

pregnancy, childhood, and hemolysis (such as that caused by malaria) (11). For example, the World Health Organization recommends a daily folate intake of 400 μg for adults and 800 μg during pregnancy, while nutritional surveys in several tropical areas indicate daily folate intakes of only 40 to 138 μg (12).

Individuals with marginal or low folate levels might be particularly susceptible to severe deficiency if photolysis of the vitamin were also to occur. Deficiency of folic acid may greatly diminish reproductive capacity. It has been estimated that 10 to 60 percent of pregnant women are deficient in folate (11). If severe enough, this deficiency may be fatal, and it is said to cause significant maternal mortality in tropical countries (11). Less severe deficiencies have been associated with major obstetric complications (abruptio placentae and placenta previa), congenital abnormalities, perinatal mortality, premature delivery, and repeated miscarriages (11). Folate deficiency in infancy and early childhood results in growth retardation, hematologic abnormalities, and failure to thrive (13). Thus, severe folate deficiency may have a profound influence on reproductive capacity and therefore on the process of natural selection.

The possibility that dark skin color protects against nutrient photolysis also fits well with the solar spectral distribution and with the light transmission spectra of human stratum corneum and epidermis (14). Analysis of the midday UV spectrum shows that the greatest intensity of light occurs at wavelengths longer than 330 nm. At shorter wavelengths intensity declines very rapidly, becoming only 0.01 percent of peak relative energy at 300 nm (14), and almost no solar radiation shorter than 295 nm reaches the earth's surface (15). Skin from both Negroes and Caucasians is highly effective in screening UV wavelengths below 280 nm. Between 280 and 320 nm, melanized skin is more effective in blocking transmission of light, but the difference in transmission between white and black skin is most marked at wavelengths greater than 320 nm (14), which are known to cause rapid photolysis of folate (7). In contrast, the carcinogenic and antirachitic effects of light are observed for wavelengths between 280 and 320 nm (15). Thus, melanized skin provides much more relative protection against the nutrient-destroying, intense, longer wavelengths of sunlight than from the shorter, less intense, mutagenic, and vitamin D-forming wavelengths.

These observations provide support for the idea that heavily pigmented skin

may protect against extensive photolysis of certain crucial metabolites, such as folate. The protection of light-sensitive vitamins and other nutrients against UV-induced photodecomposition provides an alternative explanation for the maintenance of dark skin color among members of human groups indigenous to areas of intense solar radiation.

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Tentaculites: Evidence for a Brachiopod Affinity?

Abstract. *Transmission electron microscope studies of fractured surfaces reveal that the shells of Tentaculites are constructed of calcite with a ridge and groove structure and cross-bladed fabric heretofore unique to some articulate brachiopods. A possible affinity with brachiopods or phoronids is suggested for Tentaculites.*

Tentaculites is a genus of annulate cone-shaped fossils (Fig. 1a) that are found in rocks ranging in age from Ordovician to Devonian. The systematic position of this problematic group is unknown and has been the subject of much speculation since they were first described by E. F. von Schlotheim in 1820. Tentaculitids have been variously placed among the annelids, mollusks, crinoids, coelenterates, foraminifera, brachiopods, and trilobites (1, 2). Currently, *Tentaculites* is precariously classified with the cephalopods in the phylum Mollusca (3, 4). The purpose of this report is to present new evidence suggesting that some tentaculitids may instead be related to articulate brachiopods.

The conical shells of *Tentaculites* are made of calcite arranged in a concentrically laminated fashion and sometimes penetrated by pores, canals, or pseudopores. The preservation of the microstructure and the general absence of recrystallization indicate that the calcite is original rather than an alteration product of aragonite or magnesium cal-

cite. In spite of the excellent preservation of many specimens of *Tentaculites*, there have been surprisingly few attempts at examining the fine structure of the shell with the electron microscope. Only the work of Blind (3) is noteworthy in this regard, although Hurst and Hewitt (5) described but did not figure their scanning electron microscope results. Blind examined the laminated shell in the scanning electron microscope, figuring the microscopic layers of calcite in his plate 12, figure 7 (3). He compared this structure to that of the "brick-wall" aragonite typical of molluscan nacre (mother-of-pearl). Although the morphological similarity may be appropriate (in cross section) the difference in mineralogy makes the comparison awkward for taxonomic purposes. Such fidelity of morphological preservation in any calcite transformed from aragonite is without precedent.

With this difficulty in mind, a reexamination of the fine structure of *Tentaculites* was undertaken with the transmission electron microscope. Using a single-

stage platinum-carbon replica technique, freshly fractured surfaces of the shells were examined. The material studied included specimens of *Tentaculites carteri* Clarke from the Devonian Gaspé Sandstone of Quebec, Canada (6), and *Tentaculites* sp. from the Devonian of Poland (7).

The results were startling and completely unexpected. The laminated structure of these tentaculitid shells is surprisingly similar to that of many articulate brachiopods (8-13), especially those of the order Strophomenida (12, 13). Such brachiopods construct major parts of their shells with calcite having a unique structure known as cross-bladed fabric (10). The unique aspects of this structure are that, in plan view, crisscross sets of grooves and ridges are created by layers of calcite blades as they alternate in building up the laminations of the shell. When exceptionally well developed over broad, flat regions of the brachiopod shell (Fig. 1b), the fabric produces a pearly luster simulating that of the aragonite of molluscan nacre. In such instances the groove and ridge structure acts as an optical diffraction grating, often displaying iridescent colors (8). But in other regions the typical cross-bladed fabric may become disordered and poorly developed (9). The long narrow blades are then represented by more irregular equant crystal units. Nevertheless the characteristic groove and ridge structure remains clearly identifiable (Fig. 1c). It is this latter structure that one finds preserved on freshly fractured surfaces of the curved and annulate tentaculitid shells (Fig. 1, d to f). The unique grooves and ridges are seen crisscrossing the layers of the tentaculitid shells in an irregular fashion, perhaps as required by the curvature restriction. The structure is evident in different species from such widely separated regions as Poland (Fig. 1d) and Canada (Fig. 1, e and f).

This groove and ridge, cross-bladed fabric, even when poorly developed, was heretofore unique to the articulate brachiopods. It has not been found to date in any other group of organisms, including the aragonitic nacre of mollusks. It is not found in foliated calcite of molluscan origin nor in the laminated calcite

of some bryozoans. Its presence in the shells of *Tentaculites* is therefore significant.

Does this mean that *Tentaculites* should be classified among the brachiopods? If shell microstructure is a taxonomic character of high priority, then one could quickly place *Tentaculites*

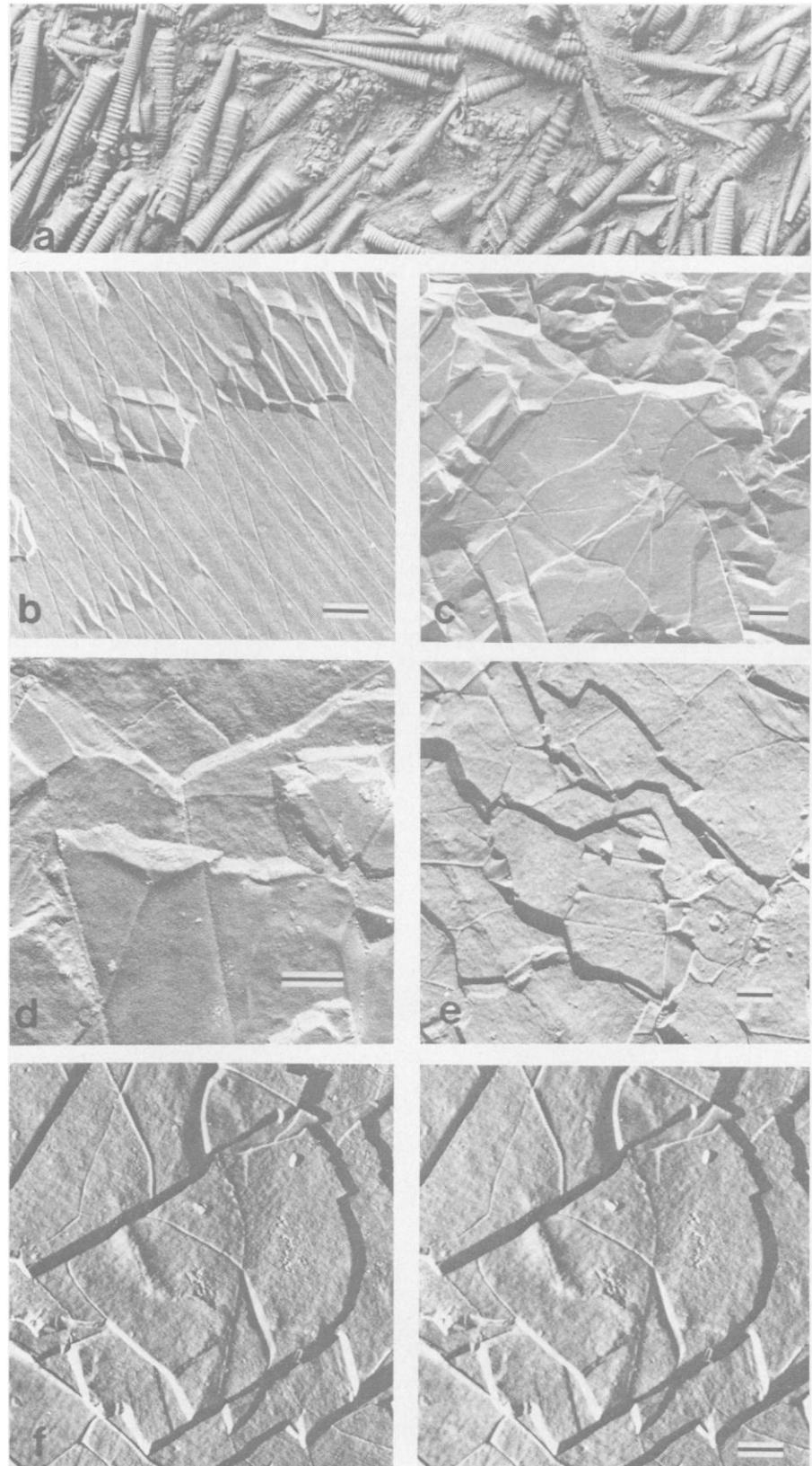


Fig. 1. (a) Aggregated specimens of *Tentaculites attenuatus* Hall from the Devonian Arkona Shale; Arkona, Ontario, Canada ($\times 2.5$). (b) Fractured surface of well-developed cross-bladed fabric in the shell of *Pholidostrophia nacrea* (Hall). Note the crisscross ridge and groove structure (scale bar, $1 \mu\text{m}$). (c) Poorly developed cross-bladed fabric, also from *P. nacrea* (Hall). Ridge and groove structure is irregular but still discernible. (d) Cross-bladed fabric on fractured surface of *Tentaculites* sp. (Poland). Compare with plate 57, figure 6 of Armstrong (10) (scale bar, $1 \mu\text{m}$). (e) Fractured surface of *T. carteri* Clarke also with cross-bladed fabric on each layer (scale bar, $1 \mu\text{m}$). (f) Stereopair of *T. carteri* Clarke. Note the crisscross ridge and groove structure on each shell layer (scale bar $1 \mu\text{m}$).

among the brachiopods of the order Strophomenida in the sense of Williams (12, 13). On the other hand, *Tentaculites* does not look like a brachiopod, as it is not a bivalved organism in the usual sense of the word. If there were indisputable evidence of a hinged operculum (3) it might be plausible to suggest it as homologous to one of the brachiopod valves. But contrary to the findings of Blind (3), with none of the specimens of *Tentaculites* that I studied is there any evidence of an operculum—attached or unattached.

The suggestion that *Tentaculites* might be the spines of a brachiopod was broached in 1831 by von Buch (14), who incorrectly considered them to be the spines of *Leptaena lata*. The strophomenide shell fabric has been reported from broken productid spines (12), and Lyashenko (1) noted the similarity of the tentaculitid wall structure to that of the brachiopod spine. But the major problem with the spine hypothesis is the fact that tentaculitids are not found associated with any brachiopods from which they were clearly a part. Conversely, no brachiopods have been found with spines that are grossly similar to *Tentaculites*. The absence of undoubted muscle scars [the drawings of Lardeux (15) notwithstanding] limits a clear interpretation of the shell as a housing for an entire organism, although some phoronids are able to move freely within their unmineralized tubes (16). The tubes of free-living annelid worms are open at both ends.

Perhaps the *Tentaculites* were specialized brachiopods or perhaps they were calcified phoronid tubes. Neither of these suggestions is compelling, but neither are the alternatives in the literature. Interestingly, the brachiopods and the phoronids have often been placed together (along with the bryozoans) in the phylum Tentaculata, the validity of which is supported by recent biochemical data (17). On the basis of shell fine structure and mineralogy, *Tentaculites* are clearly more closely related to articulate brachiopods than to mollusks or annelids. Sadly, there are as yet no known living phoronids having calcified tubes with which to compare them.

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Lymphocyte Ecto-5'-Nucleotidase Deficiency in Agammaglobulinemia

Abstract. *Fresh peripheral blood lymphocytes from eight patients with congenital agammaglobulinemia demonstrate reduced ecto-5'-nucleotidase activity when compared to the mean activity of normal subjects and patients with other forms of immunoglobulin deficiency. A specific defect of ecto-5'-nucleotidase is further suggested by normal values for lymphocyte ecto-adenosinetriphosphatase and ecto-nonspecific phosphatase. The data provide evidence for an enzyme deficiency in this X-linked, B lymphocyte deficiency syndrome.*

Inherited enzyme deficiencies in purine nucleotide degradation have been associated with immune deficiency states involving disorders of thymus-dependent (T) and thymus-independent (B) lymphocyte function. The absence of adenosine deaminase (E.C. 3.5.4.6) has been associated with a severe immunodeficiency syndrome involving defective B and T lymphocyte activity (1), whereas the absence of the next enzyme of the degradative pathway, purine nucleoside phosphorylase (E.C. 2.4.2.1), is characterized by a T lymphocyte deficiency (2). A third possible disorder, the decreased activity of 5'-nucleotidase (E.C. 3.1.3.5) on the external surface of the lympho-

cyte, has been observed in a heterogeneous group of patients with hypogammaglobulinemia (3, 4).

To distinguish whether 5'-nucleotidase deficiency is associated with a specific form of lymphocyte dysfunction, we measured lymphocyte ecto-5'-nucleotidase in patients with hypogammaglobulinemia subdivided into definable disease categories. All eight males with congenital agammaglobulinemia have deficient lymphocyte ecto-5'-nucleotidase with values ranging from 30 to 48 percent of normal activity (Fig. 1). One other male infant, who did not meet all the criteria for congenital agammaglobulinemia, had low ecto-5'-nucleotidase ac-

Table 1. Activity of plasma membrane bound enzymes in lymphocytes. Intact lymphocytes from normal subjects or patients with congenital agammaglobulinemia were prepared as described in Fig. 1. Ecto-adenosinetriphosphatase was assayed in 0.25×10^6 cells with 150 mM NaCl, 0.75 mM $MgCl_2$, 8 mM KCl, 1 mM 5'-adenosine triphosphate, and 80 mM tris-HCl, pH 8.5, in a total volume of 150 μ l at 37°C for 60 minutes. After the incubation period, the reaction mixture was cooled to 4°C and centrifuged for 3 minutes. One hundred microliters of supernatant was removed for an inorganic phosphate assay (14). The reaction was linear with time to 120 minutes and with cell number. Ecto-nonspecific phosphatase activity was measured in 0.5×10^6 lymphocytes in a reaction mixture which contained 150 mM NaCl, 70 mM tris-HCl at pH 7.0, and 4 mM *p*-nitrophenylphosphate in a total volume of 275 μ l at 37°C for 30 minutes. The reaction was stopped with 700 μ l of 0.4M NaOH. Change in optical density at 410 nm measured the enzymatic release of *p*-nitrophenol. The assay was linear with time to 30 minutes and with cell number from 0.1×10^6 to 1.0×10^6 lymphocytes.

Subjects	Ecto-enzyme					
	Adenosinetriphosphatase [μ mole hour ⁻¹ (10^6 cell) ⁻¹]			Nonspecific phosphatase [nmole hour ⁻¹ (10^6 cell) ⁻¹]		
	Value	Range	N	Value	Range	N
Normal	0.12	0.03 to 0.26	10	36.1	12.5 to 70.2	9
Congenital agammaglobulinemia	0.12	0.06 to 0.22	5	40.1	10.5 to 103.0	9