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INVERTEBRATE ZOOLOGY

A Species of Sea Anemone *Sagartia elegans* (Dalyell, 1848) (Anthozoa, Actiniaria, Sagartiidae) that is New for the Black Sea and is Capable of Clonal Reproduction

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Abstract—In the Black Sea, the sea anemone *Sagartia elegans* (Dalyell, 1848) has been found for the first time in the Gulf of Odessa (46°32′ N, 30°48′ E) and karst caves and grottos of the Western Crimea (45°21′ N, 32°30′ E). Previously, *S. elegans* was known to inhabit coastal waters of Iceland, the British Isles, and continental Europe from Scandinavia to the Adriatic Sea. According to the available data, this gonochoristic species tends to asexual somatic reproduction through laceration: juvenile polyps develop from separated fragments of the pedal disc. A rich color polymorphism is observed. The numerous clonal populations that are found in caves consist of variously sized and similarly colored polyps. All of them descended from one parental individual.

Keywords: Black Sea, Gulf of Odessa, Western Crimea, karst caves, *Sagartia elegans*, Sagartiidae, Acontiaria, Thenaria

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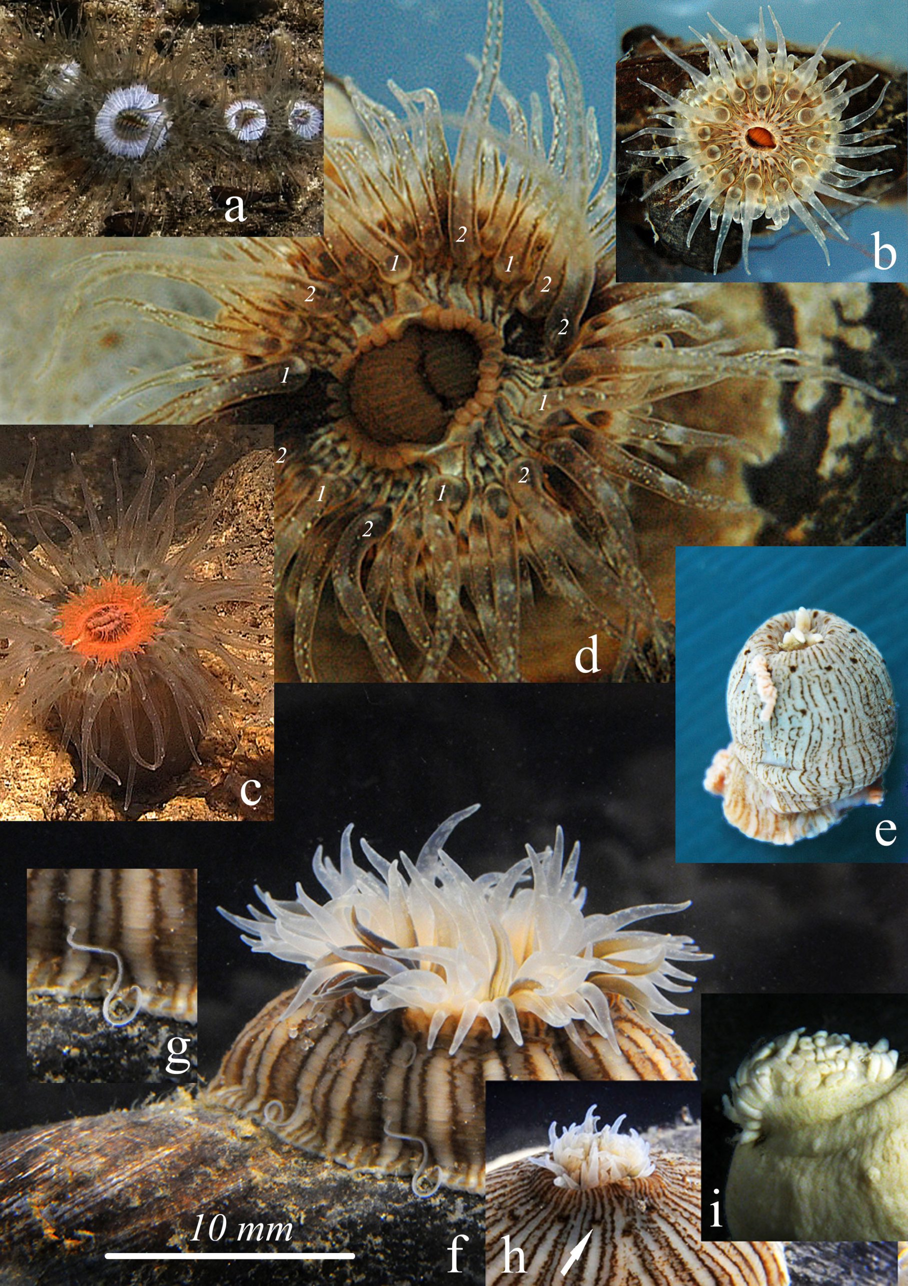
Inspection of the underwater caves and grottos of the Tarkhankut Peninsula in Western Crimea by divers and the analysis of video materials that were recorded in 2006–2011 allowed us to reveal sea anemones that had not occurred in waters of the Black Sea previously. In one of the caves, three sea anemones of an unknown species were found along with *Actinia equina* (Linnaeus, 1758), which is common for Black Sea waters; two specimens were fixed for further identification. At a distance of 1.5 km from the previous cave, over a thousand individuals of this species with greatly varying colors occupied an area of several square meters in the dark offshoot of a half-submerged karst grotto (Figs. 1a and 1c). A few very large individuals, whose height in the straightened state exceeded 10 cm, were found in a rock niche at a depth of 1.5 m. At this site, 20 specimens were collected for this study. Judging by visual evaluation, the density of this sea anemone population increased in subsequent years.

In 2009, a few sea anemones of this species were recorded in the Gulf of Odessa at depths of 11–14 m (Figs. 1b, 1d, 1f, and 1h), but the animals there did not form aggregations and occurred singly. As is known, many species of the sublittoral fauna that live at great depths in the open sea can rise up to a depth of nearly zero in shadowed sites such as caves, as occurred in the case above.

MATERIAL AND METHODS

Samples that were collected between 2008 and 2011 in underwater caves of the Tarkhankut Peninsula near Atlesh (45°21′ N, 32030′ E), Western Crimea, and a few individuals that were picked by divers from mussel shells in waters off the Malyi Fontan district (46°32′ N, 30°48′ E, within the city of Odessa, Gulf of Odessa) in the Black Sea, served as the material for the description of the polyp structure and measurements of stinging capsules. At the laboratory of the Odessa Hydrobiological Station the material was photographed and the external morphological characters of live and fixed specimens were studied. The study of the anatomical and histological characters of the polyps at the Marine Research Laboratory of the Zoological Institute of the Russian Academy of Sciences (ZIN RAS) in St. Petersburg was based on nine specimens that were fixed with a 10% formaldehyde solution (Nos. 11200–11208 according to the incoming catalog at the Sponges and Coelenterates Department of ZIN RAS). A few dozen histological sections that were stained according to Pacini's method were made [2, 40]. Photographic and video materials that were recorded during diving operations by one of the authors, O.A. Kovtun, were also used in the identification of animals. Video recording of sea anemones in nature was performed with a digital Sony 3CCD camcorder in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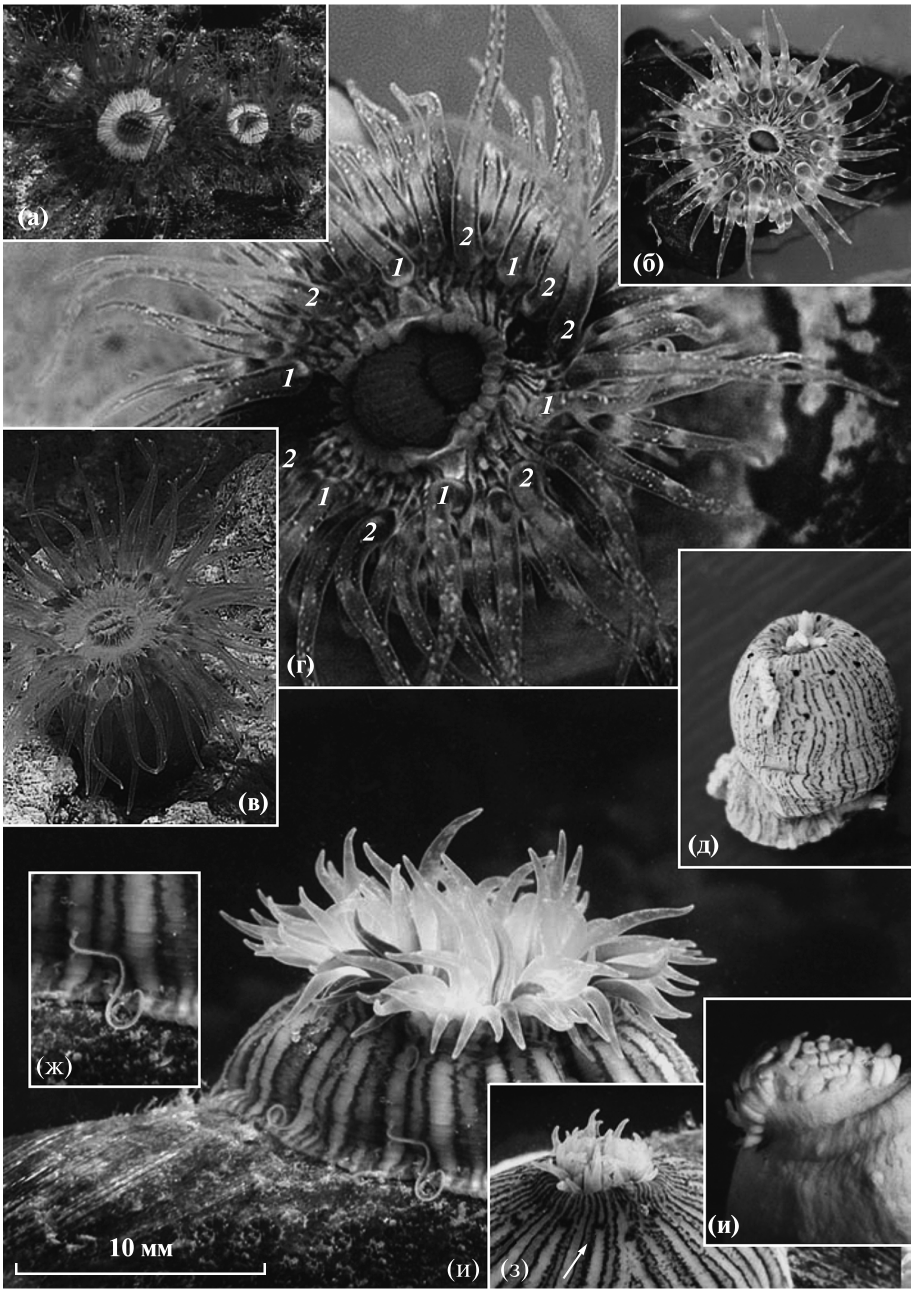


Fig. 1. Live sea anemones *Sagartia elegans* from the underwater cave of the Western Crimea (a, c) and from the Gulf of Odessa (b, d, f, h), as well as formalin-fixed specimens (e, i). a, similarly colored individuals that apparently belong to the same clone; b, polyp with the regular hexamerous arrangement of tentacles; c, individual from a brightly colored clone was in the neighborhood of polyps that were similar in color; d, a polyp showing a deviation from the regular hexamerous symmetry (*1*, *2* are the tentacles of the first and second cycles); e, shrunken fixed polyp with dark spots, which indicate holes of cinclides, still seen on the body (the spots fade out after a few months of being stored in formalin); h, shrunken live polyp with a row of dark spots, indicating the holes of cinclides, seen in the upper part of the column (hole is indicated by arrow); f, slightly shrunken live polyp with three discharged acontia seen in the upper part of the body (under the tentacles) and over the pedal disc; g, winding thread of acontium, thrown out through a cinclide. (Photo by O.A. Kovtun).

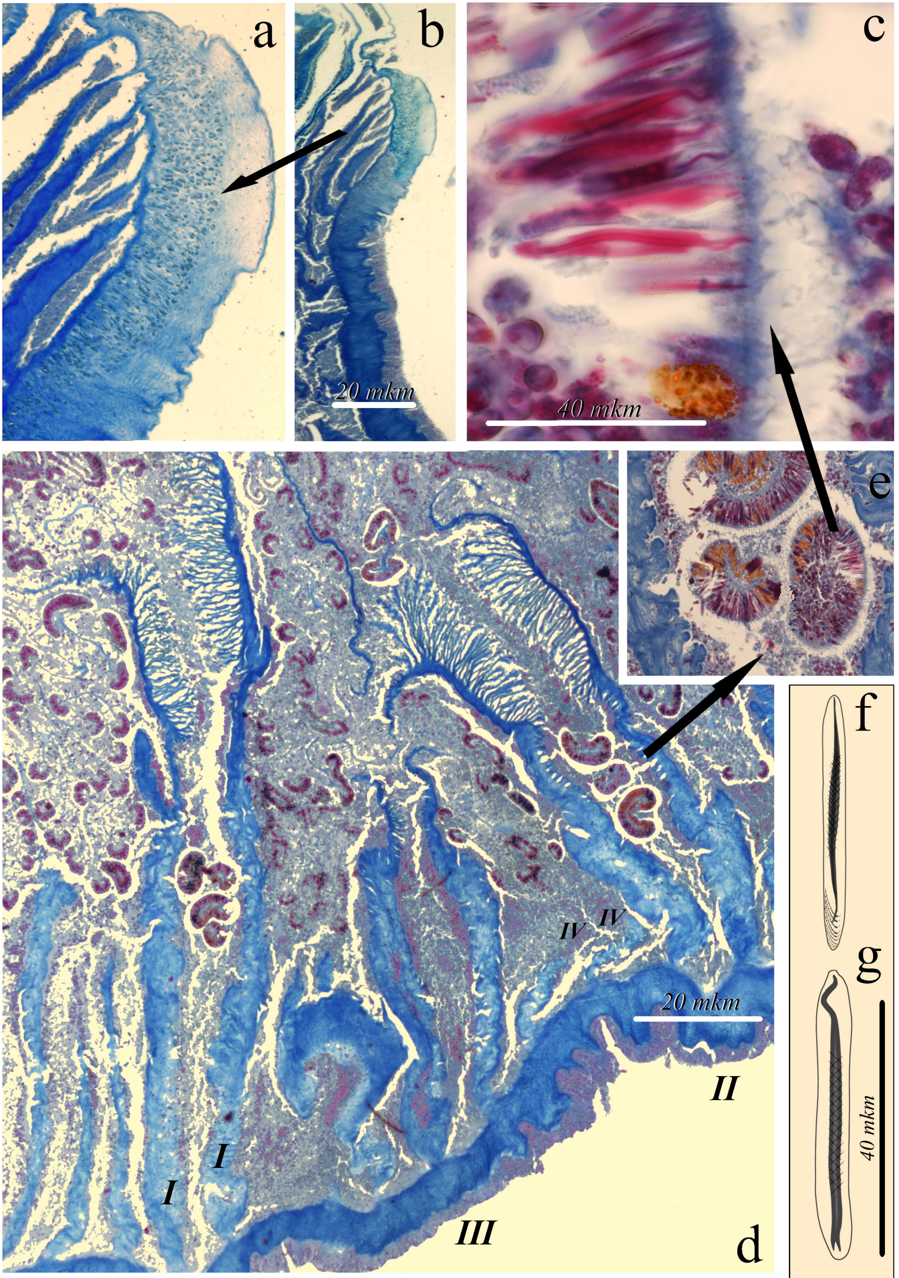
a waterproof housing. Stinging capsules (nematocysts) were measured on temporary preparations using a Nomarsky microscopy. Photographs of histological sections were taken through a Leica DM6000 B microscope, equipped with a Leica DFC295 digital camera.

DESCRIPTION

Sagartia elegans (Dalyell, 1848)

(Figs. 1 and 2)

Act. [Actinia, subgen. Isacmaea Ehr.] *rhododactylos* mihi: Grube, 1840, S. 3–4, Fig. 1 (original description).



a
b
20 mkm
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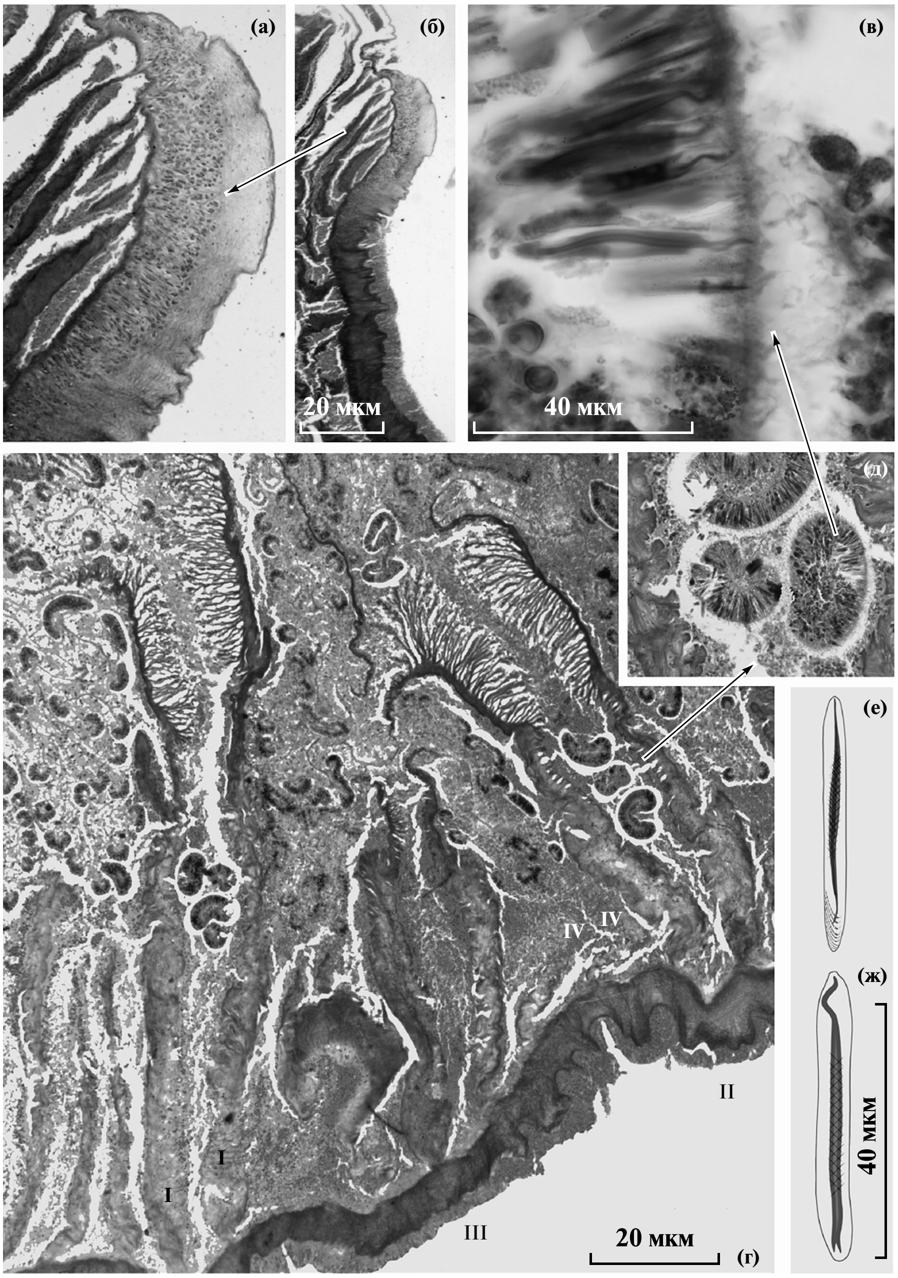

Fig. 2. Histological sections of *Sagartia elegans*, stained by Pacini's method (a–e), and nematocysts of acontia (a drawing from a temporary macerated preparation): b-rhabdoid (f) and p-rhabdoid (g). a, b, mesogloeal sphincter; c, nematocysts in acontia; d, cross section of the column: *I–IV* are the mesenteries of the first to fourth cycles; e, cross section of acontia. (Photo by B.A. Anokhin).

Sagartia rhododactylos [sp. n.][1] (A.E. Grube, 1840)—Pax, Müller, 1955a, p. 80; 1955b, p. 121; 1962, S. 209–211.+

Actinia elegans [sp. n.]: Dalyell, 1848, pp. 225–226; Pl. XLVII, figs. 9–11 (original description).

Sagartia elegans (Dal.)—Haddon, 1889, pp. 304, 323.

Sagartia elegans (Dalyell)—Nafilyan, 1912, pp. 19–24, Fig. 2; Evans, 1924, pp. 121–125; Stephenson, 1928, pp. 13, 94, text Figs. 8C, 12A, 30, pl. XIII, Fig. 2; 1929a, pp. 137–167, text-fig. 6; 1929b, pp. 178–189, text Figs. 2–4, 6–8, pl. I, Fig. 2; 1929c, p. 137; 1935, pp. 306–324, text Figs. 99A–C, 100–102, pl. XVIII, Figs. 1–7, pl. XIX, Figs. 1–5, 8, pl. XXI, Fig. 3, pl. XXXI, Fig. 1; Carlgren, 1949, p. 101; Schmidt, 1972, S. 46–48, Abb. 25d; Manuel, 1988, pp. 143–145, pl. 2A, Figs. 5H, 49A–D; Shaw,

[1] See the Taxonomic notes section.

1989, pp. 189–199; 1991, pp. 519–525; England, 1991, pp. 692, 695; Williams, 1991, pp. 540, 542; 1996, pp. 339, 345–346, 350; 1998, pp. 361, 364–368; 2000, pp. 49–68; Ates et al., 1998, p. 269; Faasse, Blauwe, 2002, pp. 95–96; Hartog, Ates, 2011, pp. 25–26.

Actinia miniata mihi: Gosse, 1853a, p. 127 (original description).

Sagartia miniata (Gosse)—Gosse, 1858, p. 415.

Sagartia miniata—Gosse, 1860, pp. 41–47, pl. II, Figs. 2–4; Stephenson, 1920, pp. 439–440, 545, text Figs. 2–9, 13–17, 21, pl. XXII Figs. 1–5, 9.

Heliactis miniata Gos.—Andres, 1883, pp. 147–148; 1884, pp. 141–142.

Actinia nivea mihi: Gosse, 1853b, pp. 93–96, pl. I, Fig. 8 (original description).

Sagartia nivea—Gosse, 1855a, pp. 274–275; 1860, pp. 67–72, pl. 2, Figs. 1, 8.

Sagartia nivea (Gosse)—Gosse, 1858, p. 415; Stephenson, 1920, p. 545.

Actinia rosea mihi: Gosse, 1853b, pp. 90–93, pl. I, Figs. 5–6 (original description).

Sagartia rosea—Gosse, 1855a, pp. 274–275; 1860, pp. 48–53, pl. I, Figs. 4–6.

Sagartia rosea (Gosse)—Gosse, 1858, p. 415; Stephenson, 1925, p. 905, text Figs. 18, 22.

Actinia venusta [sp. n.]: Gosse, 1854, pp. 281–283 (original description).

Sagartia venusta—Gosse, 1855a, pp. 272–274, pl. 28, Figs. 7–9; 1855b, p. 294, pl. XXVIII, Fig. 7; 1860, pp. 60–66, pl. I, Fig. 7.

Sagartia venusta (Gosse)—Gosse, 1858, p. 415; Stephenson, 1920, p. 545.

Actinia ornata [sp. n.]: Wright, 1856, pp. 70–72, pl. 6, Figs. 1–3 (original description, junior homonym; none Holdsworth, 1855, pp. 236–237).

Sagartia ichthystoma (Gosse): Gosse, 1858, p. 415 (original description).

Sagartia ichthystoma (Sp. nov.)—Gosse, 1860, pp. 57–59, pl. II, Fig. 7.

Sagartia ichthystoma Gosse—Pennington, 1885, p. 153.

Actinia n. sp. ?*pulcherrima* mihi: Jordan, 1855, pp. 86–87; Andres, 1883, p. 391 (original description); 1884, p. 390.

?*Sagartia rockalliensis*[2]: Carlgren, 1924, pp. 27–28 (original description).

External Structure

The shape of the body is typical for most sea anemones and is rather variable. The main cylindrical part of the body, the column, is narrower than the pedal disc, the diameter of which in large polyps may reach 3.5 cm but commonly does not exceed 10–15 mm. A column up to 3 cm in diameter frequently reaches a height of 4.5 cm. In our samples, most of the live sea anemones were not higher than 3.5 cm; the crown of the stretched tentacles was up to 2 cm in diameter. Since these animals tend to stretch themselves up in darkness, the tallest polyps of those found in the caves reached 10 cm in height, despite the fact that their body weight was not the highest. The column wall is not differentiated into segments. It can be covered with an undurable film of mucous excretions, but does not form a firm cuticle. The column is smooth; when the animal shrinks, longitudinal and transversal wrinkles and vertical rows of rounded protuberances appear on its surface. The bright spots that are covered with an adhesive secretory epithelium, which had been mentioned by many authors as being typical for other Sagartiidae and are weakly developed in *Sagartia elegans*, were not seen on our specimens. Only a few of our fixed sea anemones had noticeable small prominences on the surface of the column (Fig. 1i), which apparently corresponded to cinclides that bulge out slightly as the body shrinks due to fixation (Figs. 1e and 1h). In the upper one-third part of the body and right above the pedal disc, the body is perforated with cinclides, which are openings for releasing water and discharging acontia. In many individuals cinclides are marked with a dark pigment and are clearly seen in live (Fig. 1h) or recently fixed polyps (Fig. 1e). Moreover, cinclides are also indicated by thread-like or spiral-wound acontia that protrude from them (Figs. 1f and 1g). The external edge of the pedal disc is striated with lines of attachment of mesenteries. In the upper part, the column wall passes into the base of the external (abaxial) tentacles. The tentacles are medium in length and nearly half the oral-disc diameter. The unusually long catch-tentacles that sometimes occur in individuals of the British population (Manuel, 1988) were not found in our material. Large individuals have six cycles of tentacles, nevertheless strict hexamerous symmetry in their arrangement, viz., $6 + 6 + 12 + 24 + 48 + 96 = 192$, is almost never observed (Fig. 1b). Already in the first two cycles, there are usually more or fewer tentacles than the numbers in the formula (in Fig. 1d, two closely situated tentacles of the second cycle are seen on the dark sector of the oral disc). After examining hundreds of live specimens, Stephenson [50] and Manuel [33] stated that polyps with regular symmetry are extremely rare in this species. The latter author added that the rarely found uncommonly large polyps with the hexamerous symmetry had probably never undergone division.

Anatomical Structure

A typical mesogloeal sphincter is located in the upper part of the column (Figs. 2a and 2b). The radial muscles of the oral disc and longitudinal muscles of the tentacles are ectodermal. Our comparatively small

[2] See the section Taxonomic notes.

specimens (with diameters of about 1 cm in the fixed state) developed four cycles of mesenteries (Fig. 2d), despite the fact that five cycles of mesenterial pairs were mentioned in earlier works. The three older cycles are usually perfect, but according to Stephenson [50], the number of perfect pairs of mesenteries varies in the same manner as the number of tentacles, which is obviously related with the division of an individual, which is frequently followed by a breakdown of symmetry. The numbers of mesenteries in the upper (distal) and lower (proximal) parts of the column are approximately equal. The mesenteries from the first to the fourth cycle, including the directive pairs, bear gonads. The retractor muscles on all the mesenteries are diffuse (Fig. 2d); parietobasilar muscles are weak, while basilar ones are strong. Even small mesenteries of the final cycle can bear acontia (Figs. 2c–2e).

The coloration of the sea anemones of this species varies greatly. There are five more or less clearly differentiated color morphs known from European coastal waters, viz., *nivea* (the oral disc and tentacles are white), *rosea* (the disc is orange, brownish-olive or whitish, tentacles are pink, crimson, sometimes with violet hue or white stripes), *venusta* (the disc is orange, tentacles are white), *miniata* (the oral disc and tentacles have a distinct pattern with brownish hues; the external tentacles are orange or red, without any pattern), and *aurantiaca* (disc is bright orange or grey, with paired wedge-shaped spots at the base of the internal tentacles, which are bright orange). The detailed description of morphs and individuals with frequently occurring transitional coloration, composed by Stephenson, [50, pp. 309–314, pl. 18, 19, 21], was supplemented by Ates [5]. In the twilight of a cave or shadowed grotto, almost every stretched sea anemone becomes transparent and pale. Only a few individuals have an oral disc that is colored with orange–red, white, or dark pigment; the dark and light sectors are often located asymmetrically. According to our observations, in the Crimean underwater caves, this species was represented by the morphs *rosea* (Figs. 1a and 1c) and *miniata* (Figs. 1b and 1d); in the Gulf of Odessa, we observed only the *miniata* morph.

Differential Diagnosis

In its appearance and many of its anatomical features, the species *Sagartia elegans* differs slightly from the closest related representatives of Sagartiidae, especially from juvenile *Cereus pedunculatus*. Only the adult *C. pedunculatus* polyp is much larger, has many more tentacles (up to 768) as well as a larger number of mesenteries in the upper (distal) part of the body than in the lower part [12, 50]. In addition to this species, *S. elegans* is similar to *Sagartia troglodytes, Sagartiogeton undatus*, and *S. entellae*. As a reliable character for species diagnosis, Schmidt [41] suggested using stinging capsules of acontia, which in *S. elegans* are substantially larger than those in all the species above, *p*-rhabdoids (= *p*-mastigophores[3]. The two types of rhabdoids (*p*-rhabdoids, *b* rhabdoids) were designated by Carlgren as *p*- and *b*-mastigophores.)[4]) 39–80 × 4.0–9.0 µm; *b* rhabdoids (= *b*-mastigophores) 24–44 × 2.6–5.0 µm. In our polyp from the Black Sea, *S. elegans*, dimensions of nematocysts in acontia were similar but differed a little, viz., *p* rhabdoids 41–49 × 4.5–5.5 µm and *b*-rhabdoids 23–47 × 2.0–5.0 µm.

According to Schmidt [41], the ratio of the length of the capsule to that of the *p*-rhabdoid shaft that is thrown out after shooting can be a distinctive sign, as well as the dimensions of the stinging capsules. These ratios in the considered species are as follows: approximately 1 : 1 in *Sagartia troglodytes*; approximately 4 : 5 in *Cereus pedunculatus*; approximately 3 : 4 in *Sagartiogeton undatus* and *S. entellae*; from 2 : 3 to 3 : 4 in *Sagartia elegans*. All the four Sagartiidae species can also be distinguished by haplonemes (anisorhize Haplonemen, a German term used by Schmidt for designation of this type of nematocysts) that occur in the epithelium of the body wall: they are absent in *S. elegans* and *Sagartiogeton entellae* while they differ clearly in shape and size in all the other mentioned species [41, Abb. 3a, 3c].

Ecology

Sagartia elegans occurs within the range of the intertidal zone, where it settles in shadowed sites and under stones and up to the 60-meter depth; it was found at a depth of 185 m only one time (see the Taxonomic notes section below). Like many shallow-water animals, *S. elegans* frequently settles in rock crevices and on porous stone or stones that were perforated by rock-boring animals. The polyp inserts its pedal disc into such holes. Its oral disc, which protrudes from the shelter, can be quickly retracted at any irritation. At convenient sites this species forms abundant settlements, which we observed, particularly in Crimean caves. Western European researchers have also described *S. elegans* on silted or sandy bottoms, where the largest specimens were found. This sea anemone lives there along with similar but more numerous *S. troglodytes* and *Cereus pedunculatus*. In some places in the sublittoral zone *S. elegans* is very abundant on open rock surfaces.

As of the present, *S. elegans* in the Black Sea has been found only near the western coast of the Crimea and in the Gulf of Odessa. The inspected Crimean caves are actually tunnels in limestone that were hollowed out by water. *S. elegans* occupies the farthest sites from the entrance, where even scattered day light never penetrates. Sea anemones sit on the ledges of side walls and mainly on the upper sides of cornices. The water depth at their locations does not exceed

[3] We use the classification of nematocysts proposed by Weill [51, 52], revised and updated by Carlgren [9, 11] and Bozhenova [1]

3 m; only *Actinia equina* can occur at deeper levels of these caves. The surface of the stones that are chosen by *S. elegans* is mostly uneven and gnawed by polychaetes or the boring sponge *Pione vastifica*. Other kinds of fouling are small colonies of hydroid polyps, the sponge *Haliclona cinerea*, and juvenile bivalve mollusks (Mytilidae), which constitute not more than 10% of the projective cover of the substrate. The Marbled Rock Crab *Pachygrapsus marmoratus* and the Warty Crab *Eriphia verrucosa* are repeatedly observed among sea anemones. In 2009, the Common Prawn *Palaemon serratus*, a rare species in the Black Sea, whose behavioral aspects still remain almost unstudied, was found among sea anemones in a cave for the first time. In the caves where *S. elegans* was revealed, the salinity reaches 17.8‰; the water temperature at our diving works varied from 15 to 24°C. In the winter season, the temperature of the water in the studied area drops below 5°C. In the Gulf of Odessa, the water temperature at a depth of 10 m varies from 1 to 22°C, and salinity varies from 5.3 to 17.5‰.

Dutch researchers, after analyzing findings of *S. elegans* for many years, made the conclusion that the abundance of this species in many sites along the coast of the Netherlands decreases significantly, sometimes up to complete vanishing, in cold winters but is capable of rapid reproduction or re-colonization after a few warm years [6]. It is more probable that the unsteadiness of the populations in the Black Sea, which are at the edge of species range, is the reason that *S. elegans* was not encountered there previously. Only a dedicated inspection of underwater caves, which serve as a shelter for rare animals that tolerate aberrant habitat conditions and reach a high population in the absence of competitors, enabled us to find this species in these waters.

Reproduction

Sagartia elegans is a gonochoristic species, which, according to the published data, spawns its eggs into the water [34, 41, 47]. As well, laceration is a typical means of its somatic reproduction: pieces of an animal's pedal disc frequently come off during creeping and subsequently grow into new individuals. Unlike *S. elegans*, the closely related species *S. troglodytes*, which also inhabits waters along the European coast, does not breed asexually. Stephenson [47] believes that in *S. elegans*, laceration is the prevailing means of supporting its population. We also noted numerous clonal groups of animals that consisted of individuals that were similar in color and varied in size, which apparently had descended from a common old polyp (Fig. 1a). However, molecular analyses that could confirm the genetic identity of individuals in these variously colored clonal lines have not been performed yet.

Distribution

The species is distributed along the coasts of Iceland and Western Europe, viz., the British Isles, Scandinavia, in the Kattegat Strait and the North Sea [10, 35, 50], southward along the Atlantic coast of France [19] to the Mediterranean Sea, where it is known to inhabit waters off Banyuls sur Mer [18] and Marseille [32], the northern Adriatic Sea [38], and the Gulf of Genoa [8]. Our work is the first evidence of the presence of *S. elegans* in the Black Sea.

Taxonomic Notes

The species name *rhododactylos* (*Actinia rhododactylos* Grube, 1840) has a priority over *elegans*. However due to the incompleteness of the description by Grube, the status of this name is doubtful [3, 17, 41] and it is considered as a synonym of the species that is discussed only conditionally. The specimens that were collected later in the Adriatic Sea not far from the type locality and referred by Pax [38] to *Sagartia rhododactylos*, judging from his comments and Grube's original text [27], undoubtedly belonged to *S. elegans* by Dalyell [13]. Therefore, the ecological and geographical data that were published by Pax and Müller were taken into account in this work.

The description of *Sagartia rockalliensis* by Carlgren [7] was based on the study of 29 specimens from a single station of the French expedition. Later, the author of the species referred this deepest finding (185 m) to *S. elegans*, the type species of the genus *Sagartia* [10, p. 9, Remarks]; despite the establishment of the bathymetric range, the distribution of the species of less than 42 m had not been broadened. Later researchers also considered *S. rockalliensis* as a synonym of *S. elegans* [17].

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