Acritarchs

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Acritarchs are a heterogeneous, unicellular microfossil group with probable phytoplanktic affinities. Research into this polyphyletic group was initiated by Alfred Eisenack, whose extensive studies were based originally on Lower Palaeozoic glacial erratics (Eisenack 1931, etc.), but subsequently included some material from Gotland (Eisenack 1954, 1959, 1974). As yet there has been no systematic study of acritarchs from the Silurian of Gotland, either taxonomically or biostratigraphically, and this contribution is thus the first attempt to determine the composition of assemblages through a substantial portion of the sequence.

From the Vattenfallet section 24 samples have been investigated, of which 14 were processed and analyzed by the Instituto de Investigaciones Palinológicas in León, Spain; the remainder (15.95 m and above 20 m) were processed and analyzed at the Geological Survey of Sweden. The samples came from the standard series of rock samples (see Jaanusson, this volume); the level of the samples is indicated by a black rectangle along the rock column (Fig. 14).

Since variation in the flotation constants may alter the reproducibility of results, the essential steps are listed here.

(1) Except in the centrifugal flotation, constant temperature is not essential; however, to obtain constancy in settling rates, flotation – including breaking the centrifuge – must be carried out at 4° C (\pm 1° C) because, although both viscosity and density of the heavy liquid vary quite considerably in the interval 6 to 25° C, around 4 to 6 degrees they do not vary practically. The heavy liquid is aqueous zincbromide, not stabilized with acid, measured density = 2.0 at 20° C.

(2) Two flotations: the first for thirty minutes at 6500 G, distance between meniscus and bottom of tube 7.5 cm, diameter of tube 16 cm; the second in pointed, heavy duty 12 ml tubes, volume of liquid 10 ml, thirty minutes at 2500 G.

Acritarchs are abundant and preservation is good, although many specimens show the three-dimensional deformation typical for a calcareous matrix. They are colourless to light yellowish or greenish-brown. Apart from most specimens of the *Multiplicisphaeridium piriferum*-group – most of whose thickwalled, mostly cystbearing, central stages are still globular in form – almost all others forms are compressed.

Each sample was processed at least twice and counts were made with two preparations from separate processing runs. The counts thus obtained are very similar and show that neither detectable operator nor laboratory errors were introduced.



Fig. **[**4.



Fig. [5.

Annotated floral list

Apart from the new species described in the taxonomic section of this paper, there are illustrations of all taxa in published literature. The illustrations referred to in the taxonomic discussion below are those which best identify the forms from Gotland. Acritarchs are rather variable in morphology, and different variants often display a patchy distribution pattern in their geographical and chronological provinces. Therefore, the illustrations listed hereafter are not necessarily those of the holotypes of the species.

Group Acritarcha Evitt, 1963

Subgroup Acanthomorphitae Downie, Evitt & Sarjeant, 1963

Baltisphaeridium polygonale (Eisenack, 1931) Eisenack, 1959: cf. Cramer, 1970, Pl. 23:328.

Gracilisphaeridium encantador (Cramer, 1970): Variants with long processes (Fig. 16A); variants with short processes (Fig. 16B).

G. gracile, new species (variants with spatulate to awlshaped processes): See taxonomic section.

"Hystrichosphaeridium" wimani Eisenack, 1968: See Fig. 16C.

Micrhystridium fragile Deflandre, 1947: As M. stellatum, but with processes shorter than the body diameter.

M. longispinosum breve (Downie, 1963) Cramer et al. (herein): This group is morphologically similar to *M. longispinosum parvum*, but is distinguished by the length and greater number of its processes (generally slightly shorter than the body diameter and most commonly fifteen or more), and the thinner, often wrinkled vesicle walls, which are generally finely scabrate (Fig. 16D).

M. longispinosum parvum (Downie, 1963) Cramer et al. n. comb. (herein): cf. Downie, 1963, Pl. 91:2 (Gotland forms generally have a more spherical body than Downie's illustration). Most commonly, the processes number eight to twelve, and are about twice as long as the body diameter. The vesicle wall is smooth to scabrate and relatively stiff.

M. stellatum Deflandre, 1945: This group comprises single-walled forms, of which the body form is determined by the number of processes. These are up to twice as long as the body diameter and are never trabeculate. There are six or more processes. – "*Micrhystridium stellatum*" (large forms), see Fig. 17A.

Multiplicisphaeridium arbusculiferum (Downie, 1963): cf. Downie 1963, Pl. 91:5.

M. brevifurcatum (Eisenack, 1954) Cramer, 1970: cf. Eisenack 1954, Pl. 1:2; Eisenack et al. 1973, figure on p. 547.

"M." sp. a: These forms are similar to but definitely not conspecific with the Ordovician species *Baltisphaeridium brevispinosum* (Eisenack, 1931)



Fig. 16. A. Gracilisphaeridium encantador (Cramer, 1970) Eisenack et al., 1973, long forms. Vattenfallet, Lower Visby Marl, 1.1 m, grid number 760001 A03, Axiomat 85.6×24.5, ×1000. B. Gracilisphaeridium encantador (Cramer, 1970) Eisenack et al., 1973, short forms. Vattenfallet, Upper Visby Marl, 2.1 m, grid number 760002 A03, Axiomat 90.8×28.1, ×1000. C. "Hystrichosphaeridium" wimanii Eisenack, 1968. Vattenfallet, Upper Visby Marl, 4.9 m, grid number 760002 A02, Axiomat 92.1×31.4, ×1000. D. Micrhystridium longispinosum breve (Downie, 1963) Cramer et al. (herein). Vattenfallet, Upper Visby Marl, 2.1 m, grid number 760002 A03, Axiomat 79.8×13.6, ×1000.

Eisenack, 1958, illustrated in Eisenack et al. 1973, figure on p. 73 (for taxonomic considerations, see Kjellström 1971). For a typical form of M. sp. a, see Fig. 19A; it differs from B. brevispinosum in its clearly palmate and relatively shorter processes.

M. denticulatum gotlandicum Cramer, 1970: cf. Eisenack et al. 1973, illustration on page 595; this group also includes forms (about 20 % in total) of *M. d.*

ontariensis Cramer, 1970 (cf. Eisenack et al. 1973, illustration on page 599); transitional forms are rare.

M. denticulatum granulosum, n. subsp.: See taxonomic section.

M. denticulatum piliferum, n. subsp.: See taxonomic section.

Other forms of *M. denticulatum:* Forms characterized by denticulate processes, smooth to microsculptured body and a habitus similar to *M. denticulatum*, without however, being attributable to any of the variants of this group yet described (cf. Eisenack et al. 1973; *M. denticulatum* and following pages).

The group comprising *M. digitatum* (Eisenack, 1938) Eisenack, 1958 (cf. Cramer 1970, Pl. 22:320, round-tipped forms; Pl. 23:321, sharp-tipped forms), *M. cylindricum* Cramer, 1970 (cf. Cramer 1970, Pl. 21:309), and *M. corallinum* (Eisenack, 1959) Eisenack, 1969 (cf. Cramer 1970, Pl. 22:319): Sharp-tipped variants of *M. digitatum* are more abundant in the lower half of the section and the round-tipped forms in the upper half; *M. corallinum* is more profusely branched in the upper portion of the section than in the lower. There are too many transitional forms, and the group is too rare for a reliable frequency count of the components.

M. eoplanctonicum (Eisenack, 1955) Cramer, 1970: cf. Cramer 1970, Pl. 8:129 (illustrated as Baltisphaeridium monterrosae – B. eoplanctonicum).

M. erraticum (Eisenack, 1954) Cramer, 1970: cf. Eisenack 1955, Pl. 315.

M. euernes (Cramer & Díez, 1972): cf. Cramer & Díez 1972, Pl. 32:12 (Gotland forms are entirely transparent, showing neither colour nor structural differentiation between body and processes).

M. fisherii (Cramer, 1968): cf. Cramer 1970, Pl. 7:118 (Gotland forms are preserved similar to *M. euernes*).

M. forquiferum (Cramer & Díez, 1972): cf. Cramer & Díez 1972, Pl. 32:20.

M. forquillum (Cramer & Díez, 1972): cf. Cramer & Díez 1972, Pl. 32:15.

M. meson (Eisenack, 1954) Cramer, 1970: cf. Eisenack 1954, Pl. 1:3 (illustrated as: *Hystrichosphaeridium intermedium*) & cf. Eisenack et al. 1973, figure on p. 681.

M. microcladum (Downie, 1963): cf. Downie 1963, Pl. 91:3.

M. parvirochesterensis (Cramer & Díez, 1972): cf. Eisenack et al. 1973, illustrations b and c on page 719 (Gotland forms are about 50 % larger than the dimensions given in Eisenack et al. 1973).

M. oligofurcatum (Eisenack, 1954) Cramer, 1970: cf. Eisenack 1954, Pl. 1:4; Eisenack et al. 1973, figure on p. 703.

Complex of *M. piriferum* (Eisenack, 1954) Cramer, 1970: The most common variants of this complex are similar to those illustrated by Eisenack 1954, Pl. 1:1; 1965, Pl. 21:1 (these have a smooth body). In addition are found, in about 1 out of 10 specimens, forms with slender smooth processes and with a scabrate body (cf. *M. p. gotlandicum* (Cramer, 1970) in Eisenack et al. 1973, figure on p.



Fig. 17. A. "Micrhystridium stellatum" Cramer et al. (herein). Vattenfallet, Upper Visby Marl, 4.9 m, grid number 760004 A03, Axiomat 78.5×27.9, ×1000. B. Multiplicisphaeridium piriferum (Eisenack, 1954) Cramer, 1970. Vattenfallet, Upper Visby Marl, 5.95 m, grid number 760005 A02, Axiomat 91.8×27.0, ×1000. C. Multiplicisphaeridium ravum (Downie, 1970), cf. Cramer, 1970. Vattenfallet, Upper Visby Marl, 9.5 m, grid number 760007 A01, Axiomat 102.3×26.0, ×1000. D. Deunffa ramusculosa Downie, 1960. Vattenfallet, Högklint b, 18.10 m, grid number 7600013 A02, Axiomat 83.7×21.0, ×1000.

733). In practically all specimens of either variant the processes are distributed without apparent topological preference; however, half a dozen specimens of fragments were found in which the processes appear to be distributed similar to the arrangement in *Cymatiogalea*, that is, in rows, bordering some kind of polygons, see Fig. 17B.

M. ramusculosum insolitum (Cramer & Díez, 1972): cf. Eisenack et al. 1973, figure on p. 757.

M. ravum (Downie, 1970): cf. Cramer 1970, Pl. 10:150 (the material from Gotland comprises two variants; an entirely psilate one and a variant with smooth, or essentially smooth, processes but with a granulate body (Fig. 17C).

M. visbyense (Eisenack, 1959): cf. Eisenack, Cramer & Díez 1973, p. 831 (drawing).

Subgroup Netromorphitae Downie, Evitt & Sarjeant, 1963.

Deunffia furcata Downie, 1960: cf. Cramer 1970, Pl. 1:5 (Gotland forms have process-stems that are quite variable in length; the majority, however, fall between such extremes as illustrated by Cramer 1970, Pl. 1:5 & 1:15).

D. monospinosa Downie, 1960: cf. Cramer 1970, Pl. 1:15.

D. ramusculosa Downie, 1960: See Eisenack et al. 1973 (Fig. 17D).

Domasia amphora Martin, 1969: cf. Cramer 1970, fig. 18:q, r (described as Domasia hermosa).

D. elongata Downie, 1960: cf Cramer 1969, Pl. 1:20 (Gotland forms tend to have strongly trabeculate processes; furthermore, there is no difference in wall thickness between processes and body).

D. limaciforme (Stockmans & Willière, 1963) Cramer, 1970: cf. Stockmans & Willière 1963, Pl. 1:15 (Gotland forms almost always have clearly trabeculate processes; in addition, the processes may be up to 50 % longer than in the illustration referred to).

D. rochesterensis Thusu, 1973: cf. Thusu 1973, Pl. 104:2 (Gotland forms have somewhat thicker primary processes than those in Thusu's illustration).

D. trispinosa Downie, 1960: cf. Downie 1960, Pl. 1:17 (Gotland forms have processes up to twice as long as those in Downie's illustration).

Eupoikilofusa filifera (Downie, 1959): cf. Downie 1959, Pl. 11:6; cf. Eisenack et al. 1970, figure on p. 361.

Leiofusa algerensis Cramer, 1970, Pl. 11:5.

L. sp. a: A species that does not belong to either of the above Leiofusa species, but cannot be identified more closely.

L. tumida Downie, 1959: cf. Downie 1959, Pl. 11:5.

Subgroup Polygonomorphitae Downie, Evitt & Sarjeant, 1963.

Veryhachium europaeum Stockmans & Willière, 1960: This group comprises single-walled forms with a tetragonal body and a process at each corner. The processes are about as long as the short edge of the body. The ectoderm is entirely sculptureless and the processes are never trabeculate.

V. trispinosum (Eisenack, 1938) Deunff, 1954: This morphological group comprises smooth forms with a convex, straight or concavely triangular body, and with processes of a length that varies from approximately 50 to 200 % of that of a body edge. In contrast to *Domasia* spp., the processes are never trabeculate.

Veryhachium valiente Cramer, 1964: This group comprises single-walled forms with a square to rectangular body and with a process at each corner. The processes are about as long as the short edge of the body. The ectoderm is entirely sculptureless and the processes are never trabeculate.

Subgroup Herkomorphitae Downie, Evitt & Sarjeant, 1963.

Cymatiosphaera granulosa, n. sp.: See taxonomic section.

C. heloderma Cramer & Díez, 1972: cf. Cramer & Díez 1972, Pl. 32:22.

C. wenlockia Downie, 1959: cf. Downie 1959, Pl. 11:4.

Dictyotidium spp.: See Fig. 18A.

Subgroup Pteromorphitae Downie, Evitt & Sarjeant, 1963.

Duvernaysphaera aranaides (Cramer, 1964) Cramer, 1970 b: cf. Eisenack et al. 1976, figure on p. 239.

Pterospermella martinii (Cramer, 1967): cf. Cramer & Díez 1968, Pl. 21:82–87.

P. sp.: A species not identical with P. martinii but not identifiable at present.

Subgroup Uncertain

Tunisphaeridium tentaculaferum (Martin, 1966) Cramer, 1970: cf. Deunff & Evitt 1968, Pl. 1:1–12.

Remarks on frequency of the acritarchs

Acritarchs are present in great abundance in every sample up to 20.5 m. Higher in the sequence the frequency decreases considerably, and the slides prepared from the uppermost samples contain only a few specimens (27.0–27.1 m and Högklint d) or are barren (26.8–26.9 m). The decrease in frequency is also reflected in taxonomic diversity, which is high in the main lower part of the section but low in the upper part of Högklint b and in Högklint c.

Some common species (forming at least 10 per cent of the acritarchs in several samples) show proportionally small fluctuations in frequency throughout most of the section (*Domasia elongata*, *Micrhystridium longispinum parvum* and *Multiplicisphaeridium denticulatum gotlandicum*) whereas the relative frequency of some other common species (*Domnasia trispinosa*, *Veryhachium trispinosum*) fluctuates greatly from sample to sample. Short forms of *Gracilisphaeridium encantador* (up to 42 per cent) and *Multiplicisphaeridium ramusculosum* (up to 11 per cent) show high frequencies in the lower, calcilutitic part of the Upper Visby Marl and *Domasia limaciformes* (up to 26 per cent) together with *Veryhachium europaeum* (up to 19 per cent) in the Högklint Limestone. In Högklint *b Multiplicisphaeridium corallinum* (up to 16 per cent) and the round-tipped forms of M. digitatum (up to 17 per cent) are abundant in some beds. No other species forms 10 per cent or more of acritarchs in any sample.

Description of selected taxa

Gracilisphaeridium encantador (Cramer, 1970) Eisenack et al., 1973 Fig. 16A-B

1970 Baltisphaeridium encantador – Cramer, pp. 189–190, Pl. 19:296–299, fig. 61. 1972 Baltisphaeridium encantador – Cramer & Díez, p. 147. 1973 Gracilisphaeridium encantador – Eisenack et al., pp. 513–514, Pl. 4:A-C.

Discussion. – This species shows two morphological maxima within an array of transitional forms. We have called these: "G. encantador, long forms" (Fig. 16A), and "G. encantador, short forms" (Fig. 16B). As long forms we have classed all specimens whose process length exceeds the body diameter. These have, in general, long, well developed loops, three or four per process. Furthermore, the number of processes is lower than in the short forms. The short forms have processes of a length equal to, or shorter than, the body diameter. The loops are quite small. (It appears logical to us that the unlooped specimens – that is, specimens whose processes show an even number, six or eight, of short simple palmate pinnae – represent forms of which the loops are broken). In fact, all kinds of combinations of loops and palmate pinnae may occur on the same specimen. Both long and short forms always have a sculptured body. This feature distinguishes fragments of G. encantador from Micrhystridium longispinosum breve (Fig. 16D).

Distribution. – In addition to Vattenfallet, long forms of G. encantador are known from the very latest Llandoverian Alger Shale and equivalents of Ohio and Kentucky (Cramer & Díez 1972); from the early Wenlockian Rochester Shale of Ontario and New York; from the Wenlockian portion of the Ekwan Formation (both in outcrop and subsurface material) around the southern part of the Hudson Bay, Canada.

Gracilisphaeridium gracile n. sp.

Fig. 18B

Holotype. - Specimen figured as Fig. 18B, Vattenfallet, Upper Visby Marl, 2.1 m.

Diagnosis. – Central portion of vesicle spherical, clearly differentiated from the processes. Process distribution regular and without apparent topological preference. Approximately fifteen heteromorphic processes visible in optical section. The morphology of the processes is rather variable: some have three or four loops (as in *G. encantador*), some have an even or uneven number of slender, whiplike palmate pinnae (the uneven number suggests that these pinnae are not – or not all – fragments of damaged loops), and some of the processes have one single long whiplike pinna. The latter processes are awl-shaped, invertedly club-shaped, or have an elongated, inverted bulbous form. The final whiplike pinna is situated on the extreme tip of these processes.



Fig. 18. A. Dictyotidium sp. Vattenfallet, Upper Visby Marl, 21.0 m, grid number 760002 A03, Axiomat 89.1×24,8 ×1000. B. Gracilisphaeridium gracile n. sp., holotype. Vattenfallet, Upper Visby Marl, 2.1 m, grid number 760002 A03, Axiomat 84.5×26.5, ×1000. C. Multiplicisphaeridium denticulatum granulosum n. subsp., holotype. Vattenfallet, Upper Visby Marl, 4.9 m, grid number 760004 A02, Axiomat 89.7×31.3, ×1000. D. Cymatiosphaera granulosa n. sp., holotype. Vattenfallet, Upper Visby Marl, 2.1 m, grid number 760002 A03, Axiomat 88.6×18.1, ×1000.

The processes which bear loops and whiplike pinnae, or which bear solely whiplike pinnae, are normally slenderly columnar, but some are awl-shaped, or even bulbous. The process stems are hollow, and the process cavities are in free and direct communication with the central vesicle cavity, or - in forms which bear a cyst - may be separated from the vesicle cavity by the continuation of the endoderm, but apparently without a union structure. In forms without a cyst, the vesicle wall is unilayered and of uniform thickness (about 0.5 μ m). The sculpture distribution on the ectoderm surface is subregular: the processes are psilate, but the body portion of the vesicle is ornamented by a variable sculpture of elements ranging from microscabrate to scabrate. (The sculpture is identical to that of *G. encantador* illustrated in Eisenack et al. 1973: Pl. 4.)

Internal cysts are spherical, more rigid and darker than the ectoderm. The endoderm surface is smooth, and the cyst wall is about 1 μm thick.

Dimensions. – Diameter of body part of vesicle, up to 40 μ m; diameter including processes, up to 75 μ m (generally 50 to 60 μ m).

Distribution. – Early Wenlockian of Gotland; Wenlock portion of Ekwan Formation, Hudson Bay area, Canada.

Multiplicisphaeridium denticulatum granulosum n. subsp. Fig. 18C

Holotype. - Specimen figured as Fig. 18C, Vattenfallet, Upper Visby Marl, 3.0 m.

Diagnosis. - Central portion of the vesicle spherical, rigid, clearly differentiated from the processes. Processes essentially homogeneous and regularly distributed, varying in number from three to more than twenty; most commonly there are about eight. They are long, slender, and quite flexible, originating from the body without a basal thickening or expansion, and standing perpendicular to the body. The branching pattern is, as in all variants of M. denticulatum, simply manate, but varies in complexity from unbranched to slightly branched. All pinnae are concentrated at the distal portions of the processes. Processes and large pinnae are hollow and their cavities are in free and direct communication with the body cavity. In simple stages, the vesicle wall is unilayered, and the ectoderm surface shows a subregular sculpture distribution in that the processes are psilate or bear a sparse cover of widely spaced microdenticules of similar denticulate elements whose elevation does not exceed 0.3 μ m, but the body surface is covered by a dense pattern of roundedly granulate to vertucate sculptural elements. (These elements are not of the denticulate kind.) The ectoderm is about 0.5 μ m thick. Cysts are spherical, closely concentric to the body ectoderm. The endoderm has a smooth surface, and its thickness is about 1 μ m. It is considerably less transparent than the ectoderm and much more rigid.

Dimensions. - Overall diameter approximately 120 µm.

Distribution. – Early Wenlockian of Gotland; Wenlockian portion of Ekwan Formation, Hudson Bay area, Canada.

Comparison. – The granulate to vertucate sculpture on the body of M. d. granulosum distinguishes it from other variants of M. denticulatum.

Multiplicisphaeridium denticulatum piliferum, n. subsp. Fig. 19B

Holotype. - Specimen figured as Fig. 19B, Vattenfallet, Upper Visby Marl, 3.0 m.

Diagnosis. – Central portion of the vesicle spherical, rigid, clearly differentiated from the processes. Processes homomorphic and distributed regularly. There are about ten

processes. They are quite long, slender, and fairly stiff and originate from the body without basal thickenings, union structures, or expansions, and stand perpendicular to the body. The manate branching pattern varies in complexity from unbranched to rather profusely branched. Pinnae are concentrated at the distal portion of the processes. Processes and pinnae are hollow and their cavities are in free and direct communication with the body cavity. The vesicle wall is unilayered, and shows a quite subregular



Fig. 19. A. "Multiplicisphaeridium" sp. a. Vattenfallet, Upper Visby Marl, 9.5 m, grid number 760007 A01, Axiomat 93.3×26.0, ×2000. B. Multiplicisphaeridium denticulatum piliferum n. subsp., holotype. Vattenfallet, Upper Visby Marl, 4,9 m, grid number 760004 A03, Axiomat 77.1×24.6, ×1000. sculpture distribution in that the body wall is psilate to microscabrate (elements less than 0.3 μ m in height and width). The processes are smooth. A second sculpture is distributed over the body, consisting of widely spaced elements of the baculate to gemmate kind. These elements seem to be solid and are up to 4 μ m high, but usually smaller (about 2 μ m). No endoderms, cysts or excystment structures identified.

Dimensions. - Overall diameter approximately 120 µm.

Distribution. - Early Wenlockian of Gotland.

Cymatiosphaera granulosa n. sp. Fig. 18D

Holotype. - Specimen figured as Fig. 18D, Vattenfallet, Upper Visby Marl, 2.1 m.

Diagnosis. – Central body variable in form: spherical to polygonal, but most commonly spherical. The campi are of variable dimensions and outline, but tend to be subsquare to irregularly pentagonal. The surface of the campi is regularly and densely granulate to (micro)verrucate, thus creating a sunken reticulum. The depressions have a depth of about 1 μ m. The muri are normally straight-based and show smooth to slightly crenulate to almenate crests. They are smooth and show no primary folds. The body wall is about 2 μ m thick; the muri are less than 0.3 μ m thick.

Dimensions. – Body diameter 40 to 60 μ m.

Distribution. – Early Wenlockian of Gotland; Wenlockian portion of Ekwan Formation, Hudson Bay area, Canada.

Comparison. – C. heloderma Cramer & Díez, 1972 from the latest Llandoverian Alger Shale of Ohio has a foveolate sculpture on the body and often has membranes with pronounced crenulate crests; Variants of *C. granulosa* with a total of two campi may be confused with certain forms of *Pterospermella*, such as, e.g. *P. martinii* (Cramer, 1967) Eisenack et al., 1973, but are distinguished by the granulate body sculpture and absence of an equatorial cingulum-like structure.

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