Spore-Like Bodies in Some Early Paleozoic Acritarchs: Clues to Chlorococcalean Affinities

Authors: Kaźmierczak, Józef, and Kremer, Barbara

Spore-like bodies in some early Paleozoic acritarchs: Clues to chlorococcalean affinities

JÓZEF KAŹMIERCZAK and BARBARA KREMER

We present discoveries of internal bodies in problematic Silurian and Devonian organic-walled microfossils classified traditionally as polygonomorph, acanthomorph, sphaeromorph, and herkomorph acritarchs. These bodies are comparable with reproductive structures (auto- and/or aplanospores) of modern unicellular green algae (Chlorococcales). Our findings suggest that many of these microfossils may represent asexually reproducing (sporulating) vegetative cells of chlorococcalean algae. The presence of spore-like bodies in the studied acritarchs supports earlier suggestions, based on ultrastructural and biomarker studies, that some acritarchs can be affined with green algae.

Józef Kaźmierczak [jkaz@twarda.pan.pl] and Barbara Kremer [kremer@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

Introduction

Acritarchs represent an informal (i.e., non-Linnean) taxonomic category grouping organic microfossils of unclear systematic affiliation (Downie et al. 1963; Downie 1973; Tappan 1980; Martin 1993; Colbath and Grenfell 1995; Servais 1996 ; Strother 1996; Wicander 2002). The term "acritarchs" means in Greek "of uncertain origin" and it was coined in 1963 by Evitt to replace an older "ragbag" term "hystrichosphaeres" (i.e., "spiny spheres") enclosing organic-walled microfossils of unknown biological affinities (for discussion see Tappan 1980: 148).

Although the position of acritarchs in the organic world is still uncertain, many of these microfossils have been attributed to unicellular phytoplankton, mainly to dinoflagellates or green algae (particularly prasinophytes—*inter alia* Jux 1971) (for review and discussion see e.g., Tappan 1980; Martin 1993; Colbath and Grenfell 1995). Other affinities have also been considered as, for instance, cyanobacterial envelopes, alete spores, fungal spores, cysts of macroalgae, pellicles of euglenids, heterotrophic protists or even egg-cases of copepod-like crustaceans (for review see e.g., Martin 1993; Colbath and Grenfell 1995; Servais 1996; Butterfield 2005). Opinions prevail that microfossils classified as acritarchs represent a highly polyphyletic assemblage of microorganisms (Servais 1996). Recent ultrastructural (SEM, TEM), molecular (biomarkers), and micro-chemical (combined micro-Fourier transform infrared spectroscopy and micro-Raman spectroscopy) studies have suggested dinoflagellate and chlorophycean affinity for some Neoproterozoic and Early Cambrian acritarchs (Arouri et al. 1999, 2000; Talyzina and Moczydłowska 2000; Talyzina et al. 2000; Marshall

et al. 2005; Javaux and Marshall 2006; Willman and Moczydłowska 2007). One of the four structurally distinct types of vesicle walls recognized in Early Cambrian acritarchs by Talyzina and Moczydłowska (2000) was a multilayered wall of a common spherical acritarch *Leiosphaeridia* sp. In these authors opinion, its outer laminated layer resembling the trilaminar sheath ultrastructure typical of many extant green algae suggests chlorococcalean affiliation. Multilayered wall ultrastructure has also been observed, and considered as indicative for chlorophycean affinity, in much older acritarchs from the Neoproterozoic (Ediacaran) deposits of the Officer Basin in Australia (Willman 2009; Willman and Moczydłowska 2007), the c. 1.5–1.4 b.y. old Mesoproterozoic Roper Group of Australia, and the broadly coeval Ruyang Group of China (Javaux et al. 2004). It appears, in light of all these recent studies using micro-scale analytical techniques, that chlorophyte and dinoflagellate affiliation of many acritarchs can be considered as most probable.

The purpose of the present paper is to demonstrate that some early Paleozoic microfossils ascribed to acritarchs may represent not, as commonly inferred, cysts or other resting stages of the above mentioned groups of planktonic microalgae, but remnants of vegetative algal cells, as has been suggested for some much older enigmatic organic-walled microfossils ascribed also to acritarchs (e.g., Butterfield 2005; Javaux and Marshal 2006; Javaux et al. 2003). We hope that the new data presented below may help to clarify the biological affinities of some representatives of the main acritarch divisions as defined recently by Dorning (2004).

Institutional abbreviation.—ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Acta Palaeontol. Pol. 54 (3): 541–551, 2009

DOI: 10.4202/app.2009.0022

Material and methods

The acritarch material presented in this report derives from early Paleozoic marine deposits of Poland and Germany. Most of the studied acritarch specimens come from Early Silurian (Llandoverian) black radiolarian cherts and siliceous shales cropping out in the Holy Cross Mountains (central Poland) (Kremer 2001; Kremer and Kaźmierczak 2005) and Bardzkie Mountains (Sudetes region, southwestern Poland) (Kremer and Kaźmierczak 2005). A part of the examined Silurian acritarchs stems from the Llandoverian black radiolarian cherts and siliceous shales of southern Germany (Frankenwald) and has been collected in the quarry "Steinbruch WNW Döbra" near Schwarzenbach Am Wald (for geographic and stratigraphic details see Stein 1965; Horstig and Stettner 1976). The remaining specimens derive from a core of Late Devonian (Frasnian) limestones drilled by a deep borehole Sosnowiec IG-1 (Upper Silesia, southern Poland). These are early post mortem calcified acritarchs (Kaźmierczak and Kremer 2005) previously for a long time described as "calcispheres". The Silurian cherts and shales underwent thermal alteration of various intensity making the biomarker signatures no longer recognizable (Bauersachs et al. 2009). The remnants of acritarch organic walls in the Devonian limestones are preserved as irregular loose net of carbonaceous (kerogenous) flakes (Kaźmierczak and Kremer 2005). They cannot be extracted in an amount satisfactory for biomarker analysis. A variety of preparatory and imaging techniques has been applied to these rocks in the present study. Standard palynological technique was used (HF-dissolution) for recovery of acritarchs from the cherty samples which were subsequently examined with the use of optical transmitted light microscope on cover-glass preparations (Fig. 1). Observation of acritarchs in petrographic thin-sections—a method rarely used in routine acritarch studies—has proved to be particularly effective in recovery of the internal structures in acritarchs derived both from calcareous (Fig. 2) and siliceous rocks (Figs. 3A, B, 4, 5B, D, 6A, B). Slight etching with HF of polished platelets of acritarch-bearing Silurian cherts was also effective for the 3-D Philips XL-20 scanning electron microscope (SEM) imaging of acritarch structural details (Fig. 5A, C, E, F). SEM at 25 kV voltage was used to examine samples of air-dried etched surfaces sputtered with a 10 to 15 nm thick layer of platinum or carbon.

Raman mapping and spectra (Fig. 6C–G) were done using a confocal microscope alpha300 R (www.witec.de; WITec, Jungingen, Germany) with a piezo scan stage (100 × 100 × 20 µm, PI, Germany). The system is equipped with a 100× microscope objective for measuring in air with a working distance of 0.26 mm and a numerical aperture NA = 0.90 (Nikon, Düsseldorf, Germany). The depth of focus was about 1 µm for spectra, and 4 and 5 µm for mapping. Raman spectra were collected from individual carbonaceous grains on polished rock plates and petrographic thin
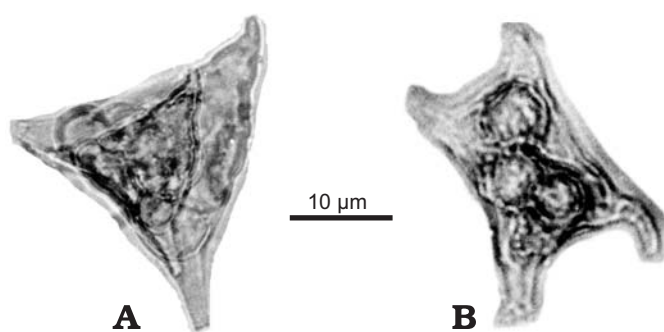

Fig. 1. Examples of early Silurian (Llandoverian) polygonomorph and acanthomorph acritarchs with internal structures resembling spores (auto- and aplanospores) of modern unicellular green algae. **A**. *Veryhachium* specimen with well-visible internal body displaying shape similar to the mother cell (autospore); ZPAL Ak. 2/Zal01. **B**. *Neoveryhachium*-like specimen enclosing spheroid bodies reminiscent of aplanospores; ZPAL Ak. 2/Zal02. Both from Zalesie Nowe (Holy Cross Mountains, central Poland); residuum of HF-dissolved black radiolarian cherts. Transmitted light photomicrographs.

sections under magnification for 100 s. For each sample several spectra were collected. The measurements were performed by focusing the laser beam on the organic matter (OM) beneath the surface.

Observations

We report novel observations of internal bodies in acritarch taxa which, according to a classification proposed recently by the Acritarch Classification Working Group of the International Commission on Palaeozoic Microflora (Dorning 2004), can be attributed to polygonomorph, acanthomorph, sphaeromorph, and herkomorph subgroups. Chemical maceration of early Silurian cherts (Fig. 1) and thin-sections of late Devonian calcispheric limestones (Fig. 2) have revealed internal bodies in representatives of such common polygonomorph and acanthomorph acritarch form-genera as *Veryhachium*, *Neoveryhachium*, and *Baltisphaeridium*. The internal bodies in these forms occur either as groups composed of several spherical or subspherical structures filling sometimes entirely the vesicle (Figs. 1B, 2A) or as large, often singular structures displaying shapes more or less similar to the acritarchs enclosing them (Figs. 1A, 2B–D, 4A). In thin-sections of early Silurian cherts spherical internal bodies, two to eight in number, have been identified in representatives of sphaeromorph acritarchs classified to the common form-genus *Leiosphaeridia* (Fig. 3A, B). These internal bodies are larger where only two of them are present (Fig. 3A), but significantly smaller where their number is higher (Fig. 3B). Similar spherical and subspherical internal bodies, between one to eight and more in number, have been found in forms classified to herkomorph and acanthomorph acritarchs and those attributed to prasinophytes (as members of the form-genera *Cymatiosphaera* and *Dictyotidium*). We studied them in early Silurian cherts in petrographic thin-sections (Figs. 4A–D, F–I, 5B, D, 6A, B) and in SEM images of HF-etched platelets (Fig. 5A, C, E, F).
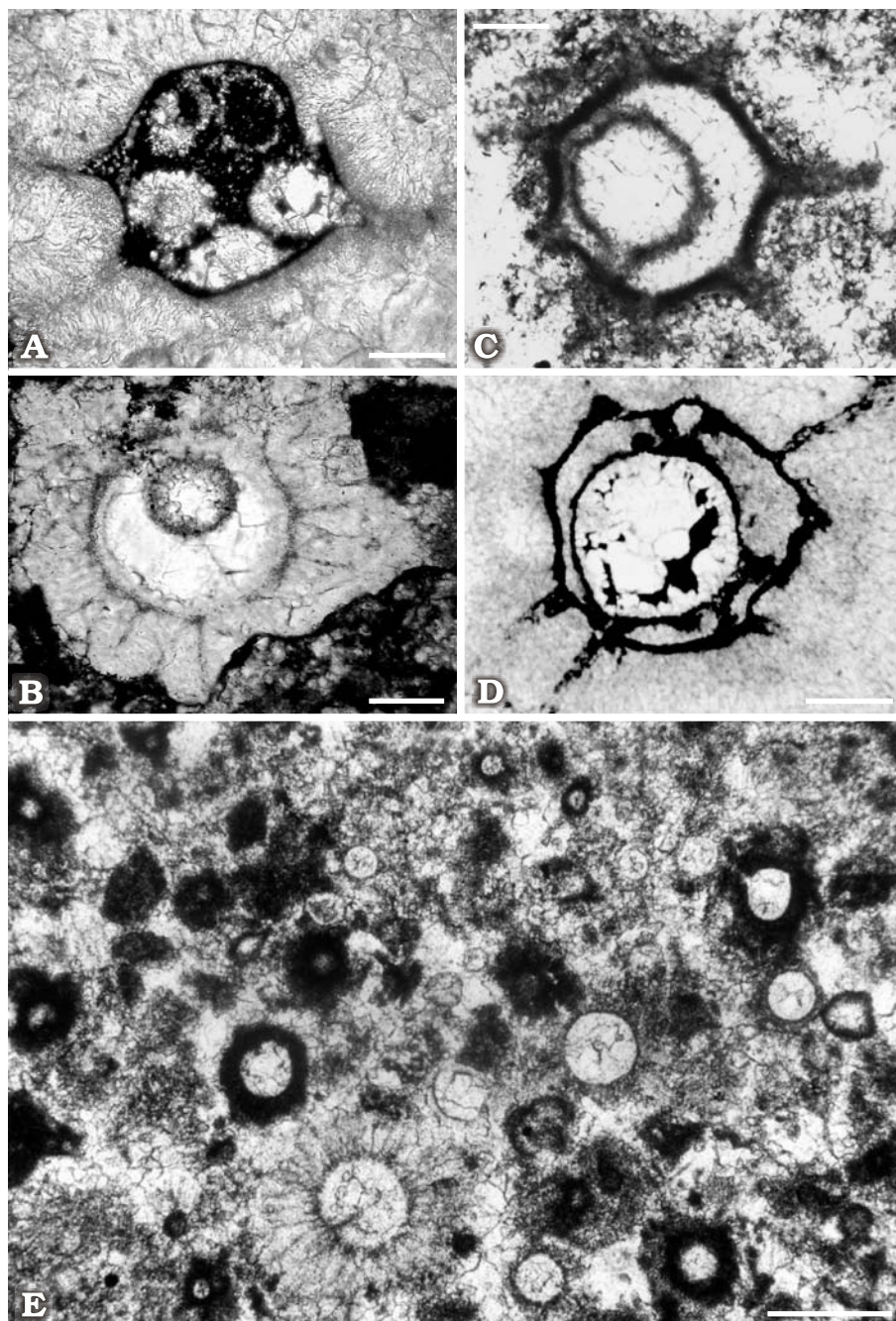
Fig. 2. Cross sections of late Devonian (Frasnian) early post mortem calcified acritarchs enclosing internal bodies comparable with spores (auto- and aplanospores) of modern unicellular green algae. All from late Devonian (Frasnian) calcispheric limestones, Sosnowiec IG-1 borehole, core depth 2389–2395 m (Upper Silesia, southern Poland). **A**. Pyritized acanthomorph (*Baltisphaeridium*-like) acritarch with internal structures resembling aplanospores. ZPAL Ak. 2/Sos1-70f. **B–D**. *Baltisphaeridium*-like acritarchs with singular acanthomorph internal bodies (autospores); noteworthy is the varying size of the internal bodies which in (C) is almost filling the vesicle volume. ZPAL Ak. 2/Sos1-17 (**B**), ZPAL Ak. 2/Sos1-70g (**C**), ZPAL Ak. 2/Sos1-60l (**D**). **E**. Photomicrograph of petrographic thin-section of the acritarch-bearing limestone to show the frequency of acritarchs in a cut-plane 800×450 µm. ZPAL Ak. 2/Sos1-50h. All transmitted light photomicrographs of petrographic thin-sections. Scale bars: A–D 10 µm; E 100 µm.

Raman spectra of kerogen carbon distribution have been obtained from walls of some of such mineral spheroids (Fig. 6C–G). They clearly indicate the presence of moderately altered carbonaceous matter almost identical to that from the acritarch wall.

Comparison and discussion

Our study shows that the internal bodies of the examined acritarchs are comparable with asexual reproductive structures (spores) occurring in many unicellular green algae (Chlorococcales) (e.g., Ettl and Komárek 1982; Komárek and Fott 1983; Ettl 1988a, b; Sluiman et al. 1989) and, consequently, acritarchs enclosing such structures can be classified to this group of microalgae. The only other group of extant unicellular microalgae approaching morphologically chlorococcaleans, and asexually reproducing also by sporulation, are xanthophytes (yellow-green algae). However, in distinction to chlorococcaleans their cell wall is composed of easily degradable pectin, never supported by sporopollenin, often containing silica, and typically formed of two overlapping halves (e.g., Ettl 1980; Hibberd 1990).

In Chlorococcales two basic modes of asexual reproduction are known. The first is the process of cell division (known also as cytotomy) where one cell divides into two
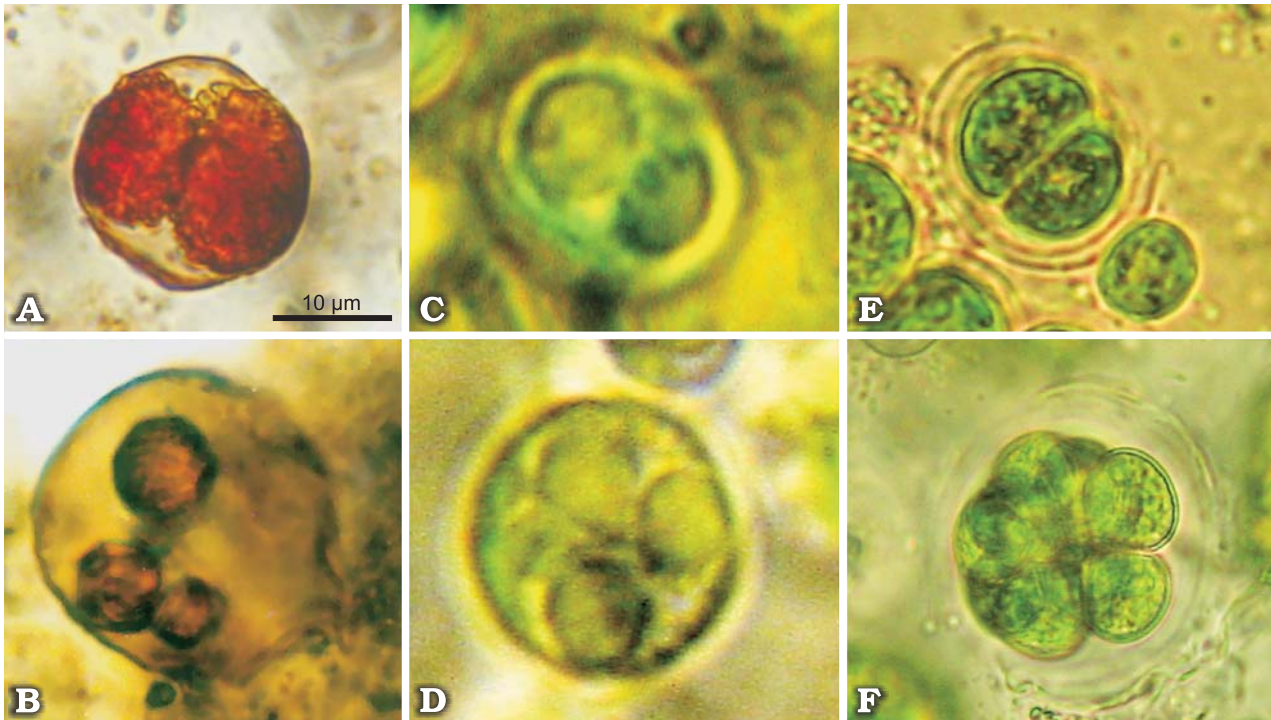
Fig. 3. Comparison of early Silurian (Llandoverian) sphaeromorph acritarchs enclosing spherical structures resembling spores (autospores and/or aplanospores) with modern unicellular green algae and capsular cyanobacteria. **A**, **B**. Petrographic thin-sections of early Silurian black radiolarian cherts. Locality Zalesie Nowe (Holy Cross Mountains, central Poland). **A**. *Leiosphaeridia*-like acritarch with two internal bodies. ZPAL Ak. 2/Zal03. **B**. Larger *Leiosphaeridia*-like specimen with three spherical internal bodies. ZPAL Ak. 2/Zal04. **C**, **D**. Modern chlorococcalean microalgae (*Chlorococcum* sp.) at two stages of spore formation. Living specimens collected from Wilanowski Pond, Warsaw. **E**, **F**. Modern capsular cyanobacteria (*Stanieria* cf. *cyanosphaera*) at various stages of spore (beocyte) formation. Yerseke Culture Collection, The Netherlands. All transmitted light photomicrographs.

parts (daughter cells) by mitosis and subsequent cytokinesis. During further growth the daughter cells use the mother cell wall and divide again. In the second process, which is known as sporulation, cells mostly divide into a number of daughter protoplasts (spore precursors), while the mother cell wall forms the sporangium. The spores of unicellular green algae (Ettl 1988a) are (i) motile (flagellated) and naked spores called zoospores, originating inside parent cell (zoosporangium) and after release transforming into new vegetative cells; (ii) non-motile (non-flagellated) spores called autospores which usually resemble the parent cell in shape and structure (but for exceptions see e.g., Ettl et al. 1967: 726). In this case the spores undergo development within the parent cell (autosporangium) and develop traits of the parent cell before release (e.g., autospores in various species of the modern genus *Tetraedron*—see Fritsch 1965; Kováčik 1975; Hindák 1980) and (iii) non-motile spores called aplanospores which develop into new vegetative cells either inside the parent cell (aplanosporangium) or after liberation from them. In distinction to autospores, aplanospores do not display morphological similarity to parent cells and are usually spherical or subspherical in shape. They can be defined as a kind of transitional stages between zoospores and autospores. Between one and several auto- or aplanospores can be produced by successive or simultaneous divisions of mother cell protoplast (Ettl 1988a, b). Typically, four or eight autospores are produced by the asexually reproducing cells;

two, 16 or 32 autospores occur more rarely and 64 exceptionally; however, the number of aplanospores can be higher (Komárek and Fott 1983; Tschermak-Woess 1989). Auto- and/or aplanospores in one sporangium are equal in size and shape as a rule but deviations caused by asymmetrical protoplast division have been observed (e.g., Hanagata et al. 1996; Huss et al. 2002), as well as deformations due to tight packing of spores before liberation (Ettl et al. 1967). While unicellular green algae reproduce both in a sexual and asexual manner, the latter mode is occurring much more frequently (Ettl 1988a; Sluiman et al. 1989).

In light of the above information, the internal bodies in the acritarch shown in Figs. 1A, 2B–D, and 6A can be attributed to autospores, whereas those illustrated in other figures to aplanospores. If the internal structure shown in Fig. 1A does not wake doubts as a potential autospore, then those in Fig. 1B can inflict impression of structures formed as a result of post mortem shrinkage of the delicate vesicle wall. Such a possibility can, however, be easily dismissed by the almost ideally spherical shape and similar sizes of the internal bodies, and, particularly, by their double membranous structure making them essentially similar to spores described from organic thalli of uniquely preserved Ordovician siphonalean green algae (Kozłowski and Kaźmierczak 1968a, b). The attribution of the spherical internal bodies in the spherical *Leiosphaeridia* (Fig. 3A, B) is less certain because they may equally represent auto- or aplanospores. Indeed, similar diffi-
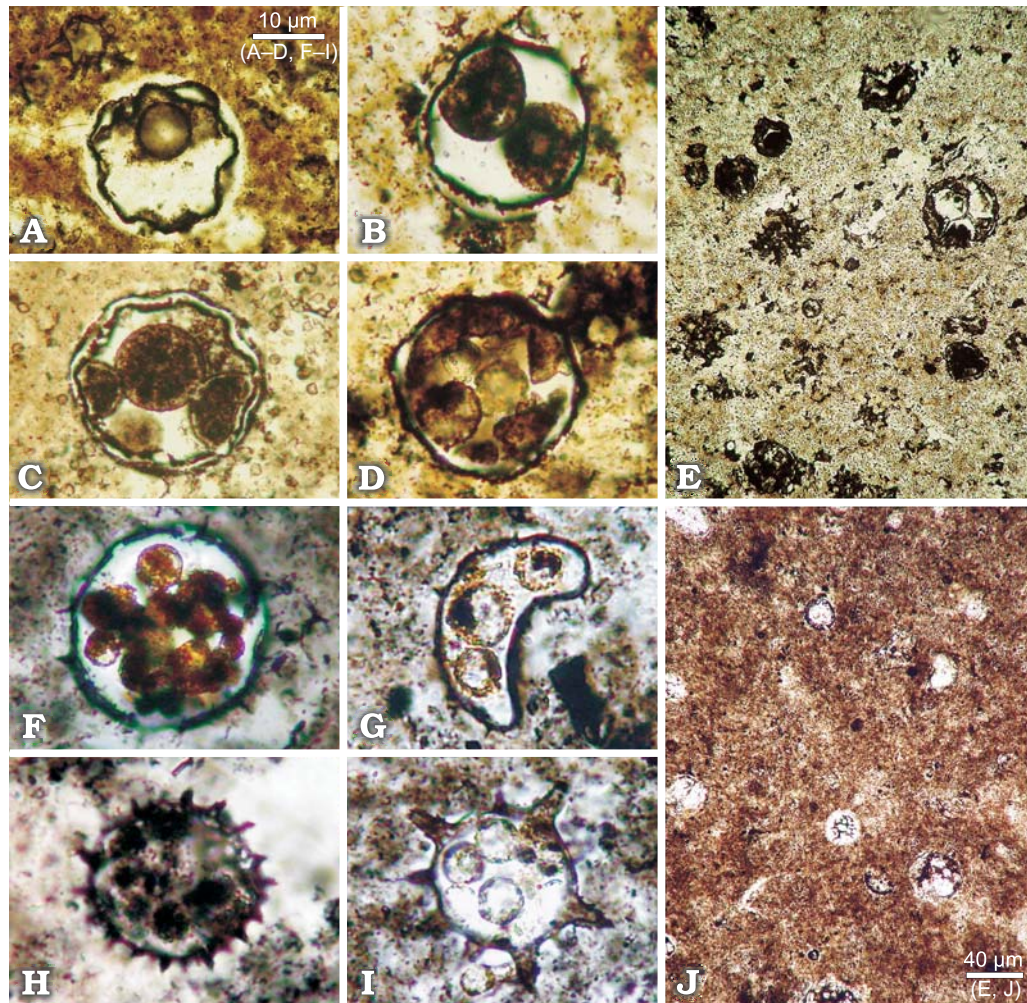
Fig. 4. Transmitted light micrographs of cross-sections of early Silurian (Llandoverian) acritarchs enclosing internal bodies comparable with spores of modern unicellular green algae. **A–D**. Examples of *Cymatiosphaera*-like acritarchs enclosing aplanospore-like bodies: singular, ZPAL Ak. 2/Lup-1802 (**A**); two, ZPAL Ak. 2/Lup-2934 (**B**); four, ZPAL Ak. 2/Lup-2939 (**C**); and eight, ZPAL Ak. 2/Lup-2928 (**D**). **E**. Photomicrograph of petrogrographic thin-section of the acritarch-bearing black radiolarian chert to show the frequency of acritarchs in a cut plane 250×350 µm; ZPAL Ak. 2/TS.Lup-2928. A–E from early Silurian (Llandoverian) black radiolarian cherts; locality Łupianka Hill near Żdanów village, Bardzkie Mountains, southwestern Poland. **F–I**. Examples of spherical and kidney-shaped spinose (*Baltisphaeridium*-like) acritarchs with varying number of spore-like bodies. ZPAL Ak. 2/Döbra04 (**F**), ZPAL Ak. 2/Döbra05 (**G**), ZPAL Ak. 2/Döbra05 (**H**), ZPAL Ak. 2/Döbra06 (**I**). **J**. Photomicrograph of petrogrographic thin-section of the acritarch-bearing black radiolarian chert to show the frequency of acritarchs in a cut plane 250×350 µm; ZPAL Ak. 2/TSDöbra01. F–J from early Silurian (Llandoverian) siliceous shales exposed in Quarry WNW Döbra, Frankenwald, Germany.

culties are met in assignment of spherical spores occurring in modern spherical unicellular green algae, for instance in representatives of the common genus *Chlorococcum* (Fig. 3C, D), where their attribution to auto- or aplanospores is practically impossible without knowing the details of cell anatomy and life cycle. In the case of singular, relatively thick-walled internal bodies occupying large volume of the acritarch mother cell (Fig. 5F), it cannot be excluded that they may represent a kind of resting spores (known as hypnospores or hypnoblasts) formed usually during unfavorable environmental conditions from modified zoospores, aplanospores or autospores (Ettl 1988a; Ettl et al. 1967).

The presence of spore-like bodies in representatives of the studied acritarch form-genera does not support opinions that these acritarchs being cysts of dinoflagellates and/or phy-comas of prasinophytes. Cysts of modern dinoflagellates do not produce spores (e.g., Pfiester 1989) and, therefore, our discoveries weaken the existing inferences linking acritarchs with these unicellular microalgae (for review see Martin 1993; Colbath and Grenfell 1995). In addition, neither morphological nor molecular studies have provided sufficient grounds for establishing firm links between acritarchs and dinoflagellates (for discussion see e.g., Fensome et al. 1990; Moldovan et al. 1996; Moldovan and Talyzina 1998; Versteegh and Blokker 2004; de Leeuw et al. 2006). Similarly, the aplanospore-like bodies occurring in the studied specimens of *Leiosphaeridia, Cymatiosphaera*, and *Dictyotidium* (Figs. 3A, B, 4A–D, 5B, D) contradict opinions linking these fossils with phycomas of prasinophytes (for review see Martin 1993). Phycomas can photo-assimilate and divide their protoplasts but occurrence
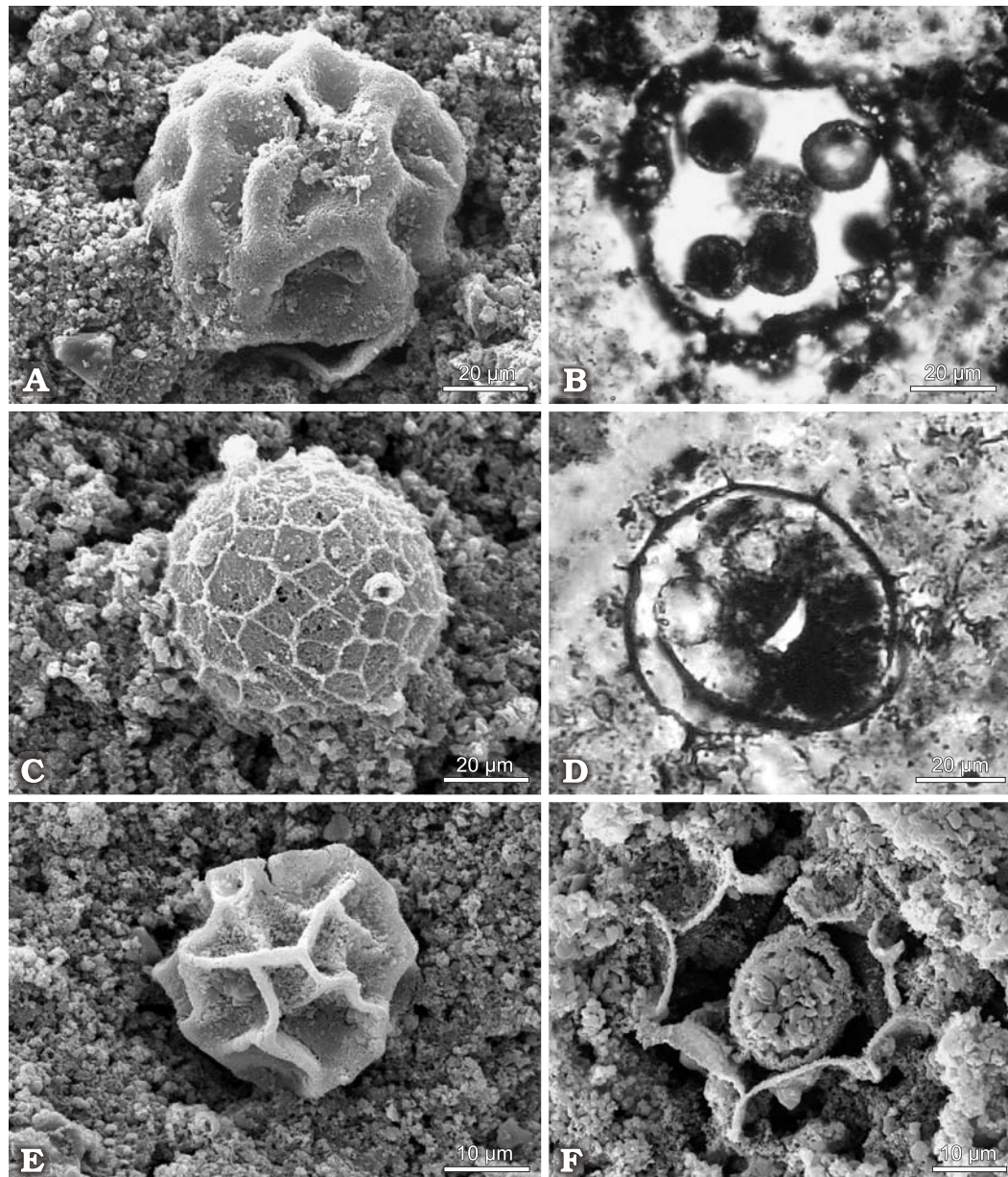
Fig. 5. Examples of early Silurian (Llandoverian) herkomorph acritarchs (classified also by some authors to prasinophytes) enclosing internal bodies comparable with spores of modern unicellular green algae. All from early Silurian (Llandoverian) black radiolarian cherts; locality Łupianka Hill near Żdanów village, Bardzkie Mountains, southwestern Poland. **A**. Specimen of *Cymatiosphaera* in SEM view. ZPAL Ak. 2/Lup19. **B**. Transmitted light micrograph of cross-section of *Cymatiosphaera*-like specimen from same sample as above enclosing spherical aplanospore-like structures. ZPAL Ak. 2/Lup26. **C**, **D**. Specimens of *Cymatiosphaera* sp., in SEM view. Inside the specimen D spheroid bodies resembling aplanospores of modern unicellular green algae are visible. ZPAL Ak. 2/13, ZPAL Ak. 2/27. **E**. Specimen of *Dictyotidium* sp., in SEM view. ZPAL Ak. 2/25. **F**. Transmitted light micrograph of cross-section of a specimen of the same taxon enclosing remnant of spherical structure resembling aplanospore or hypnospore; note the fine granular structure of the SiO$_2$ permineralized spore wall contrasting strongly with much coarser mineral substance filling the spore interior. ZPAL Ak. 2/25a. A, C, E, and F, 40 sec. HF-etched polished rock platelets.

of spores have not been observed in them (e.g., Melkonian 1989). It has also been suggested (e.g., Javaux et al. 2003) that some of the vesicular organic-walled microfossils classified to *Leiosphaeridia* may represent capsular envelopes similar to those produced by some extant coccoid cyanobacteria (Waterbury and Stanier 1978). Sporulation process in such cyanobacteria (e.g., modern *Stanieria*, see Fig. 3E, F) generates indeed internal bodies (beocytes) similar in size and number to

those occurring in our Silurian *Leiosphaeridia* specimens (Fig. 3A, B) and in modern unicellular green algae (Fig. 3C, D). However, in distinction to cyanobacterial capsules, which are composed of bands of fibrillar polysaccharide-rich mucilage (Waterbury 1979), the walls of our *Leiosphaeridia*, similarly as in other early Paleozoic members of this form-genus (e.g., Kjellström 1968; Talyzina and Moczydlowska 2000; Willman 2009), have rigid structure similar to compact cell
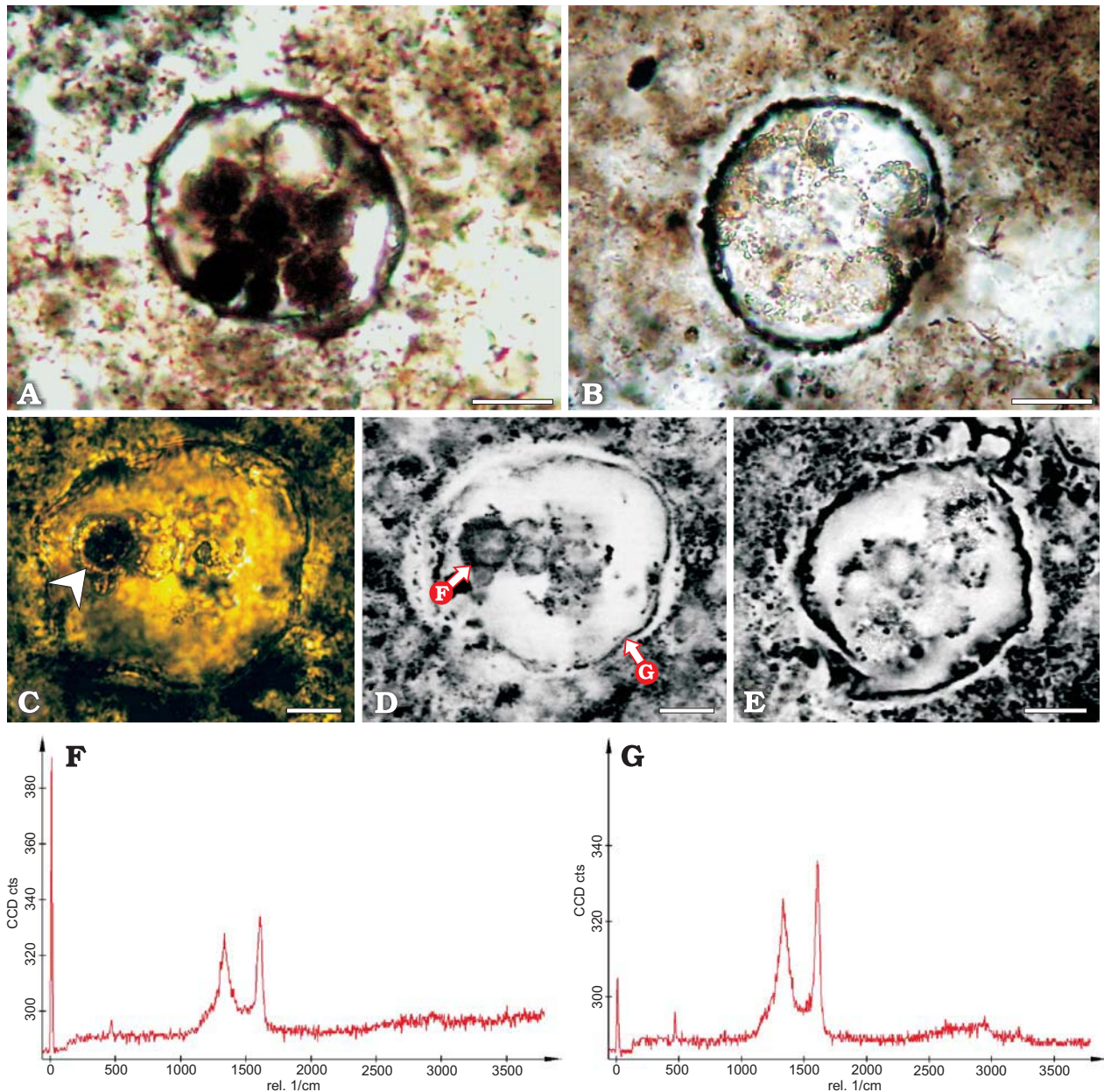
Fig. 6. Modes of preservation of spore-like bodies in early Silurian (Llandoverian) acritarchs from Quarry WNW Döbra, Frankenwald, Germany. **A**. Kerogenous spore-like spheroids in an acanthomorph specimen with one empty spheroid at the top showing an autospore-like spinose carbonaceous wall. ZPAL Ak. 2/Döbra01. **B**. Similar spheroids in an herkomorph specimen preserved as purely siliceous structures with totally degraded former carbonaceous walls delineated now by fine mineral granules. ZPAL Ak. 2/Döbra02. **C–G**. Raman confocal microscope analysis of an (?) herkomorph acritarch enclosing a spore-like spheroids (one indicated by arrow head): optical microscope view in transmitted light (**C**), two confocal Raman mappings of the same specimen, showing distribution of carbon (black color) (**D**, **E**); red arrows in D indicate points where Raman spectra from the internal body (**F**) and acritarch wall (**G**) have been obtained. Note the similarity of both spectra. ZPAL Ak. 2/Döbra03. Scale bars 10 μm.

wall structure of modern chlorococcalean algae that in addition to polysaccharides are supported by biopolymers (glycoproteins, algaenan, and sporopollenin) resistant to mechanical and biological degradation (see e.g., Atkinson et al. 1972; Dunstan et al. 1992; Burczyk et al. 1999).

Our interpretation of the internal bodies in acritarchs as possible reproductive structures is not new. Of special interest are those provided by Eisenack, who noticed singular spherical bodies in *Leiosphaeridia*-like acritarchs (Eisenack 1956: pl. 16: 3–10) and also observed presence of groups of such bodies in representatives of *Tasmanites* (Eisenack 1968: pl. 2: 7). Eisenack (1968) interpreted these bodies as possible reproductive structures ("Brutzellen"), suggesting even, as we now propose, that some of them could be compared to autospores of extant unicellular green algae (Eisenack 1968: 14–15). Other internal bodies found occasionally in acritarchs (e.g., Eisenack 1958a, b; Le Hérissé 1989; Hermann 1990; Guy-Ohlson 1996; Wood 1996; Tibbs et al.

2003; Stanevich et al. 2007) have not been accounted as biologically significant and, consequently, they have been absent from the overviews and compendia concerned with the systematic position of acritarchs (Tappan 1980; Martin 1993; Colbath and Grenfell 1995; Servais 1996; Strother 1996; Wicander 2002). Our findings of internal bodies in acritarchs confirm also earlier suppositions, based on ultrastructural and micro-chemical analyses of acritarch walls, suggesting affinities with green algae (Javaux et al. 2004; Marshall et al. 2005), and chlorococcalean affiliation of certain leiosphaerids (Talyzina and Moczydłowska 2000). The Meso-Neoproterozoic microfossil *Tappania* attributed to acritarchs (Yin 1998) has been interpreted as "an actively growing cell or germinating cyst" (Javaux et al. 2001: 67).

An interesting question arises: why do acritarchs enclose the spore-like bodies so rarely? To our knowledge, only a few examples of similar structures have been described thus far. One explanation of the rarity of these structures is that the cell walls of auto- and aplanospores in many modern chlorococcalean algae are extremely thin (2 to 21 nm) before release from parental cells (Hegewald and Schnepf 1984; Yamamoto et al. 2004) and they are not strengthened by sporopollenin (Atkinson et al. 1972). Consequently, their chances to withstand post mortem degradation are exceedingly small. Taphonomic processes were probably critical factor controlling the fossilization potential of the spore-like bodies in acritarchs. It is known that such early post mortem biodegradation processes, as autolysis, hydrolysis, dehydration and bacteriolysis, are, after burial, followed by early- and late diagenetic processes, during which the cell remnants may undergo further physical and chemical changes leading to their mechanical destruction (reworking, compaction, tectonization), kerogenization, thermal transformation, and, often, permineralization. In Fig. 6 three examples of possible effects of such taphonomic processes on the final appearance of the fossilized spore-like bodies occurring in early Silurian acritarchs are shown. The spore-like structures can be preserved as spheroids of kerogen-like substance (Fig. 6A), as empty carbonaceous vesicles resembling morphologically the mother vesicle (in this case an acanthomorph acritarch—see Fig. 6A, at the top), or as mineral (siliceous) spheroids delineated more or less distinctly by very fine mineral granules precipitated early diagenetically on the subsequently degraded organic walls of spores-like structures inside a herkomorph acritarch (Fig. 6B). Raman spectra and mappings of some of the spore-like bodies show remains of carbonaceous matter around them (Fig. 6D–G). Although Raman data, if taken alone, cannot prove the biogenic nature of the carbonaceous matter (for discussion see e.g., Schopf et al. 2007), together, however, with the morphology, size, and mode of distribution of the spheroids, they are supportive for our interpretation of these structures as possible spores.

The chemical maceration methods, often with application of centrifugation and ultrasonic cleaning of the extracted specimens, used routinely for extracting acritarchs from the mineral matrix, are an additional factor contributing to the destruction of the ultrathin-walled spores. The thin-section method was therefore most useful for finding remnants of such spores. Also slight etching of polished rock surfaces, as described by Munnecke and Servais (1996), has been proved highly promising in that regard. We recommend both these methods in the search for similar structures in other acritarch taxa.

Acritarchs became the dominant marine (phyto)plankton group in late Precambrian and Paleozoic (Knoll 1989; Molyneux et al. 1996; Willman et al. 2006), but lost their importance as primary producers during Mesozoic and Cenozoic over dominated by dinoflagellates, coccolithophorids and diatoms (Falkowski et al. 2004) which thrive also in present-day seas (Sieburth 1979). The processes responsible for this great algal exchange remain unclear, although several plausible mechanisms have been proposed (Falkowski et al. 2004; Katz et al. 2004; Riegel 2008). Many strains of extant unicellular and coenobial green algae display tendency towards mixotrophy, i.e., ability to assimilate and metabolize dissolved organic material (e.g., Droop 1974; Kirk 1998). Therefore, their abundance in many Proterozoic and Paleozoic marine sediments, compared with their scarcity in modern seas (e.g., Sieburth 1979; Raymont 1980), may suggest higher levels of dissolved organic carbon and other nutrients (eutrophy) in early Paleozoic marine environments (e.g., Riegel 2008). For instance, the co-occurrence of acritarch blooms in epicontinental Late Devonian seas with blooms of potentially mixotrophic coenobial volvocaceans (Kaźmierczak 1975; Kaźmierczak and Kremer 2005) absent in modern seas (Sieburth 1979) may offer support for such an idea.

Organic-walled microfossils ascribed to acritarchs are among the oldest morphological traces of eukaryotic life (Schopf 1968, 1992; Zhang 1986; Yan 1991; Yin 1998; Javaux et al. 2004; Knoll et al. 2006; Teyssèdre 2006). The elucidation of biological affiliation of some typical Paleozoic acritarchs as chlorococcalean algae, as shown by our findings, may therefore shed new light on the evolution of early eukaryotes among which unicellular green algae or their ancestors, are assumed to occupy a key position (Baldauf 2003; Hedges et al. 2004; Teyssèdre 2006). It has been suggested that during the Neoproterozoic and Paleozoic acritarch forms, including those shown in our paper, were the main primary producers in the seas (e.g., Knoll 1989; Molyneux et al. 1996). Therefore, their abundance in ancient seas (e.g., Colbath 1980; Dorning 1981; Vidal and Knoll 1983; Martin 1993; Strother 1996; Servais et al. 2004; Kremer 2005) might have not only influenced the evolution of the early marine ecosystem, but also the planetary biogeochemical cycles. Identifying some of them as vegetative cells of green microalgae, may, therefore, throw a new light on the understanding of basic processes ruling the evolution of Earth's biosphere. In that regard it is interesting to note that current studies on the C_{28}/C_{29} sterane ratios in the geologic record (Kodner et al. 2008) indicate far much higher than today significance of green algae in the Late Proterozoic and Paleozoic seas.

Conclusions

In our opinion, the internal bodies found in some early Paleozoic acritarchs suggest their affinity with modern asexually reproducing (sporulating) unicellular green algae (Chlorococcales) and support previous proposals linking these microfossils with unicellular green algae (Eisenack 1968; Lindgren 1981; Arouri et al. 1999; Talyzina and Moczydłowska 2000; Willman 2009; Willman and Moczydłowska 2007; Javaux et al. 2004). Consequently, these microfossils seem to represent not, as is commonly assumed, cysts of dinoflagellates or prasinophyta phycomas but vegetative green algal cells. The recognition of asexual mode of reproduction in representatives of main acritarch divisions opens, in our opinion, a new vista in biological studies of these microfossils. It seems, considering the great morphological variability observed in natural populations of green microalgae (e.g., Komárek and Fott 1983), that the extremely species-rich acritarch (para)taxonomy, based mostly on external morphological features such as shape, size and surface sculpture (ridges, processes, spines, warts, granules, flanges, etc.) can in the future be greatly simplified. The abundance and diversity of "acritarch" green microalgae in early Paleozoic seas, compared with the scarcity of unicellular chlorophytes in modern marine environments, is puzzling and supports claims explaining great secular change in marine phytoplankton composition as result of changing biogeochemical components of the environment (e.g., Riegel 2008). Summing up, we are aware that our findings offer only partial solution to the question of systematic affiliation of the enormously morphologically and, consequently, (para)taxonomically diversified group of organic-walled microfossils used to be named "acritarchs". We do hope, however, that the data presented in our paper may stimulate attempts to find similar internal structures in other representatives of these common ancient microorganisms.

Acknowledgments

References

Arouri, K., Greenwood, P.F., and Walter, M.R. 1999. A possible chlorophycean affinity of some Neoproterozoic acritarchs. *Organic Geochemistry* 30: 1323–1337.

Arouri, K., Greenwood, P.F., and Walter, M.R. 2000. Biological affinities of Neoproterozoic acritarchs from Australia: microscopic and chemical characterization. *Organic Geochemistry* 31: 75–89.

Atkinson, A.W. Jr. 1, Gunning, B.E.S., and John, P.C.L. 1972. Sporopollenin in the cell wall of *Chlorella* and other algae: Ultrastructure, chemistry, and incorporation of ^{14}C-acetate, studied in synchronous cultures. *Planta* 107: 1–32.

Baldauf, S.L. 2003. The deep roots of eukaryotes. *Science* 300: 1703–1706.

Bauersachs,T., Kremer, B., Schouten, S., and Sinnighe Damsté, J.S. 2009. A biomarker and δ^{15}N study of the thermally altered Silurian cyanobacterial mats. *Organic Geochmistry* 40: 149–157.

Burczyk, J., Śmietana, B., Termińska-Pabis, K., Zych, M., and Kowalowski, P. 1999. Comparison of nitrogen content, amino acid composition and glucosamine content of cell walls of various chlorococcalean algae. *Phytochemistry* 51: 491–497.

Butterfield, N.J. 2005. Probable Proterozoic fungi. *Paleobiology* 31: 165–182.

Colbath, G.K. 1980. Abundance fluctuations in the Upper Ordovician organic-walled microplankton from Indiana. *Micropaleontology* 26: 97–102.

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

de Leeuw, J.W., Versteegh, G.J.M., and van Bergen, P.F. 2006. Biomacromolecules of algae and plants and their fossil analogues. *Plant Ecology* 182: 209–233.

Dorning, K.J. 1981. Silurian acritarch distribution in the Ludlovian shelf sea of South Wales and the Welsh Borderland. *In*: J.W. Neale and M.D. Brasier (eds.), *Microfossils from Recent and Fossil Shelf Seas*, 31–36. Ellis Horwood, Chichester.

Dorning, K.J. 2004. Acritarch Classification Working Group Report for 2004. *In*: M. Vecoli and R. Wicander (eds.), *Acritarch Newsletter* 20, December 2004. International Commission on Palaeozoic Microflora (CIMP), 17–20. Website: http://www.shef.ac.uk/~cidmdp/ Subcom. Acritarchs and Related Forms.

Downie, C., Evitt, W.R., and Sarjeant, W.A.S. 1963. Dinoflagellates, hystrichospheres, and the classification of the acritarchs. *Stanford University Publications in Geological Sciences* 7: 3–16.

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

Droop, M.R. 1974. Heterotrophy of carbon. *In*: W.D. Stewart (ed.), *Algal Physiology and Biochemistry*, 530–559. Blackwell Scientific Publishers, Oxford.

Dunstan, G.A., Volkman, J.K., Jeffrey, S.W., and Barrett, S.N. 1992. Biochemical composition of microalgae from the green classes Chlorophyceae and Prasinophyceae. II: Lipid classes and fatty acids. *Journal of Experimental Marine Biology and Ecology* 161: 115–134.

Eisenack, A. 1956. Probleme der Vermehrung und des Lebensraumes bei der Gattung *Leiosphaera* (Hystrichosphaeridea). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 102: 402–408.

Eisenack, A. 1958a. Mikrofossilien aus dem Ordovizium des Baltikums. *Senckenbergiana Lethaea* 39: 389–405.

Eisenack, A. 1958b. *Tasmanites* Newton 1875 und *Leiosphaeridia* N.G. als Gattungen der Hystrichosphaeridea. *Palaeontographica* 110 (Abt. A, L1–3): 1–19.

Eisenack, A. 1968. Über die Fortpflanzung paläozoischer Hystrichosphären. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 131: 1–22.

Ettl, H. 1980. *Grundriß der allgemeinen Algologie*. 549 pp. VEB Gustav Fischer Verlag, Jena.

Ettl, H. 1988a. Über Definitionen und Terminologie der asexuellen Fortpflanzungszellen bei Grünalgen (Chlorophyta). *Archiv für Protistenkunde* 135: 17–34.

Ettl, H. 1988b. Zellteilung und Sporulation als wichtige Unterscheidungsmerkmale bei Grünalgen (Chlorophyta). *Archiv für Protistenkunde* 135: 103–118.

Ettl, H. and Komárek, J. 1982. Was versteht man unter dem Begriff „coccale

Grünalgen"? *Archiv für Hydrobiologie*, Supplement 60(4), *Algological Studies* 29: 345–374.

Ettl, H., Müller, D.G., Neumann, K., Stosch, H.A. von, and Weber, W. 1967. Vegetative Fortpflanzung, Parthenogenese und Apogamie bei Algen. *In*: W. Ruhland (ed.), *Handbuch der Pflanzenphysiologie*, Band 18: 597–776, Springer, Berlin.

Evitt, W.R. 1963. A discussion and proposals concerning fossil dinoflagellates, hystrichospheres, and acritarchs, II. *Proceedings of the National Academy of Sciences USA* 49: 298–302.

Falkowski, P.G., Katz, M.E., Knoll, A.H., Quigg, A., Raven, J.A., Schofield, O., and Taylor, F.J.R. 2004. The evolution of modern eukaryotic phytoplankton. *Science* 305: 354–360.

Fensome, R.A., Williams, G.L., Barss, M.S., Freeman, J.M., and Hill, J.M. 1990. Acritarchs and fossil prasinophytes: an index to genera, species and intraspecific taxa. *American Association Stratigraphic Palynologists Foundation Contributions Series* 25: 1–771.

Fritsch , F.E. 1965. *The Structure and Reproduction of the Algae*, v. 1. 791 pp. Cambridge University Press, Cambridge.

Guy-Ohlson, D. 1996. Prasinophycean Algae. *In*: J. Jansonius and D.C. McGregor (eds.), *Palynology: Principles and Applications*, v. 1, 181–189. American Association of Stratigraphic Palynologists Foundation, Salt Lake City.

Hanagata, N., Karube, I., and Chihara, M. 1996. Bark-inhabiting green algae in Japan (3) *Chlorella trebouxioides* and *Ch. angusto ellipsoidea*, sp. nov, (Chlorelloideae, Chlorellaceae, Chlorococcales). *Journal of Japanese Botany* 71: 36–43.

Hedges, S.B., Blair, J.E., Venturi, M.L., and Shoe, J.L. 2004. A molecular time scale of eukaryote evolution and the rise of complex multicellular life. *BMC Evolutionary Biology* 4: 1–9.

Hegewald, E. and Schnepf, E. 1984. Zur Struktur und Taxonomie bestachelter Chlorellales (Micractiniaceae, Golenkiniaceae, Siderocystopsis). *Nova Hedwigia* 39: 297–383.

Hermann, T.N. 1990. *Organic World Billion Years Ago*. 50 pp. Nauka, Leningrad.

Hibberd, D.J. 1990. Phylum Xantophyta. *In*: L. Margulis, J.O. Corliss, M. Melkonian, and D.J. Chapman (eds.), *Handbook of Protoctista*, 686–697. Jones and Barlett Publishers, Boston.

Hindák, F., 1980. Studies on the chlorococcal algae (Chlorophyceae). II. *Biologicke Práce* 26 (6): 5–195.

Horstig, G. von and Stettner, G. 1976. *Geologische Karte von Bayern 1:25000*. Erläuterungen zu Blatt 5735 Schwarzenbach am Wald, 1–61. Bayerisches Geologisches Landesamt, München.

Huss, V.A.R., Ciniglia, C., Cennano, P., Cozzalino, S., Pinto, G., and Pollio, A. 2002. Phylogenetic relationships and taxonomic position of *Chlorella*-like isolates from low pH environments (pH <3.0). *BMC Evolutionary Biology* 2: 13–21.

Javaux, E.J. and Marshall, C.P. 2006. A new approach in deciphering early protist paleobiology and evolution: Combined microscopy and microchemistry of single Proterozoic acritarchs. *Review of Palaeobotany and Palynology* 139: 1–15.

Javaux, E.J., Knoll, A.H., and Walter, M.R. 2001. Morphological and ecological complexity in early eukaryotic ecosystems. *Nature* 412: 66–69.

Javaux, E.J., Knoll, A.H., and Walter, M.R. 2003. Recognizing and interpreting the fossils of early eukaryotes. *Origin of Life and Evolution of the Biosphere* 33: 75–94.

Javaux, E.J., Knoll, A.H., and Walter, M.R. 2004. TEM evidence for eukaryotic diversity in mid-Proterozoic oceans. *Geobiology* 2: 121–132.

Jux, U. 1971. Über den Feinbau der Wandungen einiger paläozoischer Baltisphaeridiaceen. *Palaeontographica B* 136: 115–128.

Katz, M.E., Finkel, Z.V., Grzebyk, D., Knoll, A.H., and Falkowski, P.G. 2004. Evolutionary trajectories and biogeochemical impacts of marine eukaryotic phytoplankton. *Annual Review of Ecology and Evolutionary Systematics* 35: 523–556.

Kaźmierczak, J. 1975. Colonial Volvocales (Chlorophyta) from the Upper Devonian of Poland and their palaeoenvironmental significance. *Acta Palaeontologica Polonica* 20: 73–85.

Kaźmierczak, J. and Kremer, B. 2005. Post-mortem calcified Devonian acritarchs as a source of calcispheric structures. *Facies* 51: 554–565.

Kirk, D.L. 1998. *Volvox: Molecular-Genetic Origins of Multicellularity and Cellular Differentiation*. 381 pp. Cambridge University Press, Cambridge.

Kjellström, G. 1968. Remarks on the chemistry and ultrastructure of the cell wall of some Paleozoic leiospheres. *Geologiska Föreningens i Stockholm Förhandlingar* 90: 221–228.

Knoll, A.H. 1989. Evolution and extinction in the marine realm: some constraints imposed by phytoplankton. *Philosophical Transactions of the Royal Society of London B* 325: 279–290.

Knoll, A.H., Javaux, E.J., Hewitt, D., and Cohen, P. 2006. Eukaryotic organisms in Proterozoic oceans. *Philosophical Transactions of the Royal Society of London B* 361: 1023–1038.

Kodner, R.B., Pearson, A., Summons, R.E., and Knoll, A.H. 2008. Sterols in red and green algae: quantification, phylogeny, and relevance for the interpretation of geologic steranes. *Geobiology* 6: 411–420.

Komárek, J. and Fott, B. 1983. Chlorophyceae (Grünalgen) Ordnung: Chlorococcales. *In*: G. Huber-Pestalozzi (ed.), *Das Phytoplankton des Süßwassers*: 7. Teil 1. Hälfte. 1001 pp. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Kováčik, L. 1975. Taxonomic review of the genus *Tetraedron* (Chlorococcales). *Archiv für Hydrobiologie*, Supplement 46, *Algological Studies* 13: 354–391.

Kozłowski, R. and Kaźmierczak, J. 1968a. On two Ordovician calcareous algae. *Acta Palaeontologica Polonica* 13: 325–346.

Kozłowski, R. and Kaźmierczak, J. 1968b. Sur une Algue ordovicienne conservant le thalle organique. *Comptes Rendus de l'Académie des sciences Paris, Série D* 226: 2147–2148.

Kremer, B. 2001. Acritarchs from the Upper Ordovician of southern Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica* 46: 595–601.

Kremer, B. 2005. Mazuelloids: Product of post-mortem phosphatization of acanthomorphic acritarchs. *Palaios* 20: 27–36.

Kremer, B. and Kaźmierczak, J. 2005. Cyanobacterial mats from Silurian black radiolarian cherts: phototrophic life at the edge of darkness? *Journal of Sedimentary Research* 75: 895–904.

Le Hérissé, A. 1989. Acritarches et kystes d'algues Prasinophycées du Silurien de Gotland, Suede. *Palaeontographia Italica* 76: 57–302.

Lindgren, S. 1981. Remarks on the taxonomy, botanical affinities, and distribution of leiospheres. *Stockholm Contributions in Geology* 38: 1–20.

Marshal, C.P., Javaux, E.J., Knoll, A.H., and Walter, M.R. 2005. Combined micro-Fourier transform infrared (FTIR) spectroscopy and micro-Raman spectroscopy of Proterozoic acritarchs: A new approach to palaeobiology. *Precambrian Research* 138: 208–224.

Martin, F. 1993. Acritarchs: A review. *Biological Reviews* 68: 475–538.

Melkonian, M. 1989. Phylum Chlorophyta Class Prasinophyceae, *In*: L. Margulis, J.O. Corliss, M. Melkonian, and D.J. Chapman (eds.), *Handbook of Protoctista*, 600–607. Jones and Barlett Publishers, Boston.

Moldowan, J.M. and Talyzina, N.M. 1998. Biogeochemical evidence for dinoflagellate ancestors in the Early Cambrian. *Science* 281: 1168–1170.

Moldovan, J.M., Dahl, J., Jacobson, S.R., Huizinga, B.J., Fago, F.J., Shetty, R., Watt, D.S., and Peters, K.E. 1996. Chemostratigraphic reconstruction of biofacies: Molecular evidence linking cyst-forming dinoflagellates with pre-Triassic ancestors. *Geology* 24: 159–162.

Molyneux, S.G., Le Hérissé, A., and Wicander, R. 1996. Paleozoic phytoplankton. *In*: J. Jansonius and D.C. McGregor (eds.), *Palynology: Principles and Applications*, v. 2, 493–529. American Association of Stratigraphic Palynologists Foundation, Salt Lake City.

Munnecke, A. and Servais, T. 1996. Scanning electron microscopy of polished, slightly etched rock surfaces: a method to observe palynomorphs in situ. *Palynology* 20: 163–176.

Pfiester, L.A. 1989. Dinoflagellate sexuality. *International Review of Cytology* 114: 249–272.

Raymont, J.E.G. 1980. *Plankton and Productivity in the Oceans* (2nd edition). 489 pp. Pergamon Press, Oxford.

Riegel, W. 2008. The Late Palaeozoic phytoplankton blackout—Artefact or

evidence of global change? *Review of Palaeobotany and Palynology* 148: 73–90.

Schopf, J.W. 1968. Microflora of the Bitter Springs Formation, late Precambrian, central Australia. *Journal of Paleontology* 42: 561–688.

Schopf, J.W. 1992. Patterns of Proterozoic microfossil diversity: An initial, tentative analysis. *In*: J.W. Schopf and C. Klein (eds.), *The Proterozoic Biosphere. A multidisciplinary study*, 529–552. Cambridge University Press, New York.

Schopf, J.W., Kudryavtsev, A.B., Czaja, A.D., and Tripathi, A.B. 2007. Evidence of Archean life: Stromatolites and microfossils. *Precambrian Research* 158: 141–155.

Servais, T. 1996. Some considerations on acritarch classification. *Review of Palaeobotany and Palynology* 93: 9–22.

Servais, T., Li, J., Stricanne, L., Vecoli, M., and Wicander, R. 2004. Acritarchs. *In*: B. Webby, F. Paris, M. Droser, and I.G. Percival (eds.), *The Great Ordovician Biodiversification Event*, 348–360. Columbia University Press, New York.

Sieburth, J.M. 1979. *Sea Microbes*. 491 pp. Oxford University Press, Oxford.

Sluiman, H.J., Kouwets, F.A.C., and Blommers, P.C.J. 1989. Classification and definition of cytokinetic patterns in green algae: Sporulation versus (vegetative) cell division. *Archiv für Protistenkunde* 137: 277–290.

Stanevich, A.M., Chatta, E.N., Kornilova, T.A., and Nemerov, V.K. 2007. Habitats and probable nature of acritarchs from the Upper Riphean Chencha Formation. *Paleontological Journal* 41: 87–94.

Stein, V. 1965. Stratigraphische und paläontologische Untersuchungen im Silur des Frankenwaldes. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 121: 111–200.

Strother, P.K. 1996. Acritarchs. *In*: J. Jansonius and D.C. McGregor (eds.), *Palynology: Principles and Applications*, v. 1, 81–106. American Association of Stratigraphic Palynologists Foundation, Salt Lake City.

Talyzina, N.M. and Moczydłowska, M. 2000. Morphological and ultrastructural studies of some acritarchs from the Lower Cambrian Lukati Formation, Estonia. *Review of Palaeobotany and Palynology* 112: 1–21.

Talyzina, N.M., Moldowan, J.M., Johannisson, A., and Fago, F.J. 2000. Affinities of early Cambrian acritarchs studied by using microscopy, fluorescence flow cytometry and biomarkers. *Review of Palaeobotany and Palynology* 108: 37–53.

Tappan, H. 1980. *The Paleobiology of Plant Protists*. 1028 pp. Freeman, San Francisco, CA.

Tibbs, S.L, Briggs, D.E.G., and Prössl, K.F. 2003. Pyritisation of plant microfossils from the Devonian Hunsrück Slate of Germany. *Paläontologische Zeitschrift* 77: 241–246.

Teyssèdre, B. 2006. Are the green algae (phylum Viridiplantae) two billion years old? *Carnets de Géologie/Notebooks on Geology* A03: 1–14.

Tschermak-Woess, E. 1989. Developmental studies in trebouxioid algae and taxonomical consequences. *Plant Systematics and Evolution* 164: 161–195.

Versteegh, G.J.M. and Blokker, P. 2004. Resistant macromolecules of extant and fossil microalgae. *Phycological Research* 52: 325–339.

Vidal, G. and Knoll, A.H. 1983. Proterozoic plankton. *Geological Society of America Memoirs* 161: 265–277.

Waterbury, J.B. 1979. Development patterns of pleurocapsalean cyanobacteria. *In*: J.H. Parish (ed.), *Developmental Biology of Prokaryotes*, 203–226. Blackwell Scientific Publishers, Oxford.

Waterbury, J.B. and Stanier, R.Y. 1978. Patterns of growth and development in pleurocapsalean cyanobacteria. *Microbiological Reviews* 42: 2–44.

Wicander, R. 2002. Acritarchs: Proterozoic and Paleozoic enigmatic organic-walled microfossils. *In*: R.B. Hoover, G.V. Levin, R.R. Paepe, and A.Yu. Rozanov (eds.), Instruments, Methods, and Missions for Astrobiology IV. *Proceedings of the International Society for Optical Engineering (SPIE)* 4495: 331–340.

Willman, S. 2009. Morphology and wall ultrastructure of leiosphaeric and acanthomorphic acritarchs from the Ediacaran of Australia. *Geobiology* 7: 8–20.

Willman, S. and Moczydłowska, M. 2007. Wall ultrastructure of an Ediacaran acritarch from the Officer Basin, Australia. *Lethaia* 40: 111–123.

Willman, S., Moczydłowska, M., and Grey, K. 2006. Neoproterozoic (Ediacaran) diversification of acritarchs—A new record from the Murnaroo 1 drillcore, eastern Officer Basin, Australia. *Review of Palaeobotany and Palynology* 139: 17–39.

Wood, G.D. 1996. Biostratigraphic, paleoecologic and biologic significance of the Silurian (Llandovery) acritarch *Beromia rexroadii* gen. emend. et sp. nov., mid-continent and eastern United States. *Palynology* 20: 177–189.

Yamamoto, M., Fujishita, M., Hirata, A., and Kawano, S. 2004. Regeneration and maturation of daughter cell walls in the autospore-forming green alga *Chlorella vulgaris* (Chlorophyta, Trebouxiophyceae). *Journal of Plant Research* 117: 257–264.

Yan, Z. 1991. Shale-facies microflora from the Changzhougou Formation (Changcheng System) in Pangjiapu Region, Hebei. *Acta Micropalaeontologica Sinica* 8: 183–195.

Yin, L. 1998. Acanthomorphic acritarchs from Meso-Neoproterozoic shales of the Ruyang Group, Shanxi, China. *Review of Palaeobotany and Palynology* 98: 15–25.

Zhang, Z., 1986. Clastic facies microfossils from the Chuanlinggou Formation (1800 Ma) near Jixian, North China. *Journal of Micropalaeontology* 5: 9–16.