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Aggregates of the acritarch *Dilatisphaera laevigata*: faecal pelletization, phytoplankton bloom or defence against phagotrophy?

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ABSTRACT – Monospecific aggregates of 2–7 individuals of the Silurian acritarch *Dilatisphaera laevigata* Lister are described. Each generally consists of a central collection of vesicles surrounded by elongate, radiating processes. Acritarchs could aggregate by chance during sample processing, or they may have formed within a sporangia-like structure, although such structures are considered unlikely for *D. laevigata*. Analogies with modern algae suggest that the aggregates of *D. laevigata* could have formed by faecal pelletization in the surface waters, or by coagulation of individuals during phytoplankton blooms. In this latter instance the baculate/spinose vesicle ornament and digitate-like branching of the processes may have increased the chances of adhesion. It is also plausible that the aggregates may represent a morphological defence against predation or parasitic infection. *J. Micropalaeontol.* **22**(2): 163–167, November 2003.

INTRODUCTION

Acritarchs are an informal, probably polyphyletic, group of eukaryotic, unicellular (or apparently unicellular), organic-walled microfossils of uncertain affinity, although many may be the cysts of phytoplanktonic algae related to dinoflagellates (Evitt, 1963; Martin, 1993; Colbath & Grenfell, 1995; Moldowan *et al*., 1996; Moldowan & Talyzina, 1998).

The genus *Dilatisphaera* Lister has been recognized as having a morphology that is similar to some dinoflagellate cysts (Martin, 1966, p. 389; Lister, 1970, p. 65). However, *Dilatisphaera* was excluded from the *Cymbosphaeridium* clade of Colbath & Grenfell (1995), whose members were cited as possible candidates for Lower Palaeozoic dinoflagellates, and it also lacks the characteristic dinoflagellate cinglum, sulcus, paratabulation and archaeopyle (see Evitt, 1963, 1985).

The first aggregates of acritarchs and prasinophytes were recorded in the 1960s, although little substansive research has been completed on them. This is unfortunate, as they could elucidate aspects of the palaeobiology and palaeoecology of these groups. Clusters of the sphaeromorph microplankton *Synsphaeridium* Eisenack, *Protoleiosphaeridium* Timofeev, *Leiosphaeridia* Eisenack and *Tasmanites* Newton are well known (e.g. Eisenack, 1965, pl. 23, figs 1–2; pl. 24, fig. 1; Combaz, 1967, pl. 1, figs A–B, E–L; pl. 2, figs A–M; pl. 3, figs A–H). However, aggregates of netromorph, acanthomorph and diacromorph acritarchs have also been reported, including *Leiofusa* (now *Eupoikilofusa*) cf. *striatifera* Cramer, *Deunffia furcata* Downie, *Micrhystridium* Deflandre, *Priscogalea* Deunff, *Cymatiogalea* Deunff, *Tectitheca* Burmann and *Acanthodiacrodium* Timofeev (Combaz *et al*., 1967, pl. 1, figs N–P; Cramer, 1970, pl. 2, fig. 32; Downie, 1973, p. 245, pl. 25, fig. 1).

This study illustrates aggregates of the Silurian acritarch *Dilatisphaera laevigata* Lister, the type species of the genus. Similarities are drawn with the formation of colonies in modern algae as a defence against phagotrophy, or by the coagulation of cells through particle collision in the surface water and also through faecal pelletization. The possible functional morphology of the processes and vesicle ornamentation of *D. laevigata* is also suggested.

LOCALITY AND METHODOLOGY

Sample DB-BB/33 comes from the middle part of the Lower Bringewood Formation (*c*. 17.15 m above the base of the section), Ludlow Series, Silurian, of the Downton Gorge section, Downton-on-the-Rock, Ludlow, UK (Fig. 1A; Ordnance Survey grid reference SO 428 729–SO 431 732; see Holland *et al.*, 1963; Lawson & White, 1989). The sample was processed using a standard HCl, HF, HCl palynological technique, with heavy liquid separation (sodium polytungstate, S.G.=2.0) and sieving at 10 μm being employed to concentrate the organic residue (see Mullins, 2001).

To enable relocation, specimens were strew mounted on to nickel particle analysis grids attached to glass coverslips with Petropoxy 154 adhesive. These coverslips were fixed on to 12.5 mm diameter SEM stubs with dental wax and the specimens were sputter coated with gold-palladium for 120 seconds and then examined with a SEM. To enable study with transmitted light microscopy, the glass coverslips were inverted and attached to glass slides using Petropoxy 154 adhesive and the SEM stubs and dental wax were removed.

All figured specimens are deposited in the collection of the British Geological Survey, Keyworth, Nottingham NG12 5GG, UK (prefix MPK).

AGGREGATES OF DILATISPHAERA LAEVIGATA

Specimens of *D. laevigata* are typically recovered as individuals and comprise a central laevigate, baculate or spinose vesicle surrounded by radiating, broad-based, columnar processes (Pl. 1, figs 5–6). However, *D. laevigata* may also occur in aggregates of between two and seven individuals, with a clear skew towards pairs (Fig. 1B). The vesicles in each aggregate may be distinct, or so closely associated that they appear to form an undifferentiated central mass, although this may reflect the generally poor preservation of the material (Pl. 1, figs 1–4). In both instances the central mass is surrounded by radiating processes and the majority of the vesicles lack excystment openings, although some may show large equatorial ruptures (Pl. 1, figs 3–4).

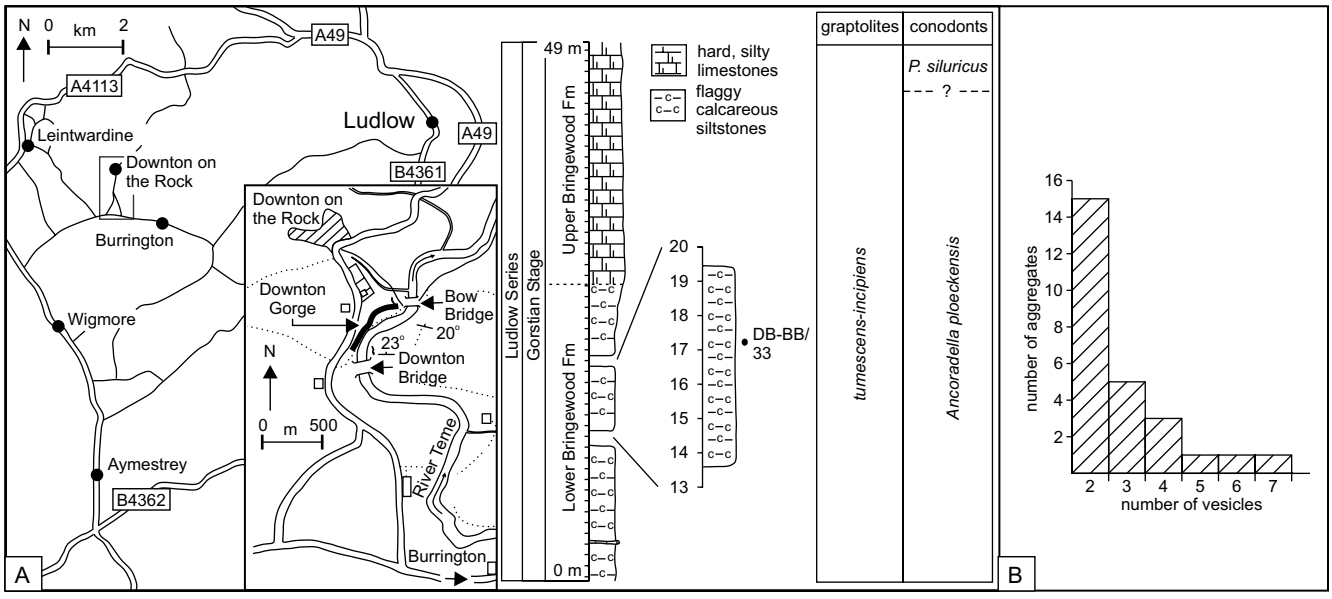


Fig. 1. (**A**) Locality map and stratigraphy of the Downton Gorge section, Downton-on-the-Rock, Ludlow, UK. The level of sample DB-BB/33 is also shown. (**B**) A histogram showing the number of vesicles present in the first 26 aggregates of *D. laevigata* observed.

DISCUSSION

Five possible scenarios may account for the aggregation of acritarchs and prasinophytes.

Chance

Aggregates may form by the clumping together of specimens during processing or slide making. This is considered extremely unlikely for *D. laevigata*, however, as the aggregates are monospecific, large numbers can occur in an aggregate, and the vesicles are commonly fused together and arranged towards the centre.

Sporangia

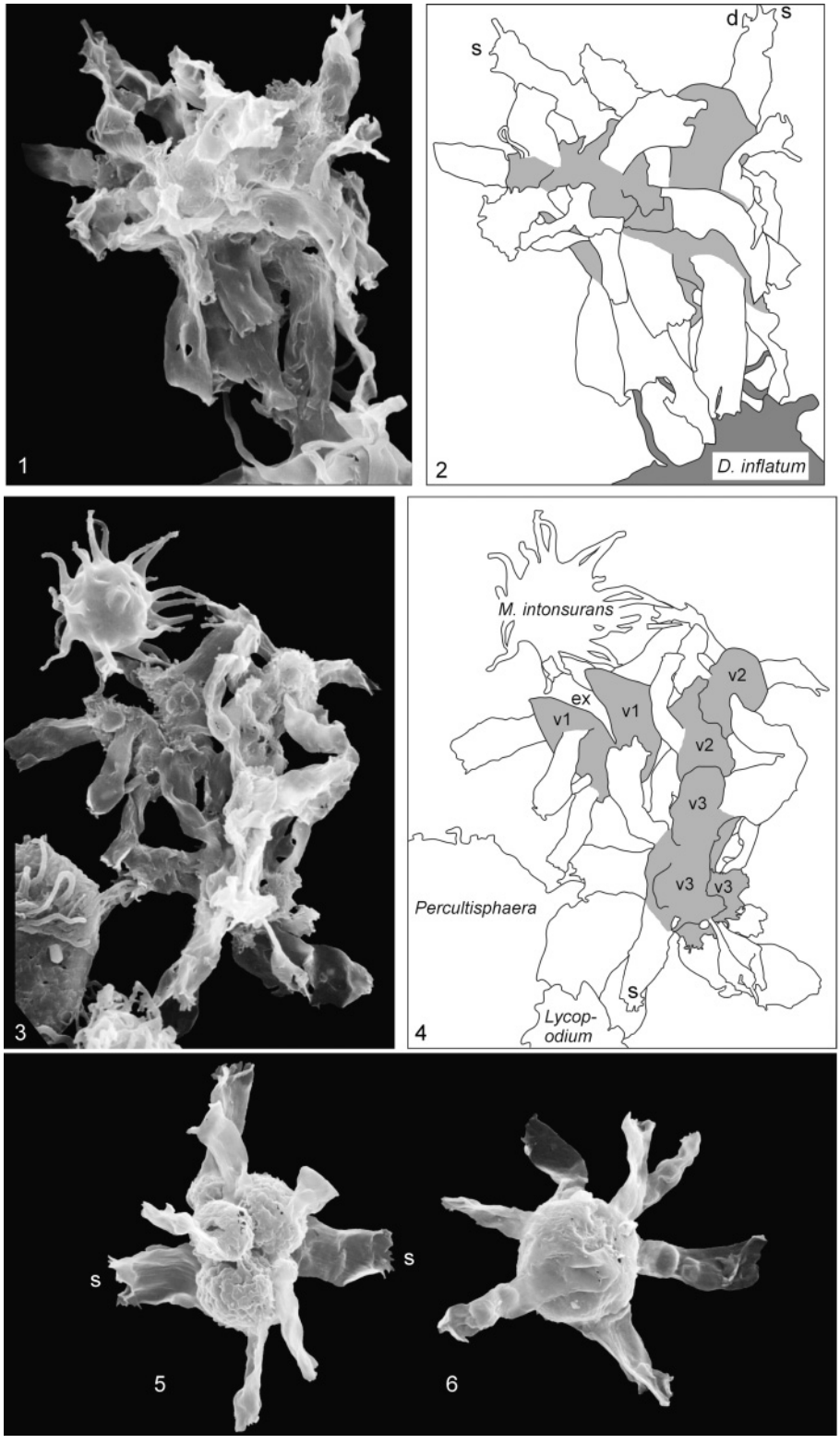
Downie (1973) considered the shape, size and occasionally the composition of aggregates, presumably sphaeromorphs, to be consistent with their production within a sporangia (like those of the Devonian non-vascular land plant *Parka*). Although it is plausible that some early sphaeromorph aggregates may represent masses of crytospores, it is considered unlikely here that acanthomorph acritarchs such as *D. laevigata* formed within a sporangia, as no modern or fossil analogue is known.

Faecal pelletization

The aggregates of *D. laevigata* could represent the faecal pellets of zooplankton (for example the graptolites) that grazed in the surface waters. Specimens of *D. laevigata* are more poorly preserved than the other microplankton in sample DB-BB/33, although this could reflect a less resistant wall composition rather than ingestion. It has been suggested that faecal pelletization would dominate the removal of phytoplankton from the surface waters during normal, non-bloom conditions (Boehm & Grant, 1998). It may be expected, therefore, that the faecal pellets produced under these circumstances would contain many species. However, the aggregates observed here are monospecific, although occasionally other acritarchs may be in random association (e.g. Pl. 1, figs 1–4). The arrangement of the vesicles towards the centre of the aggregates, lack of deformation to the processes (other than that caused by compaction and pyrite growth) and presence of excystment openings may also suggest that ingestion had not occurred (Pl. 1, figs 1–4). However, it is plausible that excystment occurred before ingestion, or that the cell contents may have remained viable even after ingestion. Porter (1977) reported that the modern green alga *Sphaerocystis schroeteri* Chodat is protected by a gelatinous sheath and may remain viable, and even benefit nutritionally, after ingestion. Similarly, the green algae *Chlorella stigmatophora* Butcher and *Stichococcus* may also remain viable after ingestion (Marshall & Orr, 1955; Gibor, 1956).

Coagulation in phytoplankton blooms

Coagulation of the acritarch-producing organisms or encysted acritarchs during bloom conditions could produce aggregates. It has been suggested that aggregates of phytoplankton may form by particle collision, with the number of cells within each aggregate being dependent on the concentration, size and species of alga (some modern algae become more sticky when nutrient limited), the initial nutrient concentration, the depth of the mixed layer, the shear rate and the hydrodynamic interactions between the cells (Kiørboe *et al*., 1990; Jackson & Lochmann, 1992; Burd & Jackson, 1997). It has also been suggested that aggregation limits the maximum concentration that actively growing populations may achieve and that it inhibits the predation of algae by accelerating the removal from the surface waters of those cells that have stopped growing (Jackson & Lochmann, 1992). Modelling also predicts that aggregation and gravitational settling dominates phytoplankton dynamics during bloom events, when the concentration of zooplanktonic predators is relatively low (Jackson & Lochmann, 1992; Boehm & Grant, 1998).



Explanation of Plate 1.

figs 1–6. *Dilatisphaera laevigata* Lister, 1970: **1,** MPK13028, aggregate with an undifferentiated mass of vesicles, DB-BB/33, stub 1, M40, ×1500; **2,** explanatory diagram of fig. 1 showing the mass of vesicles in a light grey tint and an associated specimen of *Dorsennidium inflatum* (Downie) in a dark grey tint. The spinose (s) and digitate-like (d) process branches are also shown; **3,** MPK13029, aggregate of three individuals, DB-BB/33, stub 1, P35/3, ×1500; **4,** explanatory diagram of fig. 3 showing the location of the vesicles (v1–v3, grey tint) and associated specimens of *Micrhystridium intonsurans* (Lister), *Percultisphaera* Lister and a modern *Lycopodium* spore introduced to enable quantitative analysis. The excystment opening (ex) and spinose process branching (s) are highlighted. **5,** MPK13030, single specimen with a pyrite distorted vesicle, with baculate ornament and spinose process terminations (s). DB-BB/33, stub 1, N43, ×1500; **6,** MPK13031, single specimen with a laevigate vesicle, DB-BB/33, stub 1, Q42, ×1500.

A monospecific bloom could account for the aggregates of *D. laevigata* observed here. Further, the vesicle ornament and process branching of *D. laevigata* could aid the formation of monospecific aggregates, even if a bloom contained other taxa, though increasing the chances of adhesion (see below). Within sample DB-BB/33 *D. laevigata* comprises only <3% of the total acritarch and prasinophyte assemblage. A relatively short-lived event could account for this low relative abundance, as its signal would become obscured by the subsequent deposition of other phytoplankton.

Defence

Aggregation may represent a defence against grazing or parasitic infection. From the perspective of the fossil record the acritarchs and prasinophytes appear to have formed the majority of the plankton and, therefore, perhaps the basis of the Palaeozoic food-web.

Modern algae use a number of defence mechanisms against herbivory and parasitic attack by fungi, bacteria and protists. These include very small or large cell size, rapid cell division, seasonal growth and encystment, migration through the water column, toxicity, bioluminescence, the use of sporopollenin-like polymers, the production of an encompassing gelatinous sheath and the arrangement of the organism into colonies (see Porter, 1977; Hessen & van Donk, 1993; van Donk *et al*., 1997; Graham & Wilcox, 2000).

The mutation of unicellular algae to form colonies as a defence against predation has been well documented in two modern taxa. The green alga *Scenedesmus subspicatus* Chodat is predominantly one or two-celled until the introduction of the predatory *Daphnia*, or even the medium in which *Daphnia* had been grown. *S. subspicatus* then develops eight-celled 'colonies' which dominate the cultures within 3–5 days (Hessen & van Donk, 1993). It was postulated that the the larger size and spinose armouring makes them more resistant to phagotrophy (Hessen & van Donk, 1993).

The modern green alga *Chlorella vulgaris* Beij is also unicellular, but forms globular clusters of cells with the introduction of the phagotrophic, biflagellate, chrysophyte alga *Ochromonas vallescia* (Boraas *et al.*, 1998). *O. vallescia* was unable to ingest these larger colonies and only unicells and smaller 'neonatal' colonies were consumed (Boraas *et al*., 1998).

It is plausible that the larger size of the *D. laevigata* aggregates made them inaccessible to predators. Further, the vesicles are commonly arranged towards the centre of the aggregates and are surrounded by radiating processes and these could have acted as a spinose armour to inhibit the grazing or parasitic infection of the cell contents within the vesicles.

POSSIBLE FUNCTIONAL MORPHOLOGY

The vesicle of *D. laevigata* may be laevigate, although it is more commonly spinose or baculate (Pl. 1, figs 5–6; see also Mullins, 2001). The processes are generally broad-based, columnar and they commonly have small (possibly hook-shaped) spines, or digitate-like branches at their distal extremities (e.g. Pl. 1, figs 1–6). It is possible that the interlocking of these process branches with the spinose/baculate vesicle ornament promoted cyst aggregation by increasing the chances of adhesion (see above).

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REFERENCES

Boehm, A.B. & Grant, S.B. 1998. Influence of coagulation, sedimentation, and grazing by zooplankton on phytoplankton aggregate distributions in aquatic systems. *Journal of Geophysical Research, Oceans,* **103**: 15601–15612.

Boraas, M.E., Seale, D.B. & Boxhorn, J.E. 1998. Phagotrophy by a flagellate selects for colonial prey: A possible origin of multicellularity. *Evolutionary Ecology,* **12**: 153–164.

Burd, A. & Jackson, G.A. 1997. Predicting particle coagulation and sedimentation rates for a pulsed input. *Journal of Geophysical Research, Oceans,* **102**: 10545–10561.

Colbath, G.K. & Grenfell, H.R. 1995. Review of biological affinities of Paleozoic acid-resistant, organic-walled eukaryotic algal microfossils (including "acritarchs"). *Review of Palaeobotany and Palynology,* **86**: 287–314.

Combaz, A. 1967. Leiosphaeridaceae Eisenack, 1954, et Protoleiosphaeridae Timofeev, 1959 – leurs affinitiés, leur rôles sédimentologique et géologique. *Review Palaeobotany and Palynology,* **1**: 309–321.

Combaz, A., Lange, F.W. & Pansart, J. 1967. Les "Leiofusidae" Eisenack, 1938. *Review of Palaeobotany and Palynology,* **1**: 291–307.

Cramer, F. 1970. *Distribution of selected Silurian acritarchs. An account of the palynostratigraphy and paleogeography of selected Silurian acritarch taxa.* Revista Española de Micropaleontologia, numero extraordinerio: 1–203, pls 1–23.

Downie, C. 1973. Observations on the nature of the acritarchs. *Palaeontology,* **16**: 239–259.

Eisenack, A. 1965. Mikrofossilien aus dem Silur Gotlands, Hystrichosphären, Problematika. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen,* **122**: 257–274.

Evitt, W.R. 1963. A discussion and proposals concerning fossil dinoflagellates, hystrichospheres and acritarchs. *Proceedings of the National Academy of Science USA,* **49**: 158–164.

Evitt, W.R. 1985. *Sporopollenin dinoflagellate cysts: their morphology and interpretation.* American Association of Stratigraphic Palynologists Foundation, Hart Graphics Inc., Austin, Texas, 1–33.

Gibor, A. 1956. Some ecological relationships between phyto- and zooplankton. *The Biological Bulletin, Marine Biological Laboratory, Woods Hole,* **111**: 230–234.

Graham, L.E. & Wilcox, L.W. 2000. *Algae.* Prentice Hall, New Jersey, 640pp.

Hessen, D.O. & van Donk, E. 1993. Morphological changes in *Scenedesmus* induced by substances released from *Daphnia*. *Archiv für Hydrobiologie,* **127**: 129–140.

Holland, C.H., Lawson, J.D. & Walmsley, V.G. 1963. The Silurian rocks of the Ludlow District, Shropshire. *Bulletin of the British Museum (Natural History),* **8**: 95–171.

Jackson, G.A. & Lochmann, S.E. 1992. Effect of coagulation on nutrient and light limitation of an algal bloom. *Limnology and Oceanography,* **37**: 77–89.

Kiørboe, T., Andersen, K.P. & Dam, H.G. 1990. Coagulation efficiency and aggregate formation in marine phytoplankton. *Marine Biology,* **107**: 235–245.

Lawson, J.D. & White, D.E. 1989. Standard Ludlow Series. *In:* Holland, C.H. & Bassett, M.G. (Eds), *A Global Standard for the Silurian System.* National Museum of Wales, Geological Series: 73–90.

Lister, T.R. 1970. *A monograph of the acritarchs and Chitinozoa from the Wenlock and Ludlow Series of the Ludlow and Millichope areas,*

Shropshire. Monograph of the Palaeontographical Society London, publ. no. 528, **124**: 1–100, pls 1–13.
Marshall, S.M. & Orr, A.P. 1955. On the biology of *Calanus finmarchicus*. VIII. Food uptake, assimilation and excretion in adult and stage V Calanus. *Journal of the Marine Biological Association of the United Kingdom,* **34**: 495–529.
Martin, F. 1966. Les Acritarches du sondage de la brasserie Lust, à Kortrijk (Courtrai) (Silurien belge). *Bulletin de la Société belge de geologie, de paléontologie et d'hyrologie,* **74**: 354–400.
Martin, F. 1993. Acritarchs: A review. *Biological Reviews of the Cambridge Philosophical Society,* **68**: 475–538.
Moldowan, M.J., Dahl, J., Jacobson, S.R., Huizinga, B.J., Fago, F.J., Watt, D.S. & Peters, K.E. 1996. Chemostratigraphic reconstruction of biofacies: molecular evidence linking cyst-forming dinoflagellates with pre-Triassic ancestors. *Geology,* **24**: 159–162.
Moldowan, M.J. & Talyzina, N.M. 1998. Biogeochemical evidence for dinoflagellate ancestors in the Early Cambrian. *Science,* **281**: 1168–1170.
Mullins, G.L. 2001. *Acritarchs and prasinophyte algae of the Elton Group, Ludlow Series, of the type area.* Monograph of the Palaeontographical Society London, publ. no. 616, **155**: 1–154.
Porter, K.G. 1977. The plant–animal interface in freshwater ecosystems. *American Scientist,* **65**: 159–170.
van Donk, E., Lürling, M., Hessen, D.O. & Lokhorst, G.M. 1997. Altered cell wall morphology in nutrient-deficient phytoplankton and its impact on grazers. *Limnology and Oceanography,* **42**: 357–364.