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Kofoidinium, Spatulodinium and other kofoidiniaceans (Noctilucales, Dinophyceae) in the Pacific Ocean

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Abstract

Examples of rarely reported dinoflagellates of the family Kofoidiniaceae F.J.R. Taylor (Noctilucales) from the northwest, equatorial and southeast Pacific Ocean are described and illustrated. *Kofoidinium* was the most ubiquitous genus with a maximum abundance of 10 cells L^{-1}. Specimens of this genus were identified to four species: *Kofoidinium* sp. that showed a pointed extension that emerges from the antero-ventral region and *K. velelloides*, both of which had diameters that ranged from 40 to 200 μm; *Kofoidinium pavillardii* which showed a rounded epitheca and a larger size (~300–700 μm in diameter); and another species, tentatively identified as *K. splendens*, that contained red circular inclusions. Further research is needed to clarify the characteristics that separate *K. splendens* from the other species. This study is the first to record the genus *Spatulodinium* in tropical waters and in the southern hemisphere. *S.* cf. *pseudonoctiluca* was found in the southeast Pacific Ocean, as well as other smaller specimens with a different shape or disposition of the tentacle that may belong to two other species. In the northwest and equatorial Pacific, specimens of *Spatulodinium* showed a green pigmentation that suggested the existence of the first species known in the order Noctilucales to contain its own chloroplasts. Immature stages of kofoidiniaceans, some containing symbiotic microalgae, are illustrated, as well as mature stages related to *Pomatodinium* and to unknown genera of kofoidiniaceans. Kofoidiniaceans are shown to be common and widely distributed in the Pacific, and are probably also frequent in other oceans, but are rarely recognised.

Keywords: *Kofoidinium*; *Spatulodinium*; *Pomatodinium*; Noctilucales; Dinophyta; Pacific Ocean

Introduction

The noctilucaceans, whose morphology differs strongly from that of typical Peridiniales, are of particular interest in the evolution of the dinoflagellates. After *Noctiluca scintillans* (Macartney) Kofoid, members of the family Kofoidiniaceae are the most common noctilucaceans. However information on this group has been scarce and nearly restricted to the study by Cachon and Cachon (1967b). They demonstrated that the kofoidiniaceans undergo an exceptional morphological transformation during their life cycle, e.g., they described 6 stages, *a* to *f*, in *Kofoidinium pavillardii*, and they showed that several life stages had been described as separate species (Cachon and Cachon 1967b).

Pouchet (1885) described the first kofoidiniacean, *Gymnodinium pseudonoctiluca*. He already noted the strong morphological changes of this taxon and illustrated this single species with different morphologies. One of the

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forms corresponded to a large *Amphidinium*-like cell, and the mature stage was a round or oval, laterally compressed cell with a tentacle. However, further authors considered the immature stages as separate species such as *Gymnodinium pyrocystis* Jørgensen, *G. fulgens* Kofoid et Swezy, *G. lebouriae* Pavillard and *G. viridis* Lebour (= *G. conicum* Kofoid et Swezy) (Cachon and Cachon 1967b; Konovalova and Selina 2002). Specimens from the NW Mediterranean Sea, illustrated by Pavillard (1921) under the name *Gymnodinium pseudonoctiluca*, were probably immature stages of *Kofoidinium*. Later, Pavillard found the mature stage, which he described as a member of a new genus and named it *Kofoidinium velelloides* (Pavillard, 1928). Another doubtful species, described from Canadian arctic waters, is *Kofoidinium arcticum*, known only from the first description (Bursa 1964). Cachon and Cachon (1967b) erected the genus *Spatulodinium* from *Gymnodinium pseudonoctiluca* and described the species *Kofoidinium pavillardii* Cachon et Cachon, 1967 and *K. splendens* Cachon et Cachon, 1967. They regarded *G. pseudonoctiluca* Pouchet, 1885 as the basionym for both *Spatulodinium* and *Kofoidinium* because the immature stages of these genera were similar in morphology.

Two other genera, *Pomatodinium* Cachon et Cachon-Enjumet, 1966 and *Cymbodinium* J. Cachon et M. Cachon, 1967, have been included in the family Kofoidiniaceae (Sournia 1986). *Pomatodinium* has the shape of a gastropod larva and may contain zooxanthellae (Cachon and Cachon-Enjumet 1966). The genus *Cymbodinium* has the shape of a veliger larva and only one flagellum has been observed (Cachon and Cachon 1967a). *Cymbodinium*, the least known of these genera, was first placed in the family Leptodiscaceae Kofoid and later in the family Kofoidiniaceae F.J.R. Taylor (Sournia 1986).

Information on the life cycle and detailed morphology of kofodinianceans is nearly restricted to the study based on live specimens collected by Cachon and Cachon in the coastal Ligurian Sea (NW Mediterranean). Little is known about the distribution and morphology of kofoidiniaceans in oceanic waters. However, they are probably often present in oceanic plankton samples, but are rarely recognised in the fixed condition. The present study investigates the distribution of kofoidiniaceans in several regions of the Pacific Ocean and illustrates the appearance of these dinoflagellates in fixed samples in the hope that they will be more commonly recognised and reported. The occurrence of body inclusions and tentative symbiotic microalgae is illustrated. Several life stages such as *Gymnodinium lebouriae* or *G. pseudonoctiluca* and other unidentified immature stages are illustrated. This study illustrates unknown species thought to belong to the genus *Spatulodinium* and other unknown genera of kofoidinaceans, including the first species in the order Noctilucales thought to contain its own chloroplasts.

Material and methods

Sample collection and light microscopical methods used in the northwest and Equatorial Pacific Ocean were described in Gómez and Furuya (2005) and are not repeated here. In the southeast Pacific Ocean, samples were collected during the BIOSOPE (Biogeochemistry

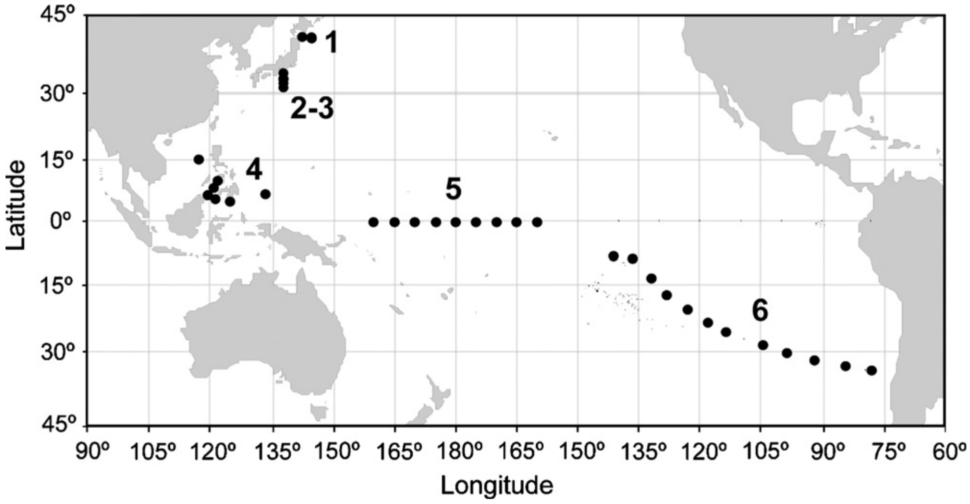


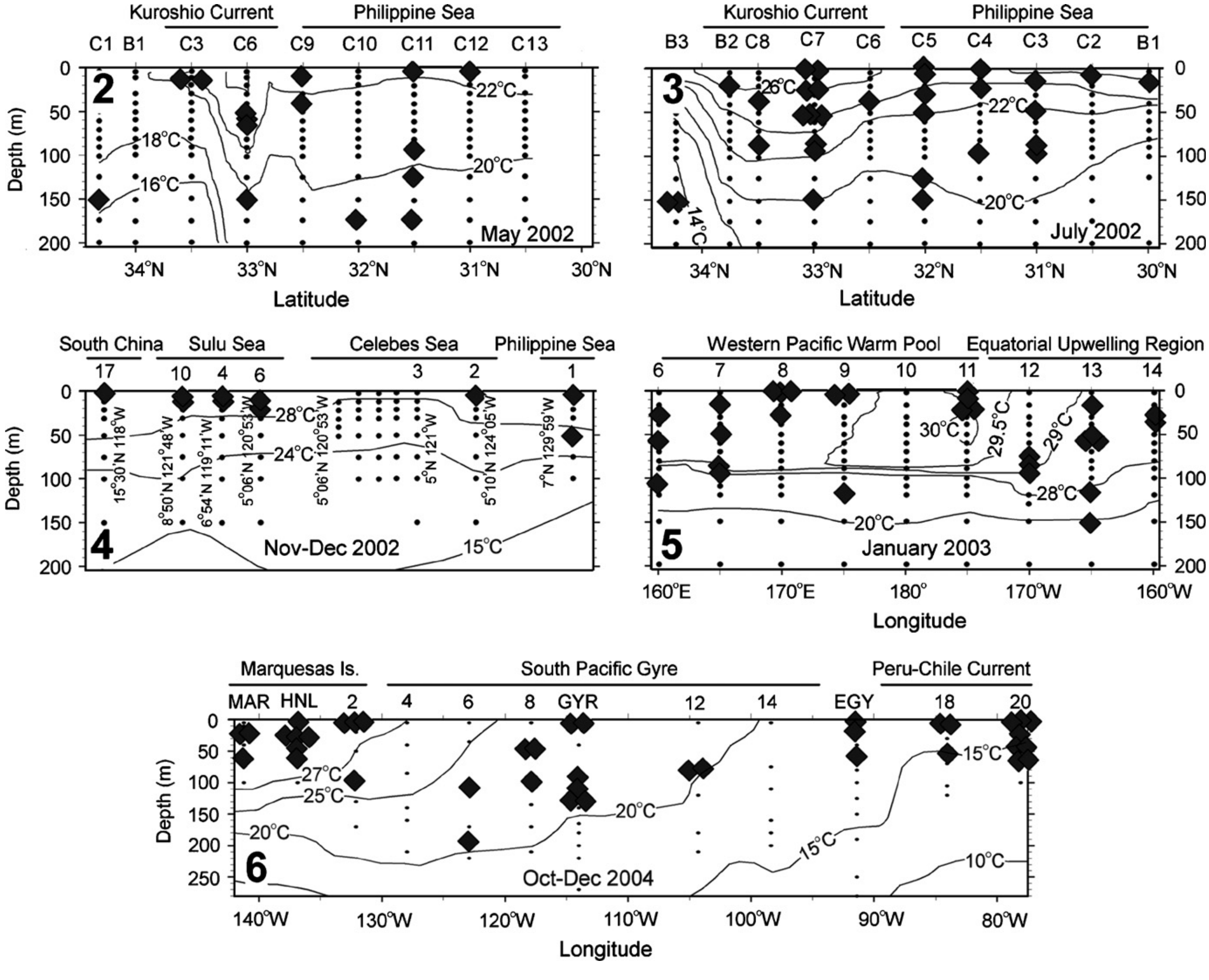
Fig. 1. Map of the station locations in the Pacific Ocean (marked by circles). 1. Oyashio Current. 2, 3. Kuroshio Current and Philippine Sea in May and July, respectively. 4. Celebes, Sulu and South China seas. 5. Western and central equatorial Pacific. 6. Southeast Pacific Ocean.

and Optics South Pacific Experiment) cruise on board R/V *L'Atalante* from the Marquesas Is. to the coast of Chile (26 October-12 December 2004) (Fig. 1). Samples from 12 stations comprised 83 samples collected by Niskin bottles from 5 to 270 m depth. These were preserved with acidified Lugol's solution and stored at 5 °C. Samples of 500 mL were concentrated via sedimentation in glass cylinders. The top 450 mL of sample was slowly siphoned off with small-bore tubing during 6 days. The remaining 50 mL of concentrate, representing 500 mL whole water, was then settled in composite settling chambers. The entire chamber was scanned at 200 × with an IX71 Olympus inverted microscope equipped with an Olympus digital camera. Each specimen was photographed and measured at 400 × with Olympus DP70-BSW software.

Results

Distribution of *Kofoidinium*

Kofoidinium was the most ubiquitous genus of noctilucaceans in the open waters of the Pacific Ocean. A latitudinal transect in the vicinity of the Kuroshio Current to the south of Japan (138°E) was investigated in May and July 2002. In May, 15 individuals of *Kofoidinium* were found from 131 samples analysed (Fig. 2), and in July, 32 specimens were found in 144 samples analysed (Fig. 3). During the cruise in the marginal seas of the western Pacific Ocean 10 specimens were observed from 81 samples (Fig. 4). In the western and central equatorial Pacific 30 specimens were found from 124 samples (Fig. 5). In the southeast Pacific



Figs 2–6. Section plots of the records of *Kofoidinium* (mature stage) in the Pacific Ocean indicated by filled rhombuses (see also Fig. 1). **2**, Records along the meridian 138°E in May. **3**, Records from the same location in July. **4**, Records from Celebes, Sulu and South China seas. **5**, Records from the western and central equatorial Pacific. **6**, Records from the southeast Pacific. Isotherms are shown.

Ocean, 42 specimens of *Kofoidinium* were found in the 83 samples analysed (Fig. 6). No kofoidiniaceans were found in the sub-arctic waters of the Oyashio Current off Hokkaido.

It is difficult to discern a pattern in the distribution of *Kofoidinium*. The highest abundance was only 4 specimens per sample (10 cells L^{-1}). In the Kuroshio Current and adjacent waters, the abundance was higher in summer than in spring (Figs 2, 3). Specimens of *Kofoidinium* were only found near the surface in the SE Asia marginal seas (Fig. 4), but in other waters they were found at depths down to 200 m. Overall, no clear longitudinal or vertical pattern in the distribution was observed, suggesting ubiquitous distribution of the organism in warm waters (Figs 2–6). The trophic conditions in these regions were described in Gómez et al. (2005). In the equatorial and southeast Pacific Ocean, the records of *Kofoidinium* tended to be more abundant in the most eutrophic regions, such as the vicinity of the Marquesas Islands and Peru-Chile Current (Fig. 6). In the Pacific Ocean the specimens were recorded in a wide range of temperature from 14 °C near the Chilean upwelling to 30 °C in equatorial surface waters (Figs 2–6).

Morphology of *Kofoidinium*

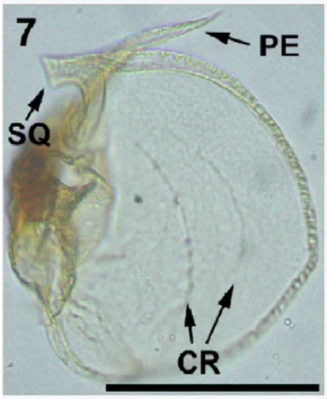
It is not easy to identify kofoidiniaceans to species due to the high morphological variability during their life cycle and the difficulties to delimit the species from preserved specimens. In the present study, the records of *Kofoidinium* have been tentatively grouped into four species: *Kofoidinium* sp., *K. velelloides* and *K. pavillardii* that are identifiable with more certainty and the more dubious *K. splendens*. The limits of this last taxon are unclear due to common morphological characters with the other species. In no case did preserved specimens of *Kofoidinium* retain the shell which is carried above the episome in life (see Cachon and Cachon 1967b).

The smaller specimens encountered ranged from 40 to 200 μm in diameter. The most extended morphology was a round to slightly ellipsoidal, laterally flattened hyposome or velum, transparent with several concentric ridges and bordered by a narrow differentiated band (Figs 7–10). The reduced episome formed a crest at the anterior margin of the cell. The nucleus was small and located in the episome. In the antero-dorsal margin appeared a short finger-like structure. The marginal differentiated band was thicker at the ends and in the antero-ventral region bifurcated forming a right angle. One extreme of this bifurcation of the marginal band was thick and formed a square-ended protrusion. The other branch was slightly curved and projected towards the episome (Fig. 7). One of the main characteristics of the Pacific specimens was the pointed extension that arises from the episome towards the ventral side of the cell. This pointed extension was flexible and tended to be in a different plane from the flattened hyposome (Figs 7 and 8). These small Pacific specimens that differed from the description of *K. velelloides* in Cachon and Cachon (1967b) are here named *Kofoidinium* sp. Specimens lacking the pointed extension, the square-ended protrusion and with a large nucleus located anteriorly in the hyposome (Fig. 10) were closer to *K. velelloides* as illustrated by Cachon and Cachon (1967b). Due to their transparency and small size, *Kofoidinium* sp. and *K. velelloides* could be more easily overlooked during sample analysis than the highly visible *K. pavillardii* (Figs 8, 9, 11–15).

Kofoidinium pavillardii is the largest species of the genus. The diameter was longer than 300 μm and reached 700 μm (Figs 8 and 11). The round hyposome occupied nearly all the cell body. The marginal hyaline band is interrupted at about 2/3 of the cell height with thicker end regions, especially the ventral one. More anteriorly than the ends of the marginal band are located two hook-shaped structures, the anchorage mechanisms that held the hemispherical transparent dome or shell (Figs 11 and 14). These delicate hyaline domes are easily detached from the cell and had presumably been lost. The ventral anchorage mechanism (Fig. 14) is bigger than the dorsal one (Fig. 11). The shape of the episome varied between the specimens, sometimes forming a prominent crest (Fig. 12), and in others more reduced (Fig. 11). The specimen in Fig. 12 has the shape of *K. pavillardii* as illustrated by Cachon and Cachon (1967b).

While the identification of *K. velelloides* and *K. pavillardii* is relatively easy, the determination of diagnostic characters

Figs 7–23. Photomicrographs of kofoidiniaceans, bright field optics. **7**, *Kofoidinium* sp. (0°, 165°W, 150 m depth) with anterior episome at the left, the hyposome at the right and the ventral projections at the top. **8-9**, *Kofoidinium pavillardii* (large cell) and *Kofoidinium* sp. (small cell) (0°, 170°E, 0 m depth); the inset in Fig. 8 shows the *Kofoidinium* sp. cell at a different focal plane. **10**, *K. velelloides*, note the prominent nucleus (0°, 160°E, 110 m depth). **11**, *Kofoidinium pavillardii*. See the ventral anchorage mechanism in the inset (34°15′N, 138° E, 150 m depth). **12–15**, *Kofoidinium pavillardii* (30°N, 138°E, 125 m depth). **13**, Detail of the dorsal margin of the hyposome. **14**, Detail of the antero-ventral region and the anchorage mechanism. **15**, Detail of the inclusions in the margin of the hyposome. **16**, *Kofoidinium splendens* (7°25′N, 121°12′E, 10 m depth). **17–21**, *K. splendens* with red inclusions (0°, 170°W, 80 m depth). **19**, Detail of the inclusions in the cell body. **20**, The arrows indicate the concentric ridges with red inclusions. **21**, Detail of red inclusions in the periphery of the hyposome. **22-23**, Unidentified pairs of kofoidiniaceans, probably stage "c" after binary fission (0°, 175°W, 30 m depth). **23**, Detail of the presumed symbiotic microalgae. AM = anchorage mechanism for shell; CR = concentric ridges; F = fibrils; PE = pointed extension; SQ = square-ended projection; TF = transverse flagellum. Scale bars = 50 μm.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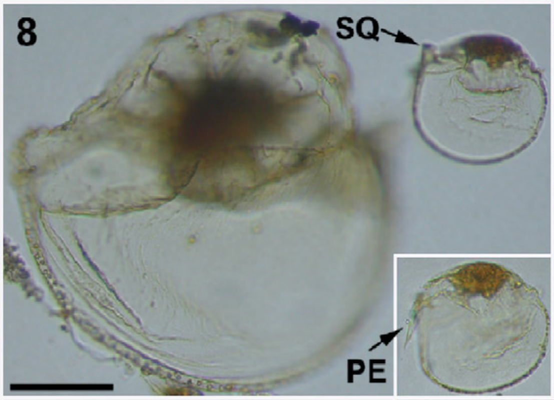
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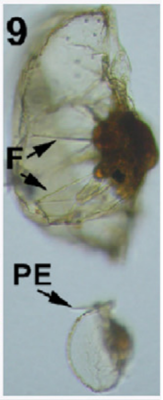
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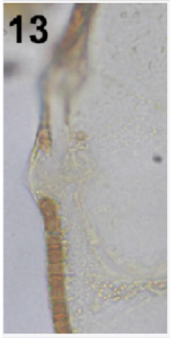
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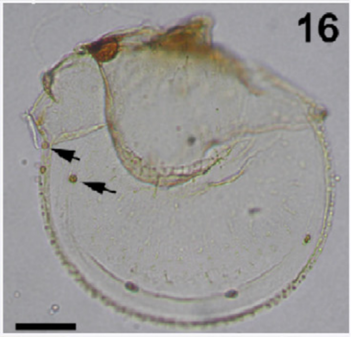
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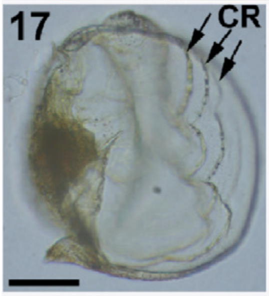
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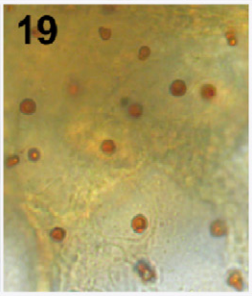
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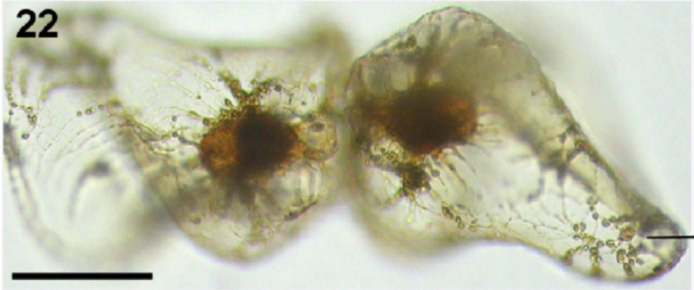
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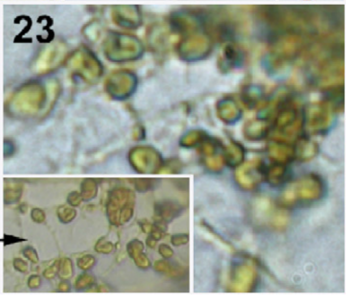
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of *K. splendens* and its validity as a species require further research. Specimens >200 μm (usually 300–400 μm) with a smoothly rounded left cingular crest have been considered as *K. splendens* (Figs 16–21). Cachon and Cachon (1967b) considered that body inclusions are characteristic of *K. splendens*. However, the specimen of Fig. 12, whose shape resembled *K. pavillardii*, had a differentiated band filled with brownish granules (Figs 13 and 15). The specimens that harbour body inclusions in the margin of the hyposome, and also in the concentric ridges or dispersed over the cell body are here assigned to *K. splendens* (Figs 16–21). According to Cachon and Cachon (1967b) these red body inclusions in the Lugol-fixed specimens are of polypeptide nature rather than lipid bodies; thus, the possibility of that these red inclusions are symbiotic microalgae may be discarded. In the present study no symbiotic microalgae were observed in mature stages of *Kofoidinium*.

No noctilucacean species has been reported to have chloroplasts (excluding chloroplasts of the ingested prey or symbiotic microalgae). Tentative symbiotic microalgae were observed in an unidentified kofoidiniacean (Figs 22 and 23). This observation was made in a pair of recently divided cells. According to Cachon and Cachon (1967b) such reproduction by bipartition is restricted to the immature cells. The presumed symbiotic microalgae were distributed along tracts and showed an ellipsoidal to rotund shape and were 5–7 μm in diameter (Fig. 23). At the same sampling station, structures that appeared to be symbiotic microalgae were found in an unidentified immature stage (Figs 24 and 25).

Distribution and morphology of *Spatulodinium*

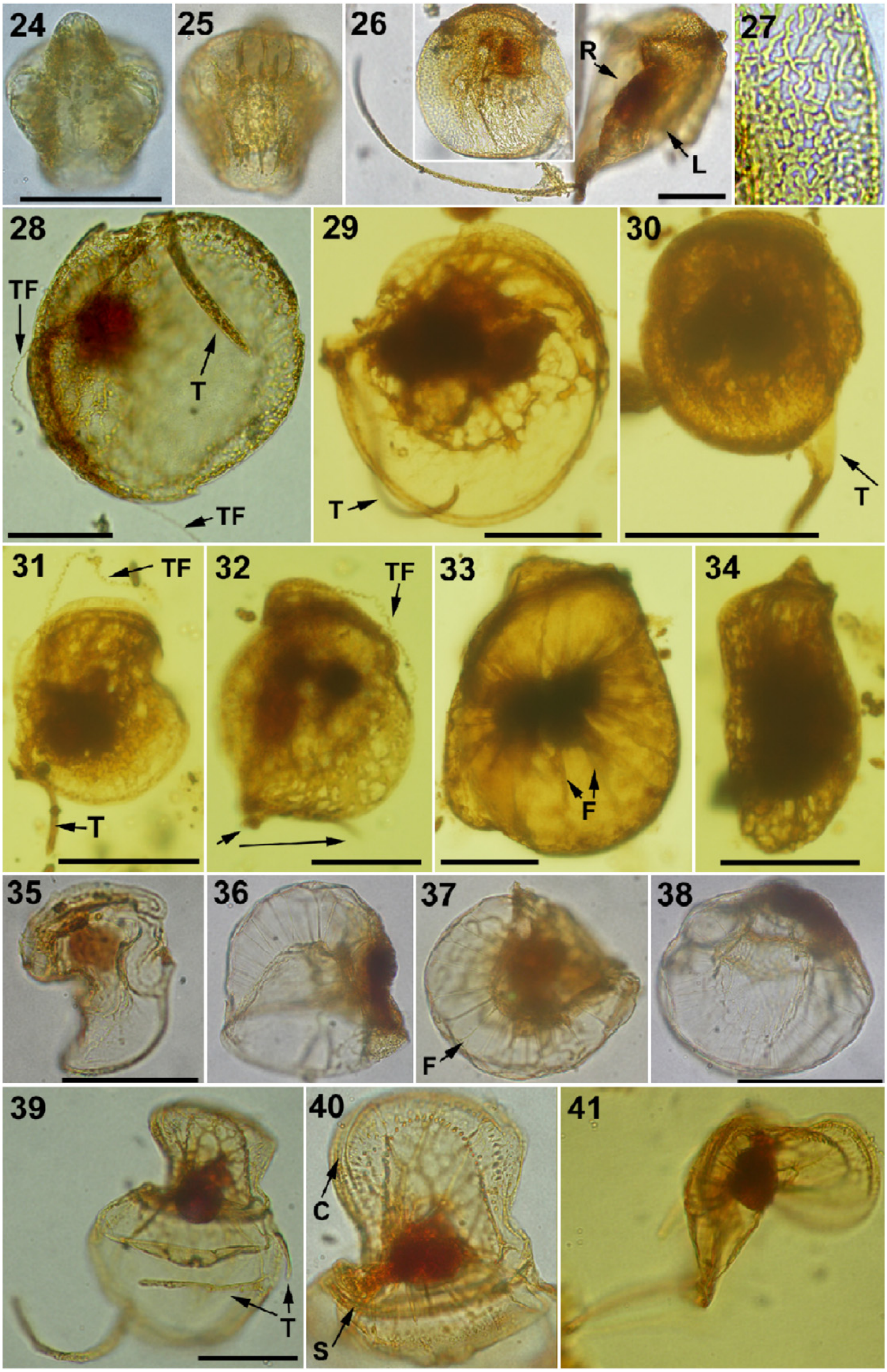
Spatulodinium pseudonoctiluca has the shape of a disc, about 100–120 μm in diameter, which has been deformed into a shallow cone by pushing in the left side so that the right side has become somewhat convex. A net of fibrils (Fig. 33) is thought to facilitate the ingestion of the prey of these heterotrophs. The main characteristic of the genus is the occurrence of a long unstriated movable tentacle projecting from the ventral side in the anterior part of the cell (Figs 26, 28–32). It is true that *Kofoidinium velelloides* (Fig. 7) and other unidentified kofoidiniaceans (Fig. 39) also have tentaculoid projections, but these differ in size or origin. Only one specimen with the morphology reported for the type species was encountered (Fig. 29). *Spatulodinium* was previously regarded as a monotypic genus only known from boreal-arctic waters from Europe to the Japan Sea. The specimen identified as *Spatulodinium pseudonoctiluca* from the Peru-Chile Current constitutes the first record of this genus in the southern hemisphere (Fig. 29).

Beyond the type species, other specimens that differed from the type of *Spatulodinium* were observed. Three specimens corresponded to a large cell (~150 μm diameter) with a long tentacle and showing a green pigmentation (Figs 26–28). In SE Asia marginal seas, only one mature specimen was recorded in the open waters of the Sulu Sea (Figs 26 and 27). Two other specimens of "green" *Spatulodinium* sp. 1 were observed in the western and central equatorial Pacific Ocean (Fig. 28). The tentacle was very long in one of the specimens (two times the cell body, Fig. 26) and shorter and with a pointed-ending in the other specimen (Fig. 28). In these "green" *Spatulodinium* sp. 1 the typical system of fibrils was not visible or was masked by the green pigmentation (Figs 27 and 28).

Other unidentified species of the genus were observed with two different morphologies. The tentacle of the type species projected from the antero-ventral region. In these other specimens the tentacle appeared to project from the posterior part of the cell. Several specimens of *Spatulodinium* sp. 2 were about one half (~50 μm) of the diameter of the type species and showed a thick tentacle with a triangular transparent halo (Fig. 30). Specimens of *Spatulodinium* sp. 3, also of smaller size than the type species, showed a *Daphnia*-like shape, with a clearly visible flagellum (Figs 31 and 32).

The highest abundance of *Spatulodinium* spp. with 7 specimens was encountered in a eutrophic region near the Juan Fernández Archipelago, associated with a surface proliferation of *Gonyaulax polygramma* Stein.

Figs 24–41. Photomicrographs of kofoidiniaceans, bright field optics. **24-25**, Tentatively identified as the immature stage of a kofoidiniacean with a green pigmentation (0°, 175°W, 60 m depth). **26-27**, "Green" *Spatulodinium* sp. 1 (7°25′N, 121°12′E, 75 m depth); inset shows the same cell in a different orientation. **27**, Detail of the green pigmentation of the same cell as in Fig. 26. **28**, "Green" *Spatulodinium* sp. 1 (0°, 160°E, 40 m depth). **29**, *Spatulodinium* cf. *pseudonoctiluca* (31°54′S, 91°27′W, 5 m depth). **30**, *Spatulodinium* sp. 2 with a tentacle that is thicker in the proximal part (33°22′S, 78°6′W, 40 m depth). **31-32**, "*Daphnia*-like" *Spatulodinium* sp. 3 with a tentacle that projects from the posterior episome region. **31**, Specimen from 31°54′S, 91°27′W, 40 m depth. **32**, Specimen from 33°22′S, 78°6′W, 5 m depth. **33**, Stage "c" of a kofoidiniacean described as *Gymnodinium pseudonoctiluca* (33°22′S, 78°6′W, 15 m depth). **34**, Stage "d" described as *Gymnodinium lebouriae* (33°22′S, 78°6′W, 5 m depth). **35**, Tentatively identified as *Pomatodinium* sp. (33°N, 138°E, 60 m). **36–38**, Unidentified kofoidiniacean (32°N, 138°E, 100 m). Figs 36 and 37 resemble illustrations of *Pomatodinium impatiens* in the description by Cachon and Cachon-Enjumet (1966); note the prominent fibrils. **39–41**, Unidentified kofoidiniacean with two long tentacles emerging from the margin of the hyposome, one smaller tentacle and a prominent anterior crest (0°, 180°, 200 m depth); note the concentric areolation in Fig. 40. C = cingulum; F = fibrils; L = left side; R = right side; S = sulcus; T = tentacle; TF = transverse flagellum. Scale bars = 50 μm.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Also immature life stages which have been described as *Gymnodinium pseudonoctiluca* (Fig. 33) and *Gymnodinium lebouriae* (Fig. 34), precursors of mature stages of both *Spatulodinium* and *Kofoidinium*, were found at the same station. Consequently these immature stages cannot be strictly ascribed to *Spatulodinium* because specimens of *Kofoidinium pavillardii* were also observed in the same location.

Morphology of other kofoidiniaceans

Cachon and Cachon-Enjumet (1966) described the shape of *Pomatodinium* as resembling a gastropod larva, but with changes of shape due to the contraction of fibrils (like those found in *Kofoidinium*, see Fig. 9); they also reported that it may contain symbiotic microalgae. They illustrated *Pomatodinium* from a few live specimens, but found the morphology varied among fixed specimens. One specimen found by us in the Kuroshio region is assumed to belong to the genus *Pomatodinium* (Fig. 35).

Another specimen was composed of two hemispherical transparent domes, one inside the other, and joined at their rims. An inner net of fibrils joined the two hemispherical domes. One of the views of the specimen (Fig. 37) was similar to the figure "d" of *Pomatodinium impatiens* in Plate I by Cachon and Cachon-Enjumet (1966). However in other views the morphology of the specimen differed from the description of *Pomatodinium*. In one view the specimen had the shape of a Roman Centurion's helmet with the nucleus located in one side of the crest (Fig. 36). In one view the specimen could be mistaken for *Kofoidinium* (Fig. 38) and provides a clear example of the need to view kofoidiniaceans from different orientations to understand their true shape.

Another unidentified kofoidiniacean (~110 μm long) showed a very distinctive shape and extensions (Figs 39–41). The nucleus was located at the base of the episome (Fig. 40). A semicircular crest with a concentric inner areolation was observed in the episome (Fig. 40). The cingulum extended along the marginal part of the crest and the sulcus along the base of the crest (Fig. 40). The margin of the hyposome did not show the differentiated band that characterises *Kofoidinium*. The specimens showed three tentaculoid extensions from the hyposome, each with rounded-tips (Figs 39 and 41). The longer extension projected from the postero-ventral part of the margin of the hyposome. At the opposite side, slightly anteriorly, emerged another long extension (Fig. 39). These extensions originated from a different position compared with the single tentacle of *Spatulodinium*. A third short finger-like extension was visible emerging from the anterior-dorsal margin of the hyposome (Fig. 39).

Discussion

How many species of *Kofoidinium*?

The existing literature on the life cycle of kofoidiniaceans is restricted to Cachon and Cachon (1967b) and Konovalova and Selina (2002), and has been largely overlooked. When Pavillard (1921) reported *Gymnodinium pseudonoctiluca* in the NW Mediterranean Sea, he was probably illustrating stage "c" of *Kofoidinium*. Later, Pavillard (1928) found the mature stage and described *Kofoidinium velelloides*; he misspelled the epithet 'velleloides' that refers the jellyfish *Velella velella* Linnaeus, but subsequently corrected it (Pavillard 1937). Pavillard (1928) reported that the size of *K. velelloides* was 350 μm long. However as reported by Cachon and Cachon (1967b) and the present study, the size of *K. velelloides* was usually less than 200 μm. This confusion may be responsible for the fact that no new species was described until 1967 and all the previous records of large specimens of *Kofoidinium* were ascribed to *K. velelloides* (Balech 1962; Fenaux 1958; Halim 1967; Rampi 1952). The description of *K. splendens* by Cachon and Cachon (1967b) did not provide sufficient definitive criteria to differentiate it from *K. velelloides*. The system of anchorage of the dome is different, but this morphological character is difficult to observe (Fig. 14). A high confusion exists in the literature. For example in the British Isles, Parke and Dodge (1976) listed *K. splendens* and no *K. velelloides* and later Dodge (1982) reported only *K. velelloides*. For *Kofoidinium splendens* Taylor (1976, p. 185) reported "*Precise distinctions between this species and K.– velleloides – Pavillard are difficult to make because of the incompleteness of the original description and the distorted condition of the type specimens of the latter*". Cachon and Cachon (1967b) reported that *K. splendens* may harbour several symbiotic zooxanthellae that are lost under eutrophic conditions as well as the red polypeptide bodies. This variability does not help in differentiating *K. splendens* from *K. velelloides*.

Cachon and Cachon (1967b) already reported specimens of *K. velelloides* of about 100 μm in length. Nearly all the previous studies that reported kofoidiniaceans were based on net sampling and subsequently these small specimens could be lost. In addition, some specimens may be overlooked during routine microscopical analysis due to their small size and transparency. In the present study specimens of *Kofoidinium* sp. of 40 μm in diameter were commonly observed. The pointed extension and the square-ended protrusion (Fig. 7) are distinctive characters that were clearly lacking in *K. velelloides* (Fig. 10).

Bursa (1964) described *Kofoidinium arcticum* in the Canadian arctic waters. Cachon and Cachon (1967b, p. 437) and Taylor (1976, p. 184) reported that *K. arcticum* is a doubtful taxon, which was described from a single formaldehyde-fixed specimen evidently deformed due to preservation. Beyond the initial description no records of *Kofoidinium arcticum* exist.

Kofoidinium splendens can be also confused with *K. pavillardii*. Both species have similar system of anchorage of the dome (Cachon and Cachon 1967b). According to Taylor (1976) *Kofoidinium lebouriae*, usually misspelled as 'lebourae', is the correct name for *K. pavillardii* because *Gymnodinium lebouriae* is considered as the basionym. Cachon and Cachon (1967b) stated that *Gymnodinium lebouriae* is stage "d" of a kofoidiniacean and consequently it is not a valid species, which added more confusion. For example Yamaji (1980, p. 107) reported the non-existent species names "*Kofoidinium lebourae* (Pavillard) Cachon et Cachon" or considered *Kofoidinium splendens* as a synonym of *Kofoidinium lebouriae*.

The observations of the present study suggest the existence of a small species with a pointed extension, here called *Kofoidinium* sp. (Fig. 7), *K. velelloides* (Fig. 10), a large species, *K. pavillardii* (= *K. lebouriae*) (Fig. 11) and a fourth species, *K. splendens* (Fig. 17), of more uncertain delimitation.

How many species of *Spatulodinium*?

Spatulodinium is a monotypic genus, only known from northern hemisphere Euro-Asian boreal and arctic waters. This study is the first to describe the genus *Spatulodinium* in tropical waters and in the southern hemisphere. In addition to the specimens with a green pigmentation that suggests the occurrence of chloroplasts (Figs 32–35), other specimens that differed from the type species were found (Figs 37–41). The monotypic character of the genus needs to be reconsidered.

In European Atlantic waters, immature stages presumed to belong to the genus *Spatulodinium* have been described as *Gymnodinium lebouriae*, *G. fulgens* and *G. conicum* (= *G. viridis*), as well as probably *G. pyrocystis* that was described with no illustration (Kofoid and Swezy 1921). In the tropical and southern Pacific Ocean, these immature stages were observed as well as other unidentified kofoidiniaceans. Kofoid and Swezy (1921) described *Amphidinium vasculum* and *A. pacificum* in tropical waters of the Eastern Pacific Ocean. These forms strongly resemble the stage "d" of a kofoidiniacean (Fig. 34). The suggestion that these large *Amphidinium* species, described from single specimens, could correspond to immature stages of *Spatulodinium* in tropical waters, cannot be discarded.

Other species of kofoidiniaceans

As well as *Kofoidinium* and *Spatulodinium*, the genera *Pomatodinium* and *Cymbodinium* have been included in the family Kofoidiniaceae. One of the specimens observed in the Pacific Ocean was ascribed to *Pomatodinium* (Fig. 35) and another specimen resembles that genus in one or two views (Fig. 37). Beyond the type locality, the Ligurian Sea, *P. impatiens* was reported from Spanish Mediterranean coasts (Margalef 1969) and the NE Atlantic Ocean (Travers and Travers 1975; Margalef 1975). In the Pacific Ocean, Sakka et al. (2002) reported *Pomatodinium* as a dominant species in an atoll lagoon in French Polynesia, but this record is questionable.

The genus *Cymbodinium* J. Cachon et M. Cachon is the least known kofoidiniacean. *Cymbodinium* was described from the coastal Ligurian Sea (Cachon and Cachon 1967b); it was further reported with no illustration from NE Atlantic waters (Parke and Dodge 1976) and an estuary in Brazil (Bergesch and Odebrecht 1997). No information on the appearance of fixed specimens of *Cymbodinium* exists. These specimens may be too distorted by fixation to be identified.

The noctilucaceans are of great interest in the phylogeny of dinoflagellates. However, the existing phylogenetic information is restricted to *Noctiluca* (Taylor 2004). Most of the species of kofoidiniaceans were previously described from the NW Mediterranean Sea. The present study reveals that there is an extensive but almost unknown diversity of noctilucaceans in the oceans of the world.

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References

Balech, E., 1962. Tintinnoidea y Dinoflagellata del Pacífico según material de las expediciones Norpac y Downwind del Instituto Scripps de Oceanografía. Rev. Mus. Argent. Cienc. Nat. "B. Rivadavia". Cienc. Zool. 7, 1–253.

Bergesch, M., Odebrecht, C., 1997. Análise do fitoplâncton, protozooplâncton e de alguns fatores abióticos no estuário da Lagoa Dos Patos. Atlântica Rio Grande 19, 31–50.

Bursa, A., 1964. *Kofoidinium arcticum*, a new dinoflagellate. Phycologia 4, 1–14.

Cachon, J., Cachon-Enjumet, M., 1966. *Pomatodinium impatiens* nov. gen. nov. sp. péridiniens Noctilucidae Kent. Protistologica 2, 23–30.

Cachon, J., Cachon, M., 1967a. *Cymbodinium elegans* nov. gen. nov. sp. péridinien Noctilucidae Saville-Kent. Protistologica 3, 313–318.

Cachon, J., Cachon, M., 1967b. Contribution à l′étude des Noctilucidae Saville-Kent, I. Les Kofoidininae Cachon J. et M. Évolution, morphologique et systématique. Protistologica 3, 427–444.

Dodge, J.D., 1982. Marine Dinoflagellates of the British Isles. Her Majesty's Stationary Office, London, 303pp.

Fenaux, R., 1958. Contribution a l'étude de *Kofoidinium velelloides*. Bull. Inst. océanogr. Monaco., 1118, 11pp.

Gómez, F., Furuya, K., 2005. Leptodiscaceans (Noctilucales, Dinophyceae) from the Pacific Ocean: first records of *Petalodinium* and *Leptodiscus* beyond the Mediterranean Sea. Eur. J. Protist. 41, 231–239.

Gómez, F., Furuya, K., Takeda, S., 2005. Distribution of the cyanobacterium *Richelia intracellularis* as an epiphyte of the diatom *Chaetoceros compressus* in the western Pacific Ocean. J. Plankton Res. 27, 323–330.

Halim, Y., 1967. Dinoflagellates of the South-East Caribbean Sea (East-Venezuela). Int. Rev. ges. Hydrobiol. 52, 701–755.

Kofoid, C.A., Swezy, O., 1921. The Free-living unarmored Dinoflagellata. University of California Press, Berkeley.

Konovalova, G.V., Selina, M.S., 2002. Life cycle of *Spatulodinium pseudonoctiluca* (Dinophyta) from Sea of Japan. Bot. Zhurnal. 87, 38–43.

Margalef, R., 1969. Composición específica del fitoplancton de la costa catalano-levantina (Mediterráneo occidental) en 1962–1967. Inv. Pesq. 33, 345–380.

Margalef, R., 1975. Composición y distribución del fitoplancton marino en la región de afloramiento del NW de África, en marzo de 1973 (Campaña "Atlor II" del 'Cornide de Saavedra'). Result. Exped. Cient. B/O Cornide 4, 145–170.

Parke, M., Dodge, J.D., 1976. Check-list of British marine algae—third revision. J. Mar. Biol. Ass. UK 56, 527–594.

Pavillard, J., 1921. Sur le *Gymnodinium pseudonoctiluca* Pouchet. C. R. Acad. Sci. Paris 172, 86–87.

Pavillard, J., 1928. *Kofoidinium velleloides* n. g. n. spec. Ann. Protistol. Paris 1, 159–161.

Pavillard, J., 1937. Les Péridiniens et Diatomées pélagiques de la Mer de Monaco de 1907–1914. Observations générales et conclusions. Bull. Inst. océanogr. Monaco 738, 1–56.

Pouchet, G., 1885. Nouvelle contribution a l'histoire des Peridiniens marins. J. Anal. Physiol. 21, 28–88.

Rampi, L., 1952. Ricerche sul microplancton di superficie del Pacifico tropicale. Bull. Inst. océanogr. Monaco. 1014, 16pp.

Sakka, A., Legendre, L., Gosselin, M., Niquil, N., Delesalle, B., 2002. Carbon budget of the planktonic food web in an atoll lagoon (Takapoto, French Polynesia). J. Plankton Res. 24, 301–320.

Sournia, A., 1986. Atlas du Phytoplancton Marin. Vol. I: Introduction, Cyanophycées, Dictyochophycées, Dinophycées et Raphidophycées. Editions CNRS, Paris.

Taylor, F.J.R., 1976. Dinoflagellates from the International Indian Ocean Expedition. A report on material collected by R/V 'Anton Bruun' 1963–64. Bibliotheca Bot. 132, 1–234.

Taylor, F.J.R., 2004. Illumination or confusion? Dinoflagellate molecular phylogenetic data viewed from a primarily morphological standpoint. Phycol. Res. 52, 308–324.

Travers, A., Travers, M., 1975. Observation en Atlantique nord-est de *Pomatodinium impatiens* Cachon et Cachon-Enjumet, Dinoflagellé Noctilucidae, décrit de Méditerranée. Rapport et Procès verbaux des réunions. Comm. Int. Explor. Scient. Mer. Medit. 20, 315–316.

Yamaji, I., 1980. Illustrations of the Marine Plankton of Japan. Hoikusha Press, Osaka.