Nova Hedwigia 77 3—4 331—340 Stuttgart, November 2003

New records of *Asterodinium* Sournia (Brachidiniales, Dinophyceae)

by

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With 22 figures and 1 table

Gómez, F. (2003): New records of *Asterodinium* Sournia (Brachidiniales, Dinophyceae). Nova Hedwigia 77: 331-340.

Abstract: New records of species of the rare planktonic dinoflagellate genus *Asterodinium* Sournia are reported. From the Mediterranean Sea and NE Atlantic Ocean: (1) three specimens of *Asterodinium* sp. sensu Sournia from the Gulf of Cádiz and Strait of Gibraltar (NE Atlantic Ocean), (2) one specimen of *Asterodinium* sp.1 from the Strait of Gibraltar, (3) three specimens of *Asterodinium* cf. *libanum* Abboud-Abi Saab from the Bay of Villefranche-sur-Mer (Ligurian Sea, NW Mediterranean Sea), (4) three specimens of *Asterodinium gracile* from the Tyrrhenian Sea and Strait of Sicily (Mediterranean Sea). Most taxa were recorded from 70 to 100 m depth, with exceptions in the Strait of Gibraltar and the Corsica Channel. From a longitudinal transect (138°E) in the Philippine Sea (NW Pacific Ocean) are reported: (5) four specimens of *Asterodinium gracile*, (6) *Asterodinium* cf. *gracile*, (7) one specimen of *Asterodinium* sp.1 and (8) *Asterodinium* sp.2. These records were collected between 50 to 175 m depths. *Asterodinium gracile* shows high morphological variation. The ecology of the genus is reviewed and discussed.

Key words: *Asterodinium*, dinoflagellate, Dinophyceae, Dinophyta, phytoplankton, Gulf of Cadiz, Strait of Gibraltar, Mediterranean Sea, Atlantic Ocean, Pacific Ocean, Kuroshio Current

Introduction

Asterodinium Sournia is a genus of photosynthetic planktonic marine dinoflagellates scarcely reported in the literature. These unarmored species are members of the family Brachidiniaceae* of the order Brachidiniales* A.R. Loeblich III ex Sournia (Loeblich III 1982, Sournia 1984) or Ptychodiscales Fensome, Taylor, Norris, Sarjeant, Wharton et Williams (Fensome et al. 1993).

DOI: 10.1127/0029-5035/2003/0077-0331 0029-5035/03/0077-0331 $ 2.50

Species of the genus *Asterodinium* have dorsoventrally flattened cells with two elongate extensions radiating from the hyposoma and three from the episoma; a well-developed nucleus and chloroplasts are present. The genus was originally described from the Mozambique Channel (SW Indian Ocean) based on *Asterodinium gracile* Sournia (type species), *Asterodinium spinosum* Sournia and an undescribed species, *Asterodinium* sp. (Sournia 1972a,b). According to Sournia (1986, p. 50) no further records of these species exist. However, Estrada (1979) reported an unidentified species of *Asterodinium* in coastal waters of the NW Mediterranean Sea and Abboud-Abi Saab (1985) found *Asterodinium gracile* in Lebanese coastal waters (Eastern Mediterranean Sea). Abboud-Abi Saab (1989) further reported the new species, *Asterodinium libanum* Abboud-Abi Saab, but with an insufficient description. To the best of my knowledge, no other documented records of species belonging to the genus *Asterodinium* have been published.

This study reports the findings of several species of *Asterodinium* collected from 1997 to 2002 in the Mediterranean Sea, Eastern Atlantic and Western Pacific Oceans and provides information on the ecology and distribution of these species.

Material and methods

New records of *Asterodinium* from Mediterranean-Atlantic waters were obtained from samples collected during the following research cruises or coastal monitoring (Fig. 1): (1) Cruise carried out 18-25 June 1997 aboard R/V "Cornide" in the Gulf of Cádiz, Strait of Gibraltar and Alborán Sea (see García et al. 2002 for sampling details); (2) cruise carried out 2-9 September 1997 aboard R/V "Thalassa" in the Strait of Gibraltar (see Gómez et al. 2000 for sampling details); (3) coastal monitoring performed at the permanent station "Point B" (80 m depth) in the Bay of Villefranche-sur-Mer (Ligurian Sea) from January 1998 to January 2000 (see Gómez & Gorsky 2003 for sampling details) and (4) PROSOPE-cruise carried out 11-30 September 1999 aboard R/V "Thalassa" in the Eastern Atlantic Ocean and Mediterranean Sea (see Dolan et al. 2002 for sampling details).

Seawater samples were collected with oceanographic bottles, preserved with acidified Lugol's solution (e.g., Hasle & Syvertsen 1997, p. 334) and stored in the dark. Only during the cruise in the Strait of Gibraltar, seawater samples were concentrated using a 5-µm pore mesh. Sub-samples (10-100 ml) were allowed to settle for 24-48 h in Utermöhl chambers (Utermöhl 1958). Cells were observed with an inverted light microscope using bright field optics.

New records of *Asterodinium* from the Pacific Ocean were obtained from samples collected during a cruise aboard R/V "Soyo-Maru" in the Philippine Sea (Fig. 2). Seawater samples were collected with Niskin bottles from 5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 125, 150, 175 and 200 m depth

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(*) The family Brachidiniaceae and the order Brachidiniales are based on *Brachidinium* F.J.R. Taylor. In the original publication of Taylor (1963) this genus was spelt *Brachydinium*, but in 1967 Taylor introduced the orthographically corrected spelling *Brachidinium* [see also Articles 60 and 61 of the current version of the International Code of Botanical Nomenclature (ICBN; Greuter et al. 2000) dealing with the correction of orthographical errors]. Contrary to Sournia's (1973) conclusion, Taylor's (1967) correction of his own orthographical error is in no way contrary to these articles and should be followed. The spelling *Brachidinium* is indicated as the correct one in the ING (Farr et al. 1979) and in NCU-3 (Greuter et al. 1993); both entries are authored by Paul C. Silva, one of the most reliable specialists in the application of the ICBN to phycological nomenclature.

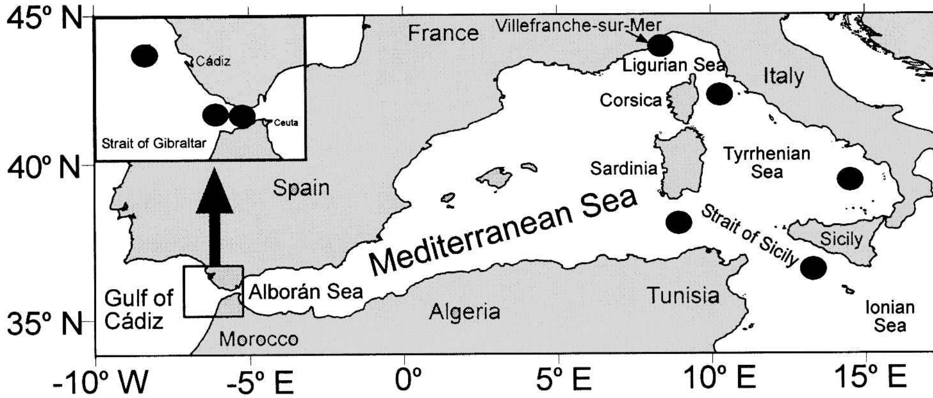


Fig. 1. Map of the Western Mediterranean Sea and Gulf of Cádiz.

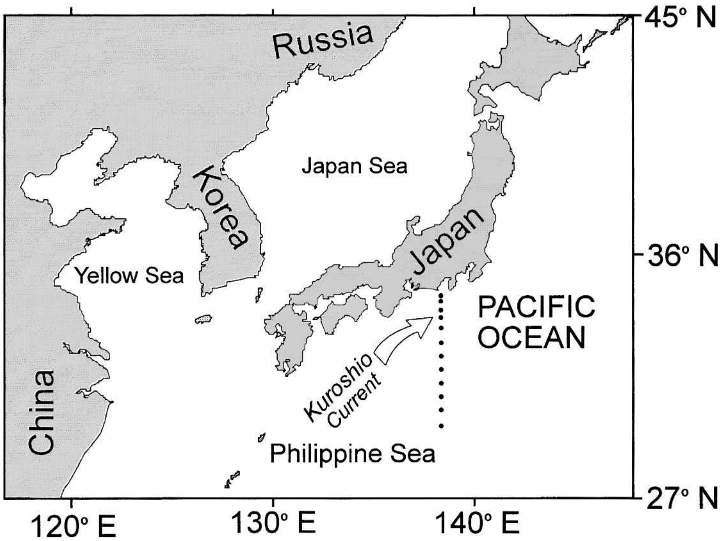


Fig. 2. Map of the NW Pacific Ocean.

along the meridian 138° from 28° 0N to 34° 20N. Nine stations were sampled from 3-20 May 2002 and nine from 3-9 July 2002. Samples were preserved with acidified Lugol's solution and stored at about 5°C. Samples were pre-concentrated by settling in glass cylinders, and concentrates were left to settle in standard sedimentation chambers. Concentrates equivalent to 400 ml were examined in a Nikon inverted microscope using bright field optics. Cells were photographed on an inverted light microscope connected to a Nikon digital camera.

Results

Asterodinium gracile Sournia

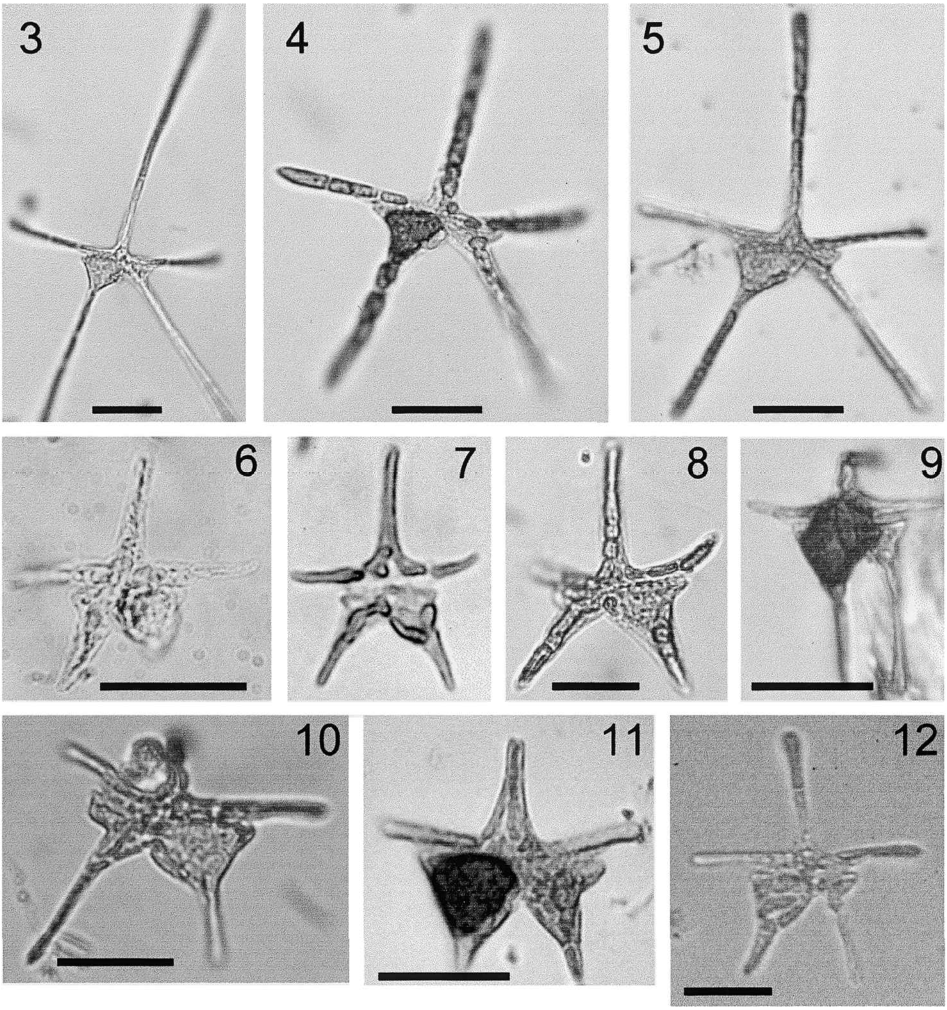
The identification is based on the drawing of *A. gracile* provided by Sournia (1972a). It is reproduced in Sournia (1986, p. 155) and in Fensome et al. (1993, p. 56) although erroneously named *Asterodinium spinosum*. To my best knowledge this is the only illustration available. In this study, it is assumed that *A. gracile* presents a high morphological variability in size and in the relative proportion of the extensions. As the extensions are flexible (especially the two lateral apical ones) the angle of the extensions with respect to the cell body is not considered as a taxonomic character. The distribution or number of chloroplasts did not seem to be usable for species differentiation.

In the Mediterranean Sea, four individuals were recorded in samples from the Tyrrhenian Sea and the Strait of Sicily collected during the PROSOPE-cruise (Fig. 1). Their maximal length was 49-52 µm and the width at the cingulum level was 21-23 µm (Figs 12, 22). All the specimens resembled *A. gracile* in shape. The lateral anterior extensions had rounded ends in all these specimens, whereas those illustrated by Sournia (1972a) had more pointed tips. Sournia's specimen of *A. gracile* had a maximum size of ~80 µm (as measured from the scale in his figure 8), thus being somewhat larger than the specimens collected in the Mediterranean Sea.

In the Pacific Ocean, 4 specimens more similar to the type material were collected from two stations located in the Kuroshio Current. At one station two specimens were collected at different depths (80 and 175 m). The specimen from 175 m depth (maximal length 90 µm, cingulum 28 µm, Figs 4, 14) was more intensely pigmented than the other one (maximal length 85 µm, cingulum 22 µm) (Figs 5, 15).

At a nearby station, two similar specimens were observed in the same sample. They showed more elongate appendices than all the other specimens (Figs 3, 13). Only one cell was measured, showing a maximal length of 160 µm, while the width of cell at the cingulum was 21 µm. The ratio between the length of the central apical extension and the cell width at the cingulum is approx. 1.3 in Sournia's (1972a) illustration. The specimen in my Figure 3 had a ratio >4, while the other specimens from the Pacific Ocean had a variable ratio ranging from 1.6-2.3. The specimens from the Mediterranean Sea also showed a ratio lower than the type material. For the present, all the cells are considered to be members of the *Asterodinium gracile* complex.

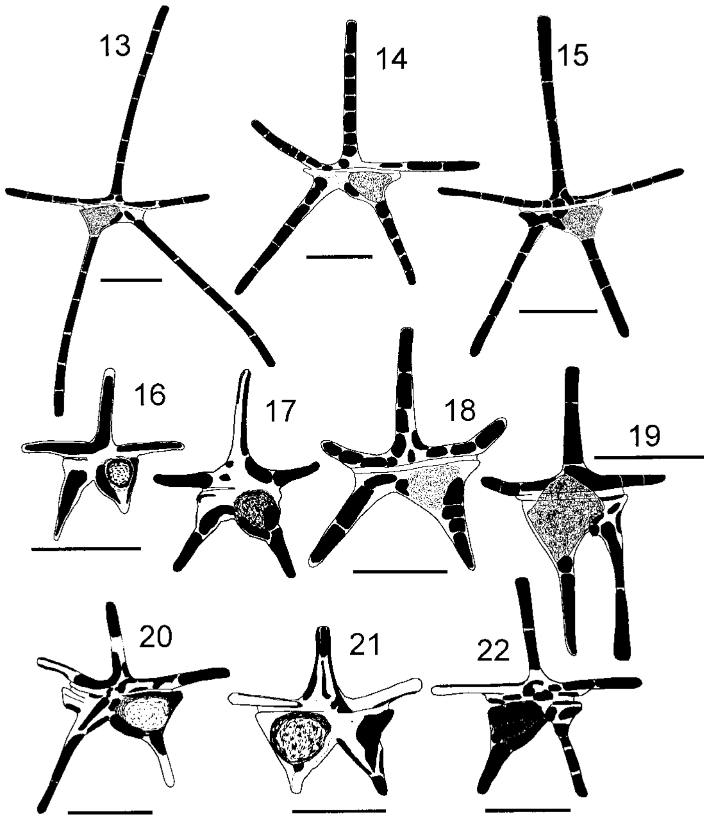
Another specimen is included in this group but here named *A.* cf. *gracile* (Figs 10, 20). It was found in offshore subtropical waters of the Philippine Sea. It differed from the specimens of the *A. gracile* complex by its shorter extensions. The width of the cell at the level of the cingulum was 27 µm. The distance between the tips of the two lateral apical arms was 52 µm and the length of the longer antapical extension was 30 µm. No precise measurement of the total length was taken due to the bending of the central apical extension, but it seems to be around ~55 µm (Figs 10, 20).



Figs 3-12. Photomicrographs of *Asterodinium* spp. Figs 3-5. *Asterodinium gracile* from the Pacific Ocean. Fig. 6. *Asterodinium* sp. sensu Sournia (1972a) from the Gulf of Cádiz. Fig. 7. *Asterodinium* sp.1 from the Strait of Gibraltar. Fig. 8. *Asterodinium* sp.1 from the Pacific Ocean. Fig. 9. *Asterodinium* sp.2 from the Pacific Ocean. Fig. 10. *Asterodinium* cf. *gracile* from the Pacific Ocean. Fig. 11. *Asterodinium* cf. *libanum* from the Mediterranean Sea. Fig. 12. *Asterodinium gracile* from the Mediterranean Sea. Scale bars 20 mm.

Asterodinium cf. **libanum** Abboud-Abi Saab

In samples collected in the Bay of Villefranche-sur-Mer (Ligurian Sea), three individuals were observed. The length was 42 µm and the cingulum was 27 µm long. This taxon is morphologically different with a less delicate appearance compared to other species of *Asterodinium* with short extensions (Figs 11, 21). It is here called *A.*



Figs 13-22. Line drawings of *Asterodinium* spp. Figs 13-15. *Asterodinium gracile* from the Pacific Ocean. Fig. 16. *Asterodinium* sp. sensu Sournia (1972a) from the Gulf of Cadiz. Fig. 17. *Asterodinium* sp.1 from the Strait of Gibraltar. Fig. 18. *Asterodinium* sp.1 from the Pacific Ocean. Fig. 19. *Asterodinium* sp.2 from the Pacific Ocean. Fig. 20. *Asterodinium* cf. *gracile* from the Pacific Ocean. Fig. 21. *Asterodinium* cf. *libanum* from the Mediterranean Sea. Fig. 22. *Asterodinium gracile* from the Mediterranean Sea. Scale bars 20 mm.

libanum, although Abboud-Abi Saab (1989) did not provide a Latin diagnosis and neither line drawings nor good quality illustrations; therefore it is difficult to compare with the original description.

Asterodinium sp. sensu Sournia (1972a)

Sournia (1972a) reported a single cell from the Indian Ocean, but he did not describe it as a new species because it was considered that the specimen was damaged.

Three specimens that strongly resemble *Asterodinium* sp. as reported by Sournia (1972a) in morphology and size were collected from the Eastern Atlantic Ocean. The first specimen was found in the Gulf of Cádiz (Figs 6, 16). Two similar specimens

Table 1. New records of *Asterodinium.*

Taxa	#	Location	Lat N	Long	depth	Date	Figure
Asterodinium gracile Sournia	1	Sardinia Channel	37° 59	8° 32 E	90	17/09/1999	
A. gracile Sournia	1	Strait of Sicily	36° 28	13° 19 E	80	18/09/1999	
A. gracile Sournia	1	South Tyrrhenian Sea	39° 12	14° 08 E	70	27/09/1999	12
A. gracile Sournia	1	Corsica Channel	41° 54	10° 26 E	30	28/09/1999	
A. cf. *gracile* Sournia	1	Offshore Philippine Sea	32° 00	138° E	90	13/05/2002	10
A. gracile Sournia	1	Kuroshio area	33° 00	138° E	80	07/07/2002	5
A. gracile Sournia	1	Kuroshio area	33° 00	138° E	175	07/07/2002	4
A. gracile Sournia	2	Kuroshio area	33° 30	138° E	100	07/07/2002	3
Asterodinium cf. *libanum* Abboud-Abi Saab	1	Villefranche Bay	43° 41	7° 19 E	50	Sept98	
A. cf. *libanum* Abboud-Abi Saab	2	Villefranche Bay	43° 41	7° 19 E	50	Sept-Oct99	11
Asterodinium sp. sensu Sournia 1972	1	Gulf of Cádiz	36° 34	6° 47 W	75	23/06/1997	6
A. sp. sensu Sournia 1972	2	Strait of Gibraltar	35° 54	5° 38 W	20	5/09/1997	
Asterodinium sp.1	1	Strait of Gibraltar	35° 58	5° 55 W	100	3/09/1997	7
Asterodinium sp.1	1	Kuroshio area	33° 00	138° E	50	11/05/2002	8
Asterodinium sp.2	1	Kuroshio area	31° 00	138° E	125	06/07/2002	9

were subsequently collected in the Strait of Gibraltar (Fig. 1, Table 1). The maximal length was 32-34 µm and the cell width at the cingulum was 14 µm. Also, the specimens collected from the Gulf of Cádiz and Strait of Gibraltar presented a 'damaged aspect', whereas other cells in the plankton appeared undamaged.

Asterodinium sp.1

This taxon differs from previous records by the presence of shorter extensions with rounded tips and with a cell body slightly more elongated than in *A.* cf. *libanum*. One specimen was collected at the Atlantic side of the Strait of Gibraltar (Figs 7, 17) (Unfortunately no size measurements were performed). A second specimen, apparently similar to the Atlantic one, was collected from the offshore subtropical waters of the Philippine Sea (Figs 8, 18). The maximal length was 51 µm and the width at the cingulum was 27 µm.

Asterodinium sp.2

From the waters of the Kuroshio Current was collected a specimen that differed from other records. Cells possessed two parallel antapical extensions, short lateral apical extensions, and a longer central apical extension (Figs 9, 19). The nucleus occupied a higher proportion of the cell body than in the other species and extended into the episoma. Due to the bending of the central apical extension, the maximum length is estimated to be around ~60 µm. The width of the cell at the cingulum was 18 µm.

Discussion

Ecological characteristics

Due to the small number of observations, it is difficult to establish the ecological characteristics of *Asterodinium*. However some trends were noticed in the vertical distribution of the taxa (Table 1).

In the Indian Ocean, Sournia (1972a,b) recorded individuals of *Asterodinium* at 100 m depth. Estrada (1979) reported an unidentified species of *Asterodinium* from surface waters of the NW Mediterranean Sea. In the Bay of Villefranche (Ligurian Sea), three specimens of *Asterodinium libanum* were collected at 50 m (at a station with a maximal depth of 80 m, see Gómez & Gorsky 2003). In the Tyrrhenian basin and the Sicily Strait, three specimens of *Asterodinium gracile* were collected in deep waters (70-90 m depth), and one individual at 30 m depth. On the Atlantic side of the Strait of Gibraltar, a specimen of *Asterodinium* sp.1 was found at 100 m depth, while in the Gulf of Cádiz, one specimen of *Asterodinium* sp. sensu Sournia (1972a) was found at 75 m depth. Concerning the records of *Asterodinium* sp. sensu Sournia (1972a) found near the sill of the Strait of Gibraltar, it should be taken into account that mixing events can alter the vertical distribution of the species (Gómez et al. 2000). *Asterodinium* species have well-defined chloroplasts and this may be an adaptation to the low irradiance levels in deep waters, since other photosynthetic deep waters species (e.g., *Ceratium platycorne* Daday) also contain higher concentrations of chlorophyll compared to taxa found in shallow water (Falkowski 1980). The most recent records clearly confirm this trend, one specimen collected at 175 m depth just below the Kuroshio axis (Fig. 4) presented a healthy aspect with more intense pigmentation compared to the shallower one (Fig. 5). It should be taken into account that the warm Kuroshio Current is characterized by highly transparent waters. Thus, the genus *Asterodinium* may be considered as a member of the shade flora (Sournia 1982).

Concerning the temporal distribution of *Asterodinium*, some trends are apparent:

Estrada (1979) reported an unidentified species of *Asterodinium* in September 1975 along the Mediterranean Spanish coasts. Abboud-Abi Saab (1985) from 3 years of monitoring in Lebanese coastal waters exclusively reported *Asterodinium gracile* in the autumn and *Asterodinium* sp. in the spring. During our biannual study of the phytoplankton composition of the Bay of Villefranche-sur-Mer, *Asterodinium* was observed only in September and October (Table 1). Since the research cruises were performed in June and September, the offshore records only appeared during these months. Late summer is the most oligotrophic period in the Mediterranean Sea and it seems to be the most favourable period for the development of these species. Gómez & Claustre (2003) mention that the recent occurrence of *Asterodinium* in the areas of the western Mediterranean Sea intensively investigated in the past (e.g., the Ligurian Sea; see Gómez 2003) could be associated with the progressive warming of the Mediterranean waters and unusual high temperatures in September 1999.

Due to the small size and delicate features such as pelliculate cells with flexible radiating arms, plankton net sampling probably damages specimens of *Asterodinium*. Their detection in oligotrophic waters requires sedimentation of large volumes of seawater with very low phytoplankton abundance. *Asterodinium* in not included in the most commonly used literature for phytoplankton identification, with the exception of Sournia (1986) and Fensome et al. (1993), and it is likely this it often escapes notice during routine analyses.

Further research should address the *Asterodinium gracile* complex; does it constitute one species with high morphological variability, depending on environmental conditions, or are different species involved?

Acknowledgements

Mediterranean and Atlantic samples were collected from cruises within the context of projects: CANIGO (EU MAS3-CT96-0060), JGOFS-France PROSOPE, and ICTIO-Alborán 97 cruise by the Spanish Institute of Oceanography. Financial support by Spanish Ministry of Science and Technology is acknowledged. Pacific Ocean samples were collected from cruises of the SOYO program by the National Research Institute of Fisheries Science, Japan. I thank the comments and suggestions by the Editor and reviewers. I acknowledge the financial support by the European Commission (ICB2-CT-2001-80002).

References

ABBOUD-ABI SAAB, M. (1985): Étude quantitative et qualitative du phytoplancton des eaux côtières libanaises. - Lebanese Sci. Bull. **1:** 197-222.

ABBOUD-ABI SAAB, M. (1989): Les dinoflagellés des eaux côtières libanaises- espèces rares ou nouvelles du phytoplancton marin. - Lebanese Sci. Bull. **5:** 5-16.

DOLAN, J.R., H. CLAUSTRE, F. CARLOTTI, S. PLOUNEVEZ & T. MOUTIN (2002): Microzooplankton diversity: relationships of tintinnid ciliates with resources, competitors and predators from the Atlantic Coast of Morocco to the Eastern Mediterranean. - Deep Sea Res. I **49:** 1217-1232.

ESTRADA, M. (1979): Observaciones sobre la heterogeneidad del fitoplancton en una zona costera del mar Catalán. - Invest. Pesq. **43:** 637-666.

FALKOWSKI, P.G. (1980): Light-shade adaptation in marine phytoplankton. - In: FALKOWSKI, P.G. (ed.): Primary production in the sea: 99-179. Brookhaven Symp. Biol. 31, Plenum Press, New York & London.

FARR, E.R., J.A. LEUSSINK & F.A. STAFLEU (eds) (1979): Index Nominum Genericorum (Plantarum), Vol. 1. - Regnum Vegetabile **100:** 1-630. Bohn, Scheltema and Holkema, Utrecht / W. Junk, The Hague.

FENSOME, R.A., F.J.R. TAYLOR, G. NORRIS, W.A.S., SARJEANT, D.I. WHARTON & G.L. WILLIAMS (1993): A classification of living and fossil dinoflagellates. -Micropaleontology, Special Publication Number 7: 1-351. American Museum of Natural History, Sheridan Press, Hanover, PA.

GARCÍA, C.M., L. PRIETO, M. VARGAS, F. ECHEVARRÍA, J. GARCÍA-LAFUENTE, J. RUIZ & J.P. RUBÍN (2002): Hydrodynamics and the spatial distribution of plankton and TEP in the Gulf of Cádiz (SW Iberian Peninsula) - J. Plankt. Res. **24:** 817-833.

GÓMEZ, F., F. ECHEVARRÍA, C.M. GARCÍA, L. PRIETO, J. RUIZ, A. REUL, F. JIMÉNEZ-GÓMEZ & M. VARELA (2000): Microplankton distribution in the Strait of Gibraltar: coupling between organisms and hydrodynamic structures. - J. Plankt. Res. **22:** 603-617.

GÓMEZ, F. (2003): Checklist of Mediterranean free-living dinoflagellates. - Bot. Mar. **46:** 215-242.

GÓMEZ F. & H. CLAUSTRE (2003): The genus *Asterodinium* (Dinophyceae) as a possible biological indicator of warming in the Western Mediterranean Sea. - J. Mar. Biol. Ass. U.K. **83:** 173-174.

GÓMEZ, F. & G. GORSKY (2003): Microplankton annual cycles in the Bay of Villefranche, Ligurian Sea, NW Mediterranean Sea. - J. Plankt. Res. **25:** 323-339.

GREUTER, W., J. McNEILL, F.R. BARRIE, H.M. BURDET, V. DEMOULIN, T.S. FILGUEIRAS, D.H. NICOLSON, P.C. SILVA, J.E. SKOG, P. TREHANE, N.J. TURLAND & D.L. HAWKSWORTH (2000): International Code of Botanical Nomenclature (Saint Louis Code). - Regnum Vegetabile **138:** 1-474. Koeltz Scientific Books, Königstein, Germany.

GREUTER, W., R.K. BRUMMITT, E. FARR, N. KILIAN, P.M. KIRK & P.C. SILVA (1993): NCU-3. Names in Current Use for Extant Plant Genera. - Regnum Vegetabile **129:** 1-1464. Koeltz Scientific Books, Königstein, Germany.

HASLE, G.R. & E.E. SYVERTSEN (1997): Marine Diatoms. - In: TOMAS, C.R. (ed.): Identifying marine phytoplankton: 5-385. Academic Press, San Diego.

LOEBLICH, A.R. III (1982): Dinophyceae. - In: PARKER, S.P. (ed.): Synopsis and classification of living organisms: Vol. 1, pp. 101-115. McGraw-Hill, New York.

SOURNIA, A. (1972a): Quatre nouveaux dinoflagellés du plancton marin. - Phycologia **11:** 71-74.

SOURNIA, A. (1972b): Une période de poussées phytoplanctoniques prés de Nosy-Bé (Madagascar) en 1971. Espèces rares ou nouvelles du phytoplancton. - Cah. O.R.S.T.O.M., Sér. Océanogr. **10:** 151-159.

SOURNIA, A. (1973): Catalogue des espèces et taxons infraspécifiques de Dinoflagellés marins actuels publiés depuis la révision de J. Schiller. I. Dinoflagellés libres. -Nova Hedwigia Beih. **48:** 1-92.

SOURNIA, A. (1982): Is there a shade flora in the marine plankton? - J. Plankt. Res. **4:** 391-399.

SOURNIA, A. (1984): Classification et nomenclature de divers dinoflagellés marins (classe des Dinophyceae). - Phycologia **23:** 345-355.

SOURNIA, A. (1986): Atlas du phytoplancton marin. Vol. I: Introduction, Cyanophycées, Dictyochophycées, Dinophycées et Raphidophycées. - Editions du Centre National de la Recherche Scientifique, Paris.

TAYLOR, F.J.R. (1963): *Brachydinium*, a new genus of the Dinococcales from the Indian Ocean. - J. South Afr. Bot. **29:** 75-78.

TAYLOR, F.J.R. (1967): Phytoplankton of the South Western Indian Ocean. - Nova Hedwigia **12:** 433-476.

UTERMÖHL, H. (1958): Zur Vervollkommung der quantitativen Phytoplankton-Methodik. - Mitt. Int. Vereinigung Theor. Angew. Limnol. **9:** 1-38.

Received 3 June 2002, accepted in revised form 8 May 2003.