

Morphology of *Brachidinium capitatum* F.J.R. Taylor (Brachidiniales, Dinophyceae) collected from the western Pacific Ocean

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Abstract – This is a first report of the genus *Brachidinium* F.J.R. Taylor from the Pacific Ocean. Of the 17 specimens of *B. capitatum* reported here, 12 were collected from the vicinity of the Kuroshio in May (2 specimens) and July (10 specimens), 3 from the western equatorial Pacific Ocean, one from the Sulu Sea, and one from Tanabe Bay, Japan. The last-mentioned specimen was observed live. For the first time, the flagella and the sulcus of a member of the order Brachidiniales A.R. Loeblich III *ex* Sournia are depicted in photomicrographs. The ventral view corresponds to that seen when the position of the nucleus is in the left side of the cell. In several specimens (confirmed by DAPI-staining) showed a secondary nucleus located in the opposite side of the dinokaryon nucleus. In the live specimen, the sulcus was visible and the lateral extensions were observed to be moveable.

***Brachidinium* / *Brachydidinium* / binucleate dinoflagellate / Pacific Ocean / phytoplankton / taxonomy**

Résumé – Morphologie de *Brachidinium capitatum* F.J.R. Taylor (Brachidiniales, Dinophyceae) récolté à l'ouest de l'Océan Pacifique. C'est la première signalisation du genre *Brachidinium* F.J.R. Taylor dans l'Océan Pacifique. Parmi les 17 spécimens de *B. capitatum* rapportés ici, 12 ont été trouvés à proximité du Kuroshio en mai (2 spécimens) et juillet (10 spécimens), 3 dans l'Océan Pacifique équatorial occidental et enfin, un seul spécimen dans la mer de Sulu ainsi que dans la Baie de Tanabe, Japon. Le dernier spécimen a été observé vivant. Pour la première fois, les flagelles et le sulcus d'un membre de l'ordre des Brachidiniales A.R. Loeblich III *ex* Sournia sont illustrés par des photomicrographies. La vue ventrale correspond à ce que l'on voit quand le noyau est du côté gauche de la cellule. Dans plusieurs spécimens, l'utilisation de la coloration au DAPI a montré un noyau secondaire situé du le côté opposé au noyau dinokaryon. L'observation du spécimen vivant a montré nettement le sulcus ainsi que la motilité des prolongements latéraux.

***Brachidinium* / *Brachydidinium* / dinoflagellé binucléé / Océan Pacifique / phytoplankton / taxonomie**

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INTRODUCTION

Brachidinium F.J.R. Taylor is a genus of photosynthetic planktonic marine unarmored dinoflagellates [usually misspelled as *Brachydidinium*, see Gómez (2003a)]. *Brachidinium* and *Asterodinium* Sournia constitute the family Brachidiniaceae, placed in 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). According to Steidinger & Tangen (1997, p. 468) *Brachidinium* has flattened cells with four elongate extensions radiating from the hyposoma and an apical process on the episoma. The sulcus has not been observed, but an incomplete cingulum and chloroplasts are present. A large, ovoid nucleus occupies most of the cell body.

The type species *Brachidinium capitatum* F.J.R. Taylor (Taylor, 1963) and one other species, *Brachidinium catenatum* F.J.R. Taylor, have been described from the southwest Indian Ocean (Taylor, 1967; see Figs 2-4). The author mentioned that the latter species might be a small neritic or summer form of *B. capitatum* (Taylor, 1967) (Fig. 4). Sournia (1972) also reported *B. capitatum* (see Figs 5-6) and described two new taxa, *Brachidinium taylorii* Sournia (see Fig. 7) and *Brachidinium brevipes* Sournia (see Fig. 8), also from the southwest Indian Ocean. According to Sournia (1972, p. 153) *B. taylorii* shows a robust aspect with thicker arms than the type species and a shorter apical protuberance. The surface of the cell is covered with fine peaks “fines côtes ou crêtes”. *Brachidinium brevipes* shows shorter arms, a very reduced central body and is also covered with fine peaks (Sournia, 1972, p. 153-4).

Subsequently, *B. capitatum* and *Brachidinium* sp. were reported from the southern waters of the Indian Ocean and the Arabian Sea, respectively (Sournia *et al.*, 1979; Tarran *et al.*, 1999). The type species was also reported from the northeast Atlantic Ocean (Margalef, 1973; Ojeda, 2000) and the Mediterranean Sea (Léger, 1971, 1972; Abboud-Abi Saab, 1985; Viličić, 1998). In the northwest Mediterranean Sea, Estrada & Salat (1989) reported *Brachidinium* as a component of the deep phytoplankton assemblages and Palau *et al.* (1991) reported *Brachidinium* sp. from a cave. *Brachidinium taylorii* Sournia was reported from the southeast Atlantic Ocean (Kruger, 1979) and the Mediterranean Sea (Margalef, 1995). The latter author also listed *Brachidinium* “transversum” but with no illustrations or additional information (Margalef, 1995).

The morphology of the species of *Bachidinium* is poorly known due to a lack of records, detailed illustrations and information on the ultrastructure (i.e., flagellum/flagella; sulcus; nuclei; etc). Taylor (1963) did not observe the flagellum/flagella or cingulum and placed *Brachidinium* in the order Dinococcales Pascher. He proposed a tentative orientation for the genus (Figs 2-3). Taylor (1980, p. 67) showed a species of *Brachidinium*, which has a poorly defined sulcus, a “longitudinal flagellum” and the dinokaryon nucleus in the left side of the cell (Fig. 9). Fensome *et al.* (1993, p. 3) included a line drawing of *B. capitatum* with two flagella (Fig. 10). They did not mention flagella or sulcus in the family Brachidiniaceae (p. 56), but illustrated dorsal and ventral views of *B. capitatum*, in which the ventral view corresponds to the position of the dinokaryotic nucleus in the right side of the cell (Figs 5-6). Fensome *et al.* (1993, p. 56) reported that the orientation was based on Sournia (1972, 1986). However, Sournia (1972, 1986) included no illustration of flagellum/flagella or sulcus of *Brachidinium*. Sournia (1972) introduced a terminology describing the orientation of the order Brachidiniales and considered that the dinokaryotic nucleus is displaced to one side and

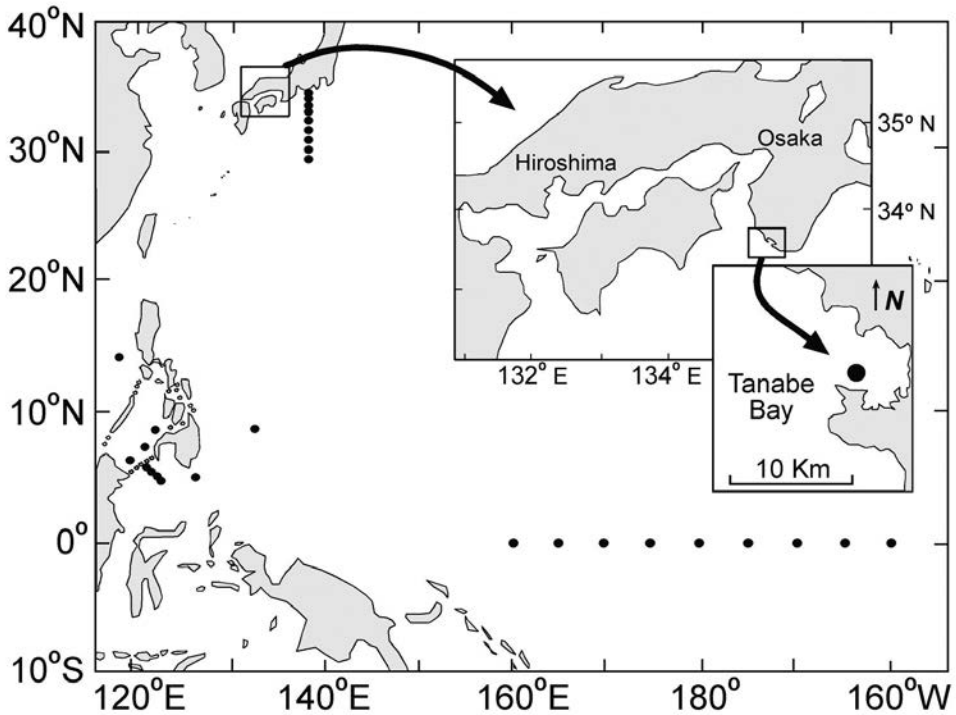
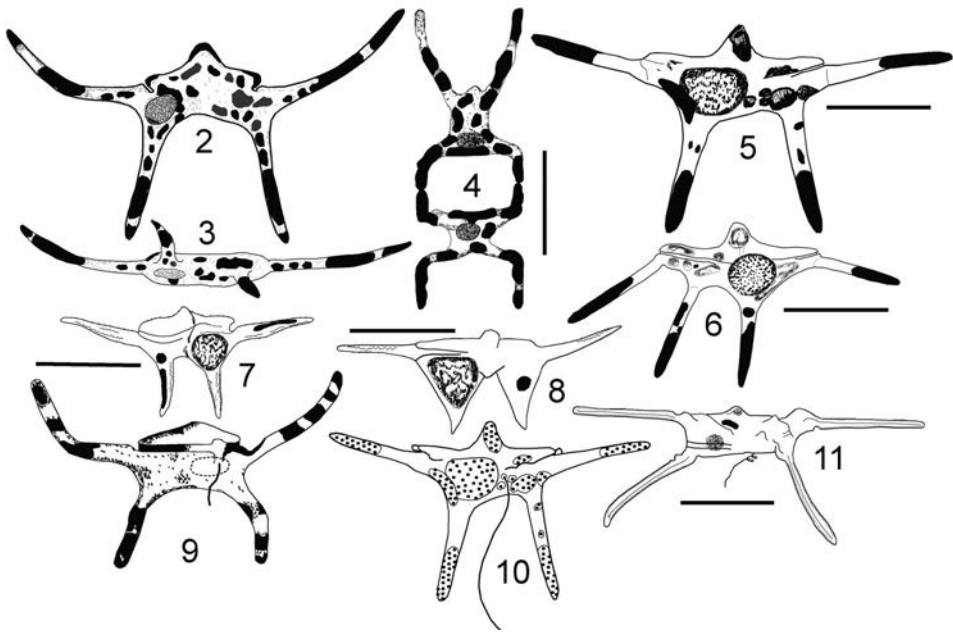


Fig. 1. Location of the sampling stations in the western Pacific Ocean. The inset shows the Tanabe Bay where a live specimen was collected.

the extensions or arms closer to the nucleus were the “left” extensions. Uncertainties remained, however, and Sournia (1986, p. 49) doubted whether the cells were dorso-ventrally or laterally flattened.

Sournia (1986, p. 50), based on the records by Léger (1971), reported that *Brachidinium* possesses at least one flagellum, but that the point of insertion remained unknown. Léger (1971) collected 30 specimens named as *B. capitatum*. However his figure, reproduced here (Fig. 11) does not seem to represent the type species. His specimen drawing has two extensions radiating from the hyposoma, and two extensions and a central process from the episoma. It is intermediate between *Asterodinium* and *Brachidinium*. Sournia (1972) commented on the possibility of an ‘optical illusion’ in the position of the cingulum. His specimen has the dinokaryotic nucleus in the left side and a hypothetical ‘sulcal’ flagellum arising from the rear and the nucleus in the right side of the cell (Fig. 11). Léger (1971) reported that he was unable to locate the insertion of the flagellum.

This study reports for the first time the flagella and the sulcus in *Brachidinium*, including photomicrographs on the moveable extensions of a live specimen, and the occurrence of a secondary nucleus (confirmed by DAPI staining).



Figs 2-11. Line drawings of several species of *Brachidinium* reported in the literature. **2.** *B. capitatum* adapted from Taylor (1963). **3.** Ventral view of *B. capitatum* according to Taylor (1963). **4.** *Brachidinium catenatum* F.J.R. Taylor adapted from Taylor (1967). **5-6.** *B. capitatum* adapted from Sournia (1972). These figures were also reproduced by Fensome *et al.* (1993), who proposed that they represented ventral and dorsal views, respectively. **7.** *Brachidinium taylorii* Sournia adapted from Sournia (1972). **8.** *Brachidinium brevipes* Sournia adapted from Sournia (1972). **9.** A ventral view of a member of the genus *Brachidinium* showing the longitudinal flagellum adapted from Taylor (1980, p. 67). **10.** A ventral view of *B. capitatum* with two flagella adapted from Fensome *et al.* (1993, p. 3) apparently based on Sournia (1972, 1986). **11.** “*Brachidinium capitatum*” adapted from Léger (1971). Scale bars 20 μ m.

MATERIAL AND METHODS

Samples were collected during several cruises in the western Pacific Ocean: 1) Two cruises on board R/V *Soyo Maru* (13-20 May and 3-10 July 2002) along the meridian 138° in the vicinity of the Kuroshio Current. Nine stations were sampled from 30° 30' N to 34° 15' N in May, and 10 stations were sampled from 30° 0' N to 34° 20' N during the July cruise. At each station, 15 depths from 5-200 m were sampled with Niskin bottles; 2) on board R/V *Hakuho Maru* (7 November-18 December 2002) in the Celebes, Sulu and South China Seas. Samples were collected using Niskin bottles at 10 stations at six depths from 0 to 150 m depth; 3) aboard R/V *Mirai* (15-28 January 2003) along the equator from 160°E to 160°W (Fig. 1). Samples were collected with Niskin bottles from 9 stations at 14 depths between 0 to 200 m depth. During all the cruises, samples were preserved with acidified Lugol's solution (Hasle and Syvertsen 1997, p. 334) and stored at 5° C. Samples were pre-concentrated by settling in glass cylinders, and concentrates settled in standard sedimentation chambers. Concentrates equivalent to 400 mL were observed with a Nikon inverted microscope equipped with a Nikon digital camera.

Several of the Lugol fixed specimens were isolated with a capillary from the chambers, transferred to a glass slide, and observed with an Olympus microscope equipped with Nomarski Differential Interference Contrast (D.I.C.) system. High magnification microphotographs ($\times 600$; $\times 1000$) were obtained with an Olympus digital camera. Several specimens were stained by adding DAPI (4,6-diamidino-2-phenylindole). DAPI specifically binds to double stranded DNA, and when excited with U.V. light the DAPI-DNA complex fluoresces a bright blue (Porter & Feig, 1980). Epifluorescence microscopy was done with Olympus and Zeiss microscopes equipped with UV excitation facility.

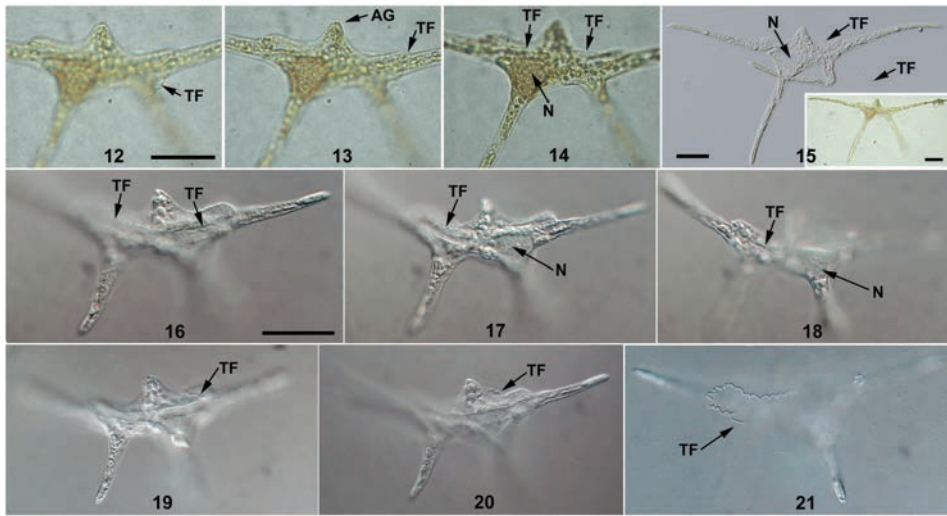
In addition, one specimen collected from the coastal waters of Japan was observed live. Seawater samples were monthly collected from a station in Tanabe Bay (see inset in the Fig. 1) at 0, 5, 10, 15 m depths and one metre above the bottom (19.5 m depth). Samples (1 l) were filtered through an 8 μm pore size Millipore cellulose acetate filter at low pressure (< 100 mmHg) to a final volume of 50 ml. This concentrate was left to settle in a composite chamber. From the bottom of the chamber, 1 ml was examined on a Sedgewick-Rafter counting chamber. The specimen was isolated with a capillary, transferred to a glass slide and cover with a glass slide. The specimen was observed and photographed with an Olympus light microscope and Olympus camera by using bright field.

RESULTS AND DISCUSSION

A total of 17 specimens of the genus *Brachidinium* were observed in the upper 90 m depth during the four cruises in the western Pacific Ocean (Fig. 1). Ten specimens were observed in the vicinity of the Kuroshio in July and only two in May. The maximum occurrence was in July ($30^{\circ} 0' \text{ N}$, 138° E at 60 m depth) with 3 specimens per sample (7.5 cells l^{-1}) (Tab. 1).

Table 1. Number of specimens recorded, date, stations, depth (m) in meters, geographic coordinates (latitude, longitude) and figures of the records of *Brachidinium* in the western Pacific Ocean.

#	Date	Sta.	(m)	Lat N	Long	Figure
1	24/1/1995	20	- 19.5	33° 42'	135° 21' E	Figs 27-28
1	10/5/2002	C3	- 5	33° 30'	138° E	
1	13/5/2002	C13	- 5	30° 30'	138° E	
2	7/7/2002	C8	- 20	33° 30'	138° E	Figs 16-21
1	7/7/2002	C7	- 50	33°	138° E	
1	7/7/2002	C6	- 5	32° 30'	138° E	
1	6/7/2002	C5	- 30	32°	138° E	
1	6/7/2002	C2	- 60	31° 30'	138° E	Fig. 26
1	4/7/2002	B1	- 10	30°	138° E	Figs 22-25
3	4/7/2002	B1	- 60	30°	138° E	
1	3/12/2002	10	- 30	8° 50'	121° 48' E	
1	15/1/2003	6	- 1	0°	160° E	
1	17/1/2003	7	- 90	0°	165° E	Figs 12-15
1	25/1/2003	13	- 80	0°	165° W	



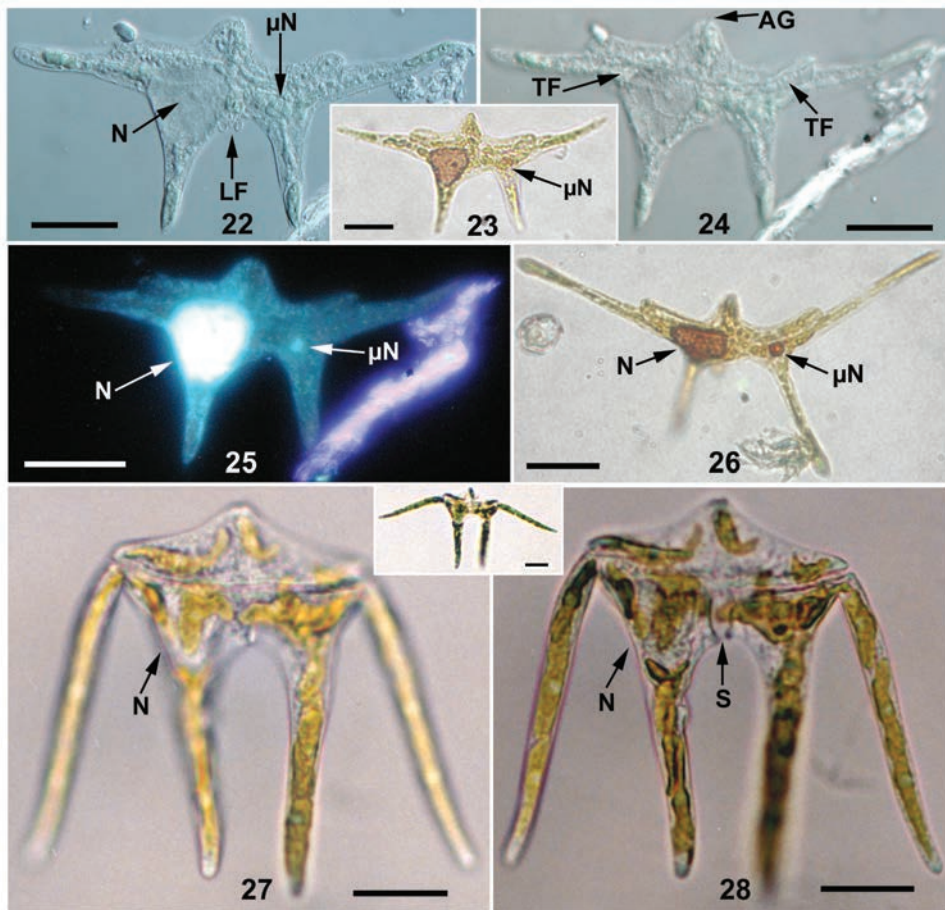
Figs 12-21. Photomicrographs of *Brachidinium* showing the transverse flagellum (TF). **12-15.** Dorsal view of a specimen under inverted microscopy (Figs 12-14), and direct microscopy (Fig. 15). See the end of the TF displaced from the cingulum and free moving in the rear focus of the cell (Fig. 12). See the cingulum groove where the TF ran (Fig. 13). Please note that TF along the cingulum does not arise from the frontal focus (Fig. 14). The specimen was transferred to a glass slide and observed with D.I.C. optic when TF appeared partially separated from the cingulum (Fig. 15). **16-21.** D.I.C. photomicrographs of the ventral view of other specimen. Figs 16-17 the TF ran all along the cingulum in the rear focus of the cell. Fig. 18, the end of the TF was observed in the central part of the cingulum in the frontal focus of the cell. Figs 19-21. The specimen was shaken until the TF was partially displaced from the cingulum in the rear focus (Figs 19-20) and the frontal focus (Fig. 21). AG= Apical groove; N= dinokaryon nucleus; TF = transversal flagellum. Scale bars 20 μ m.

All the records are considered to be of the type species, *B. capitatum*, which, although from the same sample, showed some variation in size as well as the relative angle of the extensions with respect to the cell body. The maximum length of the cells ranged from 50 to 140 μ m and the width of the cell at the cingulum was 25-55 μ m.

Cell orientation

Brachidinium is a flattened athecate dinoflagellate. The presence of long appendices, resulting in different inclinations of the cell, plus the cell transparency, make it difficult to observe ultrastructural details (such as the insertion of the flagella) by light microscopy.

The transverse flagellum (TF hereafter) was observed in several specimens by using D.I.C. optics. In one specimen, the TF was also observed under inverted microscopy when it was separated from the cingulum (Figs 12-14). The nucleus of this specimen was located in the right side of the cell. The TF was free moving, displaced from the cingulum groove in the rear (reverse) focus of the cell (Fig. 12) and turned to the front of the cell in the left extremity of the cingulum groove (Fig. 13). In the front of the cell the TF ran all along the cingulum and no insertion was observed (Fig. 14). Subsequently, the insertion of the flagellum was



Figs 22-26. Dorsal view of a specimen. **22-24.** D.I.C. photomicrographs. Fig. 22. See a part of a flagellum, possibly the longitudinal flagellum. Fig. 23. Inverted microscopy photomicrograph of the specimen. The arrow indicates the micronucleus (μ N) or secondary nucleus. Fig. 24. Frontal focus showing the TF along the cingulum. **25.** Epifluorescence photomicrograph of the same specimen stained with DAPI and illuminated with U.V. light. The arrow indicates the secondary nucleus. **26.** Inverted microscopy photomicrograph of other specimen in dorsal view. The arrow shows the secondary nucleus. Figs 27-28. Photomicrographs of the dorsal view of a specimen observed live. **27.** Frontal focus. **28.** Rear focus. An inset between the figures 27-28 shows a low magnification photomicrograph taken prior to the movement of the lateral extensions of the specimen; AG = Apical groove; N = dinokaryon nucleus; μ N = secondary nucleus; TF = transversal flagellum; LF = longitudinal flagellum; S = sulcus. Scale bars 20 μ m.

located in the rear focus of the cell. Thus, the aspect of the specimen in figures 12-14 corresponds to the dorsal view (nucleus in the right side of the cell). This specimen was later successfully transferred to a glass slide and observed under a microscope with D.I.C. The specimen appeared in the same view, also with the nucleus in the right side of the cell, but the TF was now displaced from the groove and a higher proportion of the TF was seen moving freely (Fig. 15).

D.I.C. photomicrographs of a second specimen with the nucleus in the left side of the cell were taken (Figs 16-21). Figures 16-17 show a similar focus (both right antapical and the left lateral antapical extension in focus), with the TF located along the groove. The TF did not arise from the rear focus of the cell. Figure 18 shows, in a different focal plane, the left antapical and the right lateral antapical extensions, with the TF visible in the right side of the cell along the groove. The end of the TF was located in the central part of the cell (see also fig. 21). We were unable to focus on the area of the TF origin. The flagellum did not arise from the back of the cell (Figs 16-17). This position, with the nucleus in the left side of the cell, is the ventral view. After these observations the specimen was shaken until the TF was partially separated from the cingulum. The TF turned around the left side of the cingulum (Figs 19-20) (rear of the cell, as in Fig. 16). At a different focal plane most of the TF was visible (Fig. 21). The aspect of this specimen, with the nucleus in the left side, corresponds to the ventral view (Figs 16-21).

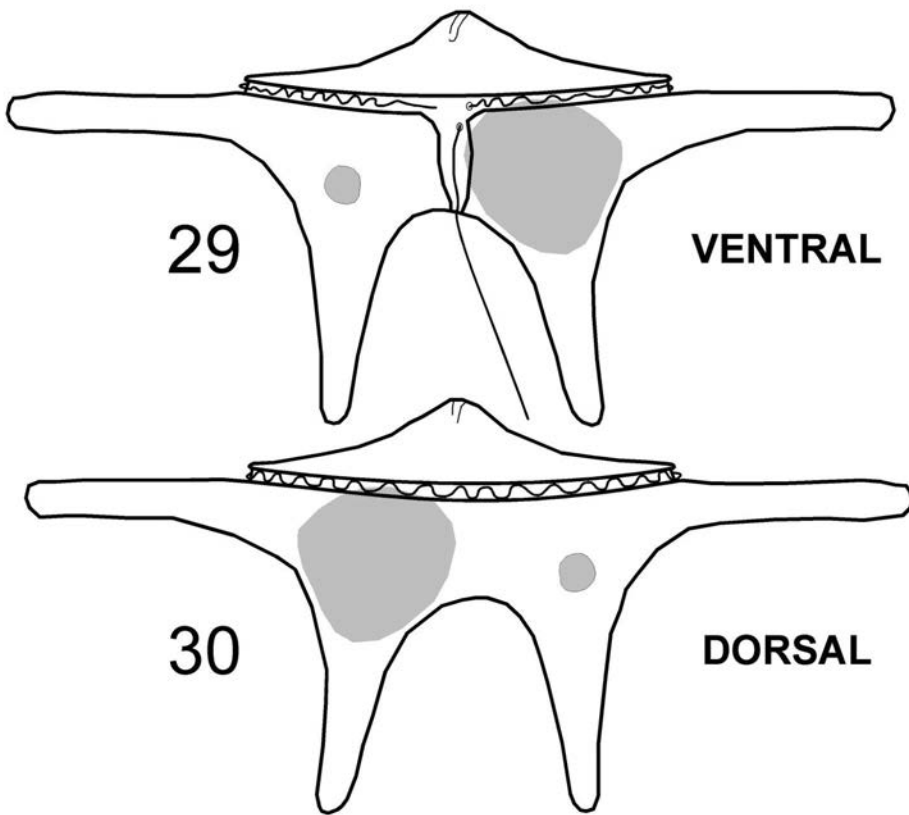
A third specimen with the nucleus in the right side was also observed with D.I.C. optics (Figs 22, 24) and inverted microscopy (Fig. 23). A part of a flagellum that could correspond to the longitudinal flagellum was observed between the two antapical extensions (Fig. 22). The TF ran along the cingulum in a frontal focus (Fig. 24). This position, with the nucleus in the right side, corresponds to the dorsal view.

An alternative method to elucidate the cell orientation is based on the location of the sulcus (ventral side). The sulcus was not visible in the Lugol-fixed specimens, but was visible in the live specimen observed with a direct microscope. The nucleus of this specimen was located in the right side of the cell (Figs 27-28). Figure 27 focusses on only one of the four extensions, corresponding to the front of the specimen. Figure 28, showing three extensions in focus (closer to the bottom glass slide), corresponds to the rear of the cell, with the sulcus being visible. Figures 27-28, with the nucleus in the right side of the cell, correspond to the dorsal view.

In these four specimens, based on the transverse flagellum or the sulcus, the ventral view corresponds to the nucleus being on the left side of the cell (Figs 29-30). The occurrence of a sulcus (Fig. 28) provides evidence of the existence of the longitudinal flagellum in the genus *Brachidinium* (partially observed in Fig. 22). This orientation is contrary to Fensome *et al.* (1993, p. 3, 56). Taylor (1980, p. 67) reported an illustration of *Brachidinium* with a weakly defined sulcus in the left side of the cell (Fig. 9). From our observations, however, the sulcus is centrally located in *Brachidinium* (Fig. 28).

Binucleate specimens

The nucleus of *Brachidinium* was relatively large, ovoid, and occupied a significant proportion of the body cell. It was clearly visible in Lugol-fixed specimens and appears darker than the rest of the cell surface (e.g., Figs 14, 23, 26), whereas it was less visible in the cell observed live (Figs 27-28). The dinokaryon nucleus was confirmed by DAPI-staining (Fig. 25). In addition, several of the Lugol-fixed specimens showed a secondary small nucleus in side of the cell opposite the dinokaryon nucleus, with both nuclei staining the same dark brown colour (Fig. 26). In a DAPI-stained specimen (Figs 22-24), the micronucleus fluoresced when excited with U.V. light and the dinokaryon nucleus appeared brighter than the micronucleus (Fig. 25). Sournia (1972) did not find chloroplasts in *Brachidinium brevipes*. Sournia (1972) and Léger (1972) reported one circular 'plast' in the opposite side of the nucleus in their line drawings (Fig. 8 and Léger



Figs 29-30. Line drawings of the ventral (Fig. 29) and dorsal (Fig. 30) views in *Brachidinium*.

(1972, p. 29)). This could be interpreted as the first evidence of the occurrence of a secondary nucleus in *Brachidinium*.

The occurrence of binucleate dinoflagellates is very rare. The freshwater dinoflagellate *Kryptoperidinium foliaceum* (Stein) Lindemann presented mononucleate and binucleate strains. *Kryptoperidinium foliaceum* contained a fucoxanthin-containing diatom as a cytoplasmic endo-symbiont (Kempton *et al.*, 2002). The origin of the secondary nucleus in *Brachidinium* was not clarified in the present study.

Live cell and moveable extensions

The extensions in *Brachidinium* are moveable, as reported by Léger (1971), based on observations by Cachon on a live specimen collected from Villefranche-sur-Mer (Ligurian Sea). We include, for the first time, photomicrographs of a live specimen of *Brachidinium*. During our microscopical observations, the specimen moved the lateral antapical extensions from the initial position parallel to the cingulum (see inset between the figure 27 and 28), to a final position with the two lateral extensions aligned with the two central antapical extensions (Figs 27-28). This last appearance was not found in our observation of the Lugol-

fixed specimens. Sournia (1972) has reported different angles of the lateral extensions from fixed specimens (Figs 5-6). The movement occurred when the specimen was observed at a high magnification with high light intensity, and took about 10 seconds.

The changes in the shape of this live specimen of *Brachidinium*, and the common changes of morphology during the life cycle of unarmoured dinoflagellates with elongate extensions (e.g., Konovalova, 2003) cast some doubts on the validity of all species of *Brachidinium* other than the type. The type species of the closely related genus *Asterodinium* is also supposed to show a high morphological variability (Gómez, 2003a). Most records of *Brachidinium* are from the 1970s, and species such as *B. catenatum* (Fig. 4) and *B. brevipes* (Fig. 8) have not been reported after the initial descriptions. The description of *Brachidinium brevipes*, with a rough surface, is based on morphological features that can be considered as intraspecific variables in other dinoflagellates. The morphology of *Brachidinium taylorii* (Fig. 7) is the same as some forms of *B. capitatum*. *Brachidinium catenatum* (Fig. 4) is a doubtful taxon according to Taylor (1967). *Brachidinium capitatum* requires further studies on the morphological variability as well as for unique characteristics such as secondary nuclei and moveable extensions.

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