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 thick-walled, mostly cyst-bearing, 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. 14.
Fig. 15.
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 Acanthomorphae Downie, Evitt & Sarjeant, 1963


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

G. gracile, new species (variants with spatulate to awl-shaped 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.


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

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).


*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. 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).


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.
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. 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)).


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


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. rochasterensi s 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).


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


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.


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

*Dictyotidium* spp.: See Fig. 18A.


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

Subgroup Uncertain


**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 ramuscosulum* (up to 11 per cent) show high frequencies in the lower, calcilutitic part of the Upper Visby Marl and *Domnasia 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

1972 *Balitisphaeridium encantador* – Cramer & Diez, 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 Llandoveryan Alger Shale and equivalents of Ohio and Kentucky (Cramer & Diez 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.
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 μm). 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. encantadorillustrated 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 μm; diameter including processes, up to 75 μm (generally 50 to 60 μm).

**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 μm, but the body surface is covered by a dense pattern of roundedly granulate to verrucate sculptural elements. (These elements are not of the denticulate kind.) The ectoderm is about 0.5 μm thick. Cysts are spherical, closely concentric to the body ectoderm. The endoderm has a smooth surface, and its thickness is about 1 μm. 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 verrucate 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. subspp., 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 \( \mu \)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 \( \mu \)m high, but usually smaller (about 2 \( \mu \)m). No endoderms, cysts or excystment structures identified.

**Dimensions.** – Overall diameter approximately 120 \( \mu \)m.

**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 \( \mu \)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 \( \mu \)m thick; the muri are less than 0.3 \( \mu \)m thick.

**Dimensions.** – Body diameter 40 to 60 \( \mu \)m.

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

**Comparison.** – *C. heloderma* Cramer & Diez, 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. martini* (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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**REFERENCES**


