

ACRITARCHS: A REVIEW

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(Received 21 January 1993; accepted 23 March 1993)

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I. INTRODUCTION

What are acritarchs? Basically, they represent an enigmatic (Greek, *akritos* = uncertain; *arche* = origin), artificial group of microorganisms, introduced as an informal category by Evitt (1963) and considered for purposes of classification as plants, so that they are covered by the Rules of Botanical Nomenclature. They are eukaryotic, unicellular, organic-walled, resistant, morphologically varied, consistently associated with water-deposited sediments, and essentially both marine and fossil. Although certainly of polyphyletic origin, the majority were probably cysts of extinct microscopic algae.

There is broad agreement that acritarchs appeared in the Precambrian, about 1400 Ma (million years ago) BP. It is certain that they achieved their maximum abundance and diversification between the early Cambrian and the late Devonian, from about 550 to 360 Ma BP and that their occurrence in more recent deposits is both relatively scarce and erratic (Fig. 1).

The question as to what they are would produce different comments from biologists and botanists on the one hand, and palaeontologists and geologists on the other. The former would emphasize the uncertain origin and affinities, the composition of the test, and the lack of an acceptable classification for a category of organisms which, because it is so broadly defined, has one of the longest known life histories. Biologists and palaeontologists together would emphasize also that during the 190 Ma or so of their 'golden age', and on account of their abundance during life, acritarchs must have played an ecologically important role at or near the base of the marine food chain, depending on whether or not they were photosynthetic. Geologically oriented workers would stress the importance of acritarchs in the mapping and reconstruction of sedimentary basins, where their main application is as indicators of relative stratigraphic age and, more debatably, of palaeogeography and palaeoenvironments. The theoretically wide geographic distribution of taxa and high durability of specimens, together with their microscopic size, so that they can be extracted from even very small fragments of sediments obtained from boreholes, appeal to geologists searching for index fossils in rocks where macrofossils are unlikely to be present. However, the use of acritarchs as biological indicators of relative time is subject to limitations that are essentially linked to the degradation and reworking that may occur before, during and after burial. This paper aims to review present knowledge of acritarchs for non-specialists but does not claim to cover all the extensive literature. The critical evaluation of acritarchs as biostratigraphic tools in defining three international chronostratigraphic boundaries (Precambrian/Cambrian, Cambrian/Ordovician and, in the Upper Devonian, Frasnian/Famennian) is intended mainly as an exercise for specialists in the field.

II. HOW TO FIND, ISOLATE AND RECOGNIZE AN ACRITARCH

(1) *Sampling*

As acritarchs are invisible in hand specimens of rock, empirical criteria determine the choice of samples likely to contain them. Apart from reworking, and regardless of the rock type, pre-Quaternary acritarchs are found primarily in near- to offshore marine environments and very secondarily in brackish water, the interpretation of Silurian fluvial deposits said to contain them (Gray & Boucot, 1989) being debatable. On the

Eon	Era	Period	Absolute age Ma	Acritarchs
Phanerozoic	Ceno-zoic	Quaternary	1.6	<p>rare records of poorly varied assemblages</p> <p>numerous records of varied assemblages</p> <p>rare records of generally poorly varied assemblages</p> <p>← oldest sphaeromorphs with excystment-like opening</p> <p>← oldest illustrated sphaeromorphs</p> <p>← ?</p>
		Neogene	23	
		Paleogene	65	
	Meso-zoic	Cretaceous	135 (140)	
		Jurassic	205	
		Triassic	250	
	Palaeozoic	Permian	290	
		Carboniferous	355	
		Devonian	410	
		Ordovician	438	
		Silurian	510	
		Ordovician	510	
		Cambrian	570 (540)	
Proterozoic	Neo-protero.	"Neoproterozoic III"	650	
		Cryogenian	850	
		Tonian	1000	
	Meso-protero.	Stenian	1200	
		Ectasian	1400	
		Calymmian	1600	
	Palaeo-proterozoic	Statherian	1800	
		Orosirian	2050	
		Rhyacian	2300	
		Siderian	2500	
	Arch-aeon			4500

Fig. 1. Acritarchs and geological time. Absolute ages from compilation by Cowie & Bassett (1988).

other hand Quaternary acritarchs, although rare, have been found in marine, continental and lacustrine strata.

Lithological criteria used when selecting rock samples depend also on the constraints of preservation, which relate mostly to the state of oxidation and thermal degradation. Depending on the purpose of the study – whether for detailed systematics or for relative dating of strata – there is some flexibility in choice of samples. Selected sediments were preferably but not exclusively deposited under calm conditions, fine-grained so as to favour preservation of ornament details, and as unweathered as possible to avoid oxidation, whether chemical or bacterial. They are principally argillaceous but may also be calcareous or silty. Acritarchs may be well preserved, in three dimensions, in phosphorite nodules and cherts. They are habitually more numerous in mudstone and shale, and the Shineton Shales (early Ordovician) at Shineton Brook, Shropshire, were estimated by Downie (1958) to contain 100000 g⁻¹. Rocks that are recrystallized, for

example dolomites, metamorphosed, such as phyllites, or reddened by oxidization, whether meteoric or not, are the most unfavourable. If independent evidence of age is available, varied and abundant acritarchs are more likely to be found in rocks of early Cambrian to late Devonian age.

(2) *Preparation*

The usual laboratory techniques employed to extract acritarchs from their enclosing sediment, and the preservation of isolated specimens demonstrate explicitly the properties of the wall. These techniques are applicable to the majority of organic-walled microfossils, with variants that depend especially on laboratory habits, the group studied and their state of preservation, as shown by Evitt (1984) and Phipps & Playford (1984). They are termed palynological (Greek, *palynein* = to sprinkle) from the original reference to the microscopic size of pollen and spores. While omitting details of the 'cooking' involved, which are nevertheless important for controlling the often exothermal reactions and eliminating the possibilities of contamination, acritarchs are extracted by dissolving from 20 to 80 g of generally consolidated sediment in strong acids of technical quality. Hydrofluoric acid (40–70%) dissolves silica, argillaceous minerals and part of the organic fraction; hydrochloric acid (35%) eliminates calcareous minerals, fluosilicates formed in the course of treatment, and pyrite if it is not too encrusted in organic walls that have resisted the HF. Acritarchs may stay for days, or even weeks, in one or other of these baths without visible sign of alteration. Like other organic elements, either amorphous or of definite shape, they are concentrated by filtration, using a mesh of 10–30 μm , and by separation using heavy liquids such as zinc bromide with density usually from 2 to 2.4.

If the acritarchs are too pale and transparent for observation using natural light, transmitted or under phase contrast, they may be darkened using histological stains such as safranin and basic fuchsin. In obstinate cases acetylation, often used to eliminate the cellulosic debris that may encumber preparations of Quaternary pollen and spores, permits them to be coloured, and they stand up well to a dehydrated mixture of 10% concentrated sulphuric acid and 90% anhydrous acetic acid. Relatively dark-brown acritarchs may be lightened by oxidation, particularly with concentrated nitric acid, which also dissolves the pyrite. This oxidation has to be optically checked and generally of short duration for, if too prolonged, it is the most radical means of destroying acritarchs, except those already black and carbonized. Specimens may withstand centrifugation up to 2000 rpm in an aqueous or alcoholic medium intended to neutralize or dehydrate the residue. They tolerate a few seconds of ultra-sonic treatment at 35 kHz, used to disperse flocculations. These latter methods are obviously unsuitable if the acritarchs are rendered fragile, either during or after sedimentation, by too strong oxidation or by contiguous perforations attributed to the activities of bacteria, especially sulphurous, and fungi. They are also inappropriate if the microfossils are fissured or show mosaic-like fracture; in this case specimens may be determined using thin sections cut parallel to the stratification (Burmah, 1968).

After palynological treatment the acritarchs are mounted between glass slides and cover glasses either in sealed, semi-permanent glycerine jelly, the refractive index (RI) of which, about 1.47, permits better observation of the most transparent, or in a stable medium. The latter consists of a synthetic resin or glue with variable RI, or Canada

Balsam, with RI from 1.52 to 1.54 to examine specimens with higher contrast. All these media except the first are also suitable for preserving dehydrated, gold-coated examples that have been examined under the SEM.

(3) *Size and morphology*

Apart from its organic wall, among the most chemically inert known and resistant even to concentrated hydrofluoric acid, how is an acritarch recognized? Criteria depend on the relatively small size and the morphology, the simplest of which is represented by the sphaeromorphs, smooth or weakly ornamented hollow balls or lenses. Acritarchs have an overall size varying from a few to several hundred micrometres, but generally between about 30 and 200 μm including processes. The record size of 3 mm, cited by Vidal (1981, 1984), is no longer acceptable. It refers to Precambrian specimens of *Chuarina* Walcott (1989), preserved as discoidal, carbonaceous impressions that have been shown by Sun (1887) to be comparable with living colonies of nostocales cyanophyte algae.

The dimensions of isolated specimens attributed to the same species and coming from the same samples of rock may occasionally vary from unity to double. This variability may depend on the stage of development attained by the living organism or on the conditions of fossilization, which may or may not preserve the original turgescence of the vesicle within the enclosing sediment. If the acritarchs occur associated in clusters, the size of different individuals is most often nearly constant.

Morphological characters which form, as is conventional in palaeontology, the basis of a systematic classification for acritarchs have been described and illustrated in detail by Tappan (1980) and are only briefly reviewed here. They depend principally on the symmetry, shape and ornamentation of the vesicle (Fig. 2) and where possible on the number of wall layers and type of opening. The hierarchical value attached to these different criteria depends upon the author, techniques of observation, and state of preservation of the acritarchs. A coherent taxonomic framework is, however, still elusive or, at best, suffers from numerous exceptions.

An acritarch is composed of a hollow central body or vesicle that lacks unequivocal intracellular structures; the original outline may be circular, oval, variably fusiform, ampulliform, triangular, quadrangular or polygonal [Pl. 1 (figs 1-8); Pl. 2 (figs 1-13); Pl. 3 (figs 1, 4-12, 14-16)]. Depending on the taxon, surface ornamentation is extremely variable in form, size and distribution. In general, when the specimen is ornamented and lacks an opening, the symmetry is radial in one or several planes, axial, with homoeomorphic or heteromorphic poles, or bilateral.

The thickness of the vesicle wall is generally a fraction of a μm , but may exceptionally reach about 4 μm and correspond to one-tenth of the diameter of the central body [Eiserhardt, 1989, pl. 1 (fig. 1), for example]. The vesicle wall is made up of one or two layers which may be joined or separate. In the latter case, the apparently hollow space must originally have contained tissue, and the terms endo-, meso- and ectophragm, implying a certain analogy with the biological vocabulary, are sometimes used. The presence of tubiform processes separating the external from the internal layer is exceptionally recorded (Miller & Williams, 1988). The structure of the vesicle wall was first known from observations at a magnification of about $\times 1000$ using the optical transmitted light microscope. Since the late 1960s, and in particular following the

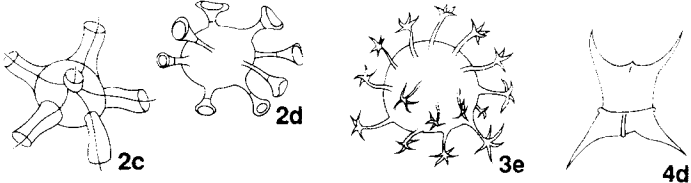
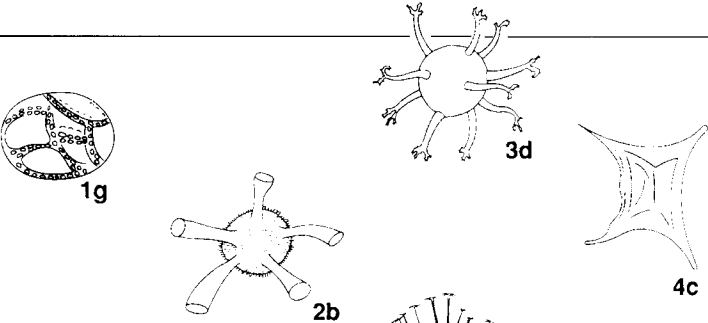
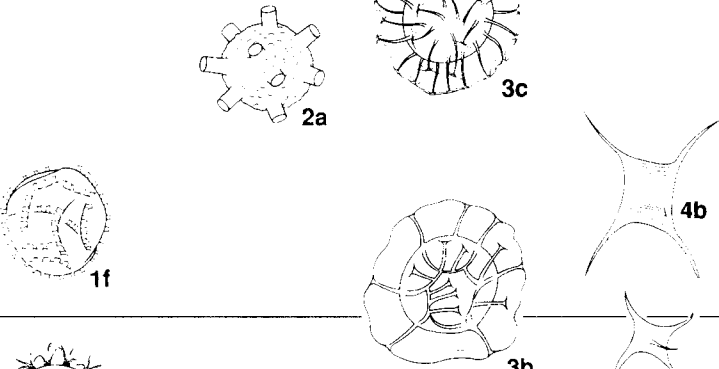
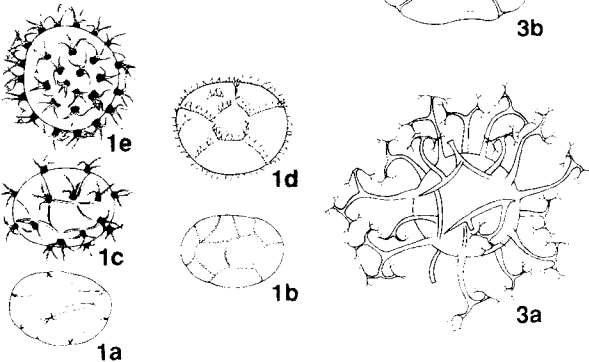
Era	Period	Examples of acritarch ornamentation
Palaeozoic (in part)	Devonian	
	Silurian	
	Ordovician	
	Cambrian	

Fig. 2. For legend see opposite.

example of Loeblich (1970), detailed descriptions and illustrations have made use of the SEM. Observations of ultra-thin sections under the transmission electron microscope, although important in principle for attempts to establish phyletic relationships, are very rare, with the notable exception of Kjellström (1968) and Jux (1969*a, b*, 1971, 1975). They involve mainly some relatively large taxa without processes, most of which, belonging to the tasmanites, are now assigned to the prasinophytes because of their lamellar, porous membrane with radially arranged canals. Paradoxically, although similar structures were observed by Jux (1971, 1975) in the membranes of four acritarch genera, including *Goniosphaeridium* and *Veryhachium*, in which processes are developed, these taxa remain, without further debate, classified with the acritarchs. In practice, interpretation of the image obtained in transmission electron microscopy is often plagued by artifacts produced during fossilization or due to preparation technique. This difficulty, added to the time-consuming preparation of selected specimens, has not so far encouraged an increase in observations of this type.

The ectophragm, with or without endophragm, forms projections that may be regularly or irregularly distributed, solid or hollow; the last-named may be septate or not, and the internal cavity may or may not communicate with that of the vesicle. The projections vary greatly in form, which may be simple or divided, distally free, coalescent or enclosed in a peripheral membrane; they differ also in ornamentation and size, ranging from a fraction of a μm to several tens or even a hundred or so. The distal extremities of the processes are generally closed and exceptionally open. The other usual surface structure consists of membranous septa more or less at right-angles to the vesicle surface. The schematic outline (Fig. 2) used as an example shows how ornamentation may vary among a selected few Cambrian to Devonian acritarchs that have a basic more or less circular or quadrangular outline. Terminology used to describe the sometimes complex, very varied, regular or irregular ornamentation, often altered during fossilization, that may be found on a single specimen is simple and habitually involves some circumlocution, for example: verrucate; echinate wall surface; diaphanous flange; nodular to blunted, spine-like branches with first to second orders of division; a 'trunk' is the basal part of a complexly divided process, etc.

Since the works of Downie (1958), Eisenack (1959) and Deunff (1961), increasing importance has been attached to the method of opening in acritarchs. An opening distinguished by the regularity of its form and, sometimes, position is recognized in numerous taxa, especially since about 530–520 Ma BP. It is often called an excystment opening by analogy with that of algal cysts, in which it permits the liberation of the protoplast. The term, which expresses the most likely hypothesis concerning the function of the opening, is practical as it excludes accidental openings. Nevertheless, some workers find it inappropriate as other microorganisms, such as invertebrate eggs

Fig. 2. A few selected Cambrian to Devonian acritarchs with, more or less, circular to quadrangular vesicle outline, showing variety of ornamentation (not to scale). Phylogenetic relationships not implied except, possibly, for 1a–f and 2a–b. 1a, *Retisphaeridium howellii*; 1b, *Cristallinium cambriense*; 1c, *Vulcanisphaera turbata*; 1d, *Cristallinium randomense*; 1e, *Vulcanisphaera africana*; 1f, *Cristallinium dentatum*; 1g, *Psenotopus condrocheus*; 2a, *Dilatitphaera wimani*; 2b, *D. williereae*; 2c, *Daillydium pentaster*; 2d, *Umbellatphaeridium saharicum*; 3a, *Timofeeva lancarae*; 3b, *Cymatiogalea velifera*; 3c, *Tunisphaeridium eisenackii*; 3d, *Cymbosphaeridium pilar*; 3e, *Ammonidium exoticum*; 4a, *Veryhachium minutum*; 4b, *Striatotheca principalis*; 4c, *Neoverhachium carminae*; 4d, *Winwaloesia ranulaeforma*.

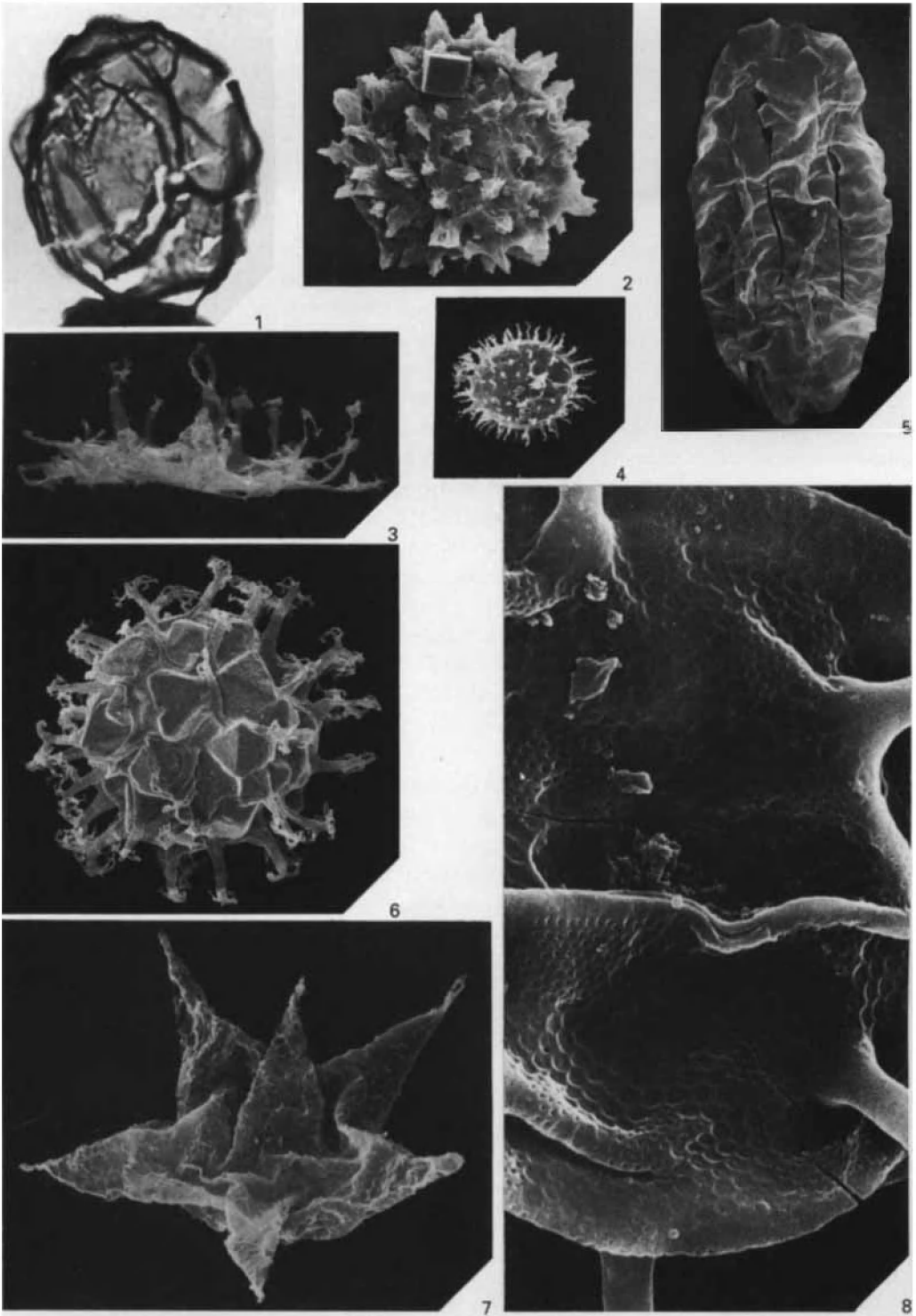


Plate 1. For legend see opposite.

(e.g. of tardigrade arthropods) or spores, particularly from terrestrial plants, may exhibit openings unrelated to excystment. In a fossil assemblage that may contain several tens of different taxa, the proportion of species with an opening is very variable but rarely exceeds one third. Furthermore, specimens of a single species found together in the same taphocoenosis do not necessarily all show an opening. By comparison with the excystment, provoked by acetolysis, of modern dinoflagellate species (Evitt, 1985, pp. 126, 127), it may be that the process of fossilization or treatment in the laboratory produces opening of the acritarch independent of the stage of maturity attained in life. On the other hand certain genera such as *Corollasphaeridium* [Pl. 3 (fig. 15)] are always seen to have a gaping opening, whereas others such as *Striatotheca* [Pl. 2 (fig. 6)] are always closed. Although acritarchs may exhibit certain similarities to dinoflagellate cysts, notably in the polygonal fields of the vesicle and/or the opening, current terminology avoids, contrary to Lister (1970), making reference to these micro-organisms. The successive appearances of the main types of excystment opening occurred from the Neoproterozoic to the Devonian. They are shown here (Fig. 3) in schematic form on the basis of selected acritarch genera and do not take into account variations due to preservation. Before excystment the form and position of the opening in acritarchs may be indiscernible (cryptosutures sensu Lister, 1970) although probably preformed at the site of a weakened area. On the other hand, the future opening may be obviously delimited by a thinning, thickening or variably developed projection of the membrane, whether ornamented or not. The presence of cryptosutures can only be reliably established if, among numerous well preserved specimens of a single species from the same sample, some lack an opening while others exhibit one that is always identical. An excystment opening preserved as a lateral or transverse split, generally

EXPLANATION OF PLATES

(Depositories of figured specimens are as follows: IRScNB b, Institut royal des Sciences naturelles de Belgique, Palaeontology, Brussels; GSC, Geological Survey of Canada, Ottawa; RUG, Rijksuniversiteit Gent, Palaeontology, Gent; NIGPAS, Nanjing Institute of Geology & Palaeontology, Nanjing.)

PLATE I

- Fig. 1. *Leiosphaeridia* sp. A sphaeromorph, showing corrosion, folds and random ruptures. Middle Cambrian, Llŷn Peninsula, North Wales. IRScNB b2563 ($\times 1000$).
- Fig. 2. *Tylotopalla deerlijkiana* (Martin) Martin, 1978. Pyrite crystal on external wall of vesicle. Early Silurian, borehole at Deerlijk, Belgium. IRScNB b2564 ($\times 1000$).
- Fig. 3. *Skiagia*? sp. Lateral view of vesicle compressed in sediment. Middle Cambrian, Llŷn Peninsula, North Wales. IRScNB b2566 ($\times 2000$).
- Fig. 4. *Heliosphaeridium* cf. *H. notatum* (Volkova) Moczydlowska, 1991. Middle Cambrian, Llŷn Peninsula, North Wales. IRScNB b2567 ($\times 1000$).
- Fig. 5. *Eliasum llaniscum* Fombella, 1977. Parallel fissures due to sediment compaction. Middle Cambrian, Llŷn Peninsula, North Wales. IRScNB b2565 ($\times 1000$).
- Fig. 6. *Timofeevia* sp. Impressions of pyrite crystals developed inside vesicle. Late? Cambrian, Derik area, southeast Turkey. IRScNB b2568 ($\times 1000$).
- Fig. 7. *Estiastra magna* Eisenack, 1959. External surface of vesicle entirely corroded. Early Silurian, Anticosti island, Canada. GSC 82887 ($\times 400$).
- Fig. 8. *Puteoscortum williereae* Martin, 1981. Detail of vesicle and base of processes; ornamentation of polygonal alveoles on external surface of vesicle; the variably distributed perforations represent a secondary character linked to preservation and fungal or bacterial activity. Late Devonian, early Famennian, Philippeville area, Belgium, IRScNB b2570 ($\times 5000$).

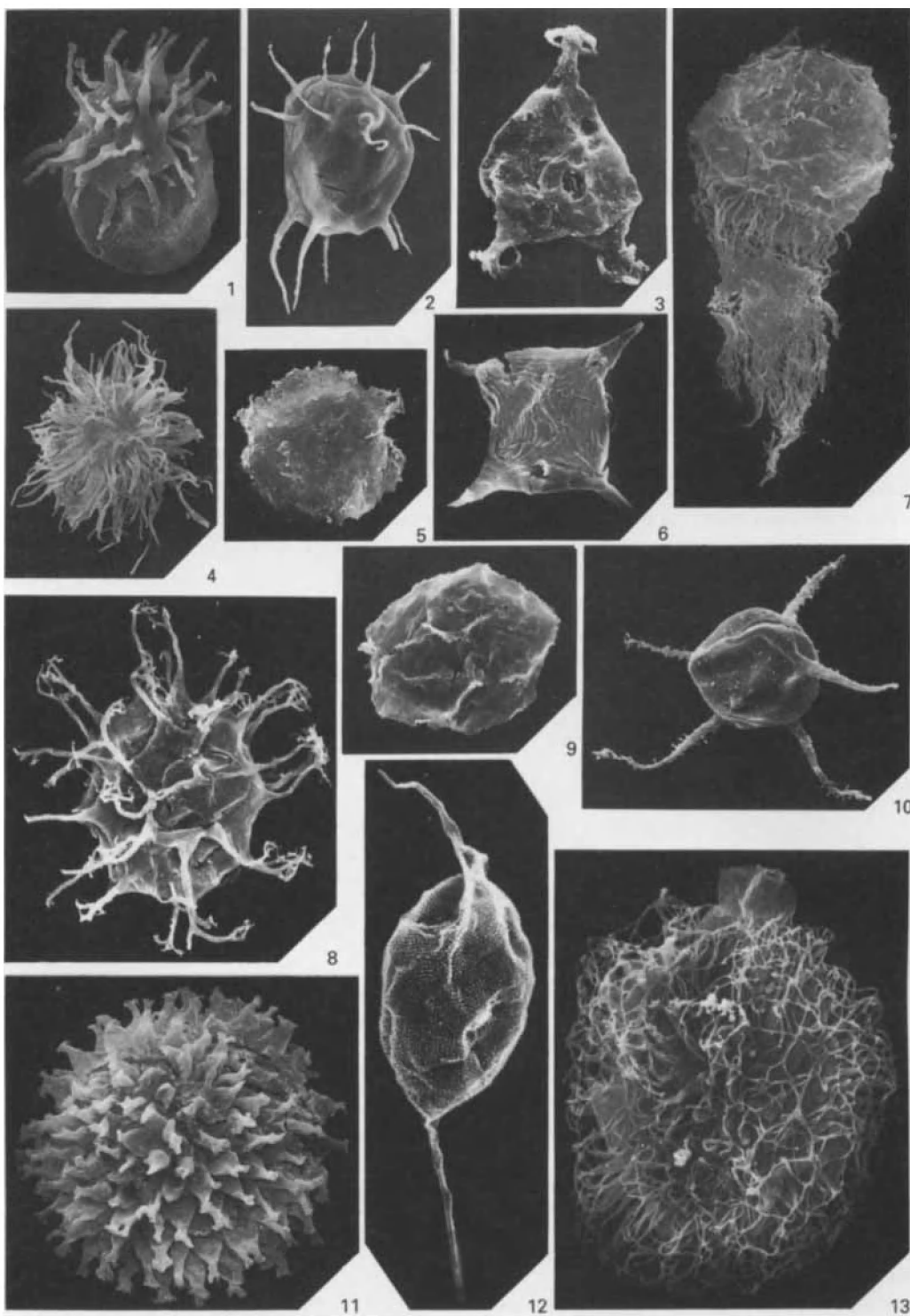


Plate 2. For legend see opposite.

straight or curved and variably gaping, may sometimes divide the vesicle into two parts. When its edge is smooth it could as well correspond to an accidental opening formed by compression. The term 'epiptych' (Loeblich & Tappan, 1969) is reserved for a simple, curved rupture, invisible before partial opening, always in the form of a flap and sometimes with a median projection corresponding to an indentation on the opposite edge. A subcircular to circular opening is called a cryptopylome (Tappan, 1980) when it is invisible before excystment. *Veryhachium* cf. *V. downiei* [Pl. 3 (fig. 6)] illustrates how badly known these means of cryptosuture are. Acritarchs resembling the latter genus in the triangular vesicle, with each of the angles prolonged to form an identical, simple process, sometimes show an opening, which in this case is always figured as a split. However the specimen illustrated here, from the Upper Devonian rocks of Belgium, possesses a clearly defined circular opening and an accidental lateral split.

Conventionally a single circular opening is said to be apical, located at or near the upper part of the specimen illustrated. When a circular excystment opening is produced by a peripheral, annular degradation of the vesicle, Vavrdová (1989) proposed use of the terms munium and munitium, depending on whether the edge of the future opening is distinctly ornamented or not. A pylome, as revised by Sarjeant (1967), of which cyclopyle (Eisenack, 1969) is a synonym, is a clearly circular or subcircular opening whose periphery, whether ornamented or not, is distinct before excystment. It is closed by a sort of lid or stopper, the operculum, which is partially or completely detached following excystment and may be observed inside the vesicle or isolated in the

PLATE 2

- Fig. 1. *Trunculumarium revinium* (Vanguetaine) Loeblich & Tappan, 1976. Late Cambrian, Random Island, eastern Newfoundland, Canada. GSC 83225 ($\times 1000$).
- Fig. 2. *Dasydiacrodium obsonum* Martin, in Martin & Dean, 1988. Late Cambrian, Dayangcha area, northeast China, IRScNB b2571 ($\times 1000$).
- Fig. 3. *Frankea sartbernardensis* (Martin) Colbath, 1986. Early Ordovician, Llanvirn, Sart-Bernard, Belgium. IRScNB b2572 ($\times 1000$).
- Fig. 4. *Elektoriskos williereae* (Deflandre & Deflandre-Rigaud) Vanguetaine, 1979. Early Silurian, borehole at Kortrijk, Belgium. IRScNB b1761 ($\times 1000$).
- Fig. 5. *Anulum squamacium* (Volkova) Martin in Martin & Dean, 1983. Middle Cambrian, Llŷn Peninsula, North Wales. IRScNB b2573 ($\times 1000$).
- Fig. 6. *Striatotheca principalis* Burmann, 1970. Early Ordovician, Montagne Noire, Hérault, France. IRScNB b1305 ($\times 700$).
- Fig. 7. *Geron guerillerus* Cramer, 1967 emend. Cramer, 1969. Early Silurian, borehole at Kortrijk, Belgium. IRScNB b1773 ($\times 1000$).
- Fig. 8. *Timofeevia lancarae* (Cramer & Diez de Cramer) Vanguetaine, 1978. Late Cambrian, Llŷn Peninsula, North Wales. IRScNB b2575 ($\times 1000$).
- Fig. 9. *Cristallinum cambriense* (Slavíková) Vanguetaine, 1978. Middle Cambrian, Přibram area, Czechia. IRScNB b2574 ($\times 1000$).
- Fig. 10. *Villosacapsula globosa* Vanguetaine *et al.*, 1983. Excystment slit slightly open. Late Devonian, early Famennian, Senzeilles, Belgium. IRScNB b2248 ($\times 1000$).
- Fig. 11. *Visbysphaera impetuosa* Martin, 1985. Late Devonian, early Famennian, Senzeilles, Belgium. IRScNB b1655 ($\times 1000$).
- Fig. 12. *Eupoikilofusa* aff. *E. ampulliformis sensu* Duffield & Legault, 1981. Early Silurian, Anticosti Island, Canada. GSC 82888 ($\times 1000$).
- Fig. 13. *Aryballomorpha grootaertii* (Martin), emend. Martin & Yin, 1988. Apical tubular extension with circular distal opening. Early Ordovician, Tremadoc, Hunjiang area, northeast China. NIGPAS, Martin & Yin, 1988, slide 2 ($\times 750$).

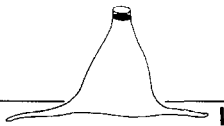
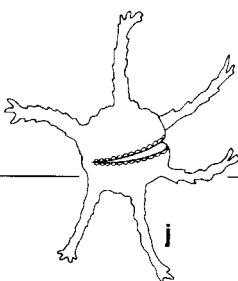
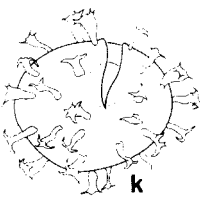
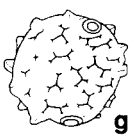
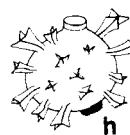

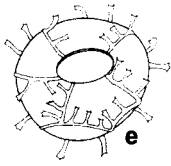
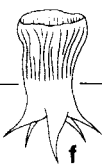
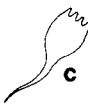



Era	Period	Main types of excystment opening
Palaeozoic (in part)	Devonian	
	Silurian	 
	Ordovician	  
	Cambrian	   
Neoproterozoic	' Neoprot. III '	
	Cryogenian	
	Tonian	

Fig. 3. Generalized successive appearance of main types of excystment opening in selected acritarchs (not to scale). a, Sphaeromorph with equivocal split, either accidental or at line of cryptosuture; b, sphaeromorph with pylome and operculum-like structure; c, *Volkovia* with munium; d, *Revintesta* with munitium; e, *Cymatiogalea* with pylome and operculum of definite contour; f, *Corollasphaeridium* with gaping opening; g, *Asketopalla* with two pylomes; h, *Polyancistrodorus* with pylome and pseudopylome; i, *Verrucosporium* with epityche; j, *Diexallophasis* with preformed split; k, *Visbysphaera* with endopylome; l, *Onondagaella* with epibystra.

palynological slide. Generally a single pylome is present; very rarely a second is located at the opposite pole. A pseudopylome is a structure only exceptionally present; comparable to a pylome, it is more or less opposite the latter but is always closed. An endopylome (Le Hérisse, 1989) corresponds to a circular, operculate opening of the endophragm, topped by a simple split in the ectophragm. The pseudopolygonal outline of openings, recalling the archaeopyle of dinoflagellates, is due to deformation and no special term is necessary. A process excystment opening is only exceptionally recorded. It involves the circular opening of a process whose distal extremity has disappeared, and is closed by a thickened plug called an epibystra (Playford, 1977).

(4) *Organic wall*

(i) *Sporopollenin-like material*

Acritarchs are composed of organic material that is mechanically resistant and whose composition is very poorly known, being chemically very inert, except to oxidation and carbonization. As the group is both artificial and polyphyletic, concentrations of specimens reliably attributed to the same species on the basis of well differentiated morphological characters would be necessary for establishing models of chemical composition and these have not been undertaken in a conclusive manner. Only Kjellström (1968) has estimated, by interpretation of absorption peaks in infrared-microspectrometry, that certain particularly ubiquitous acritarchs (*Leiosphaerida* sp.) contained probably saturated fatty acid derivatives close to those from spores and pollen grains. The heterogeneous chemical composition of acritarchs is sometimes demonstrated in ways that are still unclear; for example, by differential distributions in density gradient after centrifugation (Chaloner & Orbell, 1971, p. 287), or by fluorescent microscopy (McPhilemy, 1988). The colour and consistency of acritarchs observed under transmitted natural light are variable. They may resemble those of other microfossils or fragments of fossils originating from the same lithological specimen. The latter are represented, depending on age and conditions of deposition, by pollen, spores, fragments or larvae of graptolites, algal cyst stages of peridinin dinoflagellates and prasinophytes, scolecodonts (jaw apparatuses of polychaete worms), microforaminifera, fragments of crustacean cuticle, and *incertae sedis* such as the inappropriately named chitinozoans, whose chitin content is unproved (Vos-Foucart & Jeuniaux, 1972). This assemblage, including amorphous debris, is called a palynofacies (Combaz, 1964).

Because of its similar resistance to chemical products, and a comparable degradation due to bacterial or fungal activity, the organic matter of acritarchs is always compared with modern sporopollenin, the nature and structure of which are also incompletely established. This component of the external membrane, or exine, of modern spores and pollen is the only one capable of being preserved and fossilized; it has exceptionally been documented in vegetative cells of fresh-water chlorophytes, as reported by Horodyski *et al.* (1992, p. 190). Sporopollenin of modern plants may vary in proportion from one species to another and in composition from one group to another. The latter mainly determines the probability of preservation (Brooks, 1971, pp. 356, 358) and it is an oxidative polymer of carotenoids and carotenid esters, as first shown by Brooks & Shaw (1968). Sporopollenin has become a somewhat misused general term for the organic wall of fossil or recent unicellular groups, which persists after the dissolution

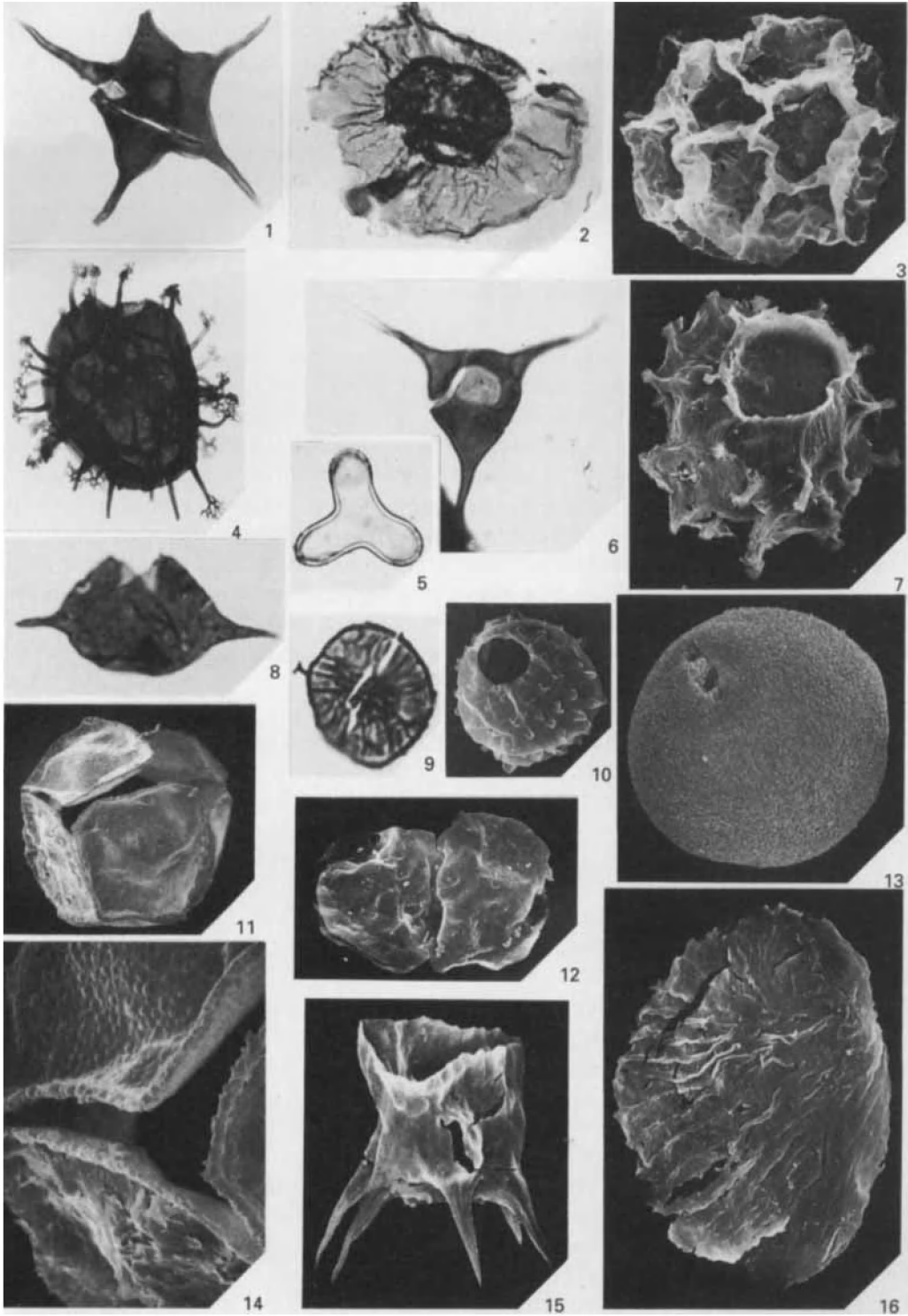


Plate 3. For legend see opposite.

of cellulose, the polysaccharides in green plants and fungi, and of chitin. The last-named, often considered as a nitrogenous derivative of cellulose, is found commonly in the exoskeleton of invertebrates, including molluscs and arthropods, and occurs also in some primitive plants, green algae and fungi. It is accepted that the sporopollenin-like wall of acritarchs is composed of polyterpenes, the polymerization of which has increased during fossilization. In practice the term is useful as it avoids circumlocution, but it masks a great deal of ignorance.

(ii) *Thermal alteration*

Sporopollenin-like material and sporopollenin may be important components of some types of kerogen, a term introduced by petroleum geochemists to designate the heterogeneous polyaromatic fraction of organic matter contained in sedimentary rocks and insoluble in the usual organic solvents (Durand, 1980, p. 15). As reviewed by Tissot & Welte (1984) kerogen contains, in addition to amorphous biogenic debris, elements indicative of two sources: one is land-derived, formed mainly of plant debris, spores and pollen grains; the other, aquatically derived, is very varied, made up of organisms or fragments of marine, fluvial or lacustrine organisms that may be plant or animal but are generally of microscopic size. Kerogen may evolve to form several types of fossil combustibles, depending on its composition, abundance, and the time during which it has been submitted to higher temperatures following burial and tectonism. That including, particularly, marine plankton preserved under reducing

PLATE 3

Fig. 1. *Palacanthus ledanoisii* (Deunff) Playford, 1977. Late Devonian, early Famennian, Senzeilles area, Belgium. IRScNB b1580 ($\times 1000$).

Fig. 2. Prasinophyte; *Pterospermella eruptio* Martin, 1985. Late Devonian, early Famennian, Senzeilles area, Belgium. IRScNB b1635 ($\times 1000$).

Fig. 3. Prasinophyte; *Cymatiosphaera* sp. Middle Cambrian, Příbram area, Czechia. IRScNB b2576 ($\times 750$).

Fig. 4. *Athabascaella playfordii* Martin, 1984, emend. Martin & Yin, 1988. Pylome. Early Ordovician, Tremadoc, Dayangcha area, northeast China. NIGPAS, Martin & Yin, 1988, slide 6 ($\times 750$).

Fig. 5. *Paucilobimorpha triradiata* De Coninck, 1986. Middle Palaeogene, Eocene, Woensdrecht borehole, southern Netherlands. RUG, De Coninck, 1986, slide 1 ($\times 1000$) (negative: J. De Coninck).

Fig. 6. *Veryhachium* cf. *V. downiei* Stockmans & Willièrè, 1962a. Pylome and compression rupture. Late Devonian, early Famennian, Villers-sur-Lesse, Belgium. IRScNB b2577 ($\times 1000$).

Fig. 7. *Cymatiogalea* sp. Transparent membrane stretched between processes; operculum *in situ*. Late Cambrian, Llŷn Peninsula, North Wales. IRScNB b2578 ($\times 1000$).

Fig. 8. *Leiofusa* cf. *L. gravida* Pittau, 1985. Compression rupture or excystment opening. Late Cambrian, St Tudwal's Island East, North Wales. IRScNB b2579 ($\times 1000$).

Fig. 9. Isolated operculum of *Cymatiogalea* or *Stelliferidium*. Late Cambrian, St Tudwal's Island East, North Wales. IRScNB b2580 ($\times 1000$).

Fig. 10. *Rhopaliophora pilata* (Combaz & Peniguel) Playford & Martin, 1984. Pylome. Early Ordovician, Dayangcha area, northeast China. NIGPAS Martin & Yin, 1988, slide 10 ($\times 2000$).

Figs 11, 14. *Cristallinium* sp. Vesicle partly open along suture lines of the polygonal plates. Middle Cambrian, Derik area, southeast Turkey. IRScNB b2581. Fig. 11 ($\times 1000$); Fig. 14, ($\times 4000$).

Fig. 12. *Synsphaeridium* sp. 1 sensu Cramer & Diez, 1972. Middle Cambrian, Llŷn Peninsula, North Wales. IRScNB b2582 ($\times 1000$).

Fig. 13. Prasinophyte; *Tasmanites* sp. with accidental opening. Middle Cambrian, Närke, Sweden. IRScNB b2583 ($\times 1000$).

Fig. 15. *Corollasphaeridium wilcoxianum* Martin, in Martin & Dean, 1982, emend. Martin, 1992. Late Cambrian, Dayangcha area, northeast China. IRScNB b2584 ($\times 1000$).

Fig. 16. *Moyeria* sp. Middle Silurian, Fosses-la-Ville area, Belgium. IRScNB b2585 ($\times 1000$).

conditions in poorly permeable, fine-grained sediments is a potential constituent of petroleum source rocks. This partial transformation of organic matter is generally produced at a depth of some thousands of metres since it requires temperatures of 60–200 °C. Except in strata that are tectonically very stable, pre-Cenozoic variations in burial depth are extrapolated. The present-day geothermal gradient measured in boreholes varies from 1 °C/20 m to 1 °C/100 m, depending on structural conditions, with an average of 3 °C/100 m.

Pyrolysis, isotopic and physicochemical analysis and organic geochemistry provide an overall analysis of all the constituents of kerogen. Microscopic techniques enable us to visualize (Combaz, 1980) a variably representative part of it, possibly including Palaeozoic acritarchs. They provide an estimate of the state of maturity, the heterogeneity of composition, and the age of the diverse organic sources, and they include: colour in transmitted natural light; reflectance of polished surfaces; and, particularly for material of Carboniferous and later age, fluorescence photometry. The first of these is the only technique currently applicable to acritarchs, which react only slightly and irregularly to the two others (Bertrand *et al.*, 1985; McPhilemy, 1988). Each of the different physical, chemical or optical techniques has its limitations, and all need to be combined (see review by Héroux, Chagnon & Bertrand, 1979) in regional reconstructions of the history of sedimentary basins and estimates of their economic potential for hydrocarbons, both liquid and gaseous.

Changes in colour and the alteration of acritarchs, like those of other microfossils partly or entirely composed of organic material, are related to the thermal history of the enclosing sediment and were, respectively, clarified and codified by Combaz (1964) and Correia (1967). The latter reproduced experimentally the darkening and progressive deterioration of the acritarch wall during increase of temperature up to 180 °C for some hundreds of hours. Although at the beginning of the experiments Correia introduced a supplementary variable by artificially oxidising the microfossils so as to bring them to an initial state of transparency, his chart does not differ fundamentally from the observations of Staplin (1969). It is, however, the latter's Thermal Alteration Index (TAI) that forms the basis of the scale, divided into six or seven parts, generally adopted for estimating visually the state of preservation (Nowlan & Barnes, 1987). Unaltered acritarchs are transparent, and from colourless to very pale yellow in immature deposits considered as possible sources of hydrocarbons of marine origin. The colours, accompanied by alteration of the ornamentation, are progressively modified up to the mature stage corresponding successively to the oil window and the wet gas-condensate. They pass through a whole range of intermediate tones of increasing intensity, from orange-yellow to progressively darker brown, before reaching black. The bases of narrow processes are always the first part to become opaque in a specimen that is still transparent though becoming brownish. This evolution takes place generally before mineral metamorphism is recognizable. At the later post- or supramature stage, capable of furnishing dry gas and becoming increasingly barren, the acritarchs attain a progressively more uniform preservation, becoming more and more fragmented until their destruction. In a single, mature sample their response to thermal alteration may vary from one taxon to another, and sometimes from one specimen to another within the same species. These apparent contradictions are due to several variables, notably differences in thickness and composition of the wall, conditions of

transport, deposition and taphocoenosis, and the nature and degree of alteration of the enclosing sediment. In addition, Moczydłowska & Vidal (1992) suggested that certain TAI discrepancies may be caused by irradiation from natural radioactive decay. Acritarchs are often considered as geothermometers, less precise than pollen grains or spores at temperatures generally estimated at from 60 to 120 or 150 °C. However, they may provide useful indications at these relatively low temperatures in the absence of other microfossils, as long as one or a few relatively abundant taxa are chosen, with vesicle at least 40 μm or so in diameter and simple, smooth, thin wall, as shown by Legall, Barnes & MacQueen (1981) and Dorning (1986).

III. BIOLOGICAL AFFINITIES

(1) *Before and after Evitt (1963)*

Successive names applied to acritarchs reflect the diverse evaluations of their biological affinities rather than the age of the deposits from which they were obtained. Acritarchs *sensu stricto* were first discovered by White (1862), who gave them the name *Xanthidium*. About 380 Ma old, they came from the 'Corniferous Limestone', of Middle Devonian age (Fisher, 1981) in New York State. Ehrenberg (1836, published 1838), the German scientist often credited with being the 'father' of the discipline of micropalaeontology, had proposed this generic name for globular, organic-walled microfossils, uniformly covered with numerous spines, that he found in translucent flakes of Upper Cretaceous chert, aged about 85 Ma, from Silesia, Poland. He erroneously interpreted *Xanthidium* as the silicified remains of Desmids, fresh-water, conjugating algae, and during the same oral communication to the Royal Academy of Berlin he surprised the scientific world by showing that rocks may contain enormous quantities of microfossils. From the same flakes of rock Ehrenberg was also the first to record fossil dinoflagellates without realizing they were cysts. In France Turpin (1837) considered, wrongly, that the spiny microspheres described by his German colleague were hard-shelled reproductive bodies of the 'Cristatelle vagabonde', a fresh-water bryozoan (colonial invertebrates). Mantell (1850), a Sussex doctor perhaps best known as discoverer of the dinosaur *Iguanodon*, also disagreed with Ehrenberg and proposed that the name *Xanthidium* be replaced by *Spiniferites* (= spine bearer). Uncertain as to the nature of the organisms in his new genus, Mantell suggested that they might represent, amongst other things, spores of marine plants. As noted by Deflandre (1947), Mantell was the first author to recognize that acritarchs are composed of organic matter.

Studying microscopic remains collected during a German oceanographic expedition, Lohman (1904) designated as 'Ova hispida' organisms similar to the 'xanthidia', attributing them to 'problematica' or plankton eggs, possibly of Crustacea, and from a culture of *Ovum hispidum hystrix* (Cleve) Lohman, 1904 he obtained *Centropages hamatus* (Lilljeborg, 1853), a pelagic marine and brackish-water copepod. Another German, Reinsch (1905) was the first to suggest that the 'xanthidia' were, in fact, dinoflagellate cysts and named them 'Palinosphären'. Nevertheless the name *Xanthidium* continued in use until replaced by the genus *Hystrichosphaera*, proposed by Wetzel (1933) to reflect the uncertain systematic position of marine Upper Cretaceous assemblages from the Baltic region studied by him. The informal name hystrichosphaerids, or hystrichospheres, widely used until the 1960s but now abandoned, is derived from that of Wetzel's genus.

From the beginning of the 1930s to the end of the 1950s researches on Palaeozoic and Mesozoic hystrichospheres multiplied. Eisenack, from 1931, and Deflandre, from 1934, were the two pioneers of this expansion and both were especially interested in the biological aspects and systematics. Unlike his German colleague, the Frenchman Deflandre (1947) was quickly convinced of the polyphyletic nature of these microfossils and noted particularly the morphological similarities between hystrichospheres and, amongst other things, the eggs of modern crustacea or worms and non-classified present-day cysts, such as *Echinum* Meunier, 1910 from the Arctic snow and ice of the Barents Sea, or belonging to the Protista. There were two practical reasons behind the increase of interest in acritarchs: the improvement of chemical techniques initiated by Eisenack (1931), which permitted the concentration of organic-walled microfossils, until then observable only in flakes of flint or in thin sections; and, from the 1950s onwards, the interest to the petroleum industry of microfossils that would permit the relative dating of borehole samples devoid of macrofossils.

In the USA, Evitt (1961, 1963) provided a major advance in the study of hystrichospheres by showing clearly that the majority of post-Palaeozoic representatives were dinoflagellate cysts formed inside motile cells; the latter have generally an external covering of cellulose or pseudocellulose, not preserved fossil. Evitt (1963, p. 300) introduced the term 'acritarch' to designate microfossils previously called 'hystrichospheres', whose affinities are still problematical, which are found mainly in Palaeozoic rocks. The original definition of the new group was as follows:

Small microfossils of unknown and probably varied biological affinities consisting of a central cavity enclosed by a wall of single or multiple layers and of chiefly organic composition; symmetry, shape, structure, and ornamentation varied; central cavity closed or communicating with the exterior by various means, for example: pores, a slitlike or irregular rupture, a circular opening (the pylome).

At the suggestion of Evitt (1963) and of Downie, Evitt & Sarjeant (1963), based on purely practical considerations in the absence of a code of nomenclature for the Kingdom Protista (or Protoctista) – which is still the case (Taylor *et al.*, 1986) – acritarchs are treated for taxonomic purposes according to the Code of Botanical Nomenclature, as are fossil dinoflagellates. Downie *et al.* (1963) emphasized that such a usage is particularly appropriate as it recognizes form-genera of uncertain position. This convention is useful since no evidence has been offered for photosynthetic pigment in acritarchs, which also lack intracellular structures such as chromatophores *sensu* Sarjeant (1974, p. 22), who preferred to use this term rather than chloroplast as it does not imply that chlorophyll is the dominant pigment.

Downie *et al.* (1963) proposed a classification for thirteen sub-groups based on external morphology and, possibly, the method of opening, then known only from observations made with the optical microscope. The result was a number of commonly used, concise, informal terms such as diacrodians, with two polar areas, and herkomorphs, in which the surface of the vesicle is divided by ridges into polygonal fields. Deflandre & Deflandre-Rigaud's (1964) proposal that the sub-groups be formalized within a para-Linnean system has not been accepted. Further variations on Downie *et al.*'s (1963) scheme, taking into account also the opening and the number of cellular walls, were subsequently introduced, notably by Staplin, Jansonius & Pocock (1965), Downie (1973) and Al-Ameri (1986). Attempts at a formal, supra-generic classification have so far produced only incomplete or inconsistent groupings, for they

do not cover the heterogeneity and variability of the taxa. To avoid these disadvantages certain authors such as Le Hérisse (1989) have proposed a dichotomous determination key applicable to acritarchs from a very limited part of the geological column, in this case the Silurian.

The pragmatic name acritarch was adopted relatively quickly by specialists who believed in its polyphyletic nature, except for Eisenack who, until 1969, preferred to use hystrichospheres for what he believed to be a coherent, natural and monophyletic group of unicellular plants. With rare exceptions, the debatable term Hystrichophyta, a separate algal class introduced and reviewed by Mädler (1963, 1967) and including some dinoflagellates, prasinophytes and acritarchs, remains unused. Diver & Peat (1979) restricted the term Acritarcha to non-spheroidal or spheroidal forms provided with ornamentation and developed especially from the Lower Cambrian onwards, and introduced a new group Cryptarcha (Greek = hidden origin) to designate, supposedly objectively, more or less spheroidal or filamentous Precambrian microfossils that lack distinct processes. The term Cryptarcha should be avoided as the essentially featureless sphaeromorphs and the hyphae, algal or fungal filaments, have persisted up to the present-day.

Loeblich (1974, p. 281) proposed that the term acritarch and any supra-generic classification should be abandoned and recommended, as did Cramer & Diez de Cramer (1972*a*), the use of an alphabetical classification of genera and species. This proposal to abandon acritarch is unjustified, in spite of its being often adopted nowadays in the USA, with the notable exception of Tappan (1980). A consequence of its adoption is that some studies of these microfossils may be disguised under headings that are uninformative, such as 'micropalaeontology', or inappropriate, such as 'microplankton' or 'microphyto-plankton', since there is no established proof that all the cells were either photosynthetic or planktonic.

Continued acceptance of the term acritarch, the abandonment of formal sub-groups, and the use of an alphabetical classification of taxa are the most convenient procedures since the phylogeny of *incertae sedis* is speculative and similar morphologies may be present within the life cycles of diverse groups of algae and of proto- and metazoans that are not phylogenetically related. Fensome *et al.* (1990, 1991) have given comprehensive lists of acritarch taxa, including those now variously admitted as prasinophyte algae. From their data and those of Tappan (1980) a current total of a few hundred genera and several thousand species of acritarchs and fossil prasinophytes may be estimated. About 2–10% of the former and 5–30% of the latter are variously considered to be green algae. Comparison with the mere thirty or so genera cited by Eisenack (1963) gives some idea of the interest aroused in this sector of micropalaeontology during recent decades.

(2) *Reassessment of some acritarchs*

As soon as a biological relationship is established for an acritarch, the taxon has to be removed from this polyphyletic group and properly reassigned. Sarjeant's (1970, p. 243) forecast that fragmentation or abandonment of acritarchs as a group could be expected within a few years is still far from being realized. A minority of acritarch genera or groups of genera has been claimed to belong, especially, to unicellular flagellate algae, dinoflagellates, prasinophytes or euglenoids. These loose terms permit, in principle, the avoidance of a botanical (suffix: yceae) or zoological (suffix: ida)

connotation, objectively unprovable for microfossils and often debatable for recent flagellates that straddle the boundary between the Plant and Animal kingdoms of Linnean classification. The dinoflagellates and prasinophytes are habitually considered, respectively, as algae by botanists and as protozoans by zoologists. At the other extreme Corliss (1984) distinguished 45 phyla grouped into 18 assemblages in the Kingdom Protista; the prasinophytes and euglenophytes are phyla and dinoflagellates form one of the 18 assemblages. The same author included, provisionally, the acritarchs among the dinoflagellates.

The essentially 'gross morphology' criteria used to classify acritarchs are relatively simplistic in relation to modern requirements and, in principle, for the classification of recent protists. The latter, although often lacking a general comprehensive approach, generally require the study of ultrastructures of subcellular components and/or their culture under diverse conditions of nutrition and temperature, as several morphological types may be variably developed during the same life-cycle, reflecting both the environment and the degree of maturity of the cell. Furthermore, data concerning the life-cycle of recent microorganisms are often very incomplete. In particular phycologists, when they record an encysted stage, rarely indicate the shape of the cysts and the nature of their wall. Micropalaeontologists, who have to deal principally with algal cysts, the most preservable as fossils owing to their sporopollenin-like wall, thus find themselves deprived of information that would enable them to propose or establish relationships with the motile stage. Some acritarchs are considered by certain workers, especially palaeobotanists, as primitive spore-like bodies originating from the first terrestrial plants. The reclassification of acritarchs among recent microorganisms of established systematic position remains rare or tentative.

(i) *Links with dinoflagellates*

Tappan (1980, pp. 231–237) recalled that the dinoflagellates are generally considered as very primitive and probably very ancient eukaryotes, notably because of the structure of the nucleus which in most cases investigated contains chromosomes formed mainly of DNA and always distinct whatever the stage of the life cycle. In other respects they appear very diversified and specialized, and therefore evolved. For example, depending on the taxa, nutrition ranges from holophytic to saprophytic; their habitat varies from free-living in ocean waters to parasitic in protists or invertebrates and swarming in certain supposedly drinkable city waters, thus demonstrating a wide spread of adaptations to very different environments involving particularly salinity and temperature.

Several stages, occasionally expressed by different morphologies, can be developed in the course of the life-cycle of modern dinoflagellates. The only one always present is a motile cell generally equipped with two dissimilar flagellae. Its external wall lacks plate patterns in the gymnodinians or is made up of plates that are generally of cellulose, easily decomposed after death. In their number and arrangement these plates form in the peridinians a tabulation that is characteristic for a genus or species and is variably reflected as paratabulation in the cyst stage, formed in the interior of the theca (encystment) and liberated following dissociation of the plates making up the latter. The cyst, termed resting spore by phycologists, is considered either as permitting resistance to adverse conditions or as a phase in alternating generations. Certain recent

cysts, because of their sporopollenin-like wall, are extremely resistant and may alone be fossilized; they are known in only a relatively limited number of species, especially among the peridinians. According to Williams & Bujak (1989, p. 849) there are at present less than 50 species of dinoflagellate cysts and more than 2000 species of thecae. After a period of rest a fossilisable cyst liberates the cellular contents through an often polygonal opening, the archeopyle, of constant shape and position within a single taxon and operculate. Evitt (1985, fig. 1.3) has shown schematically the development, including haploid and diploid phases, of the expelled protoplast. Development will end, in any case, with the formation of a motile stage, as in the pioneer experiments of Wall (1965*a*) and Wall & Dale (1968). The two latter demonstrated, by the germination *in vivo* of modern cysts of *Hystrichosphaera bentori* Rossignol, 1962 leading to the formation of motile thecae of *Gonyaulax digitalis* (Pouchet) Kofoid, 1911, that different generic and specific names had been attributed to two different stages of the same microorganism, found from the Pleistocene onwards. Following the scheme proposed by Wall & Dale (1968, pl. 1) to represent the life-history of a peridinium dinoflagellate, the life cycle of two acritarchs, *Cymatiogalea* with an operculate pylome and *Coryphidium* without opening, is shown tentatively (Fig. 4), with the unknown stages indicated.

As noted by Dale (1983), the classification of recent dinoflagellates should ideally include descriptions of the motile stages and the cyst stages, but this is rarely the case. Some cysts are no more than shapeless 'sacks' (Traverse, 1988, fig. 12.7) and are so ubiquitous that specimens can only be determined by means of culture. Considered individually, they could as well be compared with certain spores or acritarchs.

Current biological classification of living dinoflagellates is based mainly on the motile stage, almost never fossilized, and present in plankton. Palaeontological classification rests exclusively on the morphology of fossil cysts included in sediments deposited on the sea-floor. Evitt (1985, p. 42) reviewed the criteria needed for reliably attributing a fossil specimen to the dinoflagellates: size, form and composition of the cyst wall, and evidence of features corresponding to a cingulum and a sulcus, transverse and longitudinal depressions, in each of which a flagella of the motile theca was located. Some species show traces of a pattern of polygons comparable to a thecal tabulation. In several cyst forms the archeopyle is often the only remaining, usable character; its outline depends on the tabulation, which in these cases is not expressed by other characters.

Dinoflagellate cysts are very rare and equivocal in the Palaeozoic. The oldest generally accepted in treatises on micropalaeontology is *Arpylorus antiquus* Calandra, 1964, emend. Sarjeant, 1978, from the Silurian (Ludlow) of Tunisia. This record is, however, unique; formulation of the tabulation, based on 15 or so specimens, is rather speculative and the excystment opening always deformed. The presence of dinoflagellates in the Permian is exceptional (Jansonius, 1962) or dubious (Tash, 1963). Undoubted cysts are known without interruption from the end of the Triassic to the present-day and show important variations in specific diversity. It is possible if not probable that the majority of morphological resemblances between certain acritarchs and recent dinoflagellate cysts are due to convergence and do not imply any phyletic relationship. Only Dale (1977) has proved by experimental incubation that a 'living acritarch', known also under an invalid name in the Tertiary, was a dinoflagellate cyst.

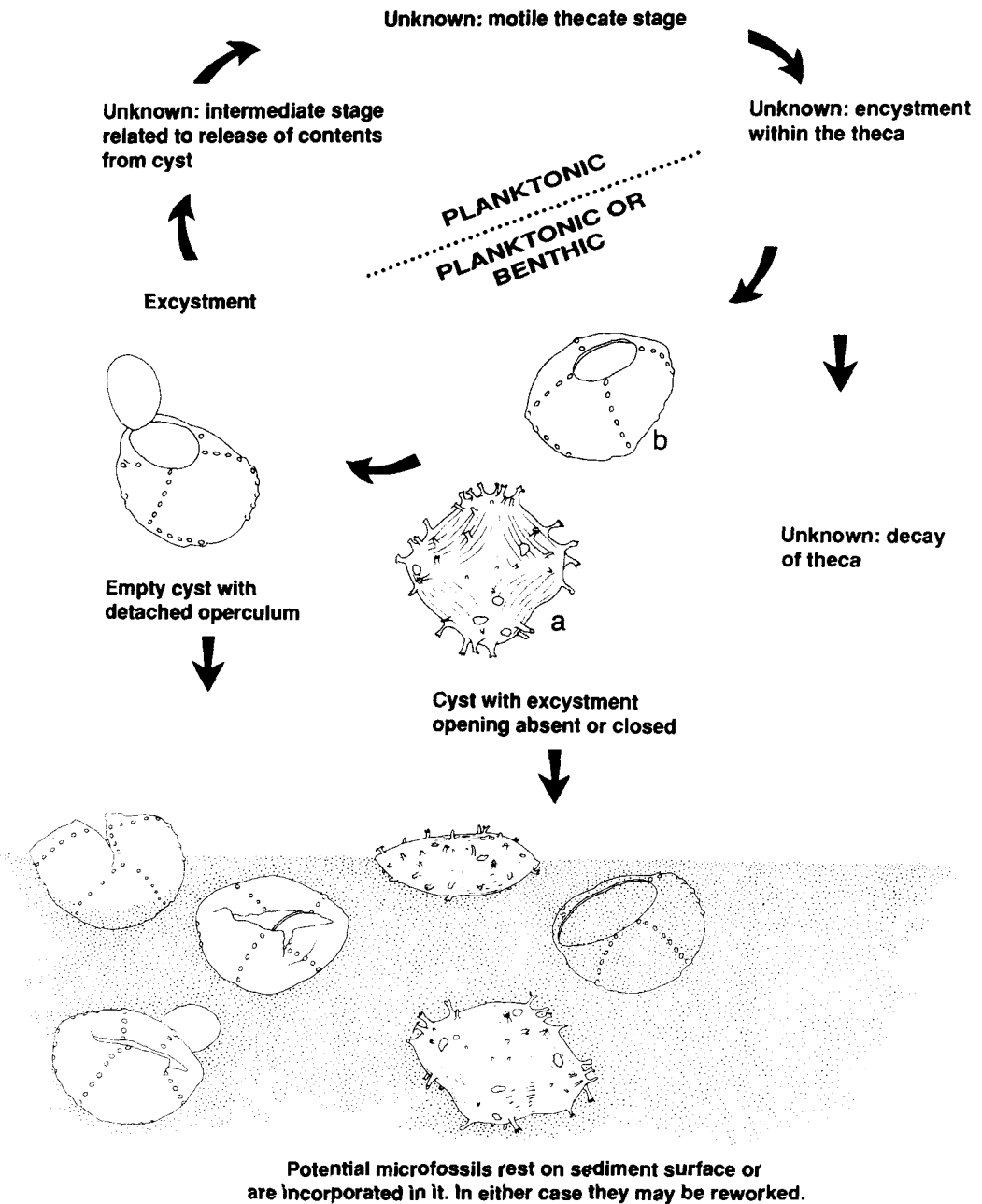


Fig. 4. Estimated life-cycle of acritarchs *Coryphidium* (a) and *Cymatiogalea* (b) by comparison with that of a living peridinin dinoflagellate.

Nevertheless, there are present-day armoured dinoflagellate species which produce cysts resembling Palaeozoic acritarchs that lived some 370 Ma BP. The cyst of *Peridinium stellatum* Wall in Wall & Dale (1978), obtained in culture, is one of a few examples. It consists of a pentagonal vesicle, each angle of which is produced to form

a conical process with simple distal extremity. According to the above authors a phyletic relationship with the acritarchs is unlikely as the recent cyst may exhibit an archaeopyle. Nevertheless a modern cyst of *P. stellatum*, extracted from recent marine sediments in New Zealand and illustrated by Baldwin (1987, fig. 20), lacks an archaeopyle and is totally comparable with some specimens of *Palacanthus ledanoisii*, aged about 370 Ma and illustrated here [Pl. 3 (fig. 1)]. However, variability of the fossil species involves the number of processes and shape of the central body, and is much greater than in recent cysts.

Lister (1970) attempted to demonstrate that acritarchs were cysts of dinoflagellates or extinct dinoflagellate-like organisms and used for their classification the criteria employed for peridininian cysts. The hoped-for result was not, however, achieved for the number of polygonally arranged processes present in certain acritarchs is variable and does not permit reconstruction of the stable tabulation of the motile stage. As the latter has a fixed formulation in the peridiniins Lister (1970) suggested that certain acritarchs, for example *Visbysphaera*, correspond to the cysts of unarmoured gymnodiniins, the motile stages of which would be unknown. Furthermore, the well-defined openings of some acritarchs, such as *Cymatiogalea*, were originally circular and match the equally circular opercula; the pseudopolygonal shapes are produced by secondary deformation during fossilization. Even when the edge of an opening is a zigzag, it corresponds to the removal of equisized polygonal plates and its outline cannot be interpreted on the basis of dinoflagellate tabulation. It is, however, possible that many acritarchs belong to extinct dinoflagellates that lack the minimum of characteristics required for recognition.

(ii) *Links with prasinophytes*

The prasinophytes are primitive algae that live especially in temperate regions, in marine, brackish or fresh water. Their reproduction, as far as it is known, is most often asexual and the majority of species contain a photosynthetic system (Norris, 1980). Genera such as *Halosphaera* Schmitz, 1878, *Pachysphaera* Ostenfeld, 1899 and *Pterosperma* Pouchet, 1893 comprise a motile, flagellate stage and an encysted stage called a phycoma. The latter possesses an external wall, made of very resistant, easily fossilized organic material, that opens at maturity along a slit and is comparable with certain acritarchs known since the beginning of the Cambrian.

Boalche & Parke (1971) and Parke *et al.* (1978), using cultures of marine species of *Pterosperma*, showed, some eighty years after the genus was introduced, that the flagellate motile stage is produced by and liberated from a non-motile, planktonic phycoma, provided with alae or an alaband. Such a phycoma bears a convincing resemblance to the acritarch genera *Cymatiosphaera* [Pl. 3 (fig. 3)], *Pterospermella* [Pl. 3 (fig. 2)] and *Pterospermopsis*, the last two of which may prove to be synonymous. Loeblich & Wicander (1976), Playford (1977) and Le Hérisse (1989) have illustrated, using the SEM, the preformed excystment slit of these alate microfossils, which is indicated by the ornamentation of its margins. Both *Cymatiosphaera* and *Pterospermella* should be considered as genera of fossil prasinophytes. The estimated life cycle of these microfossils (Fig. 5) is inspired by that given by Tappan (1980, fig. 20) but indicates also the numerous unobserved stages.

Parke *et al.* (1978, pp. 241, 251–253) also showed that the most reliable determination

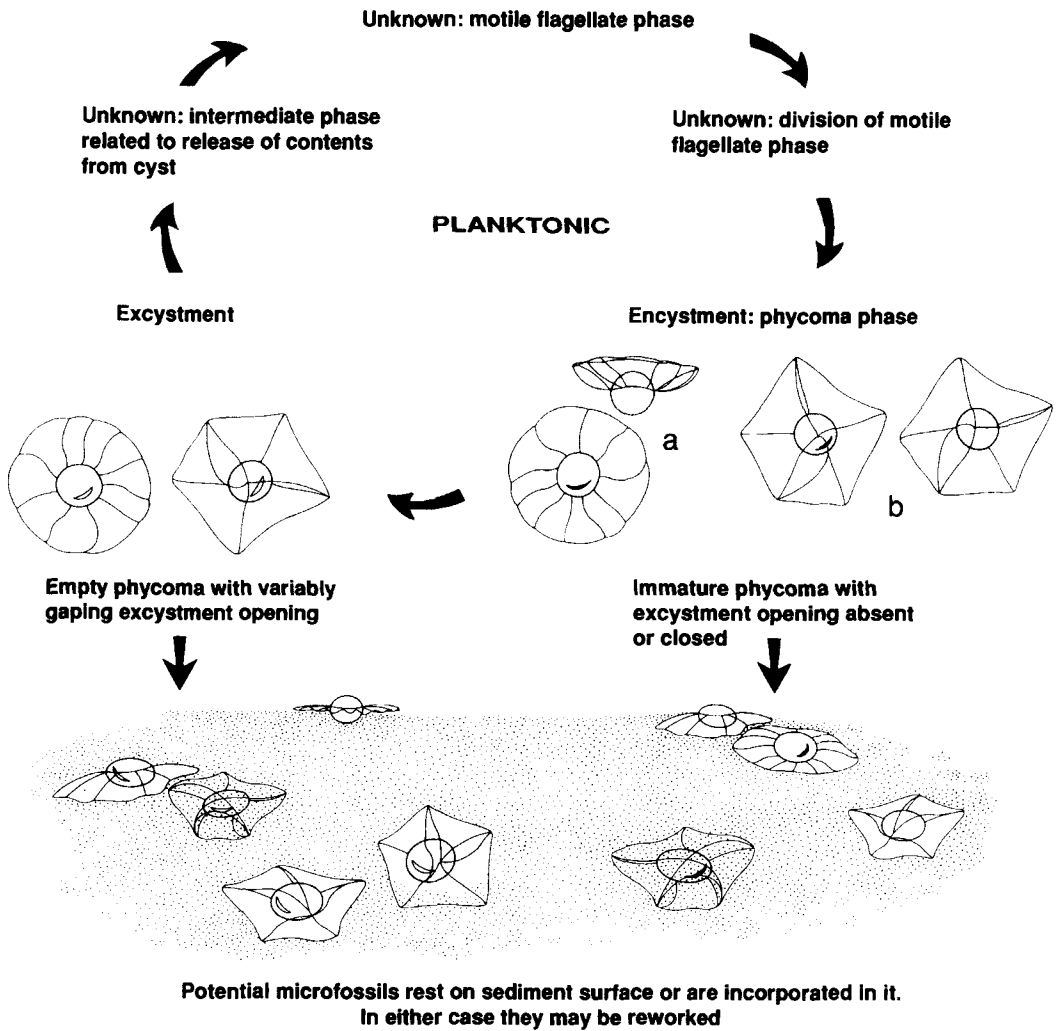


Fig. 5. Estimated life-cycle of *Pterospermella* (a) and *Cymatiosphaera* (b) by comparison with that of living *Pterosperma*, a prasinophyte alga.

of a species is based on the external wall of the phycoma after liberation of the contents, although studies *in vivo* indicate that the pattern of ala arrangement is an unstable character that may differ between parent- and daughter-phycoma [Parke *et al.*, 1978 (pl. V, figs A–D)]. The remarkable illustrations by these authors may attract the attention of those tempted to practise acritarch taxonomic oversplitting. Two examples are particularly suitable for demonstrating that the phycoma stage of the same species may vary according to its maturity or state of preservation. The photographs of Parke *et al.* [1978 (pl. VI, figs D, E)] show two views of the same phycoma of *P. rotundum* Pouchet, 1893, taken without and with pressure of the cover-slip and producing mainly differences in proportions of the body and the equatorial ala. Those of *Pterosperma euryopteron* Parke, in Parke *et al.* [1978, (pl. IX, figs. B, C)], illustrate the differences

between an empty outer wall of phycoma, with the body's slit-like opening and large folds of the ala, and a mature phycoma, with body content ready for release and narrower, shorter folds of the ala.

In a personal, subjective assessment Tappan (1980, pp. 207, 208) proposed the reclassification within the prasinophytes of several acritarchs, such as *Polyedryxium* and *Duvernaysphaera*, which have flanges sustained by projections of the vesicle. This attribution is not accepted here, given the lack of comparative illustrations of recent phycomas.

Wall (1962) made observations on living *Pachysphaera pelagica* Ostenfeld, 1899 and *Halosphaera minor* Ostenfeld, 1899 and established in particular the important variability of the wall structure in the former species (Wall, 1962, text-fig. 1 b-d), which he considered as a living representative of the fossil genus *Tasmanites*. The latter includes microscopic marine and brackish-water algae that may reach a size of some 600 μm . Their essentially organic wall is generally thick and lamellate, perforated by fairly numerous, variably developed pores [Pl. 3 (fig. 13)]. They are known from the Precambrian onwards and during this long geological history their local concentration has occasionally produced economically important algal coals, such as the 'white coals' or tasmanite in the Permian of Australia.

The history of the diverse taxonomic treatments of the tasmanitids was reviewed by Muir & Sarjeant (1971), and one need only note that whereas Evitt (1963) assigned them to the acritarchs, Downie *et al.* (1963) excluded them from that group and placed them in the green algae. Transmission electron microscope studies by Kjellström (1968) and Jux (1969*a, b*) confirmed that pore canals of the relatively thick wall are similar in *Tasmanites* and *Pachysphaera*. The methods of excystment opening, as far as they are known in a few species, do not however appear constant. *Pachysphaera* shows a slit developed some time prior to excystment and not a pylome. Specimens of *Tasmanites* may possess or lack an opening that may be termed a pylome; they may possibly have the operculum preserved, as illustrated by Eisenack [1958 (pl. 1, figs 1-4); 1962 (pl. 2, fig. 5; pl. 4, fig. 8)], or a slit [Wall, 1962 (text-fig. 2); Colbath, 1983 (figs 11, 14); Guy-Ohlson, 1988 (fig. 22D)]. In the latter case it is the structure of the wall and not the form of the opening that is accepted as a primitive generic character. By means of micromanipulation and observation under the SEM Guy-Ohlson reconstructed different stages of the life-cycle in Jurassic examples of *Tasmanites*. Assuming that the distribution of pyrite reflects the original organic content, the stages include maturation of the phycoma and the formation of motile cells, possibly with flagella-like appendages.

Since the first observations by Wall (1962), and in spite of certain contradictions linked essentially to variations in the method of opening, *Tasmanites* is accepted as a prasinophyte.

(iii) *Enigmatic sphaeromorphs*

The smooth-walled sphaeromorphs may be very abundant in the Precambrian, where they are known first in the Mesoproterozoic, about 1400 million years ago. Those of the genus *Leiosphaeridia*, commonly termed leiospheres, group together some of the dullest, most featureless acritarchs, apparently smooth, more or less circular in outline, with a thin wall that is often folded during fossilization [Pl. 1 (fig. 1)]; from a few to

several hundred μm in diameter, they generally lack a pylome or any other opening. Their notorious lack of original features unrelated to preservation has not, however, prevented numerous authors from introducing still more numerous genera and species. *Dichotisphaera* resembles *Leiosphaeridia* apart from an opening in the form of a slit that divides the acritarch into two subhemispherical parts.

Wall (1962) compared, questionably, the modern prasinophyte species *Halosphaera minor*, which has a smooth, thin wall, with *Leiosphaeridia*. His reservations were confirmed by sections viewed under the transmission electron microscope (Jux, 1969*b*) which showed a perforated lamellar structure in the former genus but not in the latter. Parke & Hartog-Adam, following culture of *Halosphaera*, showed that the cyst liberates its contents through a slit that is not visible in the immature stages [Parke & Hartog-Adam, 1965 (pl. 1, figs 18, 22)] and is comparable with that of *Dichotisphaera*, the wall of which has not, however, been observed under the transmission electron microscope.

Leiospheres have been the object of other speculative comparisons. Numerous sphaeromorphs found in near-shore to off-shore marine deposits resemble spore-like, dispersed, reproductive bodies called cryptospore sporomorphs. Apart from rare, doubtful cases accepted by Nøhr-Hansen & Koppelhus (1988), the first sporomorphs lack a trilete (Y) or monolete (I) dehiscence mark. They are claimed by Gray, Massa & Boucot (1982) to appear in the Caradoc (Ordovician), though the dating is not entirely reliable, but they are known in any case from the Ashgill (Vavrdová, 1984, 1988, 1989). Following Gray (1985) several palynologists, notably Burgess & Richardson (1991) and Strother (1991) consider that the first sporomorphs originated from non-vascular, unfossilized terrestrial plants, in particular bryophytes. However, it cannot be excluded that they belong to fresh-water or marine algae that have no modern analogues. Among the first inaperturate sporomorphs from the end of the Ordovician and the beginning of the Silurian some obligate dyads, made up of two spore bodies always joined together, resemble late Cambrian to Ordovician diacrodian acritarchs (Strother & Traverse, 1979, p. 7), or the still older *Synsphaeridium* sp. 1 *sensu* Cramer & Diez, 1972*b*, from the latest Lower Cambrian and earliest Middle Cambrian [Pl. 3 (fig. 12)]. Numerous monads, smooth, single spore bodies with no mark of dehiscence from the earliest Silurian, may be easily confused with leiospheres of any age, from which they are possibly only distinguishable by a slightly thicker wall.

It is also possible that, as suggested by Finney (1979) and Finney & Jacobson (1985) following observations on palynological preparations, certain Ordovician leiospheres with diameter at least 200–300 μm were flotation organs of the juvenile stages of graptolites, small, extinct, colonial marine animals classified as hemichordate invertebrates. Lindgren (1981) considered that the leiospheres without an opening could, in part, as well represent vegetative stages as resting cysts of flagellate algae. He showed that the pylome of certain leiospheres is similar to the flagellar pole of the modern *Trachelomonas* that had resisted acetolysis. This genus of fresh- and brackish-water euglenid exhibits a considerable polymorphism of the pellicle, illustrated by Conrad & Van Meel (1952), which is of taxonomic significance only at specific level.

Sphaeromorphs with a smooth wall, such as the leiospheres and dichotispheres, like those with reduced, spiny or granulose ornamentation, are so featureless that they are preferably, and most conveniently, classed with the acritarchs.

(iv) *Acritarchs, euglenoids or single spore-like bodies?*

Hypotheses and uncertainties relating to the biological status of acritarchs may be illustrated by the example of two closely related genera: *Moyeria*, often included with the acritarchs; and *Strophomorpha* Miller & Eames, 1982, usually considered as an inaperturate monad. *Moyeria* ranges from Ordovician (Caradoc) to Silurian (Ludlow) and is aged from about 450 to 420 Ma. It is known from the eastern USA, western Europe and Arabia (references in Gray & Boucot, 1989) in marine deposits, of variable water depth and distance from the coast, that contain also reworked older acritarchs and/or sporomorphs whose continental origin is debatable. Although Gray & Boucot accepted the rocks as fluviatile deposits and suggested that *Moyeria*, which may be abundant in them, had a continental origin or was euryhaline, their interpretation is not accepted here. This microfossil [Pl. 3 (fig. 16)] comprises a more or less ellipsoidal envelope, always seen without an opening, and the external wall carries longitudinal ridges, or muri, helically arranged so that the axis of rotation is the longitudinal axis of the vesicle. This type of spiral ornamentation is unknown in other acritarchs. From their SEM observations Gray & Boucot (1989) showed that the helical ornamentation increased from each pole towards the equatorial region. They postulated that *Moyeria* represents an active vegetative stage and not a resting cyst either of euglenophytes, of which about 75 % of modern taxa are photosynthetic, or of now extinct, unicellular eukaryotes close to the euglenoid flagellates. The latter have been studied more in fresh-water than in marine environments; their pellicle is at least ten times thinner than that of *Moyeria* and its resistance to diagenesis and to treatment with strong acids is unknown.

Strophomorpha may be found in the same Silurian (Llandoveryan) deposits of New York State as *Moyeria* (Miller & Eames, 1982), from which it is distinguished only by thicker, more pronounced and more closely-spaced ridges. The former genus is generally classified among the spore-like fossils but was considered by Gray & Boucot (1989) to be more euglenoid than the latter. In the Llandovery of Wales Burgess (1991, p. 593) found *Strophomorpha* to be most abundant in deeper marine deposits rather than in near-shore strata. The criteria of facies distribution tend to support the hypothesis that the taxon is more likely to be a thick-walled acritarch of supposedly marine origin.

(v) *Recent incertae sedis and crustacean eggs*

Resistance to acids and the potential for fossilization have been demonstrated in only very isolated cases of recent algae and invertebrate eggs. For example, Atkinson *et al.* (1972, p. 107) showed that sporopollenin is variably developed in different life stages, vegetative cells and resting cysts of chlorococcales (*Chlorellas*), and drew a parallel between the presence of sporopollenin and the development of trilaminar wall components. The latter characteristic is known in other green algae, the volvocales, which have not been the subject of chemical analyses, and the trilaminar wall is exceptional among acritarchs. Some morphological comparisons may be established between fossil acritarchs and recent *incertae sedis* of continental origin that withstand treatment with strong acids. They come from Holocene deposits that are peaty

(Churchill & Sarjeant, 1962) or lacustrine (Harland & Sarjeant, 1970) in Australia, and peaty in England (Sarjeant & Strachan, 1968). In palynological preparations from archaeological late Holocene lake deposits and peats in Friesland, northern Holland, Van Geel, Hallewas & Pals [1983, (pl. 6, figs 181–183)] found unicellular organisms similar to acritarchs, not only sphaeromorphs and acanthomorphs but also polygonomorphs from Palaeozoic marine deposits.

In recent deposits from the Wadden, in northern Holland, and from the North Sea off the Belgian coast Jan De Coninck (pers. comm.) found eggs of the copepod *Centropages hamatus*, illustrated by Lohman (1904) as *Ovum hispidum hystrix*, that were resistant to treatment with 40% HF. Among these eggs, which have variously shaped processes as shown by Lohman, some resemble Ordovician acritarchs such as *Baltisphaeridium spinigerum*. Jan De Coninck also found other *Ovum hispidum* subspecies figured by Lohman which remain as *incertae sedis*.

IV. REWORKING AND PALAEOECOLOGY

(1) *Durable microfossils*

Strictly speaking, it is theoretically possible to drink acritarchs carried in water by natural transport since the presence of organic-walled microfossils in Chicago tap-water has been demonstrated. This relates to a curious case of deposits that have undergone three phases of reworking (Hough, 1934). Devonian prasinophytes were first deposited in black shales that no longer crop out in this region but may, as a consequence of the last Quaternary glaciation, be found as pebbles of Devonian shale included in erratic blocks of unstratified boulder clay and deposited by glaciers and ice sheets. Washed out of their host strata, the spores ended in the mud of adjacent Lake Michigan where, once again in suspension, they were collected by the municipal water system. A sample from Quaternary glacial deposits in the northern Netherlands provides another undoubted case of reworking (van der Meer & Wicander, 1992). It contains, in addition to Quaternary spores and pollen, acritarchs of late Silurian to early Devonian age.

It is clearly more difficult, particularly with muddy or shaly deposits, to confirm the presence of acritarchs derived from rocks older than those from which the assemblages have been extracted, without sedimentological evidence of reworking or independent age control. Interpretations of redeposition are particularly subjective if, as often happens, the age range of taxa is only partially known and if both the allochthonous and autochthonous microfossils are of similar preservation and differ little in age. In this case the anomalous distribution of taxa may provide the only reliable argument for reworking. As an example, strata belonging to two successive graptolite zones of the earliest Silurian (Rhuddanian) in boreholes in the Brabant Massif, Belgium, were found to contain identically preserved autochthonous Silurian and allochthonous Ordovician acritarchs (Martin, 1974). The Ordovician specimens include two groups, an older of Tremadocian age, and a younger of Arenigian–Llanvirnian (undifferentiated) age. The latter is particularly present in the oldest Rhuddanian deposits, while the former is contained in the youngest strata. This stratigraphically inverted distribution of taxa indicates, as do others in the middle Ordovician (Caradoc) of Shropshire, UK (Turner, 1982), that the eroded source rocks became progressively older. In the same Brabant

Massif Silurian rocks noted above (Martin, 1974) a supposedly new acritarch species *Octogonium vanguestainii*, a nomen nudum and junior synonym of *Coryphidium bohemicum*, was believed at first to be of Rhuddanian age but has since been widely recognized in assemblages that are indubitably and exclusively Arenigian–Llanvirnian. In the case of Lower Devonian rocks from a borehole in Oxfordshire, UK, Richardson & Rasul (1978) showed that a single sample contains three or four groups of pre-Devonian acritarchs, each of characteristic age and preservation. The fact that they are found in the same taphocoenosis shows that the reworked specimens originate from several source rocks and/or source areas and may consequently play a role in palaeogeographic reconstructions. In a single Palaeozoic sample the allochthonous taxa may be more abundant than the autochthonous, and the criterion of frequency is unusable. On the other hand it is often useful for post-Palaeozoic samples. For example, in the Lower Jurassic of the Danish sub-basin dated using marine dinoflagellate zones and contemporary continental pollen and spore zones, Dybkjaer (1991) rightly maintains that the presence of a unique specimen of a species until now unknown after the Devonian and determined by her as *Diexallophasis denticulata* (senior synonym of *Diexallophasis remota*) shows reworking of deposits at least 190 Ma older.

When proposing an acritarch-based date the frequent possibility of reworking suggests that as far as possible, and in the absence of independent age control, it is preferable to use the first known appearance of the youngest taxon, even if this has to be revised later. In practice the use of overlapping species ranges introduces a supplementary variable involving the uncertainty of levels of extinction.

(2) *Life-style of acritarchs*

The wide geographic distribution of acritarchs in a large variety of essentially marine lithofacies, a palaeogeographic provincialism that was relatively weak or is poorly known, except from latest Cambrian to Ordovician (Tremadoc to Llanvirn), and their very small size suggest that they were planktonic, that is to say free-floating and submissive to water movements. By comparison with modern ecosystems (Tappan, 1980, 1986) they are most often considered to be phytoplanktonic, that is producers of organic matter and oxygen in the presence of, amongst other things, light. This interpretation rests especially on a combination of four criteria: the sporopollenin-like wall, similar to that produced by photosynthetic eukaryotes; the small size; the great abundance; and, possibly, the excessive representation of one species. This overabundance of one taxon has been observed sporadically, particularly from the Precambrian to the Ordovician, and suggests a palaeoecological control by comparison with the seasonal blooming of certain recent dinoflagellates that are responsible for phosphorescent seas or red toxic tides. The most acceptable hypothesis is that the majority of acritarchs are unicellular algal cysts, representing resistance stages under adverse conditions, and/or reproductive stages that are more demanding with reference to light, temperature, oxygenation and nutrition. The composition of live acritarch assemblages is obviously very biased in taphocoenoses. The interpretation of their palaeoecological needs and initial distribution is in any case speculative as, owing to their small size and low density, they are easily reworked. After death, like other palynomorphs, acritarchs behave as detrital particles, subject to currents and water turbulence. Deposited on the sea-floor or incorporated into soft or poorly consolidated

sediments, they may be easily retaken into suspension several times before being finally preserved in sediments very far from those representing their original habitat.

Nevertheless, acritarchs may be useful in regional reconstructions of specific marine palaeoenvironments, for their diversity and relative abundance compared with microfossils of terrestrial origin tend generally to increase progressively with distance from the coast-line. In spite of the relatively limited data Knoll (1985) proposed a reconstitution for the Neoproterozoic supratidal to open-shelf environment, with the latter containing a concentration of ornamented acritarchs. Similarly Dorning (1987) gave a preliminary synthesis linking selected acritarchs from Cambrian to Permian carbonate environments. Sphaeromorphs with thin vesicle wall would be particularly abundant in near-shore, shallow marine areas; those with thick vesicle wall would be characteristic of slope and deep water areas. In general the development of processes increases from near-shore to inner slope. In deposits of Palaeozoic basins, formed in deeper water and under less stable conditions than those of carbonate platforms, no acceptable general scheme showing relationships between different acritarch taxa and facies has been proposed. In particular, in Cambrian to Devonian deposits, where acritarchs are the most varied and abundant, comparison of regional models demonstrates apparent contradictions. Depending on the case, the latter may be due to hypothetical marine currents, reworking, or the priority subjectively given to one or other factor favouring or inhibiting acritarch development.

The principal causes invoked to explain fluctuations in the abundance and composition of live acritarch assemblages are linked principally, by comparison between remote geological times and the present day, to the proximity of the coast, water depth and nutritional factors, salinity, the distance from reefs, or fluctuations in the water mass (for references, see Moczydlowska & Vidal, 1992). Cramer & Diez (1974*a, b*, including earlier references) and Nautiyal (1977) were convinced that the distribution of, respectively, Silurian and Devonian acritarch assemblages was above all climatically controlled, on the basis of palaeolatitude models. Their generalized interpretations are nowadays more criticized than followed, for they show progressively more anomalies as the number of specimens of reliably known age increases.

V. ACRITARCHS THROUGH GEOLOGICAL TIME

The recognition and definition of time are among the basic data for both geologists and biologists as has been emphasized in many papers in recent years (references in Kauffman & Walliser, 1990), particularly in connection with studies of widespread but relatively short-term biological and geological so-called 'events'. The approximate contemporaneity of the latter becomes progressively more difficult to establish, and evidence less complete, as one descends the stratigraphic column.

The aim of the International Commission on Stratigraphy (ICS) and its satellites – a subcommission for each system and a boundary working group (BWG) for each systemic boundary – is essentially (Cowie *et al.*, 1986) to provide a uniform stratigraphic language, as stable and usable as possible, that will permit long-distance correlations required for reconstituting the evolution of the earth. The commission uses results from several disciplines whose applicability is uneven, depending on the part of the world and the interval of time involved. They include: palaeontology, radiometry, geomagnetism, seismicity, palaeobiochemistry, palaeogeochemistry and, especially from the Mesozoic onwards where data are easier to obtain and interpret by comparison

with the present day, sequence stratigraphy (references in Haq, Hardenbol & Vail, 1987) which integrates information from these sources.

In the most favourable circumstances of sediment deposition and preservation of strata, the relative dating provided by palaeontology is constrained by the endemism and facies dependence of organisms. However, in the pre-Quaternary and especially by combining data from several fossil groups, relative ages can often be more precise and refined than the absolute ages provided by isotopic analysis (review in Taylor, 1987). They are consequently indispensable for establishing the stratigraphic framework of more recently developed techniques such as palaeomagnetic and geochemical signatures.

How can acritarchs help in calibrating the geological time-scale? Downie (1984) synthesized their biostratigraphic potential and their limitations, due essentially to their being insufficiently known. Their history is illustrated by means of five examples, the first and last of which are treated in a general manner and the remainder in greater detail. These examples are: (1) the Proterozoic, as the acritarchs appeared there; (2) the base of the Cambrian, after which they became gradually more varied as a world-wide marine transgression was established; (3) the base of the Ordovician, where they show at least two palaeogeographic provinces at a time when fragmentation and movement of continental blocks increased; (4) in the Late Devonian, the base of the Famennian, which has attracted publicity due to claims that it coincided with a meteor impact that reputedly caused extinctions on a massive, even worldwide scale; and (5) from latest Devonian, when the acritarch record clearly diminished, to Quaternary.

(1) *Precambrian*

The Precambrian represents the initial 85 % of earth history and began approximately 4500 Ma BP. Palaeobiological criteria, at first absent, subsequently appeared rarely, though insufficiently distinct to be used for correlation on a large scale until the late Precambrian, very approximately about 750 Ma BP. The ICS has recently agreed (Plumb, 1991) that the Precambrian should be subdivided using chronometric time unit boundaries, defined by means of isotopic ages expressed in Ma. This policy does not take account of the errors or inaccuracies that have so far proved inevitable in absolute datings, and does not make reference to specific bodies of rocks. The new nomenclature does partly eliminate the confusion caused by the use of pre-existing regional schemes, often based on fossils of dubious value in correlation. It is, however, accepted with difficulty by palaeontologists (see Cloud, 1987) for the end of the Precambrian onwards, and especially from the beginning of the Cambrian, where the usual conventions are different.

The international recommendations of chronostratigraphy (Cowie *et al.*, 1986) require that from the Cambrian onwards a boundary – which essentially records a moment in geological time – should have its position fixed in an accessible, preferably unweathered reference section, or stratotype; the latter should be historically appropriate and sedimentation continuous and uniform, at least in principle. The position of the chosen level in the stratotype is ideally based on a point in the evolutionary lineage of a primary group of fossils, but subsidiary groups and non-biological markers helpful in correlation must also be considered.

(i) Before acritarchs

Recent decades have seen numerous researches on Precambrian microfossils, their aims being both biological, retracing the origin and evolution of life, and biostratigraphic, searching for guide taxa that permit relative dating in the absence or rarity of biogenic macrostructures. On the whole, the first of these has been more documented than the second, for the diversity of morphologically differentiated Precambrian taxa is low or poorly known.

The first undoubted evidence of Precambrian life-forms, microscopically distinct on account of their cellular membrane, was discovered by Tyler & Barghoorn (1954) in the Gunflint Formation of western Ontario, dated at about 2000 Ma BP. The same authors (Barghoorn & Tyler, 1965) illustrated numerous organic-walled microfossils from these carbonaceous Palaeoproterozoic cherts. The latter occur in eccentric laminations suggestive of stromatolites, an interpretation most often accepted by comparison with recent representatives found as shallow, benthic microbial community structures. Some microfossils from the Gunflint Formation have no modern counterparts or have subsequently been considered as pseudofossils (abiogenic) or dubiomicrofossils (questionably biogenic). Others, essentially rod-like or coccoids a few μm in size, and filamentous, branched or unbranched colonies several tens of μm long, remain attributed to procaryote moneres, lacking a distinct nucleus delimited by a membrane and reproducing asexually, mainly by binary fission. Their modern representatives are the archaeobacteria, now living in harsh environments such as the vicinity of mid-oceanic ridges, and the much more widespread eubacteria. The filamentous forms, septate or non-septate, are at best generally considered as cyanobacteria. The latter, formerly known as 'blue-green algae', are now the only procaryotes whose photosynthetic mechanism is very plant-like. Schopf & Walter (1983) accept the oldest-known cyanobacteria as coming from the Warrawoona stromatolitic cherts, about 3500 Ma BP, in Western Australia. If these ghost-like filaments are correctly interpreted they represent the oldest evidence of photoautotrophic organisms capable of releasing oxygen into the atmosphere and so playing a preeminent role in the evolution of life, about 1000 Ma after the formation of the earth.

Archaeobacteria or eubacteria, isolated or aggregated into colony-like clusters, and above all the cyanobacteria are abundant and diverse in the Neoproterozoic, as was first shown by Schopf's (1968) discoveries in the Bitter Springs stromatolitic cherts, about 850–750 Ma BP, in central Australia (see Addendum). However, the presence there of eukaryotes, capable of mitosis and meiosis, is arguable for the nucleus-like structures of cells with a diameter of about 10 μm could have been produced by degradation of protoplasts at the time of fossilization. Similarly the nearly tetrahedral cell organization could be either pro- or eukaryotic in origin (see Stewart, 1990, p. 35 for discussion and references).

(ii) Appearance of acritarchs

In the absence of a nucleus and chemotaxonomic data, the distinction between fossil procaryotes and eucaryotes rests on their cell size. The largest dimension in most modern procaryotes varies from 1–10 μm whilst it is from 10–100 μm in the majority

of eucaryotes. However, comparison of the smallest living protist eucaryote, the green prasinophyte *Micromonas* (= *Chromulina*) *pusilla*, 4 μm in length without flagella, with the largest procaryote, the spirochete *Cristispira*, up to 0.5 mm long, shows clearly that the criterion of size may be very relative. Nevertheless it is the only one morphologically usable for postulating the appearance of the oldest-known eucaryotes in the Mesoproterozoic, about 1400 Ma BP. Recognized for the first time (Horodyski & Bloeser, 1978) in limestones and shales of the Belt Supergroup in Montana, USA, they appear in palynological preparation as hollow, spheroidal envelopes some tens of μm in diameter, smooth, flattened and without preserved internal structures. Although they may also, on the basis of size and form, represent external sheets of colonial cyanobacteria (Horodyski, 1980), these sphaeromorphs are, for want of a better explanation, accepted here as being amongst the first recorded and oldest known acritarchs of reliably estimated age in the Mesoproterozoic. However, Mendelson & Schopf (1992) and Schopf (1992) have accepted their presence in the Palaeoproterozoic, from about 1800 Ma BP. It has been known since the work of Timofeev (1958) that the great majority of Proterozoic acritarchs are more or less smooth sphaeromorphs. Their ornamentation, more apparent than real, is particularly related to their laboratory preparation (agglutination of fine-grained kerogen particles) or preservation (for example, folds in *Kildinella*, corrosion in *Trachysphaeridium*, isolated microcrystals of pyrite in *Favosphaeridium*, and framboidal pyrite in *Balvinella*). This absence of authentic characteristics has not, however, prevented diagnosis of a plethora of alleged genera and species during the last 40 years. An unequivocal excystment-like opening is exceptionally recorded in Precambrian acritarchs; the oldest features comparable with a pylome and an operculum-like structure (Fig. 3) belong to sphaeromorphs dating from about 860–790 Ma BP, in the Chuar Group of Utah, USA (Vidal & Ford, 1985).

The first radiation of morphologically differentiated acritarchs is characterized particularly by the appearance of four genera: double-walled *Pterospermopsis*, *Octoedryxium* (see Addendum) and *Podolina* among the polygonomorphs, and *Vandalosphaeridium*, in which the tips of the processes support a peripheral membrane. These taxa (Fig 6), or some of them, have been recognized at levels in the Neoproterozoic ('late Riphean to Vendian'), essentially in Sweden, Norway, Greenland, the Urals, Ukraine, Siberia, Arizona, central Australia and central eastern China (see references in Vidal & Knoll, 1983; Hofmann, 1987; Jankauskas, 1989; Zang & Walter, 1992), dated to within several tens of Ma between about 800 and 600 Ma BP. Their disappearance, not yet established as synchronous, has sometimes been linked to an 'extinction episode' (Vidal & Knoll, 1983) apparently related to the Neoproterozoic glaciations (about 850–600 Ma BP). The latter, the extent and probable global diachronism of which are still only partially documented, are generally considered as having been the most geographically widespread in the history of the earth, which would then have known 'the longest winter' (Cloud, 1988). The last, and also the most important of them predates the levels where the first already diversified, soft-bodied Precambrian Ediacaran metazoans are recorded, variably dated, according to area, as about 700–570 Ma BP. The majority of the acritarch assemblages are very impoverished, dominated particularly by sphaeromorphs from the development of glaciations to around the beginning of the Cambrian, which is marked by the appearance of metazoans with biomineralized exoskeleton. Nevertheless some discoveries of acritarchs

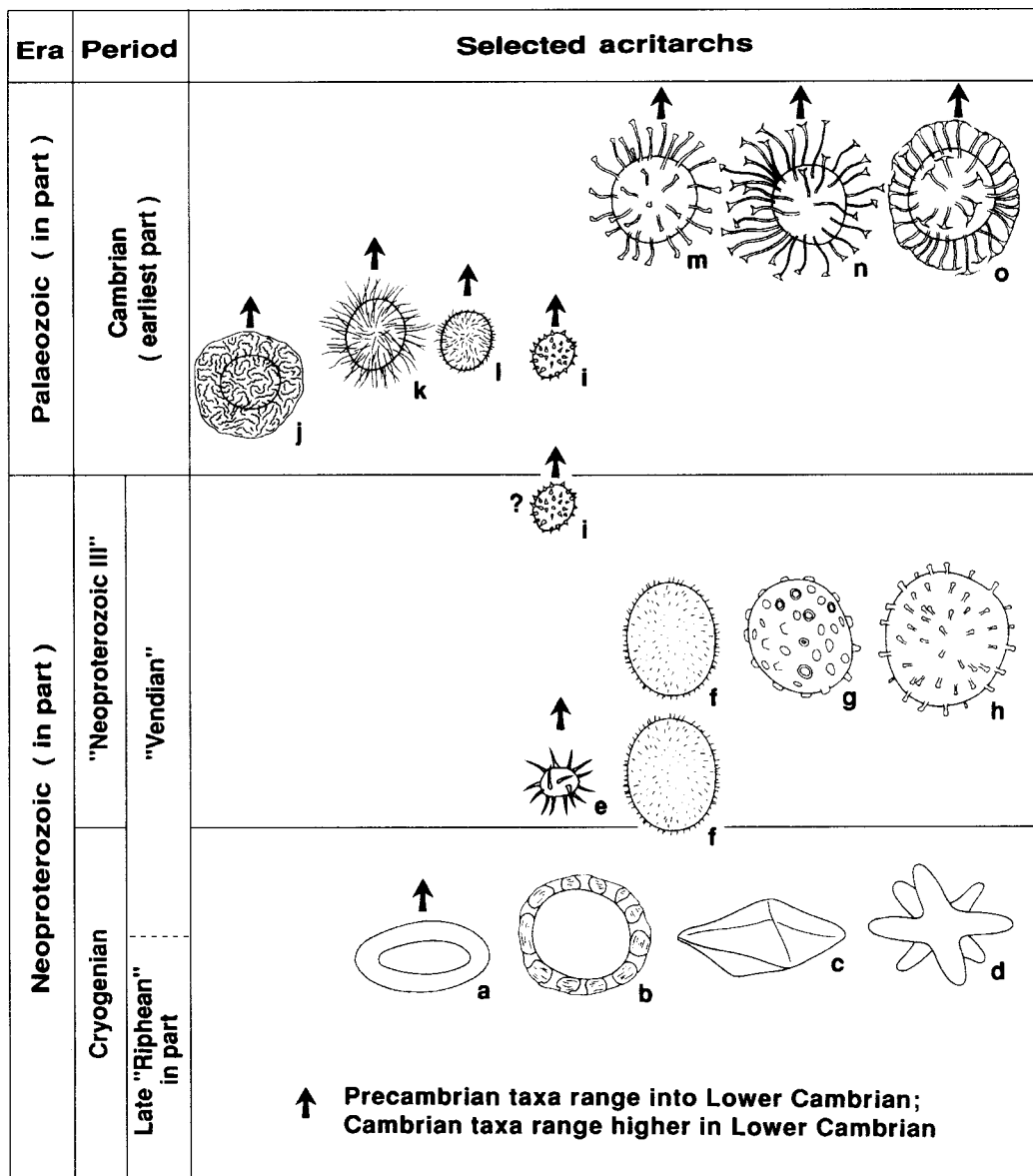


Fig. 6. Selected acritarchs from the late Precambrian (Neoproterozoic) and the Precambrian–Cambrian boundary (not to scale). a–d, widely recorded mainly in northern hemisphere: a, *Pterospirifer*; b, *Vandalosphaeridium*; c, *Octoedryxium* (see Addendum); d, *Podolina*. e–f, South China: e, 'Michhystridium'; f, cf. *Comasphaeridium*. f–h, central Australia: g, cf. *Rhopaliophora*; h, cf. *Skiagia*. i–o, successive appearances established in Eastern European Platform: i–l, pre-trilobite acritarchs; m–o, acritarchs from strata correlated with those containing oldest trilobites. i, *Asteridium tornatum*; j, *Annulum squamaceum*; k, *Comasphaeridium strigosum*; l, *C. velvetum*; m, *Skiagia orbicularis*; n, *S. ornata*; o, *S. scottica*.

with genuine, distinct ornamentation raise doubts concerning the very weak diversity of the assemblages or the supposed gigantism of latest Precambrian acritarchs. The best localized discoveries are in eastern Siberia, Hubei, and central Australia. From the Lower Yudoma Suite (about 650 Ma BP) of the Siberian Platform, Michaelis (1980) illustrated rare, small, spinose acritarchs. In the Doushantuo Formation (700–600 Ma BP) of the South China Platform, in addition to acritarchs from about 250–300 μm wide (Zhang, 1984; Awramik *et al.*, 1985), Wang (1985) and Yin (1985, 1987) have provided evidence of small '*Micrhystridium*', 10 μm or so wide, whose stratigraphic value is nil, as similarly badly preserved homoeomorphs are known also in the Palaeozoic up to the Devonian. The upper part of the Pertatataka Formation (650–600 Ma BP) in the Amadeus Basin of central Australia contains specimens with processes whose complex ornamentation (Zang & Walter, 1989) is slightly reminiscent of that of Palaeozoic taxa such as *Skiagia*, *Comasphaeridium* and *Rhopaliophora*. However, these Neoproterozoic acritarchs are clearly distinguished from the latter genera by a vesicle from 200–400 μm wide, that is about 6–10 times larger. Jenkins *et al.* (1992) have also found large, sculptured acritarchs in the Rodda Beds, late Proterozoic, of South Australia. Systematic descriptions of these rare discoveries were recently published by Zang & Walter (1992, see Addendum).

(2) Precambrian–Cambrian boundary

The pattern of oceans and continents in relation to the position of tectonic plates is very speculative for the end of the Precambrian and the beginning of the Cambrian, some 570 to 540 Ma BP (Scotese & McKerrow, 1990). Reliable palaeomagnetic and radiometric data are very rare and there are clear breaches of global biostratigraphic standards. The present tendency is to accept that the initial supercontinent, Pangaea, was starting to fragment in the late Precambrian, the end of which is, by definition, marked by the beginning of the Cambrian. The boundary is particularly difficult to define internationally for it coincides with worldwide marine transgressions interspersed with regressions (Brasier, 1982), so that a sedimentary break most often separates Cambrian from Precambrian rocks. Furthermore, because of its key position between the Proterozoic and Phanerozoic, the isotopic age of the stratotype will have to be determined. The relevant interval involves the sudden appearance of small shelly fossils and complex organic trace fossils (ichnofossils). These two groups are strongly facies controlled, the first being found particularly in carbonate sediments and the second, which has the undoubted advantage of always being found *in situ*, in siliciclastic facies.

The Precambrian–Cambrian Boundary Working Group (PCBWG), established in 1972, has long attached particular importance to the appearance of small shelly fossils, which precedes that of the trilobites. International correlation of representatives of the former group being controversial (Cowie, 1985, 1989) between the selected candidate stratotypes, in east Siberia (Ulakhan-Sugulur), China (Meishucun, Yunnan Province) and Canada (eastern Newfoundland), the choice has finally been made on the ichnofossils. After 20 years of investigation, international agreement was reached at the International Geological Congress, Kyoto, 1992. At Fortune Head, on the Burin Peninsula, Newfoundland, the Chapel Island Formation represents an apparently continuous Precambrian–Cambrian rock succession (Narbonne *et al.*, 1987). Although

the absence of reliable chemostratigraphic signals has been particularly criticized (Brasier, Anderson & Corfield, 1992), the base of the Cambrian is likely to be fixed slightly above the second member of the formation, at a point marked by the appearance of *Phycodes pedum* within the *Sabellidites cambriensis* organic tubes interval; *Sabellidites* belongs to an uncertain family of polychete annelid worms. Up to now no acritarch useful in correlation is recorded from the stratotype. The sole, rare representatives known from the Burin Peninsula (Downie, 1982) indicate, by the presence of *Archaeodiscina umbonulata*, an early but not earliest Early Cambrian age, equated with that of the earliest trilobites of the East European Platform; they come from an imprecise level in the Bay View Formation near St Lawrence (Downie, in Conway Morris, 1989, p. 15). However, either they weaken the correlation based on shelly fossils (Bengtson & Fletcher, 1983) between this formation and the three lowest members of the Chapel Island Formation, or they indicate that the level at which *Archaeodiscina* appears is globally diachronous.

What else can be said of these organic-walled microfossils, likely to be found in a great variety of rocks and so, in principle, providing an unusually valuable tool for correlating lithologically different deposits? Numerous researches on Lower Cambrian acritarchs have been carried out since 1959 in the former USSR and were reviewed by Volkova *et al.* (1979). One of the main difficulties is that each principal region tends to have its own palynological zonation. In particular, until recently (Khomentovsky, 1986; Pyatiletov & Rudavskaya, 1985), as was emphasized by Moczyłowska & Vidal (1988), lowermost Cambrian assemblages from the East European Platform are mainly, and erroneously, attributed to the Precambrian in the Siberian Platform. In the latter region Tommotian deposits, considered until 1984 (Cowie, 1985) to have potential as an internationally acceptable unit for the lowermost Cambrian, contain sedimentary breaks and no sufficiently characteristic fossils, including acritarchs (Moczyłowska, 1991). Thanks to reviews by Volkova *et al.* (1979) and especially to the contribution of Moczyłowska (1991) it is possible to indicate the appearance of significant acritarchs from the beginning of the Cambrian on the East European platform. Although the acritarch succession there is relatively the most complete known, it includes numerous breaks. The two last Precambrian 'horizons', Kotlin overlain by Rovno, are separated from each other by a hiatus. They contain ichnofossils and *Sabellidites* but lack diagnostic acritarchs, apart from the rare, questionable occurrence (Moczyłowska, 1991, p. 19) of *Asteridium* ('*Micrhystridium*') *tornatum*, a rather homoeomorphic taxon recorded in the Rovno 'horizon' by Volkova *et al.* (1979, 1983). According to data from the latter authors, *Annulum squamaceum* is the sole diagnostic acritarch that appears, as do small shelly fossils, in the first overlying 'horizon', the Lontova. The Talsy 'horizon', the last considered here as trilobites appear in it, is again separated from the underlying one by a hiatus. It contains several new genera and species of acritarchs, the most characteristic and best known of which are *Archaeodiscina umbonulata*, *Skiagia orbicularis*, *S. compressa* and *S. ornata*. In a succession of marine detrital sediments said to be essentially continuous in the subsurface of eastern Poland, Moczyłowska (1991) proposed a formal acritarch zonation for the Precambrian–Cambrian boundary and Lower Cambrian. She and Vidal & Moczyłowska (1992) also provided references to numerous works where the new biostratigraphic framework has partial application, notably in Baltoscandia, east Spitzbergen, east Greenland, northwest Scotland, and

Alberta and the Northwest Territories, Canada. It has proved partially usable also in Hubei and Yunnan provinces, south China (Zang, 1992) and in northern Spain (Palacios & Vidal, 1992). Judging from the still scattered data, there is no obvious indication of provincialism. In Poland the first varied Cambrian assemblage is represented by the *Asteridium tornatum*–*Comasphaeridium velvetum* Biozone, and includes especially *C. strigosum* and *Annulum squamaceum*. The appearance of the latter before the two eponymous species is the marker closest to the base of the Cambrian. Small acritarchs with simple spines are, considering differences in preservation, very like badly damaged specimens from the Neoproterozoic. However, the new terminology of *Asteridium* conveniently draws attention to the beginning of a palynological renewal. The *A. tornatum*–*C. velvetum* Biozone assemblage compares with that found much more poorly developed in the Lontova 'horizon'. Moczyłowska (1991) correlated this acritarch biozone with the *Platysolenites antiquissimus* (shelly fossil) Biozone, but its base is probably higher than the now favoured boundary level at the appearance of *Phycodes pedum* in eastern Newfoundland. Furthermore, this acritarch biozone, with its relatively abrupt influx of taxa, is probably separated by a sedimentary break, or lack of sampling, from the extremely impoverished sphaeromorph assemblage of the subjacent Neoproterozoic. Nevertheless, it indicates clearly the diversification of both acritarchs and prasinophytes, in particular *Cymatiosphaera* and *Pterospermella*, before the appearance of the trilobites. The succeeding assemblage, the *Skiagia ornata*–*Fimbriaglomerella membranacea* Biozone, is essentially characterized, like the Talsy 'horizon', by the rather abrupt entry of several species of *Skiagia*, including *S. orbicularis*, *S. ornata* and *S. scottica*. Despite the absence of trilobites from the relevant samples, Moczyłowska (1991) accepted that the range of this acritarch biozone corresponds to that of the *Schmidtellus mickwitzii* Biozone, below the *Holmia inusitata* Biozone.

To conclude, in the earlier part of the early Cambrian, and in ascending stratigraphic order beginning slightly above the internationally accepted systemic boundary and essentially on the basis of data from the East European Platform, the successive appearances of index acritarchs are as follows: (1) *Annulum squamaceum*; (2) *Comasphaeridium velvetum* and/or *C. strigosum*, possibly accompanied by a biostratigraphically useful diversification of prasinophytes; and (3) *Skiagia orbicularis*, *S. ornata* and *S. scottica*. The relatively sudden appearance of the genera and species specified in (2) and (3) probably indicates gaps in observations.

(3) Cambrian–Ordovician boundary

The positions of the principal continental masses and seas at the beginning of the Ordovician Period, some 510 Ma BP, are relatively a little better understood than those in preceding geological time (Scotese & McKerrow, 1991) and very different from those of modern times. The present review of the Cambrian–Ordovician boundary is based on a selection of acritarch-bearing marine strata deposited around the margins of palaeocontinents that bear names unrelated to those of the present day. Acritarch data are used subject to two conditions. First, there must be at least some reliable independent age evidence indicating proximity to the boundary, that is to say near the base of the Tremadoc Series, recognized as lowest series of the Ordovician and named after a town in North Wales. Owing to its lack of acritarch time-markers the Green

Point section, western Newfoundland, proposed as global boundary stratotype by Barnes (1988) is excluded from consideration. Second condition: the acritarchs must have been described in publications serving most often, and for want of better, as reference works for palynological dating of this stratigraphic interval at sections where there is little independent age control. The deposits discussed are as follows. (1) Warm water, low-latitude shelf areas on two distinct tectonic plates situated, respectively, in northeast China, on the north slope of the Sino-Korean Platform, and in southern Alberta, Canada, then part of the northern margin of the Laurentia palaeocontinent. (2) Epicontinental and deeper seas in intermediate latitudes related to the Baltica palaeocontinent, respectively on the East European Platform, from Öland to the Moscow Basin, and in northern Norway, part of the Scandinavian Caledonides. (3) Colder and often deeper water deposits from higher palaeolatitudes in the Algerian Sahara, then part of the Gondwanan palaeocontinent, as well as North Wales, Shropshire and eastern Newfoundland. The last three areas are associated terranes in a part of Perigondwana known as Avalonia.

At and near the Cambrian–Ordovician boundary several conodonts and planktonic graptolites, belonging respectively to the genera *Cordylodus* and *Rhabdinopora*, appear to have been cosmopolitan and are particularly useful in interregional correlation, in contrast to the trilobites, which often exhibit marked provincialism. The acritarchs also show a certain provincialism during this interval of geological time. The late Cambrian, from the base of the *Cordylodus proavus* Biozone to the base of the *C. angulatus* Biozone in the early Tremadocian, is estimated to have included four eustatic events, whose relative age may be given in terms of conodont biozones. At least the first and last of these events are very widely distributed geographically (Miller, 1992) and the third has been related to the influx of the first planktonic graptolites (Erdtmann, 1988). Conodonts, microfossils that are found especially in carbonate rocks, have been selected by the Cambro–Ordovician Boundary Working Group (COBWG) as primary guide fossils for defining the base of the Ordovician, at a level as close as possible below the first appearance of nematophorous, planktonic graptolites, macrofossils traditionally employed to define the system base in clastic facies (review in Norford, 1991). Three biozones, the bases of which have been envisaged as candidate index levels, are, in ascending stratigraphic order: *Cordylodus proavus* Biozone; *C. intermedius* Biozone (*Hirsutodontus simplex* Sub-biozone); and *C. lindstromi* Biozone. The last of these, closest to the first appearance of planktonic graptolites, is preferred, but there is some uncertainty as to whether it is everywhere contemporaneous. The present discussion attempts to evaluate the role of acritarchs in defining the same boundary.

(i) *Northern Sino-Korean Platform and northern Laurentia*

Up to the present, the section at Xiaoyangqiao, near the village of Dayangcha, Jilin province, China, has been, in spite of its stratigraphic imperfections, the most suitable – or the ‘least unsuitable’ – choice for the Cambrian–Ordovician boundary stratotype. The horizon chosen there to mark the international base of the Ordovician is at or near the base of the *Cordylodus lindstromi* Biozone *sensu* Chen *et al.* (1988), depending on a final definition of the conodont biozones, and is a little below the first *Rhabdinopora flabelliformis parabola*. Geomagnetic profiles suggest, however, that the base of the *C. lindstromi* Biozone is condensed or absent (Ripperdan & Kirschvink, 1992) and the

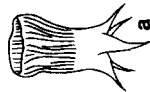





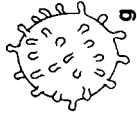

Internationally proposed base of Ordovician		Selected Cambro-Ordovician acritarchs										
Internationally proposed base of Ordovician	Base of first series of Ordovician	First appearance of selected conodonts (1,4,6), trilobites (2,3,5) and planktic graptolites (7) 1 - 6 : N. America 1,4,6,7 : N.E. China	 a	 b	 c	 d	 e	 f	 g	 h		
			Tremadoc - Europe	7. <i>Rhabdinopora fl. parabola</i>	barren	barren	barren	barren	barren	barren	barren	
			Ibexian (Canadian) N. America	6. <i>Cordylodus lindstromi</i>	barren	barren	barren	barren	barren	barren	barren	barren
				5. <i>Symphysurina</i>	barren	barren	barren	barren	barren	barren	barren	barren
				4. <i>Cordylodus intermedius</i>	barren	barren	barren	barren	barren	barren	barren	barren
				3. <i>Missisquoia</i>	barren	barren	barren	barren	barren	barren	barren	barren
			close to 6	Tremadoc - Europe	2. <i>Corbinia apopsis</i>	barren	barren	barren	barren	barren	barren	barren
1. <i>Cordylodus proavus</i>	barren	barren			barren	barren	barren	barren	barren			
			Wilcox Pass section Alberta, Canada		Xiaoyangqiao section Jilin, China		Taxon appears earlier at Chinese section					

Fig. 7. Selected acritarchs from Cambrian-Ordovician boundary sections in northern Sino-Korean Platform and northern Laurentia (not to scale). a, *Corollasphaeridium wilcoxtanum*; b, *Actinotodissus* sp. A; c, *A. achraisi*; d, *Cymatogalea* sp.; e, *Multiplicisphaeridium abnorme*; f, *Vulcanisphaera* cf. *V. africana*; g, *Buedingisphaeridium tremadocum*; h, *Dasydiacrodium* cf. *D. glabrum*.

underlying *C. proavus* and *C. intermedius* biozones have each a break in sedimentation (Miller, 1988) at or near the base.

In low-latitude areas represented by deep shelf deposits at Xiaoyangqiao and shallow shelf at Wilcox Pass, southern Alberta, Canada, *Corollasphaeridium wilcoxianum* (Fig. 7) is the most accurate Cambrian index acritarch to appear, though without any precursor, closest below the base of the Ordovician; its range begins in the upper part of the *Cordylodus proavus* Biozone. In one or other of these two regions (Martin & Yin, 1988; Martin, 1992), the first appearances of Ordovician index acritarchs, especially species of *Aryballomorpha* and *Athabascaella*, are too far from the system base to be useful in defining it internationally; indirect correlation shows them to occur higher than the biohorizons with *Rhabdinopora flabelliformis parabola* and with *Anisograptus*.

In northeast China *Corollasphaeridium wilcoxianum* forms part of impoverished assemblages containing, contrary to Yin (1986, in Chen *et al.*, 1988), taxa that are relatively long-ranging, such as *Actinotodissus achraisi* and *Cymatiogalea*, or of relatively ubiquitous shape, such as *Multiplicisphaeridium abnorme*. The base of the *Cordylodus lindstromi* Biozone marks no obvious change in composition of the acritarchs which, except for the sphaeromorphs, are very rare.

At Wilcox Pass (Martin, 1992), in an assemblage with little variety of long-ranging taxa from a section lacking graptolites, *Corollasphaeridium wilcoxianum* appears also in the upper part of the *Cordylodus proavus* Biozone, corresponding to a questionable upper part of the trilobite-based *Missisquoia* Biozone. It is accompanied by some taxa known up to the present from the Upper Cambrian and Tremadoc of mainly Baltica, Gondwana and Avalonia, such as *Vulcanisphaera* cf. *V. africana* and *Buedingii-sphaeridium tremadocum*. The *Corollasphaeridium* Biozone is succeeded, in strata dated by means of trilobites as *Symphysurina* Biozone, by an atypical acritarch assemblage composed essentially of sphaeromorphs.

(ii) *Baltica, Avalonia and Gondwana*

In regions of middle and high latitude relevant palynodata for the Cambrian–Ordovician boundary are particularly abundant, imprecise and of local value. They do not yet allow a wide range of detailed correlations to be made, nor do they permit the base of the Tremadoc to be satisfactorily established. This difficulty is due to a combination of several factors. Unwarranted datings established on mainly palynological circular arguments have been taken at their face value in subsequent publications. Until ten or so years ago (Martin & Dean, 1981) they gave the impression that numerous taxa are indicative of the Tremadoc when, in fact, they appear in the Upper Cambrian; these include particularly *Saharidia* and *Cymatiogalea*. Condensed sequences, that is strata that are very thin in relation to the time they represent, discontinuities reflecting interruptions in sedimentation, and sampling at too widely-spaced intervals may give the false impression that the appearance in force of numerous new taxa marks the base of the Ordovician. Poorly deciphered reworked assemblages are surely frequent and make for further complications. Changes of relative age attribution do not, however, involve only palynologists, for the stratigraphic ranges of bio-markers better known than the acritarchs, such as conodonts, graptolites and trilobites, are themselves subject to periodic revision.

The beginning of the Cambrian–Ordovician boundary interval considered here (Fig.

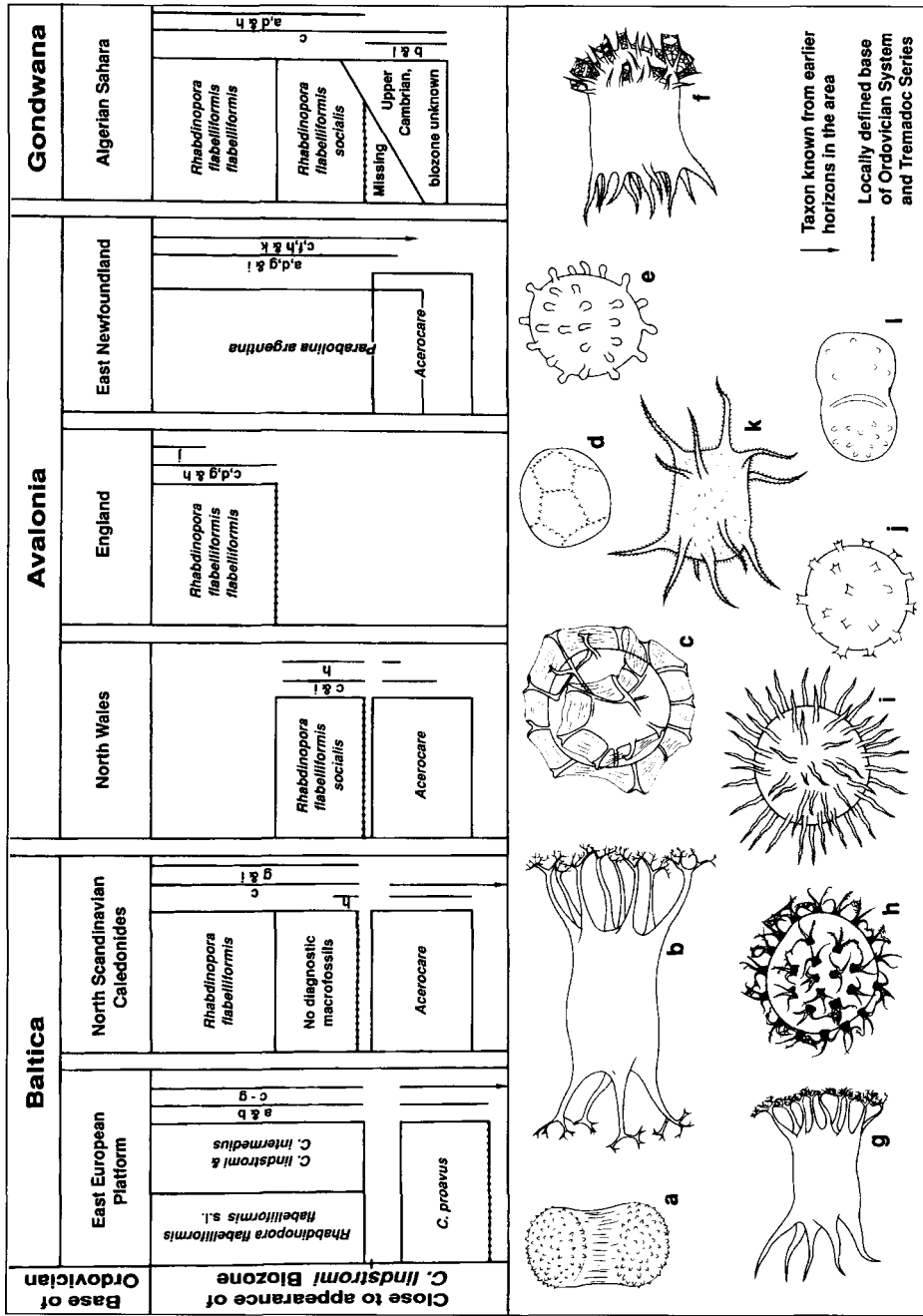


Fig. 8. Selected acritarchs in relation to the Cambrian-Ordovician boundary in Baltica, Avalonia and Gondwana (not to scale). a, *Acanthodiacroidium angustum*; b, *Arbusculidium ornatum* (= *A. ramusculosum*); c, *Cymatogalea* sp.; d, *Cymatogalea cvillieri*; e, *Buedingisphaeridium tremadocum*; f, *Ladogella* sp.; g, *Arbusculidium destombesi* (= *A. frondiferum*); h, *Vulcanisphaera africana*; i, *Baltisphaeridium crinitum*; j, *Vulcanisphaera imparilis*; k, *Actinotodissus achrasi*; l, *Dasydiacrodium glabrum*.

8) is marked either by the *Cordylodus proavus* Biozone (sub-biozone approximate) or by trilobites of the *Acerocare* Biozone (sub-biozone approximate). The end of the interval is poorly defined in terms of the last occurrence of the *Rhabdinopora flabelliformis* species-group, itself localized below the appearance of graptolites of the *Adelograptus tenellus* Biozone. A possible choice made from a few other sections or numerous other taxa would be unimportant at this stage for producing a reference scale of accurate acritarch time-markers. The results are very limited, and the present compilation indicates that until now acritarchs from the base of the Ordovician, i.e. at or near the base of the *Cordylodus lindstromi* Biozone, remain largely undocumented. With reservations *Acanthodiacrodium angustum* is, as suggested by Volkova (1989), the index taxon that is closest to the base of the Ordovician but her data are insufficient to judge if this species appears at the beginning of, or within the *Cordylodus proavus* Biozone. On the other hand, the first appearance of Ordovician acritarchs of the *Veryhachium trispinosum* 'group' *sensu* Martin (1982a) occurs above the *Adelograptus tenellus* Biozone and so is too high for consideration in defining the systemic boundary.

(a) *Baltica*. In Baltica, deposits of the Baltoscandian epicontinental sea form a highly condensed sequence with a complex pattern of sedimentary breaks, generally accepted (Jaanusson, 1982) as being due to the sporadic emergence of shallow, near-shore shelves. Volkova & Mens (1988) and, principally, Volkova (1989, 1990) studied acritarchs from diverse outcrops and, especially, boreholes in Estonia and the Moscow syncline. The latter author, using her own observations and reviewing the international literature, suggested that *Acanthodiacrodium angustum* marks the base of the Ordovician which, following general usage in the Baltic states and western Russia, she accepted as being defined by the appearance of the *Cordylodus proavus* Biozone. This level, lower than the one recommended by the COBWG, is succeeded by a hiatus, followed in turn by a condensed horizon that includes probably reworked material and may in any case contain elements of both the *Cordylodus intermedius* and *C. lindstromi* biozones as well as *Rhabdinopora flabelliformis* *s.l.* (references in Apollonov, 1991, p. 36).

In the Scandinavian Caledonides of northern Norway Welsch (1986) described acritarchs from an allochthonous unit on the Digermul Peninsula, Finmark, part of the northern European geosynclinal on the western border of Baltica. They formed the basis of a regional zonation, part of which was dated with certainty on the basis of trilobites from the lower half of the *Acerocare* Biozone (Nikolaisen & Henningsmoen, 1985), Upper Cambrian, and part as *Rhabdinopora flabelliformis* Biozone, lower Tremadoc. The first palynological level considered as Tremadocian by Welsch is separated from the last Upper Cambrian sample by at least 190 m of quartzites for which there are neither palynological nor diagnostic macrofossil data, and it marks an influx of taxa described as new or known especially from the Upper Cambrian of Gondwana and Perigondwana. The strata dated by *R. flabelliformis* (*s.l.*) contain relatively few acritarch taxa, and all were already present lower in the Digermul Peninsula sections.

(b) *Avalonia*. Although small, Wales has a special historical significance in geology as it includes the type areas of the Cambrian and Ordovician. Sediments around the Cambrian–Ordovician boundary are clastics with almost no limestone, conodonts are consequently poorly represented, and the base of the Ordovician is traditionally drawn

at the lowest occurrence of the *Rhabdinopora flabelliformis* species group. In North Wales the *Acerocare* Biozone, highest Cambrian trilobite biozone and long thought to be absent, has been proved (Rushton, 1982), though probably incomplete, in a single section at Bryn-Llin-Fawr, 25 km southeast of Tremadoc, where the rocks are slightly disturbed tectonically. The *Acerocare* Biozone is found below the first appearance of *R. flabelliformis socialis* and contains notably the trilobite *Parabolina frequens*, considered (Rushton, 1982, p. 50) to be a senior synonym of *Parabolina argentina*, a zonal index in Argentina where it is recorded below and within the range of *R. flabelliformis*. *P. frequens* is one of several trilobites, some found also in eastern Newfoundland, whose range is now accepted as extending from highest Cambrian to lowest Ordovician (Dean, 1985, p. 28). Acritarchs are extremely poorly preserved at Bryn-Llin-Fawr and do not provide reliable evidence of changes in assemblage composition at the Cambrian–Ordovician boundary (pers. obs.). They include, notably, diacrodians, herkomorphitae, *Baltisphaeridium crinitum* and *Vulcanisphaera* cf. *V. africana*.

At the section in Cherme's Dingle, Shropshire, England, the lowest levels of the Tremadoc are faulted against Lower Cambrian; they are dated by means of *Rhabdinopora flabelliformis s.l.*, the record of *R. flabelliformis socialis* by Bulman (1927, p. 28) not being subsequently confirmed. The succession is cut by faults and even though acritarchs there are abundant and well preserved, they have led to a zonation (Rasul, 1979) of no more than local application. *Acanthodiacrodium angustum* is present among the oldest taxa in the section and *Vulcanisphaera imparilis* appears in the upper part of the strata with *R. flabelliformis s.l.*

At Random Island, eastern Newfoundland (Martin & Dean, 1981, 1988), in sections that are essentially shaly, faulted and discontinuous, the Cambrian–Ordovician boundary has not yet been proved. Trilobites indicating the third highest of the four sub-biozones of the *Acerocare* Biozone were found at a single level. On the other hand *Parabolina frequens* (as *P. argentina*) and *Acanthodiacrodium angustum* were found at other levels that lack conclusive evidence of the *Acerocare* Biozone, and may belong to either the Upper Cambrian or the Tremadoc.

(c) *Gondwana*. In North Africa, except for some rare, relatively uninformative data from Moroccan outcrops dated by means of *Rhabdinopora flabelliformis* (Elaouad-Debbaj, 1988), all the supposedly Tremadocian acritarchs come from boreholes drilled by oil companies in the Algerian Sahara. Combaz (1968) attributed to the Lower Tremadoc the oldest acritarchs from the 'Grès d'El Gassi' on the basis of a comparison with those from the *Obolus* Beds of the East European Platform. Timofeev (1958) accepted erroneously a Tremadocian age for these inarticulate brachiopods, now considered (Kaljo *et al.*, 1986) as Upper Cambrian, and so distorted the age of the associated acritarchs, which include *Ooidium rossicum*. In an extension of Combaz's work Jardiné *et al.* (1974) accepted, though with reservations related especially to the significance of the fragmentary lingulids, the Tremadocian age of the first assemblage, Bo. On the other hand Legrand (1985, p. 15) showed that the age of the 'Grès d'El Gassi' varies locally from Upper Cambrian *sensu lato* to lower Tremadoc. The succeeding assemblage, B₁, dated by means of *Rhabdinopora flabelliformis*, includes the appearance of *Acanthodiacrodium angustum*; it shows also an influx of diacrodians and herkomorphitae much more varied than in assemblage Bo.

(4) *Within the Late Devonian: Frasnian–Famennian boundary*

The fossil record indicates that during the Late Devonian, some 375 to 355 Ma BP, important biological modifications took place, notably in very extensive, shallow seas around the margins of the continental masses, most of them in closer proximity than at the present day. The deposits of this epoch belong to two stages, the Frasnian succeeded by the Famennian. Using conodonts, the lower limit of the Famennian was fixed by the Subcommission on Devonian Stratigraphy (SDS) in 1989 (Oliver & Chlupáč, 1991) at the base of the Early *Palmatolepis triangularis* Biozone. The appearance of the latter is located at the beginning of a global marine regression; it precedes a radiation of new cephalopod genera and follows a succession of faunal extinctions that are relatively closely spaced within the Frasnian. This so-called 'Kellwasser crisis' (Schindler, 1990), which lasted approximately 2 Ma, began after the disappearance of large reefs and its end culminated in the *P. linguiformis* Biozone, about 370 Ma BP. Goodfellow *et al.* (1988) reviewed the possible reasons for these step-by-step disappearances, which affected especially the small coniconch (= cricoconarid) molluscs and certain trilobites, brachiopods and conodonts. The terrestrial causes most frequently invoked include principally sea level changes, glaciation, the absence of sufficiently oxygenated sea water, tectonism and volcanism. Goodfellow *et al.* (1988) showed also that an extra-terrestrial cataclysm, such as the impact of a large meteorite, has not yet been conclusively proved by means of iridium concentrations or shock metamorphic minerals. Tappan (1982, 1986) considered that the crisis was provoked indirectly by the accentuated development of terrestrial plants; increase of the latter would have progressively induced lethal disturbances of the food chain especially in the marine ecosystem. Tappan (1986, p. 551) underlined an important decline in acritarch abundance during the Frasnian. This temporary decline concerns rather the end of the Frasnian, as far as can be judged from the rare, disparate and regional data. Contrary to the opinions of Tappan and of Buggisch (1991, p. 53), Frasnian and Lower Famennian acritarchs may in fact be numerous and display a great variety of genera and species (Wicander & Playford, 1985; Lu & Wicander, 1988 for references). The majority do not yet, however, permit the two stages to be distinguished and are variably dispersed at isolated localities over five continents. Data come mainly from deposits with insufficient stratigraphic age control (Vanguetaine, 1986, for references).

Because of the refined time resolution now possible using conodont-based biozonation (Ziegler & Sandberg, 1990), this review of acritarchs at the Frasnian–Famennian boundary is based on the appearance and disappearance of species dated by means of conodont studies, a different approach from that initially proposed by Vanguetaine *et al.* (1983). The latter authors formalised, close to the Frasnian–Famennian boundary in Belgium, two successive *Visbysphaera? fecunda* and *Villosacapsula globosa* biozones. These are defined by acritarch assemblages, but take account also of the appearance of new taxa and the abundance of certain others known from older deposits, including the eponymous species of both biozones. The beginning of the *V. globosa* Biozone, accepted here as coinciding with the appearance of *Visbysphaera? occultata*, permits the recognition of late Frasnian deposits present slightly below the internationally fixed boundary. The interval considered (Fig. 9) ranges from the Late *Palmatolepis rhenana* to the Middle *P. triangularis* Biozones. No information is available for acritarchs from the candidate stratotype of the basal

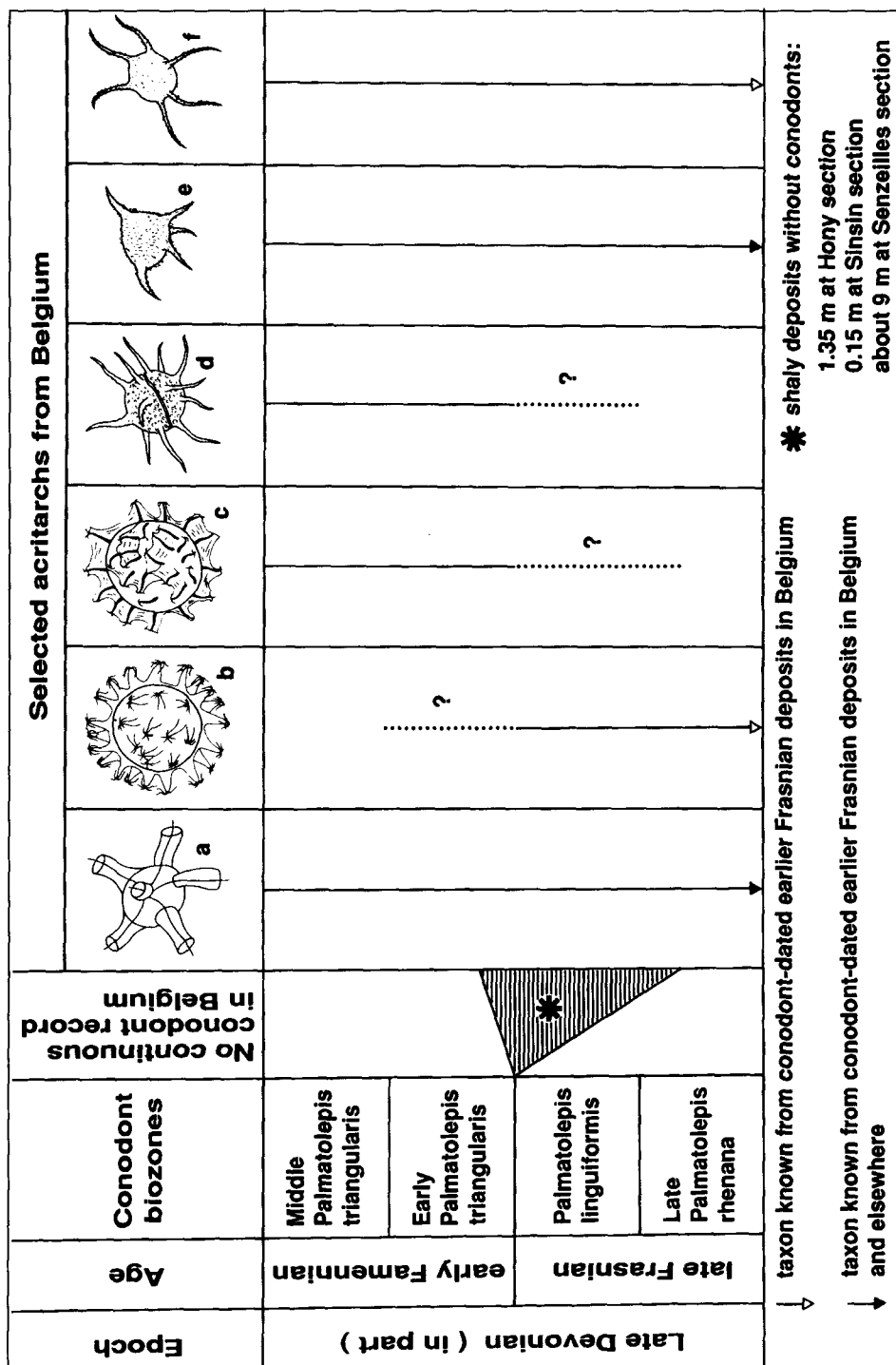


Fig. 9. Selected Frasnian-Famennian acritarchs from Belgium (not to scale). a, *Daillyidium pentaster*; b, *Visbysphaera? fecunda*; c, *V. ? occultata*; d, *Ephelopalla media*; e, *Villosacapsula ceratoides*; f, *V. globosa*.

Famennian, located at Coumiac, in the Montagne Noire, southern France (Becker *et al.*, 1989). The same is true for other outcrops considered important by the SDS and reviewed by Sandberg *et al.* (1988), apart from those in the Dinant Basin, Belgium. Among the latter, the unfaulted sections at Hony and Sinsin are here discussed. The Frasnian–Famennian boundary is situated between the last bed containing the *Palmatolepis linguiformis* Biozone, and the first bed with the Early *P. triangularis* Biozone. These two beds are separated by a shaly interval, 1.35 and 0.15 m thick at the two sections respectively, from which no conodonts were recorded. In the Dinant Basin, acritarchs considered here come also from the filled-in railway cutting at Senzeilles (Stockmans & Willière, 1974; Vanguetaine *et al.*, 1983), historically important as the base of the Famennian was drawn there by Gosselet (1877, 1888), and adjacent new reference sections (Martin, 1985; pers. obs.). The latter (Bultynck, 1988; Casier, 1992), although less condensed than at Hony and Sinsin, were not considered by the SDS as the highest Frasnian conodont biozone has not been recognized. In addition, the first level there dated as Early *P. triangularis* Biozone is located slightly more than 1 m above the early Famennian macrofaunal renewal recorded by Gosselet and contains orthocone cephalopods and numerous brachiopods. Nevertheless palynological data from the highest Frasnian at Senzeilles permit the successive appearances of two acritarchs to be better documented than at Hony and Sinsin (Vanguetaine *et al.* 1983; Streeel & Vanguetaine, 1989).

The six selected taxa (Fig. 9) are present at Senzeilles. One of them, *Daillydium pentaster*, typifies some twenty taxa whose presence and frequency cannot be used to differentiate between the Frasnian and Famennian in the Dinant Basin. This species, for example, extends from the early Frasnian (Dricot, 1968) near the village of Frasnes to the end of the early Famennian (Martin, 1981) in Famenne, a natural region situated east of the River Meuse, between the Condroz and the Ardenne. In Iowa, USA, *D. pentaster* appears towards the end of the Givetian (Wicander & Wood, in Wicander & Playford, 1985). In the Łagów region, Poland (Górka, 1974) it is present in the upper, but not uppermost, Famennian of the Holy Cross Mountains.

The other five species have a more limited range within the Upper Devonian. Of them, only *Villosacapsula ceratioides* is known elsewhere (Wicander & Playford, 1985), from an accurately dated level in the Early *P. gigas* Biozone of Iowa, USA, which is more or less equated with the early *P. rhenana* Biozone.

In the reference sections at Senzeilles the summit of the Frasnian is represented by almost 9 m of black shales containing, at most, a rare macrofauna. These deposits, often considered to represent the Frasnian–Famennian extinction event, are overlain there by less dark transitional shales. The former and the lower part of the latter, up to the appearance of *V.?* *occultata*, contain relatively rare, badly preserved acritarchs that include especially *Villosacapsula ceratioides*, *V. globosa* and *Visbysphaera?* *fecunda*. The levels at which these three species appear are imprecisely known with reference to the conodont horizons. In Belgium they are situated in the middle part of the Frasnian, below the Late *P. rhenana* Biozone. That of *Villosacapsula ceratioides* was documented in a borehole at Tournai (Stockmans & Willière, 1962a); those of *V. globosa* and of *Visbysphaera?* *fecunda* in an outcrop slightly north of Frasnes (Martin, 1982b). The first two species disappeared in the Lower Famennian above the interval considered here. At Senzeilles *Villosacapsula globosa* is present as high as shales intercalated between the Middle and Late *P. triangularis* Biozones. *V. ceratioides* disappears much later in the

lower Famennian of the Senzeilles region (Martin, 1985), in an interval dated by means of rhynchonellid brachiopods between the *Ptychomaletoechia gonthieri* and *P. omaliusi* biozones. Data are slightly contradictory regarding the upper limit of the range of *Visbysphaera? fecunda*; this is below the Early *P. triangularis* Biozone at Senzeilles. At Hony (Streel & Vanguetaine, 1989) it is situated in shaly deposits which overlie the last bed containing the *Palmatolepis linguiformis* Biozone and which, on sedimentary criteria (Sandberg *et al.*, 1988), are attributed to the latest Frasnian. At Sinsin, following Streel & Vanguetaine's rectification (1989) of the stratigraphic position of samples given by Vanguetaine *et al.* (1983, p. 143), the species is present very slightly above the last bed containing the Early *Palmatolepis triangularis* Biozone as determined by Sandberg *et al.* (1988). It has not been found (Martin, 1985) in lower Famennian strata dated by means of rhynchonellids. The appearances of *Visbysphaera? occultata* and of the succeeding *Ephelopalla media* are also imprecise in terms of conodont zonation. At Senzeilles they are probably older than in the sections at Hony and Sinsin. In the new sections they appear successively in the transitional shales situated below the first Famennian levels with abundant brachiopods and orthocone cephalopods that precede the first level containing the Early *P. triangularis* Biozone as determined by Bultynck (in Casier, 1992, p. 115).

According to Claeys, Casier & Margolis (1992*a*) an asteroid impact responsible for the disappearance of Frasnian faunas would be indicated at Senzeilles by a level with glass microspherules. The latter is, however, of very doubtful value for dating any possible impact as it is found above the Famennian macrofaunal renewal and the first bed containing the Early *P. triangularis* Biozone; neither does it affect the composition of the acritarch assemblages. At Hony, microspherules morphologically and chemically identical with the above are present (Claeys, Casier & Margolis, 1992*b*) below the first bed with the Early *P. triangularis* Biozone, which lacks diagnostic acritarchs (Streel & Vanguetaine, 1989) and is, in any case, older than the horizon at Senzeilles.

To conclude, in the vicinity of the Frasnian–Famennian boundary in the Dinant Basin, the successive appearances of *Visbysphaera? occultata* and of *Ephelopalla media* at the end of the Frasnian precede the extinction of *Visbysphaera? fecunda* at the beginning of the Famennian. If the presence of the latter in or slightly above the Early *P. triangularis* Biozone is not due to reworking, this local observation does not match with the scheme of events proposed by Walliser (1986), according to which the appearance of one or several species follows, on a global scale and after an interval, the relatively rapid extinction of one or several taxa belonging to the same group.

(5) *From latest Devonian to the present*

(i) *Latest Devonian–Carboniferous*

The most important wave of irreversible acritarch extinctions occurred, as noted by Downie (1979), during the late Famennian, between about 365 and 355 Ma BP. Detailed data are particularly sparse and do not establish whether the change was relatively sudden or gradual during this interval. They show, however, that apart from a few regional exceptions, for example in Belgium (Vanguetaine, 1978) and Tibet (Gao, 1986), acritarchs became much less frequent, notably in Ohio (Wicander, 1974), the Algerian Sahara (Jardiné *et al.*, 1974) and Western Australia (Playford, 1976). In addition the latter show always a clear diminution in diversity at both generic and

specific level. The time index acritarchs are particularly poorly documented on a global scale. The taxon that is most morphologically characteristic and whose stratigraphic age is acceptably verified, *Tornacia sarjeantii*, ranges from the beginning of the late Famennian in Belgium (Paproth *et al.*, 1983, pp. 193, 194; Vanguetaine, 1986) and from well before the beginning of the early Famennian in Western Australia (Playford & Dring, 1981). In the Carnarvon Basin it occurs in imprecisely dated deposits. Conodonts indicate probably early Frasnian, though an interval from late Middle Devonian to the beginning of the Late Devonian cannot be excluded. The species is known as late as early Carboniferous but may, as suggested by Vanguetaine (1986), be reworked there.

No new taxa with distinct characteristics have been published for the Carboniferous, about 355 to 290 Ma BP. The absence of renewal in the group is striking, both locally and globally. Assemblages become more and more sporadic and restricted, comprising notably taxa with long stratigraphic range and/or reworked, such as those illustrated from the early Carboniferous of Wales by McNestry (1988) and Davies, McNestry & Waters (1991). In the middle Carboniferous (Westphalian) the featureless shape of polygonal to globular specimens with simple processes has been illustrated particularly from Belgium (Stockmans & Willièrè, 1962*b*) and England (Spode, 1964).

(ii) *Permian–Triassic*

From late Palaeozoic to early Mesozoic, some 290 to 205 Ma BP, Permian and Triassic acritarchs are found in deposits that are imprecisely dated stratigraphically or of different ages at scattered localities worldwide (Jacobson *et al.*, 1982, for references). They may be locally much more numerous than in the Carboniferous but, as first observed by Wall & Downie (1963) for the early Permian in Yorkshire and by Jansonius (1962) for the early Trias in western Canada, they are always simple, show little diversity, and are essentially related to *Michrhystridium* and *Veryhachium*. Nevertheless Sarjeant (1973) estimated that acritarchs from incomplete sequences in the Salt and Surghar ranges of western Pakistan permit recognition of a Permian–Triassic boundary, marked by local frequency fluctuations of taxa that are long-ranging or new, with little variety. On a global scale, in the absence or extreme rarity of dinoflagellates or any other palynological criteria, the exclusive abundance of featureless forms noted above tends to indicate an undifferentiated interval from Permian to middle Trias.

From late Triassic to the end of the Cenozoic, acritarchs are rarely found in large numbers. Their value as chronostratigraphic indices is considered negligible by comparison with the refined resolution permitted, in marine environments, by the dinoflagellates. Studied mostly by means of the light microscope, they represent a group with insignificant diversity and include specimens that are reworked or strongly resemble Palaeozoic taxa.

(iii) *Jurassic–Cretaceous*

Attempts to document exhaustively the spectrum of acritarchs in the Jurassic and Cretaceous (Stancliffe, 1990, Wheeler & Sarjeant, 1990, and Marheinecke, 1992 for references) have proved generally disappointing and show mainly ubiquitous forms. Only Habib & Knapp (1982) have carried out detailed SEM studies of the membrane

ornamentation in small acritarchs. The latter abound in borehole samples from the western North Atlantic dated as early Lower Cretaceous to early Upper Cretaceous by means of dinoflagellates and nanoplankton. Their vesicle is generally from 4 to 10 μm in diameter, and the processes no more than 2 μm long. The great majority of genera and all species are new. The taxa, unknown elsewhere, have enabled their authors to distinguish nine regional acritarch biozones and to refine the time-scale based on dinoflagellates. Comparable results are not yet available elsewhere.

(iv) *Cretaceous–Tertiary boundary*

Following the work of Alvarez *et al.* (1980), the Cretaceous–Tertiary boundary, some 65 Ma BP, has been commonly cited as a classic example of mass extinction linked, rightly or wrongly, to a spectacular cataclysm of extra-terrestrial origin. As shown by Tappan (1982) the data from phytoplankton are highly equivocal. In particular, the dinoflagellate cysts were virtually unaffected. The surviving acritarchs, representatives of a group that had flourished from the early Cambrian almost to the end of the Devonian, contribute nothing to the argument.

(v) *Cenozoic*

Regional correlations are still sometimes based on fluctuations in abundance of Cenozoic acritarchs with rather featureless morphology. The first appearances of some rare taxa are sporadically relevant to the biozonation, as the following selection shows. De Coninck (1991) has established a succession of eleven biozones for the Ypresian Stage of the Paleogene, between about 53 and 45 Ma BP, in the Belgian Basin and adjacent areas. The bases of the first and of the penultimate are each defined by the appearance of an acritarch, respectively *Pseudomasia trinema* and *Paucilobimorpha triradiata*, the remaining nine biozones being founded on dinoflagellates. The level of appearance of *P. triradiata*, widespread in Eocene deposits younger than Ypresian, is both the most recent and the best documented. The species is morphologically very characteristic [Pl. 3 (fig. 5)], with three small lobes which diverge in the same plane from a common centre and have extremities ornamented with spines. In the Neogene, at the beginning of the Miocene in the Norwegian Sea (Manum *et al.*, 1989), a biozone containing mostly dinoflagellates is nevertheless named after an acritarch, *Ascotomocystis granosa*, the appearance of which marks the base of the zone. In the Quaternary, from middle early to late Pleistocene in the Bering Sea and northern North Pacific (Bujak, 1984), the appearance of three relatively ubiquitous acritarch species, with pylome but lacking processes, forms part of the definition of the *Spiniferites frigidus* Biozone, named for a dinoflagellate. In more recent Holocene deposits acritarchs occur only as exceptional curiosities.

VI. SUMMARY

1. Acritarchs are a polyphyletic group of unicellular organisms, essentially marine and fossil, with a very resistant organic membrane; the majority probably represent the cysts of microscopic, extinct eukaryote algae. This review gives a general account for the non-specialist of their characteristics and affinities, but focuses, using selected examples, on their role as biostratigraphic tools for the specialist.

2. Invisible to the naked eye, up to several tens of thousands of acritarchs per gram of rock may be extracted and concentrated from a wide variety of sediments, especially argillaceous or even calcareous, but preferably fine-grained, unweathered and only slightly recrystallized or metamorphosed.

3. Always hollow and without unequivocal intracellular structures, acritarchs are extremely variable in: overall size, from a few to several hundred μm , with numerous divergent morphological modifications from a basic spherical form; the type and development of ornamentation; the number of cellular walls; and the method of opening, attributed to excystment. Acritarchs are classified according to criteria that are relatively simple compared with the modern demands of phycologists. For convenience they are treated under the International Code of Botanical Nomenclature, recognizing the existence of form genera of uncertain position. The lack of a comprehensive taxonomic framework is not surprising, given the number and variety of unclassifiable microorganisms resistant to HF that may be included in the acritarchs.

4. The sporopollenin-like wall of acritarchs, like the sporopollenin of modern plants, is chemically very inert except to oxidation, carbonization and bacterial or fungal activity. Of poorly-known composition but very probably including highly polymerized polyterpenes, it may form an abundant component of Palaeozoic kerogen, a potential source of hydrocarbons. The codification of colour changes and preservation in selected acritarchs may enable the optical evaluation of palaeotemperatures lower than about 120–150 °C and of the degree of maturity of possible oils.

5. The first known acritarchs *sensu stricto*, although discovered in 1862, were designated as such in 1963, after having been given a variety of names reflecting mainly assessments of their biological affinities. In spite of some attempts to abandon it, the name acritarch is still the most correct as it is the least ambiguous for designating the great majority of examples.

6. The reclassifying of acritarchs among microorganisms of known systematic position remains speculative or tentative. It is possible that many acritarchs represent cysts of extinct dinoflagellates, without archaeopyle or indication of a stable tabulation. Laboratory culture of *Pterosperma* has shown that *Cymatiosphaera* and *Pterospermella* have to be considered not as acritarchs but as phycoma of prasinophytes. The ultrastructure of the wall in *Tasmanites* is similar to that of *Pachysphaera*, another recent prasinophyte. Comparisons with euglenoids or spore-like bodies of the first terrestrial plants are indirect and that with eggs of recent crustaceans remains fortuitous.

7. The composition of live acritarch assemblages is most often heavily biased in taphocoenosis. In fact, because of their very small size and low density, these microfossils are frequently found reworked in strata younger than those in which they were originally deposited. If their distributions are sufficiently documented, they can be useful as provenance indicators in palaeogeographic reconstructions.

8. Acritarchs' mode of life is thought to be best compared with that of planktonic photosynthetic algae. General schemes seeking to explain variations in their abundance and distribution in deposits formed during the distant geological past are based especially on extrapolations from complex combinations of factors that govern the distribution of modern marine phytoplankton.

9. With a worldwide geographic distribution and a record only partly influenced by

facies control, the acritarchs exhibit, geologically speaking, an extraordinarily long life span, from the Mesoproterozoic to the present day. In spite of the examples of reworking, rarely objectively verifiable, and the still relatively small number of detailed data with reliable independent age control, it is known that acritarchs, among a great number of ubiquitous forms, include time index taxa whose levels of appearance permit the calibration of very remote geological time and the establishment of regional or global correlations. These biostratigraphic indices, certainly present in the Neoproterozoic but still little known, are best demonstrated from around the beginning of the Cambrian to slightly before the end of the Upper Devonian, a time of maximum abundance and diversity for the group.

At the beginning of the Early Cambrian in the East European Platform, and probably slightly above the international systemic boundary, drawn at the appearance of the ichnofossil *Phycodes pedum* in eastern Newfoundland, the acritarchs display a radiation of original diversity which occurs at three levels and contrasts with the worldwide impoverished sphaeromorph assemblages of the latest subjacent Neoproterozoic. The first level is marked especially by the appearance of *Annulum squameum*, the second by the diversification of *Comasphaeridium*, and the third, which is the clearest and most geographically widespread, by the appearance of *Skiagia orbicularis*, *S. ornata* and *S. scottica*, which coincides approximately with that of the trilobites.

The Cambrian–Ordovician boundary is not yet agreed internationally but should be near the appearance of the *Cordylodus lindstromi* conodont Biozone, slightly below the first occurrence of nematophorous planktonic graptolites. *Corollasphaeridium wilcoxianum* is the index acritarch whose appearance is closest to, and slightly below, this boundary, in the upper part of the *Cordylodus proavus* Biozone. The species enters at this level in the north Sino-Korean Platform (Jilin province) and northern Laurentia (Alberta). It has not been recorded in Baltica, Avalonia and Gondwana, where the acritarch assemblages are better documented, more varied and different on the whole from those of northeastern China and western Canada. With reservations, it may be that in marine deposits associated with these three palaeocontinents, the lower limit of the range of *Acanthodiacrodium angustum* is located within the *Cordylodus proavus* Biozone.

In the Late Devonian, the Frasnian–Famennian boundary is fixed internationally by means of conodonts, at the base of the Early *Palmatolepis triangularis* Biozone, which succeeds the *Palmatolepis linguiformis* Biozone. Regionally, in the Dinant Basin, Belgium, no index acritarch is known to appear at the base of the Lower Famennian. On the other hand, at Senzeilles the appearances of *Visbysphaera? occulta* and of *Ephelopalla media* occur successively at the end of the Frasnian in deposits undated by means of conodonts but attributable to the end of the late *Palmatolepis zhenana* Biozone and to the *P. linguiformis* Biozone.

In the course of the upper Famennian, and from the end of the Late Devonian onwards, known assemblages are essentially sporadic, unvaried and of reduced or local stratigraphic value. The last species that is autochthonous, morphologically unmistakable and of worldwide distribution appears in the middle Neogene (Ypresian).

VII. ACKNOWLEDGEMENTS

I thank particularly William T. Dean, who translated and critically read the French manuscript. The text was also reviewed in its entirety by Pierre Bultynck and Charles Downie, and in part by Jan de Coninck, who kindly permitted me to use some of his unpublished data, and Jean Rommelaere.

At the Institut royal des Sciences naturelles de Belgique I am indebted to Hugo De Potter for treatment of the palynological samples; to Julien Cillis for SEM manipulation; to Wilfried Miseur for photographic prints; and last, but not least, to Harry Van Paesschen, who made the drawings and text-figures.

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IX. APPENDIX

ALPHABETICAL LIST OF CITED ACRITARCHS AND FOSSIL PRASINOPHYTE TAXA

[References listed by Fensome *et al.* (1990) are not included in the present bibliography unless they are cited in the text. References not listed by these authors are marked with an asterisk (*) and included in the References. Names and references within quotes indicate combinations not accepted by Fensome *et al.* (1990) but used here.]

- Acanthodiacrodium angustum* (Downie) Combaz, 1968
- Actinotodissus achrasi* (Martin) Yin, in Chen *et al.*, 1986
- Actinotodissus* sp. A in Martin 1992*
- '*Ammonidium exoticum* (Deunff) Lister, 1970'
- Annulum squamaceum* (Volkova) Martin in Martin & Dean, 1983
- Arbusculidium destombesii* Deunff, 1968
- Arbusculidium frondiferum* Deunff, 1968
- Arbusculidium ornatum* (Combaz) Fensome *et al.*, 1990
- Arbusculidium ramusculosum* (Combaz) Fensome *et al.*, 1990
- Archaeodiscina umbonolata* Volkova, 1968
- Aryballomorpha* Martin & Yin, 1988
- Aryballomorpha grootaertii* Martin, 1984 emend. Martin & Yin, 1988
- Ascostomocystis granosa* Matsuoka, 1983
- Asketopalla* Loeblich & Tappan, 1969
- Asteridium* Moczydlowska, 1991*
- Asteridium tornatum* Moczydlowska, 1991*
- Athabascaella* Martin, 1984 emend. Martin & Yin, 1988
- Athabascaella playfordii* Martin, 1984 emend. Martin & Yin, 1988
- Baltisphaeridium crinitum* Martin in Dean & Martin, 1978
- '*Baltisphaeridium spinigerum* Górka, 1969'
- Baltinella* Shepeleva, 1962
- Buedingiisphaeridium tremadocum* Rasul, 1979
- Comasphaeridium* Staplin, Jansonius & Pocock, 1965
- Comasphaeridium strigosum* (Jankauskas) Downie, 1982
- Comasphaeridium velvetum* Moczydlowska, 1988
- Corollasphaeridium* Martin in Dean & Martin, 1982 emend. Yin, in Chen *et al.*, 1986
- Corollasphaeridium wilcoxianum* Martin in Martin & Dean, 1982 emend. Martin, 1992*
- Coryphidium* Vavrdová, 1972
- Coryphidium bohemicum* Vavrdová, 1972
- '*Cristallinium* Vanguetstaine, 1978'
- '*Cristallinium cambriense* (Slavíková) Vanguetstaine, 1978'
- Cristallinium dentatum* (Vavrdová) Fensome *et al.*, 1990
- '*Cristallinium randomense* Martin in Martin & Dean, 1981 emend. Martin, in Martin & Dean, 1988'
- Cymatiogalea* Deunff 1961 emend. Deunff, 1964
- Cymatiogalea cuvillieri* Deunff, 1961
- Cymatiogalea velifera* (Downie) Martin, 1969
- Cymatisphaera* O. Wetzel, 1933 ex Deflandre, 1954
- Cymbosphaeridium pilar* (Cramer) Lister, 1970
- Daillydium pentaster* (Staplin) emend. Playford in Playford & Dring, 1981
- Dasydiacrodium glabrum* Combaz, 1968
- Dasydiacrodium obsonum* Martin in Martin & Dean, 1988
- Dichotisphaera* Turner, 1984
- Diexallophasis* Loeblich, 1970
- Diexallophasis remota* (Deunff) emend. Playford, 1977
- '*Dilatitsphaera wimani* (Eisenack) Le Hérissé, 1990'
- Dilatitsphaera williereae* (Martin) Lister, 1970 emend. Martin, 1990*
- Duvernaysphaera* Staplin, 1961 emend. Deunff, 1964
- Elektoriskos williereae* (Deflandre & Deflandre-Rigaud) Vanguetstaine, 1979 emend. Martin, 1990*

APPENDIX—cont.

- Eliasum llaniscum* Fombella, 1977
Ephelopalla media (Stockmans & Willière) Martin, 1985*
Estiastra magna Eisenack, 1959
 'Eupoikilofusa aff. *E. ampulliformis* sensu Duffield & Legault, 1981 in Martin, 1988'
Favosphaeridium Timofeev, 1959 ex Timofeev, 1966
Fimbriaglomerella membranacea (Kirjanov) Moczydłowska & Vidal, 1988
Frankea sartbernardensis (Martin) Colbath, 1986
Geron guerillerus Cramer, 1966 ex Cramer, 1969
Goniosphaeridium Eisenack, 1969 emend. Turner, 1984
Heliosphaeridium notatum (Volkova) Moczydłowska, 1991*
 'Kildinella Shepeleva & Timofeev, 1963 ex Timofeev, 1966'
Ladogella Golub & Volkova, 1985 emend. Di Milia, Ribecai & Tongiorgi, 1989*
Leiofusa cf. *L. gravida* Pittau, 1985
Leiosphaeridia Eisenack 1958, emend. Turner, 1984
Micrhystridium Deflandre 1937 emend. Lister, 1970
 'Moyeria Thusu, 1973'
Multiplicisphaeridium abnorme Yin in Chen *et al.*, 1986
Neoveryhachium carminae Cramer, 1970
Octoedryxium Rudavskaya, 1973
Onondagaella Cramer, 1966 emend. Playford, 1977
Ooidium rossicum Timofeev, 1957
Palacanthus ledanoisii (Deunff) Playford, 1977
Paucilobimorpha triradiata De Coninck, 1986
Podolina Herman in Timofeev, Herman & Mikhailova, 1976
Polyancistrodorus Loeblich & Tappan, 1969
Polyedryxium Deunff, 1954 emend. Deunff, 1971
Psenotopus condrocheus Tappan & Loeblich, 1971
Pseudomasia trinema De Coninck, 1969
Pterospermella Eisenack, 1972
Pterospermella eruptio Martin, 1985
Pterospermopsisimorpha Timofeev, 1966
Pterospermopsis W. Wetzel, 1952 emend. Sarjeant, 1984
Puteoscortum williereae Martin, 1981
Retisphaeridium howellii Martin in Martin & Dean, 1983
Revinotesta Vanguetaine, 1974
Rhopaliophora Tappan & Loeblich, 1971
Rhopaliophora pilata (Combaz & Peniguel) emend. Playford & Martin, 1984
Saharidia Combaz, 1968
Skiagia Downie, 1982
Skiagia compressa (Volkova) Downie, 1982
Skiagia orbicularis (Volkova) Downie, 1982
Skiagia ornata (Volkova) Downie, 1982
Skiagia scottica Downie, 1982
Stelliferidium Deunff, Górka & Rauscher, 1974
Striatotheca Burman, 1970
Striatotheca principalis Burman, 1970
Synsphaeridium sp. 1 sensu Cramer & Diez, 1972b*
Tasmanites Newton, 1875
Timofeevia Vanguetaine, 1978
Timofeevia lancarae (Cramer & Diez de Cramer) Vanguetaine, 1978
Tornacia sarjeantii Stockmans & Willière, 1966
Trachysphaeridium Timofeev, 1959 ex Timofeev, 1966
Trunculumarium revinium (Vanguetaine) Loeblich & Tappan, 1976
Tunisphaeridium eisenackii Loeblich & Tappan, 1978
Tylopalla deerlijkiana (Martin) Martin, 1978*
Umbellasphaeridium saharicum Jardiné *et al.*, 1972
Vandalosphaeridium Vidal, 1981
 'Veryhachium Deunff, 1954 ex Downie, 1959'
Veryhachium cf. *V. downiei* Stockmans & Willière, 1962a
Veryhachium minutum Downie, 1958
Villosacapsula ceratioides (Stockmans & Willière) Loeblich & Tappan, 1976
Villosacapsula globosa Vanguetaine *et al.*, 1983
 'Visbysphaera Lister, 1970 emend. Le Hérisse, 1989'
Visbysphaera? fecunda Vanguetaine *et al.*, 1983
Visbysphaera impetuosa Martin, 1985
Visbysphaera? oculata Martin, 1985
Volkovia Downie, 1982
Vulcanisphaera africana Deunff, 1961
Vulcanisphaera imparilis Rasul, 1976
Vulcanisphaera turbata Martin in Martin & Dean, 1981
Winwaloeusia ranulaeforma Martin, 1985

X. ADDENDUM

A monograph by Zang & Walter (1992) extends the coverage in their 1989 paper (p. 509 herein) and concerns particularly the Late Proterozoic topic reviewed in this article. They illustrate, notably, the relatively large variability of acritarchs in the Amadeus Basin, southern part of the Northern Territory, central Australia. The great majority of these acritarchs come from subsurface Neoproterozoic samples, and all were observed using palynological preparations. The oldest assemblages are from the Bitter