SHELL-MATERIAL VARIATION IN THE AGGLUTINATED FORAMINIFER *TROCHAMMINA PACIFICA* CUSHMAN

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CONTENTS

I. ABSTRACT

Test construction, reproduction, and rate of growth in specimens of *Trochammina pacifica* cultured without mineral grains are analogous to those of specimens supplied with sediment. Newly formed test chambers consist of fragile, organic membranes. Control specimens show selectivity for grain size but not for mineral composition. The median grain size of disaggregated control specimens agreed closely with the median grain size of the supplied sediment. The grain size in a test, however, increases gradually as individuals become larger during ontogenetic development. These findings are applicable to taxonomic analyses and to the paleoecological interpretation of fluctuating, shallow-water, marine environments and their depositional history.

II. INTRODUCTION

Agglutinated foraminifers constitute a major group of the protozoan order Foraminiferida, ranging from at least the Lower Cambrian to the Recent. Nevertheless, little is known of the biology of living species in regard to life cycles, cytology, or degree of selectivity in choosing the materials used in wall construction. The greatest obstacle to previous experiments with agglutinated foraminifers has been the difficulty in maintaining living cultures over extended periods (Freudenthal, Lee and Pierce, 1963; Hedley, 1964). Life studies are especially important for agglutinated species whose taxonomy heretofore has been based almost entirely on morphological features of the test. Some authors even have regarded mineralogical content as of taxonomic value (Avnimelech, 1952; Hofker, 1953). Investigation of the degree of selectivity, and compositional variations of the wall material is thus necessary to determine 1) their significance in taxonomic and phylogenetic studies especially those of fossil species, for which morphologic criteria are emphasized; 2) the effects upon such biologic functions as growth and chamber development; and 3) the influence upon distribution.

Laboratory studies of living foraminifers were initiated by the author in 1962. Among the species selected for study were *Trochammina inflata* (Montagu) and *T. pacifica* Cushman. Specimens of *T. inflata* collected from lagoonal areas of southern California contained occasional chambers devoid of mineral grains. This lack of agglutinated material is thought to be due primarily to 1) low pH affecting the cementing mechanism or some other protoplasmic function; and/or 2) a paucity of material available for test construction. Partial dissolution of early chambers of living and dead specimens of *T. inflata* probably results from chemical changes related to decaying organic matter within the test or the adjacent sediment.

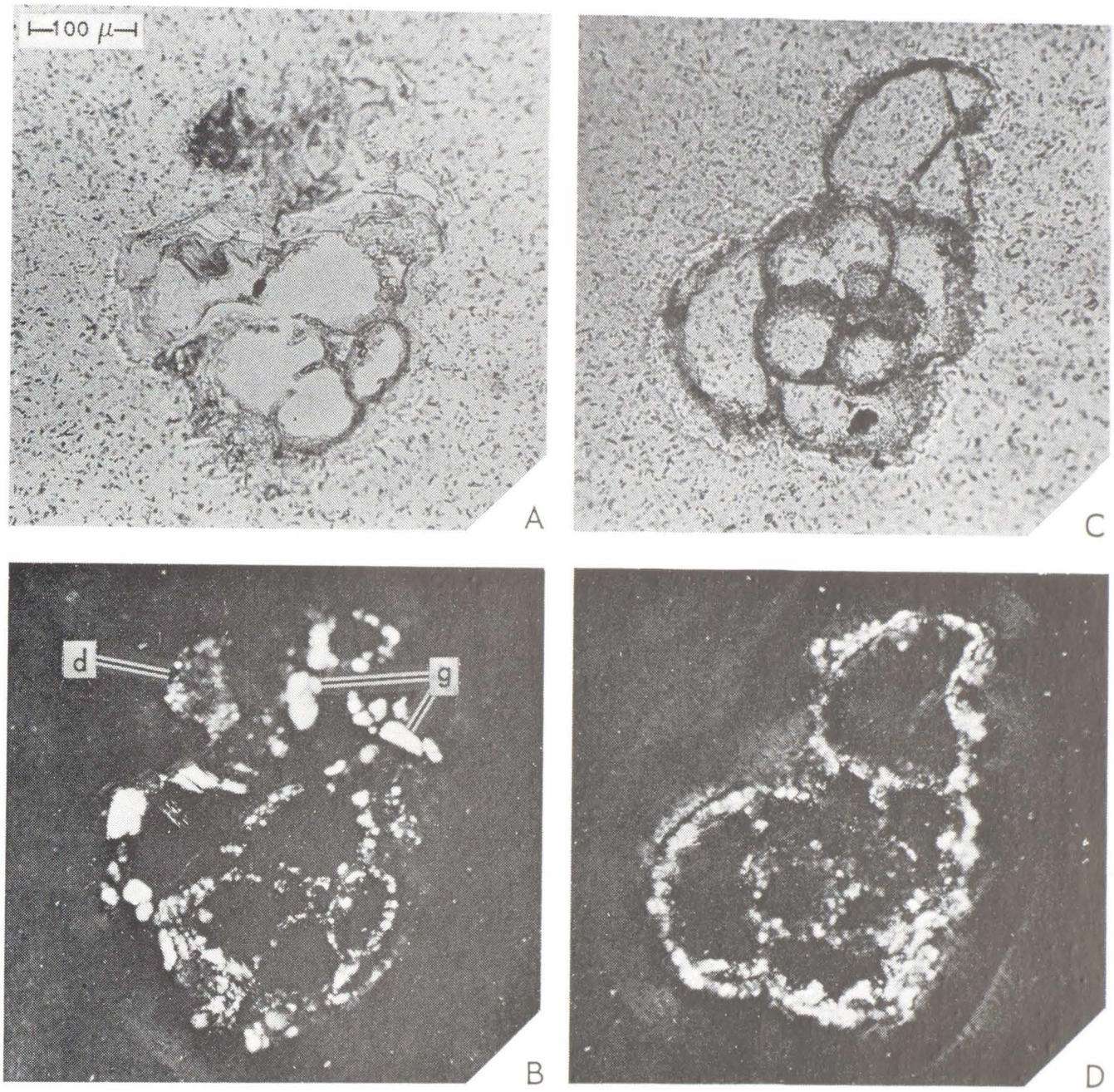

Figure 1. *Trochammina pacifica* Cushman. A. Oblique axial section of test specimen with collapsed final chambers. B. Same specimen under crossed nicols. d, diatom mass; g, transferred grains. C. Oblique axial section of control specimen showing chamber arrangement. D. Same specimen under crossed nicols showing grain orientation.

In contrast living specimens of *T. pacifica* obtained from near-shore open-ocean localities in southern California never have chambers devoid of mineral grains, nor have such specimens been reported previously, to the author's knowledge. In addition, *T. pacifica* occurs in marine environments where a continuous supply of sediment should preclude preadaptation to sediment-free test construction.

These observations prompted the present investigation, in order to determine the effect of the absence of mineral grains on the growth and reproduction of *T. pacifica.* This paper is a continuation of earlier laboratory studies (Sliter, 1965; Douglas and Sliter, 1965) designed to investigate ecologic, phylogenetic and evolutionary relationships of living foraminifers that are applicable to paleontology.

III. Materials and Methods

Collections of *Trochammina pacifica* were made at Malaga Cove, California, from water depths of 4 to 5 meters. Surface water temperatures at Malaga Cove during 1957-1958 ranged from 12.8° to 19.5°C, and the salinity from 33.4 to 33.9 parts per thousand (Reiter, 1959). Median grain diameter of the near-shore sediment during this period was 0.57 mm, and the Trask sorting coefficient averaged 1.8.

Fresh collections of *T. pacifica* were placed in 30 gallon circulating aquaria at

about 18°C. Agnotobiotic stock cultures were maintained in unaerated 180 ml covered custard dishes containing 100 ml of filtered, unbuffered sea water (salinity about 33 parts per thousand) and a fine-grained sand substrate. All stocks and experiments were kept at a temperature of 18° ± 2°C under constant illumination in the range of 200 ft-c. Experimental and control animals were transferred by pipette to 60 by 15 mm petri dishes inoculated with *Nitzschia angularis* Smith. The medium in all cultures was carefully changed weekly so as not to disturb the animals or the diatom culture.

Successive generations were cultured from September 1965 to September 1966. Test and control animals were maintained from January to September 1966.

The total generation time of *Trochammina pacifica* cultured under these conditions remained stable at about 70 days. Reproducing specimens averaged 14 chambers. Experimental animals of 7-8 chambers were transferred to petri dishes devoid of sand substrate. Upon attaining 14 chambers, most experimental and control specimens were stained with rose bengal, imbedded in Selectron 5003, and thin-sectioned for biologic and petrographic study.

The photomicrographs used in this paper were taken with a Zeiss Photomicroscope using Agfa 35 mm Isopan Iff black and white film.

Cultures were examined with a Leitz binocular stereoscopic microscope at magnifications of 25×, 50×, 100× and 150×. Cytology and thin-sections were examined with an American Optical Co. Microstar binocular microscope at magnifications of 35×, 100×, 430× and 970×.

IV. Discussion of Results

Sediment deprivation resulted in no significant difference in the rate of chamber addition and reproduction or the size of individual chambers. Experimental animals continued chamber development at a rate analogous to control specimens and reproduced upon attaining 13-14 chambers. New chambers were covered by a brown organic membrane resembling that observed in *Astrorhiza limnicola* Sandahl by Buchanan & Hedley (1960). Chambers formed by the organic membrane in *Trochammina pacifica* are extremely fragile and collapse easily upon desiccation, commonly forming irregular crusts on the surface of older chambers (fig. 1A). The flexible membrane was left bare or was thinly covered by diatom frustules or random quartz grains "cannibalized" from earlier portions of the test periphery (fig. 1B).

The wall structure of control specimens, examined microscopically under both normal and polarized light, shows a progressive increase in grain size with specimen size. Early chamber walls were constructed from the finer-sized grains of the supplied sediment, but the later chambers were formed from the largest grains. Voids in all chamber walls and septa are densely packed with progressively smaller grains (figs. C, D). The selective use of grains of varying size suggests a relationship between the mass of protoplasm available for pseudopodial development and the size of the incorporated grains. An opposite effect has been reported, however, in *Discobotellina biperforata* Collins, where a progressive decrease in grain size from early to later stages of growth was noted by Stephenson & Rees (1965).

The median grain-size from disaggregated control specimens agrees closely with the median size of the supplied sediment. These results agree with previous grain-size analyses of agglutinated foraminifers, although these had been cited as evidence of non-selective grain incorporation, in reference to the substrate (Buchanan, 1960; Buchanan & Hedley, 1960).

V. Conclusions

These experiments demonstrate that *Trochammina pacifica* is capable of sustaining life functions such as continued growth and reproduction with or without mineral grains for periods of at least half its life cycle. The apparent ability of this species to reproduce under these conditions is of ecologic importance. Reproduction is known to have the narrowest tolerance limits of any vital function. In foraminifers this has been demonstrated most notably by Bradshaw (1957, 1961). His laboratory experiments with *Ammonia beccarii tepida* (Cushman) have shown that whereas the organism can survive wide variations of temperature and salinity, reproduction occurs only over a much lesser range of physical condi-

tions. The presence or absence of agglutinated particles seemingly is of secondary importance as a limiting factor in the distribution and vital functions of *T. pacifica.* The data do not preclude, however, the value of a semirigid, agglutinated test as protection for the organism from elements of the external environment.

Several additional observations have application to biological and paleontological investigations of agglutinated foraminifers. Agglutinated material is of lesser importance in generic and specific taxonomy of *T. pacifica* and certain other agglutinated foraminifers (Slama, 1954; Buchanan and Hedley, 1960), as the size and quantity of available detrital grains may vary. The experiments have shown that *T. pacifica* is nonselective in the composition of mineral grains utilized in test construction. Grain size selectivity is noticed, however. Thin-section examination suggests a direct relationship between the size of the organism and the size of the incorporated grains (fig. D); the larger the specimen, the larger the grains. As the preferred grain size changes with growth, the average of the completed test resembles the substrate composition. Hence, this size selectivity is not recognizable in the grain-size analyses of dispersed specimens. Additional experiments are needed, as noted by Hedley (1964, p. 16), to test the selectivity of certain agglutinated species which utilize specific elements of the substrate in test construction.

The dominance of agglutinated foraminifers in marsh environments has been correlated with the low pH resulting from organic decay (Walton, 1955; Phleger, 1960). Emery (1960) indicated that the average calcium carbonate content in the marsh surface is only about 0.6 percent, but in the adjacent tidal channels it may be as high as 80 percent. Reports of the recovery of "chitinous" uncalcified foraminifers from marsh, bay and lagoonal environments of the Atlantic coast by Echols & Wegweiser (1967), and the Gulf Coast by Kane (1967) are no doubt related to the low pH.

Ronai (1955) studied the brackish-water foraminifers from the New York Bight and divided the agglutinated species into three groups. One group, containing species of *Trochammina,* was characterized by more "chitinous" tests than the other two categories. In addition, many specimens of *Trochammina* in a given sample would "deflate" or collapse while others would not. Although these features may likewise be related to low pH, "deflated" tests also resulted from the present experiments. Sediment distribution in marsh areas should be reflected in the tests of agglutinated foraminifers. Sedimentary analyses of two of the marsh collection localities in southern California have been reported by Stevenson & Emery (1958) and Warme (1967). These and other marsh studies have shown that organisms living in the high marsh areas are submerged only by the highest spring tides. Sediment in these areas consists of the finest silt and may be greatly diluted by the concentrated vegetation and surface algal mats. Wind blown sand is present only in areas adjacent to offshore barriers and spits. Foraminifers thus resting on dense algal mats and wetted only from beneath may construct tests with organic walls or utilize wall materials from earlier portions of the test. These specimens would readily collapse upon desiccation, to resemble the "deflated" forms described by Ronai (1955). Similar occurrences should be sought in marsh and bay environments with particular emphasis placed on sediment and chemical analysis. In addition, an attempt should be made to obtain organic-walled remains from Tertiary samples, which at present, may be overlooked or lost in sample preparation.

Differences in the agglutinated test material of single specimens, as of *T. inflata* from southern California, or the presence of morphologically similar organic-walled specimens may indicate fluctuating environmental conditions such as in a lagoon or tidal marsh. Test differences might also reflect the introduction of a new sediment source, or possibly indicate transportation into an adjacent environment.

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REVIEWS

IDENTIFICATION OF MINERAL GRAINS; CONTROLS OF METAMORPHISM

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IDENTIFICATION OF MINERAL GRAINS, by Meurig P. Jones and Marston G. Fleming. Published by Elsevier Publishing Company, Amsterdam, London and New York, 1965, vi + 102 pp., $5.50

The identification of mineral grains by a systematic determinative method is presented in this laboratory manual. The procedure follows a series of simple, semi-quantitative steps followed by micro-chemical tests, sufficiently diagnostic to identify most mineral species. The flow scheme and tables have been used successfully by students at Imperial College, London, for more than five years.

CONTROLS OF METAMORPHISM, edited by Wallace S. Pitcher and Glenys W. Flinn. Published by John Wiley & Sons, Inc., New York, 1966, 368 pp., $13.50

This volume contains the papers presented at a symposium titled "Controls of Metamorphic Crystallization" which was held in January 1964 in the Department of Geology, University of Liverpool, under the auspices of the Liverpool Geological Society. Emphasis was placed on the physico-chemical processes involved in the formation of metamorphic rocks rather than on field relationships. Twenty writers contributed to the published symposium; 230 persons attended the sessions.