

Palaeoecology of the Early Permian strata at Heimefrontfjella, Dronning Maud Land, Antarctica

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Abstract: Palaeopalynological studies form an integral part of the geological investigation of the Late Paleozoic sedimentary history of Dronning Maud Land. During the examination of organic residues prepared from different localities at Heimefrontfjella, the freshwater green alga *Botryococcus* was found. Exceptionally well-preserved colonies of *Botryococcus* were recorded in several samples at two sections of Early Permian age, Lidkvarvet and Locality A. These colonies vary in form and stage of development. By analogy with observations on recent material the following palaeoecological conclusions are drawn: 1) varying environmental and climatic conditions over a length of time existed at Lidkvarvet, and 2) very short ephemeral aquatic conditions existed intermittently at Locality A.

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Introduction

In 1987 a geological project commenced under the auspices of the Swedish Antarctic Research Programme, SWEDARP. It focuses specifically on the petrography, geophysics and biostratigraphy of the Late Palaeozoic sedimentary history of Dronning Maud Land (Fig. 1). Although Upper Palaeozoic sedimentary rocks have been studied widely from the

Transantarctic Mountains (e.g. by Barrett *et al.* 1972, La Prade 1970, 1972, Matz *et al.* 1972 and Walker 1983) only some sequences have been documented from the Dronning Maud Land region of East Antarctica (Jukes (1972), Hjelle & Winsnes (1972), Wolmarans & Kent (1982), Clarkson (1981) and Olausen (1985)). Upper Palaeozoic sedimentary rocks occur at three different areas in western Dronning Maud Land, namely

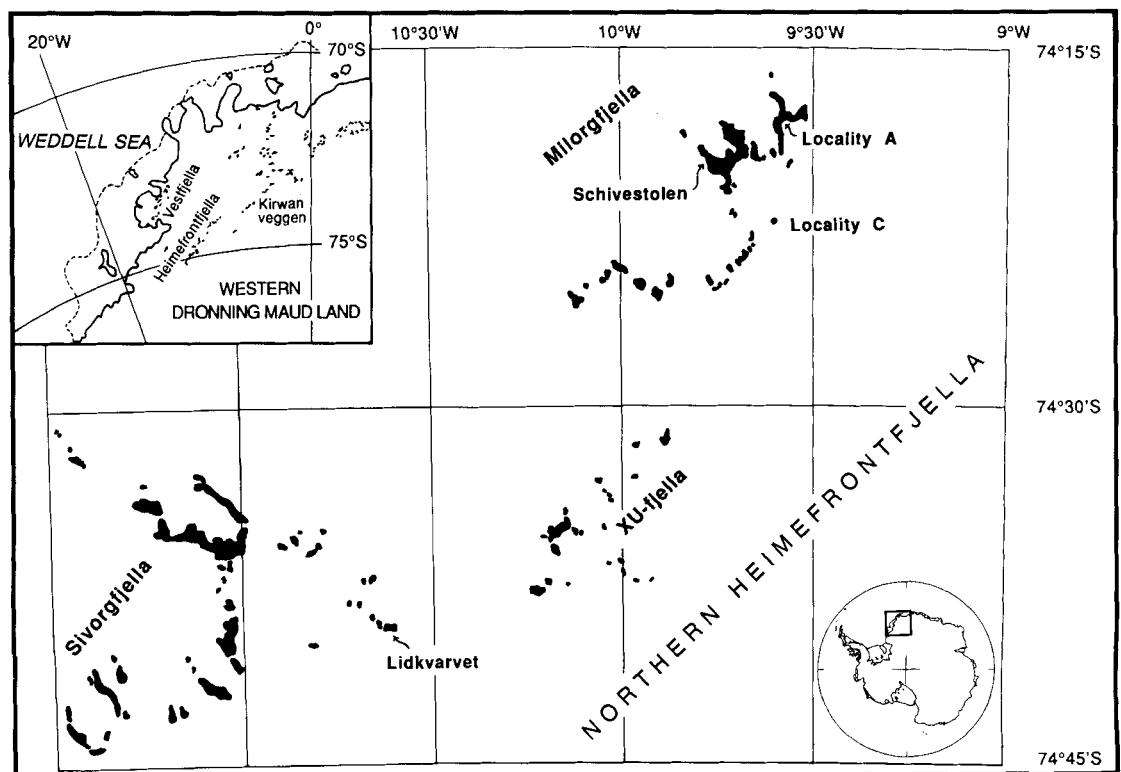


Fig. 1. Map of part of western Dronning Maud Land, showing the investigated localities mentioned in the text.

in Heimefrontfjella, Vestfjella and Kirwanveggen (Fig. 1). The localities in Heimefrontfjella, which were first described by Jukes (1972), were visited during the SWEDARP 1987/88 and 1988/89 expeditions and comprehensive collecting was carried out (Larsson & Bylund 1988, Larsson 1990). The Vestfjella area was investigated during the SWEDARP expeditions 1988/89 and 1989/90 (Larsson 1990, 1991) and the Kirwanveggen area was visited during the 1990/91 SWEDARP expedition (Ahlberg *et al.* 1992). Samples were collected for palynological investigation during all of these expeditions and were processed using standard methods (Guy-Ohlson *et al.* 1984, Vidal 1988).

Microscopical examination (transmitted light and scanning electron microscopy (SEM)) of the organic matter recovered from these samples revealed a variety of palynomorphs (organic-walled microfossils) (Larsson *et al.* 1990) and palynofacies (Lindström 1994). The palynomorphs are relatively well preserved and consist mainly of dispersed pollen grains and spores, acritarchs and microalgae (Larsson *et al.* 1990, figs 8–10, Lindström in press).

Palynostratigraphical studies of four localities at Heimefrontfjella, namely localities A, C, Schivestolen and Lidkvarvet, suggest that they are of various Early Permian ages (Larsson *et al.* 1990 and Lindström 1994), whereas the sedimentary rocks at Vestfjella are of early Late Permian age (Lindström in press).

Among the palynomorphs recorded is the green microalga *Botryococcus* (Figs 2–3). This has no biostratigraphic value, having been recorded from deposits ranging in age from Precambrian to Recent (Konzalova 1973, Combaz 1980, Tappan 1980), but it is a useful palaeoenvironmental indicator. From comparative studies with recent *Botryococcus* this unicellular microalga is known to be of colonial growth and to vary in form, size and stage of development. It has been successful as an early colonizer and has easily adapted to various aquatic habitats in which it has grown. The different forms are related to environmental changes. As the microalga has changed little with time, and no evolutionary change has been detected, it is believed that the fossil forms can be used for palaeoecological interpretation. It has been recorded in several samples, but only at two different localities in Heimefrontfjella (Fig. 1), namely at Locality A and Lidkvarvet, which are both assigned to the Early Permian, i.e. Asselian–Tastubian (Larsson *et al.* 1990, Lindström 1994). The lithologies of the sequences present at these two localities are summarized in Fig. 4.

The aim of this paper is to demonstrate how different developmental stages of *Botryococcus* in selected samples may be used for interpreting the Early Permian depositional environments represented by the Heimefrontfjella succession. This is done by analogy to observations from comparative studies on the modern day microalga.

Morphology, growth and life history of the modern microalga *Botryococcus*

The present knowledge of the morphology, growth and life history of *Botryococcus*, as well as its environmental and adaptive characteristics have been summarized by Guy-Ohlson (1992).

The microalga is unicellular and the individual cell (autospore) is oval to pear-shaped, 5–15 µm long and has a cellulose wall. It is known to occur as colonies of various sizes from 10–100 µm across. A single autospore cell produces oil and secretes its own cup. It then divides longitudinally into two daughter cells. Thereafter a second longitudinal division occurs perpendicular to the first, producing a group of four daughter cells with autospores in the same plane arranged irregularly over the surface of the colony (Guy-Ohlson 1992, pl. I). This arrangement ensures that each cell is in contact with the water and able to photosynthesize. The cups are initially very thin, but increase in thickness and number of lamellae, whilst the thimble (inner part of the cup) is in contact with a living cell or until it is superseded by those of the daughter colonies. A difference in rate of cell division changes the appearance of the colony considerably as it alters the thickness of the cups. Such factors must be taken into account when using growth and developmental stages of *Botryococcus* for environmental interpretation.

An entire colony is imbedded in a mucilaginous sheath composed of fatty acids. Copious amounts of liquids accumulate within the sheath and add to the buoyancy of the colony. A chitin-like polymer has also been isolated from the sheath. The presence of such compounds probably gives the alga its resistance to desiccation and its ability to fossilize.

Small colonies are often formed under culture conditions, whereas much larger, closely adherent, branched compound colonies may occur in natural conditions. It is believed (Temperley 1936) that branching results when a colony contains too many cells to form a single globule. The oldest mother cell is then stretched to form a link between two closely united clusters. In time each cluster divides into two, by the stretching of the next pair of mother cell cups, until a botryoidal colony is formed. Large clusters of these compound colonies may be aggregated together, apparently in mucilaginous continuity.

Living colonies may fuse to form a rubber-like substance in which the thimbles of successive generations can still be seen, forming the skeleton of the colony, while the fatty cups have fused to form a structureless background. Older parts of certain colonies appear to have “growth rings”. Colonies of *Botryococcus*, in which the matrix had become structureless, were found when freshly collected modern material (“unfixed”) was kept sealed without access to atmospheric oxygen under daylight conditions in a glass tube (Guy-Ohlson 1992, pl. II).

The reproductive strategy of the alga is very successful and, as far as is known, is only vegetative — either by the formation of autospores or fragmentation of any type of single or compound colony. Under favourable natural conditions, growth is relatively slow, taking at least one week to double the biomass, whereas,

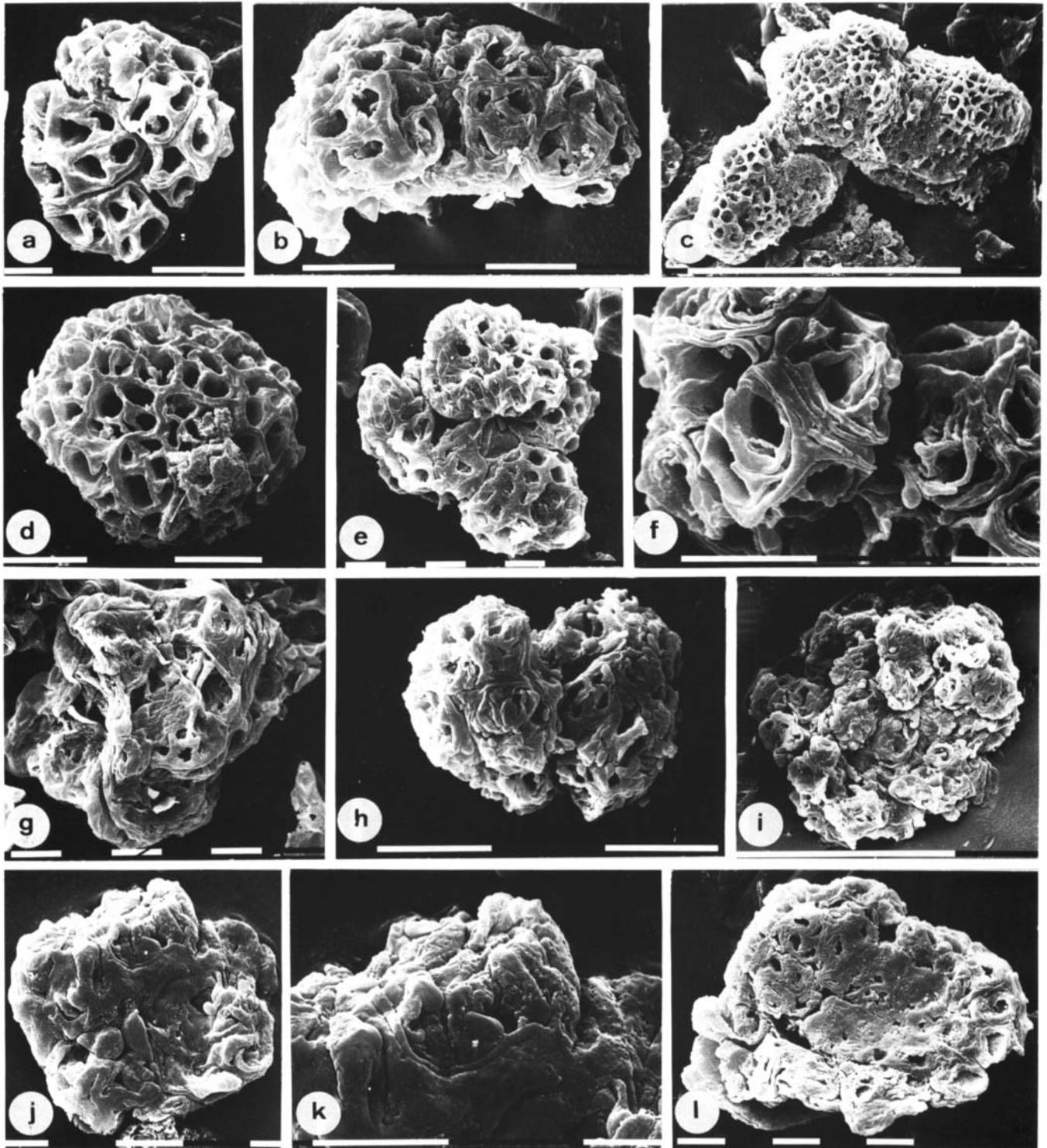


Fig. 2. Scanning electron micrographs of Early Permian colonies of the microalga *Botryococcus* from Lidkvarvet. Scale bar represents 10 μ m in all micrographs except (c) and (i) where it represents 0.1mm. (a)–(c): sample ANT 89-82; (d)–(l): sample ANT 89-80. (a), (b), (d) and (e): young, simple colonies without autospores (c): compound colony without autospores (f): part of colony showing well preserved growth rings (g): colonies showing autospores preserved (j)–(l): mother cups of the colonies have fused or commenced to fuse into structureless masses within the respective colonies. a. Specimen LO 6891 t, ANT 89-82/SEM 93–13. b. Specimen LO 6892 t, ANT 89–82/SEM 93–13. c. Specimen LO 6893 t, ANT 89-82/SEM 93–13. d. Specimen LO 6894 t, ANT 89-80/SEM 93–14. e. Specimen LO 6895 t, ANT 89–80/SEM 93–14. f. Specimen LO 6896 t, ANT 89–80/SEM 93–14. g. Specimen LO 6897 t, ANT 89-80/SEM 93–14. h. Specimen LO 6898 t, ANT 89–80/SEM 93–14. i. Specimen LO 6899 t, ANT 89–80/SEM 93–14. j. Specimen LO 6900 t, ANT 89-80/SEM 93–14. k. Specimen LO 6901 t, ANT 89–80/SEM 93–14. l. Specimen LO 6902 t, ANT 89–80/SEM 93–14.

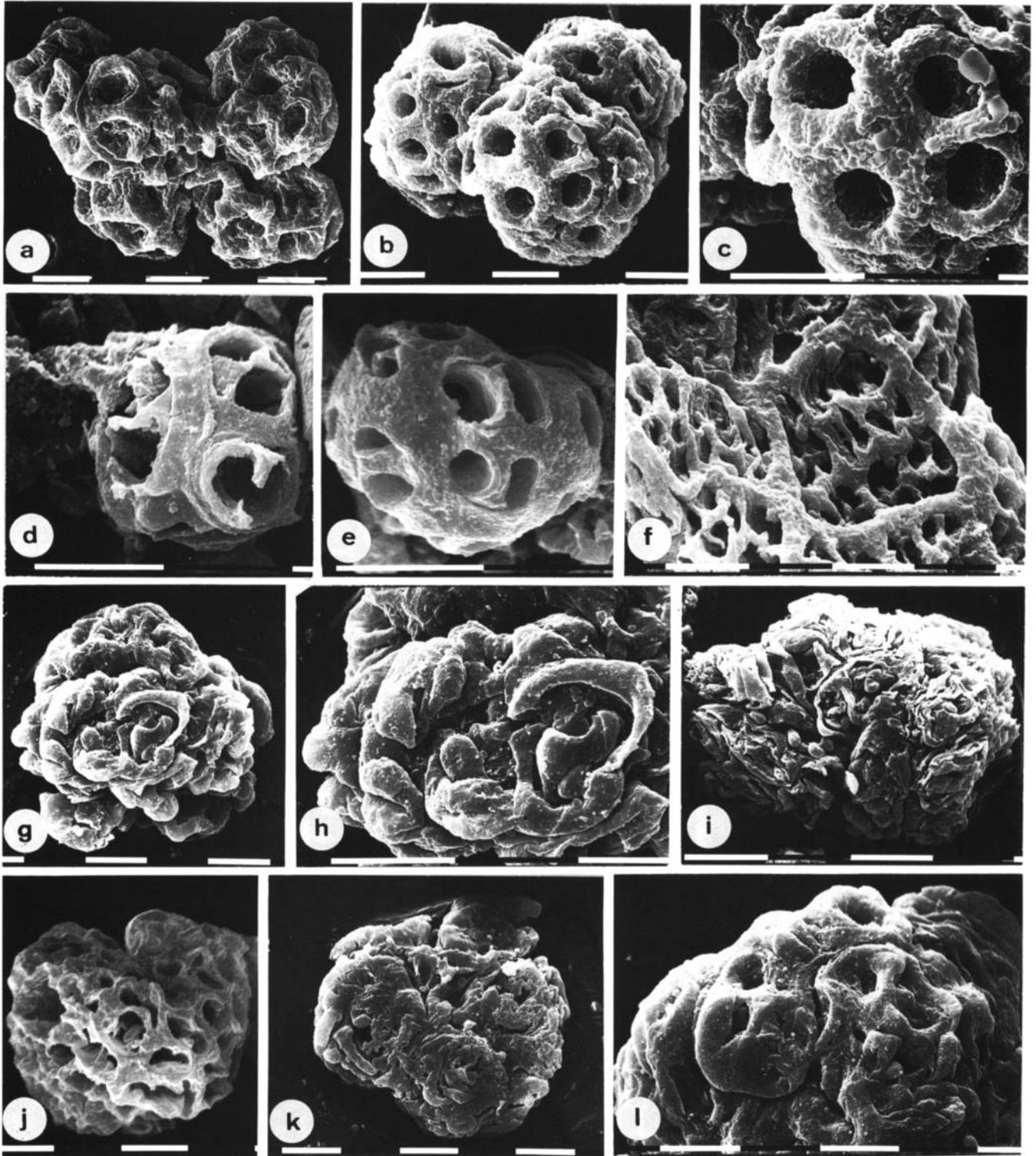


Fig. 3. SEMs of *Botryococcus* colonies of Early Permian age from Locality A. Scale bar represents 10 μ m in all micrographs. **a–c.** sample ANT 88–46; **d–e.** sample ANT 88–44; **f–i.** sample ANT 88–10; **j.** sample ANT 88–07; **k–l.** sample 88–02. **a–c.** young, excellently preserved compound colonies **d–e.** very young, simple, small, poorly preserved colonies **f–g.** compound colonies exhibiting different growth forms **h–i.** autospores present in compound colonies **j.** small, simple, skeleton-like colony **k–l.** young, compound colonies, probably with restricted access to oxygen. **a.** Specimen LO 6903 t, ANT 88–46/SEM 93–21. **b.** LO 6094 t, ANT 88–46/SEM 93–21. **c.** LO 6905 t, ANT 88–46/SEM 93–21. **d.** LO 6906 t, ANT 88–44/SEM 92–27. **e.** LO 6097 t, ANT 88–44/SEM 92–29. **f.** LO 6908 t, ANT 88–10/SEM 92–28. **g.** LO 6909 t, ANT 88–10/SEM 93–17. **h.** LO 6910 t, ANT 88–10/SEM 93–17. **i.** LO 6911 t, ANT-10/SEM 93–17. **j.** LO 6012 t, ANT 88–07/SEM 92–29. **k.** LO 6913 t, ANT 88–02/SEM 93–19. **l.** LO 6914 t, ANT 88–02/SEM 93–19.

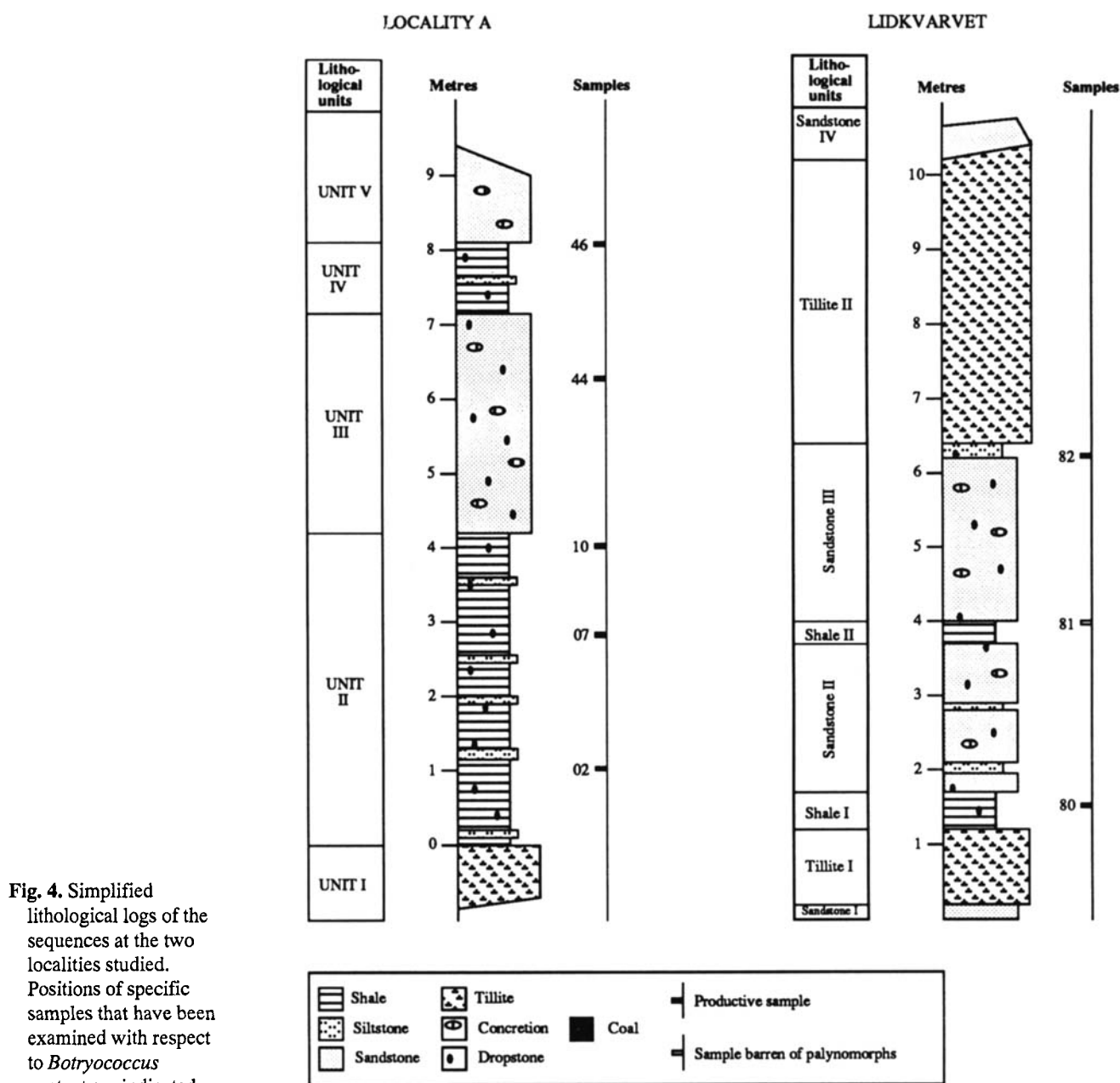


Fig. 4. Simplified lithological logs of the sequences at the two localities studied. Positions of specific samples that have been examined with respect to *Botryococcus* content are indicated.

by using growth-promoting substances (Xu & Yu 1988), the biomass can be doubled in less than half a day.

Environment and adaptive characteristics of modern *Botryococcus*

Today *Botryococcus* is commonly encountered in inland freshwater bodies, such as lakes, ponds and ditches as well as in bogs and wet mud. It also occurs in brackish waters. It is known to bloom and may form floating "mats" several centimetres thick and covering several hundred square metres. It competes most successfully with other planktonic organisms in shallow water in areas of relatively low rainfall, but where climatic

conditions vary widely throughout the year. The alga is recorded from regions which vary from tropical to subarctic.

The alga alters colour in response to seasonal changes, which affect light intensity and nitrate content of the water, and age and reproductive stage of the colony. The differences in colour reflect changes in both storage products and content of pigments.

The colonies sink when the water is disturbed by wind and return to the surface when calm conditions prevail again. When colonies die they float on the surface and may be driven by wind towards shore-lines and accumulate there. In Australia such accumulations occur and form gelatinous deposits called coorongite. This dark green to black rubbery material, first mistaken for weathered oil, originated from blooms of

Botryococcus stranded around the edges of small ephemeral lakes east of Coorong Lagoon, South Australia. These lakes formed between Pleistocene beach ridges after periods of exceptional rainfall.

Another behavioural response, which Temperley (1936) suggested is controlled by the salinity of the water, is the branching of the colonies. He found that branching usually occurs when the colony is about 30 µm in diameter and composed of 30 individual cells. The experiments of Brown *et al.* (1969) suggest, however, that branching is controlled by the reproductive status of the colony. The work of Xu & Yu (1988) shows the formation of mucilaginous connections to be associated with certain strains of the alga during biotechnological cultivation and is correlated with the growth substances involved.

Several adaptations are considered to have contributed to the survival of *Botryococcus*, e.g. the ability to withstand changing environmental conditions and store large amounts of reserve food and the possession of components resistant to desiccation. Continuous vegetative reproduction may also have contributed to its survival and explain how *Botryococcus* has retained the same form for so long.

Thus, from a study of the developmental stages and type of colony formed by the modern alga, a great deal of ecological information can be obtained. If, on examining geological samples, different developmental stages in the life history (Guy-Ohlson 1992, fig. 1), and/or different types of colonial growth are found, by analogy, it should be possible to infer, however tentatively, specific environmental and ecological conditions.

Occurrence, palaeoenvironmental and palaeoecological significance of fossil *Botryococcus* in the Permian succession of Heimfrontfjella

The different developmental stages and type of colony found in each of the investigated samples at Lidkvarvet and Locality A, are summarized in Fig. 5. Scanning electron micrographs of examples from each sample are shown in Figs 2 & 3.

If quantitative aspects are also taken into consideration and comparisons made with the living microalga then, by analogy, specific palaeoecological conditions may be tentatively interpreted. These are summarized and presented in Fig. 5.

At Lidkvarvet, sample ANT 89–82 yielded young, simple colonies as well as various sizes of compound colonies. Open, skeleton-like colonies were present, but no growth rings were recorded. A few large compound colonies with autospores preserved in the mother cups were also recorded. These finds indicate that the same kind of climatic and/or environmental conditions existed for a length of time. No colonies whatsoever were recorded in sample ANT 89–81, but sample ANT 89–90 yielded several different types of developmental stages and colonies. Fig. 2d shows a young, simple colony with no autospores present, whereas Fig. 2e is a young compound colony but also with no autospores present. Both of these indicate only brief periods of growth. Excellently preserved “growth rings” are illustrated in Fig. 2f and suggest longer periods of growth,

as well as favourable conditions for preservation. Figs 2h–i illustrate varying sizes of compound colonies, but both with autospores preserved *in situ* in the mother cups of the colonies. Colonies in which the original mother cups have fused, or commenced to fuse, into structureless masses within the colony (Figs 2j–l) suggest reduced levels of oxygen, and perhaps very slow burial in a quiet, undisturbed depositional environment. The fact that various different types of colony and developmental stages are present in one and the same sample suggests, by analogy with living material, that different “seasonal” conditions of environment and/or climate are represented and existed for such a period of time that the aquatic conditions were not merely ephemeral. Judging from the specimens found, the alga obviously thrived in its habitat, though quantitatively it was not especially common and no algal blooming was detected.

At Locality A, sample ANT 88–46 yielded young, small colonies which were extremely well preserved and still had autospores preserved in the mother cups of the colonies. Very short periods of time, probably ephemeral aquatic conditions with rapid burial have been interpreted for this sample. In sample ANT 88–44, only a few, very young, simple, small, poorly preserved colonies of the same type were recorded. Two of these are illustrated in Figs 3d & e. They indicate a very short life span to obtain this minute colonial growth, i.e. from second to fourth cell divisions. The preservation suggests that conditions were not congenial to growth and the size and developmental stage may well point to ephemeral freshwater conditions having existed for this particular sample. Different forms of compound colonial growth were found in sample ANT 88–10 and are interpreted as being the result of variable environmental and climatic conditions. Sample ANT 88–07, on the other hand, yielded only a few, small, simple skeleton-like colonies which could indicate short ephemeral freshwater conditions. Young compound colonies with autospores present were recorded in sample ANT 88–02, and are interpreted as indicating a relatively long period of quiet, undisturbed deposition. Possible restricted access to oxygen during growth and deposition is indicated by the state of preservation (Figs 3k & l).

Comparisons with other localities

There are no records of *Botryococcus* in samples from the other localities investigated in Dronning Maud Land. As for the rest of Antarctica, and other investigated sequences of the same age on the Gondwanan continent (South Africa, South America, India and Australia), although recorded, no detailed studies of *Botryococcus* have been undertaken, so direct comparisons are not possible. This is also the case for other parts of the world, although records of occurrence were taken into account by Pacaud (1977) in his reconstruction of an Early Permian coal landscape of the Autun Basin in France (Pacaud 1977). Floating algal mats of *Botryococcus* are indicated in his reconstruction.

There are, however, detailed studies of different developmental stages of *Botryococcus* found for other geological periods of different palaeogeographical location

Fig. 5. Comparison of *Botryococcus* colonies found in selected samples at Lidkvarvet and Locality A with the tentative palaeoecological interpretations.

LOCALITY	SAMPLE	% <i>Botryococcus</i> of Total Organic Content	TYPES OF COLONIES & DEVELOPMENTAL STAGES							Remarks	Examples	Palaeoecological Interpretations		
			Simple			Compound		Skeleton-like Colonies						
			young	old	young	old	Largest size μm	Auto-spores	Apparent				Not Apparent	
L I D K V A R V E T	ANT89-82	3%	X	-	X	X	-	140	(X)	X	-	Variable sizes of compound colonies; open skeleton, no growth rings; a few large compound colonies with autospores in mother cups. Variety of colony types present in one sample.	Fig. 2 (a)-(c)	Same kind of climatic and/or environmental conditions for a length of time - refer to size of largest compound colony.
	ANT89-81	-	-	-	-	-	-	-	-	-	-	No colonies recorded - sample barren of palynomorphs apart from so called palynodebris.	-	-
	ANT89-80	1%	X	X	X	X	X	150	X	X	X	Compound colonies; empty skeletons with tendency to form structureless mass, excellent preservation of "growth rings". Autospores present in certain compound colonies. Variety of colony and type of colonial growth in one sample, large number of colonies present	Fig. 2 (d)-(l)	Different "seasonal" conditions of environment and/or climate prevailed for a length of time. Structureless mass indicative of restricted access to oxygen, perhaps very slow burial in peaceful, undisturbed depositional environment
L O C A L I T Y A	ANT88-46	< 1%	-	-	X	-	-	30 (30-35)	(X)	X	-	Young small colonies (>30 μm), extremely well preserved; autospores found in mother cups.	Fig. 3 (a)-(c)	Very short period of time represented, probably ephemeral aquatic conditions with rapid burial
	ANT88-44	< 1%	X	-	-	-	-	15	-	X	(X)	Only a few, very young, simple, small colonies (10-15 μm) recorded. One example found up to 20 μm .	Fig. 3 (d)-(e)	Very short period of time for length of life: probably did not grow well in this habitat.
	ANT88-10	2%	-	-	X	X	X	80	X	X	X	Compound colonies, some with autospores in mother cups; different forms of colonial growth present.	Fig. 3 (f)-(j)	Variable environmental and climatic conditions suggested by different growth forms.
	ANT88-07	3%	X	-	-	-	-	40	-	-	X	Very few, small, simple skeleton-like colonies.	Fig. 3 (k)-(l)	Short ephemeral conditions; poor preservation.
	ANT88-02	3%	-	-	X	-	-	70	X	-	-	Young, compound colonies (up to 60 μm) with autospores present.	Fig. 3 (k)-(l)	Possibly restricted access to oxygen: relatively long period of quiet, undisturbed deposition.

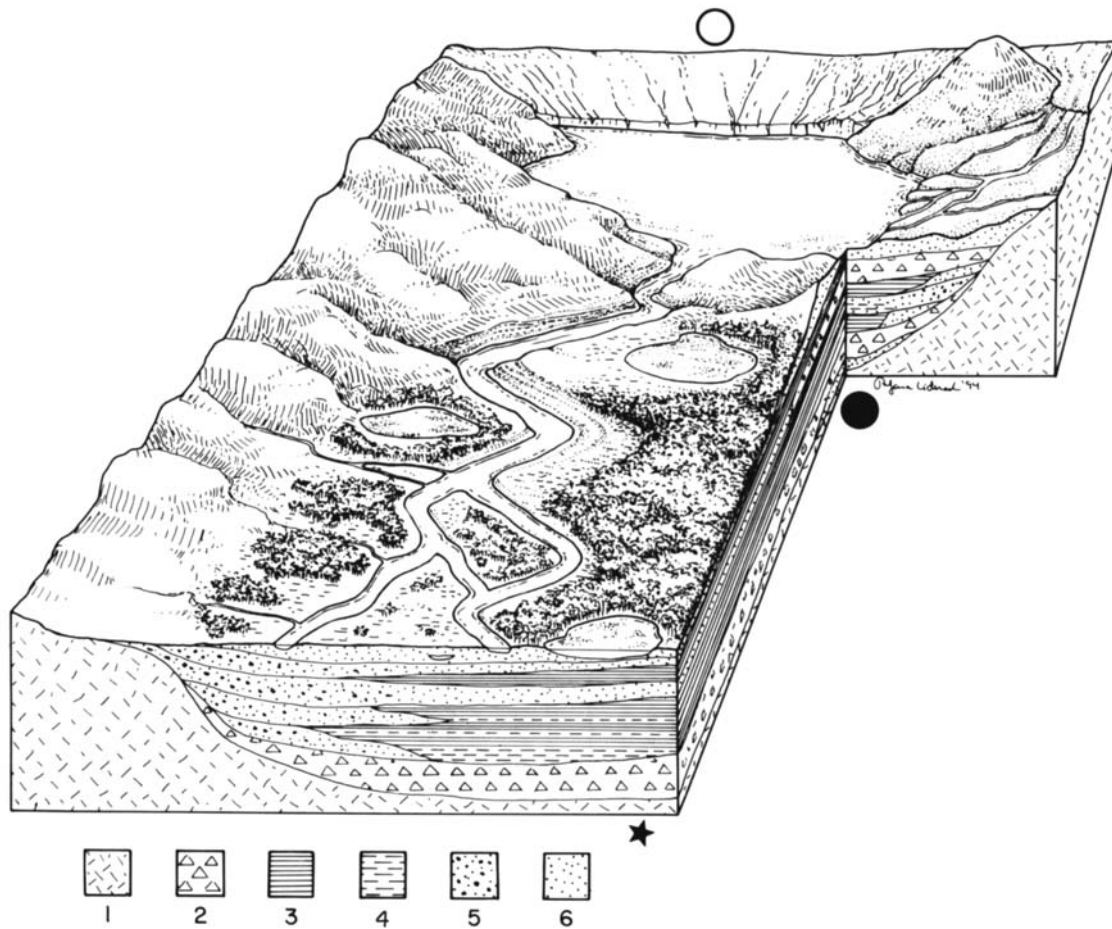


Fig. 6. Simplified composite schematic reconstruction representing an Early Permian landscape at Heimefrontfjella based on palynological evidence. Not drawn to scale. Numbers in legend refer to: 1. gneiss, 2. tillite, 3. shale, 4. siltstone, 5. conglomerate, 6. sandstone. The hypothetical site of Locality A is envisaged to be in the foreground of the reconstruction and is marked by an asterisk, while that of Lidkvarvet is in the background and indicated by a filled circle. The glacier is denoted by an open circle. Drawn by P. Lidmark.

and geological age, e.g. at the Jurassic/Cretaceous boundary in southern Sweden (Erlström *et al.* 1991, pl. 6) and where the depositional environment was interpreted as quiet, undisturbed lagoonal conditions. A reconstruction of this paleoecological interpretation is given in Erlström *et al.* (in press).

Based on palynological evidence (Lindström in press, Lindström 1994) and the present study of the *Botryococcus* colonies, it is possible to present a very simplified, composite schematic reconstruction of an Early Permian landscape (Fig. 6) as it might have been at Heimefrontfjella.

The sedimentary rocks at Locality A are interpreted as having been deposited in a periglacial environment (Plumstead 1975, Lindström 1994). The shale and siltstone comprising Unit II (Fig. 4) is believed to represent a glacial lake deposit, whereas the sandstone, comprising Unit III, probably formed under higher energy freshwater depositional conditions. The uppermost shale, Unit IV, is thought to represent a shallow,

quiet, at times undisturbed environment, e.g. an ephemeral pool or small temporary lake (Larsson *et al.* 1990, Lindström 1994).

At Lidkvarvet the glacial influence appears to be much stronger, with the presence of two tillite-units (Larsson 1990). This is also suggested by the palynomorph content which generally is much more poorly preserved than at Locality A (Lindström 1994). The sedimentary rocks at Lidkvarvet may represent glacial lake deposits, with the shale and siltstone units representing calmer conditions. In Fig. 6 the hypothetical site of Locality A is envisaged in the foreground of the reconstruction and is marked by an asterisk, while that of Lidkvarvet is in the background and indicated by a filled circle.

Conclusion

Botryococcus is usually bypassed in micropalaeontological analyses with a mere recording of its presence denoting a freshwater influence on the depositional environment. By carrying out detailed scanning electron microscopic studies of different fossilized developmental stages of this green microalga and by comparing them with those of the modern microalga it has been attempted to show, at least tentatively, some of the possibilities for interpretation of the depositional conditions and palaeoecology.

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