Cysts and Life Cycle Considerations of the Thecate Dinoflagellate *Fragilidium*  

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ABSTRACT


Thecate dinoflagellates of the genus *Fragilidium* excysted under laboratory conditions from two types of morphologically distinct hypnocysts isolated from sediments of the Indian River lagoon, Brevard County, Florida. Observations of individual motile organisms showed that ecdysal cysts were formed from the thecate (armored) stage and pellicle cysts were formed from the gymnodinoid (prearmored) stage. The duration of ecdysal encystment was typically between eight and nine hours when a thecate individual encysted and between seven and eight hours when a cyst was formed from the "gymnodinoid" stage. All cells observed excysting from ecdysal cysts were in the "gymnodinoid" stage with distinct longitudinal and transverse flagella and fully developed cingular and sulcal grooves. The results of this study provide field evidence for the presence of hypnocysts, ecdysal, and pellicle cysts in the life cycle of *Fragilidium.* The formation of ecdysal and pellicle cysts may provide several benefits for life in an estuarine system where conditions can change significantly in a relatively short period of time. A theca/cyst cycle is suggested for the genus *Fragilidium.* Similar theca/cyst cycles can be expected to occur in other dinoflagellates.

ADDITIONAL INDEX WORDS: Dinoflagellate cysts, *Fragilidium,* theca-cyst cycle.

INTRODUCTION

Cyst formation in dinoflagellates, as for most free-living protozoans, is believed to serve a number of functions and may have a variety of causes. For example, encystment may allow organisms to survive adverse conditions, such as nutrient depletion and fluctuations in pH, temperature salinity, and dissolved oxygen (see, for example, WAGTENDONK, 1955; CORLISS and ESSER, 1974; and SARJEANT, 1974). Fall-winter dormancy in an encysted stage followed by excystment in spring or summer allows the species to recolonize an area year after year. Also, species dispersal may be effected by physical transport of cysts, thus increasing their geographical range. Furthermore, some dinoflagellate cysts are part of the sexual reproductive cycle (WALL and DALE, 1966, 1968; SARJEANT, 1974; STEIDINGER, 1975; ANDERSON and WALL, 1978).

This paper is concerned with the cysts of the motile, thecate dinoflagellate *Fragilidium* Balech ex Loeblich, 1965. The generic name, *Fragilidium,* refers to the characteristic ease with which the dinoflagellate undergoes ecdysis (sheds its thecal plates) to produce a spheroplast (BALECH, 1959). The spheroplast (thin-walled cyst), with the excysted plates maintained at a distance by a gelatinous material, is relatively featureless (SWIFT and WALL, 1972; STEIDINGER et al., 1967) and is here referred to as an ecdysal cyst.

MATERIALS AND METHODS

Cysts were isolated from sediment samples and collected from the Indian River lagoon system, Florida. Dates of collection, sampling procedures, locations of the sample sites, and storing of samples
are discussed by Owen and Norris (1982).

Cysts were isolated from the processed samples with a micropipette under a compound light microscope. Similar cysts were transferred into capped culture tubes containing sea water (30 °/°S) enriched with MML-MI medium. The cysts were incubated at 22°C with a 14:10 hour light:dark cycle of cool white fluorescent lights. Six different types of cysts were incubated in this manner. After five weeks, motile dinoflagellates had been established in four of the six culture tubes. Two of the cyst types gave rise to strains of Fragilidium. In the other two, strains of Polysphondylium and Gonyaulax were established (Owen, 1979). About 30 motile, thecate individuals of Fragilidium were placed in depression slides containing MML-MI enriched sea water and sealed with petroleum jelly, either singly or in pairs. They were maintained under the same light and temperature conditions as the cultures and observed under a compound light microscope for from one day to four weeks.

RESULTS

Strains of Fragilidium were established from two morphologically distinct hypnocysts (resting cysts) isolated from sediments in the late winter and early spring. These hypnocysts have not been previously described in the literature. The first was a spherical to ellipsoidal cyst ranging from 54 to 60 \( \mu m \) in diameter and up to 62 \( \mu m \) in length (Plate 2, see color insert). The smooth outer cyst wall appeared to consist of two layers and was approximately three (3 \( \mu m \)) thick.

The cysts contained brown microgranular cytoplasm, a red colored body, and numerous small lipid bodies and/or starch grains. Tests were not conducted to determine the exact nature of the small spherical cell inclusions. In several of the cysts isolated, the brown microgranular cytoplasm exhibited Brownian motion. The actual process by which the organisms excysted from either type of hypnocyst was not observed. Both types of hypnocysts have been isolated from sediments of embayments on the west coast of Florida and successfully excysted (L. Walker, Florida Department of Natural Resources, Personal Communication to K.C.O.).

The motile, armored dinoflagellates readily excievated (underwent ecdivsis) when observed under the microscope. The thecal plates were shed and held at a distance from the cyst, apparently by some type of mucoid or gelatinous material. The spherical, smooth, thin-walled ecysisal cysts so formed were from 48 to 60 \( \mu m \) in diameter. Similar cysts are illustrated by Steidinger et al. (1967) and described by Balech (1959).

When ecysisal cysts were isolated in sealed depression slides, excystment occurred from eight to nine hours after cyst formation. A dinoflagellate in the prearmored “gymnodinoid” stage was released from the cyst. The cingulum and sulcus, along with the transverse and longitudinal flagella were formed prior to excystment. The biflagellated organism was fully motile when it emerged from the cyst. Had conditions been suitable for maturation, the organism could have been expected to develop a theca. However, all the observed specimens (approximately 30) of Fragilidium spp. excysted while in the “gymnodinoid” stage, only moments after excystment. The outer covering, which appeared as a sheath was shed in the same manner as the fully developed thecal plates. However, since the organism lacked plates, the cysts are referred to here as pellicle cysts.

The pellicle cysts were thin walled but more elongate than the ecysal cysts; being approximately 60 \( \mu m \) long and 54 \( \mu m \) wide. After seven to eight hours of apparent dormancy, the organisms excysted, emerging in the gymnodinoid stage with longitudinal and transverse grooves and flagella present. None of the dinoflagellates matured to the armoured stage but rather alternated between the “gymnodinoid” stage and the pellicle cyst, possibly due to culture stress. After a maximum of five days of this cycle, excystment no longer occurred. After two weeks of dormancy, the cytoplasm began to clump into golden brown globules. By the end of four weeks, all the cytoplasm had been incorporated into globules. However, the cyst wall was uneven and showed signs of deterioration.

DISCUSSION

Based on observations involving approximately 30 species of dinoflagellates, Wall and Dale (1968) developed the concept of the theca-cyst cycle. This
The theca-cyst cycle of Fragilidium is more complex than the simple alternation set forth by WALL and DALE (1968). The apparent theca-cyst cycle of Fragilidium is schematically illustrated in Figure 1. As occurred in the species observed by WALL and DALE (1968), Fragilidium presumably “over-winters” as a benthic hypnocyst and excysts in the spring/summer to form the motile, biflagellated cell. When this organism is disturbed or encounters stressed conditions, it exuviates to form an ecdysal cyst, with encystment occurring from eight to nine hours later. If conditions are favorable, the excysted gymnodinoid individuals will form a pellicle cyst. Based on laboratory observations, the duration of this encysted stage is slightly shorter, lasting from seven to eight hours. Also based on laboratory observations, this motile cell-ecdysal/pellicle cyst cycle may be repeated many times during a summer season or shorter period if under stress.

The asexual ecdysal cysts formed by Fragilidium offer several advantages to an organism in an estuarine or lagoonal environment. First, the molted thecal fragments, held at a distance from the cyst by the gelatinous material, increase the buoyancy of the cyst and tend to keep the non-motile, inactive organism suspended. Second, the rapidity of encystment allows Fragilidium to respond almost instantaneously to environmental disturbances. The short period of encystment, i.e. between seven and nine hours, helps the organism to survive relatively brief perturbations attributable to factors such as tides.
or heavy land run-off. In addition, the forceful shedding of the thecal plates or prevalvate membrane may help the organism escape accidental entrapment by suspended materials and possibly frighten would-be predators.

The theca-cyst cycle in *Fragilidium* shows that, for this genus, the cycle includes the formation of ec dysal and pellicle cysts (with encystment periods as short as seven hours). The identification of ec dysal cysts in other dinoflagellates, such as *G. tama ren sis*, suggests that similar complex theca-cyst cycles may be encountered in dinoflagellates other than *Fragilidium*.

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**LITERATURE CITED**


**ADDENDUM**

This article is a revision of a paper submitted to the now defunct journal *Litoralia* in November 1983 and published in the summer of 1984. WALKER (1984) independently published a summary of research on dinoflagellate life cycles. Asexual cysts, including pellicle cysts, were discussed in that review. WALKER (1984) attributed several survival advantages to asexual cysts, some of which are similar to benefits mentioned in our paper.