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A review of the systematic position and stratigraphic value of Muellerisphaerida

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KEY WORDS – *Muellerisphaerida*, *Phosphatization*, *Systematics*, *Stratigraphy*, *Ordovician-Lower Devonian*, *Turkey*.

ABSTRACT – *The Muellerisphaerida are pelagic microfossils that are morphologically similar to spherical spinose acritarchs and, particularly, to spherical radiolarians. However, their diameter (including spines) is generally 5-20 times larger than that of acritarchs, and the double-layered shell consists of calcium phosphate with some organic matter that may be absent in muellerisphaerids from metamorphic rocks. A pylome, often closed by a cap, may be present (only in Papinochium Ters & Deflandre, 1966). Most similar are radiolarians which are of similar size and may have a double-layered shell and pylomes; however, radiolarians with phosphatic test are unknown. Late Precambrian spiny spherical microfossils with secondarily phosphatized organic shells are morphologically very similar but distinct in shell composition and distribution (not present in the Cambrian, wherein phosphatized microfossils are common). Muellerisphaerida are known from Ordovician-Lower Devonian rocks of North America, Greenland, Sweden, Great Britain, France, Germany, Czech Republic, Austria, Hungary, Turkey, and Tasmania. Muellerisphaerida are stratigraphically useful, especially for dating metamorphic cherts; and have been used for stratigraphic determinations in tectonically complex areas of Turkey. In the Karaburun Peninsula, Silurian Muellerisphaerida occur in distal turbiditic cherts within a turbidite-olistostrome sequence. These beds ("Karareis Formation") were previously assigned to the Scythian-Anisian (Lower-Middle Triassic). In the Bolkardağ Unit of the Taurides, similar cherts from a turbidite-olistostrome unit were dated by Muellerisphaerida as Late Silurian to earliest Devonian, thus providing evidence of a Caledonian instead of Variscan orogeny.*

RIASSUNTO – [Una rassegna sulla posizione sistematica e il valore stratigrafico dei Muellerisphaerida] – *I Muellerisphaerida sono microfossili pelagici morfologicamente simili ad acritarchi spinosi e molto simili a radiolari sferici. Tuttavia, il loro diametro (con le spine) è generalmente 5-20 volte più grande di quello degli acritarchi e la vescicola a doppia parete è formata da fosfato di calcio con una componente di sostanza organica che può essere assente nei muellerisferidi di rocce metamorfiche. Un piloma, spesso chiuso da un opercolo (solo in Papinochium Ters & Deflandre, 1966) può essere presente. I più simili sono i radiolari che hanno le stesse dimensioni, possono avere una vescicola a doppia parete e un piloma; tuttavia, radiolari con uno scheletro fosfatico sono sconosciuti. Microfossili sferici spinosi del tardo Precambriano con vescicola organica secondariamente fosfatizzata sono morfologicamente simili ma distinti in composizione e distribuzione (non sono presenti nel Cambriano, dove microfossili fosfatizzati sono comuni). I Muellerisferidi sono conosciuti dall'Ordoviciano al Devoniano inferiore del Nord America, Groenlandia, Svezia, Gran Britannia, Francia, Germania, Repubblica Ceca, Austria, Ungheria, Turchia e Tasmania. Essi sono stratigraficamente utili, specialmente per la datazione di rocce silicee metamorfiche. I Muellerisphaerida sono stati usati per determinazioni stratigrafiche in aree tettonicamente complicate della Turchia. Nella penisola di Karaburun, Muellerisphaerida siluriani sono stati trovati in diaspri turbiditici distali entro una sequenza turbiditica ad olistostromi. Questi livelli ("Karareis Formation") erano stati precedentemente assegnati allo Scitico-Anisico (Trias Inferiore-Medio). Nella Unità Bolkardağ dei Tauridi, diaspri turbiditici distali entro una sequenza turbiditica ad olistostromi sono stati datati al Siluriano Superiore-Devoniano basale con Muellerisphaerida. Questa datazione fornisce la prova di una orogenesi Caledoniana invece che Variscica.*

INTRODUCTION

Muellerisphaerida are phosphatic microfossils of unknown systematic position that occur exclusively in Ordovician to Devonian pelagic rocks, especially in oceanic cherts. They can easily be retrieved from low-grade metamorphic cherts from which it is difficult to obtain other stratigraphically important fossils. For instance, from low-grade metamorphic Silurian cherts of the Balaton Highland and the Velence Mountains of Hungary, only one of 18 muellerisphaerid-bearing samples yielded other microfossils; viz., a few indeterminable, strongly corroded simple cone-shaped conodonts. Radiolarians are common, but cannot normally be isolated by dissolution of metacherts, and are only recognizable as indeterminable spheroids in thin sections. Acritarchs are also

present in these rocks as indeterminable spheroids without spines and, like the ill-preserved radiolarians, are not useful stratigraphically. Consequently, the muellerisphaerids have a high potential as biostratigraphic markers in low-grade metamorphic oceanic cherts. However, more data on the stratigraphic distribution of Muellerisphaerida are necessary.

Unlike conodonts, which were stratigraphically very important long before their systematic position was recognized, the natural affinity of the muellerisphaerids is pivotal for their stratigraphic evaluation. Hüsken & Eiserhardt (1997) made a comprehensive compilation of the muellerisphaerid features that they considered indicative of a secondary phosphatization; they concluded that muellerisphaerids occur only in a special, phosphorous-overload facies. If correct, this hypothesis would effectively exclude

any stratigraphic application of the muellerisphaerids. Accordingly, a careful assessment of all the arguments advanced by Hüsken & Eiserhardt (1997) is necessary. A cognate question is: do the muellerisphaerids belong to microfaunas or to the phytoplankton? This question, however, is not relevant to the possible stratigraphic use of the muellerisphaerids because both fossil phytoplankton and microfauna may be stratigraphically efficacious.

MAZUELLOIDS VS. MUELLERISPHAERIDA

Aldridge & Armstrong (1981) figured, without taxonomic description or diagnosis, spherical phosphatic microfossils from Greenland and informally named them mazuelloids. It is clear that these authors did not intend to introduce a new taxon: "for ease of reference, we informally name them mazuelloids" (Aldridge & Armstrong, 1981, p. 532). Whereas Evitt (1963) recommended that the term *Acritarcha* should be treated under the International Code of Botanical Nomenclature (ICBN), Aldridge & Armstrong (1981) did not propose the treatment of mazuelloids under either the ICBN or the International Code of Zoological Nomenclature (ICZN). Therefore, the mazuelloids do not, as a taxon, conform with the rules of either code. Similar informal names are used especially in the German language; e.g., "Strahlentierchen" (for *Radiolaria* and closely related spiny Protista) and "Muschelkrebse" (for *Ostracoda*, *Conchostraca* and other bivalved crustaceans).

Muellerisphaerida Kozur, 1984 was established with original taxonomic description as an ordinal taxon in accordance with ICZN rules (Kozur, 1984). Because the order Muellerisphaerida is not a category of "mega-acritarchs", hence not a junior synonym of *Acritarcha* Evitt, 1963, the taxonomic name Muellerisphaerida is preferred to the informal term mazuelloids (which does not formally connote a taxon). As the Muellerisphaerida is also a taxon in the sense of botanical nomenclature, it could be used in the very improbable case (see below) that its members are attributable to phytoplankton.

MAIN FEATURES OF MUELLERISPHAERIDA

Muellerisphaerida are spherical microfossils with shell diameter of 100–200 µm and total diameter of 120–400 µm (including projecting spines). The shell's two wall layers are only slightly separated and are connected by numerous short beams. The spines, of varying length, are hollow, often double-layered in their basal part but single-layered for their remaining length; otherwise the entire spine is single-layered. They always originate in the inner layer, wherein, opposite to the spine, a funnel-shaped depression is present. The spines never continue inside of the inner layer as in many radiolarians.

The shells and the spines consist of radially arranged crystallites of calcium phosphate with some organic matter. The latter constitutes the fragile innermost layer of the test (often not preserved) and is also present between the crystallites. This organic matter causes the black colour of the muellerisphaerids. Under increasing metamorphic overprint, when the conodonts become white and clear (alteration index 7–8), the muellerisphaerids also change to white. The phosphate may be replaced by silica, causing unmetamorphosed muellerisphaerids to become white, wholly or in part.

PRIMARY VS. SECONDARY PHOSPHATIZATION

Aldridge & Armstrong (1981) and Kozur (1984) assumed that the calcium phosphate of the Muellerisphaerida is primary, whereas Hüsken & Eiserhardt (1997) regarded them as being entirely and secondarily phosphatized. Hüsken & Eiserhardt (1997) assumed that this secondary phosphatization of a large amount of microfossils can only occur in a special phosphorous-overload environment to which the Muellerisphaerida should be restricted. This would exclude or at least strongly inhibit future biostratigraphic application of these microfossils. Therefore, hypotheses favouring primary phosphatization or high phosphorous content of the organic shell, and especially those arguments for a general secondary phosphatization of an organic test, require detailed scrutiny. A definite decision is difficult because there is no unequivocal criterion for distinguishing a primary phosphatic shell from one produced by secondary phosphatization.

EVIDENCE FOR PRIMARY PHOSPHATIZATION

The arguments for primary phosphatization are as follows.

1) Muellerisphaerida are accompanied by non-phosphatized microfossils. In Lower Devonian pelagic limestones of the Strázsa-hegy in northern Hungary, the Muellerisphaerida comprise about 1% of the microfossil content which includes ostracods, foraminifers, conodonts, acritarchs, sponge spicules, holothurian sclerites, and small gastropod and bivalve shells. In this association, the Muellerisphaerida comprise about 10% of the non-phosphatic microfossils (i.e., of the above-listed microfossils except conodonts). Whereas all muellerisphaerids are phosphatic, the dominating primary non-phosphatic microfossils are invariably non-phosphatized. This indicates that the Muellerisphaerida have either a complex shell consisting of organic and phosphatic matter, or an organic shell with high phosphate content. In the latter case, a selective phosphatization of only the Muellerisphaerida would be possible.

A similar example, from the Silurian of Greenland, was presented by Aldridge & Armstrong

(1981). Their well-preserved microfossil association, derived from limestone with very little phosphate, contains *Muellerisphaerida* with phosphatic shells, whereas all other microfossils, including organic-walled Chitinozoa, are not phosphatized. The chitinozoans show minor silicification but no trace of calcium phosphate.

In the only example where the author has found secondary growth of calcium phosphate on *Muellerisphaerida* shells, other fossils, even remnants of macrofossils (in this case graptolites) are also phosphatized.

2) *Muellerisphaerida* are always three-dimensionally preserved. In organic-walled, secondarily phosphatized microfossils this would be the exceptional preservation because in that case they must be always phosphatized before burial.

3) Cross sections or broken surfaces of *Muellerisphaerida* show an organic layer (if preserved) always located at the inner side of the inner phosphatic layer. This indicates a primary layering with an organic inner layer and phosphatic outer layers. An organic layer was never found inside the phosphatic layers. However, in secondary phosphatization the organic matter would be surrounded by calcium phosphate and be well-preserved because secondary test-phosphatization would constitute the best protection for original organic structures.

4) If the calcium phosphate of the *Muellerisphaerida* is carefully dissolved, a fragile, spongy shell of organic material remains undissolved. This indicates that intergrowth of organic material and calcium phosphate was original. In secondarily phosphatized organic material (as in many Cambrian arthropods) the preservation of the organic material is excellent, if the phosphatic material is dissolved. Its surface under high magnification is smooth and the material may retain original elasticity.

5) The typical kidney-like form of amorphous calcium phosphate is recognizable in those *Muellerisphaerida* (and other microfossils) in which the shell is overgrown by secondary calcium phosphate. But even in this case, the original form of the spines is preserved.

6) If the *Muellerisphaerida* were primarily organic-walled "mega-acritarchs" with secondarily phosphatized shell, their main preservation should be organic-walled without phosphatization. However, by very careful palynological preparation, fragile organic-walled *Muellerisphaerida* are sometimes preserved, in a mode corresponding to their inner organic wall layer. The shell, however, is reduced to a spongy material (Priewalder, 1987), indicating that supporting phosphatic material was dissolved. Also the surface itself is always spongy, suggesting that a covering phosphatic layer was dissolved.

In thin sections, *Muellerisphaerida* always consists of calcium phosphate layers and, if preserved, an inner organic layer. This kind of preservation should,

however, be a very rare exception if the *Muellerisphaerida* are actually "mega-acritarchs" with secondarily phosphatized organic wall. Moreover, in this case it is hard to understand why accompanying acritarchs are never phosphatized.

Published data (Aldridge & Armstrong, 1981; Kozur, 1984; Priewalder, 1987) and studies by the author on Turkish material have shown that the *Muellerisphaerida* possess a primary phosphatic-organic shell. Secondary phosphatization of such a shell is sometimes evident; therefore, the calcium phosphate content may increase by secondary phosphatization. However, the above-mentioned preservational features and the chemical composition excludes the notion that the *Muellerisphaerida* have entirely secondarily phosphatized shells. This does not preclude the possibility that the *Muellerisphaerida* had very short live stages without any mineralized shell (which, as in ostracods, would have only a slight chance of fossilization).

EVIDENCE FOR SECONDARY PHOSPHATIZATION

The arguments for secondary phosphatization compiled by Hüsken & Eiserhardt (1997) must be very carefully evaluated because they may indicate either very short live stages without mineralized shell or, less probably, a primary organic shell with high phosphorus content that can be selectively phosphatized, even if other fossils will not be phosphatized. As discussed below, however, these arguments do not invoke unequivocal criteria for secondary phosphatization of an exclusively organic-walled primary shell.

1) The wall material was originally elastic and deformable because there are plastic deformations without breakage.

Plastic deformation without breakage of many microfossils, such as ostracods and radiolarians, often occurs in fine-grained sediments. This is especially common in phosphatic fossils, like conodonts, where the plastic deformation is sometimes sufficiently strong to inhibit identification.

In primary organic-walled microfossils, plastic deformations are the rule, and entirely undeformed specimens the exception. This is also the case in *Acritarcha*, when observed especially on polished, slightly etched rock surfaces (Munnecke & Servais, 1997). Deformation during palynological preparation can be discounted. The percentage of plastically deformed *Muellerisphaerida* is considerably less than is the case with other organic-walled microfossils, including *Acritarcha*, and only slightly more so than with microfossils having thin mineralized shells of comparable thickness. On the other hand, the examples of plastic deformation are impressive (Kozur, 1984; Priewalder, 1987; Hüsken & Eiserhardt, 1997), looking rather similar to plastic deformation of organic-walled microfossils. Forms with plastically deformed shells consist of only one layer. This is also

the case for plastically deformed distal parts of spines, even if the undeformed shell has several layers.

The ratio of plastically undeformed to plastically deformed specimens, and the kind of plastic deformation clearly negate the hypothesis that all *Muellerisphaerida* are secondarily phosphatized organic-walled fossils, and moreover do not support the assumption that *Muellerisphaerida* were phosphatic during their entire life cycle. The best explanation is that, during a brief interval in their life cycle, the *Muellerisphaerida* possessed a one-layered organic-walled shell, whereas in the longer part of the cycle they bore a mineralized shell with several layers. The life-interval without mineralized shell could be an earlier ontogenetic stage or could have resulted repeatedly during discontinuous growth, as in arthropods equipped with a mineralized shell. Also, organic-walled eggs and cysts may be mineralized at a mature stage.

2) Elevated parts of fracture zones are rendered smooth by thick phosphatic armouring, whereas unelevated parts are rough and angled in response to the degree of their environmental exposition.

Actually, the opposite should be the case in secondary phosphatization. The exposed part should not be secondarily phosphatized or very insignificantly so; while the sediment-covered part should show stronger secondary phosphatization. This can be demonstrated in those few *Muellerisphaerids* that possess secondary phosphatic armouring of the shell (Kozur, 1997, pl. 3, figs. 3, 4). In Turkish Upper Silurian material, the exposed parts are not secondarily phosphatized and the lower parts show strong secondary phosphatization as manifested by the typical kidney-like surface structures.

3) Neighbouring vesicles may grow together. Processes may show secondary "overgrowth" on surfaces of adjacent spheres.

This feature provides no evidence for secondary phosphatization of a primarily organic *Muellerisphaerid* test. In very rich radiolarian assemblages, this is a very common preservational mode of otherwise well-preserved radiolarians. The spines of one specimen are so firmly attached to the surface of one or more other specimens that they cannot be separated without destroying the shells. This circumstance occurs much more frequently in radiolarians than in *Muellerisphaerida*, but does not indicate that these radiolarians had an originally organic-walled shell that was secondarily silicified; the shell was, in fact, originally siliceous. Except for radiolarians, this feature occurs in the same frequencies in *Muellerisphaerida* as in other spine-bearing microfossils with an originally mineralized shell (e.g., spiny ostracods). This feature may also be also present in the originally phosphatic conodonts, where morphotypes that do not belong to the same apparatus may have become attached to each other. It results from a diagenetic process that particularly affected forms with original-

ly mineralized hard parts including spines or pointed teeth, and would be an argument favouring original phosphatic shells in the *Muellerisphaerida*.

4) Idiomorphic apatite crystals may be "penetrated" by spines; or such crystals may be partly enclosed by the outer vesicle wall.

This provides no evidence for secondary phosphatization of an organic shell. The apatite crystals need a phosphatic "germ" for growth inception. Thus, they are, for example, seen to have grown on phosphatic spines, not on spines composed of organic matter. Therefore, the phosphatic spines "penetrate" the apatite crystal. This feature is very common in radiolarians, where quartz crystals are "penetrated" by radiolarian spines or quartz crystals fill the inner part of a radiolarian shell; and it often hinders precise determination of the radiolarians. Moreover, this phenomenon is common in conodonts, in which the denticles and other parts of the conodonts often "penetrate" idiomorphic apatite crystals; and it demonstrates the original phosphatic composition of these microfossils. Hence, this feature is indicative of a mineralized (phosphatic) shell in the *Muellerisphaerida*, at least during the growth of the apatite crystals.

5) Phosphatic facies interdependence. Many observations indicate that apatitic microspheres are correlative with a special phosphorous-overloaded environment. Moreover, some characteristic morphotypes seem to characterize distinct strata or occur exclusively in certain local horizons.

This observation is based on an Upper Silurian to upper Lochkovian regression-transgression regime from the "Orthoceratenkalk" to the "Transgressionsbrekzie" in the Frankenwald. But this is an exceptional occurrence for *Muellerisphaerida*. These microfossils mostly occur in pelagic deep-water to moderately deep-water lydites and limestones lacking phosphorous overload, having neither phosphate nodules nor any secondarily phosphatized microfossils. This was clearly indicated by Aldridge & Armstrong (1981) and is confirmed by the present author's observations. Moreover, the "special phosphorous-overloaded environment" should lead to a very conspicuous blooming of phytoplankton, but the phytoplankton frequency is unrelated to presence or absence of *Muellerisphaerida*. On the other hand, rocks with common secondarily phosphatized microfaunas are mostly devoid of *Muellerisphaerids*.

6) Occurrences of *Muellerisphaerids* and acritarchs are mutually exclusive, thus proving the special phosphorous-overloaded environment for the occurrence of *Muellerisphaerida*.

This observation by Hüsken & Eiserhardt (1997) is partly correct but their conclusion cannot be confirmed. Shallow- and brackish-water environments are often very rich in Acritarcha, but never contain *Muellerisphaerida*. The same is true for phosphorous-overloaded, very shallow water deposits. By contrast, intra-oceanic cherts may host very few or no

Acritarcha, but often abundant *Muellerisphaerida*. Thus, the occurrence or preservation of *Muellerisphaerida* is dependent on water depth, not on a phosphorous-overloaded environment. The *Muellerisphaerida* is an exclusively pelagic group that is most common in oceanic cherts, also in pelagic limestones. Thus, acritarchs and *muellerisphaerids* favour different biotopes, independent of the phosphorous supply in the different environments. Moreover, the generally mutually exclusive occurrences of acritarchs and *muellerisphaerids*, assumed by Hüsken & Eiserhardt (1997), cannot be confirmed. *Muellerisphaerida* are especially common in dark-coloured radiolarites deposited in oceanic deeps, and in siliciclastic turbidites of accretionary complexes not greatly distant from the continent. These environments also supported *Acritarcha* (in both Hungary and Turkey). Hüsken & Eiserhardt's (1997) viewpoint, that the occurrence of *muellerisphaerids* and acritarchs mutually excludes one another, is partly an "artefact" caused by different preparation methods. The phosphatic test of the *Muellerisphaerida* cannot be preserved by palynological preparation methods. After dissolving the phosphatic part of the shell, the organic part has a fragile spongy structure (Priewalder, 1987) and is retained only by careful palynological preparation. For this reason, *Muellerisphaerida* were not found in the cherts of the Szalatnak borehole (Hungary), where they were known in thin sections (Oravecz, 1964; Góczán, 1971). In hydrofluoric acid dissolving of the cherts for conodonts, very rich *Muellerisphaerida* faunas were dissolved. Even by very painstaking palynological preparation, a large part of the *Muellerisphaerida* component will be eliminated. Limestone samples prepared by conventional palynological methods may yield fragmentary or intact organic shells (with spongy wall structure) of *Muellerisphaerida*. When such samples are treated with acetic acid, large quantities of well-preserved *Muellerisphaerida* can be produced, as previously recognized by Priewalder (1987). On the other hand, *Muellerisphaerida* are mostly dissolved by acetic acid from limestones or by hydrofluoric acid from cherts. In both cases *muellerisphaerids* and acritarchs are in the insoluble residues, but by washing with 0.063 mm and 0.1 mm sieves the small acritarchs are totally lost, whereas the much bigger *muellerisphaerids* can be picked out from the residues >0.063 mm or >0.1 mm.

Despite mutual exclusion by facies reasons and selective loss during laboratory preparation, acritarchs and *Muellerisphaerida* occur together in some facies, especially in pelagic limestones and in cherts of siliciclastic accretionary complexes. Black cherts of the Szalatnak borehole (southern Hungary) yielded well-preserved *Muellerisphaerida* by dissolution with HF and washing through a 0.063-mm sieve (acritarchs being lost during the washing); and the same rocks produced *Acritarcha* (but no *muellerisphaerids*) by

palynological preparation. Seemingly, the organic matter of the *muellerisphaerids* became so fragile during the metamorphic overprint that it is unobtainable by palynological preparation. This is a good example of mutually exclusive occurrences of *muellerisphaerids* and acritarchs by application of different preparatory methods using samples hosting both microfossil categories. In Lower Devonian limestones of the Uppony Mountains (northern Hungary), acritarchs and *muellerisphaerids* co-occur, both in low frequencies. Organic-walled remnants of *Muellerisphaerida* and *Acritarcha* were obtained by palynological preparation from the same samples of Silurian rocks in Bohemia (written comm. by the reviewer, A. Le Hérisse, Brest).

No criterion for secondary phosphatization, as compiled by Hüsken & Eiserhardt (1997), can be regarded as providing real evidence that the *Muellerisphaerida* originally possessed an organic-walled test that was totally phosphatized secondarily. However, an unmineralized shell in certain live stages cannot be excluded and is probable.

SYSTEMATIC POSITION OF MUELLERISPHAERIDA

Systematic position and classification of the *Muellerisphaerida* are controversial. In connection with the assumed secondary phosphatization of the *muellerisphaerid* test, Hüsken & Eiserhardt (1997) pointed out several times that a classification dependent on morphological features is of little value (i.e., because of secondary phosphatization). This opinion is based on the unproven hypothesis of secondary phosphatization of all *Muellerisphaerida*; in any case, phosphatization generally does not change the morphology, but rather preserves it. Thus, phosphatized (or silicified) ostracods are classified using the same morphological criteria as are ostracods with calcitic or organic valves.

Because all *Muellerisphaerida* have a phosphatic spherical shell which is mostly smooth, the number, size, and shape of the spines provides the sole means for classification (Sannemann, 1955; Ters & Deflandre, 1966; Kozur, 1984, 1997; Le Hérisse *et al.*, 1991). Only the rare forms with ribs on the shell provide an additional useful classificatory criterion, also adopted by the above-mentioned authors.

The statement by Hüsken & Eiserhardt (1997) that zooplankton affinities would be "in contrast to the present state of knowledge" cannot be supported. Almost invariably, microfloras are not secondarily phosphatized, whereas secondarily phosphatized microfaunas are fairly common. In fact, the phosphorous content of the soft parts of faunal elements greatly exceeds that of flora, and secondary phosphatization of fossils starts in those organisms or parts thereof having the highest phosphorous content. Thus, even if general secondary phosphatization of *muellerisphaerids* could be proved, this would strong-

ly favour an animal origin for them; a primary phosphatic test would give the same evidence.

Hüsken & Eiserhardt (1997) mentioned five factors favouring the acritarch nature of the Muellerisphaerida, but none can be regarded as convincing, as discussed below.

1) Elastic property would be an evidence for originally organic wall material.

This cannot be concluded from plastic deformation of some Muellerisphaerida, if the majority of the specimens are not plastically deformed but preserve their spherical shape without deformation or show brittle deformation. As pointed out above, mineralized hard parts can be also plastically deformed in fine-grained sediments. Furthermore, the possibility exists that animals have, in some short life stages, unmineralized or weakly mineralized shells, as known in arthropods. Another possibility is that they were eggs with an organic shell during initial development and acquired additional phosphatic layers at maturity. Most importantly, an organic-walled test does not exclude an animal origin, as such tests are not restricted to Acritarcha or phytoplankton. Major microfossil groups, such as Thalamia and Conchostraca, have a readily preservable organic-walled shell/test and may have organic-walled, often spiny eggs (e.g. Conchostraca) or even teeth of organic material, such as scolecodonts (teeth of Eunicida and Phyllodocida) and arthropods. Many microfaunas include taxa with both organic-walled and mineralized tests/shells, e.g. Chrysomonadina, Foraminifera, Radiolaria, and Ostracoda.

2) The narrow gap between the two shell layers of the muellerisphaerids is assumed to be the site of the organic layer.

Secondary phosphatization would preserve this layer better than in any unphosphatized acritarch. In reality, however, no organic layer has so far been observed as occupying the narrow gap between the two shell layers of any muellerisphaerid (nor even in specimens preserving the organic layer on the inner side of the phosphatic shell). On the other hand, no phosphatized acritarch was found among millions of organic-walled acritarchs. The much larger size of the

muellerisphaerids does not favour phosphatization against the much smaller acritarchs.

Some surface sculptures on the outer shell layer, e.g., ridges, have no expression on its inner side. This would mean that a smooth organic wall was not only covered by phosphate on its inner and/or outer side, but, in some cases, regular ribs were developed on the outer side by secondary phosphatization which is impossible. Moreover, if the gap between the two shell layers was the original organic-walled component, then the phosphatic connecting beams and walls between the two phosphatic layers must be originally gaps in the organic-walled shell that would then partially consist of isolated plates.

3) Arealation of some muellerisphaerids.

This rare feature of muellerisphaerids gives no exclusive or decisive link to acritarchs because arelation is at least as frequent in Paleozoic radiolarians.

4) Exceptional fibrous processes on one specimen of muellerisphaerids indicate a link to certain Ordovician acritarchs that have the same feature.

This feature is also present in radiolarians.

5) Pylomoid apertures resemble the cyclopyles of many acritarch taxa.

Pylomes occur in many radiolarian taxa, where they are at least as common as in Acritarcha.

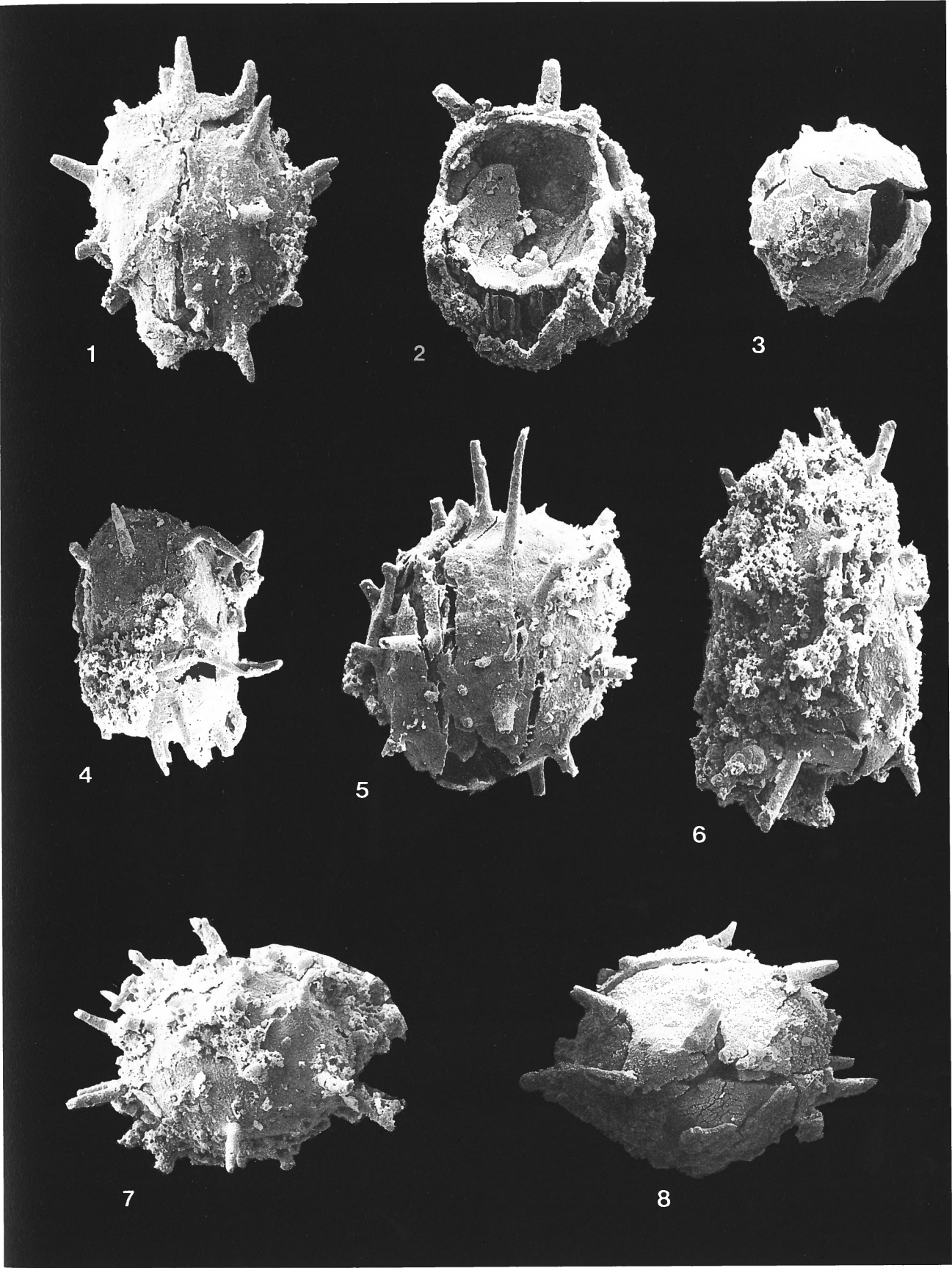
Thus, none of the muellerisphaerid features asserted by Hüsken & Eiserhardt (1997) as constituting evidence for acritarch affinity (and hence of phytoplankton character) are restricted to acritarchs and phytoplankton. The combined totality of these features also does not favour an acritarch attribution, because all of them are known in Radiolaria that are very similar in size and morphology to Muellerisphaerida.

Muellerisphaerida are not Acritarcha *sensu* Evitt, 1963 and later definitions mentioned by Servais *et al.* (1997). Evitt (1963) stated that Acritarcha are small microfossils (without clearly defining precisely how small). However, if acritarchs are small, then the 5-20 times larger Muellerisphaerida (with distinct size gap) must be considered large or very large. The second difference is that the Muellerisphaerida are fully or at least mostly phosphatized, while the Acritarcha are

EXPLANATION OF PLATE 1

- Figs. 1, 2, 8 - *Papinochium robustispinosum* (Kozur, 1984). 1) no organic matter preserved, cracked by slight deformation, rep.-no. 23-2-97/III-29; 2) broken specimen, inner view, no organic matter preserved, rep.-no: 23-2-97/III-34; 8) little organic matter preserved, rep.-no: 23-2-97/III-28.
- Fig. 3 - *Sannemannisphaera rarispinosa* Kozur, 1984, cracked by slight deformation, rep.-no. rep.-no: 23-2-97/III-31.
- Fig. 4 - *Papinochium dubium* (Ters & Deflandre, 1966), shell cracked by deformation, spines partly plastically deformed, broken and intact., rep.-no: 23-2-97/III-33.
- Figs. 5-7 - *Papinochium* sp. B *sensu* Le Hérisse *et al.*, 1991; 5) numerous deformation cracks, rep.-no: 23-2-97/III-30; 6) strongly deformed, with cracks, surface largely covered by rock material, rep.-no: 23-2-97/III-32; 7) deformation cracks, rep.-no: 23-2-97/III-27.

All illustrated specimens are from sample KB64, Wenlock low-grade metamorphic, dark distal turbiditic radiolarite in a sequence of lydites, shales, and bentonites (altered felsic tuffs), roadcut on road to Bilecik (Yükselen), Bolakdağ Unit. Magnifications × 200.



non-mineralized. If the *Muellerisphaerida* possess an originally phosphatized shell during the greater part of their life cycle, as is assumed by this author, then the *Muellerisphaerida* would definitely be excluded from the *Acritarcha*. However, even if this phosphatization of the *Muellerisphaerida* is secondary, the shell of the *Acritarcha* and *Muellerisphaerida* must have had a basically different composition; this favours a general phosphatization in *Muellerisphaerida* and excludes a phosphatization in *Acritarcha*. In both cases, therefore, a very high-rank systematic difference is indicated between these fossil groups. Whereas lack of phosphatization in *Acritarcha* is in agreement with their assumed phytoplankton character, the general phosphatic (primary or at least partly secondary) test of the *Muellerisphaerida* strongly supports their animal origin (see below).

All features cited by Hüsken & Eiserhardt (1997) as indicating the acritarch nature of the *Muellerisphaerida* also occur in the zooplanktic radiolarians. Moreover, *muellerisphaerids* are of similar average size to radiolarians and are ca. 5–20 times larger than acritarchs. Two-shelled spumellarian radiolarians are very common and some have the same narrow gap with many connecting beams.

However, radiolarians with hollow spines (tubes) are generally rare and the spines often continue inside the inner shell (but not necessarily in tubes). The main difference from radiolarians is the phosphatic shell, never present in radiolarians. If this shell was secondarily phosphatized, the similarity to the radiolarians would be still more marked, particularly as there are some radiolarians lacking a mineralized skeleton.

If all *Muellerisphaerida* have a secondarily phosphatized, primarily organic-walled shell, then no morphological distinction from *Radiolaria* is possible. However, as a radiolarian specialist, the present author would not assign the *muellerisphaerids* to radiolarians for phylomorphogenetic reasons, even if they possess a totally secondarily phosphatized test. The shell-bearing radiolarians evolved during the Tremadoc from spicular radiolarians. The first primitive radiolarian shells are rather loose latticed shells with internal spicules and compact external spicules (Kozur *et al.*, 1997). Radiolarians with compact (not latticed) shells and hollow spines (tubes) or arms, morphologically very similar to or identical with *Muellerisphaerida*, are derived forms that evolved much later. All *muellerisphaerids*, including the primitive Ordovician forms, have a compact (not latticed), double-walled shell and hollow spines which do not continue inside the shell. A derivation of these shells from ancestors with spicular skeleton can be discounted.

The ancestors of the *Muellerisphaerida* were probably forms with the same size and morphological character and had an organic-walled shell with or without a low calcium phosphate content. In late

Precambrian rocks, there are organic-walled microfossils of the size, shape, and sculpture as *Muellerisphaerida* (Sergeev, 1998; Yin, 1998). These partly retain their original organic composition and are partly secondarily phosphatized. They could be forerunners of the *Muellerisphaerida*. However, throughout the Cambrian, neither these forms nor *Muellerisphaerida* are present, despite the fact that microfossils with original phosphatic or secondarily phosphatized tests are common in pelagic limestones. Therefore, the Precambrian forms may be unrelated to the *Muellerisphaerida*.

As discussed above, zooplankton affinity is strongly supported both in the case of a primary phosphatic shell (phosphatic hard parts of plants are unknown) and in the case of a secondary phosphatic shell (secondary phosphatization is virtually unrecorded among plant microfossils). However, it is not possible to assign the *Muellerisphaerida* to any known animal class. The possibility that they are eggs or cysts (Kozur, 1997b) cannot be excluded. In the former case, they would have had an organic-walled shell during early ontogeny and a shell with both phosphatic and organic layers in the mature stage.

STRATIGRAPHIC IMPORTANCE OF THE MUELLERISPHAERIDA

Well-dated *Muellerisphaerida* are known from pelagic Ordovician to Lower Devonian rocks of Austria, Czech Republic, France, Germany, Great Britain, Hungary, Sardinia, Sweden, Turkey, Greenland, Yukon Territory (Canada), and Tasmania (Aldridge & Armstrong, 1981; Bachmann & Schmid, 1964; Burrett, 1985; Deflandre & Ters 1970; Dufka, 1991; Eisenack, 1934; Góczán, 1971; Göncüoğlu & Kozur, 1998a, b; Holmer, 1987; Hüsken & Eiserhardt, 1994, 1997; Kozur, 1984, 1997a, b, 1998b; Le Hérisse, 1992; Le Hérisse *et al.*, 1991; Loydell *et al.*, 1988; Norford & Orchard, 1985; Oravec, 1964, 1965; Priewalder, 1987; Reichstein & Schwab, 1962; Sannemann, 1955; Ters & Deflandre, 1966). Original reports from Givetian rocks (Sannemann, 1955) were re-dated as upper Lochkovian by Hüsken & Eiserhardt (1997). Reportedly Upper Devonian occurrences from a limestone-tuff-breccia section (Hüsken & Eiserhardt, 1997) may reflect reworking or perhaps questionable identifications (Reichstein & Schwab, 1962). However, M. Reich, Greifswald (pers. comm.) has found *Muellerisphaerida* in well-dated Upper Devonian deposits.

In Turkey, 23 of investigated 50 samples of unmetamorphosed and low-grade metamorphic Silurian to Lower Devonian lydites yielded *Muellerisphaerida* (by comparison only four of the samples yielded conodonts); whereas 25 samples of Upper Devonian lydites did not produce any *Muellerisphaerida* (one yielded a juvenile *Palmatolepis*). If *muellerisphaerids* are genuinely present (not reworked) in the Upper Devonian, they

must indeed be rare. Several hundreds of Carboniferous and Permian chert samples did not yield any *Muellerisphaerida*. In pelagic Ordovician to Lower Devonian limestones, *Muellerisphaerida* are of rare occurrence, but they may be rich in specimens and partly also in species. Large amounts of Carboniferous and Permian dark-coloured pelagic limestones and cherts failed to produce any *Muellerisphaerida*.

Accordingly, the proven range of *Muellerisphaerida* is Ordovician (not, as yet, Tremadoc) to Devonian. Upper Devonian occurrences have to be confirmed by accompanying conodont faunas and reworking has to be excluded.

The strongest known diversification of the *Muellerisphaerids* was in the Llandovery to Lochkovian interval. Ordovician forms have generally short, simple spines. In the Pragian, only *Papinochium*, with long, narrow spines, has been found. The limited data on the stratigraphic range of the known *Muellerisphaerid* taxa does not permit establishment of a *Muellerisphaerid*-based zonation, but for the Silurian to Pragian interval such a zonation may result from future investigations.

MUELLERISPHAERIDS IN STRATIGRAPHIC RECONSTRUCTIONS: A TURKISH EXAMPLE

Muellerisphaerids have yielded important stratigraphic data in oceanic Silurian to Lower Devonian sequences of Turkey. According to the general view, the area south of the Izmir-Ankara Belt was in Palaeozoic times a shallow-water shelf marginal to Gondwana. All deep-water rocks of this area have previously been assigned to the Mesozoic. This dating is partly correct, even if some Palaeozoic oceanic sequences have been regarded as Triassic. Thus, all deep-water rocks of the Karaburun Peninsula (Karaburun Zone) were assigned to the Scythian-Anisian siliciclastic Karareis Formation (e.g., Erdoğan *et al.*, 1995). However, discoveries of *Muellerisphaerids* have shown that many lydites, both of the ribbon chert-shale sequence and of the siliciclastic turbidites with cherts, are of Silurian-Early Devonian age (Kozur, 1997a, b, 1998b; Göncüoğlu & Kozur, 1998a, b). This was later confirmed by conodonts and radiolarians (Kozur, 1997b, 1998a), but *Muellerisphaerids* are much commoner in black cherts than conodonts, and the predominating radiolarians often cannot be dissolved out of the rocks. Thus, for achieving approximate datings of Silurian-Lower Devonian lydites, *Muellerisphaerids* are very suitable. They can be also extracted from metalydites of phyllitic sequences from which it is difficult to retrieve radiolarians and conodonts.

In the Bolkardağ Zone Özcan *et al.* (1990) first recognized a Palaeozoic deep-water sequence with radiolarites and a turbidite-olistostrome complex which they assigned to a Variscan oceanic and flysch

series. However, the initial investigation of deep-sea lydites and shales with intercalations of altered tuffs from this sequence in the environs of Konya yielded *Papinochium dubium* (Ters & Deflandre, 1966), *Papinochium robustispinosum* (Kozur, 1984), *Papinochium* sp. B *sensu* Le Hérissé, Comble & Moreau-Benoit, 1991, and *Sannemannisphaera rarispinosa* Kozur, 1984. These forms are known from the late Llandovery to Wenlock of France and Hungary (Ters & Deflandre, 1966; Deflandre & Ters, 1970; Kozur, 1984; Le Hérissé *et al.*, 1991) indicating the presence of a Caledonian-time ocean. Subsequently, numerous additional samples were investigated (Göncüoğlu & Kozur, in prep.). Some of these samples yielded conodonts, mainly long-ranging Silurian to Lower Devonian forms, but also such Silurian indices as *Dapsilodus obliquicostatus* (Branson & Mehl). Thus, the previous dating by *Muellerisphaerida* was confirmed.

Low-grade metamorphic cherts of this unit did not yield any conodonts. However, these beds contain *Muellerisphaerida* which are poorly preserved, strongly deformed (Pl. 1), and in part thermally altered (white tests). Nevertheless, they were determinable and indicate the same age as the unaltered forms.

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