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revbiolmar@gmail.com

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## Rarely reported dinoflagellates of the genera *Ceratium*, *Gloeodinium*, *Histioneis*, *Oxytoxum* and *Prorocentrum* (Dinophyceae) from the open southeast Pacific Ocean

Dinoflagelados raramente citados de los géneros *Ceratium*, *Gloeodinium*, *Histioneis*, *Oxytoxum* y *Prorocentrum* (Dinophyceae) en aguas abiertas del Pacífico sur-oriental

Fernando Gómez<sup>1</sup>, Hervé Claustre<sup>2,3</sup> and Sami Souissi<sup>4</sup>

<sup>1</sup>Laboratoire d'Océanographie Physique et de Biogéochimie, CNRS UMR 6535, Centre d'Océanologie de Marseille, Université de la Méditerranée, 163 Avenue de Luminy, Case 901, 13288 Marseille, France

<sup>2</sup>UPMC Univ. Paris 06, UMR 7093, Laboratoire d'Océanographie de Villefranche, Quai de la Darse, 06230 Villefranche-sur-Mer, France

<sup>3</sup>CNRS, UMR 7093, LOV, 06230 Villefranche-sur-Mer, France

<sup>4</sup>Laboratoire d'Océanologie et de Géosciences, Station Marine de Wimereux, Université des Sciences et Technologies de Lille-Lille1, 28 avenue Foch, BP 80, 62930 Wimereux, France  
fernando.gomez@fitoplancton.com

**Resumen.-** Se ilustran y brevemente describen dinoflagelados raramente citados de los géneros *Ceratium*, *Gloeodinium*, *Histioneis*, *Oxytoxum* y *Prorocentrum* procedentes de un transecto de ~8000 km entre el archipiélago de las Islas Marquesas y las costas chilenas. Se han encontrado diecinueve especies del género *Oxytoxum* y siete especies de *Histioneis*. Se proporcionan por primera vez microfotografías de *Histioneis hyalina*, *H. cf. pulchra* y un espécimen identificado como *Histiophysis* sp., un género que no había sido citado desde su descripción original. Más allá de los típicos especímenes unicelulares de *Prorocentrum*, se describe un comportamiento colonial en *Prorocentrum dentatum* que presentaba células alineadas. Colonias de pares de células elipsoidales o esféricas embebidas en una matriz hialina se han adscrito a *Gloeodinium marinum*. *Ceratium lanceolatum* se encuentra por primera vez en el Pacífico Sur desde su descripción original. Se proporcionan microfotografías de *Ceratium carnegiei*, *C. divaricatum* y *C. lanceolatum*.

Palabras clave: *Exuviaella*, *Histiophysis*, fitoplancton, protistas, Pyrrhophyta

**Abstract.-** Rarely reported dinoflagellates of the genera *Ceratium*, *Gloeodinium*, *Histioneis*, *Oxytoxum* and *Prorocentrum* from a ~8000 km transect between the Marquesas Islands Archipelago and the Chilean coast are briefly described and illustrated. Nineteen species of the genus *Oxytoxum* and seven species of the genus *Histioneis* were identified to species level. Photographic records of *Histioneis hyalina* and *H. cf. pulchra* are for the first time reported. One specimen ascribed to *Histiophysis* sp., a genus never reported since the first description, is illustrated. Beyond the single-cell specimens of *Prorocentrum*, a colonial behavior was observed. A small species, identified as *Prorocentrum dentatum*, was encountered forming rows. Colonies of pairs of ellipsoidal or spherical cells embedded in a hyaline matrix have been ascribed to *Gloeodinium marinum*. *Ceratium lanceolatum* is for the first time reported in the South Pacific Ocean since the first description. Photographic records of *Ceratium carnegiei*, *C. divaricatum* and *C. lanceolatum* are reported.

Key words: *Exuviaella*, *Histiophysis*, phytoplankton, protist, Pyrrhophyta

## Introduction

The studies on the dinoflagellate composition in the southeast Pacific Ocean are mainly restricted to the coast of South America (Hermosilla 1973a, Muñoz & Avaria 1980, Ochoa & Gómez 1997), and the archipelagos of Galápagos and Juan Fernández (Marshall 1972, Hermosilla 1973b). In contrast, the dinoflagellates of the open waters of the southeast Pacific are one of the least investigated in the world's oceans. The Albatross Expedition (1904-5) occupied stations in the open

southeast Pacific. Based on net samples, Kofoid described numerous new thecate dinoflagellates in his elaborated monographs (Kofoid 1907, Kofoid & Michener 1911, Kofoid & Adamson 1911, Kofoid & Skogsberg 1928, Kofoid & Adamson 1933). The results of the Carnegie Expedition (1928-9) in the subtropical southeast Pacific were restricted to large unarmoured dinoflagellates of the order Peridiniales, especially the genus *Ceratium* (Graham 1942, Graham & Bronikovsky 1944). Steemann Nielsen (1934) also investigated the genus *Ceratium* based on materials from the Dana Expedition (1928-30).

Rampi, from samples of the Dana Expedition and other cruises in the tropical Pacific, described several new dinoflagellates (Rampi 1948, 1950, 1952). Balech (1962) investigated the dinoflagellates from the Downwind Expedition (1957-8). These studies were based on material collected with coarse net hauls, and often restricted to surface waters. Hasle (1960) constituted an exception because she investigated the phytoplankton composition based on bottle samples at three stations in the central equatorial Pacific.

Recent studies in the high-nutrient low-chlorophyll region of the central and eastern equatorial Pacific were accompanied of scarce detailed studies on the dinoflagellate composition, often only identified at suprageneric levels (Chavez & Buck 1990). Iriarte & Fryxell (1995) listed species of dinoflagellates from the central equatorial Pacific and Hardy *et al.* (1996) reported a few dinoflagellates identified at the genus level from the surface of the South Pacific Gyre. Despite its oceanographic interest, very little is known about the dinoflagellate composition in the open southeast Pacific.

Within this context, a cruise along a transect of ~8000 km from the Marquesas Is. Archipelago to the Chilean coasts provided the opportunity to observe numerous species of dinoflagellates that have been rarely reported in the literature. Previous studies were focused on

unarmoured dinoflagellates (Gómez 2006, 2007a, Gómez & Furuya 2007). This study illustrates and briefly describes the records of the genera *Gloeodinium* Bouquaheux, *Histioneis* Stein, *Histiophysis* Kofoid & Michener and *Oxytoxum* Stein as well as the most interesting taxa of the genera *Ceratium* Schrank and *Prorocentrum* Ehrenberg from the open southeast Pacific.

## Material and methods

Samples were collected during the BIOSOPE (Biogeochemistry and Optics South Pacific Experiment) cruise on board R/V *L'Atalante* from the Marquesas Is. to the coast of Chile off Concepción (26 October-12 December 2004) (Fig. 1). One hundred samples from 14 stations were collected by Niskin bottles between 5 and 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 × magnification with an IX71 inverted microscope equipped with an Olympus digital camera (Olympus, Tokyo, Japan). Each specimen was photographed and measured at 400 × magnification with Olympus DP70-BSW software.

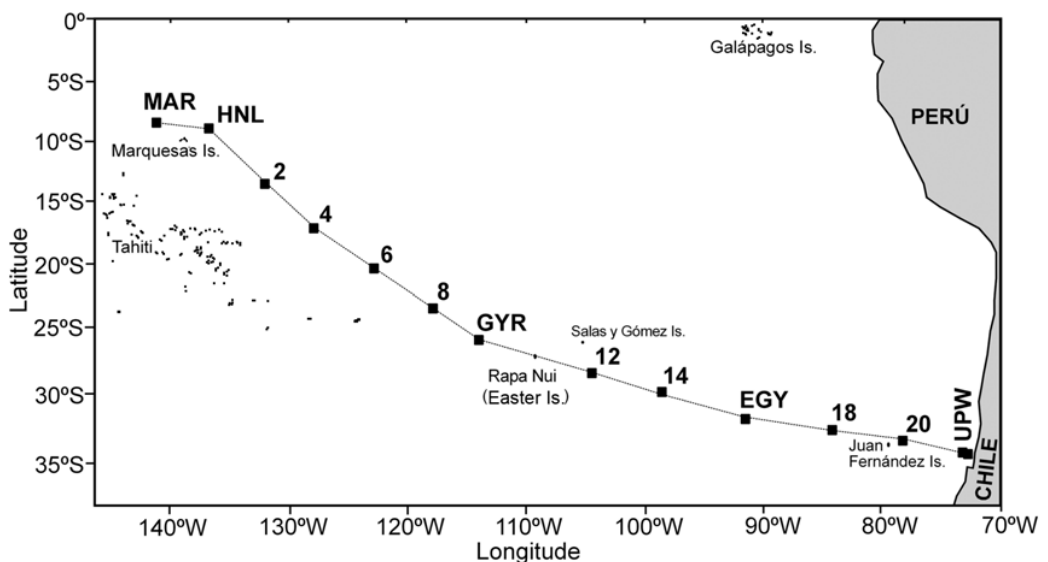


Figure 1

Map of the sampling stations occupied (solid squares) in the southeast Pacific Ocean

Mapa de las estaciones de muestreo, señaladas por cuadrados, en el Pacífico sur-oriental

## Results

### *Oxytoxum*

*Oxytoxum* was one of the most ubiquitous dinoflagellate genera in the open waters of the southeast Pacific. A total of 19 species were identified and other specimens were not identified at the species level (Table 1). Each species is briefly described and illustrated (Figs. 2-38).

The type species, *O. scolopax*, showed an epitheca with a small domed structure with a spine onto the top. Specimens of ~70 µm in length were in good agreement with the original description (Figs. 6, 7). Other very elongated (~120 µm long) specimens were also ascribed to *O. scolopax* (Figs. 4-5). Several specimens were also closed *O. scolopax*, although they did not show the bladder-like swelling at the base of the antapical spine that characterized *O. scolopax*. The epitheca had the shape of a long, drawn-out cone with slightly concave sides that tapered to an antapical spine (Figs. 2-3). These specimens with a robust appearance in comparison to the type species were ascribed to *O. longiceps* (Figs. 2-3). The possible synonymy between *Oxytoxum sceptrum* (Stein) Schröder and *O. longiceps* needs to be investigated.

Another specimen of ~60 µm in length was in agreement with the original description of *O. challengeroides* (Fig. 8). Other specimen showed a biconical shape, tapering sharply at apex and antapex, with the widest dimension at the cingulum (Fig. 9). The species *O. subulatum* Kofoid and *O. milneri* Murray & Whitting were characterized by pointed apex, often long and tapered into asymmetrical point often long. The specimen in Fig. 9 showed intermediate characteristics between *O. milneri* and *O. diploconus*. It has been tentatively identified as *O. diploconus* based on the consideration that the apex was shorter than in *O. milneri* (Fig. 9).

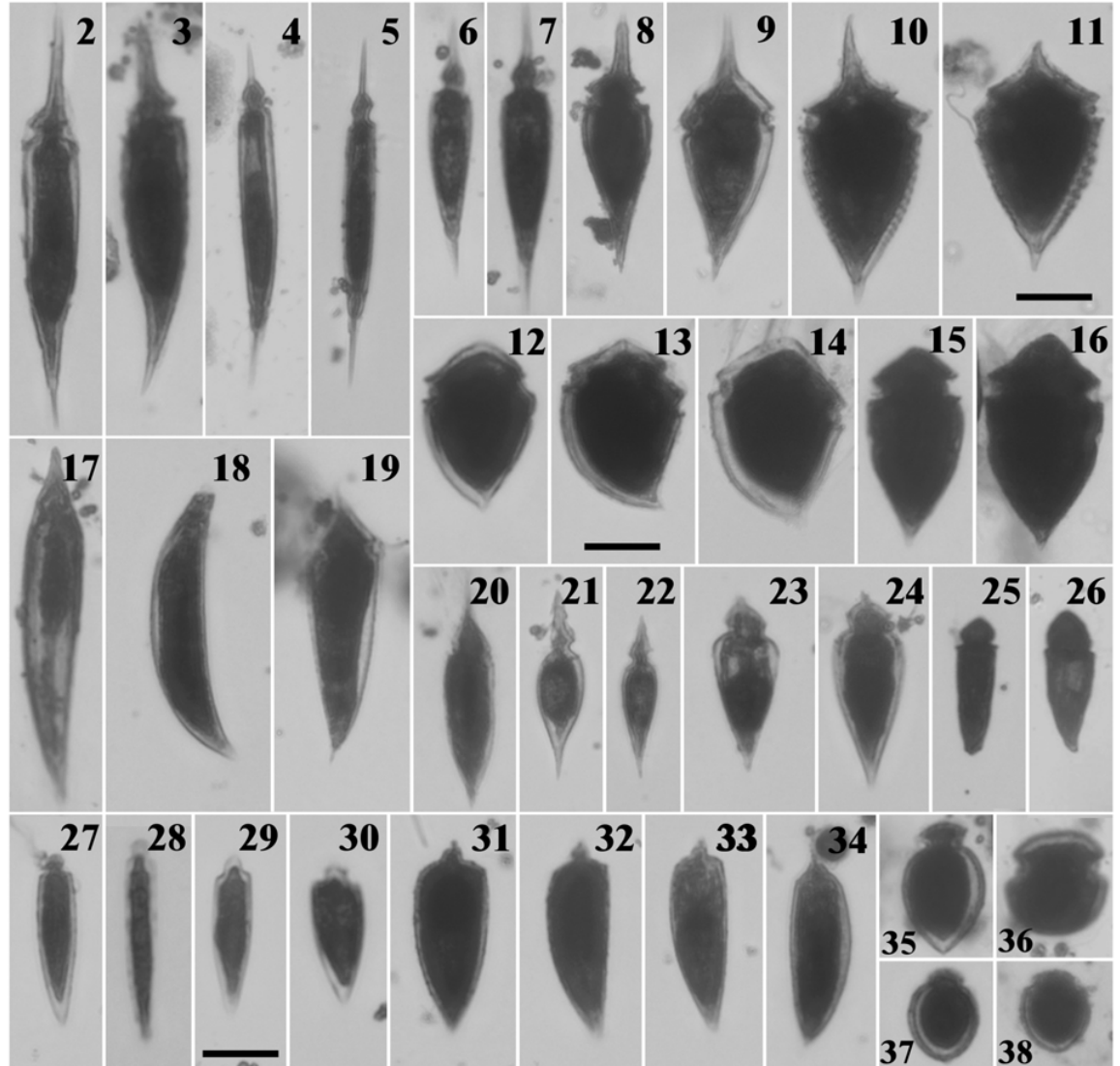
Other medium size species were twice as long as broad (Figs. 10-11). The cingulum showed a displacement of about one cingulum width, deeply excavated, and showed striae at right angle to the margins of the hypotheca (Figs. 10-11). Two taxa, *O. tessellatum* and *O. elegans* agreed to this description. *Oxytoxum michaelsarsii* Gaarder, a tentative synonym of *O. tessellatum*, is characterized by a hypotheca with convex sides anteriorly becoming slightly concave toward the antapex. At first sight, the main difference between *O. tessellatum* and *O. elegans* was the length of apical spine that it is shorter in *O. tessellatum*. The specimen in Fig. 10 has been ascribed to *O. elegans*, despite the apical horn is more developed than in the original description. The specimen with a less pointed epitheca has been ascribed to *O. tessellatum* (Fig. 11).

Other specimens showed sub-circular cell body with an obtusely angled apex and a sub-acute antapex. The epitheca was low and lacking the acute apical spines, the cingulum was deep, and displaced one width and the length ~50 µm (Figs. 12-14). One of the specimens showed the hypotheca nearly straight (Fig. 12) with a shape intermediate between *O. reticulatum* (Stein) Schütt and *O. belgicae* Meunier. *Oxytoxum frenguelli* was more robust than *O. reticulatum*. The epitheca of *O. areolatum* Rampi showed a concave outline, whereas the epitheca was nearly straight in the other species. The intraspecific morphological variability of the species is unknown, and it is difficult the separation of these species. *Oxytoxum latum* Gaarder and *O. frenguelli* may be conspecific. *Oxytoxum frenguelli* may be also a morphotype of *O. reticulatum*. The specimen of the figure 12 has been ascribed to *O. cf. frenguelli*.

Another specimens of ~50 µm in length showed a higher displacement of the cingulum than in *O. frenguelli* and the hypotheca was bent (Figs. 13-14). *Oxytoxum cristatum* Kofoid is characterized by the bent hypotheca, and the epitheca also bent in the opposite direction of the hypotheca. *Oxytoxum compressum* has an elongated and curve hypotheca. These morphological characters strictly did not fit with the specimens in Figs. 13 and 14. They have been ascribed to *O. curvicaudatum*. In contrast, *O. constrictum* is one of the most distinctive species of the genus due to the constriction in the hypotheca. The specimens of *O. constrictum* observed in this study showed a variable length (Figs. 15-16).

One specimen with a scarcely marked cingulum, and the epitheca apparently encapsulated has not been identified. It is uncertain whether it corresponded to an *Oxytoxum* species (Fig. 17). *Oxytoxum curvatum* was characterized by a blunt apical region, and a long curved hypotheca (Fig. 18). Another species showed elongated hypotheca bent in the extreme with a pointed spine (Fig. 19). The hypotheca was conical with a straight outline, and a spine. The general appearance resembled a robust specimen of the species *O. elongatum* Wood. The length of the specimen of the Fig. 19 was 70 µm, whereas the size of *O. elongatum* in the original description was higher than 150 µm. *Oxytoxum longum* was also longer and the epitheca was rounder than in the specimen in Fig. 19.

Fig. 20 illustrate a specimen of swollen outline, and it cannot be discarded that it may constitute an unarmoured dinoflagellate such as *Amphidinium sphenoides* Wulff. The specimen has been tentatively identified as *O. cf. parvum*, although its cingulum was not well marked. Other specimens showed morphology



Figures 2-38

Photomicrographs of *Oxytoxum* spp. and two unarmoured dinoflagellates, bright field optics. See Table 1 for the location of the records. (2-3) *O. longiceps*. (4-5) Elongated cell of *O. scolopax*. (6-7) *O. scolopax*. (8) *O. challengeroides*. (9) *O. diploconus*. (10) *O. elegans*. (11) *O. tessellatum*. (12) *Oxytoxum* cf. *frenguelli*. (13-14) *O. curvicaudatum*. (15-16) *O. constrictum*. (17) Tentative *Oxytoxum* sp. (18) *O. curvatum*. (19) Elongated *Oxytoxum* sp. (20) Tentative *Oxytoxum* sp. (21-22) *O. parvum*. (23-24) *O. turbo*. (25-26) Unidentified *Amphidinium*-like cells. (27-28) *Oxytoxum* cf. *longum*. (29-30) *O. variabile*. (31-32) *O. caudatum*. (33-34) *O. cf. caudatum*. (35) *O. cf. laticeps*. (36) *O. cf. sphaeroideum*. (37) *O. cf. globosum*. (38) *O. cf. crassum*. All the micrographs at the same magnification. Scale bar of 20  $\mu$ m

Microfotografías de *Oxytoxum* spp. y dos dinoflagelados atecados, óptica de campo claro. Véase la localización de los registros en la Tabla 1. (2-3) *O. longiceps*. (4-5) Célula alargada de *O. scolopax*. (6-7) *O. scolopax*. (8) *O. challengeroides*. (9) *O. diploconus*. (10) *O. elegans*. (11) *O. tessellatum*. (12) *Oxytoxum* cf. *frenguelli*. (13-14) *O. curvicaudatum*. (15-16) *O. constrictum*. (17) Tentativamente *Oxytoxum* sp. (18) *O. curvatum*. (19) Célula alargada de *Oxytoxum* sp. (20) Tentativamente *Oxytoxum* sp. (21-22) *O. parvum*. (23-24) *O. turbo*. (25-26) Células no identificadas cercanas a *Amphidinium*. (27-28) *Oxytoxum* cf. *longum*. (29-30) *O. variabile*. (31-32) *O. caudatum*. (33-34) *O. cf. caudatum*. (35) *O. cf. laticeps*. (36) *O. cf. sphaeroideum*. (37) *O. cf. globosum*. (38) *O. cf. crassum*. Todas las fotografías a la misma escala. Barra de escala de 20  $\mu$ m

Table 1

Geographic coordinates (latitude, longitude, depth) of the records of dinoflagellates from the southeast Pacific Ocean illustrated in the figures 2-79

Coordenadas geográficas (latitud, longitud, profundidad) de los registros de dinoflagelados del Pacífico sur-oriental ilustrados en las figuras 2-79

Taxon	Latitude	Longitude	Depth	Figure
	South	West	(m)	
<i>Oxytoxum longiceps</i> Schiller	28°31'	104°18'	210	2
<i>Oxytoxum longiceps</i> Schiller	31°52'	91°24'	5	3
Elongated <i>Oxytoxum scolopax</i> Stein	33°21'	78°06'	25	4
Elongated <i>Oxytoxum scolopax</i> Stein	30°02'	98°23'	160	5
<i>Oxytoxum scolopax</i> Stein	13°32'	132°07'	100	6
<i>Oxytoxum scolopax</i> Stein	28°31'	104°18'	180	7
<i>Oxytoxum challengeroides</i> Kofoid	23°32'	117°52'	210	8
<i>Oxytoxum diploconus</i> Stein	13°32'	132°07'	5	9
<i>Oxytoxum elegans</i> Pavillard	26°01'	114°01'	120	10
<i>Oxytoxum tessellatum</i> Stein	8°23'	141°14'	50	11
<i>Oxytoxum</i> cf. <i>frenguelli</i> Rampi	30°02'	98°23'	5	12
<i>Oxytoxum curvicaudatum</i> Kofoid	31°52'	91°24'	125	13
<i>Oxytoxum curvicaudatum</i> Kofoid	28°31'	104°18'	165	14
<i>Oxytoxum constrictum</i> (Stein) Bütschli	33°21'	78°06'	40	15
<i>Oxytoxum constrictum</i> (Stein) Bütschli	30°02'	98°23'	200	16
Tentative <i>Oxytoxum</i> sp.	33°21'	78°06'	40	17
<i>Oxytoxum curvatum</i> (Kofoid) Kofoid	17°13'	127°58'	5	18
Elongated <i>Oxytoxum</i> sp.	32°42'	84°04'	120	19
Tentative <i>Oxytoxum</i> sp.	32°42'	84°04'	60	20
<i>Oxytoxum parvum</i> Schiller	9°	136°51'	5	21
<i>Oxytoxum parvum</i> Schiller	17°13'	127°58'	40	22
<i>Oxytoxum turbo</i> Kofoid	20°27'	122°53'	220	23
<i>Oxytoxum turbo</i> Kofoid	9°	136°51'	100	24
Unidentified <i>Amphidinium</i> -like cell	23°32'	117°52'	100	25
Unidentified <i>Amphidinium</i> -like cell	26°01'	114°01'	270	26
<i>Oxytoxum</i> cf. <i>longum</i> Schiller	33°21'	78°06'	15	27
<i>Oxytoxum</i> cf. <i>longum</i> Schiller	31°52'	91°24'	5	28
<i>Oxytoxum variabile</i> Schiller	13°32'	132°07'	100	29
<i>Oxytoxum variabile</i> Schiller	13°32'	132°07'	20	30
<i>Oxytoxum caudatum</i> Schiller	8°23'	141°14'	40	31
<i>Oxytoxum caudatum</i> Schiller	9°	136°51'	60	32
<i>Oxytoxum</i> cf. <i>caudatum</i> Schiller	9°	136°51'	40	33
<i>Oxytoxum</i> cf. <i>caudatum</i> Schiller	30°02'	98°23'	5	34
<i>Oxytoxum</i> cf. <i>laticeps</i> Schiller	33°21'	78°06'	100	35
<i>Oxytoxum</i> cf. <i>sphaeroideum</i> Schiller	33°21'	78°06'	5	36
<i>Oxytoxum</i> cf. <i>globosum</i> Kofoid	17°13'	127°58'	85	37
<i>Oxytoxum</i> cf. <i>crassum</i> Schiller	8°23'	141°14'	20	38
<i>Histioneis</i> cf. <i>striata</i> Kofoid & Michener	31°52'	91°24'	40	39
<i>Histioneis joergensenii</i> Schiller	30°02'	98°23'	75	40
<i>Histioneis</i> sp. (dorsal view)	32°42'	84°04'	75	41
<i>Histioneis</i> cf. <i>crateriformis</i> Stein	20°27'	122°53'	170	42
<i>Histioneis</i> cf. <i>crateriformis</i> Stein	31°52'	91°24'	40	43
<i>Histioneis</i> cf. <i>crateriformis</i> Stein	31°52'	91°24'	190	44
cf. <i>Histiophysis</i> sp.	33°21'	78°06'	60	45
<i>Histioneis cleaveri</i> Rampi	28°31'	104°18'	80	46
<i>Histioneis cleaveri</i> Rampi	9°	136°51'	40	47
<i>Histioneis cleaveri</i> Rampi	9°	136°51'	30	48



(Cont. Table 1)

<i>Histioneis</i> cf. <i>pulchra</i> Kofoid	32°42'	84°04'	105	49-50
<i>Histioneis longicollis</i> Kofoid	31°52'	91°24'	60	51
<i>Histioneis hyalina</i> Kofoid & Michener	8°23'	141°14'	40	52
<i>Prorocentrum</i> sp1. (pear-shaped)	20°27'	122°53'	190	53
<i>Prorocentrum</i> cf. <i>compressum</i> (hyaline)	33°21'	78°06'	40	54
<i>Prorocentrum</i> sp2. (small)	13°32'	132°07'	100	55
<i>Prorocentrum</i> cf. <i>rhathymum</i> Loeblich III, Sherley & R.J. Schmidt	33°21'	78°06'	5	56
<i>Prorocentrum</i> cf. <i>rhathymum</i> Loeblich III, Sherley & R.J. Schmidt	31°52'	91°24'	40	57
<i>Prorocentrum dentatum</i> Stein	9°	136°51'	30	58-60
<i>Gloeodinium marinum</i> (ellipsoidal cells)	8°23'	141°14'	20	61-62
<i>Gloeodinium marinum</i> (sphaerical cells)	28°31'	104°18'	80	63-64
<i>Ceratium</i> cf. <i>lineatum</i> (Ehrenberg) Cleve	9°	136°51'	15	65
<i>Ceratium divaricatum</i> var. <i>balechii</i> Hernández-Becerril (= <i>C. balechii</i> Meave, Okolodkov & Zamudio)	8°23'	141°14'	40	66
<i>Ceratium divaricatum</i> var. <i>balechii</i> Hernández-Becerril	8°23'	141°14'	60	67
<i>Ceratium divaricatum</i> var. <i>balechii</i> Hernández-Becerril	8°23'	141°14'	50	68
<i>Ceratium divaricatum</i> var. <i>balechii</i> Hernández-Becerril	8°23'	141°14'	10	69
<i>Ceratium divaricatum</i> var. <i>balechii</i> Hernández-Becerril	34°38'	72°28'	5	70
<i>C. divaricatum</i> (Lemmermann) Kofoid var. <i>divaricatum</i>	33°21'	78°06'	5	71
<i>C. divaricatum</i> (Lemmermann) Kofoid var. <i>divaricatum</i>	33°21'	78°06'	5	72
<i>Ceratium lanceolatum</i> Kofoid	33°21'	78°06'	40	73
<i>Ceratium lanceolatum</i> Kofoid	33°21'	78°06'	40	74-75
<i>Ceratium carnegiei</i> Graham & Bronikowsky	33°21'	78°06'	5	76-77
<i>Ceratium carnegiei</i> Graham & Bronikowsky	8°23'	141°14'	20	78
<i>Ceratium carnegiei</i> Graham & Bronikowsky	8°23'	141°14'	40	79

close to the species *O. parvum*, *O. longiceps* and *O. sceptrum*. According to the original descriptions, the length of *O. longiceps* and *O. sceptrum* were higher than 70  $\mu\text{m}$ , while the specimens observed in this study were 30-50  $\mu\text{m}$  in length. Based on the size and the shape similarities, the specimens were in agreement with the description of *O. parvum* (Figs. 21-22). Another specimen showed a hemispherical epitheca with apparently a short spine. The hypotheca was long, swollen below the cingulum, and pointed at the base. These specimens were ascribed to *O. turbo* (Figs. 23-24). The anterior position of the cingulum of some elongated specimens of *Oxytoxum* may be confused with unarmoured dinoflagellates such as *Amphidinium*-like cells (Figs. 25-26).

Figs. 27-34 showed specimens with a minute epitheca compared with the longer, wider, and pointed hypotheca. The longer specimens have been ascribed to *O. longum* (Figs. 27-28), and the smaller ones with a hypotheca with wide shoulders were ascribed to *O. variabile* (Figs. 29-30). The size of *O. variabile* was highly variable ranging from 15 to 30  $\mu\text{m}$  in length. The species *O. caudatum* showed a small domed epitheca, with small apical spine, and hypotheca with an acute antapex that may be centred (Fig. 31) or curved (Figs. 32-33). The contour of the hypotheca of *O. caudatum* did not show wider shoulders, and the antapex had a spine (Fig. 34). The species *O.*

*coronatum* Schiller differed from *O. caudatum* on the occurrence of small spines in the epitheca that may be lost due to sample treatment. The occurrence of spines is a poor diagnostic character, and it cannot be discarded the conspecificity of both taxa.

More difficult is the identification of small *Oxytoxum* species with ovate hypotheca (Figs. 35-38). The use of nets for sampling probably results in severe underrepresentation of these small species. Based on light microscopy, the delimitation among the species *O. sphaeroideum*, *O. ovum* Gaarder, *O. pachyderme* Schiller, *O. crassum*, *O. minutum* Rampi and *Oxytoxum viride* Schiller was difficult. *Oxytoxum laticeps* (= *O. mediterraneum* Schiller) was one of the most distinctive species of this group (Fig. 35). The hypotheca was relatively large, roundly lenticular with a pointed antapex with convex sides, and the length was 30  $\mu\text{m}$  (Fig. 35). Another specimen with a round cell body and nearly median cingulum has been ascribed to *O. cf. sphaeroideum* (Fig. 36). The specimen of the Fig. 37 has been tentatively identified as *O. cf. globosum* (Fig. 37), and the specimen of the Fig. 38 as *O. cf. crassum*.

#### *Histioneis* and *Histiophysis*

Only twelve specimens of *Histioneis*, ascribed to seven species, were encountered. One specimen was devoid of

cell contents, and another specimen was a transition form between *Dinophysis* Ehrenberg and *Histioneis* (Table 1). All the records are here illustrated (Figs. 39-52). One specimen, with a cherry-shaped body, the fission rib ( $R_2$ ), and the third rib ( $R_3$ ) forming two loops, was ascribed to *H. cf. striata* (Fig. 39). *Histioneis joergensenii* showed a sub-rotund cell body, the  $R_2$  bending posteriorly, anastomosing with  $R_3$  about halfway (Fig. 40). Another specimen related to the *H. longicollis*-group appeared attached to an aggregate (Fig. 41). Three specimens have been ascribed to *H. crateriformis*, being closer, if not conspecific, with *H. reticulata* Kofoid (Figs. 42-44). The hypotheca was semicircular, and the cingulum broad with  $R_3$  ventrally deflected. The development of the left sulcal list varies among the specimens (Figs. 43-44) with the  $R_3$  well developed in the larger specimen (Fig. 44).

Another specimen showed intermediate characteristics between *Dinophysis* and *Histioneis* (Fig. 45). The left sulcal list was very developed as usual in species of *Histioneis* such as *H. tubifera* Böhm in Schiller. The cell body was circular and convex on the top. The shape of the cell body and scarce development of the cingular chamber was unusual in *Histioneis*. In contrast to *Histioneis*, the specimen did not harbor unicellular cyanobacteria in the scarce developed cingular chamber. This specimen has been ascribed to the genus *Histiophysis* Kofoid & Skogsberg (Fig. 45).

The eastern tropical Pacific Ocean is the type locality of numerous species of *Histioneis*. Several specimens corresponded to *Histioneis cleaveri*, described by Rampi (1952) from the central equatorial Pacific (3°S, 175°W). Two specimens that matched with the initial description were encountered in the proximities of the Marquesas Is. Archipelago (Figs. 47-48) and one specimen in the Humboldt Current (Fig. 46). The morphology of other specimen coincided with the original description of *H. longicollis* (Fig. 51). Another specimen, devoid of cell contents, corresponded to *H. hyalina* (Fig. 52). The largest specimen of *Histioneis* observed in this study (120  $\mu\text{m}$  long) showed a saddle-shaped cell body, higher dorsally (Figs. 49-50). The specimen resembled *H. cymbalaria* Stein as illustrated in Stein (1883, plate 22, figure 7). Stein apparently illustrated three different species under the name *H. cymbalaria*, and it is difficult to establish to which illustration corresponded to *H. cymbalaria*. Stein did not provide information on the size and the type locality of the specimens. The dorsal view of the specimen did not agree with the dorsal view of *H. cymbalaria* in Stein (1883) (Fig. 50). The specimen has been tentatively identified as *H. cf. pulchra* (Figs. 49-50).

### **Prorocentrum**

The species of the genus *Prorocentrum* were nearly absent in the severe oligotrophic waters of the South Pacific Gyre, except the ubiquitous *P. rostratum* Stein. A few specimens, all lacking the apical spine, were encountered in the more eutrophic conditions, near the Marquesas Is. Archipelago and the Humboldt Current (Table 1). The most extended morphology was an ellipsoidal shape, scarcely marked anterior region, and lacking the anterior spine. Most of the specimens resembled benthic species of *Prorocentrum* (Figs. 53-57), although it should be noted that the sea floor was deeper than 4000 m depth in the sampling stations.

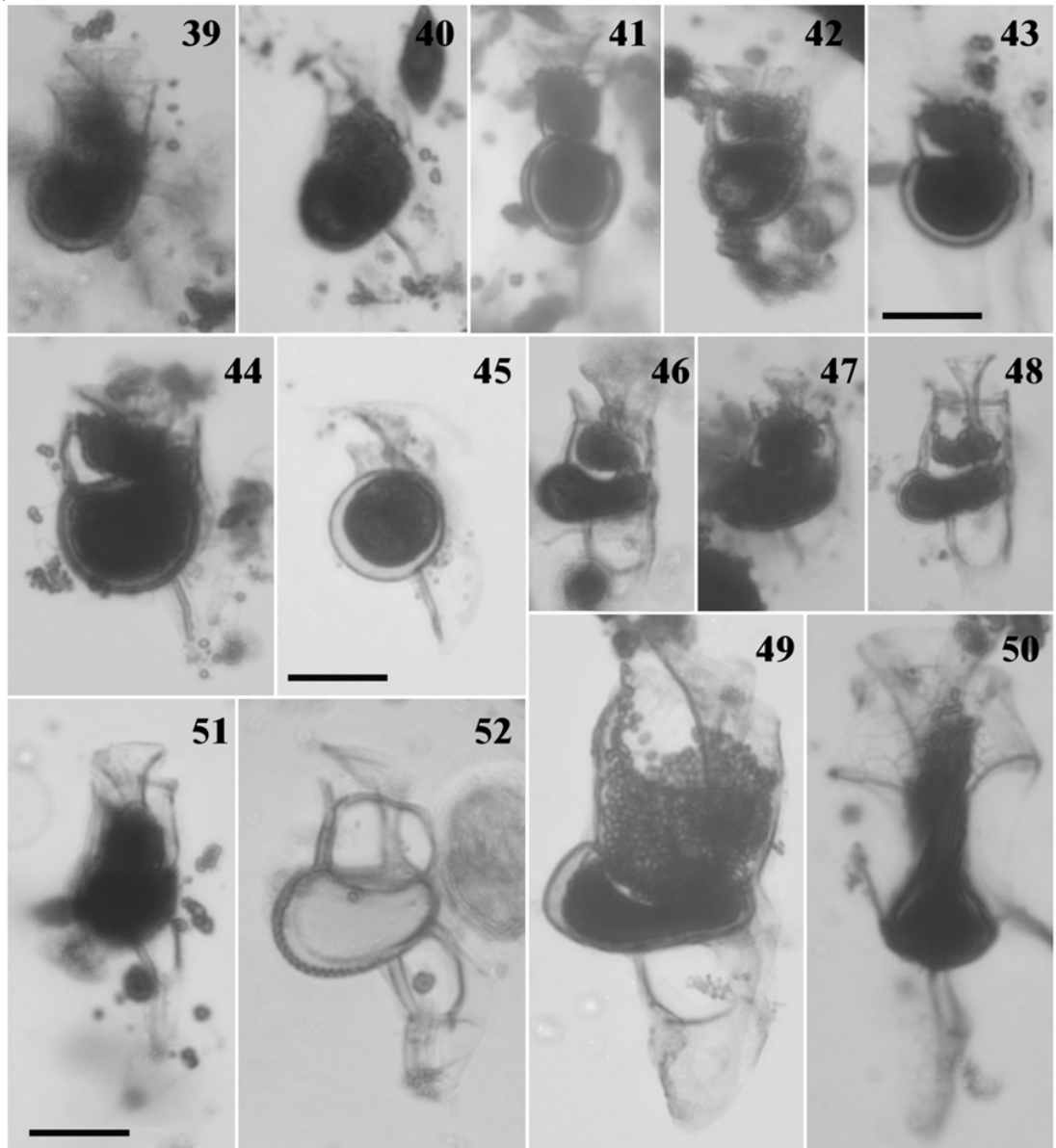
One specimen showed hyaline pyriform valves of 70  $\mu\text{m}$  in length (Fig. 53). Another specimen with highly hyaline valves of 60  $\mu\text{m}$  long and 50  $\mu\text{m}$  wide has been tentatively ascribed to *Prorocentrum cf. compressum* (Fig. 54). Another of the specimens showed smaller size (~30  $\mu\text{m}$  long) (Fig. 55). Two larger specimens of *Prorocentrum* were encountered near the Juan Fernández Archipelago (Fig. 56) and the Humboldt Current at 2000 km off Chile (Fig. 57). The dimensions were 55  $\mu\text{m}$  long and 33  $\mu\text{m}$  wide. The cells appeared more pigmented in the anterior part. These specimens resembled *Prorocentrum cf. rathymum* (Figs. 56-57).

One *Prorocentrum* species from the surrounding waters of the Marquesas Is. Archipelago showed up to seven cells in a line (Fig. 58). These rows of cells may be longer, although the labile junctions may be fragmented due to sample treatment. The anterior extreme of one specimen was in contact with the posterior part of the other specimen (Figs. 59-60). The shape of the specimens showed a variable degree of elongation. The cell size was 18-20  $\mu\text{m}$  long and 8-10  $\mu\text{m}$  wide (Fig. 60). These specimens have been ascribed to *Prorocentrum dentatum* (Figs. 58-60).

### **Gloeodinium**

A colony of two pairs of ellipsoidal cells embedded in mucilage of ~200  $\mu\text{m}$  long and ~150  $\mu\text{m}$  wide was encountered offshore the Marquesas Is. Archipelago (Fig. 61). Each cell was 40  $\mu\text{m}$  long and 25  $\mu\text{m}$  wide (Figs. 61-62). Other jelly of ~300  $\mu\text{m}$  long and ~200  $\mu\text{m}$  wide containing 10 pairs of spherical cells was encountered in the offshore boundary of the Humboldt Current (Figs. 63-64). Each cell showed a spherical hyaline capsule of 21-24  $\mu\text{m}$  in diameter. It showed a more irregular contour inside the capsule. The central part of the capsule of ~12-13  $\mu\text{m}$  was irregularly circular, and highly pigmented, resembling the nucleus of a dinoflagellate. These

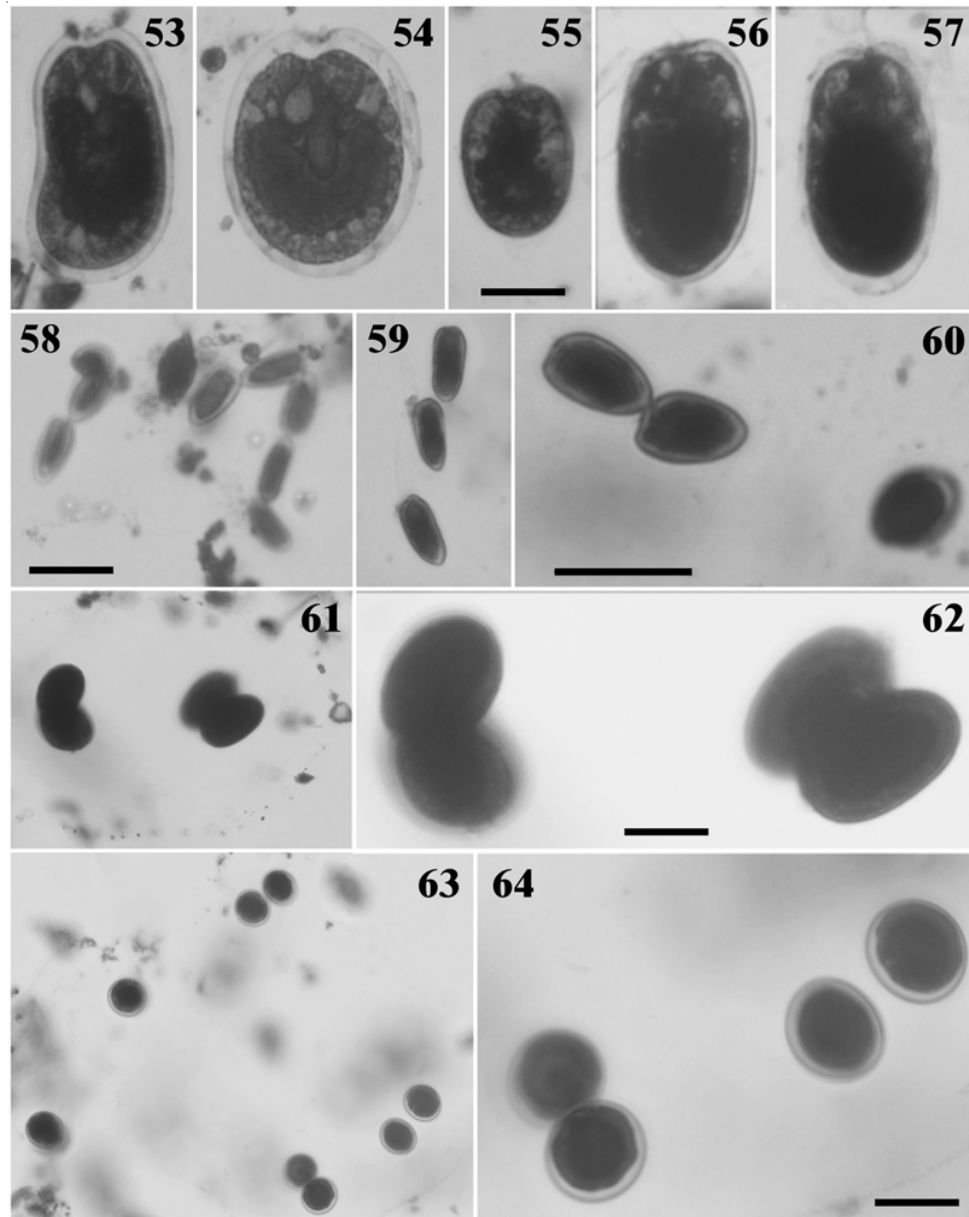




Figures 39-52

Photomicrographs of *Histiopsis* spp. and *Histiophysis* sp. in right lateral view, except figures 41 and 50 in dorsal view, bright field optics. See Table 1 for the location of the records. (39) *H. cf. striata*. (40) *H. joergensenii*. (41) *Histiopsis* sp. (dorsal view). (42-44) *H. cf. crateriformis*. (45) Tentatively identified as *Histiophysis* sp. (46-48) *H. cleaveri*. (49-50) *H. cf. pulchra* in lateral and dorsal views, respectively. (51) *H. longicollis*. (52) *H. hyalina*. All the micrographs at the same magnification. Scale bar of 20  $\mu$ m

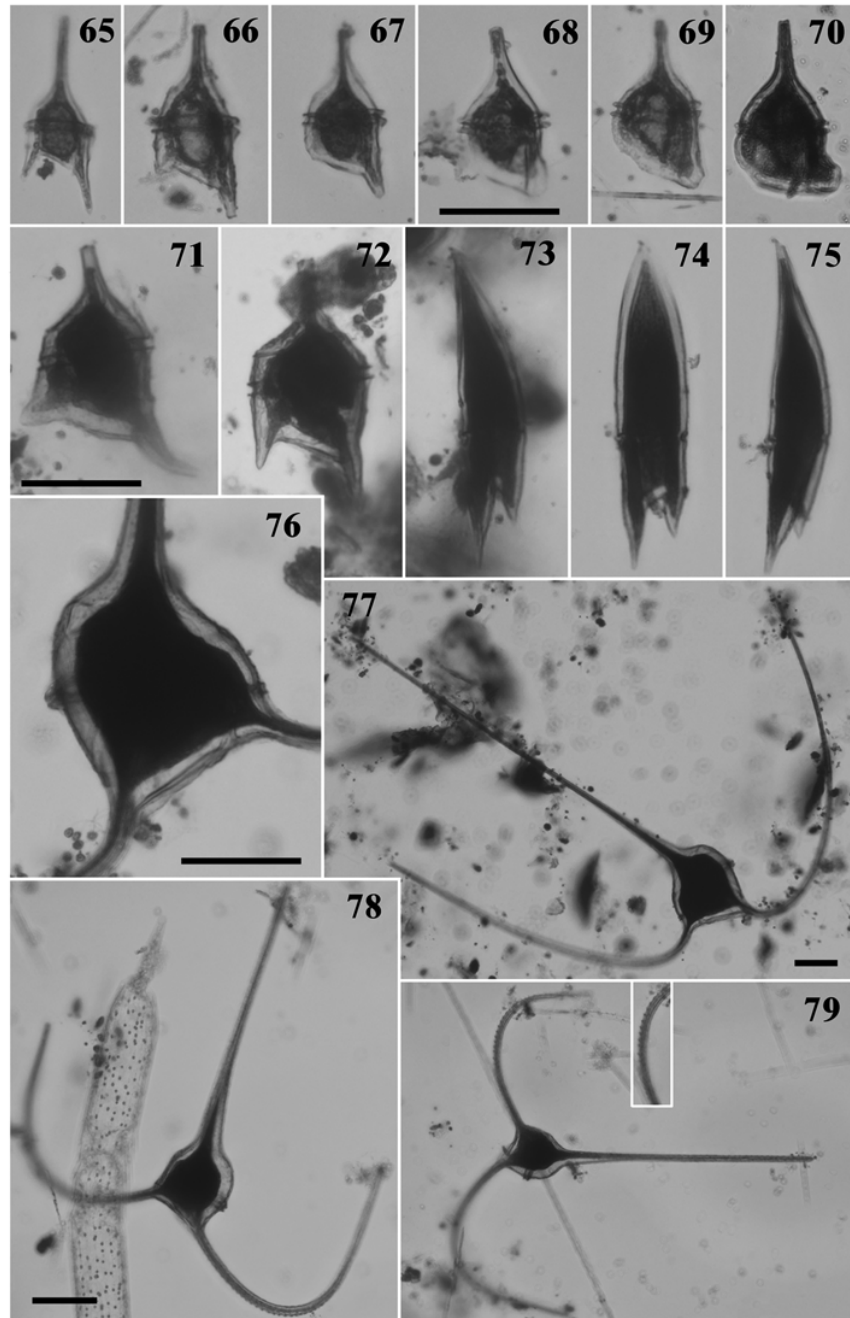
Microfotografías de *Histiopsis* spp. y *Histiophysis* sp. en vista lateral derecha, excepto las figuras 41 y 50 en vista dorsal, óptica de campo claro. Véase la localización de los registros en la Tabla 1. (39) *H. cf. striata*. (40) *H. joergensenii*. (41) *Histiopsis* sp. (vista dorsal). (42-44) *H. cf. crateriformis*. (45) Tentativamente identificado como *Histiophysis* sp. (46-48) *H. cleaveri*. (49-50) *H. cf. pulchra* en vista lateral y dorsal. (51) *H. longicollis*. (52) *H. hyalina*. Todas las fotografías a la misma escala. Barra de escala de 20  $\mu$ m



**Figures 53-64**

**Photomicrographs of *Prorocentrum* spp. and *Gloeodinium marinum*, bright field optics. See Table 1 for the location of the records. (53) *Prorocentrum* sp1. (54) *Prorocentrum* cf. *compressum*. (55) *Prorocentrum* sp2. (56-57) *Prorocentrum* cf. *rhathymum*. (58-60) *Prorocentrum dentatum*. (61-62) Ellipsoidal cells of *Gloeodinium marinum*. (63-64) Sphaerical cells of *G. marinum*. Figs. 53-59, 62, 64 at the same magnification. Scale bar of 20  $\mu$ m**

Microfotografías de *Prorocentrum* spp. y *Gloeodinium marinum*, óptica de campo claro. Véase la localización de los registros en la Tabla 1. (53) *Prorocentrum* sp1. (54) *Prorocentrum* cf. *compressum*. (55) *Prorocentrum* sp2. (56-57) *Prorocentrum* cf. *rhathymum*. (58-60) *Prorocentrum dentatum*. (61-62) Células elipsoidales de *Gloeodinium marinum*. (63-64) Células esféricas de *G. marinum*. Figs. 53-59, 62, 64 a la misma escala. Barra de escala de 20  $\mu$ m



**Figures 65-79**

**Photomicrographs of *Ceratium* spp., bright field optics. See Table 1 for the location of the records. (65) *C. cf. lineatum*. (66-70). *C. divaricatum* var. *balechii* (= *C. balechii*). (71-72) *C. divaricatum* var. *divaricatum*. (73-75) *C. lanceolatum*. (76-79) *C. carnegiei*. Figs. 65-75 at the same magnification. Scale bar of 50  $\mu$ m**

**Microfotografías de *Ceratium* spp., óptica de campo claro. Véase la localización de los registros en la Tabla 1. (65) *C. cf. lineatum*. (66-70) *C. divaricatum* var. *balechii* (= *C. balechii*). (71-72) *C. divaricatum* var. *divaricatum*. (73-75) *C. lanceolatum*. (76-79) *C. carnegiei*. Figs. 65-75 a la misma escala. Barra de escala de 50  $\mu$ m**

observations coincided with stages of the life cycle of *Gloeodinium marinum* described by Bouquaeux (1971) (Figs. 63-64).

### *Ceratium*

A total of 30 species of the genus *Ceratium* were recorded (see checklist in Gómez *et al.* 2007). This study focuses on the species *C. divaricatum* due to its assumed high morphological variability, and another two species, *C. lanceolatum* and *C. carnegiei* that are rarely reported in the literature (Table 1).

The specimens of *Ceratium divaricatum* showed a high morphological variability or they may represent more than one species (Figs. 66-72). One of these forms was described as a separate species under the name *C. balechii* by Meave *et al.* (2003) or as the variety *C. divaricatum* var. *balechii* by Hernández-Becerril & Alonso-Rodríguez (2004). In the equatorial upwelling region near the Marquesas Is. Archipelago, numerous specimens with a triangular epitheca, a very short apical horn (Figs. 66-70), and the right antapical horn absent (Figs. 67, 69) or reduced (Figs. 66, 68) were encountered. The right antapical horn tended to be more than developed than the left one (Figs. 66-70). The right antapical horns were directed posteriorly (Fig. 66) or laterally in one specimen from the Chilean coastal upwelling (Fig. 70). In this study, Figs. 66-69 corresponded to specimens of the same station near the Marquesas Is. Archipelago. The cell body of the species *C. lineatum* was closer to the shape of these specimens. However, the records of *C. cf. lineatum* did not co-occur with these specimens. *Ceratium cf. lineatum* was smaller in size (40 µm wide, Fig. 65) than these specimens assigned to *C. divaricatum* var. *balechii* (= *C. balechii*) (Figs. 66-70).

Several robust and larger specimens with an irregular contour of the epitheca and the apical horn truncate were encountered in the proximities of the Juan Fernández Archipelago (650 km off Chile) (Figs. 71-72). One of the specimens showed the right antapical more developed than the left one, and both forming an angle of ~45 degrees with respect the cingulum (Fig. 71). Another specimen showed the antapical horns directed laterally (Fig. 72). These two specimens, with a robust and coarse appearance, showed the outline of the epitheca more irregular has been ascribed to *C. divaricatum* var. *divaricatum* (Figs. 71-72).

*Ceratium lanceolatum* is an extremely rare taxon with highly distinctive lanceolate shape. Two specimens were collected at 40 m depth from the same sample in the proximities of the Juan Fernández Archipelago (Figs. 73-75). Both specimens were similar in shape and size (130 µm long and 28 µm wide) (Figs. 73-75).

*Ceratium carnegiei* is a distinctive species, large (>400 µm long) and robust. It was described from the tropical southeast Pacific Ocean. Despite these characteristics that facilitate the collection by net hauls, the records of this species has been scarce. The most distinctive feature is the relatively large volume of the epitheca compared to its nearest relatives (Figs. 76-77). The specimens showed small spines on the posterior proximal regions of the antapical horns (Figs. 78-79). Only three specimens were observed. Two specimens were encountered near the Marquesas Is. Archipelago (Figs. 78-79) and other specimen in the Humboldt Current near the Juan Fernández Archipelago (Figs. 76-77).

## Discussion

The tropical and subtropical open waters of the southeast Pacific Ocean are one of the least investigated of the world's oceans. The historical Expeditions in the southeast Pacific Ocean collected samples from the surface or vertical net hauls (Kofoid & Michener 1911, Kofoid & Skogsberg 1928, Kofoid & Adamson 1933, Graham & Bronikovsky 1944, Rampi 1948, 1950, 1952, Balech 1962). These coarse net hauls under-represented the smaller species, and destroyed other large delicate species or colonial forms. One of the most useful and detailed study in the region was carried out by Hasle (1960) that investigated the phytoplankton from bottle samples at three stations in the central equatorial Pacific at 145°W, 0-2°N.

### *Oxytoxum*

The studies on the genus *Oxytoxum* have been relatively scarce despite the high diversity in the open warm ocean. The differentiation of the genera *Corythodinium* Loeblich Jr. & Loeblich III and *Oxytoxum* is still unresolved. Overall, nineteen species were recorded and other specimens were not identified at the species level (Table 1). Hasle (1960) reported 8 species: *Oxytoxum caudatum*, *O. curvatum*, *O. laticeps*, *O. longum*, *O. milneri* Murray & Whitting, *O. sceptrum*, *O. scolopax* and *O. variabile*. All these species are illustrated in this study, although *O. cf. milneri sensu* Hasle is here ascribed to *O. diploconus*. The species *O. subulatum* or *O. milneri* were characterized by a pointed apex, often long, and tapered into an asymmetrical point. Hasle (1960) illustrated *O. cf. milneri*, but her specimen was more robust and the apex more pointed than in the original description of *O. milneri*. Balech (1988) illustrated a slightly premedian cingulum for *O. diploconus* and median cingulum in *Corythodinium cf. milneri*. There was not data on the size of *O. diploconus* in the original description (Stein 1883). In this study it has been considered the record as *O. diploconus* (Fig. 9) instead of *O. cf. milneri* as reported



by Hasle (1960). It cannot be discarded the conspecificity of *O. milneri*, *O. subulatum* and *O. diploconus*.

According to Hasle (1960) the most abundant species was *O. variabile* that reached 4000 cells L<sup>-1</sup> which size ranged from 15 to 30 µm in length. Rampi (1952) from a close location reported the larger species *O. elegans*, *O. sceptrum*, *O. scolopax*, *O. sphaeroideum* and *O. tessellatum*, whereas *O. variabile* was absent. Hasle (1960) was based on bottles samples, whereas Rampi was based on net sampling that may under-represent the small size species such as *O. variabile*. The epithet of the species is representative of the high variability in size and shape assumed in *O. variabile*, and even may be confused with unarmoured dinoflagellates such as *Amphidinium* Claparède & Lachmann. The species *O. gracile* has been regarded as a synonym of *O. variabile* (Hasle 1960). *Oxytoxum gracile* showed wider shoulders in the hypotheca than *O. variabile*. The specimens in this study were closer to the original description of *O. gracile* (Figs. 29-30). *Oxytoxum variabile* and *O. gracile*, described from the cold waters of the shallow Adriatic Sea, showed a short apical spine in the epitheca that was absent in the specimens illustrated by Hasle (1960). From an ecological point of view, the type locality of both taxa strongly differed from the environmental conditions of the central Pacific Ocean. It is uncertain whether *O. variabile* was the same species in these two contrasted environments. After Hasle (1960) this taxon has been reported as *O. variabile* in the equatorial Pacific Ocean (Desrosiers 1971, Iriarte & Fryxell 1995). The species *O. gladiolus* Schiller had a similar shape, and the epitheca had not an apical short spine, and it was described from warm waters of the Atlantic Ocean (Stein 1883), and reported near the Hawaii Is. Archipelago (Lemmermann 1905). In this study, following previous studies, the specimens have been ascribed to *O. variabile*. Further research is needed to clarify the identity of this taxon.

In the central equatorial Pacific, Iriarte & Fryxell (1995) listed *O. caudatum*, *O. curvatum*, *O. laticeps*, *O. milneri*, *O. cf. sceptrum*, *O. scolopax*, *O. tonollii* Rampi, *O. turbo* and *O. variabile*. *Oxytoxum tonollii* was also observed in this study, although it is considered an inverted specimen of the genus *Amphidoma* Stein (Taylor 1976). From the North Pacific Gyre, Venrick (1982) listed *Oxytoxum curvatum*, *O. curvicaudatum*, *O. constrictum*, *O. elegans*, *O. laticeps*, *O. adriaticum* Schiller, *O. globosum*, *O. longum*, *O. parvum*, *O. scolopax*, *O. cf. sphaeroideum*, *O. subulatum*, *O. turbo* and *O. variabile*. *Oxytoxum adriaticum* strongly resembled one of the varieties of *O. sphaeroideum* described from the Hawaii Is. Archipelago (Lemmermann 1905).

One of the specimens of *Oxytoxum* showed a discontinuity in the outline of the epitheca (Fig. 13) that was illustrated by Balech (1988, plate 82, Fig. 8) under the name *Corythodinium* sp. This morphology was also illustrated by Wood (1968) for *O. curvicaudatum*. This study is the first to illustrate *O. challengeroides* since the initial description (Fig. 8). The specimen in Fig. 12 was more robust than *O. areolatum*, and less elongated than *O. strophalatum* Dodge & Saunders. The specimen was ascribed to *O. cf. frenguelli* (Fig. 12).

### *Histioneis*

Despite more than one hundred species of the genus *Histioneis* has been described, little is known about one of the most numerous dinoflagellate genera. The specimens are often referred as *Histioneis* sp. in the literature due to the difficulties in the delimitation of the species (Gómez 2007b). Twelve specimens of *Histioneis* were encountered in this study. This is a scarce number of records when compared to other geographical areas. For example, Gómez (2005) found 17 of specimens a single seawater sample of 400 ml from the North Philippine Sea. The records of *Histioneis* could be more numerous by using net sampling. However, smaller specimens may be under-represented and the delicate sulcal list may be damaged. From the twelve specimens encountered, four specimens were recorded in the upper 30-40 m depth, three specimens at 170-190 m depth, and two specimens of the same species appeared at 40 and 190 m depth at the same sampling station (Figs. 43-44). It is difficult to establish a clear pattern in the distribution of the genus *Histioneis*.

*Histioneis cf. crateriformis* and *H. cleaveri* were the most represented species (Table 1). Gómez (2005) tentatively found a specimen of *H. cf. cleaveri* in the western equatorial Pacific. This taxon was not cited since the description by Rampi (1952) in the southern equatorial Pacific. These new observations confirm the validity of *H. cleaveri*. More doubts appeared with *H. crateriformis*, a taxon of difficult identification due to the scarce development of the left sulcal list. It is difficult to establish a separation from close relatives such as *H. reticulata* and *H. pachypus* Böhm in Schiller and also *H. mediterranea* Schiller (Gómez 2007b).

Stein (1883) reported three different lateral figures and one ventral view for *H. cymbalaria*. Later, Schiller (1933) described *H. skogsbergii* Schiller based on one of the lateral views, and the ventral view illustrated by Stein for *H. cymbalaria*. Kofoid & Skogsberg (1928) considered other of the Stein's figures (plate 22, fig. 10) of *H. cymbalaria* very close to *H. hyalina*. This study is the first to report a photographic record of *H. hyalina*



(Fig. 52). The specimen observed was devoid of cell content. This record showed that *H. hyalina* is a distinctive taxon, and different from *H. cymbalaria sensu* Stein. Other specimen identified as *H. pulchra* (49-50) was also close to one of the figures of *H. cymbalaria* by Stein (1883). Abé (1967) proposed *H. pulchra* as a synonym of *H. mitchellana* Murray & Whiting. Abé considered that the figures of *H. mitchellana* by Kofoid & Skogsberg (1928) also illustrated *H. pulchra*. Recently Gómez (2005) illustrated *H. mitchellana*. *Histioneis mitchellana* and *H. pulchra* should be regarded as separate species until further research.

### ***Prorocentrum***

*Prorocentrum rostratum*, a highly distinctive species, was the most ubiquitous *Prorocentrum* species in the open southeast Pacific. However, it resulted more difficult the identification of other species with an ovate shape and lacking spines, resembling benthic or epiphytic species of *Prorocentrum*. The net sampling may under-represent these *Prorocentrum* species. Based on net sampling, Rampi (1952) only listed *Exuviaella compressa*, *E. lenticula* Matzenauer and *Prorocentrum rostratum*. Based on bottles samples, Hasle (1960) recorded *Exuviaella baltica* Lohmann, *E. compressa*, *P. obtusidens* Schiller, *P. rostratum*, *E. vaginula* Stein and described the new species *Exuviaella aequatorialis* Hasle. Venrick (1982) listed *Prorocentrum* cf. *compressum*, *P. dactylus*, *P. obtusidens*, *P. rostratum*, *P. cf. triestinum* and *P. vaginulum*. Iriarte & Fryxell (1995) listed *Prorocentrum compressum*, *P. maximum*, *P. obtusidens* and *P. rostratum*. Beyond the ubiquitous *P. rostratum*, the specimens lacking apical spine with oval shape in the open tropical Pacific Ocean have received the name of *P. compressum*. In the proximities of the region investigated by Hasle, Rampi (1952) and Iriarte & Fryxell (1995) reported *P. lenticulatum* (Matzenauer) F.J.R. Taylor. Hasle (1960) described the new species *Exuviaella aequatorialis* with almost circular outline of 19  $\mu\text{m}$  in diameter, and two distinct notches in the flagellar pores. Dodge (1975) over-synonymized the species of the genus *Prorocentrum*, and erroneously proposed *E. aequatorialis* as a synonym of *P. balticum* (Lohmann) Loeblich III, and *P. lenticulatum* as a synonym of *P. compressum* (Bailey) Abé *ex* Dodge. However, *E. aequatorialis* should be considered as a synonym of *P. lenticulatum*.

A colonial behavior was observed in specimens encountered forming rows of cells (Figs. 58-60). The specimens were small (18-20  $\mu\text{m}$  long, 8-10  $\mu\text{m}$  wide), showing a different degree of elongation. The anterior part was asymmetrical, with one side more developed than the other one (Fig. 60). The junction among the

specimen was weak, and this may be responsible of the lack in other studies due to the breakage using drastic methods such as net sampling. The illustration and description of *P. maximum* in Hasle (1960), also listed by Iriarte & Fryxell (1995), coincided with single-cell specimens of the species observed forming rows in the central equatorial Pacific Ocean (Figs. 58-60). Dodge (1975) erroneously synonymized *P. maximum* and *P. mexicanum* Osorio-Tafall (Cortés-Altamirano & Sierra-Beltrán 2003).

The morphology of the specimens of the figures 58-60 was close to species reported as *P. obtusidens* in the central Pacific Ocean (Hasle 1960, Venrick 1982, Iriarte & Fryxell 1995). According to Schiller (1933) the length of *P. obtusidens* was 36  $\mu\text{m}$ , while the colonial specimens in this study were about one half of the length of *P. obtusidens* (Figs. 58-60). The shape of the specimens agrees with *P. triestinum sensu* Taylor (1976) that reported a smaller size than in the original description. Dodge (1975) and Hernández-Becerril *et al.* (2000) considered *Prorocentrum obtusidens* as a synonym of *P. dentatum*. Hernández-Becerril *et al.* (2000) illustrated a two-cell chain of *P. dentatum* of similar size to those in this study (<20  $\mu\text{m}$  in length) (Fig. 60). From the year 2000 *Prorocentrum dentatum* has been observed to cause large blooms in Chinese coastal waters (Tang *et al.* 2006). This species, later named as *Prorocentrum donghaiense* Lu, often showed 4-cell chains (Lu *et al.* 2005) as reported in this study (Figs. 58-59). Le Gall *et al.* (2008) have established cultures of *Prorocentrum minimum* (Pavillard) Schiller and *P. dentatum* from material collected during this cruise in the SE Pacific Ocean.

### ***Gloeodinium***

The colonies of *Gloeodinium* were first reported in the Atlantic Ocean as unidentified cysts by Schütt (1895). In the Sargasso Sea, an oligotrophic environment as the South Pacific Gyre, Gaarder (1954) illustrated tentative pairs of spherical cyst of dinoflagellates embedded in mucilage. Gaarder (1954) suggested a relation to the specimens of *E. compressa* embedded in mucilage that she also found. Hasle (1960) reported for *Exuviaella compressa* 'Four cells were found embedded in a jelly mass in the same way as depicted by Gaarder (1954)'. Two Norwegian researchers, Gaarder (1954) and Hasle (1960), by using similar methodology found cells ascribed to *Prorocentrum* embedded in mucilage from bottle samples of the sub-tropical Atlantic and the equatorial Pacific, respectively. Previous studies based on net hauls would easily destroy these delicate structures (Figs. 61-64). These unidentified colonies also appeared in the western Mediterranean Sea (Margalef *et al.* 1954). In the

French Mediterranean coast, Bouquaheux (1971) described these mucilaginous colonies of pairs of cells as a part of the life cycle of the new species *Gloeodinium marinum*. Taylor (1976) also reported colonies of *Gloeodinium* from the Indian Ocean, with no further records in the literature.

### *Ceratium*

Most of the species of the genus *Ceratium* are large, robust, and easy collectable by using nets. Consequently *Ceratium* is one of the best known genera of dinoflagellates. The identification at the species level is relatively easy, although some species showed a high intraspecific morphological variability. The identification of the species of *Ceratium* is mainly based on the length and orientation of the horns and the delimitation between species and varieties may be difficult. Several species showed a pronounced phenomenon of dichotomy, and exuviations of the horns as described by Kofoid (1908) for *C. divaricatum*, often confused with *C. dens* Ostenfeld & Schmidt. The variety *Ceratium divaricatum* var. *balechii* proposed by Hernández-Becerril & Alonso-Rodríguez (2004) was previously described as the new species *C. balechii* Meave, Okolodkov & Zamudio (Meave *et al.* 2003). This new species was defined based only on morphometric differences that may result insufficient for a highly variable taxon. Hernández-Becerril & Alonso-Rodríguez (2004) reported as diagnostic character that the base of the apical horn was continuous in the variety *C. divaricatum* var. *divaricatum* and well-defined in *C. divaricatum* var. *balechii*. In this study, the two tentative varieties of *Ceratium divaricatum* appeared in two geographically distant populations. *Ceratium divaricatum* var. *balechii* appeared in the Marquesas Is. Archipelago and the Chilean upwelling off Concepción, whereas the form *C. divaricatum* var. *divaricatum* was encountered in the offshore Humboldt Current. The morphology and size of the specimens of these separate populations were rather different to be considered as only varieties. The different morphological characteristics and geographical separation of the populations suggested that these varieties may be truly separate species. However, studies based on clone cultures and molecular phylogeny are needed to clarify the status of *C. balechii*.

*Ceratium lanceolatum* was described by Kofoid (1907) off Perú. This study is the first to report a photographic record of *C. lanceolatum* from the South Pacific. Hernández-Becerril (1988) reported this taxon from the Pacific coasts of México. Kofoid (1907) reported a transdiameter of 19-22  $\mu\text{m}$  and a length of 95-122  $\mu\text{m}$ .

The length of the specimens from the Humboldt Current was similar to the original description off Perú, although the transdiameter was slightly wider (Figs. 73-75). *Ceratium lanceolatum* was absent in the extensive collections from the Dana Expedition by Steemann Nielsen (1934), Rampi (1952), neither from the Carnegie Expedition by Graham & Bronikovsky (1944). After Kofoid, Gaarder (1954) found one specimen of *C. lanceolatum* in the tropical North Atlantic Ocean. She reported a transdiameter of 56  $\mu\text{m}$  and a length of 285  $\mu\text{m}$ . The specimen illustrated by Gaarder (1954) seems to be closer to *C. schroeteri* B. Schröder. Later Wood (1968) reported *C. lanceolatum* from the northern waters of Brazil. The length was 100-150  $\mu\text{m}$  and the shape was similar to the original description.

*Ceratium carnegiei* is a large and distinctive species. This taxon was known from the tropical Indian Ocean (see references in Taylor 1976). Gaarder (1954) found one specimen in the tropical North Atlantic Ocean. Despite its high size and distinctive cell body shape, no further records of *C. carnegiei* have been reported in the Atlantic Ocean.

The decline of taxonomical studies in open ocean waters is responsible of that numerous species, even large and distinctive ones, were absent from the literature since decades. Numerous species are considered rare, although this is due to lack of studies where these species can be found.

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