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Observations on the wall structure and the excystment mechanism of acritarchs

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ABSTRACT — Systematic studies on acritarchs of Ordovician, Silurian and Devonian ages of North Africa, the British Isles and Podolia showed varieties of six types of wall structures and five types of excystment mechanism. These are well documented in this study and may form the main basis for a natural classification in future work.

MORPHOLOGICAL FEATURES

The morphology of acritarchs has been mainly studied by Lister (1970), concerning excystment mechanism, vesicle ornamentation and process morphology (see Cramer, 1970; Downie, 1973). Jux, in a series of publications since 1969, engaged in the study of wall structure and its relation to natural classification. The study of the forms living in clusters was discussed mainly by Downie (1973). The present study is based on observations of acritarchs from the Palaeozoic of North Africa, the British Isles and Podolia. Its aim is to further investigate the question of the wall structure and excystment mechanism in the acritarchs and to assist in the formalisation of a rigid basis for their natural classification.

WALL STRUCTURE

The studies by Jux from 1969 to date show that the ultra thin section by transmitted electron microscopic technique shows that the wall of *Tasmanites, Veryhachium, Leiosphaeridia, Baltisphaeridium* and *Goniosphaeridium* have a similar structure and this, therefore, indicates a genetic relationship between them. They have a uniform wall, laminated with narrow radial pores. This type of wall structure is found in the living alga *Pachysphaera*. Therefore, a genetic relationship between algae and these forms may be postulated.

In this study, assemblages of acritarchs were studied mainly be optical microscopy and some of them showed a homogeneous and single wall layer e.g. *Micrhystridium*. Other assemblages have complex wall structures; the genus *Visbysphaera* and the genus *Diexallophasis* show walls of double layers. These layers are termed the outer wall, ectoderm and inner wall, endoderm. Membranous assemblages, e.g. *Tunisphaeridium* and *Pterospermella* have an outer wall termed outer membrane, periderm.

Such a variety of walls are grouped here in many different types and illustrated diagramatically in Figs. 1 and 2. These wall types are as follows:

1. **Tasmanites wall** (Pl. 1, fig. 4)
This type is composed of one wall of thick and uniform nature with radial pores which can be seen optically and under the S.E.M. The thickness of the wall is variable, possibly reaching one seventh (1/7) of the total body diameter. It is seen in the genus *Tasmanites* and the living alga *Pachysphaera*. The taxa possessing this type of wall have a spherical body shape without major projections. The walls of some sphaeromorphs have also been shown by Jux (1975) to have the same characteristics as the genus *Leiosphaeridia*.

2. **Baltisphaeridium wall**
This type is composed of two layers which are difficult to observe except within the process position. In this position, only the outer wall forms the process. The vesicle cavity and the process cavity are separated by plugging of the base of the process by the inner wall. The inner wall is composed of a uniform lamina with radial pores which could only be observed by peel section of the wall under the S.E.M. (Jux, 1975). The taxa possessing this type of wall have a spherical body with processes, e.g. the Ordovician genus *Baltisphaeridium*.

3. **Veryhachium wall** (Pl. 1, fig. 11)
This type is composed of one thin, uniform wall with radial pores that are only seen by peel section (Jux, 1977). The process cavity is continuous with the central cavity. The taxa possessing this type of wall have spherical, polygonal or elongated geometrical form. Examples are the Palaeozoic genera *Veryhachium, Multiplicisphaeridium* and *Leiofusa*.

4. **Pterospermopsis wall** (Pl. 1, figs. 1, 5, 9)
This type is composed of a tasmanites wall forming circular or ovate shaped vesicles with membranous

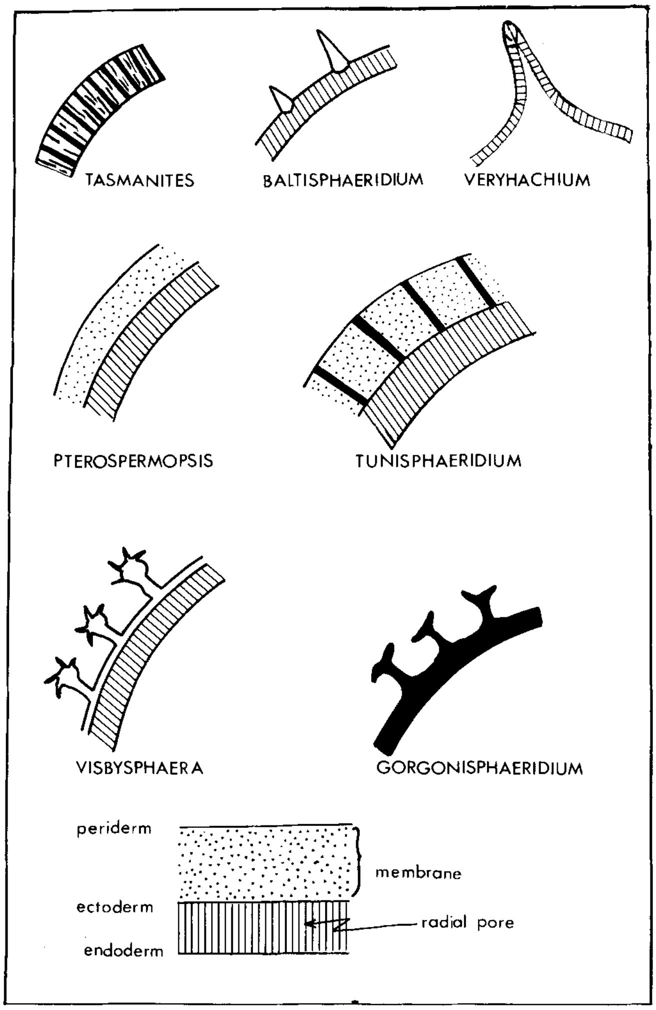


Fig. 1. Types of wall structures in the acritarch groups.

extensions. The membrane divides vesicle into fields, of a circular or polygonal geometrical form (Fig. 2). This wall can be subdivided into two types. The first, the Pterospermella type includes the genus *Pterospermella* with a lateral membranous extension as a flange or wing, and also includes *Cymatiosphaera* and *Fimbriaglomerella* with polygonal alae or lists dividing the vesicle surface into many polygons. If the membrane has projections from the endoderm to the inside of the periderm to support the membrane then this is the Tunisphaeridium, second type of wall, e.g. as found in *Tunisphaeridium*. The Baculatireticulatus type of wall is used for specimens with projections on the corners of the polygonal alae to support two lists in their intersections, e.g. *Baculatireticulatus, Dictyotidium* and *Ovnia* (Fig. 2). The similarity in appearance and pattern of alae in taxa composed of this type of alae to the living genus *Pterosperma* Boalch & Parke, 1971 indicates that these taxa belong to the Prasinophacean algae. The list and the wing are distinguished under the optical microscope by lighter colour from the central body and of a semitransparent appearance.

5. **Visbysphaera wall** (Pl. 1, figs. 3, 7)

This type is composed of two layers clearly distinguished under the optical microscope. The outer layer is thin and transparent and the inner layer is thicker possessing a tasmanitid type wall. Only the outer layer extends to form the processes. The processes are hollow and their cavities are separated from the central cavity by the inner layer. The shape possessed by this type of wall is either spherical or polygonal, e.g. *Visbyphaera, Triangulina* and *Azontobranchion*.

6. **Gorgonisphaeridium wall** (Fig. 1)

This type is composed of unilayered, highly condensed material and with radial pores (Jux, 1977). They have processes of rigid and condensed material extending from the vesicle wall with no process cavity. The processes are either of a branching type as in the Lower

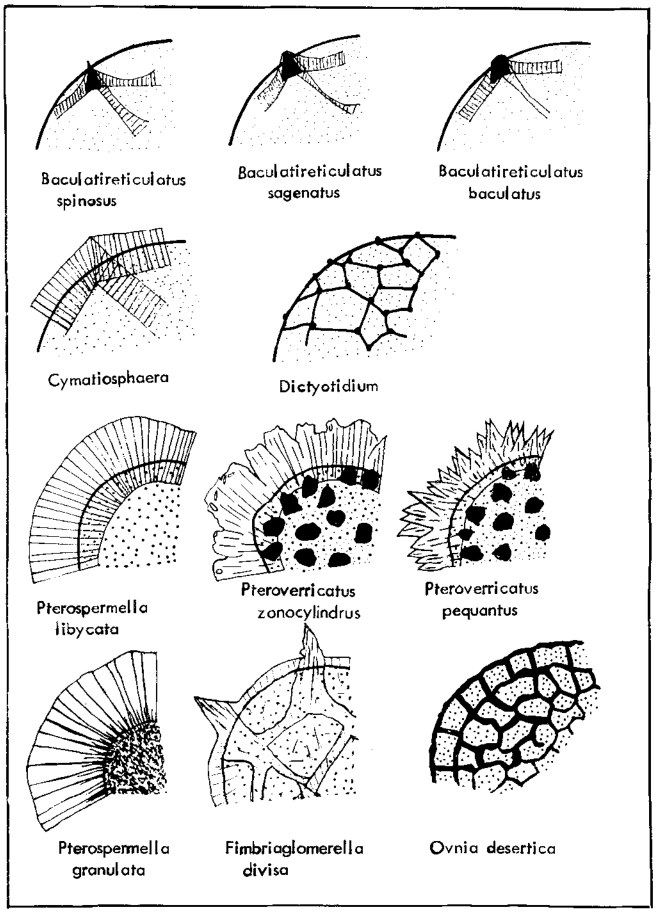


Fig. 2. Diagrammatic drawing of quartered area of the vesicles of some taxa from the Pterospermopsis group that shows distinct morphological variations of the membranous list (lined area) and the vesicle (dotted area). All the figures are as they appeared under optical transmitted light microscopy. After Al-Ameri, 1984.

Palaeozoic genus *Gorgonispaeridium*, filose type as in the Lower Palaeozoic genus *Acanthodiacrodium* and the Palaeozoic genus *Electoriskos* or with short and wide base processes as in the Upper Palaeozoic genus *Buedingisphaeridium*.

Studies such as that of Kjellstrom (1968) show that some walls described above consist of condensed fatty acid derivatives, similar to the "sporopollenin" material.

EXCYSTMENT MECHANISM

The importance of the excystment mechanism in determining the relationships of dinoflagellates was shown by Evitt (1961) and discussed in detail by him later (Evitt, 1967). It is possible that this is also true for acritarchs (Lister, 1970; Downie, 1973). Fig. 3 shows different types of excystment mechanism and some records are showing in Pl. 1.

The main categories of excystment mechanism are:–

1. **Archaeopyle**

A name introduced by Evitt (1961) for excystment openings formed by the loss of one or more plates from a dinoflagellate cyst, e.g. dinoflagellates of Mesozoic and Tertiary age and *Apylorus antiquus* of Silurian age. Some varieties may show a semiarchaeopyle opening which is recorded in the Palaeozoic genus *Cymatiosphaera* with polygonal opening (Pl. 1, fig. 9; Fig. 3i); some species of the genus *Cymbosphaeridium* possess an opening that is located in a distal process position (Pl. 1, fig. 7) and the same may occur in the genus *Oppilatala*. These records, however, are not clear enough to be identified as an archaeopyle.

2. **Cyclopyle** (Pl. 1, figs. 4, 12)

This name was introduced by Eisenack (1969) for openings with a circular outline, e.g. the openings in *Tasmanites, Peteinosphaeridium* and *Cymatiogalea*. Some variants were recorded with a collar, notably *Polyancistrodorus*.

3. **Epityche**

This term was introduced by Loeblich & Tappan (1969) for the excystment structure formed by a curving split allowing a flap to open, e.g. the opening in *Veryhachium* (Fig. 3a-d and 3h; Pl. 1, fig. 10). A number of variants have been subsequently noted. Cramer (1970) distinguished C-shaped and S-shaped splits in *Veryhachium* and Lister (1970) stressed the progressive development of a small circle split in many genera, notably *Micrhystridium*. These are cryptosutures and their appearance forms a large flap which may often break off.

4. **Median Split** (Pl. 1, fig. 8; Fig. 3e-g)

A few forms open by splitting into two equal halves, e.g. in the genera *Orthosphaeridium* and *Leiofus*. Some variants have been recorded by Reaugh (1978) in the genus *Diexallophasis denticulata* which show a split. Both sides of the openings are ornamented by small and closely spaced bumps which form a scalloped pattern along the opening.

5. **Epibystra**

This term was introduced by Playford (1977) for an excystment structure formed by the split of the cup of one end of the pulvenoid processes into a zigzag line of opening, e.g. the genus *Pulvenosphaeridium* (Fig. 3m; Pl. 1, fig. 6).

SUBDIVISONS OF THE GROUP "ACRITARCHA"

The group Acritarcha may be divided into many major subgroups equivalent to the types of wall structures illustrated in this study (Fig. 1). Other characteristic features are also used to identify the subgroups and help to further subdivide the subgroups into the heirarchical scale of classification. Accordingly, the subgroups defined by Downie, 1973 are very useful, but some have to be combined. For example, Downie's subgroups of *Tasmanites, Pachysphaera, Navifusa* and *Leiosphaeridia* could be combined into one "Tasmanite subgroup"; *Veryhachium, Micrhystridium, Leiofusa* and *Multiplicisphaeridium* into "Veryhachium subgroup"; and *Lophosphaeridium, Gorgonisphaeridium* and *Electoriskos* into "Gorgonisphaeridium subgroup". The rest of the subgroups erected by Downie are considered valid. These are the subgroups of "Baltisphaeridium", "Pterospermopsis" and "Visbysphaera". The Geron subgroup is erected as new, having a unique wall structure.

The proposed subgroups from this study can be briefly described as follows:

Tasmanites subgroup

These are acritarchs with a tasmanitid type of uniwall. Usually they are spherical to ovoidal forms with cyclopyle or epityche openings, e.g. *Tasmanites* (Pl. 1, fig. 4; Pl. 2, fig. 7) and *Leiosphaeridia* (Pl. 1, fig. 10).

Baltisphaeridium subgroup

Members of this group have a tasmanitid inner wall and hyaline outer wall that is difficult to distinguish from the inner wall except at the place of projection, where only the outer wall forms the processes. Thus, the process cavity is separated from the central cavity. These members usually have a cyclopyle type of opening, e.g. *Baltisphaeridium*.

Pterospermopsis subgroup

This group has been defined by Downie, 1973 as the group with characteristic alae dividing the vesicle surface into fields. These alae are hyaline lateral extensions from the vesicle. Taxa of this group can be further subdivided into different families on the basis of spinose projections from the vesicle into the hyaline extension:

1. *Pterospermella family*. This is characterised by the presence of thin septa (list) that divide the vesicle wall into fields. There are no records of thickened areas or thick spines in the intersection of two or more of the septal alae. This group includes *Cymatiosphaera* (Pl. 1, fig. 9), *Pterospermella* (Pl. 1, fig. 1) and *Pteroverricatus* Al-Ameri, 1984 (Fig. 2).
2. *Baculatireticulatus family*. This is characterised by the presence of spines, projecting from the vesicle wall. These spines are connected together by septae and divide the vesicle surface into numerous fields, e.g. *Ovnia* (Fig. 2), *Baculatireticulatus* (Pl. 1, fig. 5), *Dictyotidium* (Fig. 2) and *Tunisphaeridium* (Fig. 1).

Veryhachium subgroup

This group characteristically has a spinous body with very thin and tasmanitid wall structure. Excystment is by epityche, cryptosuture or splitting. Its uniwall continues to form the processes and is therefore characterised by the free extension of the body cavity into the processes. Taxa of this group can be further subdivided into different families on the basis of morphological shape and excystment opening:
1. **Veryhachium family.** Characterised by a polygonal body, with three or more spines and excystment by epityche. Examples are *Frankea, Striatotheca* and *Veryhachium* (Pl. 1, fig. 9).
2. **Micrhystridium family.** Characterised by a spherical to oval shape of the body, with many spines, excystment by epityche or splitting. Examples are *Micrhystridium, Multiplicisphaeridium* and *Ammonidium.*
3. **Leiofusa family.** Characterised by elongated body shape with one or two spines. Opening is by splitting (lateral or median) or flap epityche (C-shape). Examples are *Anomaloplaisium, Dactylofusa* and *Leiofusa* (Pl. 1, fig. 8).
4. **Acanthodiacrodium family.** Characterised by the polarity of its processes. There are many processes in each pole. Downie (1973) mentioned that there does not appear to be a consistent method of opening, but splitting does occur along clear lines. Examples are *Acanthodiacrodium, Arbusoulidium, Dasydiacrodium* and *Schizodiacrodium.*

Visbysphaera subgroup

This group is characterised by a clearly distinguished double wall. The inner wall is thicker and hence darker in colour than the outer wall, as viewed optically. The outer wall only forms the process, thus the vesicle cavity is separated from the process cavity by the inner

Explanation of Plate 1

Scale = 20μm in all figures
All the specimens are from Libyan material

Fig. 1. *Pterospermella* sp., from the Upper Llandoverian, showing equatorial flange of pterospermopsis type of wall.

Fig. 2. *Buedingisphaeridium pyramidale* Lister, 1970, from the Ludlovian showing the gorgonisphaeridium type of wall.

Fig. 3. *Visbysphaera jardineae* (Cramer) Jardine *et al.* 1974, from the Lower Devonian showing the double wall character of the visbysphaera type.

Fig. 4. *Tasmanites avelenoi* Sommer, 1953, from the Upper Llandoverian showing the thick tasmanites wall.

Fig. 5. *Baculatireticulatus baculatus* Al-Ameri, 1984, from the Ludlovian showing the pterospermopsis type of wall with perpendicular and netted membranous list, and bacula in each corner of each polygon.

Fig. 6. *Pulvenosphaeridium* sp., from the Lower Devonian showing the Veryhachium type of wall and epibystra type of opening.

Fig. 7. *Cymbosphaeridium pilaris* Lister, 1970, from the Downtonian, showing the visbysphaera type of wall and cyclopyle type of opening.

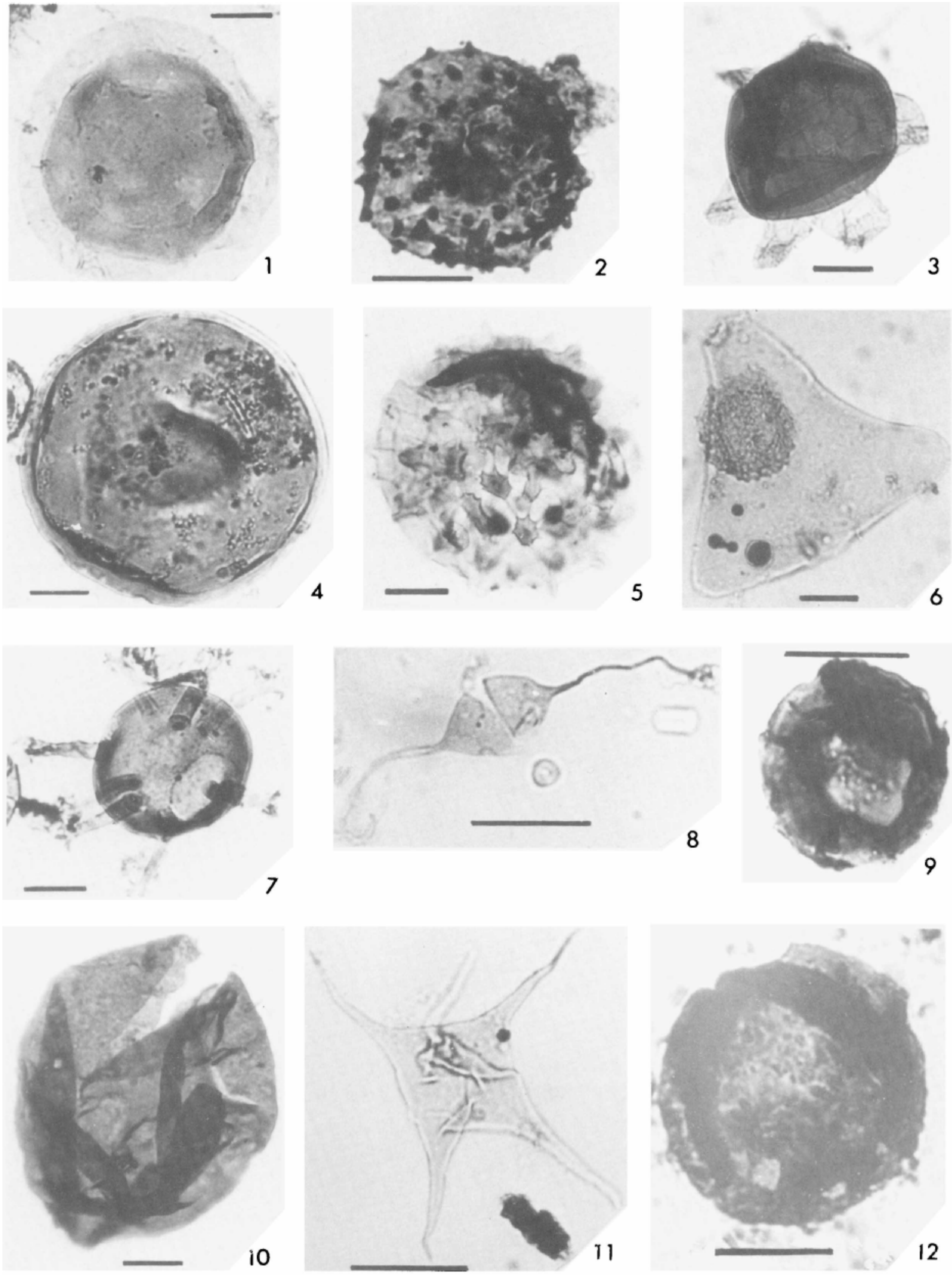
Fig. 8. *Leiofusa bernesgae* Cramer, 1964, from the Ludlovian, showing the veryhachium type of wall and median split type of opening.

Fig. 9. *Cymatiosphaera* sp., from the Llandoverian, showing the semiarchaeopyle type of opening and the pterospermopsis type of wall with vertical lists along the borders of the polygons.

Fig. 10. *Leiosphaeridia laevigata* Stockmans & Willierie, 1963, from the Upper Ordovician showing the epityche type of opening.

Fig. 11. *Veryhachiam rhomboidium* Downie, 1959, from the Downtonian showing the veryhachium type of wall.

Fig. 12. *Aremoricanium* sp. from the Ordovician showing the cyclopyle type of opening with neck.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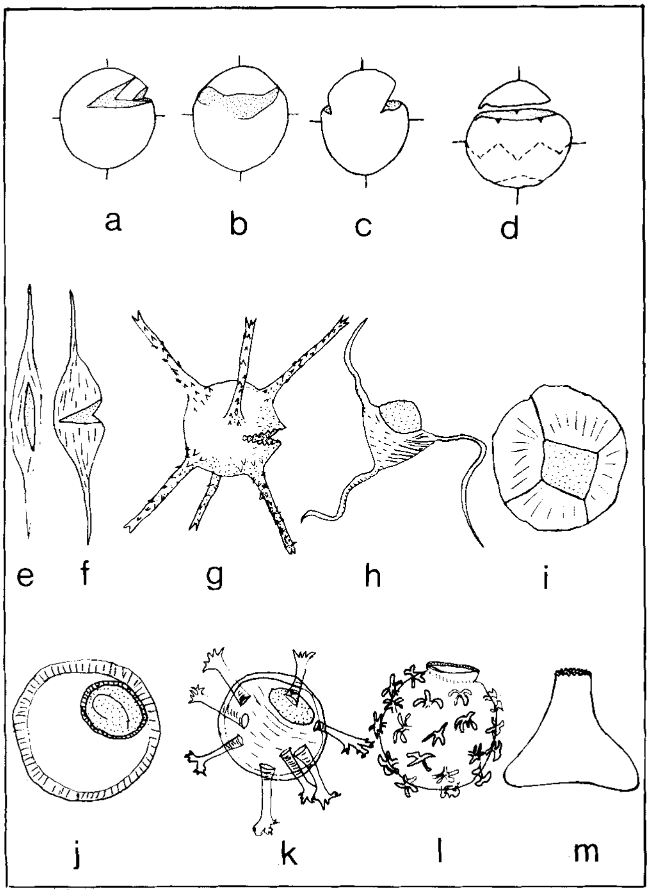

Fig. 3. Excystment apertural openings in acritarchs: a-d, Epityche; a, lateral view; b, dorsal view; c, ventral view; d, opening by obvious suture; e-g, Median split; e, lateral split; f, equatorial split; g and m, zigzag face; h, Epityche; i, Pseodo-Archaeopyla; j-l, Cyclopyle; j; in thick wall; l, with collar; m, Epibystra.

wall. The excystment mechanism is by cyclopyle or cryptosuture (small-circle epityche). Taxa of this group can be subdivided into four families on the basis of body shape and opening.

1. **Visbysphaera family.** Characterised by spherical to oval shape with cryptosutural opening, e.g. *Cymbosphaeridium* (Pl. 1, fig. 7) and *Visbysphaera* (Pl. 2, figs. 8, 9).
2. **Triangulina family.** Characterised by polygonal body shape and cryptosuture opening, e.g. *Onondagella, Ozontobranchion* and *Triangulina* (Pl. 2, fig. 5).
3. **Diexallophasis family.** In this type, an inner layer is infrequently developed. In addition, the processes are inclined to have small excrescences and a peculiar type of digitate terminal branching. The excystment opening can be by cryptosuture or median split. It includes *Florisphaeridium, Diexallophasis* (Fig. 3g) and *Tylotopalla*.

Gorgonisphaeridium subgroup

Members of this subgroup have unilayered and solid ornaments, i.e. with no cavity. Excystment opening is rare and if present, a splitting tip will occur. This subgroup can be subdivided on the basis of wall thickness and the branching termination:

1. **Gorgonisphaeridium family.** This type is characterised by a thick wall (1μm or more) and broad processes which have a tendency to dichotomise, e.g. *Gorgonisphaeridium* (Pl. 2, figs. 1-3), *Echthymapala* and *Barathrisphaeridium*.
2. **Electoriskos family.** This type is characterised by a thin wall (less than 1μm), the processes are wire-shaped and do not dichotomise, e.g. *Electoriskos* (Pl. 2, fig. 6), *Fillisphaeridium, Comasphaeridium* and *Solita*.
3. **Lophosphaeridium family.** This type is characterised by a thick wall (1μm or more), a short, wide base and solid ornaments that do not dichotomise. Ornaments

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Explanation of Plate 2

Scale = 20μm in all figures
All the specimens are from Libyan material

Figs. 1-3. *Gorgonisphaeridium* sp., from the Upper Llandoverian.

Fig. 4. *Geron guerrilerus*, from the Lower Ludlovian.

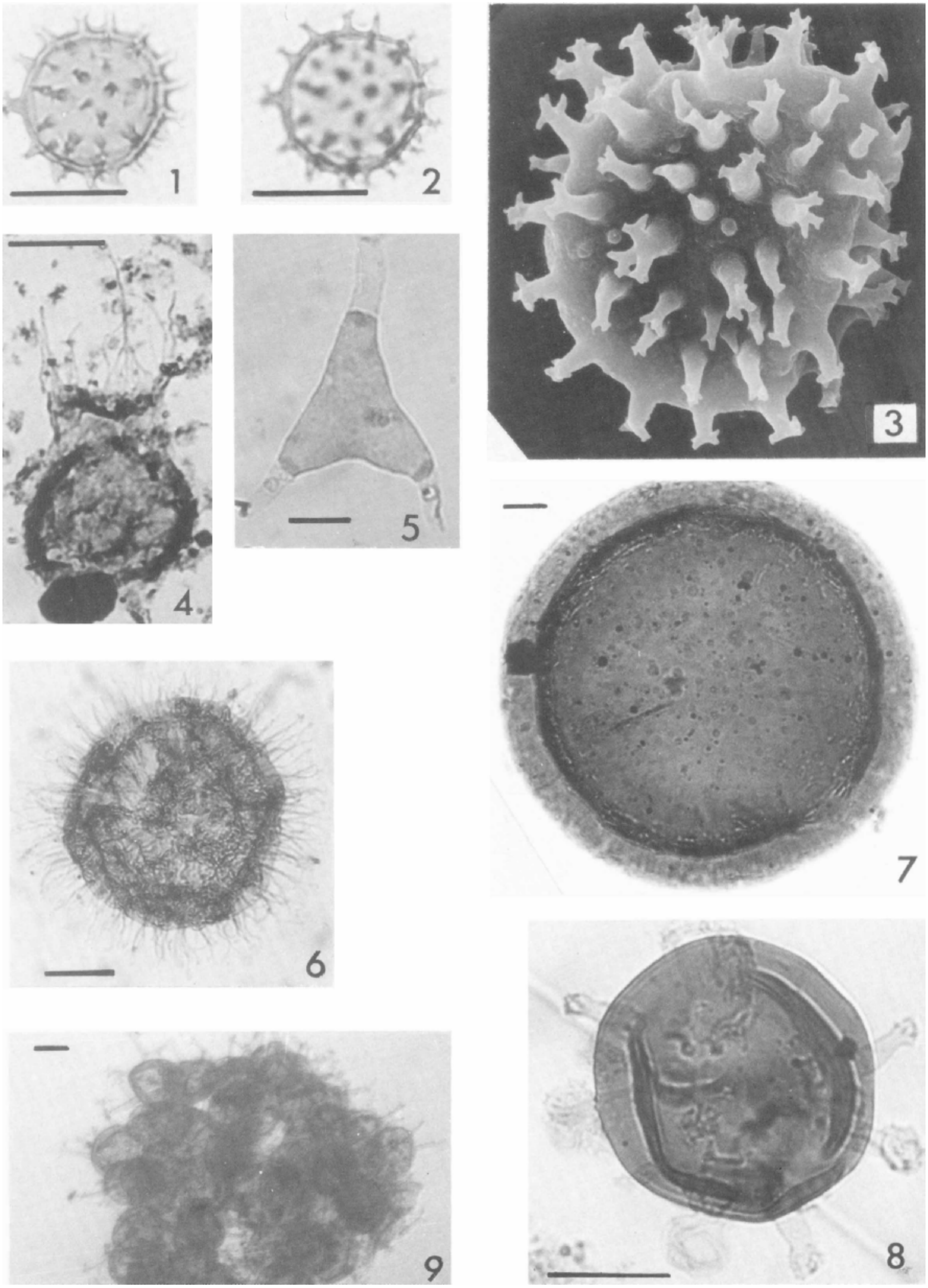
Fig. 5. *Triangulina* sp., from the Upper Ludlovian.

Fig. 6. *Electoriskos* sp., from the Lower Devonian.

Fig. 7. *Tasmanites roxi*, from the Downtonian.

Fig. 8. *Visbysphaera dilatisphaera*, from the Ludlovian.

Fig. 9. *Visbysphaera* sp., in cluster association from the Downtonian.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can be tubercles, verrucae, baculae, clavate or granulate. Excystment is by small circle epityche (cryptosuture type), e.g. *Buedingisphaeridium* (Pl. 1, fig. 2).

Geron subgroup

Members of this group are characterised by a wall structure consisting of an endodermal layer of a spherical to oval vesicle enclosed in an outer peridermal layer that may have one or more circular openings with a neck. Solid processes originate from the endoderm to the outer layer of the periderm. No excystment opening was recorded within the endodermal layer. Examples of this type are *Geron, Carminella, Riculasphaera* and *Aremoricanium*.

CONCLUSIONS AND DISCUSSION

It is evident from this study and from Downie, 1973 that the acritarchs have major distinctive features, in particular wall structures and the excystment mechanisms which both form the basis of this study. These features are recorded as being stable within a taxon although there are many different types and varieties of wall structures and openings. These types and varieties represent functional adaptations; examples are the radial pores for taking up nutrients, processes for keeping the organism afloat on the sea surface and for attachment with other organisms, and the hyaline peridermal layer for moving up and down within the ocean. Moreover, to confirm the functional adaptation of the acritarch wall type, my article in 1983 related acritarch taxa directly to the palaeoenvironments, especially the distance from shore and the relationship to open and closed marine environments. Among those acritarchs, it is possible to suggest some relationship between the wall type and the environment. Accordingly, acritarchs with a tasmanitid wall lived very near to the shore or in shallow water depths with direct influence of the wave and current action, while acritarchs with a pterospermopsid type of wall lived in the outer neritic zone with a depth of about 100-200m with no effect of wave and current action. The acritarchs of baltisphaerid and veryhachid wall types lived in the inner neritic zone within a depth of about less than 100m under the indirectt effect of wave and current action.

The excystment opening in the acritarch is for the release of the living cell from the vesicle cavity to form the new generation, while the vesicle settles down in the substrate and becomes fossilised within the sediment. The adaptations of the various types of openings to the environment need further studies, but in order to clarify the problem, these openings may be related to the type of wall, e.g. *Visbysphaera* has a cyclopyle type of excystment opening, *Veryhachium* has a median split or epityche and *Tasmanites* has a cyclopyle or epityche while in *Gorgonisphaeridium* the excystment mechanism is difficult to observe.

Thus, the wall structures and excystment openings are very useful for defining the affinities of acritarchs and as the main basis for classification. Their use for affinity delineation can be understood by comparison with known taxa from Mesozoic and Tertiary ages. For example, comparison of the tasmanited wall with the living alga *Pachysphaera* is evidence of an algal origin for the acritarchs, and comparison of *Pterospermopsis (Pterospermella)* with the living genus *Pterosperma* indicates that these taxa belong to the prasinophycean algae. Additional evidence of this relationship is seen in the similarity of some of the acritarch openings to the dinoflagellate archaeopyle, that could relate acritarchs to the Pyrhophyta and to the dinoflagellates (class Dinophacea), especially the naked dinoflagellates. Additional features (from previous work), such as vesicle cavity, tabulation, living in clusters, sculptures, major surface features (including processes, lists, flanges, clathria and collars) and the body shape and symmetery are also helpful in the classification of acritarchs.

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