

STUDIES ON *CYCLOTELLA MENEGHINIANA* KÜTZ.

III. The Frustule*

BY T. V. DESIKACHARY AND V. N. R. RAO

(University Botany Laboratory, Madras-600005, India)

Received January 13, 1973

INTRODUCTION

DIMENSIONS, structure and markings (areolae or punctae) of the diatom frustule have for a long time been considered to be relatively stable and reliable features of importance in taxonomy. But, studies on diatoms in the last few decades have shown clearly the presence of a certain degree of variability in these characters, bringing into question the validity of a number of species. Variations may occur during auxospore formation (Hustedt, 1956; *see also* Geitler, 1966), or during progressive diminution in size of a diatom (Conger, 1966; Stoermer, 1967; Rao and Desikachary, 1970; *see also* Hustedt, 1937). The cell may become shortened in one or more axes and smaller cells of a species may become more compact and show deviation from the larger cells (Geitler, 1932; Hendey, 1951; Hustedt, 1956, 1967; Rao and Desikachary, 1970; *see also* Trainor *et al.*, 1971). Variability in a taxon may also be brought about by environmental factors (*see* Hustedt, 1956).

Lund (1945, 1946) points out that orientation and density of striae also may show variation in cells of different sizes of the same species and if sufficient number of specimens are not examined, extremes of sizes may be mistaken for different varieties or even species. This statement is of great significance in the taxonomy of this group. Studies on natural population or in cultures (Braarud, 1944; Wallace and Patrick, 1950; Peterson, 1950; Belcher *et al.*, 1966; Seaton, 1970; *see* Leboime, 1957; Wood, 1959; Hendey, 1964; Hartmann, 1967; Trainor *et al.*, 1971; *see also* Cholnoky, 1960; Pringsheim, 1967), have revealed that many varieties, forms and sometimes even species are only growth forms of other known taxa of the same genus.

Electron microscope studies have revealed that variations in valve ornamentation exhibited by one and the same species through its different

* Memoir No. 159 from the Centre for Advanced Studies in Botany.

phases may encompass features which are considered characteristic of other species. Holmes and Reimann (1966) studied *Coscinodiscus concinnus* and found that while frustules of post-auxospore condition resembled *C. concinnus*, frustules of mid-growth condition resembled those of *C. granii*. Frustules of pre-auxospore condition were still different and had not been previously described. As an extreme example of variability may be mentioned, the case of *Nitzschia alba* studied by Lauritis *et al.* (1967). Dividing cells of *Nitzschia alba* yielded both *Nitzschia* type and *Hantzschia* type of cells. They, therefore, suggested that *Hantzschia* and *Nitzschia* are not taxonomically distinct and that *Hantzschia* spp. are but a stage in the vegetative life-cycle of species of *Nitzschia* (see also Geitler, 1968). These many observations point out that a thorough study of the diatom is necessary to understand the extent of variability of a taxon and to assess the stability of the different characters used in separating infra-generic taxa.

Cyclotella meneghiniana Kütz., exhibits a great deal of variation in cell dimensions during its life-cycle (Rao and Desikachary, 1970). Frustules of varying diameters of an estuarine clone of this species were studied with light and electron microscopes. The results are presented here.

MATERIAL

Frustules of *Cyclotella meneghiniana* were cleaned with cold dilute sulphuric acid (see Desikachary, 1956). This treatment was found advantageous as it did not disturb the girdle bands very much. Frustules were also cleaned by using hot concentrated sulphuric acid with little potassium nitrate. Uncleaned formalin preserved frustules were also studied. A RCA EMU 3 model electron microscope with an accelerating voltage of 50 kV and 100 kV was used for EM pictures. Scanning electron micrographs (SEM) of both cleaned and uncleaned frustules were taken with the kind help of Dr. F. E. Round and Miss Patricia A. Sims, while one of us (TVD) was in the United Kingdom.

OBSERVATIONS

Cyclotella meneghiniana Kütz.—Description

Frustules discoid in valve view, rectangular in girdle view, with an undulate central area; margin well defined; coarsely striated; striae 8-9 in $10\ \mu$, wedge-shaped; central area well defined from an areolated marginal area; smooth or with a number of punctae; 5-100 μ diameter (7-10 μ in Kützling, 1884; 10-20 μ in van Heurck, 1884; 10-30 μ in Hustedt, 1930 a;

7–30 μ in Cleve-Euler, 1951; 5–100 μ in Reimann *et al.*, 1963). Varieties are known which are otherwise similar to the type but having cells with varying diameter ranges and with other features like presence of intercalary bands, *e.g.*, *v. laevissima* (van Goor) Hust. (Hustedt, 1930 *b*, p. 100), absence of undulation, *e.g.*, *f. plana* Fricke (*see* Hustedt, 1930 *b*, p. 100) or the presence of central pores and their number, *e.g.*, *C. meneghiniana*, *v. meneghiniana*, *f. unipunctata* Cleve-Euler, and *f. binotata* Grun. (Cleve-Euler, 1951; pp. 48–49).

Structure of Frustule

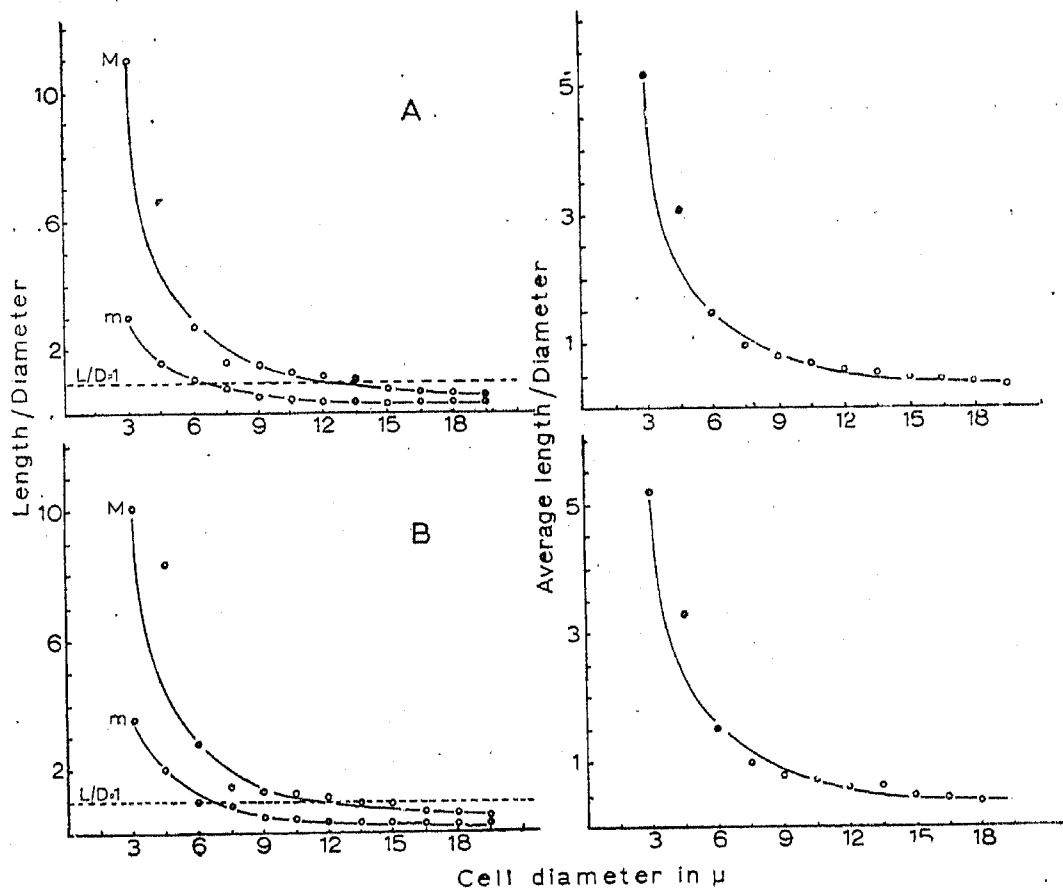
Frustules of a single clone studied at different stages in the progressive diminution show the following trends: reduction in the number of areolae per cell, neighbouring areolae tending to gradually coalesce to form broader ones, costae becoming less prominent making it difficult to demarcate the individual areolae, and from a gradual reduction in the smooth central area to a total obliteration of it (Plate III). Frustules of the small cells very much resembled similar small cells of *Cyclotella cryptica* (*cf.*, Badour, 1968, p. 22, Fig. 3) in their structure.

Pores in the central area.—The number of central pores vary from one to many. Generally only one pore is noticed in cells with small diameters, one to two pores in cells with about 15 μ diameter, and variable from two to ten, in cells above 15 μ diameter (*see* also Hasle, 1962). However, the size of cell and the number of pores are not generally correlatable as cells with the largest diameter do not always have the largest number of central pores. In some cells these are even totally absent (Plate IV). These pores appear to be simple in large cells but compound and branched in small cells (Plate III, Figs. 4–7 and 9).

Valve margin.—The valve at its margin, *i.e.*, where it bends to form the valve mantle, is provided with regularly placed groups of 2–4 dissimilar spines. Usually the one uppermost, proximal to the valve face is larger and the others smaller. These arise opposite the costae. In addition, a number of other smaller blunt tubercular protruberances and a number of smaller pores are distributed on the costae (Plate V, Fig. 2). In between the costae are the arched areolae which extend into the mantle, often up to the edge of the valve (Plate V, Fig. 3). From inside, the costae are clearly seen as structural elements supporting the entire valve face (Plate V, Fig. 4). Traversing each of these costae is a single canal whose internal opening is clearly on the costa and the external opening is located in between the groups of spines at the rim of the valve referred to above. Thus, there are as many

Cell Dimension

Normally centric diatoms are discoid. While describing *Cyclotella meneghiniana* and its varieties and forms the length or the height of the frustule is given as 1/6 of the cell diameter (Cleve-Euler, 1951). They are rarely as long as broad appearing more or less quadrate in girdle view. A 1 : 1 ratio of length : diameter is not found in the larger cells but may be seen in cells with intermediate diameters. However, cells with smaller diameters (3.0–6.0 μ) are distinctly elongated on the perivalvar axis. This length is more than double the maximum length of a single valve, i.e., the length that would normally obtain at the time of separation of the daughter cells immediately after cell division (Rao and Desikachary, 1970). We have studied two other clones of *C. meneghiniana*, one obtained from a beach

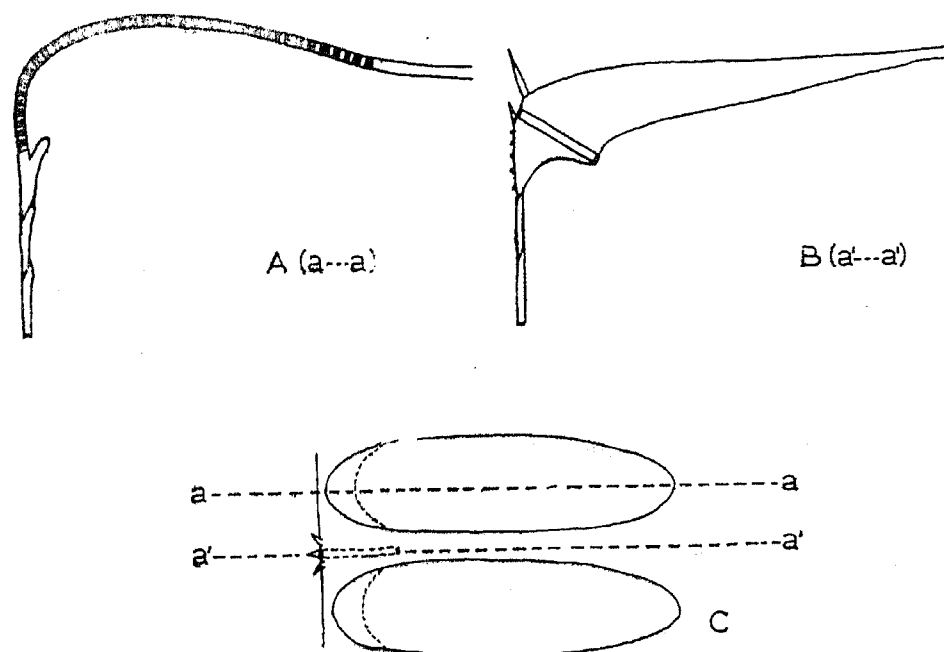


TEXT-FIG. 2. A. *Cyclotella meneghiniana* (Beach pool clone). B. *C. meneghiniana* (Garden pond clone).

Left: Two curves showing the minimum (m) and maximum (M) lengths/diameter (L/D) recorded for cells of different diameters.

Right: Curve showing the relationship of cell diameter to average length/diameter.

distinct canals as the costae which open to the inside as well as to the outside. In some uncleaned frustules small fibrous material emanated from these pores. They, thus, appear to be mucilage canals. Viewed externally, there are many small pores, often irregularly distributed at the valve margin. Text-Figure 1 gives a diagrammatic representation of the structure of the valve, which is somewhat different from the layout presented by Round (1970). Similar canals have been described in a few other diatoms (see Round, 1970; Hasle, 1972).



TEXT-FIG. 1. A-C. Diagrammatic representation of the marginal area of the valve showing the position of areolae, costa, mucilage canal and the spines. A. Cross-section through the region $a-a$, in C. B. Cross-section through the region $a'-a'$ in C.

As the number of areolae gets reduced with progressive reduction in size, there is a corresponding reduction in the number of groups of marginal spines. In some smaller cells these appear to be totally eliminated while in other similarly small cells these are present but not as prominently as in the larger cells.

Pervalvar elongation.—Large cells seem to have only a single girdle band. But as the cells become smaller and smaller in their diameter (especially cells with $3-6\mu$ diameter) the valves are elongated on the pervalvar axis. This elongation is unrelated to cell division and is brought about by addition of intercalary bands. These are not, however, distinguishable from the primary girdle band.

A study of the freshly divided cell reveals that the newly formed theca, hypotheca of the daughter cells, is more or less completely tucked into the old thecae, the epithecae (Plate VI, Figs. 5 and 8). Owing to the moving away of the two epithecae the newly formed hypothecae become gradually pushed out as it were until we get a clear view of them. It is nearly impossible to distinguish the primary girdle band and the later secondarily formed intercalary bands. Nevertheless, it seems evident, that in all such cases the full complement of bands is formed at the time of division or immediately thereafter with the gradual pushing out of the hypothecae. The number of bands changed with the frustule diameter which in turn largely depended on the generation to which the epitheca belonged. These bands are punctate and have simple pores (Plate VI, Fig. 3; Plate VII, Figs. 1, 2).

In many small cells, the valve face is narrower than the connecting band which is broader at the region where the two thecae overlap. It is not also thick and inelastic, but thin and broadening and attains a near barrel-shaped condition (see Plate VI, Figs. 3, 5, 6, 8; Plate VII, Figs. 4, 5).

Round (1971) has given certain schematic representations of the mode of formation of the connecting bands. The writers are not in agreement with him on these, but would like to discuss it in a later communication.

Organic skin.—Desikachary (1962) in his X-ray studies on *Cyclotella meneghiniana* and other diatoms first pointed out the possibility of the presence of an organic skin on the frustule, whose removal was necessary to reveal the crystalline character of the α -silica of the frustule (see also Desikachary and Dweltz, 1961). According to him an endogenous formation of frustule would leave an organic skin external to the frustules during withdrawal or retraction of the cytoplasm to render the frustule external to the protoplast. Desikachary, however, did not then give any evidence of its actual presence. Since Desikachary first made this suggestion presence of an organic skin has been demonstrated in *Cylindrotheca fusiformis* and *Navicula pelliculosa* (Reimann *et al.*, 1965, 1966) (also in *Stephanodiscus* sp. and *Hantzschia* sp.; see Round, 1970).

The present study in *C. meneghiniana* confirms the presence of an organic skin. Uncleaned frustules were studied in the scanning electron microscope. Frustules exhibited clearly a thin membrane external to the silica shell (Plate V, Fig. 1). The membrane became clearer in areas where it had peeled off partially exposing the inner silica shell. This skin gets removed on treating with acids.

pool and the other from a garden pond. These had similar frustule dimensions as those in the estuarine clone, *i.e.*, $43.5-3.0 \mu$ diameter. Text-Figure 2 shows the average minimum and maximum lengths obtained for different cell diameter based on measurements taken for a large number of cells grown in Reimann medium (Reimann *et al.*, 1963, p. 76). As in the case of the estuarine clone here also the average length of cell was more or less constant in cells of larger diameters while it increased in cells with smaller ($3.0-6.0 \mu$) diameters.

DISCUSSION

The present study on *Cyclotella meneghiniana* reveals that characters that are considered important in the demarcation of this species are not very stable and frustules of the diatom examined at various stages during its life-history, exhibit features which are often considered characteristic of other varieties of *C. meneghiniana* or even other species of *Cyclotella*. This conclusion is very similar to the one arrived at by Holmes and Reimann (1966) on *Coscinodiscus concinnus*.

The number of central pores within the clone is found to be variable. Doubts arise on the validity of one or more forms or varieties of *C. meneghiniana* separated on the basis of number of central pores or nature of the central area (*see also* Reimann *et al.*, 1963).

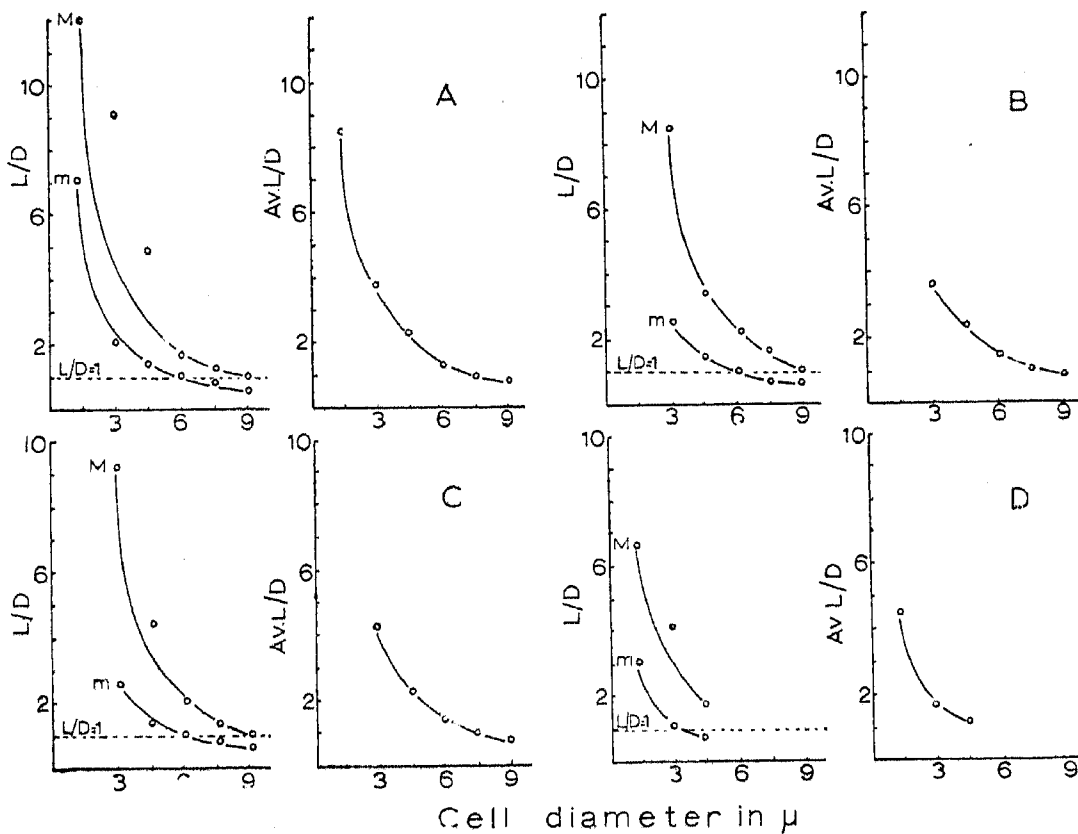
Cyclotella meneghiniana v. meneghiniana is generally described (*see* Hustedt, 1930) as having no intercalary bands. *C. meneghiniana v. laevis-sima* has two intercalary bands, one to each valve. The number of intercalary bands does not appear to be a fixed feature as the intercalary bands increase in stages with progressive reduction in frustule diameter. Hence, varieties established on the presence or absence of number of intercalary bands may not be valid.

Larger cells of *C. meneghiniana* have an undulated central area. But it is very hard to find such undulations in the smaller valves and we believe that this character is useful only to a limited extent in separating taxa. Thus, the validity based on this feature of the frustule, (*cf. f. plana*) becomes doubtful.

Toman (1948) described a new species, *Cyclotella pratii*, in which he observed that cells were distinctly elongated on the perivalvar axis. He considers this feature characteristic of his species to separate it from small celled *Cyclotella* spp. As is now evident from the present study it is possible

that *C. pratii* is an extremely small form of *C. meneghiniana* with elongated condition. It has not been possible to obtain material of this diatom.

In fact similar perivalvar elongations have been observed in other small *Cyclotellas* which were studied for purposes of comparison. These are *Cyclotella meneghiniana* (1020-la; Göttingen Culture Collection, W. Germany), *Thalassiosira fluviatilis* reidentified as *Cyclotella cryptica* (1070-1; Göttingen Culture Collection, W. Germany) and *C. cryptica* (1269, Indiana Culture Collection, Indiana, U.S.A.). Text-Figure 3 shows the relationship of average length to cell diameter and minimum and maximum lengths obtained for different cell diameters of these isolates grown in Reimann medium. Attempts



TEXT-FIG. 3. A. *Cyclotella cryptica* (Indiana); B. *C. cryptica* (Göttingen); C. *C. meneghiniana* (Göttingen); D. *C. nana* (Göttingen).

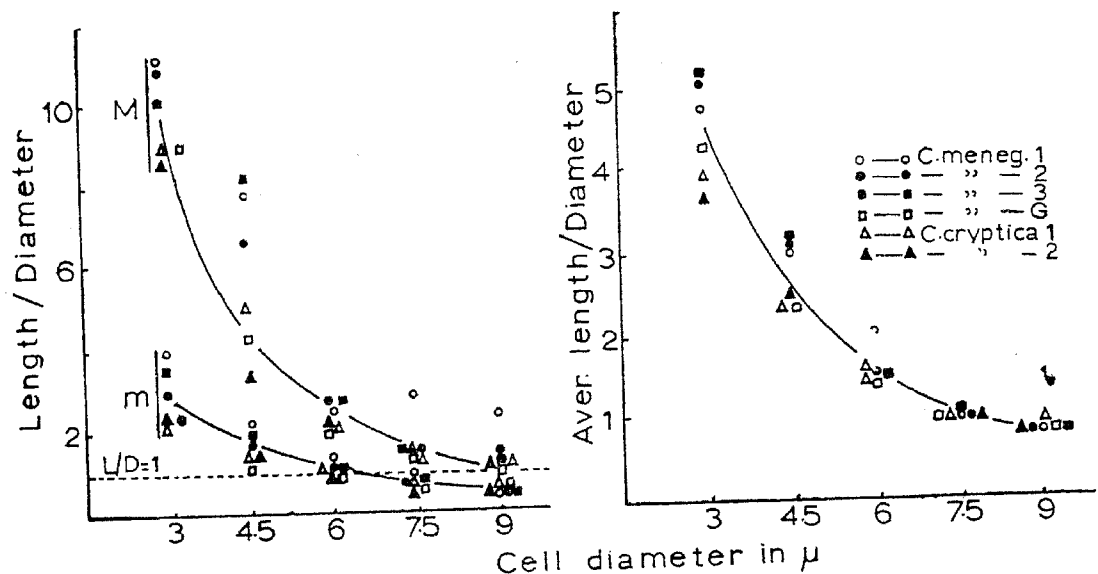
Left: Two curves showing minimum (m) and maximum (M) lengths/diameter (L/D) recorded for cells of different diameters.

Right: Curve showing the relationship of cell diameter to average length/diameter (Av. L/D).

to induce auxospore formation in these isolates have failed and a study of full range of cell diameters was not possible. Nevertheless, it was possible to

compare their behaviour with smaller cells of the Indian isolates grown in Reimann medium. All the isolates showed a similar length/diameter relationship as the Indian *C. meneghiniana* (Text-Fig. 4).

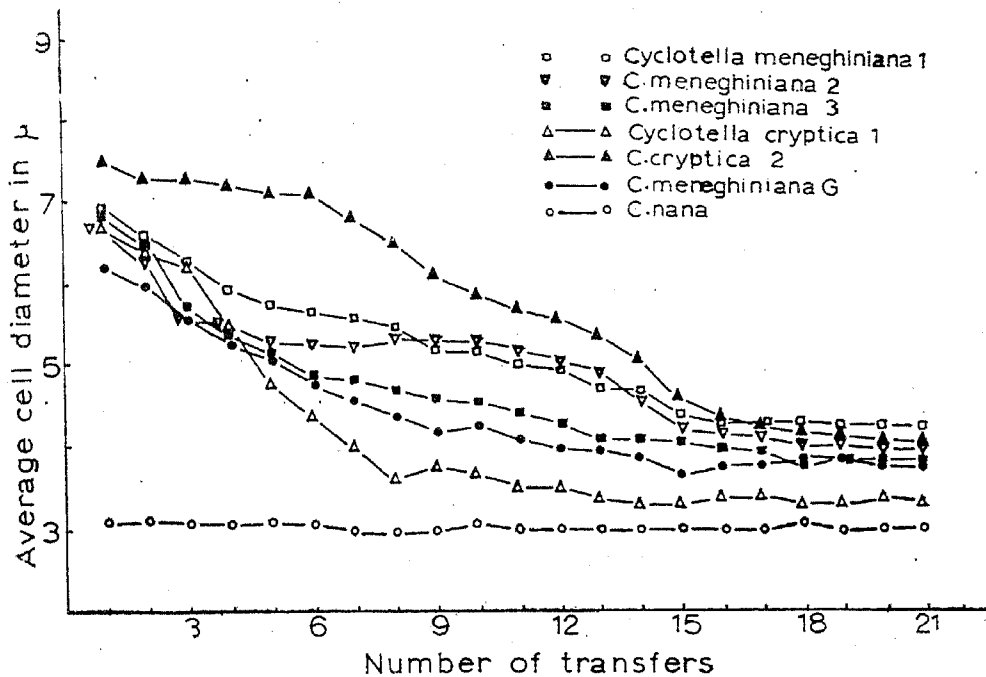
These isolates maintained themselves indefinitely for several subcultures at the lowest size range when grown in Reimann medium. Their behaviour is similar to the one observed in the Indian isolates (Text-Fig. 5). We have referred earlier to the elastic and barrel nature of the girdle band in the small cells of *C. meneghiniana*. In these isolates also many small cells had very thin girdle bands (*cf. also* Lewin and Lewin, 1960; Plate III, Fig. 29 B; Guillard and Ryther, 1962; Plate II, Fig. 2 B; Badour, 1968, Fig. 6). We consider that the elasticity and the resultant barrel-shaped condition of the girdle bands in smaller cells are responsible for the maintenance of a constant minimum size during their continued growth in culture.



TEXT-FIG. 4. Two graphs showing similarity in the minimum (m) and maximum (M) length diameter and average length/diameter in cells of *C. meneghiniana* and *C. cryptica*. *C. meneghiniana*: 1. Cooum estuary, Madras; 2. Beach Pool, Madras; 3. Garden Pond, Madras; G. Göttingen. *C. cryptica*: 1. Indiana; 2. Göttingen.

C. nana (1020-1b; Göttingen Culture Collection, W. Germany) also maintained a constant size (*see* Text-Fig. 5) and showed perivalvar elongation (*cf.* Text-Fig. 3). When obtained *C. nana* had reached the smallest diameter range which it maintained throughout. From the study of Guillard and Ryther (1962) it is evident that *C. nana* had larger cells. It is interesting to note that they themselves noted perivalvar elongation in smaller cells of

this alga. Pervalvar elongation seems to occur in other small *Cyclotellas* also and we do not consider *C. pratii* a distinct species but conspecific with *C. meneghiniana*.



TEXT-FIG. 5. Average diameter of cells of *Cyclotella meneghiniana*, *C. cryptica* and *C. nana* grown in Reimann medium for 21 months with monthly transfers.

C. meneghiniana: Isolates from 1. Cooum estuary, Madras; 2. Beach Pool, Madras; 3. Garden Pond, Madras; G. Göttingen. *C. cryptica* 1. Indiana; 2. Göttingen.

Reimann *et al.* (1963) described a new species, *Cyclotella cryptica* which is similar to *C. meneghiniana*. Light microscope studies revealed no apparent distinction between these two. However, electron microscope studies showed that in smaller cells of *C. cryptica* the areolae seemed to invade into the central area and in the smallest valves the central area was completely obliterated. This, they considered as a distinguishing feature to separate the two species. EM pictures of *C. meneghiniana* given by Reimann *et al.* (1963) appeared to be those of cells of about 15 μ diameter. They did not give pictures of smaller cells. In the present study, in smaller cells of *C. meneghiniana* (cells less than 10 μ diameter), the areolae tend to become less clearly demarcated and in the smallest cells the central area is very nearly obliterated, presenting a condition similar to that seen in *C. cryptica*. While frustule structures of *C. cryptica* as described by Reimann *et al.* (1963) are very distinct from frustule structures obtained in our study, some electron micrographs of frustules of *C. cryptica* published recently (Badour, 1968; Figs. 3, 4, Hasle, 1972, Fig. 4) bear a very close resemblance to our *C. meneghiniana*, suggesting

that the two species are conspecific. A study of whole range of sizes grown in the same medium is essential for a proper comparison between the two species. Although we had obtained cultures of *C. cryptica* (when obtained these had only small cells), it has not been possible to study larger cells as attempts to induce auxospore formation in this diatom were unsuccessful. Nevertheless, variations in frustules of these two species are quite similar. Recently Schultz and Trainor (1970) studied variation in frustule ornamentation in a particular clone, 03 A, originally identified as *C. cryptica*. Frustules of the same clone had different valve patterns. *C. meneghiniana* pattern was found characteristic of the largest valves. Smaller cells had valve patterns of either *C. meneghiniana* or *C. cryptica* with an occasional one with a valve of each type. They considered that the variation in valve pattern was environmentally influenced and possibly salinity was involved. Thus, the observations made by us in the present study, on variations in *C. meneghiniana*, and the evidences presented by Schultz and Trainor (1970) very strongly suggest that *C. cryptica* may after all be a variant of *C. meneghiniana*.

Studies on clonal populations and over the entire size range exhibited by a diatom appear to be necessary for a proper understanding of the variations and in the assessment of its taxonomic distinctiveness. As more and more diatoms are studied similar taxonomic problems may crop up in other species and genera.

ACKNOWLEDGEMENTS

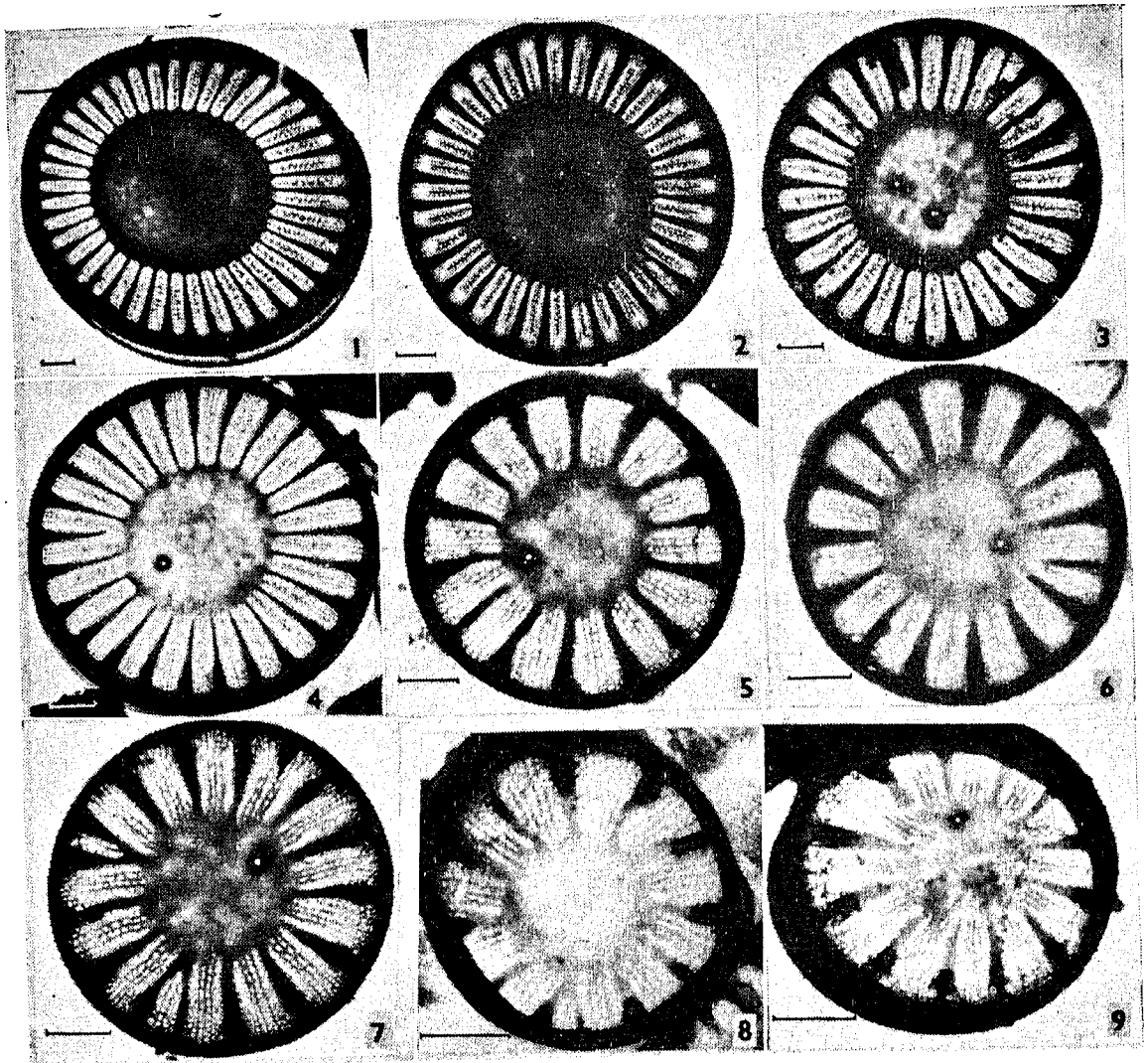
Our grateful thanks are due to Prof. R. Starr of the Indiana Culture Collection, U.S.A., for the culture of *Cyclotella cryptica* and to Dr. W. Koch, University of Göttingen for cultures of *C. cryptica*, *C. meneghiniana*, and *C. nana*. Stereoscan pictures were first taken when one of us (TVD) was in the U.K. on a British Council grant. We thank Dr. F. E. Round, Department of Botany, University of Bristol, Bristol and Miss Patricia A. Sims, British Museum (Natural History), London, for their kind help in taking scanning electron micrographs. Pictures, taken by Miss P. A. Sims, are published with the permission of the Trustees of the British Museum (Natural History).

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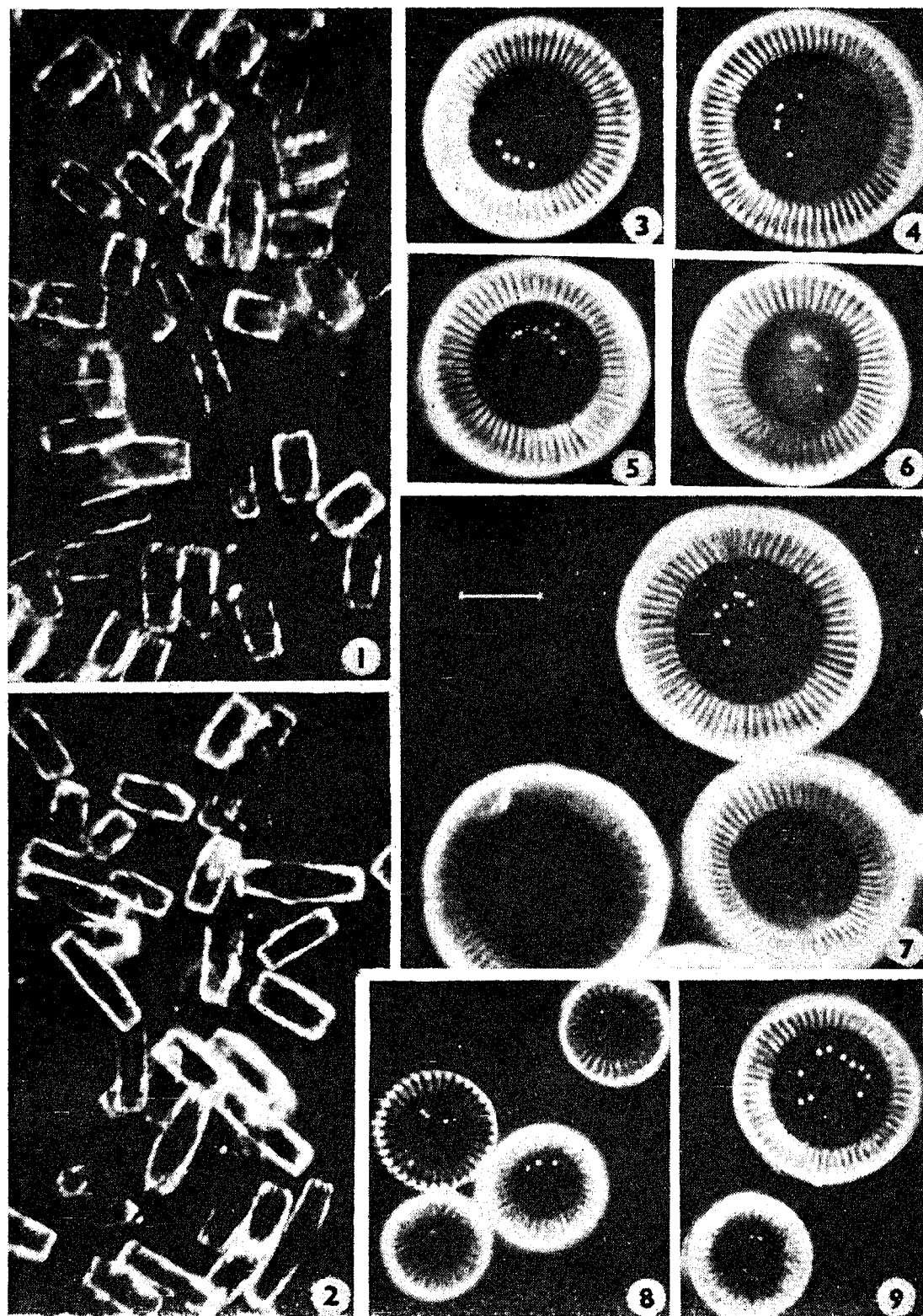
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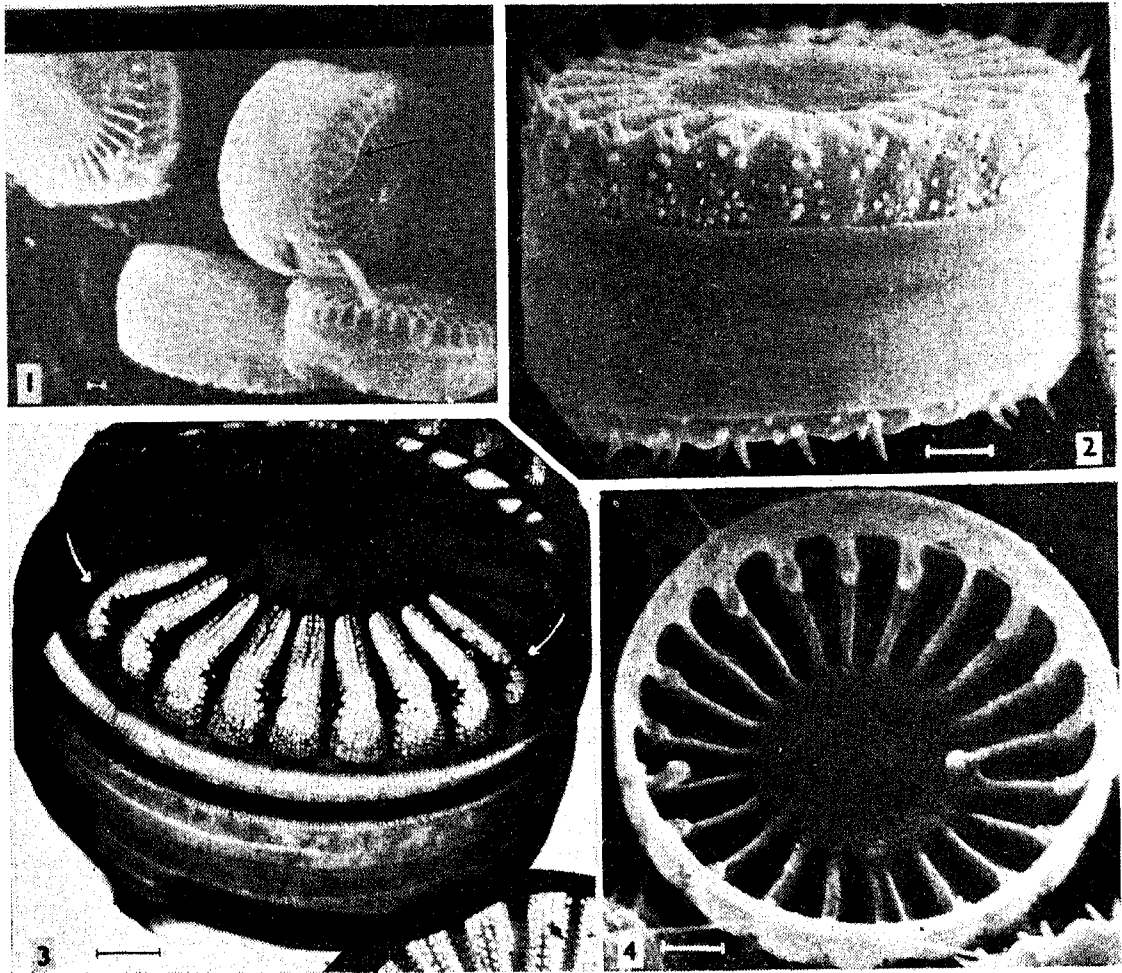
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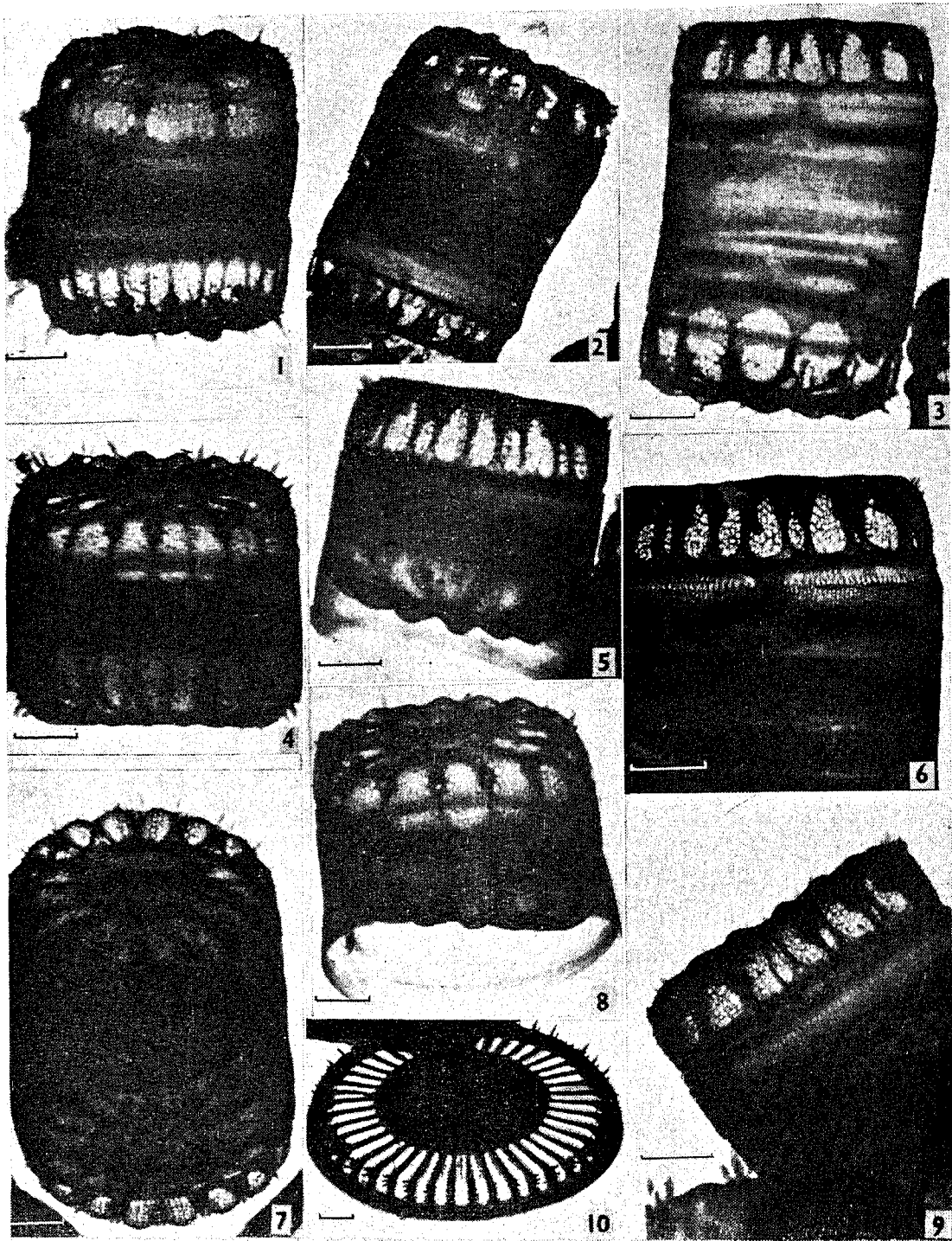
FIGS. 1-9. *Cyclotella meneghiniana*. Electron micrographs of frustules of different diameters showing variations in areolae. Scales represent 1 μ .



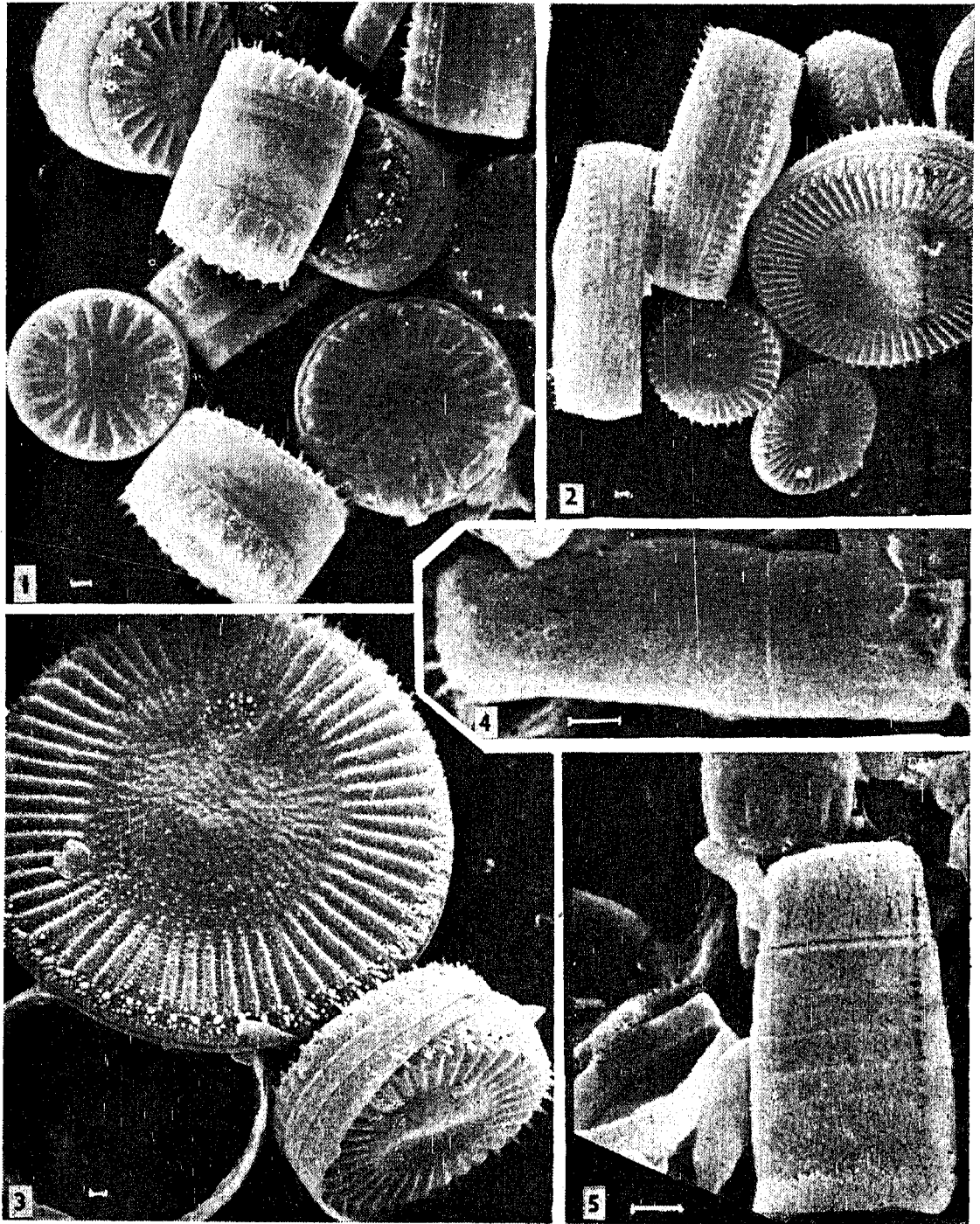
FIGS. 1-9. *Cyclotella meneghiniana*. Photomicrographs of frustules of different diameters under dark field illumination. Figs. 1 and 2. Showing frustules with perivalvar elongation; Figs. 3-9. Frustules showing varying number of punctae in the central area. Scale represents 10μ .



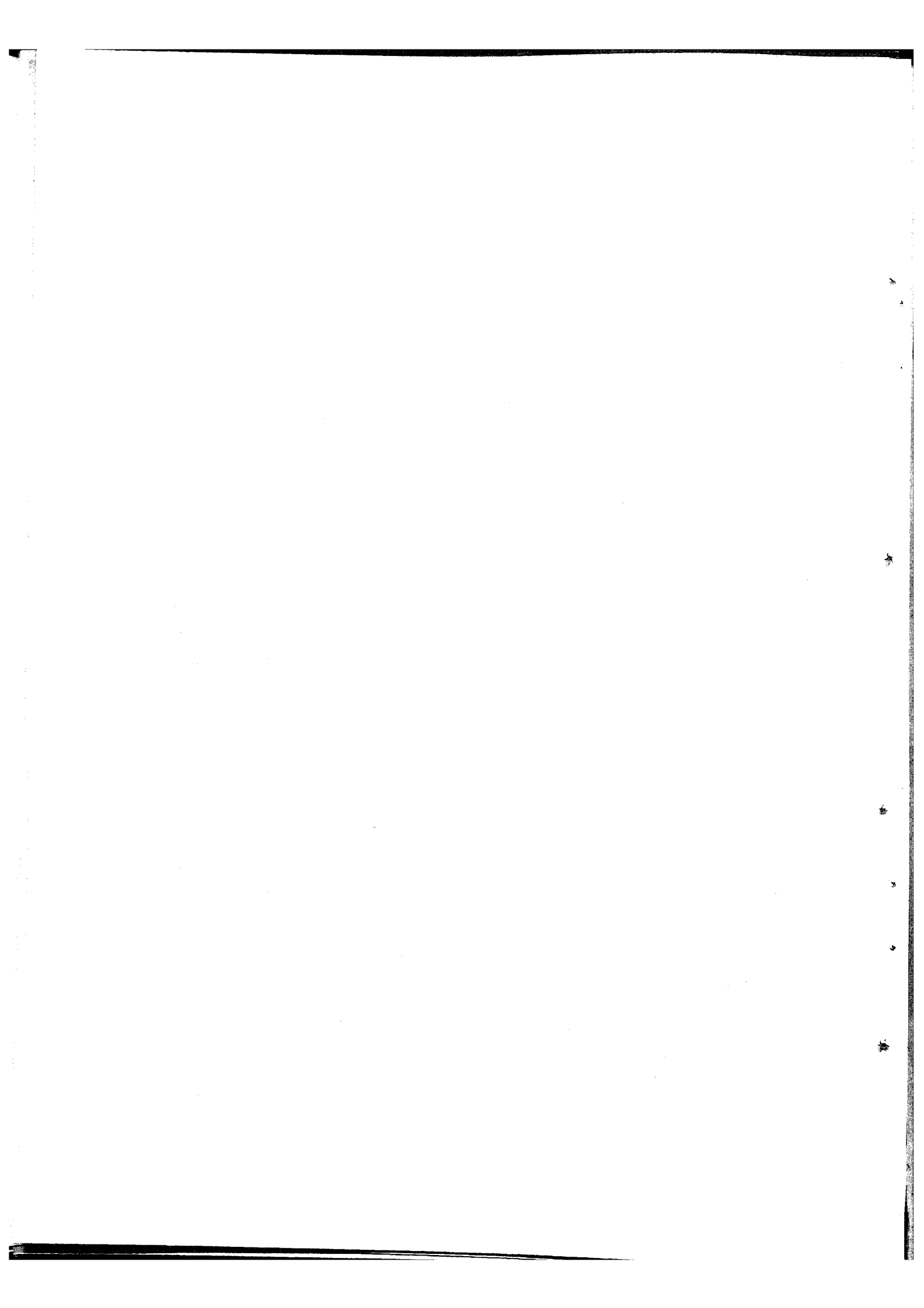
FIGS. 1-4. *Cyclotella meneghiniana*. Fig. 1. Scanning electron micrograph of uncleaned frustule showing organic skin external to the silica frustule, arrow indicates the organic skin. Fig. 2. Scanning electron micrograph of cleaned frustule showing the rim of valve with spines; Fig. 3. Electron micrograph of the mantle region of the frustule clearly showing areolae extending upto the edge of the mantle. Arrows indicate the position of the spines on the costae and the mucilage canal opening, on the rim of the valve. Fig. 4. Scanning electron micrograph showing the inner side of the valve with the mucilage canal opening on each of the costae. Scales represent 1 μ



FIGS. 1-10. *Cyclotella meneghiniana*. Figs. 1-9. Electron micrographs showing girdle view of frustules. Fig. 10. Electron micrograph of a single valve. Scales represent 1 μ .



FIGS. 1-5. *Cyclotella meneghiniana*. Scanning electron micrographs of frustules with different diameters. Note the varying 'lengths' (perivalvar elongation) of the frustules in cells with different diameters. Scales represent 1 μ .



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3961/73. Published by B. S. Venkatachar, Editor, 'Proceedings of the Indian
Academy of Sciences', Bangalore and Printed by V. J. F. Jesudason at the
Bangalore Press, Bangalore-560018
