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THE BIOLOGY OF DESMIDS

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Subsequent experiments in mineral media containing varying concentrations of strontium alone and with barium, and also barium and calcium have, however, revealed no indication that any of the crystals in these cells contained this rare element, though all again showed barium and sulphur to be their major constituents.

Most observations on the intriguing problem of vacuolar crystal movements have been made on *Closterium* species with spherical vacuoles. Their continual activity is well documented and as a result of careful analysis it became clear that although one component is purely physical and determined by Brownian movement, superimposed on these are other, more irregular motions. Over a hundred years ago, Schumann (1875) suggested that, at least in part, the latter was a consequence of perivacuolar activity of the cytoplasm. He supported this view by stressing that the crystals are not scattered throughout the vacuole but aggregate as a single mass in its centre. Cytoplasmic currents can be readily seen by virtue of the granules entrapped in the cytoplasm which circulate, especially round spherical vacuoles (Fig. 31). They not only change the shape of the vacuole, but the pressures developed by them are transmitted to the crystals inside. These small shock waves, though unequal, are said to be felt in a centripetal direction from all sides. Because of their inequality they cause the crystals to exhibit their characteristic agitation, and because they originate on all sides, the centre of vacuole is clearly the natural place for their aggregation.

Fischer (1883) also considered that it was cytoplasmic movement that caused crystal movement and demonstrated a correlation between crystal agitation and cytoplasmic activity. By adding ammonia, which arrests cytoplasmic movement without causing plasmolysis, to *Closterium* cells, Fisher noticed that the movement of the crystals became less intense, and indeed appeared to show only Brownian movement. Wurtz (1942) carried out similar observations but killed the cells with formalin or alcohol. Cytoplasmic activity then stopped immediately but the Brownian movement of the crystals, observed by Fischer was still visible. Even when cytoplasm and chloroplasts had contracted the crystals still exhibited activity and it was only when the vacuolar fluid increased in viscosity following this drastic treatment that all movement stopped. That crystal activity has a component other than purely physical Brownian movement would seem to have been confirmed by Frey (1926) by simple observations on spherical vacuoles. By inclining his microscope from the vertical to the horizontal position, he noticed that by the resulting sudden change in the direction of gravity, the crystals accumulated at the base of the vacuole but from this mass, occasional crystals were projected from out of the heap. This author concludes that 'ce sont plutot des courants centripetes, sans

doubte des jets d'excretion qui se superposent au mouvement brownien'.

Wurtz has followed in detail crystal movement in the elongated conical vacuoles of *C. diana*e and finds that in the basal region, crystal activity is constant, though jerky, and attributable to Brownian movement and does not extend beyond the middle of the vacuole. Suddenly, however, one or two crystals appear to travel by a slow and even movement along the length of the vacuole before resuming their Brownian movement, though he comments that this had nothing in common with the projections described by Frey since the displacement was neither as slow, nor as regular. Wurtz carefully recorded the position of individual crystals at regular intervals and in the case where there were 2 large and 3 small crystals, it was the small crystals which were entrained most easily in these slow, regular but intermittent movements (Fig. 32). With these he also recorded a rolling rotation, though this did not seem to be complete or regular. He also noted that, in accordance with Einstein's law, the Brownian movement of the small crystals was more intense than that of the large ones.

It has already been mentioned (p. 72) that Wurtz repeated with *C. diana*e Frey's experiments in which the microscope was placed horizontally instead of vertically. The crystals fell to the bottom of the vacuole, but in accordance with Stokes' law, the large granules fell more rapidly than the small ones. Indeed, the latter took up to 3 min to reach the bottom. Some, however, adhered to the vacuole wall and fell much more slowly than if following Stokes' law. Also, though most of the crystals remained as a group after this radical change in cell orientation, on the base of the vacuole, the small ones still showed the entrainment movements already described. Wurtz invokes Schumann's (1875) explanation of cytoplasmic activity for such movements of the vacuolar contents.

Wurtz has described the changes in the shape of the conical vacuoles of *C. diana*e already alluded to (p. 71). The basal part of the vacuole does not change shape, but he records changes in the shape of the lateral margins due to undulations caused by the cyclosis of the cytoplasm around the vacuole which occur in successive waves. This activity causes marked changes in the pointed upper part of the vacuole which changes shape endlessly. Sometimes the vacuole may fragment and then merge, become markedly pointed at its extremity; also small diverticulae may be produced from the side, producing small independent vacuoles. These then fuse producing again in a few moments an entire vacuole. All such changes are rapid, thus giving an impression of great instability, and appear to be attributable to the actions of the surrounding cytoplasm (see also Leblond 1928).

OTHER CELL VACUOLES

In the introduction to their five volume work 'The British Desmidiaceae'

West and West (1904, p. 5) state that 'the cell protoplasm occupies a large proportion of the interior of the wall and a portion of it always completely lines the inner surface of the cell wall.' The protoplasm contains numerous granules, largely of nutritive nature, and it exhibits a well-marked 'circulatory movement'. Personal experience indicates that especially in certain large species of *Closterium* (e.g. *C. didymotocum*) these movements may be more vigorous than in any other plant cells normally used to demonstrate cyclosis to laboratory classes. Very small granules (mitochondria?) can be seen in these cytoplasmic streams which also surround the apical vacuoles in the genera *Closterium* and *Pleurotaenium* (Fig. 31). However, also carried in the stream may be granules of the size and angular shape of the crystals enclosed within the terminal granules (Fig. 33). (See also p. 70.)

The Wests also comment later that 'when desmids are kept alive for

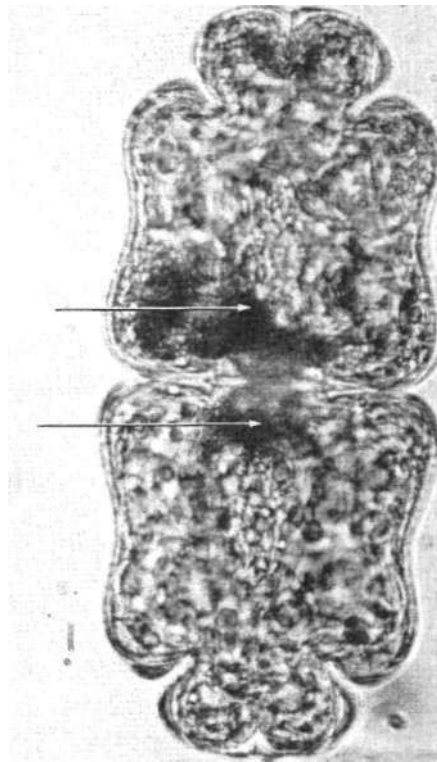


Fig. 33. A photomicrograph of a freshly gathered specimen of *Euastrum crassum* (Breb.) Kiitz. showing (arrows) dark patches of swarming granular material surrounding cell vacuoles.

some time, especially under abnormal circumstances, the protoplasm develops numerous vacuoles, often of large size, all of which become filled with a dense, swarming mass of granular material'. Observations of living material from Scottish lochs has revealed swarming masses of granules to be present even in material examined within a few hours of collection. It has also been found that they are present much more commonly in large than small desmid cells. Moreover, it is questioned whether the violently jiggling granules occur, as the Wests state, within the vacuoles but instead occur within the cytoplasm surrounding the vacuoles. For example, recently examined material from the metaphyton associated with *Sphagnum subsecundum* in the Dubh Loch, Loch Lomond, Scotland, has revealed that, particularly in cells of *Euastrum crassum* and *E. ansatum* (Figs 33 and 34), also of *Xanthidium armatum* (Fig. 38: 4), these granules are so dense in certain parts of the cell that when examined with a x 40 objective they appear as brownish patches. Higher magnification reveals the intense activity described by the Wests, but as shown in the accompanying illustrations, and especially in the side view of *E. ansatum* (Fig. 34), the granules are clearly exterior to the vacuoles. Masses of swarming granules have been observed in cells of *Pleurotaenium ehrenbergii* and these also appeared as brown patches under low magnification (Fig. 34). It should be noted that the position of the granules and their abundance differ in adjacent semicells and some cells (for example *Penium cucurbitum* var. *scoticum*) an aggregation of small swarming granules was observed in only one semicell.

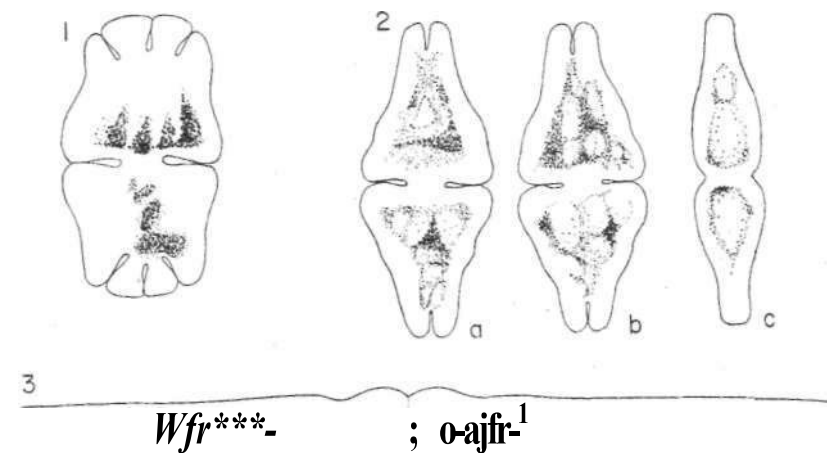


Fig. 34. Line drawings from living material of *Euastrum crassum* (Breb.) Kiitz. (1) *E. ansatum* Ralfs (2 a-c) and *Pleurotaenium ehrenbergii* (Breb.) de Bary (3) showing the position of granular swarms (mitochondria?) surrounding the cytoplasmic vacuoles.