Diversity and Distribution of Noctilucoid Dinoflagellates (Noctilucales, Dinophyceae) in the Open Mediterranean Sea

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Summary. The noctilucoid dinoflagellates have been investigated in the open waters of the Mediterranean Sea. Kofoidinium spp., Spatulodinium spp. and Scaphodinium mirabile were found in nearly all the stations. The genera Craspedotella, Leptodiscus, Petalodinium and Pomatodinium were recorded for the first time in the eastern Mediterranean basin. An undescribed small species of Kofoidinium (40–60 µm in diameter) with a pointed extension represented about 1/3 of the genus records. The monotypic character of the genus Spatulodinium needs to be reconsidered because numerous specimens differed from the type species. One of these undescribed species showed a distinctive hyposome and an extremely long tentacle (up to 1600 µm long). A leptodiscacean that showed an arrowhead-shaped contour is found for the first time in the Mediterranean Sea. There is a considerable diversity of noctilucaceans yet to be described.

Key words: Biodiversity, Craspedotella, Dinophyta, Kofoidiniaceae, Leptodiscaceae, Kofoidinium, Leptodiscus, Noctiluca, Petalodinium, Pomatodinium Scaphodinium, Spatulodinium.

INTRODUCTION

Noctiluca scintillans (Macartney) Kofoid is the first dinoflagellate to be described. This aberrant species lacks, at least in some life stages, typical dinoflagellate characters such as the ribbon-like transversal flagellum or condensed chromosomes. In contrast to Noctiluca that is widespread in eutrophic coastal waters, the other noctilucaceans have a predominantly tropical to warm-temperate oceanic distribution (Cachon and Cachon 1967, 1969; Gómez and Furuya 2005, 2007). All the Noctilucales differ markedly from the rest of the dinoflagellates, notably by the presence of contractile muscle-like fibrils involved in cell shape changes and movements. Based on the gene sequences of N. scintillans, the phylogenetic position of the noctilucaceans has been controversial. Some studies placed Noctiluca within one of the clades of the dinoflagellate order Gymnodiniales (Saldarriaga et al. 2004) and other phylogenies have placed it as an early diverging lineage within dinoflagellates, branching after Oxyrrhis and before the core dinoflagellates (Liu and Hastings 2007, Fukuda and Endoh 2008, Zhang and Lin 2008, Gómez et al. 2009, Ki 2010). Additional sequences of other genera such as Kofoidinium Pavillard, Spatulodinium J. Cachon et M. Cachon and Abedinum Loeblich Jr. et Loeblich III (=Leptophyllus J. Cachon et
Cachon-Enjumet) revealed that the Noctilucales emerged before the dinoflagellate core and the weakly supported monophyly of three well-supported noctilucoid clades (Gómez et al. 2010). *Noctiluca* branched among species of *Spatulodinium*. This does not support the split of the Noctilucales into the families Noctiluceae and Kofodiniaeeae, especially in what refers to the conservation of *Noctiluca* as the only representative of its own family (Gómez et al. 2010).

Most of the Noctilucales have been described from the NW Mediterranean and knowledge is almost completely restricted to the coastal studies by Cachon and Cachon (1967, 1969). Since their observations, the records of noctiluaceans have been scarce and several genera have never been reported after the initial descriptions. This study describes the diversity and distribution of the noctilucoid dinoflagellates in the open waters of Mediterranean Sea. The results reveal that the species diversity is underestimated. For example, one of the most common species of *Kofodinium* remains to be described, as well as numerous species of the monotypic genus *Spatulodinium* and some leptodiscaceans.

### MATERIALS AND METHODS

Samples were collected during the BOUM (Biogeochemistry from the Oligotrophic to the Ultra-oligotrophic Mediterranean) cruise on board R/V *L’Atalante* from the south of France to the south of Cyprus (20 June–18 July 2008) (Fig. 1). Seawater samples were collected by Niskin bottles from 30 stations. At each station 6 depths were sampled between 5 and 125 m and an additional sample at 250 m depth. These were preserved with acid 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 settled in composite settling chambers. The sample was examined at 100 × magnification with a Nikon inverted microscope (Nikon Eclipse TE200) and the specimens were photographed with a digital camera (Nikon Coolpix E995).

### RESULTS AND DISCUSSION

#### *Kofodinium* spp.

*Kofodinium* was the most ubiquitous genus of noctiluaceans in the open waters of the Mediterranean Sea. As a general trend, the abundance of *Kofodinium* spp. was higher in the upper 25 m depth and slightly increased between 100–125 m depth (Fig. 2B). *Kofodi-
knowledge this is the first record in the Eastern Mediterranean Sea (Gómez 2003).

**Spatulodinium spp.**

The species of *Spatulodinium* were present in most of stations and preferentially in the upper 75 m depth (Fig. 2C). The abundance was low with a maximum 12 individuals $L^{-1}$ in the Balearic Sea (Sta. A) at 75 m depth. The genus *Spatulodinium* is currently restricted to one species, *S. pseudonoctiluca* (Pouchet) J. Cachon et M. Cachon, known from the coastal waters of the northern hemisphere (Cachon and Cachon 1967, Gómez and Souissi 2007). In the open waters of the Mediterranean Sea, none of the 52 specimens of *Spatulodinium*...
confirmed to the morphology that usually presented the type species. In order to facilitate the comparison, a Lugol-fixed specimen from the coastal Mediterranean Sea is here illustrated (Fig. 4A). While the morphology of the Lugol-fixed specimens of *S. pseudonoctiluca* from coastal waters is quite constant, there was a high diversity of size, shape of the hyposome and position and length of the tentacle in the specimens collected in open waters (Figs 4B–I). Some specimens corresponded to the life stage known as *Gymnodinium lebouriae* with the tentacle (Fig. 4I) or lacking the tentacle (Figs 4K–L). The life stage precursor of *G. lebouriae* may appear in pairs of smaller cells joined at the elongate episome (Fig. 4J).

Among the high species diversity of *Spatulodinium*, six individuals showed a very distinctive morphology that differed from the other species (Figs 4M–V). The most distinctive character was an extremely long extension that seems to be analogue to the tentacle of the other species of *Spatulodinium*. The cell diameter was 80 µm and the tentacle that represented about 20 × times the cell diameter (up 1600 µm) is the longest known extension among the dinoflagellates (Fig. 4M). All the specimens were collected below 75 m depth and one of them at 250 m depth (Fig. 2C). While the other species of *Spatulodinium* showed a shallower distribution and the cell body was pigmented due to the occurrence of chlorophyll *a* (Gómez and Souissi 2007, Gómez et al. 2010), this undescribed species was apochlorotic. The hyposome showed concentric rings and was bordered by a differentiated band with septae (Figs 4O–P). The lack of plastids and the hyposomal bands resembled *Kofoidinium*. At least one species of *Kofoidinium* showed a short extension (Figs 3A–E) that may be analogous with the tentacle of *Spatulodinium*. Despite these common features with *Kofoidinium*, the specimens have been tentatively ascribed to the genus *Spatulodinium*.

*Spatulodinium* contains one species in current taxonomic schemes. Molecular data are available for *S. pseudonoctiluca* from live specimens collected in the type locality, English Channel, and the coastal NW Mediterranean Sea (Gómez et al. 2010). Other sequences were obtained from a distorted ethanol-fixed specimen collected from the open Balearic Sea. The general appearance and size was close to some specimens here illustrated (Figs 4D, G). The phylogenetic distance between both species of *Spatulodinium* was high and *Noctiluca* branched between them (Gómez et al. 2010). This confirmed that among these Mediterranean species there is, at least, a second species for the genus *Spatulodinium*.

**Leptodiscaceae**

The leptodiscaceans are the less known of the noctilucaceans. After *Kofoidinium pavillardii*, *Scaphodinium mirabile* Margalef (71 individuals) was the most common noctilucacean in the open Mediterranean Sea. The highest abundance (28 cells L$^{-1}$) was recorded in the Balearic Sea (Sta. 20) at 50 m depth (Fig. 2D). As previously illustrated by Gómez and Furuya (2004), most of the Lugol-fixed specimens appeared folded (Figs 5A–E). Observations of live specimens revealed that the specimens fold as a response to environmental stress such as the fixation.

Four specimens of *Petalodinium porcelio* J. Cachon et M. Cachon were observed (Fig. 2E). As occurred in *Scaphodinium*, the specimens of *Petalodinium* appeared folded in the fixed material (Figs 5F–J). Two of the specimens collected from the Levantine Basin constituted the first records in the eastern Mediterranean Sea. These scarce records do not allow establishing any trend on the distribution.

The distinctive reticulation of myo-fibrils that characterized *Petalodinium* was also observed in an undescribed leptodiscacean collected at 250 m depth in the Levantine basin (Sta. 8). The specimen (130 µm long) showed an arrowhead-shaped outline and the proximal extremity bifurcated. The margins of the cell appeared folded as far as the region of the nucleus (Figs 5K–L). This undescribed species was also recorded at 100 m depth from the South China Sea as illustrated by Gómez and Furuya (2005).

A total of 17 specimens of the medusoid leptodiscacean *Leptodiscus* were observed (Fig. 2F). The highest abundance (10 individuals L$^{-1}$) was recorded at 50 m depth in the Balearic Sea (Sta. A) (Figs 2F, 5M–P). One specimen collected from the Ionian Sea constituted the first record of this genus in the eastern Mediterranean Sea.

Four specimens of *Crasedotella* were observed from two stations in the Ionian Sea at 125 m depth (Figs 2F, 5Q–R). *Crasedotella pileous* was described from the tropical Pacific Ocean (Kofoid 1905). Cachon and Cachon (1969) found *C. pileous* in coastal waters and also in very deep waters (4300 m depth) in the Mediterranean Sea. The specimens observed in this study were similar to those observed in the Pacific Ocean by Gómez (2007).
Figs 4A–V. Photomicrographs of Spatulodinium spp., bright field optics. A – Spatulodinium pseudonoctiluca from the Berre lagoon, coastal NW Mediterranean Sea; B–L – other species of Spatulodinium; B – Sta. 3, 175 m depth; C – Sta. 19, 25 m; D – Sta. 1, 25 m; E – Sta. 7, 25 m; F – Sta. 1, 5 m; G–H – Sta. 6, 25 m; I–L – immature stages of Spatulodinium; I – Gymnodinium lebouriae with tentacle, Sta. 21, 75 m; J – Sta. 24, 100 m; K–L – Sta. A, 25 m; M–V – undescribed Spatulodinium species with a long tentacle; M–N – Sta. 20, 125 m; O–P – Sta. 10, 125 m; Q – Sta. 25, 250 m; R – Sta. 25, 75 m; S–T – Sta. A, 100 m; U–V – Sta. 5, 125 m. Scale bar: 50 µm.
Figs 5A–R. Photomicrographs of leptodiscaceans, bright field optics. A–E – several specimens of *Scaphodinium mirabile*; F–J – specimens of *Petalodinium porcelio*; F – Sta. 20, 125 m depth; G – Sta. 24, 5 m; H – Sta. 11, 25 m; I–J – Sta. 8, 100 m; K–L – undescribed arrowhead-shaped leptodiscacean, Sta. 8, 250 m; M–P – specimens of *Leptodiscus medusoides*; M – Sta. 20, 74 m; N – Sta. 7, 100 m; O – Sta. 15, 50 m; P – Sta. 4, 100 m; Q–R – *Craspedotella* sp.; Q – Sta. 12, 125 m; R – Sta. B, 125 m. Scale bar: 50 µm.
The fragility, transparency and polymorphism of the leptodiscaceans are responsible for the scarce records, going unnoticed in the world’s oceans. It is not easy to identify noctiluaceans to species due to the high morphological variability during their life cycle and the difficulties to delimit the species from preserved specimens. This study illustrated some species for the first time since the studies by Cachon and Cachon (1967, 1969) and other undescribed species that preferentially inhabit in deep waters. There is a considerable diversity of noctilucoid dinoflagellates yet to be described.

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