'HYSTRICHOSPHERES' (ACRITARCHS) AND SPORES OF THE WENLOCK SHALES (SILURIAN) OF WENLOCK, ENGLAND

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ABSTRACT. In the examination of twenty-five assemblages obtained from samples from the Wenlock Shales of Wenlock, several thousands of 'hystrichospheres' (acritarchs) and about 100 spores were found. These are allocated to sixteen genera and over sixty-five species and varieties are recognized. The restricted ranges of some of the species and the marked variation in the proportion of others present allow these assemblages to be grouped into three main types. One assemblage type is confined to the Lower Wenlock Shales (Buildwas Beds), one to the Middle Wenlock Shales (Coalbrookdale Beds), and one to the Upper Wenlock Shales (uppermost Coalbrookdale and Tickhill Beds).

SOME account of the occurrence of 'hystrichospheres' (acritarchs) in the Wenlock Shales has already been given by the author (Downie 1959, 1960). The latter paper was concerned with the description of a few novel forms from the lowest part of the Wenlock Shales; the former dealt fully with an assemblage from the middle part. The present paper is more comprehensive, 'including the description of hystrichosphere' assemblages from twenty-five samples spaced throughout the Wenlock Shales and an account of the differences in the character of these assemblages as they follow each other through the rock succession.

New facts about the affinities of the hystrichospheres have necessitated their reclassification and proposals put forward by Downie, Evitt, and Sarjeant (1963) have been adopted in this paper. The name 'hystrichosphere' is no longer appropriate for the forms dealt with here and is replaced by the term 'acritarch' (Evitt 1963): formal classification into orders is replaced by a less rigid supra-generic grouping not based on type genera.

Location of the samples. The thickness of the Wenlock Shales below Wenlock Edge is difficult to estimate accurately. Pocock *et al.* (1938) estimate it to be about 1,000 feet; measurements made by the author west of Much Wenlock indicated 950 feet and this figure is used in this account. The difficulty in measuring the thickness is partly due to the absence of a continuous section through the formation, indeed some parts of the sequence are rarely exposed and in order to get samples more or less evenly spaced throughout the sequence the sampling localities are spread for quite a considerable distance along the strike (text-fig. 1). Because of this and the difficulty in accurately measuring the thickness there is some uncertainty about the precise position of the samples in the sequence. Their positions (text-fig. 1) are based on direct field measurements when circumstances permitted, and in other instances on geometric calculations. Although the possible errors for some of the samples in the middle of the sequence may be about 20 feet plus or minus, there is no doubt about the relative positions of any of the samples, and the assemblages obtained from them can be placed in the correct chronological order.

In general the spacing of the samples is about 100 feet. Closer spacing would have

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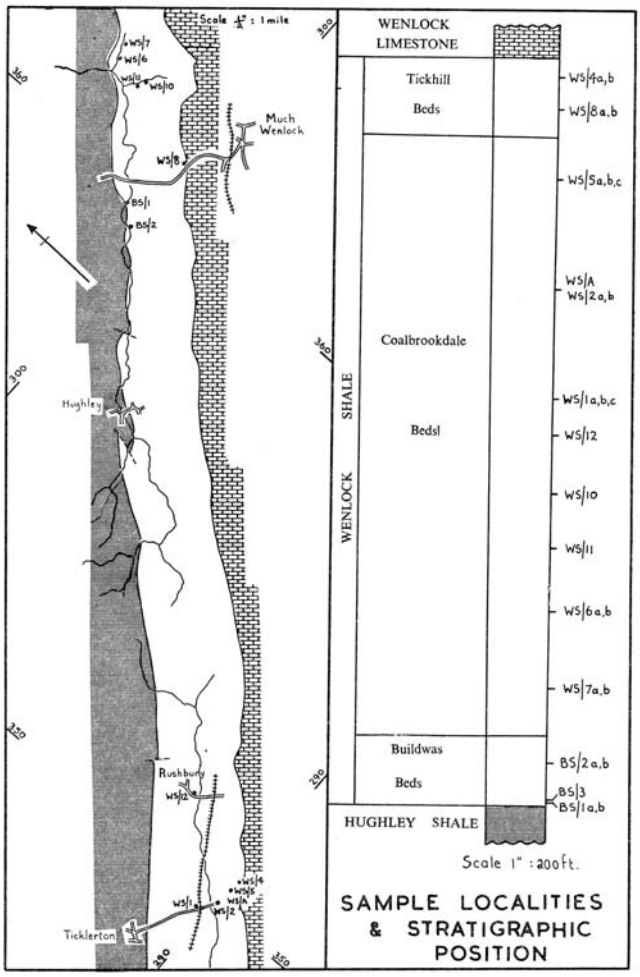


TEXT-FIG. 1. Map and section showing the location of the samples collected.

been ideally more desirable but the results show that except near the base and near the top, where the spacing is already fairly close, the character of the assemblages changes only slightly. At a number of localities two or even three samples have been taken at vertical intervals of about 1 or 2 feet in order to check that the nature of the microflora was not varying erratically over short periods. In every case the results confirmed the relative constancy of the character of the assemblages over these short ranges.

The localities from which samples were collected are as follows:

BS/1a Soft grey shale, 4 feet above base of Wenlock Shales, Harley Brook, 100 yards downstream from bridge at Domas. G.R. 33/596008.
BS/1b As for BS/1a, but 5 feet above base of Wenlock Shales.
BS/3 As for BA/1a, but 6 feet above base of Wenlock Shales.
BS/2a Calcareous nodule, *c.* 55 feet above base of Wenlock Shales, Harley Brook, 150 yards upstream from bridge at Domas. G.R. 33/594006.
BS/2b As for BS/2a, but 56 feet above base of Wenlock Shales.
WS/1a Somewhat weathered shale, roadside exposure where railway crosses road from Ticklerton to Eaton. G.R. 32/497901.
WS/1b One foot above WS/1a.
WS/1c One foot above WS/1b.
WS/A Calc. grey mudstone, section in lane behind Eaton Church. G.R. 32/501900.
WS/2a Three feet below WS/A.
WS/2b One foot above WS/2a.
WS/4a Grey mudstone, lane section above Eaton Church, 105 feet below Wenlock Limestone.
WS/4b One foot below WS/4a.
WS/5a Calc. grey mudstone, lane section above Eaton Church, 89 feet stratigraphically below WS/4a. G.R. 32/505899.
WS/5b As for WS/5a.
WS/5c One foot below WS/5a.
WS/6a Grey mudstone, small stream section half mile east of old mill at Sheinwood. G.R. 33/624028.
WS/6b One foot above WS/6a.
WS/7a Grey mudstone, small stream section 250 yards east of old mill at Sheinwood. G.R. 33/618027.
WS/7b One foot above WS/7a.
WS/8a Calcareous grey mudstone, road section at Harley Hill, 30 feet below base of Wenlock Limestone. G.R. 33/610003.
WS/8b One foot above WS/8a.
WS/10 Grey mudstone, stream section in Whitwell Coppice, 500 yards above junction with Sheinton Brook. G.R. 33/6120021.
WS/11 Grey mudstone, stream section in Whitwell Coppice, 70 feet stratigraphically below WS/10. G.R. 33/619020.
WS/12 Grey mudstone, road section 200 yards south of Rushbury Church. G.R. 32/514918.

Treatment of the samples and general character of the residues. The samples were prepared by first removing the carbonates in dilute hydrochloric acid and then dissolving the silicates in hydrofluoric acid. Subsequent oxidization was generally omitted. The Wenlock Shales consist of a relatively uniform series of more or less calcareous grey mudstones which readily break down when treated with hydrochloric acid followed by hydrofluoric acid.

The residues which are obtained contain abundant acritarchs; only one sample was checked quantitatively: this yielded about 5,000 acritarchs per gramme of rock. Accompanying the acritarchs was a smaller number of spores, chitinozoa, scolecodonts, graptolite fragments, and organic debris of various kinds. Only the acritarchs and spores are dealt with in this paper.

DISTRIBUTION OF THE SPORES

There is as yet no generally agreed principle whereby spores are to be separated on an objective morphological basis from certain of the acritarchs and in the Lower Palaeozoic taxonomic procedure has not been stabilized. In this paper only those microfossils which are indubitably the reproductive organs of higher plants are considered as spores, the

presence of triradiate marks on one surface being the main determining character. But a number of other forms are present in the Wenlock Shales which, although lacking this character, in other ways resemble the spores of plants more highly organized than the algae. They are nevertheless grouped with the acritarchs because of the difficulty of distinguishing acritarchs from spores without triradiate marks.

Spores in the sense defined above are not numerous; altogether just over a hundred were observed, all belonging to one species with a single exception. Although they are never common the spores appear to range throughout the Wenlock Shales and may form as much as 4 per cent. of the whole assemblage. Table 15 shows how the proportion present varies and it will be seen that they tend, in general, to be a little more common in the higher than in the lower beds.

All the spores observed, except one, belong to the species *Punctatisporites? dilutus* Hoffmeister, previously described only from the Lower Silurian of Libya (Hoffmeister 1959). The Wenlock forms (Plate 92, fig. 13) agree almost exactly with those from Libya and many show the darkening at the equator described by Hoffmeister. In no instance, however, is this sufficiently clearly set off from the rest of the exine to justify attributing any of the specimens to *Ambitisporites avitus* which accompanies *P.? dilutus* in the Libian assemblage.

The only other spore with triradiate markings was found in WS/12 and was a form of *Lophotriletes* somewhat similar to *L. minuscula* Naumova but with thinner exine and with an ornament of fine irregular verrucae. The distribution of the spores is shown in Table 3.

SYSTEMATIC DESCRIPTIONS AND DISTRIBUTION OF THE ACRITARCHS

Acritarchs always form the greater part of the assemblages. They vary greatly in shape and have been divided into a large number of species and genera: these are grouped according to their more obvious morphological features.

Group ACRITARCHA Evitt 1963
Subgroup SPHAEROMORPHITAE Downie, Evitt, and Sarjeant 1963

(1) *Smooth spheres* (*leiospheres*)

These fossils have in the past been classified with the hystrichospheres (Eisenack 1958) but they are a polyphyletic group, few if any having any affinity with the dinoflagellates. Although most are likely to be planktonic organisms of various kinds or their reproductive stages, others may well be spores of more highly organized plants.

Several thousands were observed in the Wenlock Shales where they form from 20 to 99 per cent. of the total assemblage, but generally about one-third (Table 15). It is not known what significance, if any, is to be attached to these fluctuations in the proportions of leiospheres present. The increases may be due to chance 'flooding' of the sample from a local source or to secular changes in the composition of the plankton. The complete dominance of samples from locality WS/1 by leiospheres was so remarkable that its reality was checked in three separate rock samples from the locality. All were similar in that they yielded no spores or spiny acritarchs. Unfortunately no

unweathered samples could be got at this locality and the effects of weathering cannot be eliminated as a factor in producing these unusual samples. However, it may be significant that both the preceding and succeeding samples show a much higher content of leiospheres than average.

There is no notable variation in the species of leiospheres present throughout the succession. By far the most common is *Leiosphaeridia wenlockia* Downie, which is always at least twice as common as all the others considered together and may be twenty times as common. In extending observations of this species throughout the Wenlock Shales no need has arisen to alter the range of variation stated in Downie (1959) but it should be noted that pl. 3, fig. 4, in that paper shows a common and distinctive variant, probably due to preservation, having its surface distorted into numerous swellings and its interior occupied by a number of pyrite grains. It is doubtful if more than one or two of the many hundreds of specimens examined have a pylom and since the wall may sometimes be a little thicker or thinner than the 1 μ stated in the diagnosis it is very doubtful if *Protoleiosphaeridium orbiculatum* Staplin is a distinct species.

Leiosphaeridia cf. *microsystis* (Eisenack) Downie 1959, although rare by comparison with *L. wenlockia*, is generally quite common and has been found to occur throughout the Wenlock Shales. Its size range is now known to be from 40 to 75 microns which brings it into conformity with Eisenack's typical *L. microcystis*; there is, however, good reason for maintaining a distinction since the Wenlock forms never appear to have a pylom but open by splitting cleanly along a great circle (Downie, 1959, pl. 12, fig. 1).

Next in importance is *Leiosphaeridia* sp. cf. *Protoleiosphaeridium diaphanum* Staplin which probably also ranges throughout the Wenlock Shales generally in smaller but occasionally in slightly greater numbers than *L.* cf. *microcystis* (see Table 1). They closely resemble the species described by Staplin (1961) but are larger, 50 to 80 microns as against 40 to 50 microns for the Devonian forms.

There are a few other forms present but these are rare not being represented by more than one or two in populations of about a thousand. They appear to be of little interest. The distribution of the leiospheres is shown in Table 1.

TABLE 1. Recorded occurrences of *Leiosphaeridia*

Locality	BS/1	BS/3	BS/2	WS/7	WS/6	WS/11	WS/10	WS/12	WS/1	WS/2	WS/5	WS/8	WS/4
L. wenlockia	687	61	71	178	146	45	35	90	148	1,202	122	213	326
L. cf. *microcystis*	80	38	10	31	2	8	5	19	26	37	4	11	61
L. cf. *diaphanum*	..	15	..	4	5	5	3	6	1	43	9	7	3
L. spp.	5	..	..	2	..	1	..	1	..	4	2	4	3

(2) *Ornamented leiospheres*

In every assemblage there is a number of microfossils resembling the leiospheres described above but ornamented with solid spines and tubercles which are short in relation to the size of the body. They are provisionally placed in the genus *Lophosphaeridium* Timofiev and in general form about 3 per cent. of the whole assemblage.

Seven species are considered here; others exist but are too rare to be of any importance. Of these seven species, four, *L.* sp. cf. *P. papillatum* Staplin, *L. triangularum* sp. nov., *L. granulosum* (Staplin), and *L. citrinum* sp. nov., range throughout the Wenlock Shales,

L. granulosum apparently extending into the Devonian. Of the three other species, one, *L. microspinosum* (Eisenack), has been found only in the lower and middle part of the Wenlock Shales, and, by Eisenack, and in the Upper Llandovery of Estonia. The existence of a similar form in the Upper Ludlow (Eisenack 1955) suggests, however, that the species may range right through. The other two species are probably characteristic of the upper levels of the Wenlock Shales, *L. pilosum* sp. nov. was found only in samples from locality WS/4, and *L.* sp. cf. *P. cryptogranulosum* Staplin was confined to this locality also. The distribution of these forms is shown in Table 2.

TABLE 2. Recorded occurrences of *Lophosphaeridium*

Locality	BS/1	BS/3	BS/2	WS/7	WS/6	WS/11	WS/10	WS/12	WS/1	WS/2	WS/5	WS/8	WS/4
L. cf. *cryptogranulosum*	..	..	..	..	..	..	..	..	..	..	..	..	11
L. granulosum	63	1	4	8	25	3	3	6	2	24	13	8	13
L. citrinum	12	..	3	4	7	..	..	..	..	8	1	..	7
L. cf. *papillatum*	2	1	5	2	..	1	..	1	..	5	2	2	12
L. triangulatum	..	1	..	..	..	..	1	1	..	..	..	..	2
L. pilosum	..	..	..	..	..	..	..	..	..	..	..	..	8
L. microspinosum	2	7	6	2	2	..	..	..	..	8	..	..	..

SYSTEMATIC DESCRIPTIONS

Genus LOPHOSPHAERIDIUM Timofiev 1959

Type species. Designated here: *L. rarum* Timofiev 1959.

Remarks. Timofiev did not designate a type species for his genus, the first named of his two species is selected here. The genus is characterized by its solid tubercules which distinguish it from *Leiosphaeridia*. Some forms occurring in the Wenlock with short solid spines with rounded or capitate ends are also included here provisionally.

Lophosphaeridium granulosum (Staplin)

Synonym. Protoleiosphaeridium granulosum Staplin 1961.

Remarks. Several hundred individuals were seen from samples ranging throughout the Wenlock Shales. They appear to be identical to the Devonian species, although they may range up to 40 microns in size.

Lophosphaeridium sp. cf. *P. cryptogranulosum* Staplin

Remarks. This form, of which eleven examples were found in samples from locality WS/4, resembles in most respects *Protoleiosphaeridium cryptogranulosum* from the Devonian, but being generally about 25 microns in size, it is consistently larger. Its outline is always subquadrate and it is quite possible that though no triradiate marks were seen, that this form is in fact the spore of a higher plant.

Lophosphaeridium citrinum sp. nov.

Plate 92, fig. 3

Diagnostic. Vesicle ellipsoidal, lemon yellow in colour. Ornament of capitate spine

(pilae). Body size about 40 by 30 microns; spine length 1 to 2 microns, spacing 1 to 2 microns.

Holotype. Slide 5, position 080.450.

Locality. Wenlock Shales, WS/4a.

Remarks. The species is not uncommon, over forty individuals having been found, and it appears to range throughout the Wenlock Shales. It is clearly a leiosphere since most of the examples show a pylom whose diameter is about 20 per cent. of the test length.

Lophosphaeridium pilosum sp. nov.

Plate 92, fig. 2

Diagnosis. Vesicle thin-walled ellipsoidal subcircular. Ornament of closely spaced short solid spines. Body colour lemon-yellow. Body size 35 to 40 microns, spine length 3 to 4 microns, spacing 1 micron.

Holotype. Slide 9, position 000.630.

Locality. Wenlock Shales. WS/4a.

Remarks. This species, of which eight examples are known, has been found only in samples from locality WS/4. It resembles *P. microsaetosum* Staplin but is more ellipsoidal and has a denser pile of spines. It also bears some resemblance to *L. citrinum* sp. nov., but the ornament is saetose and generally denser.

Lophosphaeridium sp. cf. *P. papillatum* Staplin

Plate 92, fig. 12

Remarks. This species is known from over thirty specimens spread throughout the Wenlock Shales. The body is a pale yellowish-green colour and circular to subtriangular in outline. It may well be a spore from one of higher plants but no triradiate marks have been seen. Its ornament consists of short solid spines 1 to 2 microns in length and 1 to 2 microns apart. It resembles both *P. papillatum* and *P. microsaetosum* of Staplin but is rather smaller than either, the body measuring from 18 to 28 microns. Furthermore, the subtriangular outline is distinctive.

Lophosphaeridium triangulatum sp. nov.

Plate 92, fig. 1

Diagnosis. Vesicle subtriangular in outline, pale yellow-green in colour. Ornament of solid spines up to 5 microns long and 5 microns apart. Body size from 18 to 25 microns.

Holotype. Slide 8, position 050.620.

Locality. Wenlock Shales, WS/4a.

Remarks. This species is rare, only five examples having been found, but it probably ranges throughout the Wenlock Shales. It resembles closely *L.* cf. *papillatum*, differing only in size and spacing of the spinose ornament. Like *L.* cf. *papillatum* it may well be a spore.

Lophosphaeridium microspinosum (Eisenack)

Plate 92, fig. 11

Synonyms. *Hystrichosphaeridium microspinosum* Eisenack 1954.
Baltisphaeridium microspinosum Downie 1959.

Remarks. This species with its ornament of short solid spines and pilae must be grouped with the forms discussed above since it differs markedly from the typical forms of *Baltisphaeridium* with their relatively long hollow spines. Twenty-eight examples have been found in the Wenlock Shales most of them in the lower horizons and none above locality WS/A, about 300 feet from the top. This is in accord with the occurrence of Eisenack's type material in the Upper Llandovery, but the occurrence of a similar form in the Upper Ludlow suggests that it may eventually turn up in the Upper Wenlock.

Subgroup PTEROMORPHITAE Downie, Evitt, and Sarjeant 1963

Only eleven specimens of acritarchs with a characteristic equatorial flange were found, all belonging to the genus *Pterospermopsis* which appears to range throughout the Wenlock Shale, but is probably more common in the upper part (see Table 3). Three types were found, the most common being *P.* cf. *onondagaensis* Deunff (Downie 1959). The others are a small colourless form from locality WS/2 and a form with a quadrate outline from WS/12.

TABLE 3. Recorded occurrences of spores, *Tasmanites*, and *Pterospermopsis*

Locality	BS/1	BS/3	BS/2	WS/7	WS/6	WS/11	WS/10	WS/12	WS/1	WS/2	WS/5	WS/8	WS/4
Punctatisporites? dilutus	..	1	..	7	22	3	1	4	..	10	6	12	41
Lophotriletes sp.	..	..	..	..	..	..	..	..	..	..	..	..	1
Tasmanites spp.	..	3	..	3	1	1	1	..	..	30	..	5	1
Pterospm. cf. *onondagaensis*	..	1	..	..	..	..	..	..	..	6	2	1	..
Pterospm. spp.	..	..	..	..	..	..	..	1	..	1	..	..	..

Subgroup HERKOMORPHITAE Downie, Evitt, and Sarjeant 1963

The only acritarch genus present with flanges dividing the surface into polygonal fields is *Cymatiosphaera* which is fairly common throughout the Wenlock Shales forming up to 4 per cent. of the whole assemblage. The commonest species, *C. wenlockia*

TABLE 4. Recorded occurrences of *Cymatiosphaera* spp.

Locality	BS/1	BS/3	BS/2	WS/7	WS/6	WS/11	WS/10	WS/12	WS/1	WS/2	WS/5	WS/8	WS/4
C. octoplanus	..	2	..	2	2	..	1	1	..	8	..	1	3
C. cubus	2	1	1	3	..	..	1	4	..	9	3	2	2
C. prismatica	..	1	..	..	..	..	..	..	..	3	..	..	..
C. pavimenta	..	..	..	..	..	2	..	..	..	14	1	1	2
C. wenlockia	3	2	..	3	2	2	1	3	..	7	1	..	7
Other spp.	4	1	1	2	2	..	..	..	..	1	1	2	..

Downie, and the closely related *C. cubus* Deunff and *C. octoplana* Downie, appear to be present through the whole sequence. Among the other species present *C. pavimenta*

(Deflandre) and *C. prismatica* Deunff have been found only in the middle part of the sequence. The latter is, however, rare, and was, furthermore, first described from the Devonian so that it has little stratigraphical significance. Other forms found are too rare to merit description at present.

Subgroup NETROMORPHITAE Downie, Evitt, and Sarjeant 1963

This group of acritarchs with distinctly elongate vesicles includes the genera *Leiofusa*, *Deunffia*, and *Domasia*.

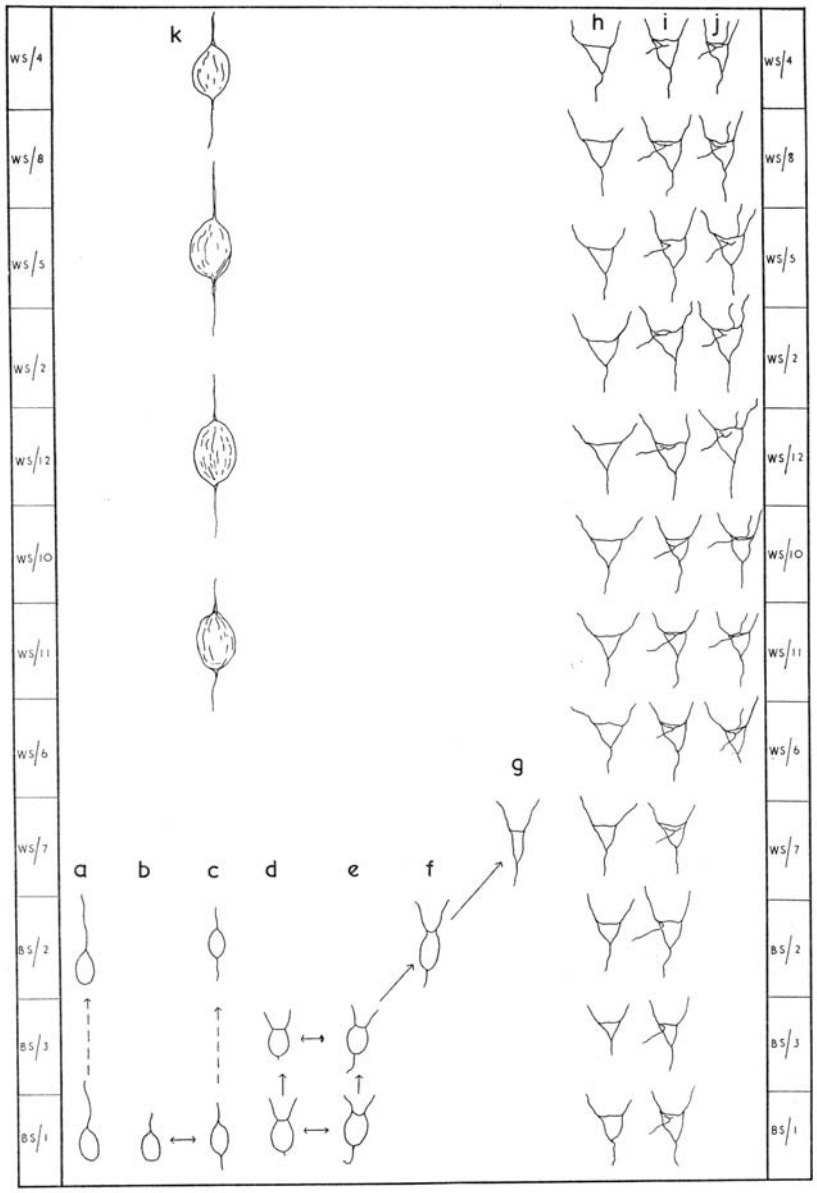
The leiofusids are represented by *L. filifera* Downie and *L. tumida* Downie which differ only in the proportions of the body. Since publishing the first account of these forms it has been found that there is complete gradation between the two and that intermediate forms predominate at some horizons (see Table 5). The stouter bodied

TABLE 5. Proportion of different types of leiofusids expressed as percentage total number of leiofusids present

Locality	*L. filifera* narrow body breadth/length 20–35%	*L. filifera* wide body breadth/length 35–65%	*L. tumida* spherical body breadth/length +65%
WS/4	18	70	12
WS/8	50	29	21
WS/5	90	10	..
WS/2	70	20	10
WS/1	..	..	..
WS/12	84	..	16
WS/10	86	7	7
WS/11	92	4	4
WS/6	100	..	..
WS/7	100	..	..
BS/2	100	..	..
BS/3	100	..	..
BS/1	..	..	..

forms are not, however, always present, being confined to locality WS/11 and higher levels where they increase in importance at the expense of the slim-bodied forms, and eventually become dominant. These leiofusids, of which several hundred were seen, tend as a whole to become abundant in the upper levels and in sample WS/4b form over 14 per cent. of the total assemblage.

A difficult taxonomic problem is set by the few small leiofusids that occur in the Buildwas Shale. Four examples were found, all measuring about 40 microns in overall length. They are morphologically almost identical to small specimens of *L. tumida* which, however, usually exceeds, often greatly, 100 microns in length. In the Buildwas Shale these small leiofusids are associated with *Deunffia* and *Domasia* and in body size, shape, and texture all three are identical (text-fig. 2). There seems little doubt that they are closely related and that these small leiofusids are homoeomorphs of *L. tumida* more closely related to *Deunffia* and *Domasia* than to *L. filifera*. Apart from slight, and



TEXT-FIG. 2. The stratigraphic distribution and possible relationships of some acritarchs. a, *Deunffia monospinosa*; b, *Deunffia brevispinosa*; c, *Leiofusa* cf. *tumida*; d, *Domasia bispinosa*; e, *Domasia trispinosa*; f, *Domasia elongata*; g, *Veryhachium elongatum*; h, *V. trispinosum*; i, *V. europaeum* var. *wenlockium*; j, *V. formosum* var. nov.; k, *Leiofusa tumida*. The arrows indicate where morphological transition is probable.

possibly unreliable, differences in the texture of the wall there appears to be no morphological character to distinguish them from *L. tumida*, but because of their associations they are referred to here as *L.* cf. *tumida*.

Deunffia and *Domasia* are closely related and were found only in the Buildwas Beds at the base of the Wenlock Shale. There they were quite common, especially at locality BS/2 where they form over 22 per cent. of the whole assemblage. The morphological relationship of the forms present and their distribution is shown in text-fig. 2 and it is clear that those from BS/2 are quite distinct from the assemblages from BS/1 and BS/3. *Deunffia monospinosa* has not been found at BS/3 but it probably occurs throughout the Buildwas Beds. *Domasia bispinosa* and *D. trispinosa* were found only in the two lowest localities, BS/1 and BS/3. *Deunffia brevispinosa* and *D. ramusculosa* were confined to BS/1 while *Domasia elongata* and *Deunffia furcata* were found only in samples from BS/2.

The distribution of these forms is shown in Table 6.

TABLE 6. Recorded occurrences of *Domasia*, *Deunffia*, and *Leiofusa*

Locality	BS/1	BS/3	BS/2	WS/7	WS/6	WS/11	WS/10	WS/12	WS/1	WS/2	WS/5	WS/8	WS/4
Domasia elongata	..	..	19	..	..	..	..	..	..	..	..	..	..
D. trispinosa	5	3	..	..	..	..	..	..	..	..	..	..	..
D. bispinosa	1	4	..	..	..	..	..	..	..	..	..	..	..
Deunffia monospinosa	19	..	7	..	..	..	..	..	..	..	..	..	..
Dnf. brevtspinosa	11	..	..	..	..	..	..	..	..	..	..	..	..
Dnf. ramusculosa	7	..	..	..	..	..	..	..	..	..	..	..	..
Dnf. furcata	..	..	63	..	..	..	..	..	..	..	..	..	..
Leiofusa filifera	..	5	3	8	1	23	13	5	..	28	38	11	108
L. tumida	..	..	..	..	..	1	1	1	..	3	..	3	16
L. cf. *tumida*	2	..	2	..	..	..	..	..	..	..	..	..	..

Subgroup POLYGONIMORPHITAE Downie, Evitt, and Sarjeant 1963

(1) *Acritarchs with polygonal bodies*

The veryhachids in the Wenlock Shales are mostly small but throughout the succession they are generally abundant (Table 8). Of the eight species recognized, *Veryhachium rhomboidium* Downie, *V. trispinosum* (Eisenack), and *V. europaeum* Stockmans and Willière var. *wenlockium* (Downie) are the most common and range all through the sequence. *V. rhomboidium* is quite distinct from the other veryhachids in the Wenlock but is probably closely related to *Baltisphaeridium longispinosum* var. *parvum* with which it is commonly associated. *V. trispinosum* and *V. europaeum* var. *wenlockium* are probably the three- and four-spined varieties of the same organ or organism; the five-spined variety being *V. formosum* Stockmans and Willière, which is less common and confined to locality WS/6 and higher horizons (text-fig. 2). Apart from the appearance of the five-spined forms in the Coalbrookdale Beds there is little change in the composition of this complex throughout the sequence (Table 7).

Among the other forms present, *V.* cf. *balticum* has been found only twice and is too rare to be of any importance. *V. elongatum* sp. nov., *V. bulbosum* (Deflandre), and *V. trisphaeridium* sp. nov., however, appear to have restricted ranges; *V. elongatum* being confined to the lower Coalbrookdale Beds, *V. bulbosum* to the lower and middle Coalbrookdale Beds, and *V. tripartitum* to the Tickhill Beds. The distribution of these forms is shown in Table 8.

Veryhachium rhomboidium Downie

Remarks. This species is now considered as a form species with homoeomorphic repetitions at widely separated horizons (Wall and Downie 1963). The description of the Silurian forms (Downie 1959) needs no alteration, but it should be noted that rare examples with shorter or longer spines than stated in the diagnosis do occur.

TABLE 7. Changes in the *V. trispinosum–V. europaeum–V. formosum* complex

Locality	BS/1	BS/3	BS/2	WS/7	WS/6	WS/11	WS/10	WS/12	WS/1	WS/2	WS/5	WS/8	WS/4
Percentage of forms with:													
3 spines (*V. trispinosum*)	19	15	30	31	35	13	9	3	..	13·4	23	31	28
4 spines (*V. europaeum*)	81	85	70	69	63	83	91	97	..	86	64	63	68
5 spines (*V. formosum*	..	..	..	..	2	4	..	..	..	0·6	13	6	4

TABLE 8. Recorded occurrences of *Veryhachium*

Locality	BS/1	BS/3	BS/2	WS/7	WS/6	WS/11	WS/10	WS/12	WS/1	WS/2	WS/5	WS/8	WS/4
V. rhomboidium	45	24	10	15	6	1	4	..	..	5	6	30	8
V. europaeum var. *wenlockium*	17	19	19	31	38	58	41	29	..	144	25	69	39
V. formosum var. nov.	..	..	..	..	1	3	..	..	..	1	5	6	2
V. trispinosum	4	3	8	14	21	9	4	1	..	22	9	34	16
V. elongatum	..	..	..	15	..	1	..	..	..	..	..	..	..
V. bulbiferum	..	..	..	1	3	3	..	1	..	2	..	..	..
V. cf. *balticum*	..	..	..	..	..	..	1	..	..	1	..	..	..
V. tripartitum	..	..	..	..	..	..	..	..	..	..	..	2	4
V. spp.	5	1	..	1	..	1	1	..	..	1	4	..	1

Veryhachium europaeum Stockmans and Willière var. *wenlockium* (Downie)

Synonym. V. tetraedron var. *wenlockium* Downie 1959.

Remarks. The reasons for transferring this form to *V. europaeum* are discussed in Wall and Downie 1963. A small number of specimens whose spines are shorter than allowed for in the original diagnosis have been found.

Veryhachium trispinosum (Eisenack)

Remarks. The forms from the Wenlock Shale allocated to this species are closely akin to *V. europaeum* var. *wenlockium*, differing only in the number of spines. Both are probably only parts of a variable group of organs or organisms belonging to one interbreeding species.

The Wenlock specimens of *V. trispinosum* are smaller than the typical forms of Eisenack and have slightly more constricted spine bases. In these respects they resemble more closely *V. reductum* Jekhowsky, which, however, has shorter spines. *V. trisulcum* Deunff differs in having a markedly inflated test with a tendency to have an inequilateral outline. The Wenlock forms are therefore retained in *V. trispinosum*.

Veryhachium elongatum sp. nov.

Plate 92, fig. 10

Diagnosis. A species of *Veryhachium* with three simple spines about equal in length to the body. The body is elongate, length about three times the width, subtriangular in outline.

Dimension. Body length 7 (10) 16 microns, width 4–7 microns; spinebody length ratio 1·0 to 2·5.

Holotype. Slide 1, position 280.515.

Locality. Wenlock Shales, WS/7b.

Remarks. This small species is associated in samples from WS/7 with *V. trispinosum* which it resembles except for its elongated body. This body is, however, distinctly triangular which distinguishes it from *Domasia elongata* which it also resembled in size, spine number, and length. It is indeed intermediate in morphology between *Veryhachium* of the *V. trispinosum–V. trisulcum* group and Domasia of the *D. trispinosa–D. elongata* group and it is interesting to note that it follows *D. elongata* immediately in the sequence (text-fig. 2).

Altogether over fifteen individuals were found in samples from WS/7 and a single one from a sample from WS/11.

Veryhachium trisphaeridium sp. nov.

Plate 92, fig. 7

Diagnosis. A species of *Veryhachium* with three simple spines and an equilateral thin walled subtriangular test. The spines are equal in length or longer than the sides of the test. The test is constricted midway between the spine bases forming a Y-shaped furrow clearly visible when the spines are more or less in the same plane.

Dimensions. Body size about 15 microns; spinebody length radio, 1·0 to 1·7.

Holotype. Slide 2, position 198.623.

Locality. Wenlock Shales, WS/8b.

Remarks. In size and shape this species resembles *V. trispinosum* from the Wenlock Shales, differing in the presence of the grooves which divide the test into three rather bulbous apical parts. It is not a common form and the six known examples all come from the Tickhill Beds at the top of the Wenlock Shales.

(2) *Acritarchs with body formed by fusion of the process bases*

This group includes forms belonging to the genera *Estiastra* and *Pulvinosphaeridium*. *Estiastra*, hitherto represented by a single species from the Upper Llandovery of the Baltic, occurs at two distinct levels in the Wenlock Shales. *E. barbata* sp. nov. occurs in considerable numbers but only in the lowest horizons of the Buildwas Beds, *E. granulata* sp. nov. is less common and was found only from locality WS/4 in the Tickhill Beds (Table 13). *Pulvinosphaeridium* has been found only as a rare constituent in samples from locality WS/A, but its distribution in the rocks of the Baltic area shows it to range from the Upper Llandovery to the Ludlow (Eisenack 1959).

Estiastra barbata sp. nov.

Plate 92, fig. 8

Diagnosis. A species of *Estiastra* 80 to 130 microns across with four to eight processes. The surface of the processes ornamented with varying density by small hollow spines up to 2 microns in length.

Holotype. Slide 3, position 135.452.

Locality. Wenlock Shales, BS/3.

Remarks. This species resembles the type species *E. magna* Eisenack in overall shape but it is much smaller and is ornamented with small spines.

Estiastra granulata sp. nov.

Plate 91, fig. 8

Diagnosis. A species of *Estiastra* 100 to 150 microns across with eight to twelve processes. The walls are thin, generally crumpled, and ornamented with a fine ornament of small closely spaced granules.

Holotype. Slide 9, position 120.615.

Locality. Wenlock Shales, WS/4a.

Remarks. This species resembles *E. magna* Eisenack but is smaller, paler in colour, and has a finely granular surface.

Pulvinosphaeridium oligoprojectum Downie

Remarks. No more specimens of this species have been found in the Wenlock Shales since it was first described (Downie 1959) but subsequently discussion with Professor Eisenack suggests it is a junior synonym of *P. pulvinellum* Eisenack which ranges from the Llandovery to the Ludlow.

Subgroup ACANTHOMORPHITAE Downie, Evitt, and Sarjeant 1963

(1) *Acritarchs with relatively large spherical bodies and hollow spines* (*Baltisphaeridium*)

(*a*) *Spines smooth and generally simple*. This group embraces two large variable species of acritarchs, varieties of which are likely to appear at many horizons. The long process forms in the Wenlock Shales are allocated to varieties of *B. longispinosum* (Eisenack), the forms with shorter processes to *B. brevispinosum* (Eisenack). Both of these species range throughout the Wenlock Shales and are nearly always present in considerable numbers (Table 9). Variation in the numbers present and in their relative proportions does not appear to have any stratigraphical significance in the Wenlock

EXPLANATION OF PLATE 91

Figs. 1–7. *Baltisphaeridium* spp. 1, *B. granulatispinosum* sp. nov.; holotype, ×520; locality BS/3. 2, *B. longispinosum* var. *parvum* var. nov.; holotype, ×550; locality BS/3. 3, *B. microcladum* sp. nov.; paratype, ×600; locality BS/3. 4, *B. longispinosum* var. *paucispinosum* var. nov.; holotype, ×550; locality WS/5. 5, *B. arbusculiferum* sp. nov.; holotype, ×700; locality WS/4. 6, *B. ravum* sp. nov.; holotype, ×400; locality BS/2. 7, *B. granulatispinosum* sp. nov.; a form with markedly cladate processes, ×575; locality BS/3. 8, *Estiastra granulata* sp. nov.; holotype. ×500; locality WS/4.

Shales, except that the forms of *B. longispinosum* are more abundant in the earlier horizons.

Baltisphaeridium longispinosum (Eisenack) var. *parvum* var. nov.

Plate 91, fig. 2

Synonymy. *Baltisphaeridium longispinosum* (Eisenack); Downie 1959 (pars), pl. 10, figs. 2, 6.
Micrhystridium stellatum Deflandre var. *inflatum* Downie 1959, pl. 11, fig. 12.

Diagnosis. A variety of *Baltisphaeridium longispinosum* having a more or less spherical body 15 to 35 microns in diameter, bearing spines longer than the test radius and five to twenty-five in number, the spines are hollow, closed at the tips, with a smooth surface and rarely branching.

Holotype. Slide 3, position 100.560.

Locality. Wenlock Shales, BS/3.

Remarks. This species is generally abundant, over 300 individuals distributed throughout the Wenlock Shales were seen. It is, however, rather more common in the Buildwas Shales. The variety resembles the typical Ordovician form in general appearance but it is

TABLE 9. Recorded occurrences of *Baltisphaeridium spp.* belonging to group (*a*)

Locality	BS/1	BS/3	BS/2	WS/7	WS/6	WS/11	WS/10	WS/12	WS/1	WS/2	WS/5	WS/8	WS/4
B. longispinosum var. *parvum*	101	37	48	10	10	16	9	2	..	12	26	18	18
B. longispinosum var. *paucispinosum*	..	..	..	..	..	1	..	..	..	4	6	..	..
B. brevispinosum var. *wenlockensis*	23	49	35	40	53	17	43	5	..	77	11	18	17
B. brevispinosum var. *granuliferum*	..	1	2	6	2	2	..	..	..	8	..	1	..
B. brevispinosum var. *nanum*	2	3	2	4	5	1	1	1	..	3	2	..	1

consistently smaller and a pylome has never been observed. Furthermore, branching spines rarely occur, broad processes are absent and in general these appear more flexuous than those of the typical Ordovician forms.

Some examples from the Wenlock show morphological transitions to other species occurring there. For example some with six regularly disposed processes differ from *V. rhomboidium* only because the test is ellipsoidal and not polygonal. Fortunately this difficulty rarely arises and only in samples from locality BS/1 where there were 12 of these intermediaries among 101 specimens of *B. longispinosum* and 40 of *V. rhomboidium* did it assume any importance.

Some small forms of *B. longispinosum* var. *parvum* with more markedly flaring spine bases are difficult to separate from *Micrhystridium stellatum* Deflandre. It can in fact be done only on an arbitrary basis and for this reason *M. stellatum* var. *inflatum* is considered synonymous with *B. longispinosum* var. *parvum*.

In the Ordovician Eisenack found that it was convenient to make an arbitrary distinction between *B. longispinosum* and forms with short processes. The same is the case in the Wenlock and the distinction between *B. longispinosum* var. *parvum* and *B. brevispinosum* var. *wenlockensis* is based mainly on the length of the processes. Forms near the boundary (processes equal to the radius in length) are, however, less common than typical forms except in samples from BS/3 where they predominate.

Baltisphaeridium longispinosum (Eisenack) var. *paucispinosum* var. nov.

Plate 91, fig. 4

Diagnosis. A variety of *B. longispinosum* with a more or less spherical body 15 to 35 microns in diameter, bearing spines longer than the test diameter. Spines hollow, unbranched and closed at the tips, less than five in number.

Holotype. Slide 1, position 210.448.

Locality. Wenlock Shales, WS/5c.

Remarks. This form of which only eleven examples have been found occurs mainly near the top of the Coalbrookdale Beds. It may be connected with *B. eoplanktonicum* but the intermediate forms with some branched and some unbranched spines are rare. Six were found, five of which were from locality WS/5, the only place where this supposed transition is substantially supported.

Baltisphaeridium brevispinosum (Eisenack) var. *wenlockensis* Downie

Remarks. This variety is one of the commonest in the Wenlock Shales and one of the most variable. The body size ranges from 15 to 40 microns, its shape from spherical to ellipsoidal, the process length from one-fifth to three-quarters of the diameter and number from about twelve to forty in optical section; their tips may be sharply pointed, hair-like, rounded or capitate. *B. brevispinosum* var. *granuliferum* Downie belongs to the same plexus, but *B. brevispinosum* var. *nanum* Deflandre appears to be less closely connected with its widely spaced relatively short processes. All of these varieties range throughout the Wenlock Shales and there is no change in the emphasis of the variation that has any stratigraphic significance.

TABLE 10. Recorded occurrences of *Baltisphaeridium spp.* belonging to group (*b*)

Locality	BS/1	BS/3	BS/2	WS/7	WS/6	WS/11	WS/10	WS/12	WS/1	WS/2	WS/5	WS/8	WS/4
B. granulatispinosum	26	14	6	22	11	26	9	1	..	43	60	71	73
B. robustispinosum	1	2	..	3	9	2	..	..	..	2	..	..	..

(*b*) *Spines, branched or unbranched, ornamented with small tubercles.* This group includes two species, *B. granulatispinosum* sp. nov. and *B. robustispinosum* Downie. The former is the more common and over 350 examples have been found. They are distributed throughout the Wenlock Shales but are clearly more common in the upper part. Some rather distinctive varieties are included in this species but they do not appear to be restricted in their stratigraphical distribution and are relatively rare. *B. robustispinosum* is represented by only twenty specimens and is entirely absent in the samples from the upper part of the Wenlock Shales, most of them being found in the lower part of the Coalbrookdale Beds (Table 10).

Baltisphaeridium granulatispinosum sp. nov.

Plate 91, figs. 1, 7; text-fig. 3*c*

Synonym. B. longisposum (Eisenack); Downie 1959 (pars), pl. 10, fig. 1.

Diagnosis. A hollow spherical, ellipsoidal or rarely polygonal test with hollow spines

about equal or greater in length than the test diameter. Spines simple, rarely branching, but terminating in nearly every instance in short finger-like digitations. Invariably the surface of the spines along all their length is ornamented with granules about 1 micron in size.

Dimensions. Body size 18(30)36 microns; ratio spine lengthbody size 0·8(1·2)2·0; number of processes 5(8)12.

Holotype. Slide 3, position 030.540.

Locality. Wenlock Shales, BS/3.

Remarks. Typical members of this species have spines unbranched except at the tip where they fray into small finger-like processes. Varieties with the tips closing to a point are very rare (10 in 364) as are those with markedly cladate spines (14 in 364).

Baltisphaeridium robustispinosum Downie

Remarks. This species is distinguished from *B. granulatispinosum* by its broader stouter processes and generally coarser ornament of granules. In addition the spine tips terminate by constricting suddenly to a hair and never break up into small digitations.

Since the species was originally described on the basis of two specimens (Downie 1959) others have been found which indicate that it would be desirable to extend the original diagnosis to include forms whose body size ranges from 20 to 40 microns with six to twelve spines visible in optical section, their length varying from 20 to 100 per cent. of the text diameter.

TABLE 11. Recorded occurrences of *Baltisphaeridium spp.* belonging to group (*c*)

Locality	BS/1	BS/3	BS/2	WS/7	WS/6	WS/11	WS/10	WS/12	WS/1	WS/2	WS/5	WS/8	WS/4
B. meson group (including *B. oligofurcatum* and *B. brevifurcatum*	1	6	1	1	..	..	..	..	..	5	..	1	..
B. dilatispinosum	..	3	..	..	..	..	..	..	..	..	..	..	..

(*c*) *Forms with dark spherical bodies and pale-coloured short processes*. Only a few specimens of this type have been found but they are of some interest since they are very similar to the forms described from the Upper Visby Marl (Upper Llandovery) of the Baltic by Eisenack (1954). From there he described three intergrading species, *H. brevifurcatum*, *H. intermedium* (= *B. meson*), and *H. oligafurcatum* (Pl. 92, fig. 9). Examples of all three have been found in the Wenlock Shales together with a new species *B. dilatispinosum* which resembles *B. piriferum* (Eisenack) from the Upper Visby Marl. These hystrichospheres are too few in number to make any definite assertions about their stratigraphic range (Table 11) but so far *B. dilatispinosum* has been found only at locality BS/3 and the others are mainly concentrated in the Buildwas Beds.

Baltisphaeridium meson (Eisenack)

Remarks. Since allocating certain forms from localities WS/A and WS/2 to *B.* cf. *meson* (Downie 1959) because of their smaller size, other specimens have been found indicating that they are inseparable from the typical Baltic forms.

Baltisphaeridium dilatispinosum sp. nov.

Plate 92, fig. 4

Diagnosis. Body spherical, walls stout and dark, processes pale, relatively short, distally inflated. The distal part bears numerous small spines.

Dimensions. Body size 50 to 60 microns; process length 10 to 12 microns, width 6 to 8 microns, number in optical section fourteen to twenty-two; spines on processes 1 to 1·5 microns, 2 microns apart.

Holotype. Slide 3, position 190.480.

Locality. Wenlock Shales, BS/3.

Remarks. Three individuals of this species were included in statistical counts of the assemblages but a number of others were seen. All were confined to samples from locality BS/3. The general shape of the test and the processes shows a close resemblance to *B. piriferum* (Eisenack) which does not, however, have any small spines ornamenting the bulbous processes.

(*d*) *Forms with smooth branching spines.* A great variety of acritarchs with branching processes occur in the Wenlock Shale. Some have already been discussed in previous sections; the remaining ones are considered here. They include *B. ramusculosum* (Deflandre), *B. eoplanktonicum* (Eisenack), *B. digitatum* (Eisenack), *B. ravum* sp. nov., *B. cladum* sp. nov., *B. arbusculiferum* sp. nov., and *B. microcladum* sp. nov., as well as some other varieties so far too rare to merit description. In all about 300 examples were found, their abundance decreases markedly upwards.

B. eoplanktonicum, originally described from the Ludlow by Eisenack, was represented by forty-five specimens and occurred in similar proportions throughout the Wenlock Shales. *B. ramusculosum* was more common with 150 examples and was more numerous in the lower horizons, especially near the base of the Coalbrookdale Beds. Since it was first described by Deflandre from the Wenlock it has been recorded from the Devonian by Deunff. *B. cladum* (6 examples) and *B. ravum* (34 examples) are restricted to the Buildwas and lowest Coalbrookdale Beds. *B. microcladum* (26 examples) has a similar distribution but isolated examples have been found as high as locality WS/5. *B. arbusculiferum* (12 examples), on the other hand, has been found only in the Tickhill Beds. *B. digitatum* (5 examples) has been found only at high levels but it is rare and it clearly has a wider range since it has been found by Eisenack in the Llandovery of the Baltic as well as in the Wenlock Limestone. Their distribution is shown in Table 12.

EXPLANATION OF PLATE 92

Figs. 1–3, 11–12. *Lophosphaeridium* spp. 1, *L. triangulatum* sp. nov.; holotype, ×900; locality WS/4. 2, *L. pilosum* sp. nov.; holotype, ×660; locality WS/4. 3, *L. citrinum* sp. nov.; holotype, ×660; locality WS/4. 11, *L. microspinosum* (Eisenack), ×540; locality BS/3. 12, *L.* sp. cf. *P. papillatum* Staplin, ×900; locality WS/4.

Figs. 4–6, 9. *Baltisphaeridium* spp. 4, *B. dilatispinosum* sp. nov.; holotype, ×500; locality BS/3. 5, *B. cladum* sp. nov.; holotype, ×1,000; locality BS/3. 6, *B. microcladum* sp. nov.; holotype, ×540; locality BS/3. 9, *B. oligofurcatum* (Eisenack), ×540; locality BS/3.

Figs. 7, 10. *Veryhachium* spp. 7, *V. trisphaeridium* sp. nov.; holotype, ×1000; locality WS/8. 10, *V. elongatum* sp. nov.; Holotype, ×1000; locality WS/7.

Fig. 8. *Estiastra barbata* sp. nov.; holotype, ×500; locality BS/3.

Fig. 13. *Punctatisporites? dilutus* Hoffmeister, ×700; locality WS/4.

Baltisphaeridium eoplanktonicum (Eisenack)

Remarks. As well as typical forms of this species with 4 spines one example was found with 3, one with 5, and five with 6 spines. These forms differed from the typical ones in no other respect.

TABLE 12. Recorded occurrences of *Baltisphaeridium spp.* belonging to group (*d*)

Locality	BS/1	BS/3	BS/2	WS/7	WS/6	WS/11	WS/10	WS/12	WS/1	WS/2	WS/5	WS/8	WS/4
B. ravum	..	3	29	..	2	..	..	..	..	..	..	..	..
B. eoplanktonicum	6	3	6	..	..	1	3	3	..	24	7	2	1
B. ramusculosum	29	19	2	36	28	6	1	2	..	19	2	5	1
B. cladum	..	3	2	1	..	..	..	..	..	..	..	..	..
B. microcladum	13	6	1	3	..	1	1	..	..	..	1	..	..
B. arbusculiferum	..	..	..	..	..	..	..	..	..	..	..	2	10
B. digitatum	..	..	..	..	..	..	..	..	..	3	1	..	1

Baltisphaeridium ravum sp. nov.

Plate 91, fig. 6; text-fig. 3*c*

Diagnosis. Test spherical rather dark greyish-yellow in colour, processes long cylindrical, pale coloured, flaring at the tips and breaking up into numerous digitations.

Dimensions. Text diameter 30 to 55 microns; process lengthbody size 60 to 100 per cent.; number of processes in optical section six to twelve, width of processes 3 to 4 microns, length of digitations 3 to 4 microns.

Holotype. Slide 4, position 200.450.

Locality. Wenlock Shales, BS/2a.

Remarks. This species resembles *B. ramusculosum* but is larger, the contrast it shows between body and process colour and texture is another distinction. The style of branching also differs (text-fig. 3*c*), *B. ramusculosum* in general having wide-angled regular bifurcations, often to the fourth order, whereas *B. ravum* has less frequent narrow-angled bifurcations and irregular distal digitation.

TABLE 13. Recorded occurrences of *Estiastra*, *Pulvinosphaeridium*, and *Polyedrixium*

Locality	BS/1	BS/3	BS/2	WS/7	WS/6	WS/11	WS/10	WS/12	WS/1	WS/2	WS/5	WS/8	WS/4
E. barbata	25	17	..	..	..	..	..	..	..	..	..	..	..
E. granulata	..	..	..	..	..	..	..	..	..	..	..	..	5
Pulv. pulvinellum	..	..	..	..	..	..	..	..	..	8	..	..	..
Polyedrixium spp.	..	..	..	..	..	..	..	..	..	..	..	1	1

Baltisphaeridium cladum sp. nov.

Plate 92, fig. 5; text-fig. 3*a*

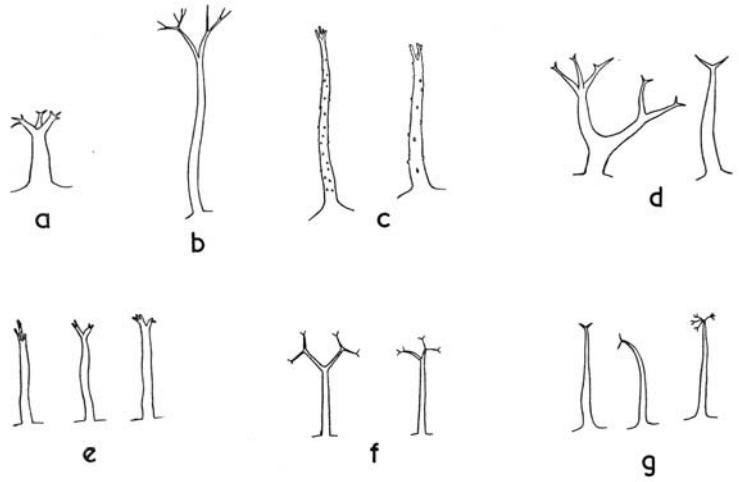
Diagnosis. Test slightly ellipsoidal, several processes with stout shanks tapering to point of forking, forks fairly wide angled, short, tips irregularly bifurcate or trifurcate.

Dimensions. Body size 18 to 25 microns; spine number in optical section ten to fourteen, spine length about 65 per cent. of test diameter.

Holotype. Slide 3, position 030.470.

Locality. Wenlock Shales, BS/3.

Remark. This species differs from *B. ramusculosum* in the slightly ellipsoidal test, the stout tapering processes and the more limited and irregular bifurcations at the tips.



TEXT-FIG. 3. Illustration of the types of processes occurring in some species of acritarchs. a, *Baltisphaeridium cladum* (12 μ long); b, *B. eoplanktonicum* (50 μ long); c, *B. granulatispinosum* (60 μ long); d, *B. arbusculiferum* (20 μ long); e, *B. ravum* (40 μ long); f, *B. ramusculosum* (20 μ long); g, *B. microcladum* (20 μ long).

Baltisphaeridium arbusculiferum sp. nov.

Plate 91, fig. 5; text-fig. 3*d*

Diagnosis. Test subspherical to subpolygonal, processes long broad tapering, forking irregular at a moderate angle, branches often long and broad; forking usually bifurcate up to fourth order.

Dimensions. Test size 15 to 30 microns; spine number in optical section six to nine, spine length 100 to 140 per cent. of test diameter.

Holotype. Slide 2, position 010.560.

Locality. Wenlock Shales. WS/4b.

Remarks. This species bears some resemblance to *B. digitatum* in the broad tapering form and mode of branching of the processes but differs in its smaller size and in the clear separation of the processes from the test.

Baltisphaeridium microcladum sp. nov.

Plate 91, fig. 3, Plate 92, fig. 6; text-fig. 3*g*

Diagnosis. Test slightly ellipsoidal, smooth or granular, spines moderately long and numerous, narrow and slightly tapering. Forking only at the tips, bifurcate, trifurcate, or quadrifurcate, branches very short and thin but second-order branching may occur.

Dimensions. Test size 20 to 45 microns; number of processes in optical section fifteen to twenty, length 30 to 50 per cent. of test diameter, branches 1·0 to 2·5 microns long.

Holotype. Slide 3, position 145.540.

Locality. Wenlock Shales BS/3.

Remarks. This species resembles *Multiplicisphaeridium*? *sprucegrovensis* Staplin but is smaller, has somewhat fewer processes, and shows greater variation in the style of branching.

(2) *Acritarchs with small spherical bodies bearing spines*

This group is represented by the genus *Micrhystridium*, of which several hundred examples were found spread throughout the Wenlock Shales. They formed a relatively small proportion of the total assemblage except in the higher levels where they became

TABLE 14. Recorded occurrences of *Micrhystridium*

Locality	BS/1	BS/3	BS/2	WS/7	WS/6	WS/11	WS/10	WS/12	WS/1	WS/2	WS/5	WS/8	WS/4
M. stellatum	1	1	..	2	12	2	5	5	..	49	11	27	18
M. eatonensis	3	..	..	..	..	..	..	..	..	14	..	..	3
M. nannacanthum	12	..	8	4	8	1	1	..	..	6	20	48	52
M. parinconspicuum	7	2	4	..	6	9	4	1	..	32	10	18	97
M. imitatum	2	1	3	..	..	1	..	..	..	20	5	26	15

abundant forming between 10 and 20 per cent. of the sample. The species present were *M. stellatum* Deflandre, *M. imitatum* Deflandre, *M. parinconspicuum* Deflandre, *M. nannacanthum* Deflandre, and *M. eatonensis* Downie. They all appear to range throughout and to become more common in the upper beds. A number of other small hystrichospheres were present but insufficiently well preserved or not present in large enough numbers to merit description. Their distribution is shown in Table 14.

Subgroup PRISMATOMORPHITAE Downie, Evitt, and Sarjeant 1963

This group of Acritarchs with polygonal tests bearing flanges on the edges of the polygons is represented by the genus *Polyedrixium*, and is very rare in the Wenlock Shales. Only two examples have been found, one quite unidentifiable specifically; the other, slightly better preserved, closely resembled *P. centrigerum* Deunff from the Middle Devonian. Hitherto *Polyedrixium* has been known only from the Devonian where it appears to be common at certain levels; the Wenlock specimens occurred near the top (Table 13).

Class CHLOROPHYCEAE

ORDER UNCERTAIN

Tasmanites appears to be present in small numbers throughout the succession (Table 3), never forming more than about 1 per cent. of the whole assemblage. It is represented mainly by *Tasmanites medius* (Eisenack) and a similar form slightly smaller in size (Downie 1959).

STRATIGRAPHIC RANGE OF WENLOCK SHALE ACRITARCHS

(*a*) *Forms confined to the Wenlock.* As far as is known thirty-eight species or varieties among the forms occurring in the Wenlock Shale have not been found at other horizons. Of these *C. pavimenta*, *B. brevispinosum* var. *nanum*, *M. imitatum*, *M. nannacanthum*, and *V. bulbiferum* have also been found in the Wenlock of France (Deflandre 1945).

(*b*) *Forms ranging from the Lower Silurian into the Wenlock. B. meson* and *L. microspinosum* occur in the Upper Llandovery of the Baltic (Eisenack 1954), *P.? dilutus* in the Lower Silurian of Libya (Hoffmeister 1959), and *M. parinconspicuum* in the Middle Silurian of New York (Fisher 1953). *P. pulvinellum* and *B. ramsculosum* seem to range throughout the Silurian.

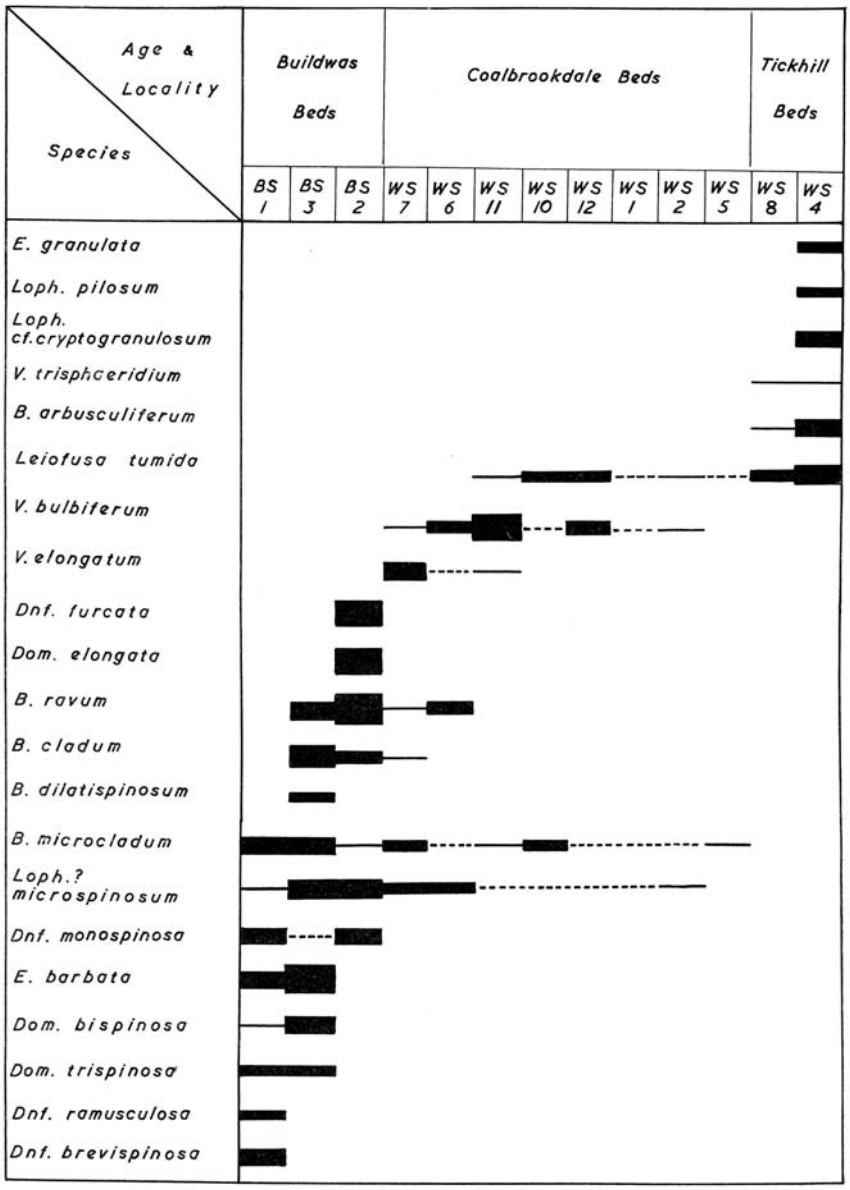
(*c*) *Forms ranging from the Wenlock into the Ludlow. P. pulvinellum*, *B. eoplanktonicum*, and *T. medius* have been recorded from the Ludlow but not from higher horizons (Eisenack 1955).

(*d*) *Forms ranging into the Devonian.* These include *P. onondagaensis*, *C. cubus*, *C. prismatica*, *Polyedrixium*, and *B. ramusculosum* (Deunff 1954, 1955) and *L. wenlockia*, *L. diaphana*, *L. cryptogranulosum*, *L. granulosum*, and *L. papillatum* (Staplin 1961).

(*e*) *Forms with longer ranges.* A small number of species have longer ranges than any of the above. *B. digitatum* ranges from the Caradoc to the Wenlock Limestone and *L. microsystis* from the Ordovician at least to the Wenlock. *V. trispinosum* and *M. stellatum* show subtle variations in morphology over a long period of time producing a number of only slightly distinct varieties. The former ranges from the Ordovician at least to the Devonian, the latter from the Wenlock to the Upper Jurassic.

(*f*) *Comparison with the Wenlock assemblage from the Montagne Noire.* Deflandre (1945) described sixteen forms from the Wenlock of France. Of these ten have been identified in the Wenlock of Shropshire; the other six (*H. staurasteroides*, *H. geometricum*, *M. mendax*, *M. tenuissimum*, *L. retigera*, and *L. aurata*) were not seen or could not be certainly identified. Of the various Wenlock assemblages those in the Coalbrookdale Beds compare most closely with that described by Deflandre.

(*g*) *Comparison with Silurian assemblages from the Baltic.* Eisenack (1954, 1955, 1959) has described 'hystrichospheres' from a number of horizons in the Silurian of the Baltic regions. From the Visby Marl (Upper Llandovery) he has recorded *B. piriferum*, *B. brevifurcatum*, *B. meson*, *B. oligofurcatum*, *B. gotlandicum*, *B. erraticum*, *B. polygonale*, *B. digitatum*, *B. visbyense*, *E. magna*, *L. microspinosum*, and *P. pulvinellum*. Of these *B. brevifurcatum*, *B. meson*, *B. oligofurcatum*, *B. digitatum*, *L. microspinosum*, and *P.*



TEXT-FIG. 4. Chart showing the stratigraphical range of some species of acritarchs.

pulvinellum have been found in the Wenlock of Shropshire and forms very close to *B. piriferum*, *B. erraticum*, *B. visbyense*, and *E. magna* also occur. All ten of the forms identical or similar to the Baltic species occur in the Buildwas Shales, only six in the Coalbrookdale Beds and only two in the Tickhill Beds. The greatest similarity is therefore to be found in the earliest beds of the Wenlock Shales.

From the Wenlock of the Baltic Eisenack has recorded *B. polygonale*, *B. visbyense*, *B. corallinum*, *B. lophophorum*, and *P. pulvinellum* of which only *P. pulvinellum* has so far been found in Shropshire.

In the *Beyrichia* Limestone (Ludlow) Eisenack found the following species *B. corallinum*, *B. erraticum*, *B. eoplanktonicum*, *B. meson*, *L.* cf. *microspinosum*, *L. media*, *P.* aff. *pulvinellum*, *Dictyotidium dictyotum*, and *D. tenuiornatum*. Of these *B. meson*, *B. eoplanktonicum*, *L. media*, *L. microspinosum*, and *P. pulvinellum* probably range all through the Wenlock Shale but *L. microspinosum* and *P. pulvinellum* have not been found in the highest beds. Forms like *B. erraticum* also occur (*B. dilatispinosum*) but they are confined to the Buildwas Shales. Nothing resembling *B. corallinum* or the two species of *Dictyotidium* has been found, and there is therefore no close comparison with any part of the Wenlock Shales, only three species being directly comparable.

COMPARISON OF ASSEMBLAGES WITHIN THE WENLOCK SHALE

It has been found that several species range throughout the Wenlock Shales without much change in the numbers present. These are *V. europaeum* var. *wenlockium*, *V. trispinosum*, *B. eoplanktonicum*, all the varieties of *B. brevispinosum*, all the species of *Cymatiosphaera*, *L. granulosum*, *L. citrinum*, *L.* cf. *papillatum*, and *L. diaphanum*. These play no part in giving character to the different assemblages.

The other forms present either have a restricted range or vary markedly in their abundance. On the basis of these latter forms the Wenlock Shale assemblages can be divided into three types.

Assemblage type 1. All the samples from the Buildwas Beds (BS/1a, BS/1b, BS/2a, BS/2b, and BS/3) yielded assemblages of this type. They contain the greatest number of forms like those described from the Upper Llandovery of the Baltic, in particular *L. microspinosum*, the *B. meson* complex (*B. oligofurcatum*, *B. meson*, and *B. brevifurcatum*), and *B. dilatispinosum*.

In general these asemblages have relatively few specimens of *Micrhystridium* (1·1 to 3·9 per cent.), few leiofusids (0·2 to 1·3 per cent.), few specimens of *B. granulatispinosum* (1·6 to 3·9 per cent.), and few spores (0 to 0·2 per cent.) (see Table 15). On the other hand, acritarchs of the *B. longispinosum* type are relatively common (8·5 to 15 per cent.), as are those with branching processes (4·1 to 10·5 per cent.). The most striking feature, however, is the presence of *Deunffia* and *Domasia* which are frequently abundant and quite absent from the other assemblage types.

Samples from BS/1a and BS/1b have the general features of assemblage type 1 but leiospheres are unusually abundant (61·6 per cent.) *D. brevispinosa* and *D. ramusculosa* are characteristic: *B. microcladum* is relatively abundant. *B. dilatispinum*, *B. cladum*, and *B. ravum* are absent. Sample BS/3 is similar to samples from BS/1a and BS/1b but leiospheres are less common (31·2 per cent.), *D. brevispinosum* and *D. ramusculosum* are

TABLE 15. Occurrence of microfossils as percentages

	WS/4	WS/8	WS/5	WS/2	WS/1	WS/12	WS/10	WS/11	WS/6	WS/7	BS/2	BS/3	BS/1
Micrhystridium	18·2	17·8	11·1	6·2	..	3·1	5·2	5·0	6·0	1·3	3·9	1·1	2·1
Polyedrixium	0·1	0·1	..	..	..	..	..	..	..	..	..	..	..
Pulvinosphaeridium	..	..	..	0·4	..	..	..	..	..	..	..	..	..
Estrastra	0·5	..	..	..	..	..	..	..	..	..	..	4·7	2·1
Baltisphaeridium Gp. (*a*)	3·6	5·5	11·0	5·3	..	4·2	27·2	14·4	16·2	12·9	22·8	24·6	10·4
Baltisphaeridium Gp. (*b*)	7·3	10·5	14·5	2·3	..	0·5	4·6	10·8	4·7	5·3	1·6	4·4	2·4
Baltisphaeridium Gp. (*c*)	..	0·1	..	0·2	..	..	..	..	..	0·2	0·2	2·5	0·1
Baltisphaeridium Gp. (*d*)	1·3	1·3	2·7	2·3	..	2·5	2·5	2·4	6·9	8·5	10·5	9·2	4·1
Veryhachium	7·0	21·1	11·8	8·9	..	16·4	26·4	29·9	16·1	16·5	9·8	12·8	6·0
Leiofusa	12·2	2·1	9·2	1·6	..	3·1	7·3	9·5	0·2	1·7	1·3	1·4	0·2
Deunffia	..	..	..	..	..	..	..	..	..	..	18·5	..	3·1
Domasia	..	..	..	..	..	..	..	..	..	..	5·0	1·9	0·5
Cymatiosphaera	1·4	0·9	1·4	2·1	..	4·2	1·5	1·2	1·4	2·1	0·5	2·2	0·7
Pterospermopsis	..	0·1	0·5	0·3	..	0·5	..	..	..	..	..	0·2	..
Tasmanites	0·1	0·7	..	1·3	..	..	0·5	0·4	0·2	0·6	..	0·8	..
Lophosphaeridium	5·3	1·5	3·8	2·3	1·1	3·1	2·0	2·0	7·9	3·4	4·7	2·8	6·6
Leiosphaeridia	38·8	36·5	32·6	66·3	98·9	60·4	22·3	23·3	35·3	46·0	21·2	31·2	61·7
Spores	4·2	1·8	1·4	0·5	..	2·0	0·5	1·1	5·1	1·5	..	0·2	..
Total	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0

absent; *B. dilatispinosum*, *B. cladum*, and *B. ravum* are present. Samples from BS/2a and BS/2b are similar to samples from BS/3 but *D. trispinosa*, *D. bispinosa*, *E. barbata*, and *B. dilatispinosum* are absent. *B. microcladum* is rare. *D. elongata* and *D. furcata* are characteristically present.

Assemblage type 2. Samples from localities WS/2a, WS/2b, WS/6a, WS/6b, WS/7a, WS/7b, WS/A, WS/10, WS/11, and WS/12 yielded assemblages of this type. All of these are from the Coalbrookdale Beds. The samples from localities WS/1a, WS/1b, and WS/1c although they contain only leiospheres are included here provisionally for it is not yet certain that their peculiar features are due to original differences in the plankton assemblages. However, in quoting proportions of various types present, samples from this locality are ignored.

The features of this assemblage are mainly negative and it grades into assemblages of type 1 which preceed it and those of type 3 which succeed it. Assemblages of this type compare most closely with those described from the Wenlock of France.

Assemblages of type 2 differ from those of type 1 in that *Deunffia*, *Domasia*, and *Estiastra* are absent, *Micrhystridium* is more common (1·3 to 6·2 per cent.), leiofusids are also more common in general (0·2 to 9·5 per cent.) and *L. tumida* is present. *Veryhachium* is more common (8·9 to 29·9 per cent.) and also spores (0·2 to 5·1 per cent.). On the other hand, *B. meson*, *L. microspinosum*, and *M. microcladum* are very rare. Acritarchs with branching processes are less common, especially in samples from the higher horizons (there is a decline from 8·5 to 2·3 per cent. in their contribution to the assemblage). *B. longispinosum* is also less common (0·6 to 6·0 per cent.). The only forms thought to be characteristically restricted to this assemblage are *V. bulbiferum* and *V. elongatum*: the latter, however, occurs only in samples from locality WS/7 at the base of the Coalbrookdale Beds.

Samples from WS/7a, WS/7b, Ws/6a, WS/6b, WS/11, and WS/10 (i.e. the Lower Coalbrookdale Beds) have the general features of assemblages of type 2, but are distinct in the relatively small proportion of leiospheres (22·3 to 46 per cent.). On the other hand, acritarchs with branching processes and those of the *B. longispinosum* type are present in relatively high proportions, this and the presence of small numbers of *B. ravum* and *B. clavum* are reminiscent of the assemblages of type 1. *V. elongata* occurs but only in samples from locality WS/7a and WS/7b.

Samples from localities WS/12, WS/2a, WS/2b, WS/A (i.e. Upper Coalbrookdale Beds) are similar to those from the Lower Coalbrookdale Beds but the proportion of leiospheres is very high (60·4 to 66·3 per cent.); the proportion of acritarchs with branching processes is small (2·3 to 2·5 per cent.) and also that of *B. longispinosum* 0·6 to 1·0 per cent.); *B. cladum*, *B. ravum*, and *V. elongata* are absent. Assemblages from localities WS/1a, WS/1b, and WS/C at a similar stratigraphic level are unique since they consist exclusively of sphaeromorphs.

Assemblage type 3. Samples from localities WS/5a, WS/5b, WS/4a, WS/4b, WS/8a, and WS/8b yielded assemblages of this type. These localities occur in the Tickhill Beds and near the top of the Coalbrookdale Beds.

In general this assemblage type differs from type 2 because of the larger proportion of *Micrhystridum* (11·1 to 18·2 per cent.), leiofusids (2·1 to 12·2 per cent.), and *B. granulatispinosum* (7·3 to 14·3 per cent.). Acritarchs with branching processes are few (1·3 to

2·7 per cent.) and so is *B. longispinosum* (1·8 to 6·2 per cent.). *V. bulbiferum*, *V. elongatum*, *B. cladum*, *B. ravum*, and *L. microspinosum* have not been found but *B. arbusculiferum*, *V. trisphaeridium*, *L.* cf. *cryptogranulosum*, *L. pilosum*, *E. granulata*, and *Polyedrixium* appear for the first time.

Samples from WS/5a and WS/5b have the general features of assemblage type 3 but *B. arbusculiferum*, *V. trisphaeridium*, *L.* cf. *cryptogranulosum*, *L. pilosum*, and *E. granulata* have not been found. *B. arbusculiferum* and *V. trisphaeridium* appear in samples from WS/8a and WS/8b and *L. tumida* becomes more common (Table 5). Assemblages from WS/4a and WS/4b also contain *L.* cf. *cryptogranulosum*, *L. pilosum*, and *E. granulata* and leiofusids intermediate in form between *L. filifera* and *L. tumida* are abundant (Table 5).

CONCLUSIONS

The acritarch assemblages of the Wenlock Shales show a more or less progressive change throughout the sequence but may be divided into three main types which succeed each other in stratigraphic order. Type 1 characterizes the Buildwas Beds, type 2 the Coalbrookdale Beds, and type 3 the uppermost Coalbrookdale Beds and Tickhill Beds.

Insufficient data is at present available to show over what area this succession of assemblage types persists and an assessment of their value in correlation must wait until several other Wenlock successions have been examined. At present all that can be said in this respect is that the assemblages from the Buildwas Beds have their closest parallel in the Upper Llandovery of the Baltic and those from the Coalbrookdale Beds in the Wenlock of France.

All the holotypes are at present in the collections of the Micropalaeontology Laboratory of the Department of Geology at the University of Sheffield.

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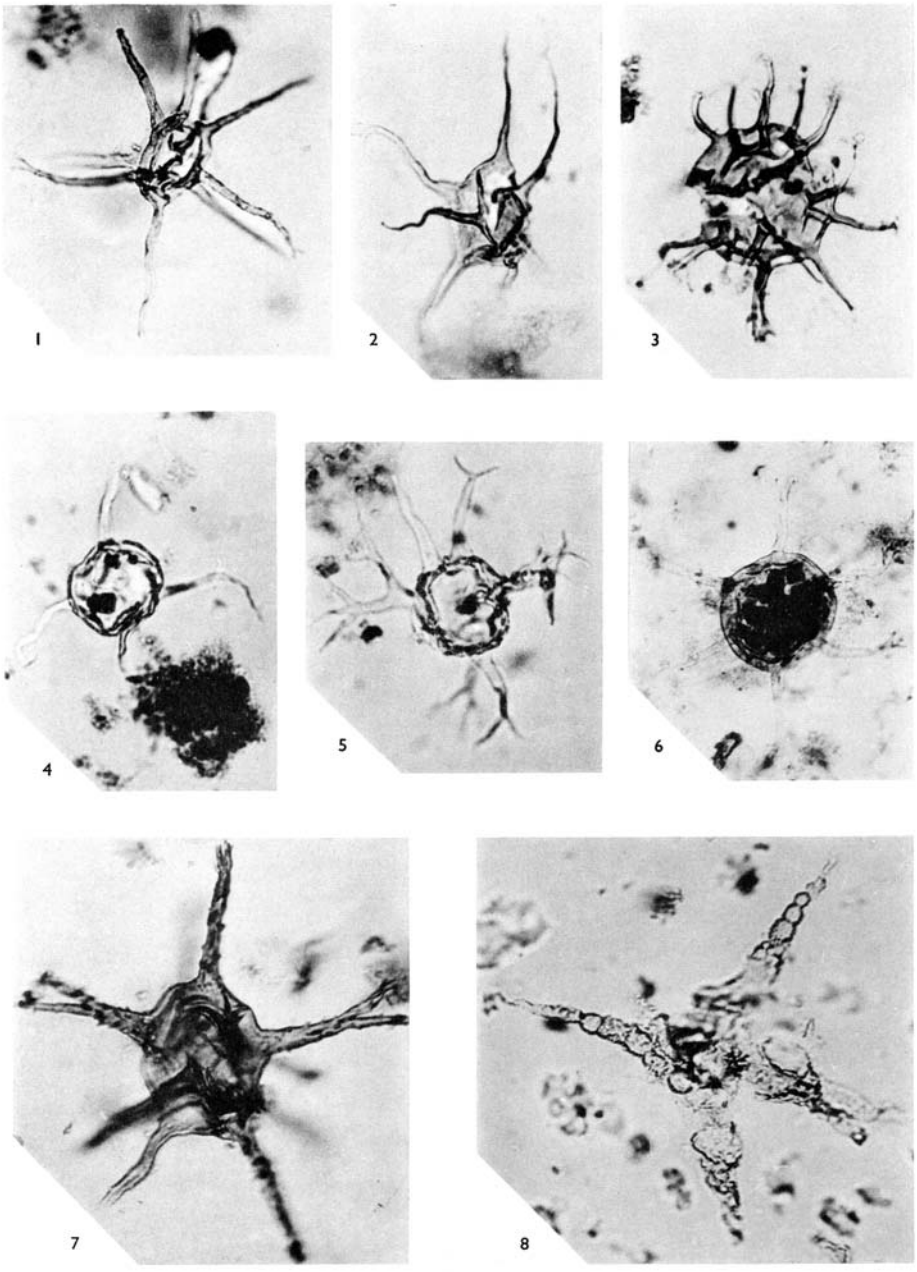
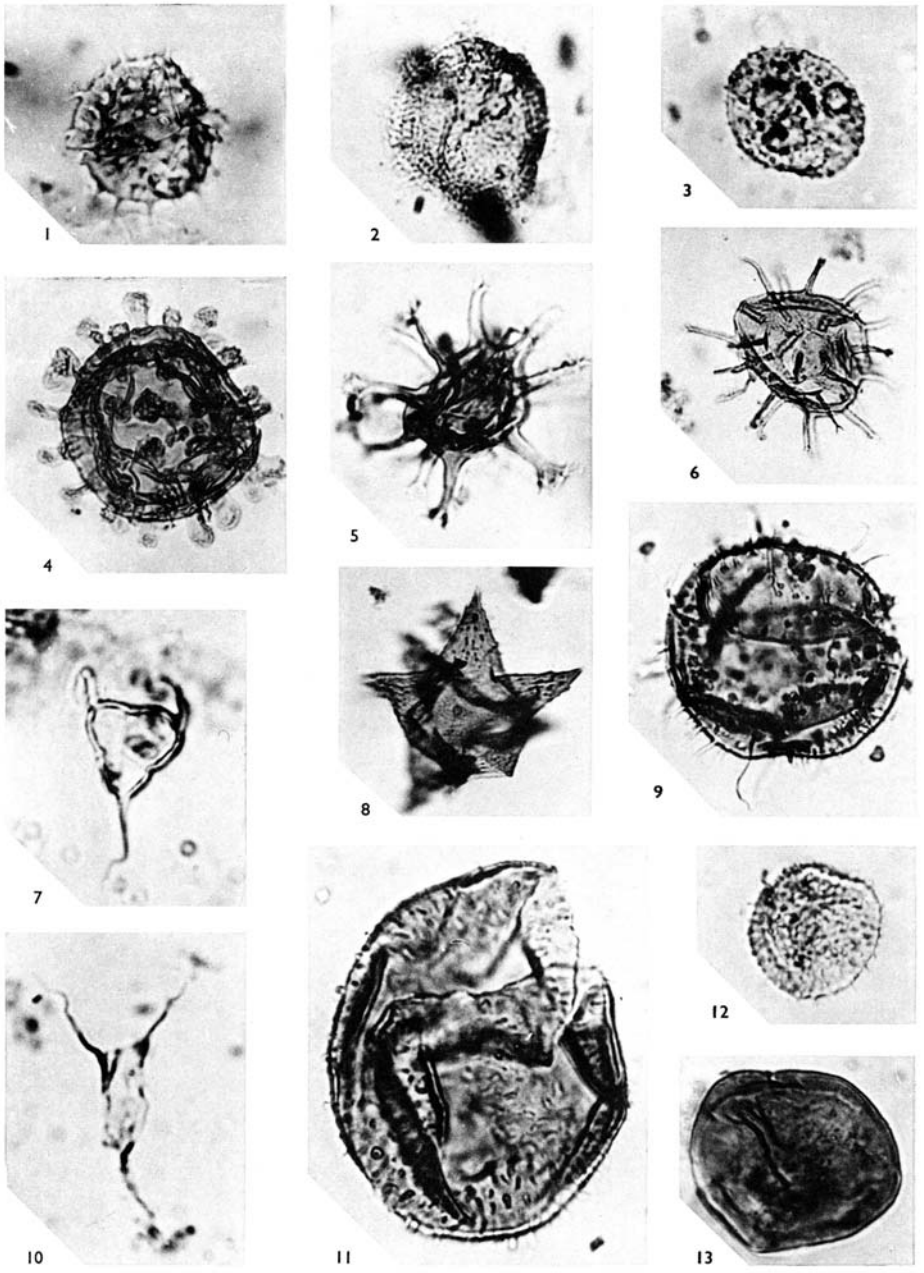


DOWNIE, Silurian 'hystrichospheres'



DOWNIE, Silurian 'hystrichospheres' and spores