

Erythrospidinium (Gymnodiniales, Dinophyceae) in the Pacific Ocean, a unique dinoflagellate with an ocelloid and a piston

Fernando Gómez

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

Received 25 June 2007; received in revised form 12 March 2008; accepted 24 March 2008

Abstract

The distribution and morphology of the dinoflagellate *Erythrospidinium* (= *Erythrospis*) was studied in the vicinity of the Kuroshio and Oyashio Currents, the Philippine, Celebes, Sulu and South China Seas, western and central equatorial and southeast Pacific Ocean. Ninety-four specimens were observed, most of them collected from depths of less than 90 m. The highest abundance (15 cells L⁻¹) was recorded in the north Philippine Sea in May (32°N, 138°E, 30-m depth). Twenty-four specimens were found in a station in the offshore Perú-Chile Current (31°52'S, 91°24'W). The transition regions between open warm waters and productive currents or upwellings seem to favour the abundance of *Erythrospidinium*. Specimens with duplicate pistons, with two protuberant ocelloids, and specimens with a piston that attains up to 20 times the body length are illustrated for the first time. All the specimens have been ascribed to the type species, *Erythrospidinium agile*, until stable taxonomical criteria are established for the species diagnosis. Despite the complexity of its organelles, the ocelloid and piston, the competitiveness of *Erythrospidinium* in the pelagic ecosystem seems to be low.

© 2008 Elsevier GmbH. All rights reserved.

Keywords: *Erythrospidinium*; *Erythrospis*; *Pouchetia*; Eyespot; Photoreceptor organelle; Pacific Ocean

Introduction

Members of the family Warnowiaceae Lindemann are gymnodinioid dinoflagellates characterised by the possession of one or several elaborate eyespots, a light-receiving organelle named the ocelloid (also misnamed the ocellus) (Greuet 1970, 1977). The genus *Erythrospidinium* P.C. Silva (= *Erythrospis* Hertwig, *Pouchetia* Schütt, in part) is characterised by a single, very elaborate, ocelloid that possesses a refractive structure capable of acting as a focusing lens, and another unusual organelle, the piston (also named prod, dart

or tentacle), capable of incessant rhythmical contractions (Greuet 1967). The piston is also known from its close relative *Greuetodinium* Loeblich III (= *Leucopsis* Greuet), a genus never reported again after the first description (Greuet 1968).

Ten species of *Erythrospidinium* have been described from warm and temperate seas. In the Gulf of Naples, Hertwig (1885) described *Erythrospis agilis* with an eyespot composed of a pigment mass and lens, and a highly contractile 'tentacle'. These organelles, later named ocelloid and piston (Greuet 1987), attain a degree of structural complexity in *Erythrospidinium* unequalled among protists. This unusual complexity generated disbelief among earlier protozoologists.

E-mail address: fernando.gomez@fitoplancton.com.

Hertwig received the criticisms of C. Vogt who considered the description of *Erythroopsis* as a vorticellid ciliate that had ingested the ocellus of a medusa (see Kofoid and Swezy 1921). The genus *Erythroopsis* did not appear in the literature during the next decade. Schütt (1895), who had not known about Hertwig's description of *Erythroopsis*, described *Pouchetia cochlea* Schütt and *P. cornuta* Schütt from an indeterminate location of the tropical Atlantic or the Bay of Naples. Pavillard (1905) illustrated *E. agilis* from French Mediterranean coasts and he considered *P. cornuta* as a synonym of the type species. Although the specimens reported by Schütt (1895) lacked the piston, Kofoid and Swezy (1921) considered that the ocelloid and epicone were distinctive characters of the genus *Erythroopsis* and they transferred *P. cochlea* and *P. cornuta* to that genus. Kofoid and Swezy (1921) also considered that Pavillard's illustration of *E. agile* corresponded to a separate species and they proposed *E. pavillardii* Kofoid et Swezy. Kofoid and Swezy (1921) described six new species: *Erythroopsis extrudens*, *E. richardii*, *E. hispida*, *E. labrum*, *E. minor* and *E. scarlatina* from Californian coasts. Kofoid and Swezy (1921) used the position, shape and coloration of the ocelloid and the presence or absence of a terminal stylet in the piston as taxonomical criteria for species diagnoses. The genus *Erythroopsis* Hertwig was a junior homonym of the sterculiacean *Erythroopsis* Lindley and all the species were transferred to the new genus *Erythropsidinium* P.C. Silva (Silva 1960). Greuet (1967, 1970, 1973, 1977) performed numerous morphological, cytological and ultrastructural studies, with the aid of electron microscopy, from material collected near the French Mediterranean coast. Greuet realised that the diagnostic characters used by Kofoid and Swezy (1921) were variable intraspecifically and he suggested that *Erythropsidinium* is a monotypic genus (Greuet 1973, p. 467). Elbrächter (1979) examined live specimens from the NW Africa upwelling and also observed that the structure, position and coloration of the ocelloid changed in the course of the cell division or individual development. Elbrächter (1979) considered *Erythropsidinium cornutum*, *E. hispidum*, *E. labrum*, *E. pavillardii*, *E. richardii* and *E. scarlatinum* as synonyms of the type species. Greuet (in Sournia 1986) showed micrographs of *Erythropsidinium* with the piston in different phases of elongation. Takayama (1998) showed a scanning electron micrograph of *E. agile* from the southern Japanese coast.

The ocelloid and the piston are of particular interest in the evolution and phylogeny of protists. The unique organelles of *Erythropsidinium* received much attention from earlier marine protozoologists (Hertwig 1885; Pavillard 1905; Fauré-Fremiet 1914; Kofoid and Swezy 1917, 1921) and further by Greuet (1967, 1970, 1973, 1977). Gehring (2005) hypothesised that the ocelloid of dinoflagellates such as *Erythropsidinium* and *Warnowia* Lindemann may be the origin of photoreceptor cells in

metazoa. He proposed that the dinoflagellates may have transferred their photoreceptor genes to cnidarians (Gehring 2005). The delicacy of this unarmoured dinoflagellate and the limited investigations in warm waters contribute to the fact that *Erythropsidinium* rarely appeared in the literature in the last three decades. Very little is known about the ecological and geographical distribution of *Erythropsidinium* and its morphology in the open ocean.

The present study reports the first estimates of the abundance, vertical and spatial distribution in several contrasting regions in both hemispheres in the Pacific Ocean between the subarctic and the equator. The appearance of *Erythropsidinium* in fixed samples is illustrated in the hope that they will be more commonly recognised and reported. A selection of specimens with especially interesting morphology is shown. This includes specimens apparently undergoing binary division, specimens with two pistons, with two ocelloids and specimens with high variability in the length of the piston. These observations are reported to contribute to our knowledge about this unique protist.

Material and methods

Samples were collected during 11 cruises in the Pacific Ocean. Sample collection and light microscopical methods used were described in Gómez and Furuya (2005, 2007) (Fig. 1). The physical and trophic conditions were described in Gómez et al. (2005) and Gómez (2007). Water samples at each station collected using Niskin bottles from depths of 0–280 m were preserved with acidified Lugol's solution and stored at 5 °C. Samples of 500 mL were concentrated by sedimentation in glass cylinders. During a 6-day settling period, the top 450 mL of the sample was progressively and slowly siphoned off with small-bore tubing. Fifty millilitre of the concentrate representing 500 mL whole water sample was settled in composite

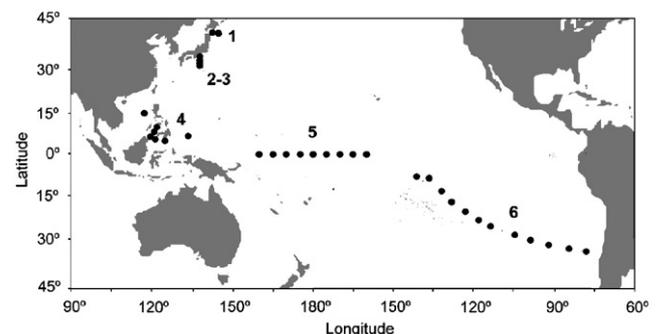


Fig. 1. Map of the station locations in the Pacific Ocean (marked by circles). 1. Oyashio Current. 2, 3. Kuroshio Current and Philippine Sea in May and July, respectively. 4. Celebes, Sulu and South China seas. 5. Western and central equatorial Pacific. 6. Southeast Pacific Ocean.

settling chambers. The entire chamber was scanned at 200 × magnification under a Nikon or Olympus inverted microscope equipped with a digital camera.

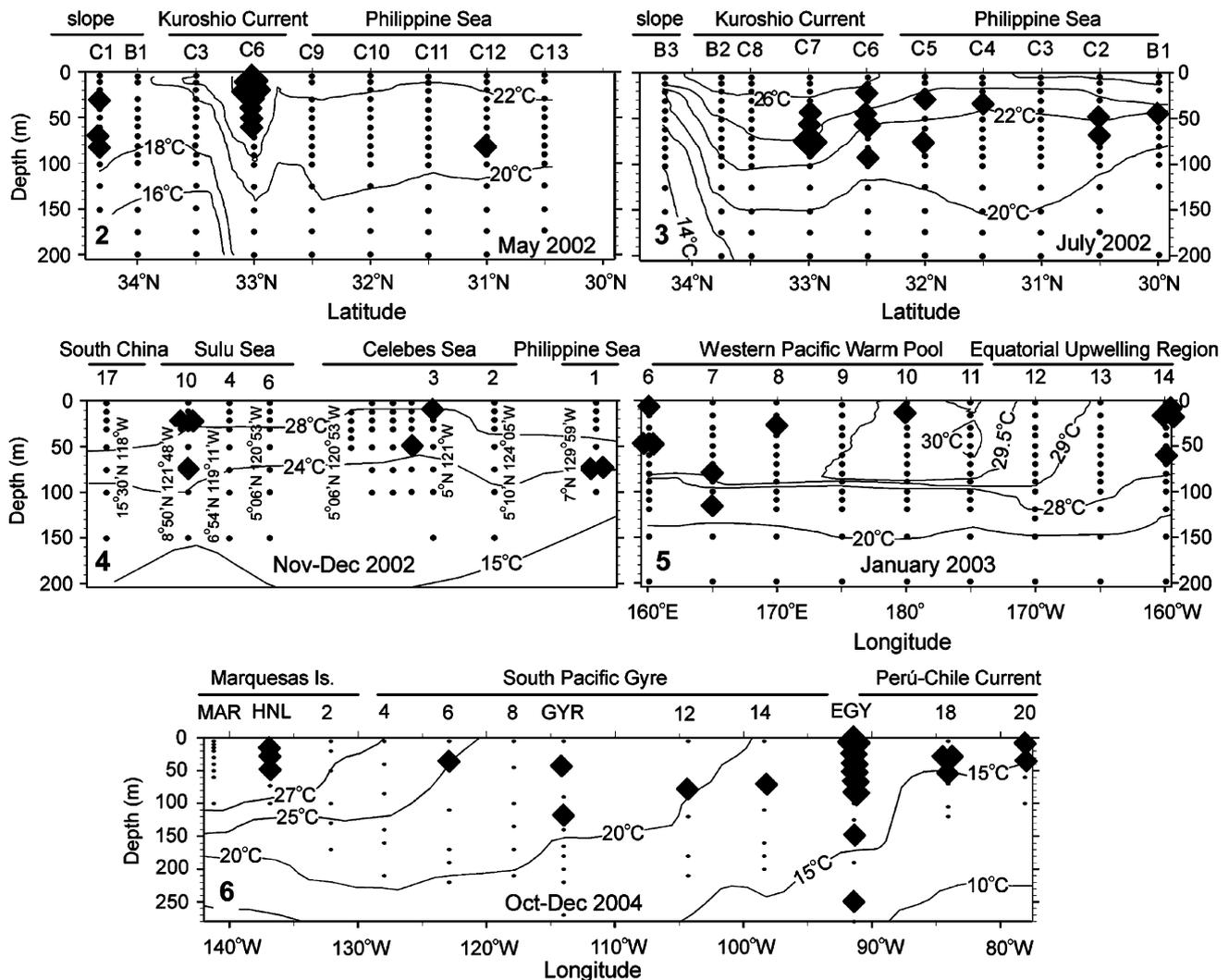
Results

Distribution of *Erythropsidinium*

Ninety-four specimens of the genus *Erythropsidinium* were collected from the open 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, 16 individuals of *Erythropsidinium* were found in 131 samples analysed (Fig. 2). During the cruise in July, the stations were re-visited and 21 specimens were found in 144 samples analysed (Fig. 3). During the cruise in the marginal seas of the

western Pacific, 7 specimens were observed in 81 samples (Fig. 4). In the western and central equatorial Pacific, 13 specimens were found in 124 samples (Fig. 5). In the southeast Pacific, 37 specimens of *Erythropsidinium* were found in the 83 samples analysed (Fig. 6). Samples from six cruises carried out off Hokkaido (north of Japan) were also analysed. No specimens of *Erythropsidinium* were observed in these cold waters under the influence of the subarctic Oyashio Current.

In the Kuroshio Current and adjacent waters south of Japan, the number of specimens was slightly higher in summer than in spring (Figs 2, 3). The highest abundance (15 cells L⁻¹) was recorded in May coinciding with the warmer surface waters of a narrow Kuroshio Current. Records of *Erythropsidinium* in the southeast Asia marginal seas were scarce and it is difficult to discern a pattern in the distribution (Fig. 4). In the western and central equatorial Pacific the records



Figs 2–6. Section plots of the records of *Erythropsidinium* 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 the Celebes, Sulu and South China Seas. 5, Records from the western and central equatorial Pacific. 6, Records from the southeast Pacific. Isotherms are shown.

were more numerous in the less oligotrophic stations of the transect, namely the westernmost station and in the equatorial upwelling region (Fig. 5). In the southeast Pacific Ocean, the records of *Erythrospidinium* tended to be more abundant in the most eutrophic regions, i.e. the vicinity of the Marquesas Islands and the Perú-Chile Current. Twenty-four specimens were recorded in a station located at the western margin of the Perú-Chile Current (31°52'S, 91°24'W) (Fig. 6). As a general trend, most of the specimens were collected in the upper 90 m depth. Only three specimens of the 94 observed were recorded below 100 m depth, two specimens in the offshore Perú-Chile Current and one specimen in the western equatorial Pacific.

Morphology of *Erythrospidinium*

Members of the genus *Erythrospidinium* have a globular gymnodinioid cell body, 70–120 µm in length (without piston) and ~45–60 µm in width (Figs 7–22). Most of the cell body is occupied by the hyposome, whereas the episome is less than 1/4 the size of the hyposome. According to the orientation proposed by Kofoid and Swezy (1917), the ocelloid is located at the left side of a cell seen in ventral view. The outline of the cell is modified by this large ocelloid, usually protuberant, premedian or directed anteriorly (Fig. 7). The ocelloid was composed of one or several hyaline lenses, the hyalosome, and a highly pigmented region, the melanosome. The nucleus was ellipsoidal and usually located at the right side of the cell. The piston projects from a postero-ventral invagination in the hyposome. The length of the piston was highly variable and its length tended to be inversely proportional to the thickness. The piston may be enlarged in the distal (Fig. 9) and/or proximal parts (Fig. 18) and with intermediate knobs (Fig. 20). The end of the piston may be capitate (Figs 7–11, 13–15), with flattened thickening or papillae (Fig. 18). The distal end of the piston may show a terminal stylet (Figs 12, 16, 17). The length and thickness of the piston were highly variable among the specimens, depending on the degree of retraction or protraction at the time when the specimens

were fixed. In some specimens the piston was very short (Fig. 22) or very long, extending for more than 20 times the body length with several knobs (Fig. 20). The contour of the cell body in some specimens showed an anterior lamella or horn. This lamella was pointed (Figs 16, 18) and arising from a peduncle with a lanceolate shape (Fig. 15). Neither chromatophores nor food vacuoles were observed.

Four of the 94 specimens showed a median constriction (Figs 10–12), interpreted as specimens undergoing division based on the photomicrographs by Greuet (1973). These specimens showed a single piston on dividing cells (Figs 10–12). As well as the piston, another specimen showed a body extension that projected posteriorly from the hyposome from another point than the piston (Figs 16, 17). Two specimens showed two pistons projecting from the same position of the hyposome. One of the specimens showed two pistons of the same length and thickness which projected posteriorly at right angles to one another (Fig. 13). Another specimen showed two pistons with slight differences in thickness (Figs 14, 15). There is no evidence to conclude that these specimens with two pistons were undergoing division.

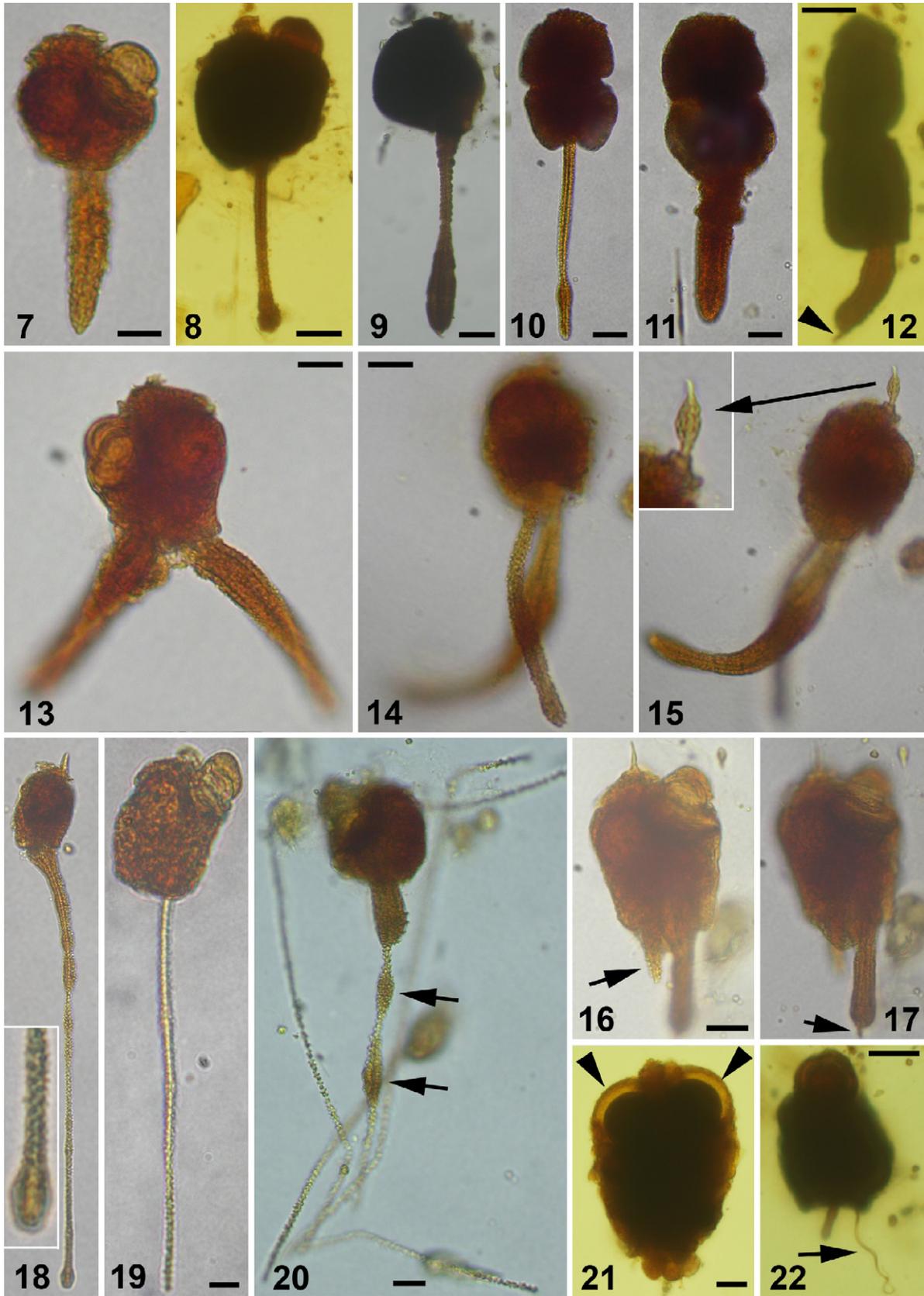
One large specimen (90 µm wide, 170 µm long) (Fig. 21), apparently with the piston lacking or fully retracted, showed two protuberant ocelloids, one at each side of the anterior cell body (Fig. 21). Another specimen showed a posteriorly directed filament (Fig. 22). The longitudinal flagellum of these dinoflagellates tends to be more labile than the transverse one and is rarely observed in preserved samples. Although the slightly undulated filament seen in Fig. 22 was unusually thick, it has been tentatively considered to be the longitudinal flagellum.

Discussion

Geographical and ecological distribution

Previous records of *Erythrospidinium* were restricted to the Italian coasts (Hertwig 1885; Schütt 1895), French Mediterranean and Atlantic coasts (Pavillard 1905;

Figs 7–22. Photomicrographs, bright-field optics, of *Erythrospidinium*. **7, 8**, Two specimens. See the ocelloid in the left side of the cell (ventral view). **9**, Specimen with an enlarged end of the piston. **10–12**, Three specimens with a central constriction, tentatively undergoing binary division. The arrowhead in Fig. 12 indicates a terminal stylet in the piston. **13**, Specimen in dorsal view with two pistons. **14, 15**, Two views of another specimen with two pistons. The inset in Fig. 15 shows a lanceolate apical extension. **16, 17**, Two views of another specimen in ventral view with a pointed apical extension; in Fig. 16 the arrow indicates a short extension from the hyposome and in Fig. 17 the arrow indicates the terminal stylet. **18**, Specimen with a pointed apical extension. The inset shows the papillae at the end of the piston. **19**, Another specimen in ventral view; in this case the piston does not have a capitate end. **20**, Another specimen in dorsal view with an extremely long piston. The arrows indicate enlargements or papillae in the proximal part of the piston. **21**, A specimen with two ocelloids (see arrowheads), and no piston. **22**, A specimen with a prominent apical ocelloid. The arrow indicates a filament that emerges from the episome, tentatively the longitudinal flagellum. Geographic coordinates of sources of these specimens (latitude, longitude): **8, 21** (31°52'S, 91°24'W); **9, 20** (30°02'S, 98°23'W); **10, 11** (33°45'N, 138°E); **12** (32°42'S, 84°04'W); **13** (30°30'N, 138°E); **14–19** (33°N, 138°E); **22** (20°27'S, 122°53'W). Scale bars = 20 µm.



Fauré-Fremiet 1914; Greuet 1973), Spanish Mediterranean coasts (Delgado 1990; Margalef 1995), Californian (Kofoid and Swezy 1921) and southern Japanese coasts (Takayama 1998), and the offshore NW African upwelling (Margalef 1975; Elbrächter 1979). The present study reports *Erythrospidinium* in all the regions of the open Pacific investigated from 34°N to 33°S, except for the cold waters of the subarctic Oyashio Current (Figs 2–6). To the best of my knowledge, this study is the first to report the genus *Erythrospidinium* in the southern hemisphere. Although *Erythrospidinium* does not reach high abundances in open waters (max. 15 cells L⁻¹), it is a widespread genus, and its distribution is underestimated through under-reporting.

Greuet (1970, 1973) reported that *Erythrospidinium* was found between May and September from French Mediterranean coasts. In the present study, the number of specimens recorded in the vicinity of the Kuroshio Current was slightly higher in July than in May (Figs. 2,3). However, the temperature does not seem the main factor that favours the occurrence of *Erythrospidinium*. The western Pacific warm pool has the warmest open-ocean temperatures (up to 30°C), and only a few specimens of *Erythrospidinium* were recorded in that region, which extended for over 2000 km (Fig. 5). The highest abundance (15 cells L⁻¹) was recorded in the transition between the warm Kuroshio Current and the highly productive slope waters off south Japan (Fig. 2). In May, the Kuroshio Current was narrower and separated from the Japanese coast by a highly productive cyclonic gyre (Gómez et al. 2005). The Kuroshio Current is enriched with potential prey for *Erythrospidinium* due to mixing with coastal waters during the eastward transit along southern Japan. This may explain why the warm-water heterotrophic dinoflagellate *Erythrospidinium* reached its highest abundance there. Twenty-four specimens were found in a station located at the western limit of the Perú-Chile Current (Fig. 6). This location constitutes a transition region between the productive Perú-Chile Current and the oligotrophic warm waters of the South Pacific Gyre. Open-ocean records of *Erythrospidinium* have previously been limited to the offshore subtropical waters of the NW African upwelling (Margalef 1975; Elbrächter 1979). Mesotrophic conditions in the transition regions between productive and warm waters seem to favour the presence of *Erythrospidinium*.

In the present study most of the stations were sampled between the surface and 200 m depth, in some cases down to 280 m depth. In these open-ocean oligotrophic waters, the deep chlorophyll maximum tends to be located in the 100–150 m depth range (Gómez et al. 2005; Gómez 2007). The highest number of prey of larger size suitable for heterotrophic dinoflagellates might be expected to occur in the deep chlorophyll maximum, usually at the bottom of the euphotic zone

(~1% of the surface irradiance). However, nearly all of the specimens of *Erythrospidinium* were collected in the upper 90 m depth, above the deep chlorophyll maxima. This could be interpreted to indicate that *Erythrospidinium* tended to inhabit in the illuminated layer where its sophisticated light-receptor is more efficient.

The morphology and life of *Erythrospidinium*

Greuet (1973) considered *Erythrospidinium* as a monotypic genus, although he used the name *E. pavillardii* instead of the type species name. Elbrächter (1979) considered *E. pavillardii* as a synonym of *E. agile*. In the present study all records have been ascribed to *E. agile*, in the absence of adequate evidence that there are any other species in this genus.

The cell morphology raises many questions about the life of these dinoflagellates. The ocelloid and piston offer exciting prospects for future research, but the present study contributes little new information on these structures. The ocelloid, which is the main morphological characteristic of the genera *Nematodinium* Kofoid et Swezy, *Proterothropsis* Kofoid et Swezy, *Warnowia*, *Greuetodinium* and *Erythrospidinium*, consists of a lens, a retinoid, and an opaque pigment cup, the entire organelle in *Erythrospidinium* measuring about 24 µm long × 15 µm wide (Greuet 1977, 1987). A specimen was seen in this study with two protuberant ocelloids, but there is no evidence that it was undergoing division. The piston, a unique organelle found in the genera *Greuetodinium* and *Erythrospidium*, is distinguished from the tentacle of other dinoflagellates because of its insertion in the post-cingular part of the ventral furrow (Greuet, 1987). Greuet (1967, 1973, 1987) described the fine structure of the piston and its powerful longitudinal extension and contraction; he concluded that the piston is exclusively used for locomotion. A specimen seen in this study had a piston extended to 20 times the length of the cell body. Further study is needed to determine the true function of this structure, because the described changes in length would be unlikely to produce significant movement of the pelagic cell unless its distal end is anchored to a larger structure. This suggests that it could be an extremely useful structure for food capture, or perhaps defence against a predator. Specimens with two pistons were found in this study, but again the significance of this is unknown.

Erythrospidinium has no chloroplasts, but it has a cytostome in the cingulum, and so is presumed to be a phagotroph. Greuet (1973) did not observe food vacuoles, although Takayama (1998) showed a food vacuole in a schematic line drawing. Several dinoflagellates have very specialised feeding mechanisms (e.g. Jacobson and Anderson 1992; Spero 1982), that may be compared with the method of feeding that Greuet (1970,

1987) suggested for *Erythrospidinium*, but none of the incidental observations in this study added new information about nutrition.

Monotypic genera and organelle complexity

The dinoflagellates are considered as “a remarkable evolutionary experiment” (Hackett et al. 2004) due to the tendency to transfer the genes of the ingested prey into its huge genome. This could explain the high morphological and structural diversity of the dinoflagellates, which have organelles from many other protist groups that are controlled by the dinoflagellate genome (Hackett et al. 2004). The high degree of ultrastructural development of the warnowiaceans might be expected to provide a high ecological success. However, the warnowiaceans never reach high abundances and speciation. According to Greuet (1973) all the genera of warnowiaceans are probably monotypic. Other groups of dinoflagellates, such as the leptodiscaceans whose morphology differs strongly from that of the typical Peridiniales, also tend to be monotypic genera (Cachon and Cachon, 1969; Gómez and Furuya 2005). The best known of the ‘aberrant’ dinoflagellates is *Noctiluca scintillans* (Macartney) Kofoid that is demonstrated to be a single species with a cosmopolitan distribution. It can be speculated that these dinoflagellates with unusual morphologies and organelles correspond to ‘evolutionary experiments’ that do not reach high competitiveness in the pelagic ecosystem and display lower speciation compared to other groups of dinoflagellates.

The unique characteristics of *Erythrospidinium* received much attention from earlier protozoologists. *Erythrospidinium* has rarely been reported in the literature during the last three decades, mainly due to the reduction of taxonomical studies carried out in warm open oceans. Nothing is known about the evolutionary origin of the exceptional organelles of *Erythrospidinium*. Molecular phylogeny techniques have been successfully applied to easily accessible species, and interaction between classical taxonomists and molecular biologists is necessary to advance understanding of protist phylogeny and evolution through studies on unusual protists such as *Erythrospidinium*.

Acknowledgements

Studies from NW and Equatorial Pacific Ocean were supported by a Grant-in-aid for Creative Basic Research (12NP0201, DOBIS) from MEXT, Japan, and in the SE Pacific Ocean within the context of the project BIOSOPE of the LEFE-CYBER. I was supported by a fellowship of the European Commission (ICB2-CT-2001-80002) held at the University of Tokyo with

Prof. K. Furuya as host. I am supported by a post-doctoral grant of the Ministerio Español de Educación y Ciencia #2007-0213. I thank M. Sleight for his suggestions for improving this manuscript.

References

- Cachon, J., Cachon, M., 1969. Contribution à l'étude des Noctilucidae Saville-Kent. Évolution, morphologique, cytologie, systématique. II. Les Leptodiscinae Cachon J. et M. Protistologica 5, 11–33.
- Delgado, M., 1990. Phytoplankton distribution along the Spanish coast of the Alborán Sea. Sci. Mar. 54, 169–178.
- Elbrächter, M., 1979. On the taxonomy of unarmored dinophytes (Dinophyta) from the Northwest African upwelling region. ‘Meteor’ Forschungs. Reihe D 30, 1–22.
- Fauré-Fremiet, E., 1914. *Erythrospis agilis* (R. Hertwig). Arch. Protist. 35, 24–46.
- Gehring, W.J., 2005. New perspective on eye development and the evolution of eyes and photoreceptors. J. Heredity 96, 171–184.
- Gómez, F., 2007. On the consortium of the tintinnid *Eutintinnus* and the diatom *Chaetoceros* in the Pacific Ocean. Mar. Biol. 151, 1899–1906.
- Gómez, F., Furuya, K., 2005. Leptodiscaceans (Noctilucales, Dinophyceae) from the Pacific Ocean: first records of *Petalodinium* and *Leptodiscus* beyond the Mediterranean Sea. Eur. J. Protistol. 41, 231–239.
- Gómez, F., Furuya, K., 2007. *Kofoidinium*, *Spatulodinium* and other kofoidiniaceans (Noctilucales, Dinophyceae) in the Pacific Ocean. Eur. J. Protistol. 43, 115–124.
- 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.
- Greuet, C., 1967. Organisation ultrastructurale du tentacule d'*Erythrospis pavillardi* Kofoid et Swezy, Péridinien Warnowiidae Lindemann. Protistologica 3, 335–345.
- Greuet, C., 1968. *Leucopsis cylindrica* nov. gen. nov. sp., Péridiniens Warnowiidae Lindemann. Considérations phylogénétiques sur les Warnowiidae. Protistologica 4, 419–422.
- Greuet, C., 1970. Étude morphologique et ultrastructure du trophonte d'*Erythrospis pavillardi* Kofoid et Swezy. Protistologica 5, 481–503, (1969).
- Greuet, C., 1973. Les critères de détermination chez les Péridiniens *Warnowia* Lindemann. Protistologica 8, 461–469, (1972).
- Greuet, C., 1977. Évolution structurale et ultrastructurale de l'ocelloïde d'*Erythrospidinium pavillardi* Kofoid et Swezy (Péridinien Warnowiidae Lindemann) au cours des divisions binaires et palintomiques. Protistologica 13, 127–143.
- Greuet, C., 1987. Complex organelles. In: Taylor, F.J.R. (Ed.), The Biology of Dinoflagellates. Botanical Monographs 21. Blackwell Science Publishers, Oxford, pp. 119–142.
- Hackett, J.D., Anderson, D.M., Erdner, D.L., Bhattacharya, D., 2004. Dinoflagellates: a remarkable evolutionary experiment. Am. J. Bot. 91, 1523–1534.

- Hertwig, R., 1885. *Erythroopsis agilis*, eine neue Protozoe. Gegenb. Morphol. Jahrb. Z. Anat. Entw. 10, 204–212.
- Jacobson, D.M., Anderson, D.M., 1992. Ultrastructure of the feeding apparatus and myonemal system of the heterotrophic dinoflagellate *Protoperidinium spinulosum*. J. Phycol. 28, 69–82.
- Kofoed, C.A., Swezy, O., 1917. On the orientation of *Erythroopsis*. Univ. Calif. Publ. Zool. 18, 89–101.
- Kofoed, C.A., Swezy, O., 1921. The Free-Living Unarmoured Dinoflagellata. University of California Press, Berkeley.
- Margalef, R., 1975. Composición y distribución del plancton marino en la región de afloramiento del NW de África, en marzo de 1973. Res. Exp. Cient. B/O Cornide 4, 145.
- Margalef, R., 1995. Fitoplancton del NW del Mediterráneo (Mar Catalán) en junio de 1993, y factores que condicionan su producción y distribución. Mem. Real Acad. Ciencias y Artes de Barcelona 927 (LV1), 1–56.
- Pavillard, J., 1905. Recherches sur la flore pélagique (phytoplankton) de l'étang de Thau. Mem. Univ. Montpellier (série mixte) 2, 1–116.
- Schütt, F., 1895. Peridineen der Plankton-Expedition. Ergebn. Plankton-Expedition der Humboldt-Stiftung 4 (M), 1–170.
- Silva, P.C., 1960. Remarks on algal nomenclature, III. Taxon 9, 18–25.
- Sournia, A., 1986. Atlas du Phytoplancton Marin. Vol. I: Introduction, Cyanophycées, Dictyochophycées, Dinophycées et Raphidophycées. Editions CNRS, Paris.
- Spero, H.J., 1982. Phagotrophy in *Gymnodinium fungiforme* (Pyrrhophyta): the peduncle as an organelle of ingestion. J. Phycol. 18, 356–360.
- Takayama, H., 1998. Morphological and taxonomical studies of the free-living unarmored dinoflagellates occurring in the Seto Inland Sea and adjacent waters. Ph.D. The University of Tokyo.