out the remainder of the summer period due to decomposition of rhizomes and death of underground perennating organs (*3*).

The data presented here indicate that significant amounts of potassium and nitrogen were retained in accumulating *Erythronium* biomass in early spring and made available through shoot decomposition in midsummer. The vernal dam hypothesis implies that had *E. americanum* not been present, nutrients in amounts equivalent to those taken up in its biomass and subsequently released by decomposition would have been subject to spring stream water flushing. This interpretation does not necessarily imply ecosystem evolution; however, it does illustrate how the adaptation of one species to a period of high nutrient availability may benefit the ecosystem through reduction of nutrient losses. Thus, even though *E. americanum* accounts for a very small proportion of the net primary production of the ecosystem, it may significantly influence the nutrient dynamics of the system.

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4. The Hubbard Brook forest is an approximately 60-year-old stand composed primarily of sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*). For a complete description of the study area see Muller (*3*); Siccama *et al.* (*5*); F. H. Bormann, T. G. Siccama, G. E. Likens, R. H. Whittaker, *Ecol. Monogr.* **40**, 373 (1970).
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11. Soil nitrate concentrations remain at high winter levels through April and approach low summer levels in May (J. Mellilo, personal communication). These values are reflected in stream water nitrate concentrations.
12. While the data were not available to calculate uptake in 1972, the similarity of uptake and release of calcium, magnesium, and nitrogen in 1973 suggests that the release values in 1972 are adequate indicators of uptake. Data for spring and annual stream water losses were provided by J. Eaton and G. E. Likens (personal communication).

13. This is a contribution of the Hubbard Brook Ecosystem Study, funded by the National Science Foundation. Preparation of the manuscript was supported by the Energy Research and Development Administration. We thank B. Green, T. Green, P. Marks, J. Mellilo, R. Pierce, T. Siccama, D. Sprugel, and G. Whitney for helpful comments on the manuscript.

13 May 1976; revised 8 July 1976

Dinoflagellates: Fossil Motile-Stage Tests from the Upper Cretaceous of the Northern New Jersey Coastal Plain

Abstract. *Fossil dinoflagellate tests have been considered to represent encysted, nonmotile stages. The discovery of flagellar porelike structures and probable trichocyst pores in the Upper Cretaceous genus* Dinogymnium *suggests that motile stage tests are also preserved as acid-resistant, organic-walled microfossils.*

The life cycle of living dinoflagellates has been shown, in some cases, to consist of a motile planktonic stage and an encysted, nonmotile benthonic stage (*1*). Dinoflagellate fossils have been thought to represent only the encysted, nonmotile stage, with the fossil itself being the cyst. To my knowledge, this report is the first discussion of morphological features (flagellar pores and probable trichocyst pores) which suggest that motile stages are also preserved as fossil dinoflagellates.

The only genus of fossil dinoflagellates that has been considered to be possibly of the motile stage is *Dinogymnium* Evitt *et al.* 1967. It was noted by Evitt (*2*) and Evitt, Clarke, and Verdier (*3*) that the cystlike tests of this genus bore morphological features that resembled those of motile stages. These features include wall canals (interpreted here as trichocyst pores) that penetrate the test wall, and a cingulum and sulcus that never appear to be interrupted by transverse structures that would inhibit the operation of a flagellum along their length. Also, fossil *Dinogymnium* tests show a striking similarity in morphology to the tests of living motile stages of the genera *Gymnodinium* Stein and *Gyrodinium* Kofoid and Swezy, which suggests that *Dinogymnium* tests may represent ancestral motile stages. Flagellar pores, however, are one of the features that must be present on a fossil form before it can be proven to be a motile stage. Until now, no such pores have been reported for *Dinogymnium* or for any other dinoflagellate.

Flagellar pores on modern dinoflagellates occur at the intersection of the cingulum, a transverse furrow, and the sulcus, a longitudinal furrow, and mark the exit of the transverse flagellum (which is restricted to the cingulum) and the longitudinal flagellum (which is restricted to the sulcus). Scanning electron microscopy of fossil *Dinogymnium* specimens

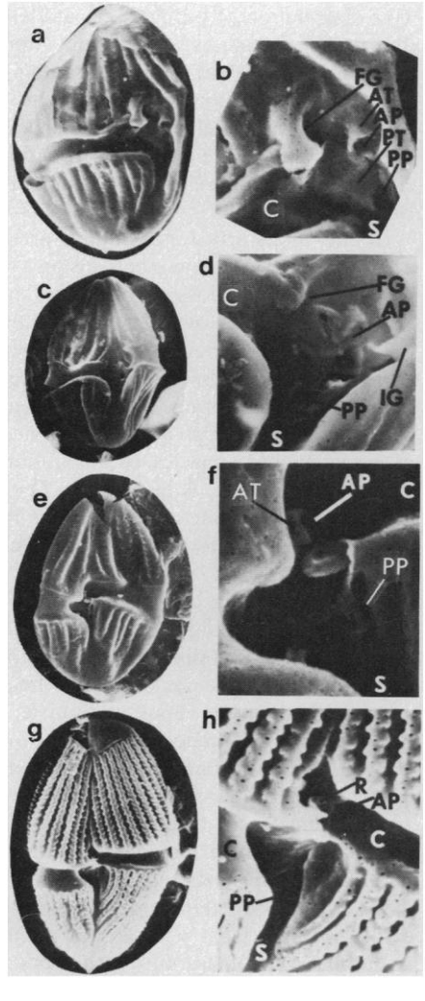

Fig. 1. The left column (a, c, e, and g) shows complete ventral views of *Dinogymnium* tests. Enlargements to the right (b, d, f, and h) show cingulum-sulcus intersections with flagellar pore structures; anterior flagellar tube (*AT*) and pore (*AP*) allowed passage of the transverse flagellum onto the cingulum (*C*); posterior tube (*PT*) and pore (*PP*) allowed passage of the longitudinal flagellum onto the sulcus (*S*); *IG*, initial grove; *FG*, final groove; *R*, half-circular ridge.

from the upper Mount Laurel Sand and the Sandy Hook Member of the Red Bank Sand (upper Campanian and lower Maestrichtian, respectively) of the northern New Jersey coastal plain near Atlantic Highlands, has revealed apparent flagellar pore structures. These consist of tubes and pores—one anterior tube and pore and one posterior tube and pore—at the cingulum-sulcus intersection. If these are flagellar pore structures, the possibility is enhanced that some motile-stage dinoflagellates are preserved as acid-resistant, organic-walled microfossils (*4*).

The most striking features at the cingulum-sulcus intersection on the midventral surface of *Dinogymnium* tests are the many curved ridges and depressions associated with the cingulum and sulcus. These ridges and depressions (Fig. 1, a to h) seem to have a functional morphology that provides a directing and confining course for both transverse and longitudinal flagella. When the positions of the flagellar pore structures are associated with the positions of the curved ridges and grooves, it is often apparent how the transverse flagellum could have been directed from the anterior pore toward the right onto the cingulum (Fig. 1, c and d) and, likewise, how the longitudinal flagellum could have been directed from the posterior pore onto the sulcus. The specimen in Fig. 1, a and b, best shows the flagellar tube and pore structures. Curved ridges and depressions are best seen in Fig. 1, c and d, where the grooves and ridges suggest three confining structures for the transverse flagellum: (i) an initial groove leading the transverse flagellum from the anterior pore onto the cingulum; (ii) the cingulum leading the transverse flagellum around the test; and (iii) the final groove, which may have confined the distal end of the flagellum to the uppermost part of the sulcus. The posterior tube and pore of Fig. 1, b and d, allowed the posterior passage of the longitudinal flagellum onto the sulcus. The morphology of the anterior pore structures does not appear as complex in the specimens shown in Fig. 1, a, b, e, and f. Figure 1a shows a specimen bearing an anterior tube and pore and a posterior tube and pore. No curved groove or ridge is observed to direct the transverse flagellum onto the higher of the two cingulum ends; a somewhat distorted final groove confines the distal end of the flagellum. Figure 1e shows a straightforward arrangement in the anterior structures, with a simple, horizontally projected tube directed to the right from the higher cingulum end toward the cingulum and no obstructions. The posterior

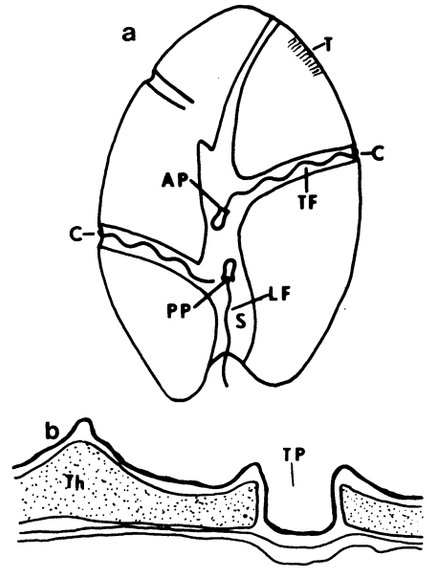

Fig. 2. (a) A recent *Gyrodinium pavillardi* shows positions of anterior and posterior flagellar pores associated with tubelike structures. The transverse flagellum (*TF*) passes from the anterior flagellar pore (*AP*) onto the higher of the two ends of the cingulum (*C*) and the cingulum confines the transverse passage of the flagellum. The longitudinal flagellum (*LF*) passes from the posterior flagellar pore (*PP*) onto the sulcus (*S*); trichocysts (*T*) are found near the cell wall. (b) The wall structure of recent *Ceratium hirundinella* shows a trichocyst pore (*TP*) penetrating the test wall (*Th*); pores may be related to wall canals observed in fossil *Dinogymnium*. The diameter of the pore is about 0.5 μm.

pore on this specimen occurs at the surface as a narrow slit that allows the longitudinal flagellum to pass onto the sulcus. Figure 1g shows a specimen with a rather complex anterior pore structure. The transverse flagellum appears to have passed ventrally from the anterior pore. In front of the pore, a half-circular confining ridge apparently directed the flagellum to the right onto the cingulum. The posterior flagellar pore allowed the longitudinal flagellum to pass uninterrupted onto the sulcus.

A comparison of these structures with those of the modern *Gyrodinium pavillardi* Biecheler (Fig. 2a) shows a similarity in flagellar pore placement and structure. The anterior flagellar pore of *G. pavillardi* allows passage of the transverse flagellum from the cell interior outward to the cingulum; the posterior flagellar pore allows passage of the longitudinal flagellum from the interior outward to the sulcus. Also associated with each pore are apparently tubular passageways.

Although the presence of flagellar pores suggests motility, this does not have to be the case. The nonmotile cysts of living forms are known to develop generally in close association with the motile test. The flagella on fossil *Dinogymnium* forms may have persisted in their activity until after the cyst was completed, at which time the flagella atrophied or were discarded. The resultant cyst remained, with relic openings through which the flagella had passed. This explanation does not seem logical in view of the complex arrangement of curved ridges and depressions associated with the flagellar pore structures; these appear to have been functional in directing the flagella onto the sulcus and cingulum of the *Dinogymnium* test.

Living motile-stage dinoflagellate tests often bear many pores that penetrate the test wall, whereas the nonmotile encysted stage is considered to be impervious. The discovery of pores (wall canals) that penetrate the test wall of *Dinogymnium* forms was first reported by Evitt (*2*, p. 357), who considered them as possible evidence of the motile stage. Wall canals

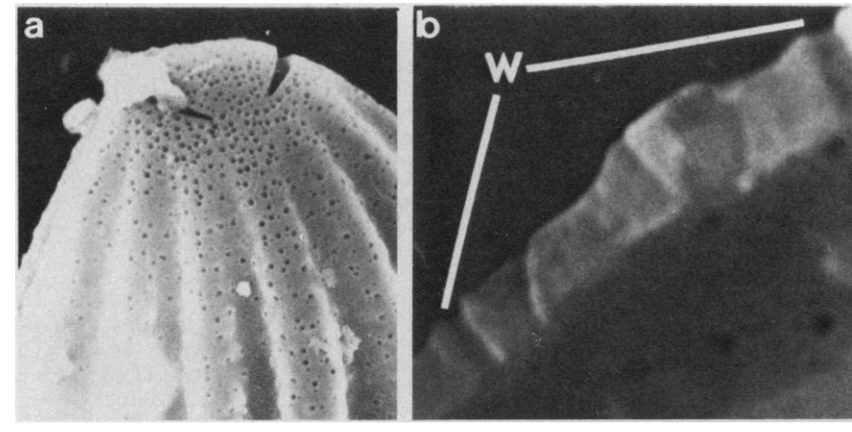

Fig. 3. A *Dinogymnium* test shows the position and structure of wall canals (the porelike openings). (a) Wall canals are most numerous near the apex (for scale, the ribs are about 3 μm wide). (b) A cross section of the test wall shows wall canals (*W*) perforating the test wall. Wall canal diameter is about 0.2 μm.

thus far observed and reported are at the limits of resolution for light microscopy and are best seen by means of interference contrast or scanning electron microscopy. Figure 3a shows a dorsal epitract bearing many wall canals that are concentrated mainly near the apex of the specimen. Figure 3b shows several wall canals, each about 0.2 μm in diameter, penetrating the test wall, which is about 0.5 μm thick.

In living motile stages, such wall canals are often associated with trichocysts—the canals are called trichocyst pores. Trichocysts have a neck that contains fibrillar strands and a body that consists of proteinaceous material. The purpose of trichocysts is not fully known, although they may function as sensing devices, defense mechanisms, or mechanisms of attachment. The positions of a few trichocysts are shown on *G. pavillardi* (Fig. 2a). Trichocyst pores are also numerous on *Ceratium hirundinella* (O. F. Muller) Schrank. In this species, the pores penetrate the test wall but are lined laterally and basally by at least one membrane (*5*). Because of this lining, the pores do not actually penetrate to the cell interior (Fig. 2b). Therefore, the wall canals in *Dinogymnium* tests may never have allowed uninhibited communication between the cell interior and the outside water; they may have been trichocyst pores lined laterally and basally by impermeable or semipermeable membranes. The trichocyst pores of *C. hirundinella* are also numerous at the lateral cell margins and on the horns (*5*). Wall canals on *Dinogymnium* tests are often concentrated near the apex (Fig. 3a) and antapex, a distribution that is similar to that found in *C. hirundinella*. The purpose of such concentrations is not known.

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4. The *Dinogymnium* specimens reported on were recovered as palynological residues from sediments that underwent a standard maceration procedure. The sediments were digested in hydrochloric and hydrofluoric acids, and organic components were oxidized in 5 percent sodium hypochlorite. The acid-resistant, organic-walled *Dinogymnium* tests were observed as strew mounts on aluminum disks under the scanning electron microscope. Specimens reported on are retained on aluminum disks and also in bulk residues at the U.S. Geological Survey Palynological Laboratory, Reston, Virginia.
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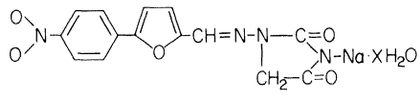
17 March 1976; revised 26 May 1976

Calcium Release from Skeletal Muscle Sarcoplasmic Reticulum: Site of Action of Dantrolene Sodium?

Abstract. *The muscle relaxant dantrolene sodium acts directly and specifically on skeletal muscle, unlike other pharmacological agents which affect the central nervous system or act at the neuromuscular junction. Dantrolene sodium markedly suppresses the release of calcium previously sequestered by skeletal, but not cardiac, muscle sarcoplasmic reticulum. No effect in the total amount of calcium accumulated was found. In situ, the drug may reduce the amount of calcium necessary for muscle contraction.*

In 1967 Snyder and co-workers (*1*) reported the synthesis of a compound which acted as a skeletal muscle relaxant. This compound, dantrolene sodium (Dantrium, Norwich Pharmacal Corp.),



1-{[5-(*p*-nitrophenyl)furfurylidene]amino}hydantoin sodium hydrate, has been found to be very beneficial in the treatment of spasticity of varying origins and degrees of muscular involvement. Patients suffering from spasticity due to stroke (*2*), multiple sclerosis (*3*), and other disorders of the central nervous system manifesting themselves in some degree of involuntary muscle spasm (*2*, *4–6*) have, in a majority of cases, responded favorably to dantrolene sodium therapy (*7*). The drug appears to be a favorable choice in such maladies because it acts only on skeletal muscle (*8–10*), with no effect on the central nervous system (*5*, *6*, *10*, *11*) (such as sedation or impair-

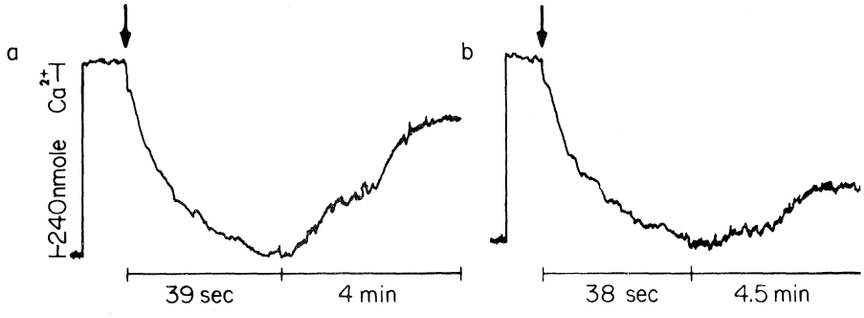


Fig. 1. Dual-wavelength spectrophotometric traces of cat tibialis anterior SR Ca^{2+} binding and release. Note that the release is spontaneous (*22*, *23*). (a) Control preparation trace. (b) Trace in the presence of $10^{-5}M$ dantrolene sodium. Reaction cuvettes contained 1.5 mg of SR, 100 m*M* KCl, 10 m*M* $MgCl_2$, 40 m*M* tris-maleate, *p*H 6.8, and 0.3 m*M* murexide in a final volume of 3 ml. Calcium, here 300 nmole, was added to the cuvette (initial upward sweep), followed by the rapid addition of Na_2ATP (arrow) to a final concentration of 0.25 m*M*. The reaction took place at 30°C and was monitored in an Aminco-Chance dual-wavelength spectrophotometer with wavelength settings at 507 and 542 nm.

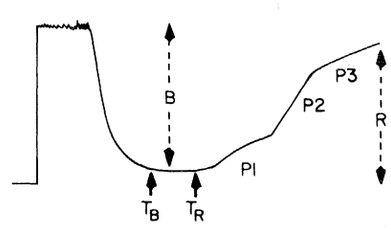


Fig. 2. Diagrammatic representation of traces from a dual-wavelength spectrophotometric recording of Ca^{2+} sequestration by SR. The numerical data represent a typical control and experimental study. Abbreviations: *B*, total Ca^{2+} bound (nanomoles per milligram of SR protein); T_B, time in seconds required for peak Ca^{2+} binding; T_R, time in seconds for initiation of Ca^{2+} release; and *P1* to *P3*, rates of Ca^{2+} release at the three phases expressed in nanomoles per milligram. Figures in brackets represent the amount of Ca^{2+} released per phase expressed as a function of the amount bound (*R*/*B*); *R* is the percentage of bound Ca^{2+} released. The values for control and dantrolene sodium Ca^{2+} sequestering studies are representative of eight separate experiments of rabbit and cat muscle SR fractions.

	B	T_B	T_R	PI	P2	P3	R
Control	197	28	39	36.5 [.186]	79.8 [.405]	15.9 [.08]	78
Dantrolene sodium	187.5	29	36	16.5 [.08]	63 [.33]	8.2 [.04]	45