

OBSERVATIONS ON THE NATURE OF THE ACRITARCHS

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The Fifteenth Annual Address, delivered March 1972

ABSTRACT. Recent studies of the acritarchs have shown that many have features in common with one or other of two major groups of planktonic algae—the prasinophyceae (tasmanitids) and the dinophyceae (dinoflagellates). However, studies of the ultrastructure, excystment mechanisms, and knowledge of their geographic and historical distribution are too incomplete at the moment to allow a worthwhile natural classification of the 300 or so acritarch genera. A rough outline of their evolution can, however, be indicated, and shows a marked diversification in the Lower Cambrian and a more rapid succession of groups through the Lower Palaeozoic.

PALYNOLOGICAL preparations, particularly of Lower Palaeozoic marine sediments, normally contain large numbers of small (10–50 μm) organic bodies with hollow interiors. Although these have a great variety of shape and particularly of ornament, such as spines and crests, their natural relationships are obscure beyond the general agreement that they are for the most part the reproductive stages (spores or cysts) of marine planktonic algae. To these fossils the name *Acritarcha* has been given and they currently include over 3000 species. Because of their abundance in the early sediments and their often characteristic appearance, they have been much studied recently in the hope of finding out more about the origin of life and in the expectation of using them for biostratigraphic correlation.

THE GROUP ACRITARCHA

Evitt (1961) published some results of his studies of typical Cretaceous hystrichospheres, i.e. type genera of the older *Hystrichosphaerida* O. Wetzel, and showed them to be not of uncertain affinity as was supposed, but the resting spores or cysts of dinoflagellates. This was amply confirmed by Wall and Dale (1968 and other works), who showed the type species of *Hystrichosphaera* to belong to the dinoflagellate genus *Gonyaulax*. In this way a large number of the organic walled microfossils classed as hystrichosphaerids of unknown affinity were transferred to the dinoflagellates.

The residue of about 600 species did not possess the necessary morphological features to justify their transfer and having no other known affinities remained an *incertae sedis* group for which Evitt (1963) coined the name 'acritarch'. Realizing that this group was probably inhomogeneous, like its predecessor the hystrichospheres, he did not formally name it according to the Rules of Nomenclature but instead established an informal category, the group *Acritarcha*.

The biological and stratigraphical interest of the acritarchs. In the short time that has elapsed since the creation of the group it has been found to be of major importance as an element in the evolution of the biomass and as a contributor to biostratigraphy.

[*Palaeontology*, Vol. 16, Part 2, 1973, pp. 239–259, pls. 24–27.]

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The importance of acritarchs arises from their early appearance in the Precambrian and the record they provide of the diversification of the algae and the origin of the plankton. They are evidently the major group of plankton during the Lower Palaeozoic, probably continuing as such until the Mesozoic. They therefore played an important role in the biological cycle, and were possibly the largest contributors to the biomass during this period. The scale of their contribution can be gauged from the fact that in marine sediments from about 1000 to 300 million years old they are to be found in numbers usually between 1000 and 10 000 per gramme, provided that diagenesis, metamorphism, or abrasion has not affected them.

On this basis Tappan (1971) has calculated their effect on the biological cycle and the consequences of their changing abundance on the atmosphere and the geochemistry of the oceans.

In biostratigraphy their importance also arises from this long continued abundance. In the Precambrian they are the most numerous of fossils. In many apparently unfossiliferous Palaeozoic rocks they provide the only biostratigraphic evidence and in most marine strata of Palaeozoic age they outnumber other common fossils. They have, like all microfossils, the advantages of small size making them useful in dating borehole and other small samples. These advantages would be of little significance were they not allied to distinct, or at least recognizable, differences in the morphology of acritarchs from different strata. The efforts to determine this have shown that assemblages of ten to fifty species are commonly found in samples and are characteristic of particular stratigraphic divisions. Zonal schemes have, however, not yet been established and much work remains to be done before their value in stratigraphic correlation can be accurately determined. This research so far has greatly increased the number of species named to over 3000 and with this increase has come some taxonomic confusion and many problems of systematics.

It is not intended here to review all of these difficulties but to concentrate on the larger more general problem of the affinities of the acritarchs and the possibility of discovering a way to effect a useful genetic classification.

Distribution of the acritarchs. As the study of the acritarchs is so recent, it is intended to give a brief review of what is known about their distribution.

It should be noted at the outset that so far the only fresh-water forms classed with the acritarchs have been found in Holocene lake deposits in Australia (Harland and Sarjeant 1970), and Pleistocene peats of England (Sarjeant and Strachan 1968). All others have been found in marine or brackish water sediments.

Among the marine environments and sedimentary rocks they are most numerous in argillites but also occur in a wide variety of carbonate and arenaceous rocks. Little work has been done on their association with particular environments and no generalizations are possible (Williams and Sarjeant 1967). In the Silurian a widespread provincial distribution, possibly climatically controlled, has been determined by Cramer (1970), affecting the continents bounding the Atlantic. There are indications, not yet confirmed, that broad provincialism of a similar kind affected Ordovician and Cambrian acritarchs as well.

Probably the most intensively studied area is that surrounding the Baltic where rocks ranging in age from the Precambrian Karelian to the Silurian have been examined, notably by Eisenack in many publications

from 1931 onwards, Timofeyev (1959, 1966, 1969), Volkova (1968), and Kjellström (1971). Assemblages from the Cambrian of the Russian platform and Poland have been described by Volkova (1969), from the Ordovician of Poland by Górka (1967, 1969), and from the Russian platform by Umnova and Vanderflit (1971). Vavrdova (1965, 1966) and Slavikova (1968) have investigated the Cambrian and Ordovician of Czechoslovakia, and Burmann (1968) has reported on some lower Ordovician forms from East Germany. In Belgium the Devonian and Carboniferous forms have been described by Stockmans and Williere in a series of papers between 1960 and 1969, Martin (1969) recorded their distribution in the Ordovician and Silurian, and Vanguetaine (1970) reported Cambrian forms. In Britain there are records of Permian acritarchs (Wall and Downie 1963), Silurian (Lister 1970), Ordovician (Rasul 1971) and Cambrian (Downie, *in press*). Mesozoic forms were described by Wall (1965). The Mesozoic acritarchs of France have been described by Valensi (1953) and Devonian and Ordovician forms by Deunff in several papers from 1951 onwards, and Silurian and Devonian forms by Rauscher (1969). In Spain the most important work is that of Cramer (1964 *et seq.*) describing Silurian and Devonian assemblages. Precambrian forms are recorded by Roblot (1964).

In Africa little is known about acritarchs from south of the Sahara, but in North Africa, Ordovician, Silurian, and Devonian forms have been repeatedly recorded notably by Deunff (1961, 1966), Combaz (1968), Magloire (1968), and Jardiné and Yapaudjian (1968).

In Asia acritarchs have been described from Cambrian and Precambrian rocks of the U.S.S.R. by several workers notably Timofeyev (1966, 1969), Lopukhin (1971), Pychova (1966). Apart from this the only records are scattered; among them, Oligocene forms from Japan (Takahashi 1964), from the Jurassic of Pakistan (Sarjeant 1967), and the Precambrian Vindhyan of India (Saluja *et al.* 1971). From Australia Combaz and Peniguel (1972) have recorded Ordovician forms but the main data from the southern hemisphere are due to the work of Brito (1967), Sommer and van Boekel (1966), and Combaz *et al.* (1967).

North American acritarchs have been studied by Cramer (1970) who reports on many Silurian occurrences in the east, and Loeblich (1970, and with various authors) has described forms from the Ordovician, Silurian, and Devonian from localities ranging from Oklahoma to New York. The Cambrian forms have been recorded by Walton (in Staplin *et al.* 1965), and Staplin (1961) has described Devonian forms from Canada.

Although this list is by no means comprehensive and indeed arbitrary to the extent that apology may be needed to authors omitted, it serves to show that, except for the southern hemisphere, a reasonably good coverage of the sedimentary rocks ranging from Precambrian to Devonian has been achieved in Europe, North America, and North Africa. Although only a few papers concerning Mesozoic and Tertiary rocks are included in the above summary these periods also have been covered, and more fully than the Palaeozoic.

STUDIES OF ACRITARCH MORPHOLOGY

In recent years several factors have led to an improved knowledge of the structure of various acritarchs. These include the discovery of extremely well preserved material like that from the Sylvan Shale of Oklahoma and the Lower Palaeozoic of Estonia, as well as improved methods of preparation producing cleaner and more easily examined specimens. The improved techniques of examination such as the use of the scanning electron microscope (see Loeblich 1970) and ultra-thin sections (Jux 1971) have also contributed in a major way.

This work has focused attention on wall structure and excystment mechanism as characters meriting special consideration in determining the relationships of the acritarchs to each other and to other organisms.

Wall structure. Too little is known about the chemistry of the substance forming the acritarchs test to help in their classification. Studies like that of Kjellström (1968)

show that some consist of condensed fatty acid derivatives, similar to the 'sporo-pollenin' material.

The wall structure does, however, show promise of being of considerable importance. The studies of Jux (1969) indicate the value of ultra-thin sections. At present these studies are limited to a very small number of genera but can be supplemented by some more obvious features visible under the ordinary microscope.

At present the following types of wall structure can be recognized:

1. *Tasmanitid*. The wall is uniform, but laminated with narrow radial pores. The wall thickness is often variable in a species, probably due to growth.

This type of wall has been shown by Jux to be present in the important Palaeozoic genera *Tasmanites* and *Baltisphaeridium*. It is also present in Mesozoic and Tertiary species attributed to *Tasmanites* and the living alga *Pachysphaera*. Optical studies suggest that the Cambrian genera *Priscogalea* and *Cymatiogalea* have a similar wall structure.

2. *Micrhystridian*. The wall is of a simple homogeneous nature and appears to be of a more or less constant thickness in a species, usually thin.

To this group belong *Micrhystridium* and *Veryhachium*, which account for a large number of acritarch species in the Palaeozoic and Mesozoic.

3. *Diacrodian*. The wall is thin and of a simple homogeneous nature. It is distinguishable from that of *Micrhystridium* only because of a tendency to split into angular plates when damaged (Lister 1970b). All the diacrodian genera could be placed here, although the plate structure has only been seen in *Acanthodiacrodium*, *Lophodiacrodium*, and *Dasydiacrodium*.

4. *Visbysphaerid*. The wall is thin and apparently homogeneous. It is distinguished from that of *Micrhystridium* because of the capacity for developing an inner body closely adpressed to the outer wall. In this way a double wall can be formed. This potentiality is nearly always realized in the genus *Visbysphaera* but only infrequently in others like *Diexallophasis*.

Excystment mechanism. The importance of the excystment mechanism in determining relationships in dinoflagellates was shown by Evitt (1961) and discussed at length by him later (Evitt 1967). It is possible that this is true also for the acritarchs, although, because the openings are often less distinctive and frequently unknown, the evidence is much less clear. Examples of openings are shown in Pl. 24.

The following categories of excystment mechanism are known:

1. *Archaeopyle*. A name introduced by Evitt (1961) for excystment openings formed by the loss of one or more plates from a dinoflagellate cyst.

These are of a few regular types distinguished by the number and position of the plates that open. The openings are frequently angular or sub-angular in outline.

EXPLANATION OF PLATE 24

All figures $\times 1000$

Fig. 1. *Acanthodiacrodium* sp. Dictyonema Beds (Tremadoc), Leningrad. Shows the beginnings of a split in the median unornamented region.

Fig. 2. *Poikilofusa* sp. Shineton Shales (Tremadoc), England. Showing a lateral epityche.

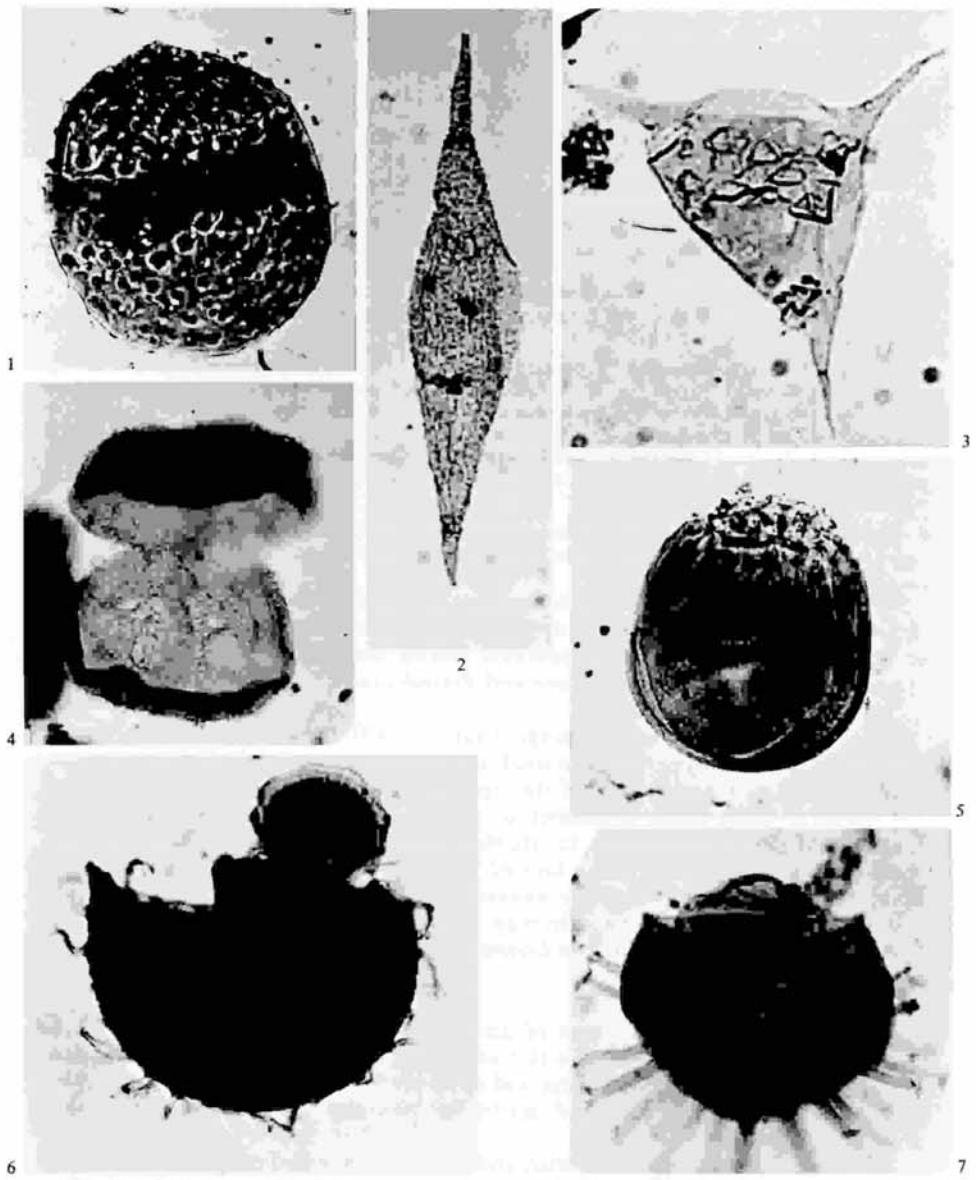
Fig. 3. *Veryhachium* sp. Shineton Shales (Tremadoc), England. Showing a lateral epityche.

Fig. 4. *Acanthodiacrodium* sp. Shineton Shales (Tremadoc), England. Shows development of split into two equal halves.

Fig. 5. *Ooidium* sp. Dictyonema Beds (Tremadoc), Leningrad.

Fig. 6. *Cymatiogalea* sp. Tremadoc, Poland. Showing thick walls, micropyle and marginal veil round operculum.

Fig. 7. *Cymatiogalea* sp. Shineton Shales (Tremadoc), England. A thinner walled specimen.



DOWNIE, Tremadocian acritarchs

These characterize dinoflagellate cysts of Mesozoic and Tertiary age, and are known in only one or two species from the Silurian and Devonian, e.g. *Arpyloris antiquus*.

2. *Cyclopyle*. This name was introduced by Eisenack (1969) for openings with a circular outline. The term pylome which had formerly been used for acritarch openings he suggested should be used as a general term for all kinds of escape apertures.

Cyclopyles are found in Palaeozoic species of *Tasmanites* and in the Ordovician genera *Baltisphaeridium*, *Peteinosphaeridium*, and *Axisphaeridium*, among others. They appear for the first time in the Cambrian, probably in the Upper Cambrian.

The openings are formed by the release of a circular operculum whose location is probably in a fixed and pre-determined position, thus allowing orientation of the cysts. This fact is not demonstrable except in a few genera, e.g. *Cymatiogalea*, which can be independently orientated by means of other characters.

Variants of the cyclopyle are found in *Priscogalea* and *Cymatiogalea* (Pl. 24, figs. 6, 7), where its diameter is unusually large, exceeding 50% of the body diameter. These large openings (macropyles) are sometimes sub-polygonal. It is also common to find the cyclopyle or macropyle surrounded by a differentiated zone, sometimes smooth, sometimes a raised rim.

3. *Epityche*. This term was introduced by Loeblich and Tappan (1969) for excystment structures formed by a curving split allowing a flap to open (Pl. 24, figs. 2, 3). These openings are commonly found in species of *Veryhachium* and *Leiofusa* where they can be shown to have a regular location.

A number of variants have been subsequently noted. Cramer (1970) distinguishes C-shaped and S-shaped splits in *Veryhachium* and Lister (1970) stresses the progressive development of a small-circle split in many genera, notably *Micrhystridium*. These are called cryptosutures and their appearance forms a large flap which may often break off.

4. *Median split*. A few forms open by splitting into two equal halves. The Ordovician genus *Orthosphaeridium* is a good example of this and it is also characteristic of many leiospheres, e.g. *Hemisphaeridium*.

Although these categories can be accepted and applied to most acritarch species, there is still difficulty arising mainly from species which have not ever been found to have natural openings. Most common among this group are the Precambrian sphaeromorphs. But *Cymatiosphaera* and *Polyedryxium*, two important Palaeozoic genera, present the same problem.

Other groups rarely show openings. Cramer (1970) reports C-shaped epityches in *Deunffia*, Rasul (1971) records a small subpolygonal opening in *Vulcanisphaera*.

In other cases the character of the opening is ambiguous. *Acanthodiacrodium*, for instance, splits along a number of planes sometimes transverse, sometimes longitudinal (Pl. 24, figs. 1, 4). In *Micrhystridium* some species, presumably with small-circle epityches, have them located very near the equator and they can only be arbitrarily separated from the median split. In *Veryhachium* and in *Leiofusa* instead of the usual epityche a split may form along one edge, and subsequent deformation of the test, particularly in *Leiofusa*, may make recognition and classification of the pylome very obscure.

Clusters. The overwhelming mass of acritarchs occur in preparation, and in the rock, as isolated individuals. This is true also of dinoflagellate cysts and modern representatives of the dinoflagellates and other planktonic algae. There is, however, a growing number of records of acritarchs occurring in monospecific clusters. Examples are shown in Pl. 25.

In the case of certain Precambrian and Cambrian sphaeromorph acritarchs (i.e. forms with more or less smooth surfaces) this has long been known, and in the Precambrian they are particularly common. These clusters take forms varying from

loose chains and aggregates of a few individuals to more or less compact discoid or spherical masses comprising scores of cells. Timofeyev (1966) created the subgroup Polysphaeritae to include them.

It is now known that many other kinds of acritarchs occur in similar associations although much less commonly. In the Cambrian or Tremadoc rounded clusters have been found of species belonging to *Micrhystridium*, *Prisogalea*, *Cymatiogalea*, *Tectitheca*, and *Acanthodiacrodium* (Pl. 25, fig. 1). In younger rocks records are even less common but *Leiofusa* is recorded in clusters from the Ordovician (Combaz *et al.* 1967) and possibly *Deunffia* and *Veryhachium* in the Silurian (Cramer 1970).

The significance of these clusters is not clear. The shape, size and in some cases the content is consistent with their production in sporangia like those of *Parka*, a non-vascular plant from the Lower Devonian (Challinor and Orbell 1971).

Other morphological features used in classification. In the sub-group created by Downie *et al.* (1963) the symmetry and shape of the body was given greatest weight, combined with the nature of the outgrowths from the body surface. These are characters that are always readily visible and can form the basis of an easily used classification. This has been extensively discussed by Cramer (1970). These features, however, probably have little significance in establishing the natural affinities of the acritarchs, the evolution of a sphere with spines being a response to very common functional requirements.

CLASSIFICATION OF THE ACRITARCHS

The problems of defining genera are considerable and complicated by confused concepts and irregular nomenclature. It would be inappropriate to review them partially and too large a work to be included here. It is proposed therefore to examine the question of supra-generic classification in the light of the morphological information set out above.

The earliest classification including the acritarchs was that of Wetzel (1933) which was subsequently added to by Eisenack. In 1954 the divisions were:

Incertae Sedis

- Order HYSTRICHOSPHAERIDA Wetzel 1933
- Family HYSTRICHOSPHAERIDAE Wetzel 1933
- Family LEIOFUSIDAE Eisenack 1938
- Family LEIOSPHAERIDAE Eisenack 1954
- Family PTEROSPERMOPSIDAE Eisenack 1954

Soon after it became conventional to treat the hystrichospheres as plants, including those subsequently to become the foundation of the acritarchs. The following families were later introduced:

- Family TASMANACEAE Sommer 1956
- Family OOIDACEAE Timofeyev 1959
- Family DIACRODIACEAE Timofeyev 1959

The last two were invalid because of legal defects.

The work of Evitt (1961) radically altered this arrangement by showing that the members of the family Hystrichosphaeridae belonged to the dinoflagellates whereas the members of the others remained *incertae sedis*. The latter formed the nucleus of the group Acritarchs.

The systematic situation was then reviewed by Downie *et al.* (1963). They suggested a number of informal subgroups to accommodate the fifty-six genera of acritarchs then named. These subgroups were based on characters easily seen, and were intended to provide a temporary classification while the data needed for a more durable and significant classification were accumulated. A somewhat similar system of groups and subgroups was later introduced by Timofeyev (1966).

These informal groups have been criticized because of their invalidity according to the 'Rules', but they have been widely adopted because many workers have recognized that a formal, valid, classification would have been, with the limited evidence available, just as arbitrary but more confusing and troublesome to discard. In fact the only subsequent formal classification, that of Mädlar (1963, 1967) cannot be used as it stands. Mädlar's classification is as follows:

- Class HYSTRICHOPHYTA Mädlar 1963
- Order TASMANALES Mädlar 1963
 - Family TASMANACEA Sommer 1956
 - Family PTEROSPHAERIDACEAE Mädlar 1963
- Order LEIOSPHAERIDALES Mädlar 1963
 - Family LEIOSPHAERIDACEAE Eisenack 1954
- Order HYSTRICHOSPHAERALES Mädlar 1963

The criticisms of this classification are that *Hystrichosphaera*, the type genus of the family, is a junior synonym of *Spiniferites* and also of *Gonyaulax*, a living dinoflagellate. *Tasmanites* and *Pterospermopsis*, the type genera of the families in the Tasmanales, most probably belong to the algal class Prasinophyceae. Some of the leiospheres may belong here too, but they appear to be a polyphyletic group.

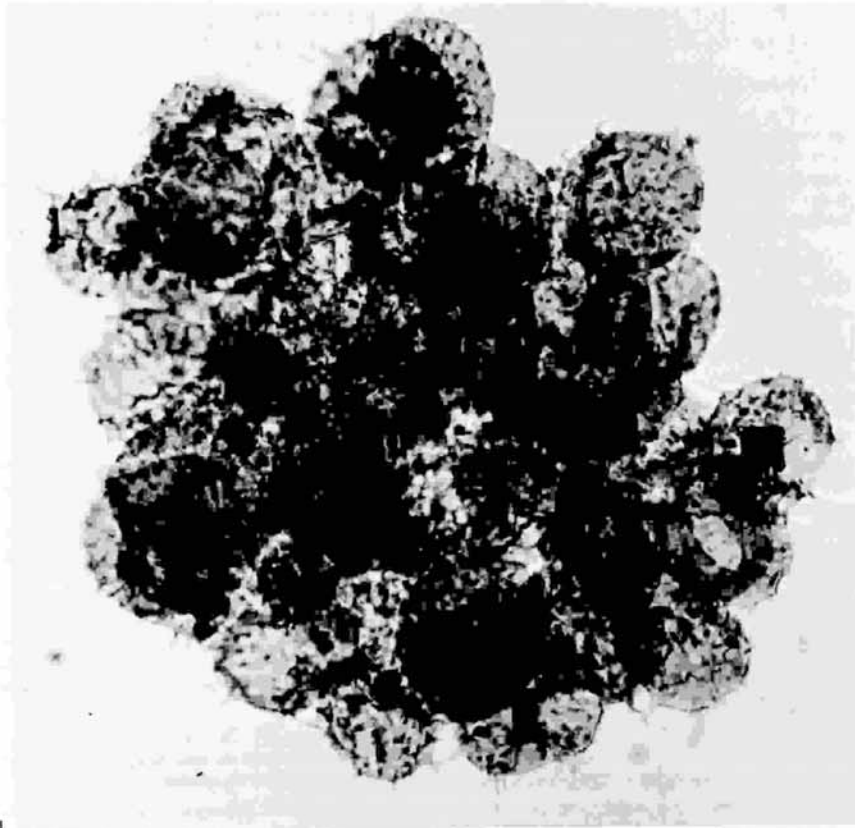
There is therefore no acceptable legal supra-generic classification of the acritarchs available as an alternative to the subgroups of Downie *et al.* (1963). Before considering the erection of such a classification with its implications of genetic relationship, it is necessary to review the present state of knowledge and examine the evidence relevant to the nature and affinities of the acritarchs.

The affinities of the acritarchs. The morphological evidence, particularly that relating to the wall structure and excystment mechanism, permits a tentative subdivision of the acritarchs into related groups. The grouping is tentative because the observations

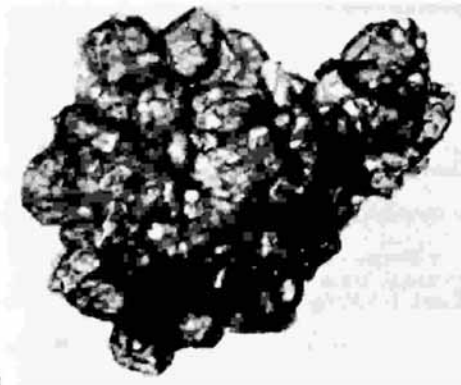
EXPLANATION OF PLATE 25

All figures $\times 1000$

- Fig. 1. Cluster of *Acanthodiacrodium* sp. Shineton Shales (Tremadoc), England.
 Fig. 2. Cluster of sphaeromorphs (*Synsphaeridium* sp.). Torridonian (Precambrian), Scotland.
 Fig. 3. Single sphaeromorph (?*Leiosphaeridia* sp.). Lower Cambrian, Scotland.



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DOWNIE, Precambrian and Palaeozoic acritarchs

are available for only a small proportion of the described species. These groups should form the basis for a more natural classification in the future.

1. *Pachysphaera* group

This group is characterized among fossils by having the tasmanitid type wall, excystment by a median (great circle) split, and the absence of alae (i.e. crests or wings).

To it belong the modern genera *Pachysphaera* and *Halosphaera* and the fossil genera *Tyttthodiscus*, *Crassosphaera*, and *Tasmanites* (pars.) (Pl. 26, fig. 3). It appears to be confined to Mesozoic and younger periods.

The group belongs to the algal class Prasinophyceae.

2. *Tasmanites* group

This group has tasmanitid wall structure, and an absence of alae. Excystment is by a cyclopyle. To it belong the Palaeozoic species of *Tasmanites*, ranging in age from Ordovician (?Cambrian) to Permian (Pl. 26, fig. 5).

Unfortunately I have been unable to determine whether or not the type species of *Tasmanites*, *T. punctatus* from the Permian of Australia, opens by a cyclopyle or a median split. The nomenclature is therefore provisional.

3. *Pterospermopsis* group

This group has characteristic alae dividing the vesicle surface into fields. Living representatives excyst by splitting along the base of an ala. No excystment structures have been recorded among fossil examples. It includes the living genus *Pterosperma* and the fossils *Pterospermopsis* (Pl. 26, fig. 4) and *Cymatiosphaera*. The latter range in age from Cambrian to Tertiary. The similarity in appearance and pattern of alae to those of various species of the living *Pterosperma* (Boalch and Parke 1971) indicates that the group belongs to the Prasinophyceae.

4. *Baltisphaeridium* group

Members of this group have a tasmanitid wall structure with spinose outgrowths from the vesicle surface. These outgrowths are commonly simple spines, but alae and irregular projections also are found. The excystment structures are cyclopyles, macropyles, and median splits. The group may be subdivided as follows:

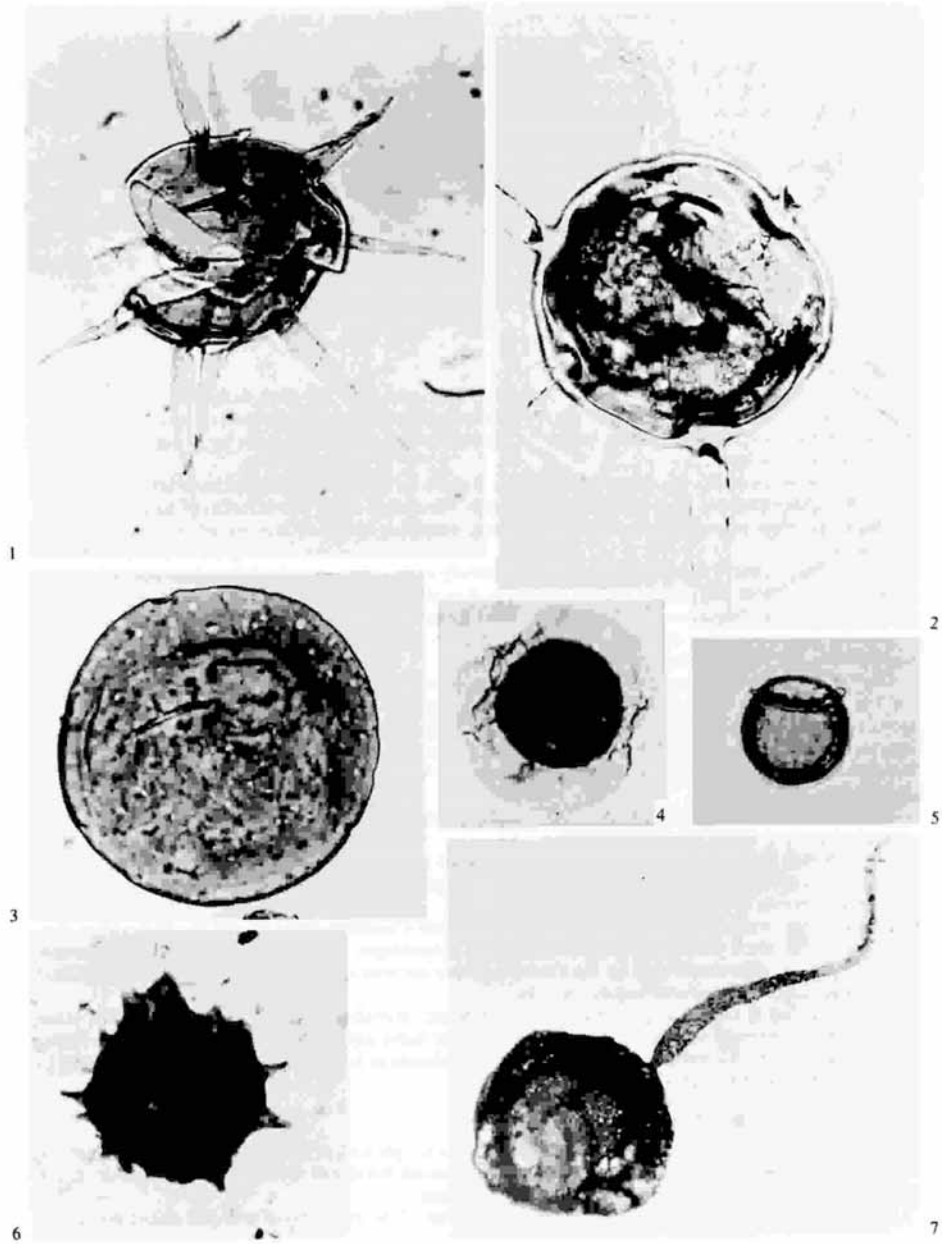
(a) *Baltisphaeridium* type. This is characterized by spinose ornament (Pl. 26, fig. 7) and cyclopyles. It includes *Baltisphaeridium*, *Peteinosphaeridium*, *Asketopalla*, *Polyancistrodorus*, and *Axisphaeridium*. It is characteristically Ordovician in age (Arenig to Ashgill), but certain Cambrian species may belong here.

(b) *Priscogalea* type. This is characterized by its macropyle. It includes *Priscogalea* and *Cymatiogalea*, and is confined to the Upper Cambrian and Lower Ordovician. *Cymatiogalea* has alae and shows a field pattern very like that of some species of the living *Pterosperma* (Boalch and Parke 1971; Rasul 1971).

EXPLANATION OF PLATE 26

All figures $\times 1000$

- Fig. 1. *Orthosphaeridium* sp. Sylvan Shale (Ashgillian), U.S.A. Shows median equatorial split.
 Fig. 2. *Orthosphaeridium* sp. Sylvan Shale (Ashgillian), U.S.A. Shows the thick wall with plugs at base of spines.
 Fig. 3. *Tasmanites* sp. Bailey Formation (Lower Devonian), U.S.A. Shows thick perforated wall with split developing.
 Fig. 4. *Pterospermopsis* sp. Bailey Formation (Lower Devonian), U.S.A. Shows equatorial alae.
 Fig. 5. ?*Tasmanites* sp. Sexton Creek Formation (Silurian), U.S.A. Shows large cyclopyle with rim.
 Fig. 6. *Aremoricanicum* sp. Sylvan Shale (Ashgillian), U.S.A. Opening is through large process at the upper end.
 Fig. 7. *Bacisphaeridium* sp. Caradoc, England. Single process shows constriction common in *Baltisphaeridium* group of acritarchs.
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DOWNIE, Palaeozoic acritarchs

(c) *Orthosphaeridium* type. This is characterized by its median split. Only the genera *Orthosphaeridium* (Pl. 26, figs. 1, 2) and *Actipilion* can be placed here so its range is confined to Middle and Upper Ordovician.

(d) *Goniosphaeridium* type. This is characterized by the body shape which tends to be polygonal, being formed by the fusion of the process bases. No openings are found (except possibly a cyclopyle in *Pulvinosphaeridium*). It includes the genera *Goniosphaeridium* and possibly also *Pulvinosphaeridium* and *Estiastra*. It would then range from Middle Ordovician to Ludlow.

The *Baltisphaeridium* group differs from the *Tasmanitid* group mainly by the possession of strong ornament. It is therefore probable that they both belong to the same class of algae.

5. *Navifusa* group

Navifusa and *Leiovalia* are elongated acritarchs without spines. They rarely show excystment structures but cyclopyles are possibly present in a few species. The wall ultra-structure is unknown.

At present the only feature associating them with the other groups so far described is the presence of the cyclopyle.

6. *Sphaeromorph acritarchs*

The previous five groups have features indicating relationship to the class Prasinophyceae. The only other acritarchs having such characters are a few species included in the smooth, round genus *Leiosphaeridia*. This genus was defined by Eisenack (1954) who distinguished it from *Tasmanites* by its simple wall structure. Both have cyclopyles.

Several species in which the excystment opening is rarely or not at all developed have been put in *Leiosphaeridia*, although there is no evidence of the way in which they open. The affinities of such forms poses a difficult problem since the structure is featureless, consisting solely of a more or less smooth round pellicle.

At the present time it is not possible to constructively review the content of the sphaeromorph group, which includes about 120 generic names. However, it is clear on the basis of excystment mechanism that some are related to the Prasinophyceae; others, like *Chytroesphaeridium*, have been classed with the dinoflagellates. A great number remains, some of which have been compared with Chlorophyceae and other algal classes, but the grounds for doing so are slender.

The sphaeromorphs appear in the Precambrian where they are extremely abundant, particularly in the Upper Proterozoic. Their widespread occurrence suggests they are marine, their morphology that they are spores. Beyond this there is little positive evidence about their nature. They have been classified into genera mainly on slight differences of surface ornament (some of which may have been diagenetically introduced), on size which ranges from 5 to 500 μ and on various obscure structures like rims, folds, and openings.

Many are found in associations, the most complete being compressed spherical groups of hundreds of individuals.

The openings are unknown until the Lower Cambrian where several uniporate and multiporate forms have been recorded (Pychova 1969). These openings appear to be irregular in shape and size and their biological meaning is not clear.

The sphaeromorphs decline in numbers from the Lower Cambrian onwards. By the Ordovician they have become a minor element in most palynological assemblages but occasionally dominate in certain facies. The decline continues until by the Devonian there are relatively few forms that need to be placed in the biologically unclassifiable sphaeromorphs.

Here the group is treated as primitive and polyphyletic, probably including ancestral forms of other algal groups represented among the acritarchs. The cluster habit supports this view. It is a habit persisting in the microhystridia, diacrodians, baltisphaerids, and leiofusids as late as the Tremadoc or Arenig and in the leiospheres to the Upper Silurian.

7. The *Micrhystridium-Veryhachium* group

This group characteristically has a spinose body with a simple wall structure: excystment is by epityche or cryptosuture (small circle epityche). Additional features are the size of the body, which is usually small, and the free extension of the body cavity into the processes.

Some members of the group are very similar to the cysts of the living *Peridinium* and naked dinoflagel-

lates (Wall and Dale 1968). It is quite possible that the affinity of the group is with the dinoflagellates (Lister 1970b).

The group ranges in time from the Cambrian possibly to Recent sediments. Its abundance in favourable facies of the Mesozoic equals that in the Palaeozoic.

8. The *Leiofusa* group

This group is in many ways similar to the *Michhystridium-Verhachium* group, differing in its elongate body shape. Opening is by splitting (lateral or median) or flap-epityche (C-shape). Deformation of the body sometimes makes recognition of the type of opening difficult.

Included in the group are several genera of somewhat disparate morphology, e.g. *Deunffia*. The range is from Cambrian to Tertiary with a clear acme in the Silurian-Devonian.

There is no direct evidence of their affinity but structurally they are similar to the *Michhystridium-Verhachium* group with which they are often associated. Relationship to this group is likely in several instances at least.

9. The *Acanthodiacrodian* group

This group is characterized by its simple wall structure, its elongate body shape, and the polarity of its ornament. There does not appear to be a consistent method of opening, but splitting does occur along clear lines and there are indications of a wall structure of plates bounded by sutures (Lister 1970a).

The possession of a tabular wall structure is reminiscent of the cysts of tabulate dinoflagellates.

The group ranges in age from Lower Cambrian to Llanvirn and possibly later. There is a clear acme around the Cambro-Ordovician boundary.

10. The *Visbysphaera* group

Members of this group open by a cryptosuture (small-circle epitiche) and have a greater or less tendency to develop an inner cyst.

It is convenient (although not perhaps justifiable on biological grounds) to subdivide them.

(a) *Visbysphaera* type. This type is rarely found without an inner cyst. The wall is therefore nearly always double (Pl. 27, fig. 5), the inner layer being relatively thick with a smooth surface, the outer layer thinner and extending outwards to form processes (usually hollow). Some individuals closely resemble dinoflagellate cysts particularly of the chorate group (mostly gonyaulacid types), e.g. *Hystrichosphaeridium*, *Cleistosphaeridium*.

Included here are the genera *Daillydium*, *Dilatysphaera*, and *Cymbosphaeridium*. Its range in time is restricted from the Silurian to the Carboniferous with a clear acme in the Upper Silurian/Lower Devonian.

(b) *Triangulina* type. This type is similar to the above, but has a triangular body (Pl. 27, fig. 4). It includes also *Ozotobrachion* and *Onondagella*.

(c) *Diexallophysis* type. In this type (Pl. 27, fig. 6) an inner cyst is only infrequently developed. In addition the processes are inclined to have small excrescences and a peculiar type of digitate terminal branching. It includes also *Florisphaeridium* and *Evittia*. Its range is confined to the Silurian and Lower Devonian.

The similarity of some species to dinoflagellate cysts indicates the possibility of a relationship. The evidence is as yet rather superficial and inconclusive.

Other acritarchs

The above groups include over 90% of the described acritarch species and genera. The remainder are not included either because there is not enough evidence about wall structure and opening, e.g. *Polyedryxium*, or because they do not fit into any of the categories established, e.g. *Duvernaysphaera* and *Quadradiium*.

THE ACRITARCH SUCCESSION

The tentative relationships expressed in the groups described above, when considered against the background of the geological time scale, permit the consideration of possible evolutionary trends. This is displayed on text-fig. 1. Several stages can

be recognized, each in succession being marked by assemblages characteristic of the period.

Period 1. This is in the Precambrian where, following an early phase of very fragmentary records, there is from about 1000 million years to the base of the Cambrian an abundant record of sphaeromorphs. These simple types cannot be assigned to any particular algal group because they have not yet evolved any differentiation of wall structure or developed any distinctive ornament. They tend to occur in clusters, and are probably spores of larger marine algae. This basic, primitive, and probably heterogeneous stock begins to show pronounced ornament near the Cambrian base and in the next period clear differentiation is possible.

Period 2. In the Lower Cambrian four innovations are found. There is the development of short spines with the appearance of *Micrhystridium*, the appearance of crests (?alae) in *Cymatiosphaera* (their structure needs closer investigation), the development of processes with a closed base in species currently classified as *Baltisphaeridium* (these Lower Cambrian species also require detailed investigation to determine their relationship to typical Ordovician *Baltisphaeridium*), and there is the development of polarity in *Leiofusa* and *Lophodiacrodium*. Thus from the Cambrian onwards the acritarchs include both prasinophycean and possible dino-flagellate groups.

The tendency to occur in clusters persists, but no opening styles have yet been clearly developed, although *Uniporata-Polyporata* are present.

Period 3. The Upper Cambrian is marked by the flourishing of the *Acanthodiacrodium* and *Priscogalea* groups. *Tasmanites* also appears and the macropyle opening is a common feature.

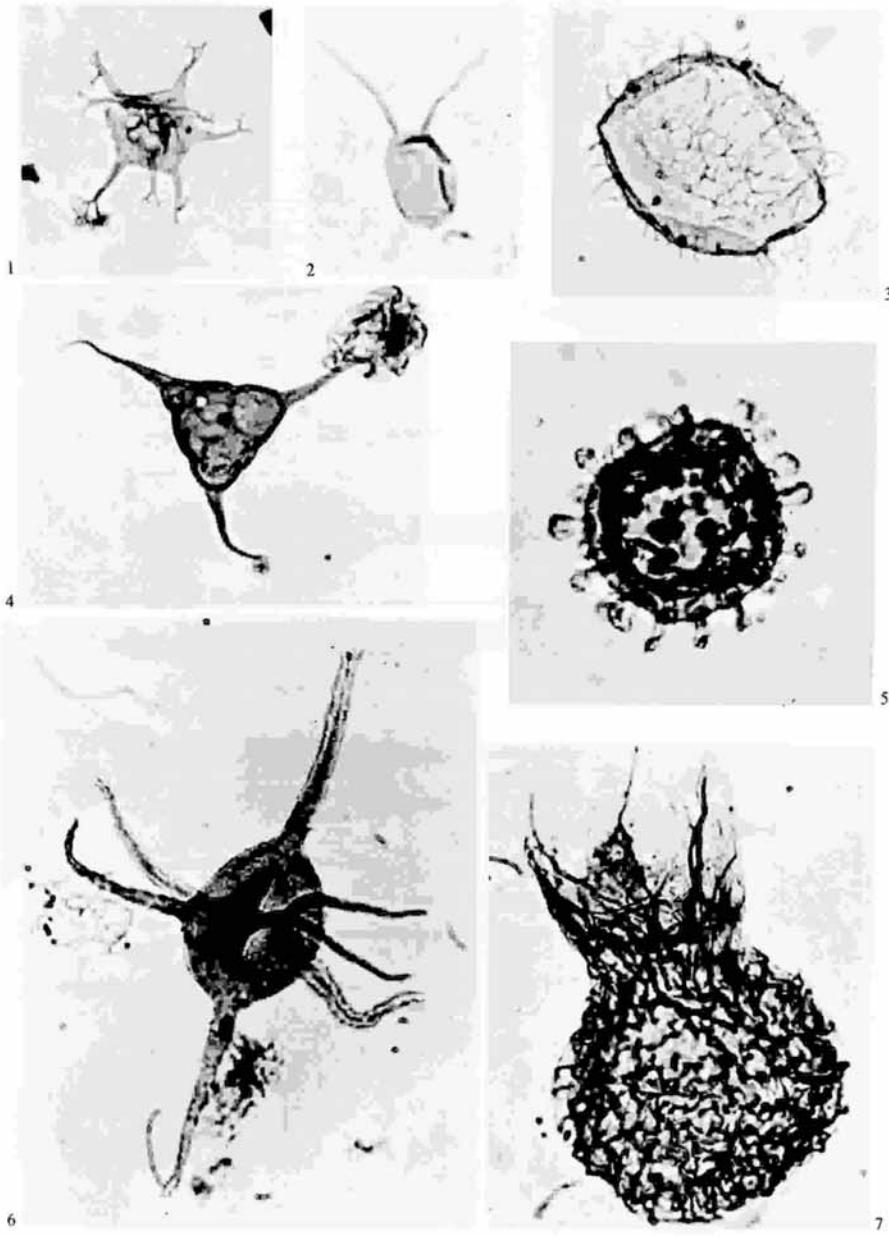
Period 4. In the Arenig the most striking feature is the increase of typical *Baltisphaeridium* types and the development of differentiates of the *Acanthodiacrodium* group which is now waning. *Veryhachium* appears in force in a rather simple form. The Upper Ordovician is distinguished by the abundance of *Baltisphaeridium* and its derivatives.

Period 5. In the Silurian the Baltisphaerids die out, and are replaced after a short interval by the *Diexallophasis* type. During the Lower Silurian, which is dominated

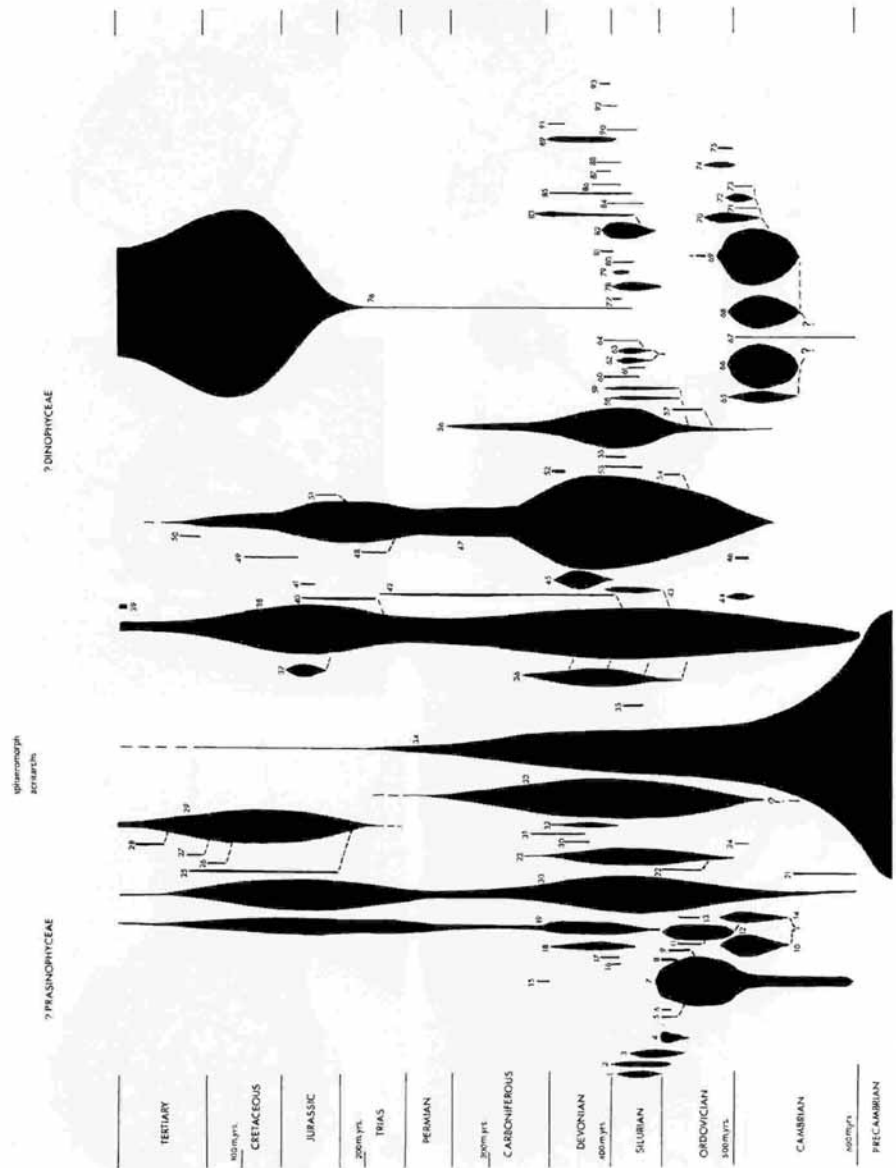
EXPLANATION OF PLATE 27

All figures $\times 1000$

- Fig. 1. *Multiplicisphaeridium* sp. Bailey Formation (Devonian), U.S.A. Single walled acritarch.
 Fig. 2. *Domasia* sp. Buildwas Beds (Silurian), England. Single walled acritarch.
 Fig. 3. *Ammonidium* sp. Bailey Formation (Devonian), U.S.A. Shows complete sub-equatorial epityche development.
 Fig. 4. ?*Triangulina* sp. Bailey Formation (Devonian), U.S.A. Shows double walled structure.
 Fig. 5. *Visbysphaera* sp. Wenlock Shales (Silurian), England. Shows double walled structure.
 Fig. 6. *Diexallophasis* sp. Neahga Shales (Silurian), U.S.A. A form with no inner body.
 Fig. 7. ?*Geron* sp. Neahga Shales (Silurian), U.S.A. A form related to *Tumisphaeridium* and *Carminella*, but difficult to classify.



DOWNIE, Silurian and Devonian acritarchs



TEXT-FIG. 1. Possible relationships among the acritarchs.

The width of the columns is approximately proportional to the number of species described from a given period. The horizontal arrangement is indicative of possible relationship. Not all genera are included partly because of synonymy problems and partly because of classification difficulties. The numbers refer to generic names as follows:

- Baltisphaerid group:**
 1, *Estiastra* 2, *Pulvinosphaeridium* 3, *Gontosphaeridium* 4, *Orthosphaeridium* 5, *Axissphaeridium* 6, *Actipilion* 7, *Baltisphaeridium* 8, *Bacisphaeridium* 9, *Aremoricanicum* 10, *Priscogalea* 11, *Asketopalla* 12, *Petemosphaeridium* 13, *Polyaucycystroderus* 14, *Cymatiogalea*.
- Pterospermopsid group:**
 15, *Tornacia* 16, *Sol* 17, *Helios* 18, *Duvernaysphaera* 19, *Pterospermopsis* 20, *Cymatiosphaera* and *Dictyotidium* 21, *Retisphaeridium*.
- Navifusa group:**
 22, *Leiovalia* 23, *Navifusa* 24, *Lunulida* 25, *Crassosphaera* 26, *Pleurozonaria* 27, *Noremia* 28, *Cooksoniella* 29, *Tasmanites-Pachysphaera* 30, *Quisquellites* 31, *Tapajonites* 32, *Maranhites* 33, *Tasmanites*.
- Sphaeromorph group:**
 34, *Sphaeromorph acritarchs*.
- Microhystridium-Veryhachium group:**
 35, *Piliferosphaera* 36, *Multiplicisphaeridium* 37, *Solisphaeridium* 38, *Microhystridium* 39, *Creberlumectum* 40, *Filisphaeridium* 41, *Comasphaeridium* 42, *Buedingisphaeridium* 43, *Elektroniskos* 44, *Vulcanisphaera* 45, *Polyedrixium* 46, *Imphiviculus* 47, *Veryhachium* 48, *Staplinium* 49, *Prismatocysta* 50, *Hidasia* 51, *Metaleiofusa* 52, *Unellium* 53, *Neoveryhachium* 54, *Sylvanidium*.
- Leiofusa group:**
 55, *Anthractrus* 56, *Leiofusa* 57, *Disparifusa* 58, *Poikilofusa* 59, *Eupoikilofusa* 60, *Dactylofusa* 61, *Baiomeniscus* and *Holothurodiagma* 62, *Deauffia* 63, *Domasia* 64, *Hemibaltisphaeridium*.
- Diacrodian group:**
 65, *Trachydiacrodium* 66, *Lophodiacrodium* 67, *Ooidium* 68, *Dasydiacrodium* 69, *Acanthodiacrodium* 70, *Tectitheca* 71, *Polygonium* 72, *Priscotheca* 73, *Arbusculidium* 74, *Dicrodia-crodium* 75, *Schizodiacrodium*.
- Dinoflagellate group:**
 76, Dinoflagellate cysts.
- Visbysphaera group:**
 77, *Percultisphaera* 78, *Diexallophasis* 79, *Florisphaeridium* 80, *Helosphaeridium* 81, *Evittia* 82, *Visbysphaera* 83, *Gorgonisphaeridium* 84, *Cymbosphaeridium* 85, *Ammonidium* 86, *Triangulina* 87, *Ozotobranchion* 88, *Onodagella* 89, *Eisenackia* and *Crameria* 90, *Dilatatisphaera* 91, *Daillyidium* 92, *Leoniella* 93, *Fimbrialomerella*.

Connecting lines indicate close relationship.
 The width of the columns roughly represents the number of species recorded from the appropriate period.

by the *Micrhystridium-Verhachium* group, there is a progressive enrichment of the assemblages by the appearance of many new forms belonging to the *Visbysphaera*, *Leiofusa*, and *Micrhystridium-Verhachium* groups. This enrichment continues into the Upper Silurian and Lower Devonian. *Arpylorus*, an Upper Silurian form with an archaeopyle, is commonly considered to be a dinoflagellate.

Period 6. The Devonian begins with rich assemblages, but there is considerable change in this period. The *Visbysphaera* group declines, but is represented by a few forms very like dinoflagellates, e.g. *Dilatysphaera* and '*Hystrichosphaeridium*'. *Leiofusa* types become rarer and are reduced mainly to simple forms. The *Verhachium-Micrhystridium* group becomes dominant by Middle Devonian and produces novel forms like the spinose *V. rosendae* group. The Middle and Upper Devonian assemblages are also enriched by *Polyeduxium* and *Senziella*, possibly derivatives from a *Verhachium* stock.

Period 7. This period begins with the Carboniferous and continues into the Triassic. It is marked by a great paucity of all organic walled plankton, following a rapid decline in the Carboniferous. In the Permian a few species of the *Verhachium-Micrhystridium* group account for nearly everything so far known.

Period 8. The period from the Upper Triassic onwards can be treated as a unit because dinoflagellates clearly of the peridinoid and gonyaulacoid stocks dominate the marine organic-walled microplankton. The acritarchs, however, persist and during the Middle Jurassic there is even a late flourishing of *Micrhystridium*. The *Pachysphaera* group appears in the Lias and several new derivatives are known in the Cretaceous and Tertiary. *Pterospermopsis* and *Cymatiosphaera* are commonly found.

The first fresh water forms appear in the Quaternary.

CONCLUSIONS

Although some idea of the natural affinities and evolution of the acritarchs can be gained by a review of the evidence currently available, it is not enough to obviate radical errors in classification such as have occurred in the past. For this reason the informal groupings should be retained, if found useful, while more data are gathered.

Already, however, it is evident that there are two main divisions of the acritarchs, both arising from primitive Precambrian stocks. One of these is related to the prasinophycean algae, the other possibly to dinoflagellates.

Acknowledgements. I would like to thank all my colleagues in the study of acritarchs for their co-operation. I am aware that many papers and genera have not been mentioned in the text; this is due only to the limited objectives of this review. I am grateful to Mr. P. Shepherd for the photography, and to Dr. S. M. Rasul for allowing me to use his prints of Shineton Shale acritarchs.

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Typescript received 31 July 1972