Studer, 1878                        | On a grapnel rope from cable laying ship ‘Faraday’ |
| *Rhizophysa conifera* | 35.715 | -17.834 | North Atlantic               | 2877      | 1874 | Studer, 1878                        | On plumb-line from His Prussian Majesty’s corvette ‘Gazelle’ world voyage |
| *Rhizophysa conifera* | 23.314 | -25.351 | North Atlantic               | 2743      | 1874 | Studer, 1878                        | As above                                          |
| *Rhizophysa conifera* | -5.068 | -8.967 | Equatorial Atlantic         | 1463      | 1874 | Studer, 1878                        | As above                                          |
| *Rhizophysa conifera* | -24.401 | -0.200 | Tropical Atlantic Ocean     | 3658      | 1874 | Studer, 1878                        | As above                                          |
| *Rhizophysa conifera* | -11.300 | 120.151 | Eastern Indian Ocean        | 3658      | 1875 | Studer, 1878                        | As above                                          |
| *Pterophysa grandis* | 36.920 | -71.918 | Eastern US coast            | 3841      | 1884 | Fewkes, 1886                        | Collected by USFC Albatross in region of Gulf Stream |
| *Bathyphysa conifera* | 39.900 | -67.091 | Georges Bank, South of      | 3316      | 1885 | GBIF Secretariat, 2019              | United States Fish Commission. Id by Nishiyama, Eric, Federal University of ABC (UFABC) |
| *Pterophysa grandis* | 28.743 | -86.434 | Gulf of Mexico              | 415       | 1885 | Fewkes, 1889                        | Collected by USFC Albatross in region of Gulf Stream |
| *Pterophysa grandis* | 30.897 | -76.151 | Gulf Stream                 | 3316      | 1885 | Fewkes, 1889                        | As above                                          |
| *Bathyphysa grimaldi* | 39.476 | -32.480 | N Atlantic, near the Azores | 2000      | 1888 | Bedot, 1893                         | Scientific results of yacht voyage by Prince Albert 1st of Monaco |
| *Bathyphysa grimaldi* | 39.423 | -33.385 | N Atlantic, near the Azores | 1557      | 1888 | Bedot, 1893                         | As above                                          |
| *Bathyphysa grimaldi* | 39.296 | -33.539 | N Atlantic, near the Azores | 1384      | 1888 | Bedot, 1893                         | As above                                          |
| *Bathyphysa grimaldi* | 39.378 | -33.726 | N Atlantic, near the Azores | 1372      | 1888 | Bedot, 1893                         | As above                                          |
| *Bathyphysa grimaldi* | 38.374 | -30.714 | N Atlantic, near the Azores | 1294      | 1888 | Bedot, 1893                         | As above                                          |
| *Pterophysa grandis* | -9.050 | 119.951 | Savu Basin, south of Flores Is | 959    | 1899 | Lens & van Rijnsdijk, 1908        | Siboga expedition. Deep Sea Trawl                        |
| *Pterophysa grandis* | -3.334 | 127.385 | Manipu-strait, Indonesia    | 1536-0    | 1899 | Lens & van Rijnsdijk, 1908        | Siboga expedition. Deep Sea Trawl                        |
| *Pterophysa grandis* | -8.717 | 127.301 | Flores Sea, Indonesia       | 828       | 1899 | Lens & van Rijnsdijk, 1908        | Siboga expedition. Deep Sea Trawl                        |

Continued
| Species (cited as) | Lat | Lon | Geographic area | Depth (m) | Year | Reference | Observations |
|-------------------|-----|-----|-----------------|----------|------|-----------|-------------|
| Pterophysa studeri | 3.45 | 125.32 | Celebes Sea, Indonesia | 2053 | 1899 | Lens & van Riemslgik, 1908 | Siboga expedition. On cable |
| Pterophysa grandis | 0.5766 | 119.14 | Makassar Strait, Indonesia | 1301 | 1899 | Lens & van Riemslgik, 1908 | Siboga expedition. Deep Sea Trawl |
| Pterophysa grandis | 2.4500 | 125.58 | West of Halmahera, Indonesia | 1327 | 1899 | Lens & van Riemslgik, 1908 | Siboga expedition. On cable |
| Pterophysa grandis | -1.1750 | 130.15 | West of Sorong, Indonesia | 1798 | 1899 | Lens & van Riemslgik, 1908 | Siboga expedition. On cable |
| Pterophysa grandis | -5.7450 | 126.45 | Banda Sea, Indonesia | 4391 | 1899 | Lens & van Riemslgik, 1908 | Siboga expedition. On cable |
| Bathyphysa conifera | 31.7649 | -25.00 | West of the Canary Islands | 0-3000 | 1904 | Leloup, 1936 | Prince Albert 1st of Monaco Scientific Expedition |
| Bathyphysa conifera | 31.6396 | -42.63 | SW of the Azores | 2000 | 1905 | Leloup, 1936 | As above |
| Bathyphysa conifera | 43.0569 | -19.41 | Off Galicia, Spain | 0-5940 | 1909 | Leloup, 1936 | As above |
| Bathyphysa conifera | 46.7164 | -5.83 | West of the Bay of Biscay | 3910 | 1910 | Leloup, 1936 | As above |
| Bathyphysa conifera | 44.4071 | -11.60 | Off Galicia, Spain | 0-1900 | 1910 | Leloup, 1936 | As above |
| Bathyphysa conifera | 37.1652 | -11.80 | East of the Azores | 0-4750 | 1910 | Leloup, 1936 | As above |
| Bathyphysa conifera | 36.8209 | -0.30 | S Balearic Basin, Mediterranean Sea | 0-2590 | 1910 | Leloup, 1936 | As above |
| Bathyphysa conifera | 32.5067 | -17.00 | Near Madeira | 0-2380 | 1911 | Leloup, 1936 | As above |
| Bathyphysa conifera | 38.2760 | -25.03 | West of the Canaries | 0-1200 | 1910 | Leloup, 1936 | As above |
| Bathyphysa japonica | 35.1814 | 139.58 | 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 | -4.70 | Just east of Strait of Gibraltar, Mediterranean | 900-0 | 1910 | Leloup, 1955b | ‘Michael Sars’ North Atlantic Deep-Sea Expedition |
| Bathyphysa conifera | 29.1149 | -25.03 | 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 | -25.75 | Just E of Mid-Atlantic Ridge | 2000 | 1910 | Leloup, 1955b | As above |

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 | 6.349 | -27.3444 | Atlantic Ocean | 4169 | 1948 | Totton, 1965 | As above |
| Bathyphysa conifera | 39.3663 | -69.6383 | Veatch Canyon, NW Atlantic | 1987 | 1994 | Janssen et al., 1995 | Observed during Johnson-Sea-Link dive 2148 |
| Bathyphysa conifera | 36.6969 | -122.0335 | Monterey Bay | 500 | 1989 | Robison, 1995 | MBARI’s ROV Ventana |
| Bathyphysa conifera | 35.0043 | 139.2251 | Sagami Bay | 306 | 2000 | JAMSTEC, 2020 | BISMAL website; two videos taken by Shinohara |
| 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 | 348 | 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 | 1325 | 2015 | Jones & Pugh, 2018 | Oceaneering Millennium ROV |

Table 1 continued...
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 gastrozoooid 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 gastrozoooids 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 gastrozoooids in the anterior region and many mature gastrozoooids (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). Tutton (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. Bathypsysa conifera appears to exhibit benthic-boundary layer coupling, as also shown by rhodaliid siphonophores (Angel, 1990). Cystonectes are known to be important predators of larval fish (Pullur, 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, foraminifers, 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 Bathymeta confirera 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.

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