

## *Amphidinium latum* Lebour (Dinophyceae), a sand-dwelling dinoflagellate feeding on cryptomonads

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An unarmoured dinoflagellate, *Amphidinium latum* Lebour found in marine tidal pools off the South African coast has been studied at the light and transmission electron microscope level. These studies have revealed that the dinoflagellate often possesses what initially appear to be chloroplasts of varying colour but are actually different species of cryptomonad cells that have been ingested by the dinoflagellate. Three types of cryptomonads (Type 1, Type 2 and Type 3) have been found in the dinoflagellate cytoplasm: 1) Type 1 is yellowish-brown in colour and possesses a nucleomorph embedded in pyrenoid matrix which is not traversed by any thylakoid bands, 2) Type 2 is blue-green in colour and possesses a nucleomorph situated external to pyrenoid matrix which is traversed by many thylakoid bands, and 3) Type 3 is bright-green in colour and possesses a nucleomorph external to pyrenoid matrix which is traversed by a single pair of thylakoids. A possible division stage of the chloroplasts has been observed in the cryptomonads within the dinoflagellate, suggesting that they may remain photosynthetically active. It was confirmed that *A. latum* is phagotrophic and feeds on several species of cryptomonads.

*Key Index Words:* *Amphidinium latum*—*cryptomonad*—*dinoflagellate*—*endosymbiosis*—*phagotrophy*—*sand-dwelling*—*ultrastructure*.

In 1925, Lebour described a small species of *Amphidinium*, *A. latum* Lebour which was originally found in a sample from Cullercoats in Europe. In her description, she mentioned that this dinoflagellate was holozoic and that all the specimens possessed green-coloured “food cells”. Her drawing clearly shows two “food cells” located in the hypcone and a pyrenoid-like structure in each food cell. The fact that all the specimens possessed the same kind of food cells seems to suggest that the dinoflagellate specifically feeds on certain species of unicellular algae.

Herdman (1924) found the same species in a sand sample from Port Erin, Isle of Man and she, by referring to Lebour’s manuscript, identified it as *A. latum*. She mentioned that the cell possessed bright green globules and also noticed an orange-coloured body somewhere in the cell. It is possible that these bright green globules are same as the Lebour’s “food cells”.

Recently, Larsen (1985) described a small species of *Amphidinium*, *A. poecilochroum* Larsen from the Danish coast. This rather peculiar dinoflagellate is characterized by possessing 4 to 8 chloroplasts of varying colour, viz. blue-green or yellow-green. Later, Larsen (1988) demonstrated that this dinoflagellate is, in fact, phagotrophic and feeds on small species of cryptophytes. Different species of cryptomonads engulfed by the dinoflagellate were responsible for the variation in “chloroplast” colour. Although the cryptomonad cells were eventually digested, this dinoflagellate is worthy of some attention, because it may represent the earliest stage of chloroplast acquisition via an endosymbiotic process (Larsen 1988).

During the course of our studies on tidal pool and sand-dwelling dinoflagellates along the Natal coast, South Africa, we often encountered a small species of *Amphidinium* whose chloroplasts were variable both in num-

ber and in colour. This unique cytological feature prompted us to undertake an ultrastructural study of this dinoflagellate which we subsequently identified as *A. latum*. In this paper, we demonstrate that *Amphidinium latum* is, as Lebour (1925) stated, holozoic and feeds specifically on cryptomonads.

## Materials and Methods

A few specimens of *Amphidinium latum* were found in a sand sample collected from the large artificial marine swimming pool at Palm Beach, Natal, South Africa (28 Sep. 1985; 24 May 1986; 14 May 1987) and considerable numbers have also been collected from sand collected from a tidal pool at Amanzimtoti, Natal (13 May 1987).

Since the sand sample from Amanzimtoti contained a large number of *A. latum*, we were able to undertake electron microscopical observations. For electron microscopy, *A. latum* cells together with other flagellates were collected by gentle centrifugation. Then they were fixed and embedded as mentioned by Pienaar and Aken (1985). Observations were made using a JEOL 100CX transmission electron microscope.

Individual cells were picked up and placed in sterilized seawater. After two weeks of starvation in seawater, cultured cryptophyte cells (*Chroomonas* sp.) were given to the dinoflagellates. The opportunities of observing phagotrophy in culture were few and we were able to observe ingestion of cryptomonad cell by dinoflagellate only once.

## Observations

### *Light microscopy*

The cell (Figs. 1-4) is broadly sac-shaped in ventral view and dorsiventrally compressed, measuring 16.0-22.0  $\mu\text{m}$  in length and 16.0-22.0  $\mu\text{m}$  in width. The epicone is small and has a moderately curved apex, while the hypocone is large and has a rounded antapex. The posterior part of the hypocone is notched by the distal end of the sulcus. The left side of the hypocone is slightly longer than the

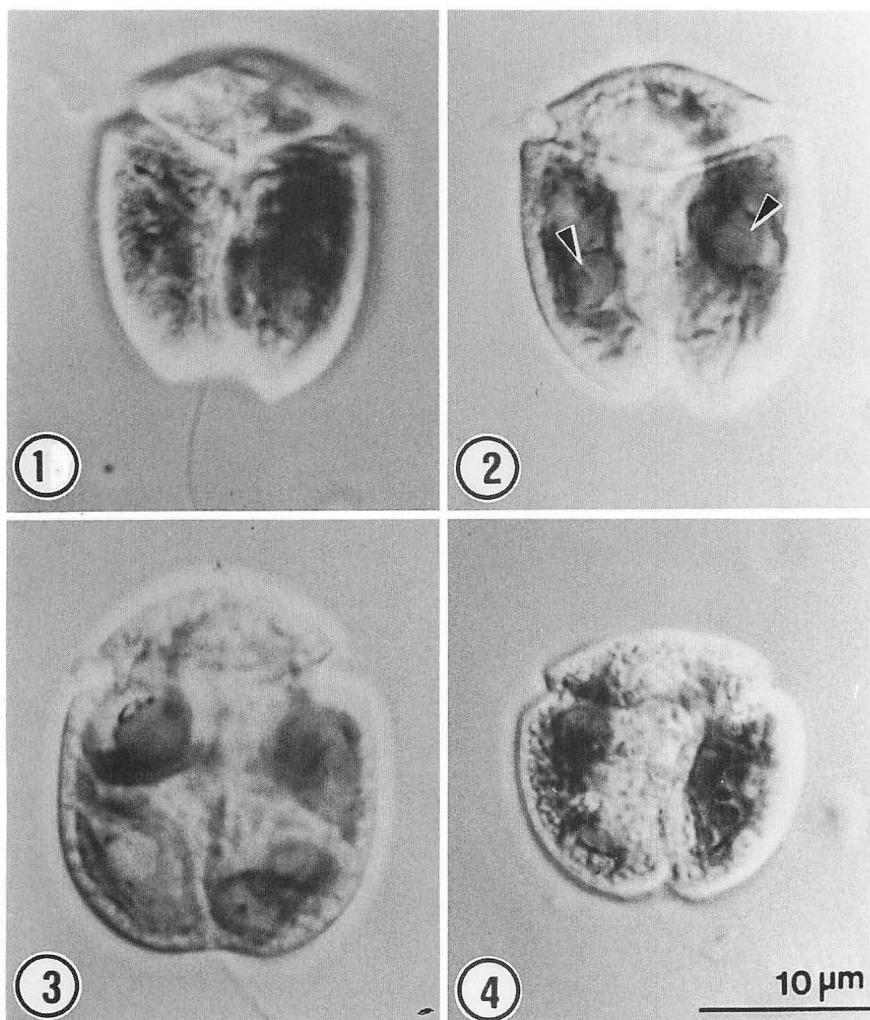
right side. The cingulum is well excavated and slightly left-handed. The sulcus is narrow and extends into the epicone nearly to the cell apex. The sulcus extends to the antapex. Although the cell shape is normally somewhat angular as shown in Figs. 1-3, the cell shape is quite variable and rounded cells (Fig. 4) have also been observed.

The nucleus is ovoid and is located in the centre of the upper portion of the cell. The dinoflagellate contains one to four coloured bodies which appear to be chloroplasts. Ultrastructural observations revealed that these "chloroplasts" are in fact cryptomonad cells which are taken up by the dinoflagellate (see below). Recently collected specimens possessed three differently pigmented cryptomonad cells, viz. yellowish-brown, blue-green and bright green. The different colours are due to the fact that a dinoflagellate can harbor three different types (species) of cryptomonads. Although the dinoflagellate may possess one to four cryptomonads, the majority of cells contain two, one on each side of the nucleus (Fig. 2). In most cases, the ingested cryptomonad cells are located in the hypocone, while in some cases, they are found in the epicone as well as in the hypocone (Fig. 3). Very rarely, a small cell was found to possess no cryptomonad cells.

Although the dinoflagellate survived for two weeks in seawater medium, it did not divide during this period. It started to divide, however, after *Chroomonas* cells were added to the culture medium. All the offsprings of the dinoflagellate possessed cryptomonad cells in their cytoplasm. Although we were able to observe only one case, the way the dinoflagellate captures and engulfs its prey seems to be similar to that reported for *Amphidinium poecilochroum* (Larsen 1988). The cryptomonad cell is captured and drawn into dinoflagellate cell through the sulcal region. The possible involvement of peduncle could not be confirmed.

### *Transmission electron microscopy*

The dinoflagellate cytoplasm contains typical dinoflagellate organelles, including a



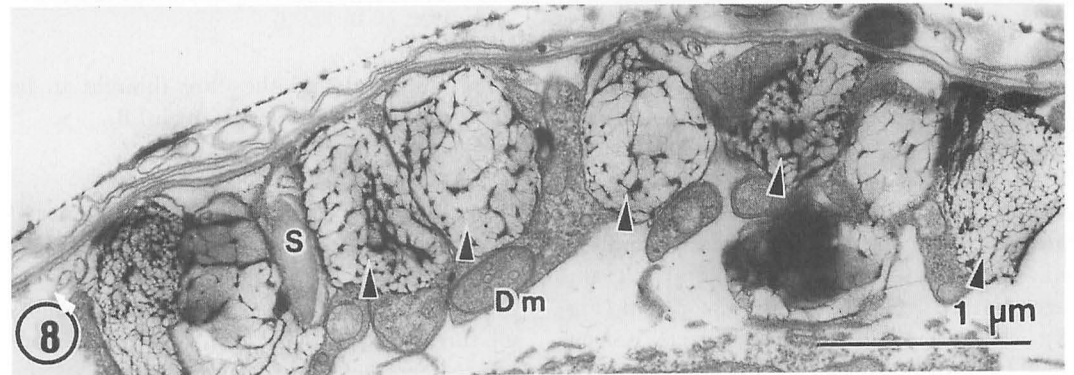
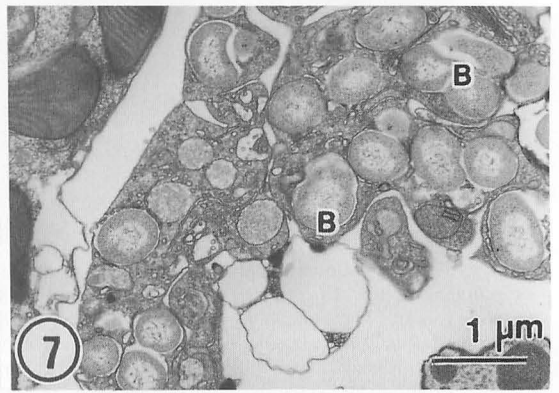
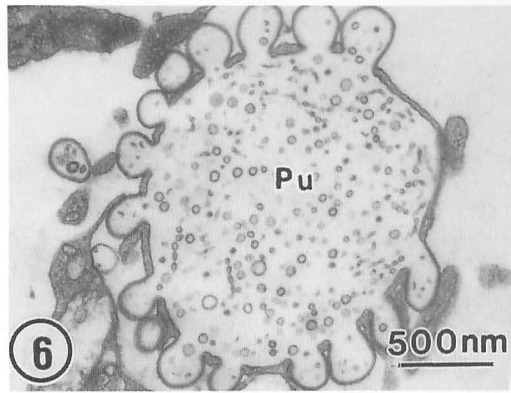
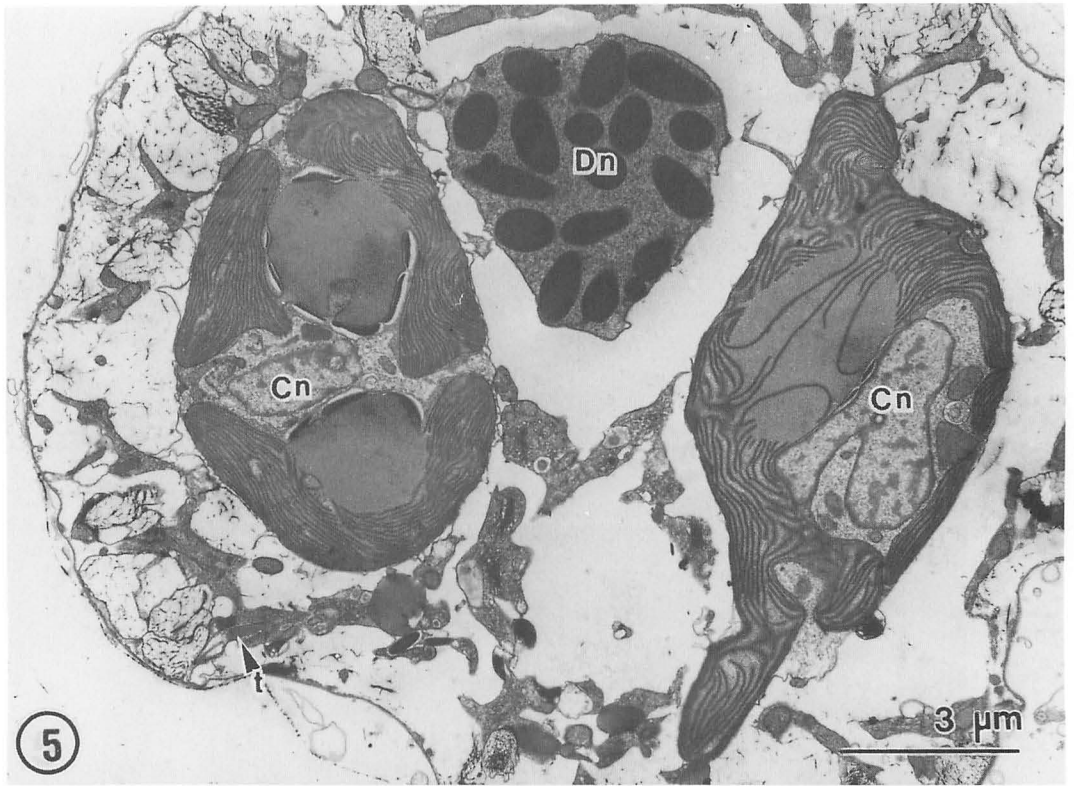
Figs. 1-4. Light micrographs of *Amphidinium latum* Lebour. Figs. 1-2. Through focus of a live cell with two cryptomonad cells. In this case, the left cryptomonad is yellowish-brown in colour, while the right one is blue-green in colour. Fig. 1 shows the slightly left-handed cingulum. Fig. 2. A distinctive pyrenoid can be seen in each cryptomonad cell (arrowheads). In the pyrenoid matrix of the left-hand side cryptomonad, a narrow slit can be seen (left arrowhead). Fig. 3. A slightly larger cell containing four cryptomonad cells—all of the cryptomonad cells are bright green in colour. Note that all these cryptomonads are relatively small compared to those of Fig. 2. Fig. 4. A rounded cell which resembles Lebour's original figure (1925, pl. II, Fig. 3).

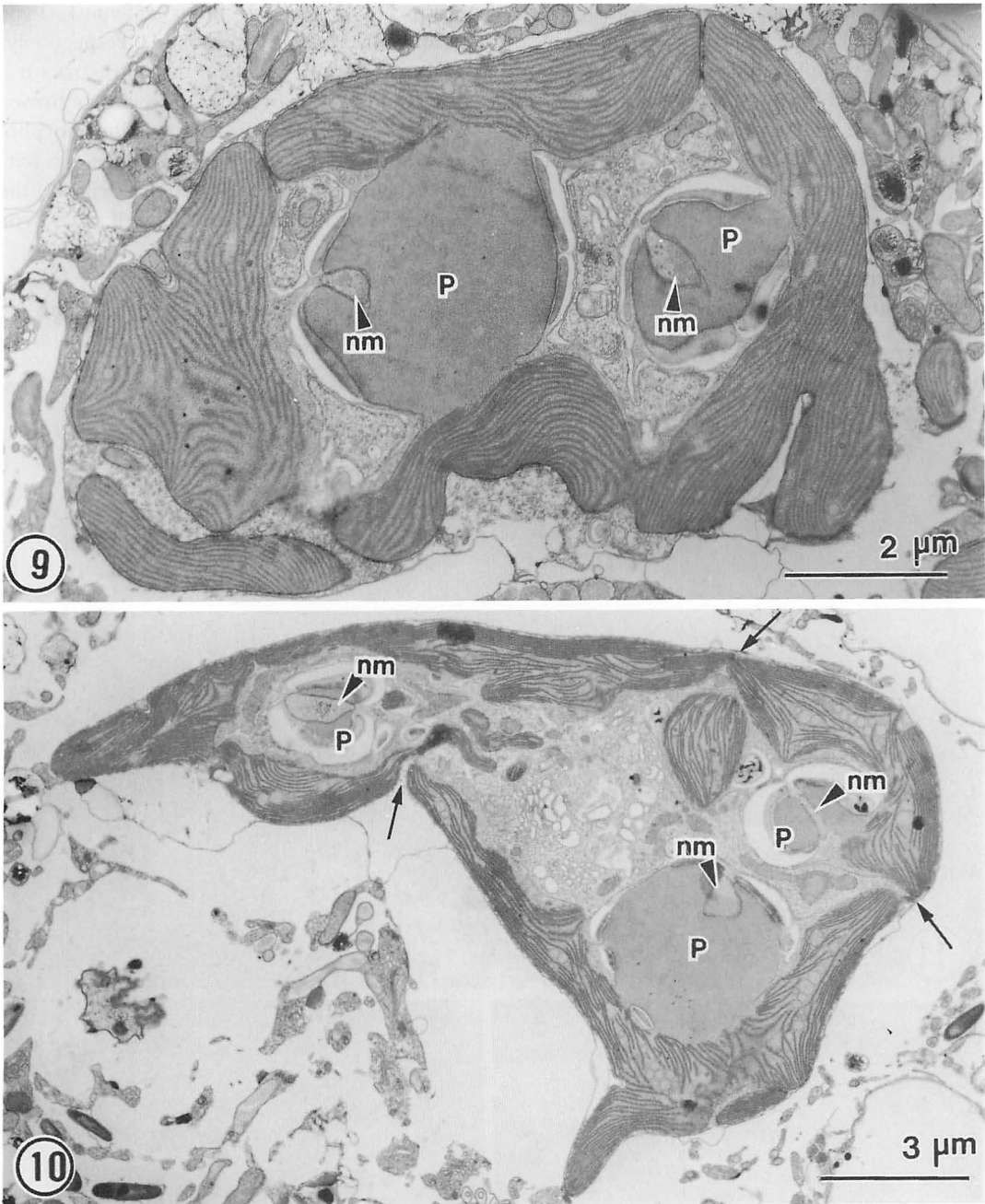
dinokaryotic nucleus (Fig. 5), mitochondria (Fig. 8), dictyosomes, trichocysts (Fig. 5) and a pusule (Fig. 6). The pusule consists of a collecting chamber and many spherical pusular vesicles (Fig. 6). Many bacterial cells which are surrounded by a single unit membrane have been observed (Fig. 7). Starch grains are scattered throughout the cytoplasm (Fig. 8). The peripheral region of the cell is occupied by many vesicles which contain an amor-

phous material and they are thought to be mucilage-producing vesicles (Fig. 8).

#### *The cryptomonad cell*

We were able to distinguish three species of cryptomonads based on their colour and ultrastructural features. Although some modifications in cell structure were evident, all three species ingested by the dinoflagellates share the features characteristic of the





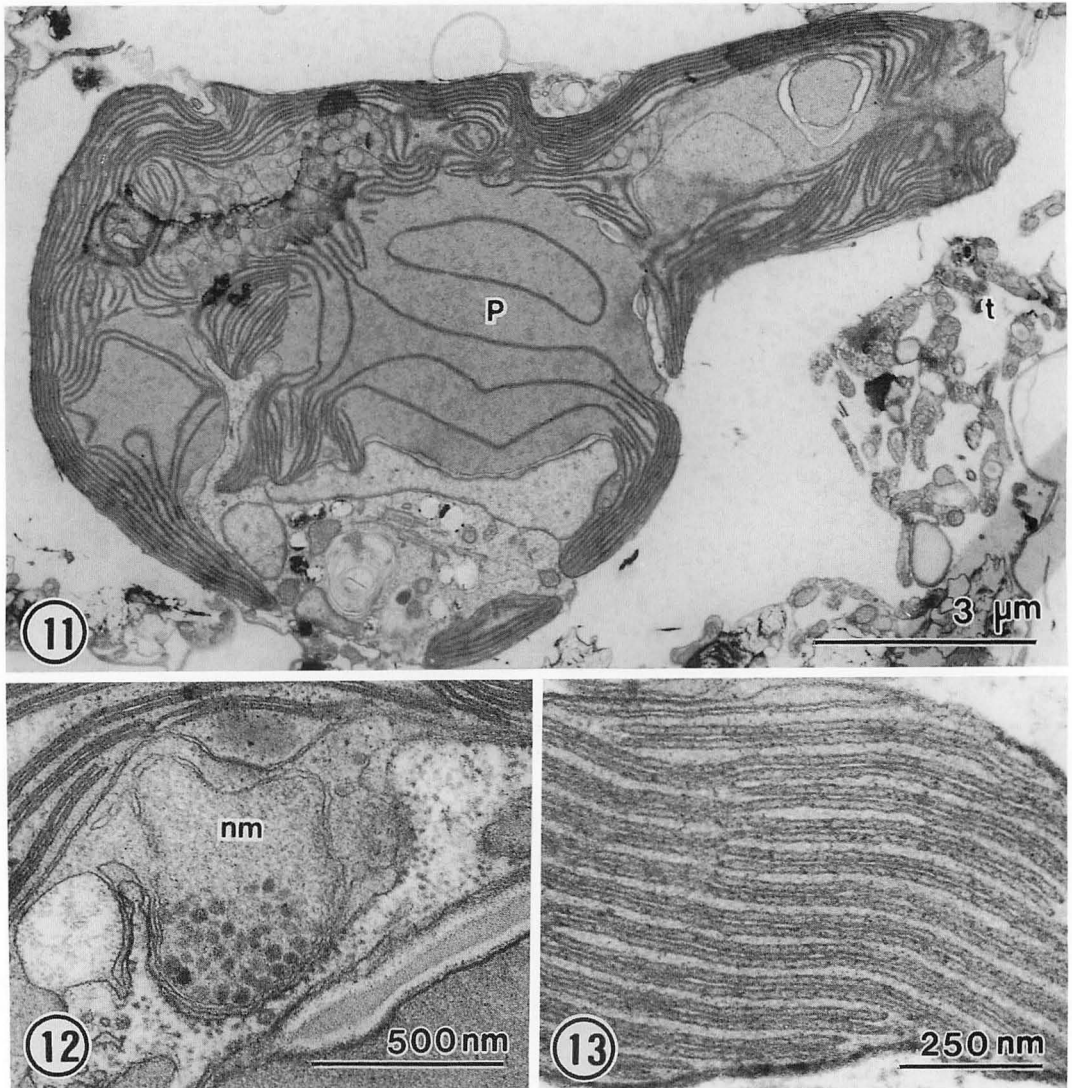
Figs. 9–10. Type 1 cryptomonad cell, showing multiple “pyrenoid (P)-nucleomorph (nm)-complex”. Note that cryptomonad cytoplasm is enclosed by a single membrane. Fig. 10. Multiplication of the chloroplast has taken place and three chloroplasts can be recognized. Each chloroplast possesses a single pyrenoid with an nucleomorph. Disjunctures of chloroplasts are indicated by arrows.

Figs. 5–8. General cell structure of *Amphidinium latum*. Fig. 5. A longitudinal section, showing a dinokaryotic nucleus (Dn) and two cryptomonad cells. (Cn = cryptomonad nucleus; t = trichocyst) Fig. 6. Pusule (Pu). Fig. 7. Bacterial cells (B) surrounded by a single unit membrane system. Fig. 8. Peripheral region of a cell, showing mucilage producing vesicles (arrowheads), starch grain (S) and dinoflagellate mitochondrial profile (Dm).

Cryptophyceae, such as the possession of a nucleomorph (Figs. 9, 11, 15), the presence of a plastidial complex enclosed by a double unit membrane (chloroplast endoplasmic reticulum), and the possession of paired thylakoids whose lumen is filled with amorphous material (Fig. 13). Cryptomonad cytoplasm is enclosed by a single membrane (Fig. 9). Ultrastructurally, the three types are readily distinguished from one another by the structure of the pyrenoid and the position of the nucleomorph.

We designate them as Type 1, Type 2 and Type 3 cryptomonad, respectively. The correlation between the ultrastructural type and the chloroplast colour was confirmed by means of light microscopy using morphological features, such as the presence of a narrow slit in the pyrenoid matrix (Type 1), the shape of starch sheaths and the cell size (Type 2 and 3).

The nucleomorph of Type 1 is embedded in the pyrenoid matrix. This feature can be



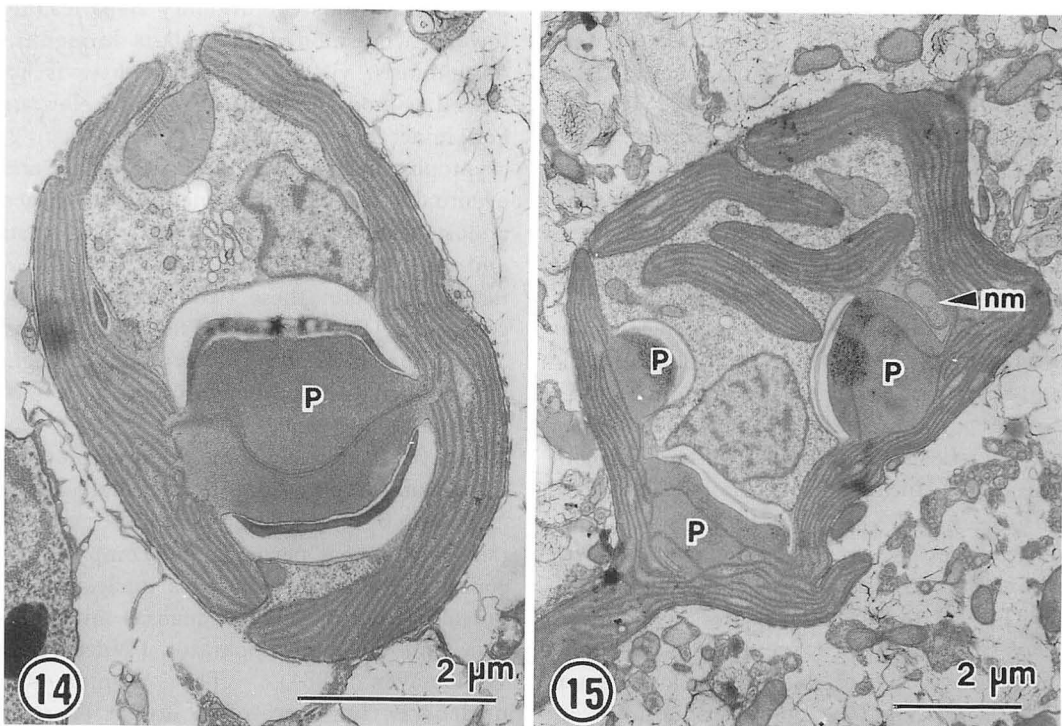
Figs. 11–13. Type 2 cryptomonad cell. Fig. 11. Longitudinal section, showing general structure of the cryptomonad cell. Fig. 12. Detail of nucleomorph. Fig. 13. Paired thylakoid bands each with a thickened lumen.

recognized as narrow slit in the pyrenoid matrix under the light microscope (Fig. 2) and thus, we were able to confirm that the yellowish-brown cell is the Type 1 cryptomonad. The pyrenoid matrix itself is not traversed by any thylakoid bands (Figs. 5 on the left, 9, 10). The number of pyrenoids per cell varies from one to three and each pyrenoid contains a nucleomorph (Figs. 9, 10). Some sections reveal that a single chloroplast possesses two pyrenoid-nucleomorph-complexes (Fig. 9). Other sections show that a single cell contains three chloroplasts. In the latter case, each chloroplast possesses a single pyrenoid with a nucleomorph (Fig. 10). In both cases, the number of chloroplasts was confirmed by serial sections. From these observations, one can infer that multiplication of the cryptomonad plastidial complex takes place in the dinoflagellate cell. Other ultrastructural modifications are the absence of the periplast, the flagellar basal bodies and the

ejectisomes.

Type 2 is characterized by possessing a pyrenoid whose matrix is traversed by many thylakoid bands (Fig. 5 on the right, Fig. 11). The nucleomorph is situated outside the pyrenoid matrix (Fig. 12). The absence of the periplast, basal bodies and ejectisomes has also been confirmed. Additionally the existence of more than one pyrenoid per chloroplast has been observed in this cryptomonad (Fig. 11). Multiplication of the nucleomorph, however, has not been confirmed.

The pyrenoid of Type 3 is single and is surrounded by conspicuous starch sheaths (Fig. 14). The shape of starch sheaths can be recognized under the light microscope. Based on the shape of the starch sheaths together with the fact that the cell size of Type 3 is relatively small compared to other two species, it is apparent that bright-green cells are the Type 3 cryptomonad. Because bright-green cell is Type 3 cryptomonad, it is, then, obvious that



Figs. 14–15. Type 3 cryptomonad cell. Fig. 14. Longitudinal section through a cryptomonad cell showing general structure of the cell. Fig. 15. Multiplied chloroplasts and pyrenoids (P). A nucleomorph (nm) can be seen near one of the pyrenoids.

the blue-green one is the Type 2 cryptomonad. The pyrenoid matrix of Type 3 is traversed by a single pair of thylakoids. The nucleomorph is situated external to the pyrenoid (Fig. 15) and the periplast, basal bodies and ejectisomes are also absent as found in the Type 1 and Type 2 species. A possible division stage of the chloroplast has been observed in this cryptophyte (Fig. 15).

## Discussion

The dinoflagellate species described here has been identified as *Amphidinium latum* Lebour based on several similarities, such as cell size (our specimens are slightly bigger than the original description), cell form, position of the nucleus and the possession of greenish "food cells". The typical cell form of our species is, however, somewhat angular and is slightly different from that of Lebour's (1925) illustration. It should be pointed out, however, that the cell form is variable and rounded cells (Fig. 4) which are similar to that of the original description (Lebour 1925) were often been observed. Furthermore, it is worthwhile noting that Lebour (1925) drew a pyrenoid-like structure in the greenish "food cells". Therefore, it is highly possible that what she described as green food cells were actually blue-green cryptophytes (not necessarily the same cryptomonad as that in our species) which had been ingested by the dinoflagellate. In this study, we have demonstrated that *A. latum* is, in fact, phagotrophic and feeds specifically on cryptomonad cells.

The cryptomonads in *Amphidinium latum* are not true endosymbionts. Attempts to obtain clonal cultures of the dinoflagellate were unsuccessful. The cryptomonads are obviously ingested by the dinoflagellate as a source of food, as in the case of *A. poecilochroum* (Larsen 1988). The process whereby *A. latum* captures the prey seems to be essentially the same as that of *A. poecilochroum* (Larsen 1988). It should be pointed out, however, that the morphology of *A. poecilochroum* is different from that of *A. latum* and they obviously belong to different species. The pres-

ence of numerous bacteria surrounded by a single membrane system suggests that *A. latum* probably feeds also on bacteria as in the case of *G. acidotum* (Farmer and Roberts 1990).

Accurate identification of these cryptomonads even at generic level is not possible, because certain key features for identification of cryptomonads, such as cell shape, arrangement of ejectisomes and periplast structure, have been lost.

Recently, some blue-green gymnodinioid dinoflagellates have been shown to possess chloroplasts or coloured bodies that appear to be chloroplasts of cryptophyte origin. These include *Gymnodinium acidotum* Nygaard (Wilcox and Wedemayer 1984), *Gymnodinium aeruginosum* Stein (Schnepf *et al.* 1989), *Amphidinium wigrense* Woloszynska (Wilcox and Wedemayer 1985) and *Amphidinium poecilochroum* (Larsen 1988). The degree of reduction of the cryptomonad cytoplasm in these dinoflagellate cells has been thought to represent various evolutionary steps leading towards acquisition of chloroplasts through endosymbiosis, viz. 1) the cryptophyte is acquired as food and some of its organelles are kept intact for some time (*A. poecilochroum*), 2) cryptophyte is acquired by dinoflagellate and eventually become permanently established endosymbiont which includes chloroplasts and other organelles (*G. acidotum* and *G. aeruginosum*, Note: these two species may be conspecific (Popovsky and Pfister 1990) and 3) only the chloroplasts of cryptophyte origin are retained as permanently established chloroplasts (*A. wigrense*).

In *Gymnodinium acidotum*, the cryptomonad cytoplasm is separated from the dinoflagellate cytoplasm by a single unit membrane and contains not only a periplastidial compartment containing chloroplasts and a nucleomorph, but also other organelles, such as mitochondria and a Golgi apparatus (Wilcox and Wedemayer 1984). The cryptomonad nucleus is, however, often absent (Farmer and Roberts 1990; Fields and Rhodes 1991). Since the cryptomonad cytoplasm is considerably modified as is the chloroplast which is



highly convoluted, the cryptomonad within *G. acidotum* is believed to be a true endosymbiont (Wilcox and Wedemayer 1984; Farmer and Roberts 1990). This situation is comparable to those of thecate dinoflagellates with a chrysophyte endosymbiont, such as *Peridinium balticum* (Levander) Lemmermann (Thomas and Cox 1973), *P. foliaceum* (Stein) Biechler (Jeffrey and Vesik 1976) and *P. quinquecorne* Abé (Horiguchi and Pienaar 1991) where the true endosymbiont is separated from host cytoplasm by a single unit membrane. However, a recent study (Fields and Rhodes 1991) has demonstrated that *G. acidotum* has to ingest new cryptomonad cells from time to time since it could only be maintained in culture when *Chroomonas* cells were supplied. These cryptomonad cells are maintained within the dinoflagellate cytoplasm for some time (at least 12 days) but then degenerate and make it necessary for the dinoflagellate to ingest further cryptomonad cells. The relationship between *G. acidotum* and its cryptomonads is, then, essentially the same as that of *A. poecilochroum* (Larsen 1988). In these species, the organelles of the cryptomonad cytoplasm seem to remain intact for some time and the chloroplasts probably remain photosynthetically active. This is also the case in *A. latum*. In *A. latum*, the chloroplast and nucleomorph undergo multiplication and, as a result, a single cell or cytoplasmic region could contain up to three chloroplasts and three nucleomorphs. This modification of the cryptomonad cytoplasm strongly suggests that the cryptomonad organelles are intact, at least, for some time after being ingested by the dinoflagellate. A similar proliferation of chloroplasts has been reported for *G. acidotum* (Wilcox and Wedemayer 1984) and the marine ciliate *Mesodinium rubrum* (Hibberd 1977). Unlike *G. acidotum*, however, all the cryptomonads in *A. latum* retained their cryptophyte nucleus.

*Amphidinium wiggense* is different from the above mentioned species in that its chloroplasts are bounded by a triple unit membrane and other cellular organelles of cryptomonad origin are completely absent (Wil-

cox and Wedemayer 1985). The chloroplasts seem to be permanently established (true chloroplast) and this might be comparable to the situation of other unusually pigmented gymnodinoid dinoflagellates, such as *Gyrodinium aureolum* Hulburt and a green dinoflagellate, *Lepidodinium viride* Watanabe *et al.* *G. aureolum* contains 19'-hexanoyloxyfucoxanthin (Bjørnland and Tangen 1979; Tangen and Bjørnland 1981) instead of peridinin, while the chloroplasts of *L. viride* contain chlorophylls a and b. The former species possesses chloroplasts of unusual ultrastructure and has no other organelles of endosymbiotic origin (Kite and Dodge 1988), while in the latter species, although the boundary between the host cytoplasm and cytoplasmic region of endosymbiont still exists, no organelles other than chloroplasts are present in the cytoplasmic region of the endosymbiont (Watanabe *et al.* 1987; Watanabe *et al.* 1990).

As far as blue-green dinoflagellates are concerned, two types of cryptomonad-dinoflagellate relationship could be recognized; the one type is like *A. latum* in that the dinoflagellate is capable of retaining intact chloroplasts for some time, but needs to capture further cryptomonad cells from time to time in order to maintain this "system", while the other type is like *A. wiggense*, where the dinoflagellate possesses permanently established chloroplasts. The intermediate situation between these two types, which is comparable to those of *Peridinium balticum*, *P. foliaceum* and *P. quinquecorne*, have not been found in blue-green dinoflagellates. In this connection, it should be pointed out that a number of unusually pigmented dinoflagellates have been described (e.g. Conrad and Kufferath 1954) and most of them have yet to be studied in detail. It would be of great interest to survey them ultrastructurally and to study them using unialgal cultures in order to verify whether these dinoflagellates contain true endosymbionts or not.

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堀口健雄\*・R. N. Pienaar\*\*：クリプト藻を補食する砂地性の渦鞭毛藻 *Amphidinium latum*  
Lebour (渦鞭毛藻綱) について

南アフリカ沿岸のタイドプールより *Amphidinium latum* Lebour と同定される渦鞭毛藻を採集し、光学顕微鏡ならびに透過型電子顕微鏡により細胞構造の研究をおこなった。その結果、この渦鞭毛藻はしばしば色調の異なる葉緑体様の構造物を有するが、それらは実は渦鞭毛藻によって補食されたクリプト藻の細胞であることが明らかとなった。3種類(タイプ1, タイプ2, タイプ3)のクリプト藻が渦鞭毛藻の細胞質の中に存在することが示された。すなわち、1)タイプ1の細胞は黄褐色を呈し、そのヌクレオモルフはピレノイドのマトリックスに埋没するタイプであり、ピレノイド・マトリックスにはチラコイドが陥入しない、2)タイプ2の細胞は青緑色で、そのヌクレオモルフはピレノイドの外側に位置し、ピレノイド・マトリックスには多数のチラコイドが陥入する、3)タイプ3は明るい緑色を呈し、ヌクレオモルフはピレノイドの外側に位置し、ピレノイド・マトリックスは1組のチラコイドが陥入する、という特徴をそれぞれ有する。葉緑体の分裂と考えられるステージが、渦鞭毛藻内部のクリプト藻の葉緑体で観察され、このことから取り込まれた葉緑体はおそらく光合成能をしばらく保持しているのではないか、ということが示唆された。本研究により、*A. latum* は摂食栄養をおこない、しかも数種類のクリプト藻を補食する性質があることが確かめられた。(\*380 長野市西長野6-ロ 信州大学教育学部, \*\*Department of Botany, University of the Witwatersrand, Private Bag 3, P.O. Wits, 2050 Republic of South Africa)

