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Ordovician acritarch genera *Peteinosphaeridium*, *Liliosphaeridium*, and *Cycloposphaeridium*: morphology, taxonomy, biostratigraphy, and palaeogeographic significance

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ABSTRACT – Lower to middle Ordovician marine strata of Öland, Sweden, contain abundant acritarch palynofloras especially notable for their diversity and excellent preservation. Quantitatively and qualitatively significant components include representatives of the peteinoid genera *Peteinosphaeridium* Staplin, Jansonius & Pocock, 1965, *Liliosphaeridium* Utela & Tynni, 1991, and *Cycloposphaeridium* Utela & Tynni, 1991, all characterized by their sphaeroidal, pylomate vesicles bearing conspicuous and distinctively laminate processes. Process morphology – pivotal to peteinoid taxonomy at genus and species levels – is analyzed in detail. It provides the main basis for taxonomic revisions and innovations, as follows: emendation of above three genera; institution of two new species, *P. angustilaminae* and *P. eximium*; elevated (sub-specific to specific) status, new combination, and emendation of *L. hypertrophicum* (Eisenack, 1976); new combination and emendation of *L. intermedium* (Eisenack, 1976); emendation of *P. bergstroemii* Staplin, Jansonius & Pocock, 1965 (type species), *P. velatum* Kjellström, 1971 (neotype designated), *L. kaljoi* Utela & Tynni, 1991 (type species), and *C. auriculatum* Utela & Tynni, 1991 (type species); the new combinations *L. pennatum* (Deunff, 1977) and *Ordoviciidium asperum* (Kjellström, 1971); and designation of a new neotype for *P. trifurcatum* (Eisenack, 1931 ex Eisenack, 1938) Eisenack, 1969. A comprehensive and critical literature survey reveals, inter alia, that certain species previously attributed to *Peteinosphaeridium* are not, or may not be, so assignable. The geographic and stratigraphic distributions of all species judged to be authentic or likely representatives of the three genera are documented. All three genera are confined to the Ordovician. From current records, *Peteinosphaeridium* extends from the lower into the upper Ordovician (uppermost Tremadoc-upper Ashgill); both *Liliosphaeridium* and *Cycloposphaeridium* are considerably more restricted stratigraphically (upper Arenig-lower Llanvirn and uppermost Arenig-mid Llanvirn respectively). Previously inferred, acritarch-based, biogeographic provinces for the lower and middle Ordovician are well-substantiated by the peteinoid evidence, in particular the differentiation of the Baltic Province from the Perigondwana Province, with different species of *Peteinosphaeridium* characterizing each and *Cycloposphaeridium* confined to the former. However, few data are available from South America, North America, North China, and Australia.

RIASSUNTO – [I generi ordoviciani di acritarchi *Peteinosphaeridium*, *Liliosphaeridium*, e *Cycloposphaeridium*: morfologia, tassonomia, significato biostratigrafico e paleogeografico] – I depositi marini dell'Ordoviciano inferiore e medio di Öland, Svezia, contengono una ricca microflora ad acritarchi, particolarmente notevole per l'alta diversità e l'eccezionale stato di conservazione. Tra i componenti quantitativamente e qualitativamente rilevanti, si annoverano rappresentanti dei generi peteinoidi *Peteinosphaeridium* Staplin, Jansonius & Pocock, 1965, *Liliosphaeridium* Utela & Tynni, 1991 e *Cycloposphaeridium* Utela & Tynni, 1991, tutti caratterizzati da una vescicola sferica, pilomata, e da cospicui processi, distintamente laminati. Viene qui analizzata in dettaglio la morfologia di questi processi, elemento cardine per la tassonomia peteinoida, sia a livello generico che specifico. Questo studio morfologico fornisce la base principale per alcune revisioni e innovazioni tassonomiche e cioè: emendamento dei tre generi sopra indicati; istituzione di due nuove specie, *P. angustilaminae* e *P. eximium*; elevamento di status (da subspecifico a specifico), nuova combinazione ed emendamento di *L. hypertrophicum* (Eisenack, 1976); nuova combinazione ed emendamento di *L. intermedium* (Eisenack, 1976); emendamento di *P. bergstroemii* Staplin, Jansonius & Pocock, 1965 (specie tipo), *P. velatum* Kjellström, 1971 (viene designato un neotipo), *L. kaljoi* Utela & Tynni, 1991 (specie tipo), e *C. auriculatum* Utela & Tynni, 1991 (specie tipo); nuove combinazioni: *L. pennatum* (Deunff, 1977) e *Ordoviciidium asperum* (Kjellström, 1971); designazione di un neotipo per *P. trifurcatum* (Eisenack, 1931 ex Eisenack, 1938) Eisenack, 1969. Una larga revisione critica della letteratura rivela, tra l'altro, che certe specie prima attribuite a *Peteinosphaeridium* non sono o possono non essere assegnabili a questo genere. La distribuzione geografica e stratigrafica di tutte le specie giudicate sicure o probabili rappresentanti dei tre generi viene qui dettagliatamente documentata. Tutti e tre i generi sono esclusivamente ordoviciani. Sulla base delle citazioni esistenti, *Peteinosphaeridium* si estende dall'Ordoviciano inferiore al medio e superiore (da un possibile Tremadoc terminale all'Ashgill superiore); *Liliosphaeridium* e *Cycloposphaeridium* hanno una ripartizione stratigrafica considerevolmente più ristretta (Arenig superiore-Llanvirn inferiore e Arenig terminale-Llanvirn medio, rispettivamente). La differenziazione in province biogeografiche, già supposta per le associazioni ordoviciane ad acritarchi, viene qui confermata con dati relativi alle specie peteinodi. In particolare, emerge chiaramente la differenziazione della Provincia Baltica dalla Provincia di Perigondwana, con differenti specie di *Peteinosphaeridium* caratterizzanti ciascuna di queste, mentre *Cycloposphaeridium* appare confinato nella prima. Troppo pochi dati, però, sono disponibili dal Sud America, Nord America, Cina del Nord e Australia.

INTRODUCTION

Medium-sized to large acanthomorphitic acritarchs featuring a morphological combination of

spheroidal vesicles, conspicuous laminate («listed», «finned», «winged», «veiled», etc.) processes, and pylomate excystment mode are characteristic and sometimes abundant components of palynofloras in

Ordovician marine strata from many parts of the world. Indeed, they have been reported in nearly 90 publications published thus far on acritarch assemblages of this age. The majority of these forms have been attributed to the genus *Peteinosphaeridium* Staplin, Jansonius & Pocock, 1965, although a number have been reassigned elsewhere and some further new combinations and new species are proposed in the present work. Also included herein are detailed considerations of two other genera, *Liliosphaeridium* and *Cycloposphaeridium* (both instituted monotypically by Uutela & Tynni, 1991), which are morphologically comparable with *Peteinosphaeridium*.

The importance of *Peteinosphaeridium* and its morphological allies in Ordovician stratigraphy and palaeogeographic syntheses invokes a need to clarify the morphology and taxonomy of this distinctive group of acritarchs. This constitutes the aim of the present paper, and, moreover, is greatly facilitated by particularly well preserved palynofloras, including abundant representatives of all three cited genera, from the well-dated early to middle Ordovician marine sequence of Öland, Sweden.

NOTE ON ORDOVICIAN SUBDIVISIONS

Cognizant of the current lack of international agreement concerning primary subdivision of the Ordovician period and system (Harland *et al.*, 1989, pp. 34-37; Cowie & Bassett, 1989; Odin, 1994, p. 66), we adopt herein an informal, though customary, three-fold categorization into early/lower, middle, and late/upper Ordovician (i.e., without initial capitalization of the qualifying adjective). In ascending order, these subdivisions respectively embrace the epochs/series Tremadoc + Arenig, Llanvirn + Llandeilo, and Caradoc + Ashgill (e.g., Fortey *et al.*, 1991, fig. 8). Since no general agreement exists on the subdivision of lower and middle Ordovician epoch/series (Harland *et al.*, 1989) we will also designate informally (with initial lower case letter) subdivisions at the age/stage level (e.g. late/upper Arenig, early/lower Llanvirn).

For this study we utilized material from four sections in northern Öland, Sweden; thus, the Baltoscandian chronostratigraphic nomenclature is also used. In Text-fig. 1 the Baltoscandian series and stages are depicted, together with their correlation (Tjernvik & Johansson, 1980; Harland *et al.*, 1989; Paris, 1992) with the British standard units. Note that the Baltoscandian three-fold subdivision of the Ordovician (Oeland, Viru, Harju) does not fit with the British standard. As regards stages and substages, we follow Jaanusson's (1960) interpretation. Since

BRITISH STANDARD				BALTO SCANDIAN			
SYSTEM - SUBS.		SERIES	GRAPTOLITE ZONES		SERIES-STAGES		
ORDOVICIAN	UPPER	ASHGILL	<i>G. persculptus</i> <i>C. extraordinarius</i>		HARJU	Porkuni	
			<i>D. anceps</i>			Pirgu	
			<i>D. complanatus</i>			Vormsi	
			<i>P. linearis</i>			Nabala	
	MIDDLE	CARADOC	<i>D. clingani</i>		VIRU	Rakvere	
			<i>C. multidentis</i>			Oandu	
			<i>N. gracilis</i>			Keila	
			<i>G. teretiusculus</i>			Jõhvi	
		LLAN-DEILO	<i>D. munchisoni</i>			Idavere	
			<i>D. artus</i>			Kukruse	
						Uhaku	
						Lasnamägi	
						Aseri	
			LOWER	ARENIG		<i>D. hirundo</i>	
	<i>D. extensus</i>	<i>I. gibberulus</i>			Volkhov		
		<i>D. nitidus</i>			Latorp	Billingen	
		<i>D. deflexus</i>					
	<i>(T. approximatus)</i>			Hunneberg			
	TREMADOC	<i>R. flabelliformis</i>		Varangu			
				Pakerort			

Text-fig. 1 - Stratigraphic units used in the text. Baltoscandian Ordovician subdivisions after Uutela & Tynni (1991, fig. 3), Paris (1992, fig. 2), Nölvak & Grahn (1993, fig. 2).

the sections studied in Öland do not exceed the middle and upper part of the Oelandian (Ontikan), only Swedish chronostratigraphic units of that interval are here reported (Text-fig. 2), together with corresponding trilobite zones and the traditional stratigraphic units, following Jaanusson (1960, p. 301) and Tjernvik & Johansson (1980, p. 175).

Series	Subser.	Stages	Substages	Trilobite Zones (Tjernvik & Johansson, 1980)	Old Swedish Units (from Jaanusson, 1960)
O E L A N D	O N T I K A N	Kunda	Aluoja	<i>Megistaspis gigas</i>	Vaginatium Limestone
				<i>Megistaspis obtusicauda</i>	
			Valaste	<i>Asaphus raniceps</i>	
			Hunderum	<i>Asaphus expansus</i>	
		Volkhov	Langevoja	<i>Megistaspis limbata</i>	Lepidurus Limestone
				<i>Megistaspis simon</i>	"Limbata" Limestone
				<i>Megistaspis lata</i>	
		Latorp	Billingen	<i>Megistaspis estonica</i>	Planilimbata Limestone
				<i>Megalaspides dalecarlicus</i>	
				Transition beds	
			Hunneberg	<i>Megistaspis planilimbata</i>	
				<i>Megistaspis armata</i>	

Text-fig. 2 - Subdivisions of the middle and upper part of the Oelandian Series commonly used in Sweden, according to Jaanusson (1960) and Tjernvik & Johansson (1980).

GEOLOGICAL SETTING, PREVIOUS WORK, AND MATERIAL STUDIED

THE ISLAND OF ÖLAND

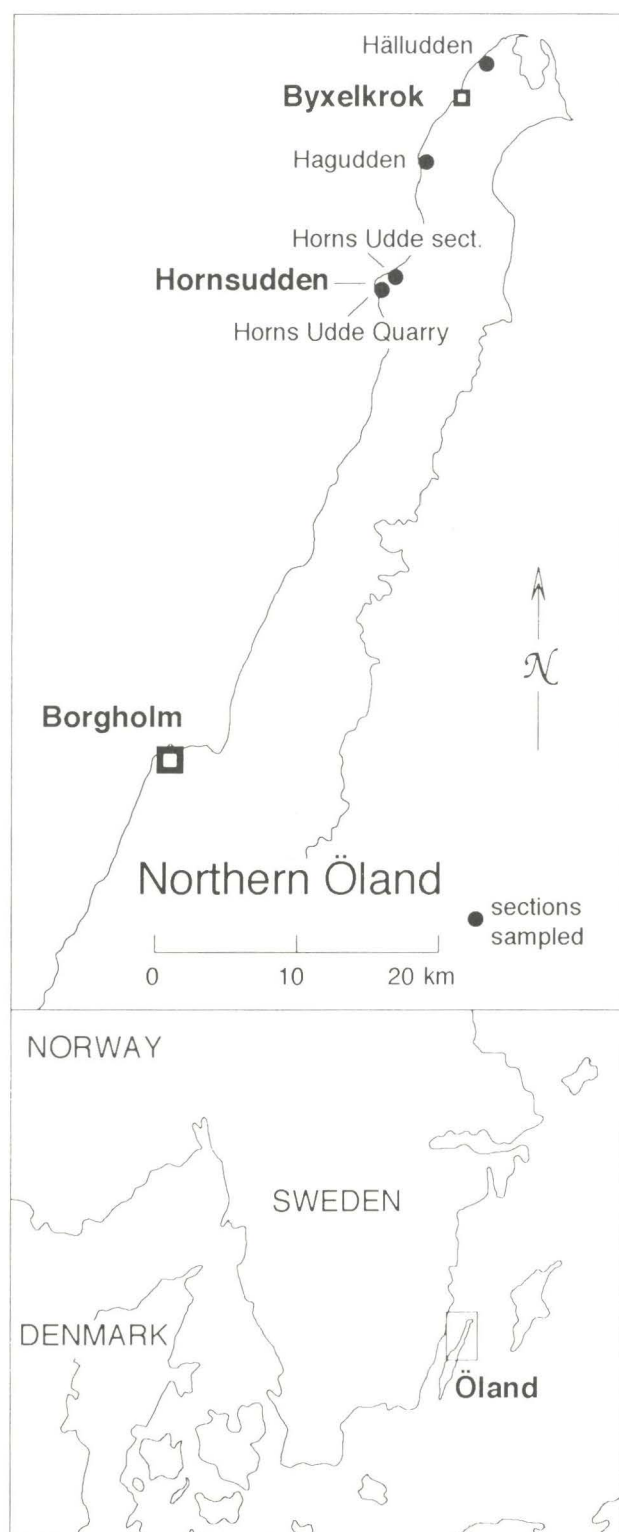
The Island of Öland is located just off the southeast coast of the Swedish mainland (Text-fig. 3) and on the western part of the East Baltic (Russian) Platform. Lower to middle Ordovician marine sediments are well-exposed as cliffs and terraces along the island's west coast. Deposited in part of the Baltic Syncline, a marginal platform depression opening southwesterly into the Danish-Polish trough (Störmer, 1967; Brangulis *et al.*, 1993), under stable, temperate, mostly shallow-marine conditions, these sediments accumulated slowly and apparently without major hiatuses during Tremadoc-Llandeilo time, forming a condensed carbonate sequence, *ca.* 44 m thick (Westergård, 1922, 1947; Tjernvik, 1956; van Wamel, 1974; Grahn, 1982). The strata, described as fossiliferous micrite and wackestone, rarely grainstone, often with abundant glauconite, are almost flat-lying and virtually undisturbed, and contain prolific, age-diagnostic faunas of trilobites, graptolites, and conodonts, together with brachiopods, nautiloids, ostracods, and cystoids. An informative stratigraphic summary is given by Stouge & Bagnoli (1990, pp. 2-4); for sedimentological and related details, see Nordlund (1988, and references cited therein).

Previous studies on Ordovician acritarch palyno-

logy of Öland comprise Staplin *et al.* (1965), Eisenack (1976), Tongiorgi (*in Bagnoli et al.*, 1988), and Ribecai & Tongiorgi (*in press*). The first utilized material from many geographic and stratigraphic sources, including Ordovician glacial erratics from Öland, one of which furnished the type species of the principal genus considered herein (*Peteinosphaeridium*). Eisenack (1976) reported on acritarchs (plus chitinozoans and other microfossils) of the Vaginatium Limestone (upper Arenig-lower Llanvirn) at Hälludden. The study by Tongiorgi (*in Bagnoli et al.*, 1988) concerned Middle Cambrian-lower Ordovician (Tremadoc) acritarch assemblages, mostly in association with conodonts, from the Furuhall section near Borgholm on the central-west coast. Ribecai & Tongiorgi (*in press*) conducted a reconnaissance study of upper Arenig-lower Llanvirn acritarchs from Horns Udde Quarry farther to the north. The present work is based on material from that quarry and from approximately coeval strata from three other nearby exposures along the northwest coast, including Hälludden (see below). Following Eisenack (1976), Grahn (1980, 1981, 1982) researched lower to middle Ordovician Chitinozoa of Öland, and these were considered briefly in a Baltoscandia-wide biozonal context by Nölvak & Grahn (1993).

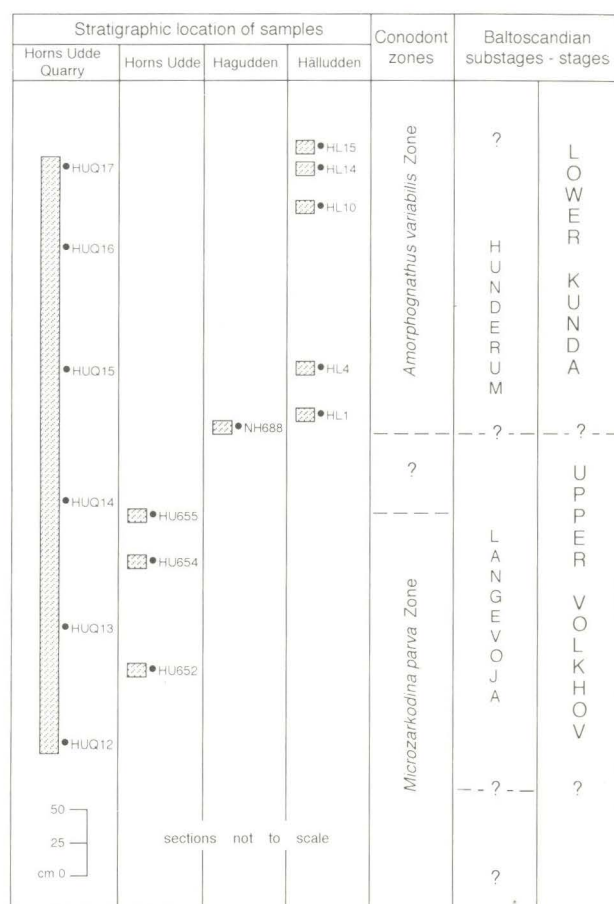
SECTIONS AND SAMPLING AT ÖLAND

Samples used in this study were collected principally from the section at Horns Udde Quarry, nor-



Text-fig. 3 - Locality map, Island of Öland, southeast Sweden.

thwest Öland, as detailed in Ribecai & Tongiorgi (in press) and depicted summarily in Text-fig. 4. Other



Text-fig. 4 - Stratigraphic positions of palynological samples collected from the section at Horns Udde Quarry (beginning 4 m stratigraphically above Flowery Sheet horizon) and relative positions of samples from Horns Udde, Hagudden, and Hälludden. Conodont zonation after Stouge & Bagnoli (1990, and pers. comm.). For correlation of Baltoscandian stages and substages see Text-fig. 1.

samples were obtained from three other sections to the north of that quarry; viz., Horns Udde, Hagudden, and Hälludden. The sequences exposed at these additional sections have been described in prior literature, as cited below; the sampling levels, related stratigraphically to the Horns Udde Quarry section, are indicated in Text-fig. 4.

A further Öland sample, mentioned previously and courteously provided by Dr. J. Jansonius, facilitated our examination of topotypic specimens of *Peteinosphaeridium bergstroemii* (type species described by Staplin *et al.*, 1965). This sample is part of an erratic boulder considered to be representative of the Schroeteri Limestone (middle Ordovician, Lasnamägi; upper Llanvirn), Parish of Stenåsa, southeast Öland (Staplin *et al.*, 1965).

Horns Udde Quarry

Located in a stone quarry ca. 1500 m southwest of the Horns Udde exposure (van Wamel, 1974), this section yielded acritarchs through an interval ca. 4.5 m thick (Ribecai & Tongiorgi, in press, fig. 2) starting ca. 4 m stratigraphically above the so-called Flowery Sheet (Bohlin, 1949; Lindström, 1971). The palyniferous beds comprise green to grey glauconitic limestones including (between 2–2.5 m above sampling base) three marly beds, each 10–20 cm thick. The top of the section is marked by a thin bed of ooids (Sturesson, 1986). From lithological and biostratigraphic evidence, the lower part of the sampled quarry section (encompassed by samples HUQ12–HUQ13) corresponds to the upper part of van Wamel's (1974) Horns Udde section.

In terms of the conodont sequence, the sampled interval extends from the *Microzarkodina parva* Zone into the lower part of the *Amorphognathus variabilis* Zone (G. Bagnoli & S. Stouge, pers. comm.) and is thus equivalent to the upper Volkhov Stage (Langevoja substage)–lower Kunda Stage (Hunderum Substage) of Baltoscandian terminology (Text-fig. 4). The top of the section may possibly reach the Valaste substage. Hence, the interval sampled is datable as late Arenig–early Llanvirn (cf. Stouge & Bagnoli, 1990).

Horns Udde

This coastal section, described in detail by van Wamel (1974, pp. 14, 16; fig. 10) and depicted also by Sturesson (1986, fig. 2), is situated some 1600 m northwest of Hornsudden (i.e., of the cape itself). Three samples were investigated for purposes of this study: HU652, HU654, and HU655, respectively 7.56 m, 8.50 m, and 8.92 m above section base (i.e., in the uppermost part of the section). These samples (Text-fig. 4) are assigned to the *Microzarkodina parva* conodont Zone (G. Bagnoli & S. Stouge, pers. comm.), i.e. to the upper Volkhov Stage (Langevoja Substage). Hence, the interval sampled is datable as late Arenig.

Hagudden

Situated 5 km south of Byxelkrok, this section is rich in shelly and conodont faunas; Stouge & Bagnoli (1990) have provided a literature review and conodont-based biostratigraphy. One sample, NH688, was utilized in the present study; it was collected 2.68 m above section base and corresponds to Stouge & Bagnoli's sample 688 at the base of the *Amorphognathus variabilis* conodont Zone (see

Stouge & Bagnoli, 1990, fig. 2), i.e. to the lowermost Kunda Stage (Hunderum Substage). Hence, sample NH688 is datable as latest Arenig.

Hälludden

The Hälludden section extends for ca. 2 km along the shore north of Byxelkrok. Nordlund (1988) has summarized previous work and provided a detailed account of the stratigraphy and sedimentology. The five samples of this study (Text-fig. 4) were collected from that part of the section exposed ca. 2.9 km northeast of Byxelkrok. Stratigraphic sampling levels are as follows: sample HL 1, 0.08 m above exposed base; HL4, 0.46 m; HL10, 1.12 m; HL14, 1.50 m; and HL15, 1.58 m. Attribution of these samples to the uppermost *Microzarkodina parva* and to lower *Amorphognathus variabilis* conodont Zones (Text-fig. 4) is based on preliminary data by G. Bagnoli & S. Stouge (pers. comm.), also verified by acritarch based correlations (C.R., unpublished). Hence, samples used here are datable as latest Arenig–early Llanvirn.

SECTIONS AND SAMPLING IN SOUTH CHINA

In addition to the Baltic samples, we also used a sample from the Yangtze Platform, southern China, originally studied by Tongiorgi, Yin Lei-ming & Di Milia (in press). This sample comes from the Daping section (ca. 26.5 km north of Yichang City, Hubei Province, South China), which comprises the whole Ordovician, represented by several, limestone-dominated formations. The very detailed, stratigraphic and sedimentological description of the whole section by Lindström *et al.* (1991) demonstrated that the Ordovician facies evolution of the Yangtze Platform and Scandinavia were similar, particularly during the middle Arenig–Llanvirn.

Sample HD2, utilized herein, comes from the Arenigian, mainly calcareous, Dawan Formation. It was collected ca. 20.25 m above section base in a shaly interval containing graptolites (notably *Axygograptus suecicus*) and trilobites and corresponding approximately, in British biostratigraphic terminology, to upper part (*Isograptus gibberulus*) of the lower Arenigian *Didymograptus extensus* graptolite Zone (An Tai-xiang, 1987).

TECHNIQUES

Approximately 250 g of each sample were processed for extraction and concentration of palynomorphs using conventional procedures. Successive treatments with hydrochloric acid (ca. 33%)

and hydrofluoric acid (ca. 40%) removed carbonates and silicates respectively. Neither oxidative nor alkali treatments were applied. Following demineralization, residues were transferred in absolute ethanol for sieving via screen meshes of 50 μm and 10 μm . Organic matter of each recovered fraction was concentrated by treatment with zinc bromide solution (S.G., 2.5) and then mounted on glass microslides in polyester resin for optical microscopy. Scanning electron microscopy was performed on both residue smears and on specimens picked individually per micromanipulator. The acritarchs proved to be abundant and exceptionally well preserved: transparent to translucent and light-coloured (mostly pale amber).

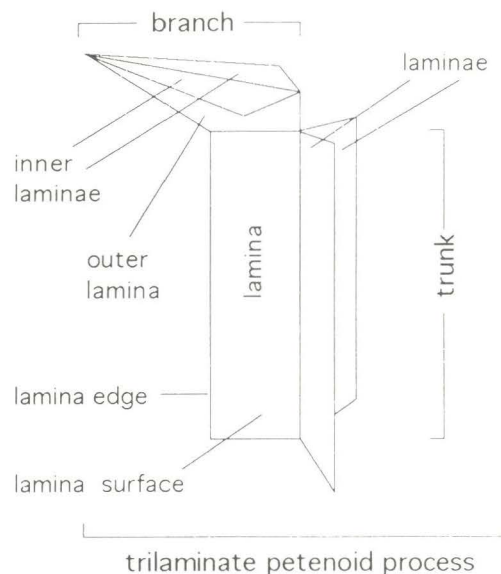
PROCESS MORPHOLOGY OF *PETEINOSPHAERIDIUM* AND RELATED FORMS

Peteinosphaeridium, *Liliosphaeridium*, and *Cycloposphaeridium* constitute a morphologically cohesive group of acritarch genera, often alluded to as «peteinoid» forms, linked by their possession of discrete solid processes composed of longitudinally and radially oriented blade-like elements. Certain other genera, not considered here in detail, may also be regarded as belonging to this same general category; viz., *Polyancistrodorus* Loeblich & Tappan, 1969 and *Asketopalla* Loeblich & Tappan, 1969 emend. Loeblich & Tappan, 1971. Details of peteinoid process morphology are elaborated below, as a prerequisite for taxonomic analysis and discrimination at generic and specific levels.

PROCESS TERMINOLOGY

For the purposes of this discussion and for ensuing systematic descriptions, morphological terms that relate specifically to the distinctive process morphology of *Peteinosphaeridium* and allied forms are given below and are illustrated in Text-fig. 5.

(a) *Lamina* (plural, *laminae*): A characteristically thin and often diaphanous, blade- or plate-like structure developed along the length of a process and constituting an integral part of the process. Laminae may be either psilate or may bear fine sculptural projections; and are normally of near-equal width on a given process. Synonymous with *peteinos* of Kjellström (1971a, p. 13) and list of some authors (e.g., Jacobson, 1978; but cf. Steidinger & Williams, 1970, p. 13, *vide* Williams *et al.*, 1978, p. 43). Various other terms, of more generalized and not always apposite connotation, have also been used; e.g., «veil», «strut», «keel», «fin», «wing» (e.g., Staplin *et al.*,



Text-fig. 5 - Terminology for laminate processes of peteinoid acritarchs. Schematic, not to scale.

1965; Jacobson, 1978; Loeblich & Tappan, 1969, 1978; Turner, 1984; Jacobson & Achab, 1985).

(b) *Lamina edge*: The outer (free) margin of a lamina.

(c) *Laminate process*: A process constituted of laminae. For example, *trilaminate processes* and *quadrilaminate processes* comprise, respectively, three and four longitudinally and radially disposed laminae oriented at 120° and 90° to each other.

(d) *Trunk*: The more or less cylindrical, prismatic, or laminate proximal portion of a branching process, i.e., excluding the branched or expanded (e.g., calical) distal portion; as per, e.g., Martin (1974), Martin & Yin Lei-ming (1988). Synonymous with *stem* of Cramer & Diez (1968, p. 552). In laminate processes, the trunk laminae are fused continuously along their inner margins, thus constituting the axial region of the trunk, while their outer margins (i.e., lamina edges) are entirely free, as are the lamina surfaces.

(e) *Branches of laminate processes* comprise, initially or entirely, three or four branches developed at the distal end of the trunk of a trilaminate or a quadrilaminate process, respectively. Branches themselves are invariably trilaminate, with one *outer branch lamina* and two *inner branch laminae* fused along their common margins, thus forming the branch axis. In each first order branch, the outer branch lamina derives specifically from the parental trunk lamina and, in any subsequent branch orders, from the outer lamina of the preceding order. Branching of laminate

processes is characteristic of categories C and D, discussed below; by contrast, categories A and B, also discussed below, incorporate simple, unbranched laminate processes.

(f) *Calyx* (plural, *calices*): Expanded, typically cup- or crown-like distal process structure (Text-fig. 6D), that is distally open and proximally (basally) closed, is more or less distinctly differentiated from trunk, and incorporates branches of one order and, in some cases, higher orders. Calyx may have an entire margin, or be dissected to varying degree (i.e., with more or less incomplete sides). Calyx-bearing processes thus appear in profile like wineglasses or trumpets, tall or squat depending on, respectively, greater or lesser elongation of the proximal (trunk) portion and on its relative width.

CATEGORIES OF LAMINATE PROCESSES

Four basic groups, discussed below, can be distinguished on the basis of the gross form of processes, which in turn reflects the nature, configuration, and interrelationships of the constituent process elements, the laminae, as defined above. The detailed morphology of the laminate processes provides objective criteria for recognition of peteinoide acritarch taxa at generic and specific levels.

A. *Elongate attenuated processes* (Text-fig. 6A)

The relatively simple, unbranched processes of this category, known currently from two species of *Peteinosphaeridium*, are composed of three or four (more commonly three) laminae that taper at their distal extremities to a common, often sharp point, sometimes extending as a more or less elongate, flexible spina or fine, hair-like termination. Process may attain maximum width at various distances from its base; or maintain relative uniformity in width until or near the distal attenuation. Laminae of a given process may not be equally developed distally; i.e., one may be narrower and almost imperceptible in the distal part of the process. In the proximity of the process base, one or more laminae may split into short, narrow, subsidiary laminae; thus, the main lamina insertion on vesicle wall assumes a characteristic Y shape. Also, the proximal parts of two adjacent laminae may occasionally more or less converge to form a C-shaped or near-circular insertion on vesicle wall; in such cases, the other process lamina(e) may be greatly diminished or even absent.

The external (free) margin of each lamina, defined above as the lamina edge, may be psilate or sculptured with echinae or other projections that

may extend into fine apical filaments. If the lamina edge is, for instance, regularly echinate, it assumes a serrate profile. The rest of the lamina surface is essentially unsculptured.

B. *Petaloid processes* (Text-fig. 6B)

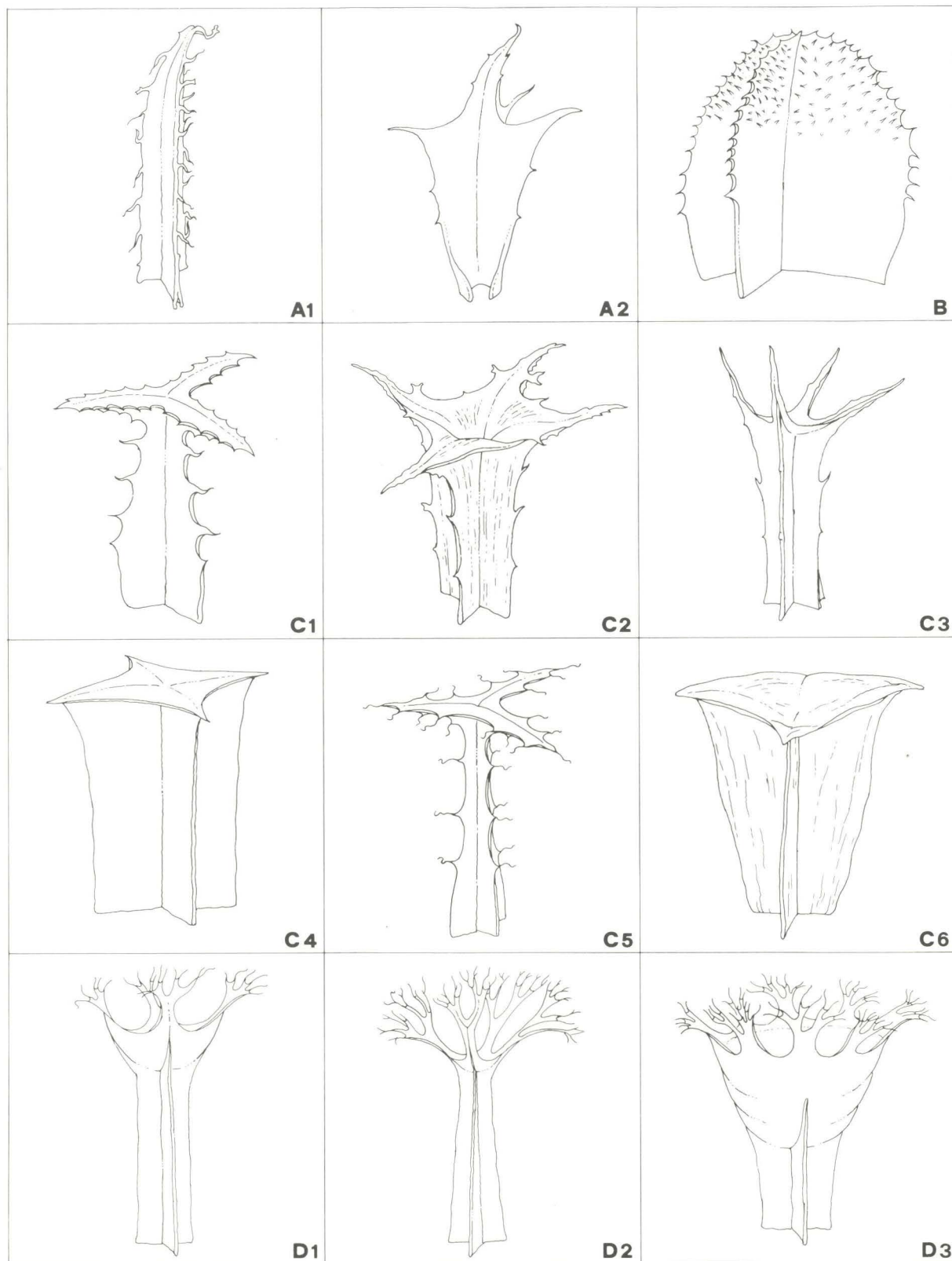
Exemplified by the type species of the monotypic genus *Cycloposphaeridium* (*C. auriculatum* Uutela and Tynni, 1991), these processes have a characteristic, broadly petal- or leaf-like shape in lateral aspect and consist of three laminae. The lamina edges diverge from a broad process base and then curve regularly to converge at the obtusely rounded, unbranched, distal process termination. The laminae of *C. auriculatum* are comprehensively and minutely sculptured (finely echinate).

C. *Near-columnar processes* (Text-fig. 6C)

This category is characteristic of 13 species of *Peteinosphaeridium*, including the type species *P. bergstroemii* Staplin, Jansonius & Pocock, 1965, emend. Category C is distinguished by processes having approximately columnar trunks – i.e., of more or less uniform width, or gradually flaring or tapering – and typically with ramifications at their distal extremities. Trunks are composed of three or four laminae (normally the latter). Close to process base, one or more laminae may bifurcate to form subsidiary laminae with resultant Y-shaped attachment to vesicle wall. Also as with category A, lamina edges may be psilate or variously, albeit finely, sculptured with, for instance, echinae/spinae or other elements, occasionally with filamentous extensions to the apices of the sculpturing elements. Numerous regularly distributed spinae developed on the lamina edges produce a distinctly serrated profile. The remainder of the lamina surface is either psilate or bears very minor sculpture.

The distal part of each process comprises three or four branches, each of which corresponds in position to a trunk lamina and projects at a minimum angle of about 90° to the trunk. Length of the branches may equal the width of the corresponding lamina or it may exceed that width. Each branch is composed of three laminae, so arranged that the outer lamina of the branch is a prolongation of one trunk lamina. These branch laminae taper distally to a blunt or sharp common point, sometimes extending as an elongate, flexible spine, that may be drawn out further as a very fine, hair-like ultimate extension.

When viewed superpositionally, both inner



Text-fig. 6 - Diagrams of laminate process categories (A-D), as represented by peteinoid species described and/or illustrated herein; not to scale. Elongate attenuated laminate processes (category A) - A1) *Peteinosphaeridium angustilaminae*; A2) *P. hymenoserum*. Petaloid laminate processes (category B) - B) *Cycloposphaeridium auriculatum*. Near-columnar laminate processes (category C) - C1) *Peteinosphaeridium armatum*; C 2) *P. bergstroemii*; C 3) *P. eximium*; C4) *P. micranthum*; C5) *P. robustiramosum*; C6) *P. velatum*. Distally elaborated processes (category D) - D1) *Liliosphaeridium hypertrophicum*; D2) *L. intermedium*; D3) *L. kaljoi*.

laminae of adjacent branches can be seen to coalesce, to a greater or lesser extent, to form a variably shaped, more or less flat or concave structure at the distal process extremity. If the branches are almost orthogonal to the trunk, a nearly flat, stellate (three- or four-rayed) structure is developed; and where the inner branch laminae are wider (and more co-extensive), a broader structure results that may be nearly square or triangular in outline. If the branches are more upwardly oriented (i.e., branch-trunk angle $>90^\circ$), the same structure is slightly concave or considerably more so. Edges of branch laminae exhibit the same features as the trunk lamina edges; i.e., the margins of the variably shaped distal structure (as viewed from above) may be smooth or sculptured, in some instances producing serrate margin.

D. Distally elaborated processes (Text-fig. 6D)

Characteristic of the genus *Liliosphaeridium*, this category incorporates the most complex morphology with respect to laminate processes. In gross terms, the processes feature a ramified and extended distal structure, defined above as a calyx, that is generally well-differentiated from the process trunk. In representatives of this category, laminae of both trunk and calyx are consistently and comprehensively psilate.

The process trunk comprises three or, more typically, four laminae; a shorter subsidiary lamina may occur between two adjacent main laminae. The trunk's maximum width is variable, interspecifically, along its length.

The distal part of each process – constituting the calyx, surmounting the trunk – is prominently ramified, embodying branches that correspond in number and location to the main trunk laminae (three or four). Branches extend upward at an angle to the trunk exceeding 90° , and with lengths greater than the trunk lamina width (often considerably so). Each branch is itself composed of three laminae, the outer of which is formed by the extension of one trunk lamina. Branches may dichotomize once or even twice, the dichotomies (i.e., products of second- and possibly third-order branching) still retaining their trilamination, with the outer lamina of each successive branch constituting the extension of the corresponding lamina from the preceding parental order.

The base of the calyx comprises the inner laminae of the initial (first order) branches that are coalescent, to varying degree, to form a concave structure (analogous to the flat to concave unit developed at the distal end of processes attributed to

category C). As noted, these branches correspond in number and position to the main trunk laminae. In successive second and possible third orders of branching, the inner laminae of adjacent branches are partially joined, thereby giving rise to a flat connection in their proximal region. At the distal limit of the calyx, the two inner laminae of each ultimate branch conjoin, beyond the trilaminate branch apex, to form distally broadening, flat, fanshaped projections that fork, mainly by repeated dichotomy, thus producing minute spinae often extending tenuously as thin filaments.

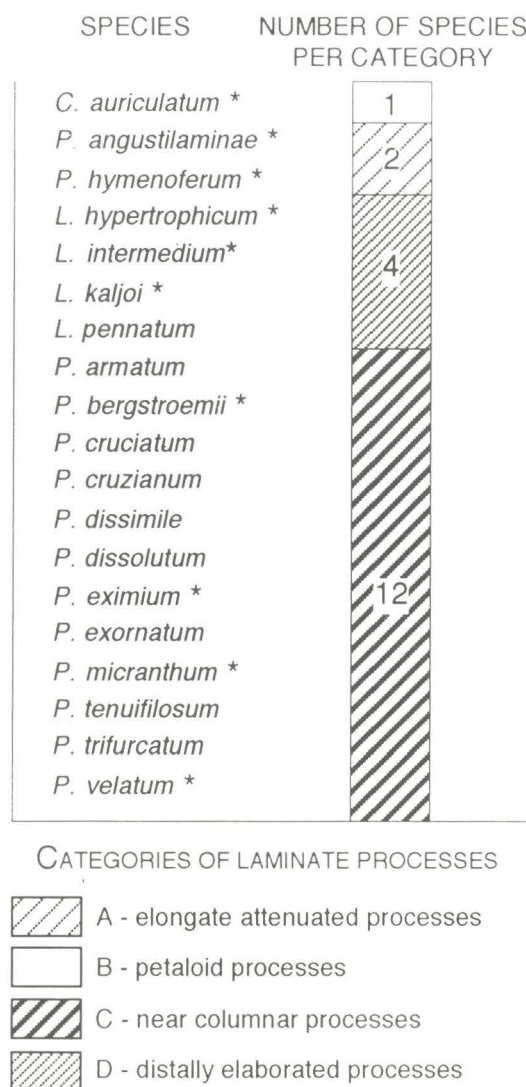
Overall, it will be evident that this fourth process category is characterized particularly by its distal ramifying complex: a variably dissected cup- or crown-like structure (calyx). In the type species *L. kaljoi* Uutela & Tynni, 1991, the calyx is particularly well developed and comprises a single branch order, in which the inner laminae of each branch extend distally (curving upwardly) as large projections fusing with neighbouring laminae to form a complete (undissected) calyx having an entire distal opening. By contrast, in the other species we attribute to *Liliosphaeridium*, the first and higher order branches remain discrete, thus forming a semi-enclosed coronal structure; i.e., a dissected, less-complete calyx.

Clearly, no rigorous boundary can be drawn between this category and some variants within category C. However, a reasonably serviceable distinction is that, in category D processes, the distal branches effectively combine to delimit, in varying degree, a more or less distinct cup- or crown-like entity.

DISCUSSION

The peteinoid species recognized herein are not evenly apportioned among the process categories (Text-fig. 7). Category C – the preponderant group by far – is represented by 13 species, all assigned to *Peteinosphaeridium*, and including type species *P. bergstroemii*. The remaining two species of that genus are attributable to category A. Category B, with its distally unelaborated petaloid processes, currently embodies one species only, *Cycloposphaeridium auriculatum*, which typifies the monotypic genus. Category D, embracing all known species of *Liliosphaeridium*, represents the most differentiated and elaborated process format, with its conspicuous distal ramifying complex constituting what is here called a calyx.

Not surprisingly, this four-fold process categorization is reflected taxonomically, primarily at generic level. The possibility clearly exists of in-



Text-fig. 7 - Distribution of laminate process categories among species assignable to the peteinoid genera *Peteinosphaeridium*, *Liliosphaeridium*, and *Cycloposphaeridium*. Asterisks denote species described herein.

corporating those species endowed with category A processes, viz., *P. angustilaminae* and *P. hymeniferum*, into a new genus, but is deferred at this time pending further work by C. Ribecai.

SYSTEMATIC PALAEONTOLOGY

TERMINOLOGY AND NOMENCLATURE

Morphological terms adopted in the systematic descriptions which follow are mostly in accord with usages promulgated by Williams *et al.* (1978), with the exception of those terms, defined above, that ap-

ply specifically to morphological characterization of the distinctive processes of *Peteinosphaeridium* and related genera.

Generic, specific, and infraspecific taxa are treated hereunder in accordance with the provisions of the current International Code of Botanical Nomenclature (ICBN; Greuter *et al.*, 1988; see also Fensome *et al.*, 1990, pp. 5-18).

REPOSITORY

All specimens illustrated herein (Pls. 1-9) are housed in the type collections of the Museo di Storia Naturale e del Territorio, Certosa di Calci, Pisa. Catalogue numbers (prefixed CPT) of that institution and other accessional details, including geographic and stratigraphic data pertaining to each specimen, are incorporated in Appendices 1 and 2.

SYSTEMATIC DESCRIPTIONS AND DISCUSSION

Synonymy listings incorporate basionym followed, where applicable, by synonyms and citation of prior emendations, together with any published records of the particular taxon that are deemed erroneous. Homonymy applies to none of the taxa discussed. Emendations to generic and specific diagnoses are proposed where significant alterations to the circumscriptions are warranted by our observations, primarily per optical microscopy, supplemented by SEM. A summary of geographic and stratigraphic occurrences of each species is provided under the heading «Distribution». This constitutes a critical appraisal insofar as obvious misidentifications are excluded, while doubtful identifications are appropriately signalled; explanatory notes in those respects appear under «Discussion» or «Remarks». Finally for each species described below, the vertical range, as confirmed or augmented critically by direct association with other fossils (principally conodonts), is specified. These supplementary biostratigraphic data derive from the Öland sections of this study. Clearly, the vertical ranges so established will almost certainly not represent the complete ranges, but will at least constitute an independently constrained portion thereof.

Group ACRITARCHA Evitt, 1963

Genus PETEINOSPHAERIDIUM Staplin, Jansonius & Pocock, 1965 emend.

1965 *Peteinosphaeridium* STAPLIN, JANSONIUS & POCKOCK, p. 194.

1969 *Peteinosphaeridium* Staplin, Jansonius & Pocock emend. EISENACK (*pars*), pp. 253-254.

Type species (by original designation) – *Peteinosphaeridium bergstroemii* Staplin, Jansonius & Pocock, 1965 emend.; from middle Ordovician, Lasnamägi Stage (upper Llanvirn) of Öland, Sweden. See discussion below under citation of *P. trifurcatum* and description of *P. bergstroemii*.

Emended diagnosis – Vesicle originally spherical or subspherical, with circular-subcircular outline. Vesicle wall essentially psilate or with very minor sculptural modification; probably bilayered, but layers evidently closely appressed. Processes conspicuous, elongate, discrete, approximately homomorphic, solid; trunk trilaminar or quadrilaminar, consisting of 3-4, thin, longitudinally and radially disposed laminae. Lamina surfaces essentially psilate; lamina edges psilate or bearing diminutive sculptural projections, e.g., echinae, bacula. Distal process termini either (a) attenuate and unbranched, with laminae tapering to a common, evexate or acuminate point, sometimes extending as a spina; or (b) more or less truncate, but with 3 or 4 ramifications (branches) emanating distally from the process trunk. In latter case, each branch constituted of 3 laminae, so arranged that the outer lamina effectively forms the extension of one trunk lamina; branch laminae tapering to an evexate or acuminate common point, sometimes extending as an elongate, flexible spina. Excystment structure consisting of well-developed pylome with simple or lipped margin and operculum.

Discussion – Following the original definition of *Peteinosphaeridium* by Staplin *et al.* (1965), summaries and discussions of its main attributes have been contributed by several authors, e.g., Tynni (1982, p. 77), Turner (1984, pp. 129-130), and Jacobson & Achab (1985, p. 190). However, none of the descriptions presented thus far, including the emendation proposed by Eisenack (1969, pp. 253-254), can be regarded as satisfactorily or unequivocally incorporating the salient morphological features. In particular, it should be noted that the invariable solidity and laminate structure of the processes are now specified, as is the presence of a pylome.

Process branching, characterizing the majority of *Peteinosphaeridium* species, is readily discernible under the light microscope. When viewed laterally, branched processes exhibit, in optical section, a T- or Y-shaped terminal configuration, resulting from distal divergence of the trunk laminae to form branch laminae (e.g., Pl. 2, figs. 1, 2, 5; Pl. 3, figs. 1, 4).

Comparison – *Liliosphaeridium* Uutela & Tynni 1991 emend. is distinguishable from *Peteino-*

sphaeridium Staplin, Jansonius & Pocock, 1965 emend. mainly on the basis of distal process morphology, the former genus being characterized by development of a calyx. Furthermore, in *Liliosphaeridium* the process laminae (including the lamina edges) are invariably psilate. *Polyancistrodorus* Loeblich & Tappan, 1969 (p. 51) differs from *Peteinosphaeridium* in possessing a «thickened antapical pseudopylome», i.e., additional to the more or less diametrically opposed «normal» pylome (but cf. Playford & Martin, 1984, p. 206). Moreover, although the solidity or otherwise of the processes of *Polyancistrodorus* was not specified by its authors, at least some of its species have hollow processes (e.g., Colbath, 1979; Playford & Wicander, 1988). *Cycloposphaeridium* Uutela & Tynni, 1991 emend. is distinct in its process morphology, as is *Asketopalla* Loeblich & Tappan, 1969 emend. Loeblich & Tappan, 1971 (p. 900) which features low «petaloid» processes unlike the elongate acanthomorphitic laminate processes of *Peteinosphaeridium*. *Ordovicidium* Tappan & Loeblich, 1971 (p. 398; see also Loeblich & Tappan, 1978, pp. 1278, 1281) has been compared and even synonymized (Eisenack *et al.*, 1976, p. 517) with *Peteinosphaeridium*, but is readily separable from the latter by reason of its hollow, non-laminate processes and its different excystment mode (simple wall-splitting); see also Eiserhardt (1992, p. 65).

Species assignable to Peteinosphaeridium

In addition to the type species (*P. bergstroemii*, described below), the following species are here considered consonant with the genus as emended above.

1. *Peteinosphaeridium angustilaminae* n. sp. (described below).

2. *Peteinosphaeridium armatum* Tongiorgi, Yin Lei-ming & Di Milia, in press (Pl. 2, fig. 1; Text-fig. 6C1 herein).

Occurrence – South China, lower Ordovician, Arenig (Tongiorgi, Yin Lei-ming & Di Milia, in press).

3. *Peteinosphaeridium cruciatum* Lu Li-chang, 1987.

One of the originally illustrated specimens (Lu Li-chang, 1987, pl. 3, fig. 8) has been attributed by Tongiorgi, Yin Lei-ming & Di Milia (in press) to their species *P. tenuifilosum* (listed below).

Occurrence – South China, lower Ordovician, Arenig (Lu Li-chang, 1987; Tongiorgi, Yin Lei-ming & Di Milia, in press).

4. *Peteinosphaeridium cruzianum* Vavrdová, 1990.

The sole illustrated specimen is not well preserved (Vavrdová, 1990, pl. 4, fig. 6; text-fig. 7) but is clearly consonant with *Peteinosphaeridium*.

Occurrence – Czech Republic, lower Ordovician, upper Arenig (Vavrdová, 1990).

5. *Peteinosphaeridium dissimile* Górká, 1969.

Based on only one «slightly damaged» specimen (Górká, 1969, pp.53-54, pl. 14, fig. 6), this species is neither well-characterized nor adequately illustrated, but nevertheless seems attributable to *Peteinosphaeridium*.

Occurrence – Poland, lower Ordovician, upper Arenig (Górká, 1969). North China, lower Ordovician, «cf.» record (Hu Yunxu, 1986).

6. *Peteinosphaeridium dissolutum* (Burmman, 1970) Eisenack, Cramer & Diez, 1979.

Apparently based on a single, diagrammatically illustrated specimen (Burmman, 1970, pp. 312-313, pl. 17, fig. 1), this species awaits more rigorous definition. Possibly conspecific are (i) the species described by Martin (1969, p. 44; pl. 5, fig. 215; pl. 6, fig. 299) under the binomen *Baltisphaeridium bergstromii* (Staplin, Jansonius et Pocock) from the Silurian of Belgium (reworked from Ordovician: Francine Martin, pers. comm. to M.T., 1993); (ii) *Peteinosphaeridium trifurcatum* (Eis.) Stapl., Jans. et Poc. in Rauscher (1974, p. 74, pl. 2, fig. 18) from the lower Ordovician (Arenig) of Montagne Noire, France; and (iii) *P. trifurcatum* subsp. *trifurcatum* in Turner (1985, p. 226, pl. 4, fig. 5) from the middle Ordovician (Llandeilo) of South Wales.

Occurrence – Germany, middle Ordovician, upper Llanvirn (Burmman, 1970).

7. *Peteinosphaeridium eximium* n. sp. (described below).

8. *Peteinosphaeridium exornatum* Tongiorgi, Yin Lei-ming & Di Milia, in press.

Occurrence – South China, lower Ordovician, Arenig (Tongiorgi, Yin Lei-ming & Di Milia, in press).

9. *Peteinosphaeridium hymeniferum* (Eisenack, 1938) Fensome *et al.*, 1990 (described below).

10. *Peteinosphaeridium micranthum* (Eisenack, 1959) Eisenack, Cramer & Diez, 1973 (described below).

11. *Peteinosphaeridium robustiramosum* Tongiorgi, Yin Lei-ming & Di Milia, in press (Pl. 4, fig. 11; Text-fig. 6C5 herein).

Occurrence – South China, lower Ordovician, Arenig (Tongiorgi, Yin Lei-ming & Di Milia, in press; Lu Li-chang, 1987, as *P. cruciatum* in part).

12. *Peteinosphaeridium tenuifilum* Tongiorgi, Yin Lei-ming & Di Milia, in press.

Occurrence – South China, lower Ordovician, Arenig (Tongiorgi, Yin Lei-ming & Di Milia, in press).

13. *Peteinosphaeridium trifurcatum* (Eisenack, 1931 ex Eisenack, 1938) Eisenack, 1969.

Typification – As discussed below under *P. bergstroemii*, loss of the holotype and rejection of Eisenack's (1959) neotype invoke the need to select a new neotype for *P. trifurcatum*. Accordingly, we designate here as neotype the specimen figured by Eisenack (1959, pl. 17, fig. 7; slide E1, G₁, 2, Nr. 5, Tb - Geol. Paläont. Inst., Univ. Tübingen, Germany) as *Baltisphaeridium trifurcatum* forma *breviradiata*, subsequently *P. breviradiatum* (Eisenack, 1959 ex Eisenack, 1965) Eisenack, 1969. The latter species includes the lost holotype of *P. trifurcatum* (Eisenack, 1969, p. 255) and is therefore to be regarded as a nomenclaturally superfluous name for *P. trifurcatum* (see ICBN Art. 63.1; cf. Art. 53.1). According to Eisenack (1959, caption to pl. 17, fig. 7), the neotype designated herein come from Rawaküll, Estonia, Jörden's Stage G₁. That implies a Lower Silurian (Juruu Stage = early Rhuddanian) age for Eisenack's holotype of *P. breviradiatum*. But in Estonia the Lower Silurian lies transgressively, mostly unconformably on Ordovician beds. The contact is characterized by evident channelling (Kaljo, 1990). Thus, reworking cannot be excluded. This is confirmed by the age of the other specimens attributed by Eisenack to the same species, which came from Ordovician erratics (called Ostseekalk), late Llandeilo-earliest Caradoc (*N. gracilis* graptolite Zone: Eisenack, 1965, p. 116) in age (Eisenack, 1965, p. 138, pl. 11, fig. 8, pl. 12, fig. 15; 1968a, p. 7, pl. 1, fig. 9); and from upper Ordovician outcrops (Rakvere Stage = upper Caradoc: Eisenack, 1968a, p. 7, pl. 2, fig. 3).

Remarks – In its customarily broad and confused connotation, with a plethora of often inadequately circumscribed subspecific components, *P. trifurcatum* has come to acquire the unfortunate and unhelpful status of a balloon taxon (*sensu* Hughes, 1970). From the present systematic text, it will be evident that many peteinoid forms that have been attributed to this «species» are more properly or definitively assignable elsewhere; e.g., to *P. bergstroemii*. Many putative records of *P. trifurcatum* represent poorly preserved and/or inadequately described and illustrated specimens that defy positive identification, in some instances even at generic level. Elevation of some of the *trifurcatum* subspecies (or formae) to full specific rank is, generally speaking, a propitious development, though some of the taxa still await satisfactory definition or typification. While not intending any unfair criticism of Eisenack (1931 *et seq.*) – assuredly a most distinguished and revered figure in microphytoplankton studies – it is clear that many of the *trifurcatum* problems originate from the pioneering nature of his researches. Compounding the difficulties are losses or destruction of much of

Eisenack's original study material, including type specimens (at least partly a consequence of World War II hostilities in his native Germany).

Occurrence – This summary is restricted to the few published reports of what are considered to be authentic specimens of *P. trifurcatum* (i.e., in the above-typified, restricted sense). Baltic region, lower to middle Ordovician (e.g., Eisenack, 1969, 1976; Kjellström, 1971b; Tynni, 1975; Górka, 1987).

Subspecies – Neither of the two currently recognized subspecies of *P. trifurcatum*, listed below, can be considered as adequately defined, but both appear distinctive enough to merit separate specific status within the genus.

(i) subsp. *cylindroferum* (Eisenack, 1968) Fensome *et al.*, 1990 features prominent, laminate, branched processes (seemingly both trilaminate and quadrilaminate) and, more particularly, a pylome with conspicuously elevated, collar-like surround (Eisenack, 1968a, p. 19, pl. 1, figs. 3, 4, pl. 3, fig. 9; Eisenack *et al.*, 1973, p. 925). Known occurrences restricted to a Baltic lower Ordovician erratic boulder (Eisenack, 1968a) and a middle Ordovician subsurface sample from Finland (Tynni, 1982).

(ii) subsp. *longiradiatum* (Eisenack, 1959) Fensome *et al.*, 1990 is characterized by very long and slender, branching processes that appear to be distinctly laminate only in their distal portions; excystment structure unknown (Eisenack, 1959, p. 202; Eisenack, 1965, p. 138, pl. 11, figs. 6, 7; Eisenack *et al.*, 1973, pp. 927-928). Reported from Baltic Ordovician erratic boulders (Eisenack, 1959, 1965; Tynni, 1975, Caradoc; Uutela, 1989, Llandeilo-Caradoc); and in situ from middle to upper Ordovician (Lasnamägi-Nabala; Llanvirn-Caradoc) of Estonia (Uutela & Tynni, 1991), upper Ordovician (Caradoc) of Russia (Umnova, 1975), and Caradoc of Portugal (Elaouad-Debbaj, 1981). From these records, the subspecies appears to be dominantly Caradoc.

14. *Peteinosphaeridium velatum* Kjellström, 1971 emend. (described below).

Species possibly assignable to Peteinosphaeridium

Doubts concerning allocation to *Peteinosphaeridium* of the first six species listed ensue chiefly from their respective diagnoses either stating or implying the presence of hollow, albeit laminate processes.

1. *Peteinosphaeridium furcatum* Combaz & Peniguel, 1972.

Occurrence – Western Australia, lower Ordovician, Arenig (Combaz & Peniguel, 1972).

2. *Peteinosphaeridium granulatum* Uutela & Tynni, 1991.

Occurrence – Estonia, middle to lower upper Ordovician, Uhaku-Idavere, Llandeilo-lower Caradoc (Uutela & Tynni, 1991).

3. *Peteinosphaeridium indianaense* Colbath, 1979.

Occurrence – U.S.A., upper Ordovician, Eden, upper Caradoc (Colbath, 1979).

4. *Peteinosphaeridium parvispinosum* Uutela, 1989.

Excystment structure unknown; lamination of processes unspecified and unclear from sole illustration (Uutela, 1989, pl. 8, fig. 71).

Occurrence – Finland, offshore middle Ordovician erratic (Uutela, 1989).

5. *Peteinosphaeridium spiraliculum* Colbath, 1979.

Occurrence – U.S.A., upper Ordovician, Eden, upper Caradoc (Colbath, 1979).

6. *Peteinosphaeridium strigosum* Vavrdová, 1986.

Occurrence – Czech Republic, middle Ordovician, lower Llanvirn (Vavrdová, 1986).

7. *Polyancistrodorus magnispinosus* Uutela & Tynni, 1991.

This multi-processed species is seemingly unipylomate, as noted by Tongiorgi, Yin Lei-ming & Di Milia (in press), and may thus be more in accord with *Peteinosphaeridium* than with *Polyancistrodorus*, which features a so-called pseudopylome additional to the normal pylome.

Occurrence – Estonia, middle Ordovician, Kunda-Kukruse, Llanvirn-Llandeilo (Uutela & Tynni, 1991).

8. *Polyancistrodorus phylloides* Uutela & Tynni, 1991.

The slightly flared processes of this species are non-furcate, and, as with *Polyancistrodorus magnispinosus* (7, above), the apparent absence of a pseudopylome invokes doubt as to generic assignment.

Occurrence – Estonia, middle Ordovician, Aseri-Lasnamägi, Llanvirn (Uutela & Tynni, 1991).

9. *Peteinosphaeridium polyfurcatum* Tynni, 1982.

Restricted material base, brevity of description, and insufficiency of illustration (Tynni, 1982, p. 79, pl. 14, fig. 103) result in poor characterization; no differential diagnosis provided. Possibly assignable to *Liliosphaeridium*.

Occurrence – Finland, Åland Islands, middle Ordovician (Tynni, 1982).

10. *Peteinosphaeridium xiphopterum* Hu Yunxu, 1986.

Excystment structure unknown or unspecified, hence generic attribution uncertain. Process morphology and other features do appear to be consonant with *Peteinosphaeridium*.

Occurrence – North China, lower Ordovician (Hu Yunxu, 1986).

Species not compatible with Peteinosphaeridium

1. *Ordoviciidium asperum* (Kjellström, 1971) n. comb.

Basionym – *Peteinosphaeridium asperum* Kjellström, 1971, p. 32, fig. 21 [1971b].

New combination based on simple-split (non-pylomate) excystment and hollow, non-laminate, furcate processes not communicating with vesicle cavity (cf. Loeblich & Tappan, 1978, pp. 1278, 1281). Górká's (1979, p. 368, pl. 17, fig. 3) record of this species, from Polish middle Ordovician strata, is a likely misidentification: processes too short and too sparsely distributed.

Occurrence – Sweden, Gotland, middle Ordovician (Kjellström, 1971b).

2. *Peteinosphaeridium? hystrichoreticulatum* (Eisenack, 1938) Eisenack, Cramer & Diez, 1973.

The questioned generic assignment (Eisenack *et al.*, 1973, p. 905) is endorsed here because of (i) uncertainty regarding laminate character of processes; (ii) unspecified or unknown excystment mode; and (iii) conspicuously reticulate vesicle wall sculpture.

Occurrence – Baltic region, erratic, Glaukonitkalk, Ordovician (Eisenack, 1938). Sweden, Öland, lower Ordovician, Volkhov, Langevoja, upper Arenig (Ribecai & Tongiorgi, in press).

3. *Peteinosphaeridium macropylum* (Eisenack, 1959) Eisenack, Cramer & Diez, 1973.

Incompatibility with *Peteinosphaeridium* ensues chiefly from (i) nonlaminate process construction (e.g., Eisenack, 1959, p. 199, fig. 9); and (ii) presence of so-called «double pylome» (Eisenack, 1976, pp. 195, 198). On these grounds, it seems likely that this species warrants recognition as a new (non-peteinoid) genus. In accord with Eisenack (1976), but not Eisenack *et al.* (1973, pp. 907-908), Swedish lower Ordovician specimens reported by Kjellström (1971a, pp. 31-32, pl. 2, fig. 3) are considered misidentified, as are those reported from Estonia by Uutela & Tynni (1991, p. 105, pl. 24, fig. 251). The specimen figured and described by Tynni (1982, p. 78, pl. 14, fig. 100; from a Finnish Ordovician erratic boulder) as *Peteinosphaeridium macropylum* f. *coronata* Tynni, 1982 seems an unlikely representative of the species.

Occurrence – Sweden, lower Ordovician, Volkhov-lower Kunda (Hunderum), upper Arenig (Eisenack, 1959; Ribecai & Tongiorgi, in press). Finland, lower to middle Ordovician, Volkhov-Kunda, upper Arenig-lower Llanvirn (Uutela & Tynni, 1991).

4. *Peteinosphaeridium nanofurcatum* Kjellström, 1971.

Uncertainty as to generic assignment results mainly from Kjellström's (1971a, p. 55) implication that processes are hollow («separation of the interior of the process from the vesicle cavity»). Moreover, the single original illustration (Kjellström, 1971a, pl. 4, fig. 5; holotype) does not clearly depict other process detail, and doubts are not allayed by further description and illustrations in Bockelie & Kjellström (1979, p. 213, figs. 14a, b). In any case, the species is surely incompatible with *Peteinosphaeridium* because, as noted by the latter authors, its excystment structure is a «median-split rupture». Uutela & Tynni's (1991, p. 101) proposed new combination with *Ordoviciidium* Tappan & Loeblich, 1971 lacked complete basionymic specification (i.e., figure number omitted; cf. ICBN, Art. 33.2); that notwithstanding, it may be premature to endorse or validate the combination in the absence of critical information on process morphology from the holotype or other topotypic material. An English Caradoc specimen recorded by Turner (1984, pp. 130-131, pl. 8, fig. 7) as *Peteinosphaeridium nanofurcatum* is of doubtful specific identity (much smaller vesicle, differently proportioned processes).

Occurrence – Sweden and Estonia, middle Ordovician (Kjellström, 1971a; Bockelie & Kjellström, 1979; Uutela & Tynni, 1991). Finland, offshore Ordovician erratics (Uutela, 1989). Canada, Newfoundland, middle Ordovician (Martin, 1978; cf. record only).

5. *Peteinosphaeridium paucifurcatum* (Eisenack, 1959) Eisenack, Cramer & Diez, 1973.

Generic assignment inappropriate because of non-laminate processes, and attribution elsewhere dependent on as yet uncertain process construction (hollow or solid?).

Occurrence – Estonia, Ordovician erratic, Glaukonitsand, B₁ (Eisenack, 1959). Finland, offshore Ordovician erratics (Tynni, 1975; Uutela, 1989). Russia, lower Ordovician (Umnova, 1975). The specimen figured by Downie & Ford (1966, pl. 17, fig. 10; lower Ordovician, Isle of Man) as *Baltisphaeridium* cf. *trifurcatum paucifurcatum* appears unrepresentative of *P. paucifurcatum*.

6. *Peteinosphaeridium? sibiricum* (Timofeev, 1966) Eisenack, Cramer & Diez, 1979.

This species is known only from a brief description and one line-drawn illustration (Timofeev, 1966, pp. 46-47, pl. 9, fig. 3). These do not facilitate attribution to *Peteinosphaeridium*, however tentatively proposed (Eisenack *et al.*, 1979, p. 101), nor indeed definitively to any other genus. For instance,

the scattered, distally funnel-like processes may or may not be solid and the excystment opening, if any, remains unspecified.

Occurrence – Siberia, middle and upper Ordovician, Mangazeisk and Delbrosk (Timofeev, 1966).

PETEINOSPHAERIDIUM ANGUSTILAMINAE n. sp.

Pl. 1, figs. 1-3; Text-fig. 6A1

1991 *Peteinosphaeridium hymeniferum* auct. non Eisenack (1938)
1969 - UUTELA & TYNNEI, pp. 104-105, pl. 24, fig. 250.

Diagnosis – Vesicle originally spherical, outline circular to subcircular; wall psilate, 0.8-1.4 µm thick. Processes solid, more or less homomorphic, elongate, unbranched, trilaminate, comprising 3 very thin, diaphanous, longitudinally and radially disposed laminae, each 0.8-3.2 µm wide at process base; mostly maintaining that width for ca. two-thirds to five-sixths of process length, then tapering distally to simple, obtuse to acute process extremity where laminae converge to common evexate to acuminate apex. Lamina edges psilate to finely sculptured (minutely echinate, granulate, elongate-baculate). Processes mostly straight or curved; distal termini often curved to coiled when markedly attenuated. Process length variable among specimens (range 14-32 µm), but fairly uniform on given specimen; bases 2.5-14 µm apart; proximal contacts angular to slightly curved. Pylome circular to subcircular, margin simple, diameter 17-24 µm; operculum not observed.

Dimensions – Vesicle diameter 43 (55) 66 µm (56 specimens measured); pylome diameter 14 (20) 24 µm (36 specimens). Process length averages 40% of vesicle diameter (range 25-54%).

Holotype – Slide HL10/50-1, S49/2; Pl. 1, figs. 2a, 2b. Vesicle 62 µm in diameter, wall 1.2 µm thick; processes 21-25.5 µm long, tips commonly recurved, bases 3-9.5 µm apart; laminae more or less constantly 1.3-2.4 µm wide for about 80-85% of distance from base, then tapering abruptly to narrowly acute distal termini; lamina edges with sparse, irregularly distributed, diminutive echinae, grana, and thread-like projections; near-circular pylome 18 µm in diameter.

Type locality and stratum – Sweden, Island of Öland, northwest coast, Hälludden, ca. 2.9 km northeast of Byxelkrok; Vaginatum Limestone, sample 10, 1.12 m above section base; *Asaphus expansus* trilobite Zone, lower or middle Ordovician, Kunda (uppermost Arenig or lowermost Llanvirn).

Etymology – Lat., *angustus* = narrow; *lamina* = lamina.

Remarks and comparison – Process length and width (i.e., width of constituent laminae) vary fairly widely, albeit continuously, among specimens of *Peteinosphaeridium angustilaminae* n. sp., but are comparatively uniform on any one specimen. This species is distinguishable from *P. hymeniferum* (Eisenack, 1938) Fensome *et al.*, 1990 (described subsequently herein) in having regularly tapering, unexpanded laminae.

The specimens described and figured by Uutela & Tynni (1991) under the binomen *Peteinosphaeridium hymeniferum* Eisenack (1938) 1969 cannot be ascribed to that species owing to their slender processes which do not show the sub-distal expansion of the laminae (emphasized by outwardly projecting major spinae) that characterizes *P. hymeniferum*. In fact, Uutela & Tynni's (1991) material exemplifies the morphology of *P. angustilaminae*, to which it is consequently here assigned.

Distribution – Estonia (Uutela & Tynni, 1991, as *P. hymeniferum*) and Öland, Sweden: lower to middle Ordovician, Volkhov-Kunda, upper Arenig to lowermost Llanvirn.

Stratigraphic range verified by co-occurrence of other fossils (Öland, Sweden) – (a) Lower limit: lowermost Kunda, lower Hunderum (uppermost Arenig), *Asaphus expansus* trilobite Zone, lower *Amorphognathus variabilis* conodont Zone, Vaginatum Limestone, Hälludden. (b) Upper limit: Kunda, Valaste (uppermost Arenig-lowermost Llanvirn), *Asaphus «raniceps»* trilobite Zone, *Amorphognathus variabilis* conodont Zone, Vaginatum Limestone, Hälludden.

PETEINOSPHAERIDIUM BERGSTROEMII Staplin,

Jansonius & Pocock, 1965 emend.

Pl. 2, figs. 2-6; Text-fig. 6C2

1938 *Hystriosphæridium trifurcatum* EISENACK (*pars*), pp. 16-19, pl. 2, fig. 3, ?figs. 8, 9 (*non* pl. 2, figs. 1, 2, 4-7, 10-14a, b).

1959 *Baltisphaeridium trifurcatum* (Eisenack) 1931 forma *typica* EISENACK (*pars*), p. 202, pl. 17, fig. 3 (*non* pl. 17, figs. 1, 2a, b).

1965 *Peteinosphaeridium bergstromii* STAPLIN, JANSONIUS & POCKOCK (*pars*), p. 194, pl. 20, figs. 13, ?14 (*non* pl. 20, figs. 16-18).

non 1969 *Baltisphaeridium bergstromii* (Staplin, Jansonius & Pocock) MARTIN, p. 44; pl. 5, fig. 215; pl. 6, fig. 299.

non 1969 *Peteinosphaeridium bergstromi* Staplin, Jansonius & Pocock, 1965 - GÓRKA, p. 53, pl. 14, figs. 7, 8.

non 1969 *Peteinosphaeridium trifurcatum* (Eis.) subsp. *typicum* Eisenack, 1969 - GÓRKA, pp. 23-25, pl. 1, figs. 1, 5, text-fig. 4.

- 1969 *Peteinosphaeridium trifurcatum* (Eisenack 1931) - EISENACK, pp. 254-255.
 1973 *Peteinosphaeridium trifurcatum typicum* (Eisenack 1959) - EISENACK *et al.* (pars), pp. 929-930.
 non 1981 *Peteinosphaeridium trifurcatum typicum* (Eisenack 1959) ? - ELAOUAD-DEBBAJ, pp. 50-51, pl. 16, figs. 15, 16.
 ? 1984 *Peteinosphaeridium trifurcatum trifurcatum* (Eisenack 1959) Staplin, Jansonius & Pocock (sic) - TURNER (pars), pp. 133-134, pl. 9, fig. 3 (non pl. 9, fig. 8).
 non 1987 *Peteinosphaeridium bergstroemii* Staplin, Jansonius & Pocock - LU LI-CHANG, p. 95, pl. 2, figs. 6, 7.

Emended diagnosis – Vesicle originally spherical; outline circular or subcircular. Vesicle wall psilate to shagreenate; mostly 1.4-2.3 μm thick, sometimes showing slight local thickening (up to 2.8 μm) about process bases. Processes solid, more or less homomorphic, elongate, flared; trunks quadrilaminate or trilaminate, consisting of 4, less commonly 3, relatively thin, longitudinally and radially disposed laminae, each *ca.* 1.4-5 μm broad at process base, broadening gradually and uniformly to reach maximum width of 4.5-13 μm distally, where 3 or 4 branches developed, each corresponding in position to a trunk lamina and projecting at minimum angle of 90° to trunk. Branch length up to *ca.* twice width of corresponding trunk lamina; branches invariably trilaminate, the outer lamina of each being the extension of one trunk lamina. Proximal portions of inner laminae of adjacent branches coalescent to form a variably shaped (quadrangular or triangular), nearplanar to concave structure at process extremity; distal portions of inner laminae often produced laterally as simple or furcant, spine-like projections. Process length within range of 18-34 μm (but fairly uniform on given specimen); proximal contacts angular or slightly curved; bases 4.8-20 μm apart, some featuring short, divergent, root-like extensions. Lamina edges psilate or with fine echinae, bacula, or flat fan-like projections, some having attenuated-prolonged, tenuous termini; lamina surfaces very minutely sculptured (microstriate) to near-psilate. Pylome circular to subcircular, margin simple or thickened to form darkened, slightly elevated, circular band up to 4.5 μm wide; operculum (rarely encountered) psilate or minutely sculptured (irregularly granulate/verrucate or faintly rugulate).

Dimensions – vesicle diameter 39 (55) 65 μm (70 specimens measured); pylome diameter 9 (17) 25 μm (46 specimens). Process length averages 43% of vesicle diameter (range 28-78%).

Holotype – Staplin *et al.* (1965), pl. 20, fig. 13; Imp. 5099-#4, slide 2 - 110.1 X 38.5.

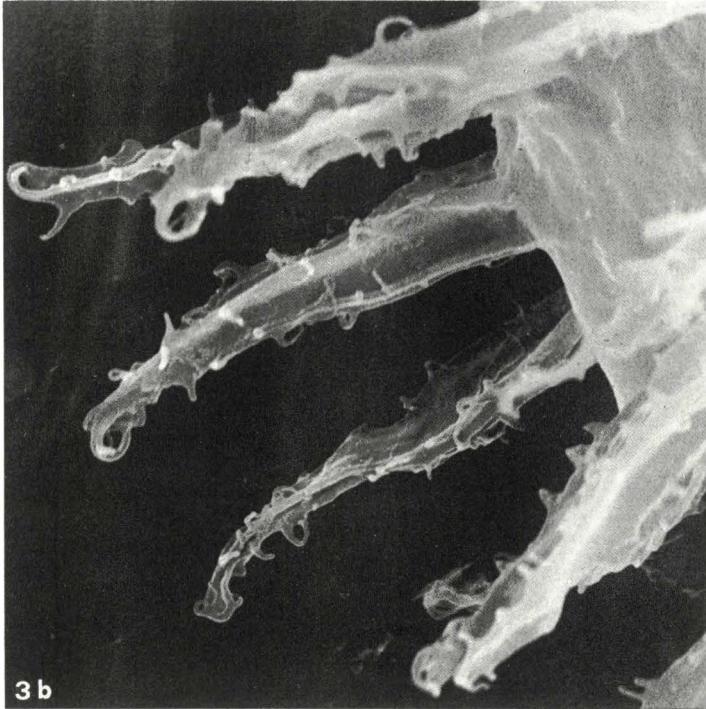
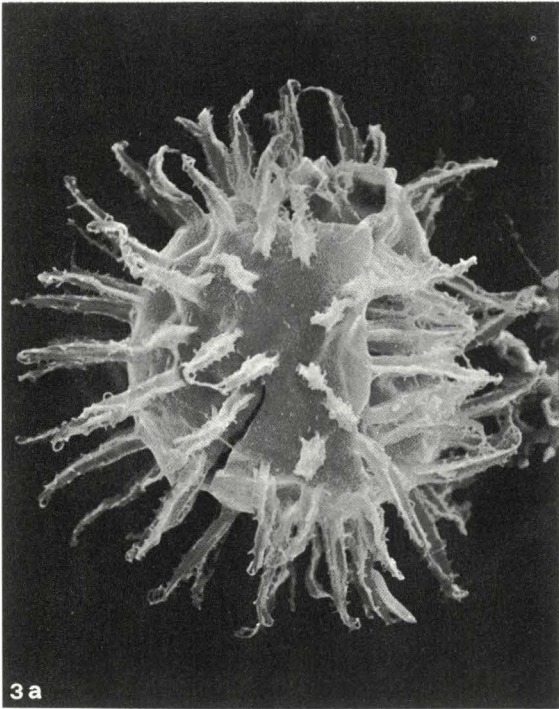
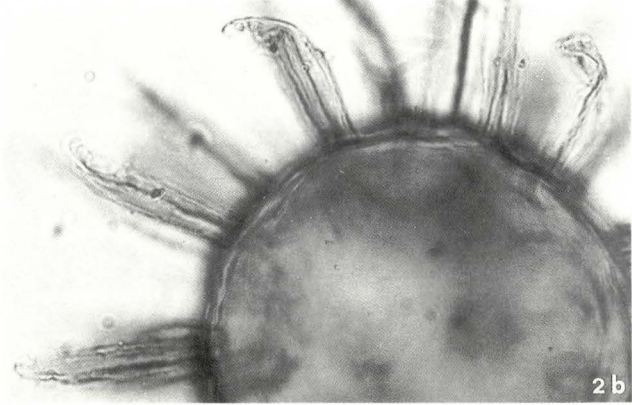
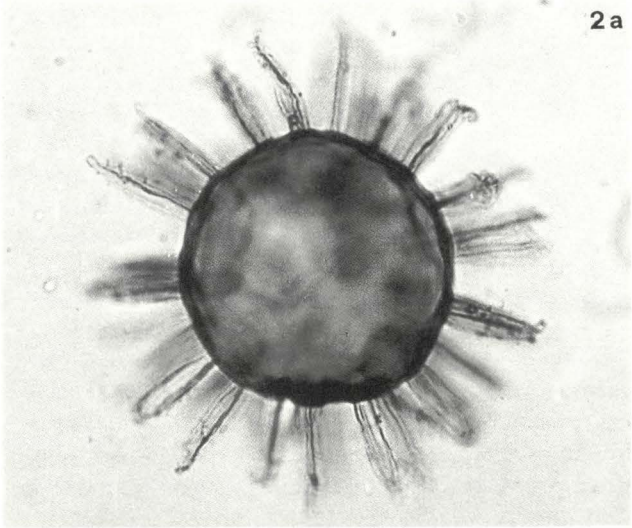
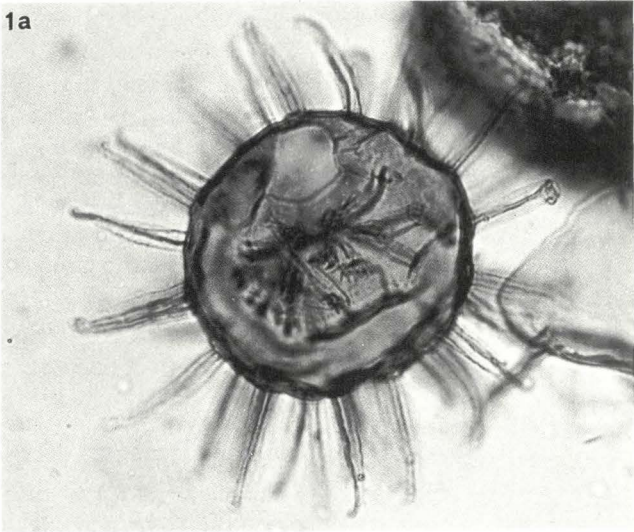
Type locality and stratum – Sweden, Island of Öland, Parish of Stenåsa; Schroeteri Limestone (erratic boulder), middle Ordovician, Lasnamägi (upper Llanvirn).

Remarks – Included in the synonymy list (above) is Eisenack's (1959) designated neotype of *Baltisphaeridium trifurcatum* (Eisenack 1931 ex Eisenack 1938) Eisenack, 1959 (see Eisenack, 1959, pl. 17, fig. 3), which is also the holotype of *B. trifurcatum* forma *typicum* Eisenack, 1959. The latter taxon is illegitimate, as noted by Fensome *et al.* (1990, pp. 129, 393), who considered that its senior synonym, by autonymy, is *B. trifurcatum* forma *trifurcatum*. Moreover, the same authors «reject(ed) the neotype under the provisions of ICBN Article 8 as being in serious conflict with the protologue». Their stated reason was that Eisenack (1959) regarded his neotype as belonging to an infraspecific taxon (*B. trifurcatum* forma *typicum*) different from the one to which he assigned the (lost) holotype, viz., *P. trifurcatum* forma *breviradiatum* Eisenack, 1959 [which he subsequently (Eisenack, 1969, p. 255) elevated to specific rank as *P. breviradiatum* (Eisenack, 1959) Eisenack, 1969]. Fensome *et al.* (1990, p. 389) recorded Eisenack's (1969, pp. 254-255) opinion that *P. bergstroemii* is taxonomic junior synonym of *P. trifurcatum*. That opinion was based essentially on perceived identity between the holotype of *P. bergstroemii* and Eisenack's (1959) neotype of *P. trifurcatum*, with which we agree [as did Eiserhardt (1992, p. 69), with respect to *P. trifurcatum* forma *typicum*]. However, the above-mentioned rejection of the 1959 neotype, and its author's re-attribution of the holotype (to *breviradiatum*) effectively invalidates the putative synonymy between *trifurcatum* and *bergstroemii*. Accordingly, the latter is here retained as the correct name, essentially in accord with Eiserhardt (1992).

EXPLANATION OF PLATE 1

Figs. 1-3 - *Peteinosphaeridium angustilaminae* n. sp. 1a) $\times 600$; 1b) detail of processes, $\times 1000$. 2) holotype; 2a) $\times 600$; 2b) detail of processes, $\times 1000$. 3a) $\times 1000$; 3b) detail of processes showing sculpture of lamina edges, $\times 4000$.

For locality, stratigraphic, and curatorial details see Appendices 1, 2.



The above emended diagnosis of *Peteinosphaeridium bergstroemii* Staplin, Jansonius & Pocock, 1965 specifies more precisely the morphology of the processes and their distal configuration, as exhibited by the holotype and by our study of numerous other specimens, including topotypic material, from the lower and middle Ordovician of Öland, Sweden. Corrosion of the psilate-shagreenate vesicle wall evidently results in its partial or comprehensive punctation. The pylomate excystment structure, not mentioned in the original circumscription, is here regarded as diagnostic for the species (as for the genus which it typifies). The diameter of the pylome, another variable feature of *P. bergstroemii*, bears no relationship to vesicle diameter. Well-preserved specimens examined under SEM display microstriate pattern on lamina surfaces, but this is not clearly discernible with optical microscopy.

Comparison – In comparison with *Peteinosphaeridium bergstroemii*, *P. eximium* n. sp. differs mainly by possessing differently shaped (grossly cylindrical) processes. *P. velatum* Kjellström, 1971 emend. bears processes having branch length about equal to width of corresponding trunk lamina; furthermore, processes are, on average, relatively shorter. *P. dissolutum* (Burmann, 1970) Eisenack, Cramer & Diez, 1979 – originally described as a subspecies of *P. bergstroemii* by Burmann (1970, pp. 312–313, p. 17, fig. 1), and evidently founded on a single specimen from German upper Llanvirn strata – is distinct from the latter species in featuring stubbier, multifurcate processes. As discussed previously (see *P. dissolutum* listing), *Baltisphaeridium bergstromii* of Martin (1969; Silurian, Belgium) is probably a reworked specimen of *P. dissolutum*. The latter species may also be represented by a Welsh Llandeilo form identified by Turner (1985, p. 226, pl. 4, fig. 5) as *P. trifurcatum trifurcatum*.

The species described by Górka (1969, pp. 23–24, text-fig. 4) as *P. trifurcatum typicum*, from a Polish Ordovician erratic, is assignable neither to *P. bergstroemii* nor to the genus because its long slender processes are nonlamine and multifurcate;

likewise, Elaouad-Debbaj's (1981, pp. 50–51, pl. 16, figs. 15, 16) record of the same subspecies from the Caradoc of Portugal. Also excluded from *P. bergstroemii*, as per above synonymy, is Górka's (1969) alleged record of that species from the upper Arenig of Poland: both of her illustrated specimens have processes with shapes and distal termini unlike those of *bergstroemii*, and at least one is attributable to *P. eximium* n. sp. However, other specimens depicted subsequently by Górka (1980, pl. 36, figs. 5, 6, non 4) from the Polish upper Llanvirn as *P. trifurcatum* are probably attributable to *P. bergstroemii*; similarly, the putative records of *P. trifurcatum* by Kjellström (1971a, p. 57, pl. 4, fig. 7; 1976, p. 36, fig. 29) from the Swedish middle Ordovician. The specific identity of Burmann's (1973, pl. 6, fig. 7) figured but undescribed, fragmentary specimen labelled «*P. bergstromii*» (from the middle Ordovician of Germany) cannot be confirmed, nor can that figured by Martin (1977, pl. 5, fig. 2) from Massif du Brabant, Belgium.

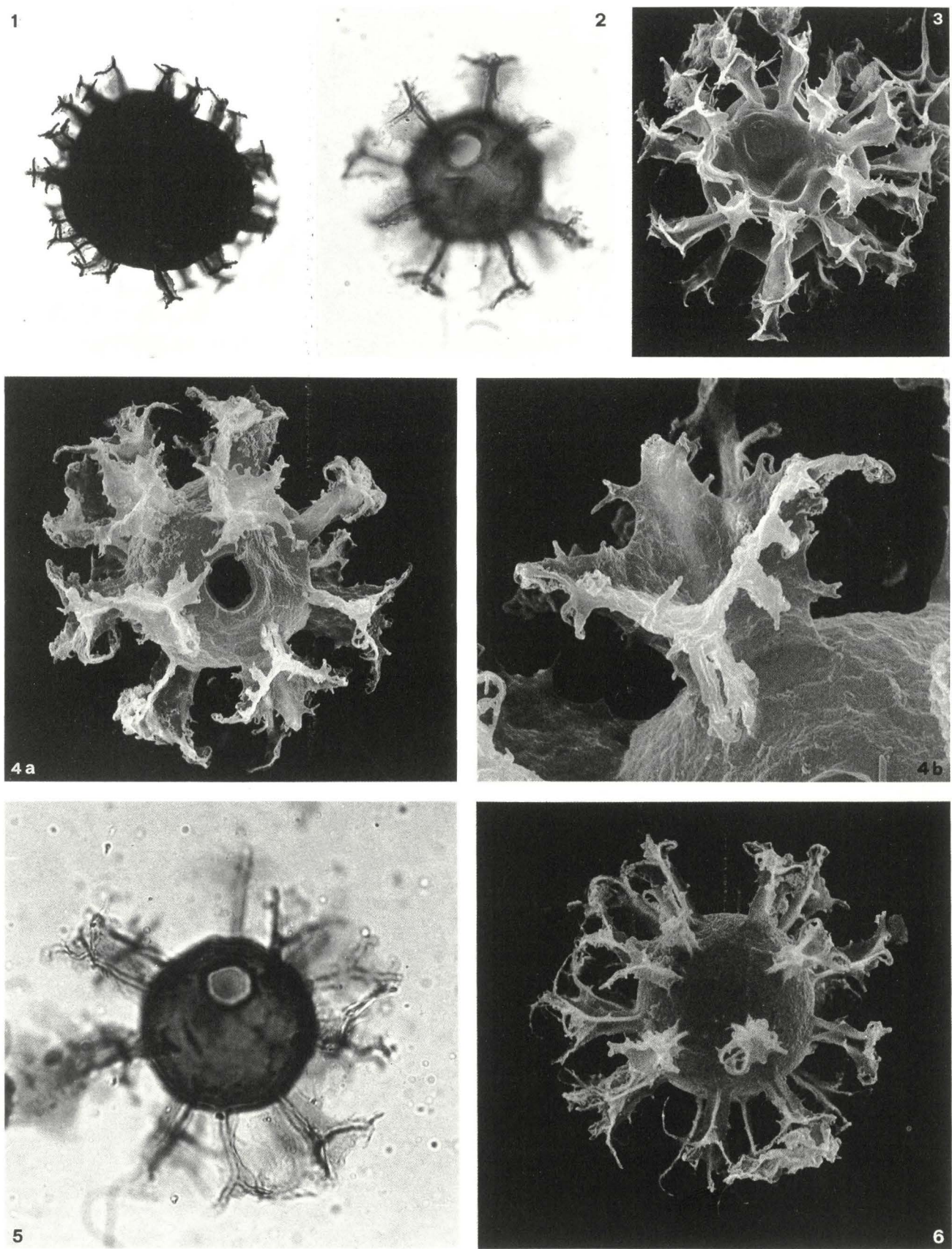
Several reports from various Arenig strata of South China require scrutiny. *P. robustiramosum* Tongiorgi, Yin Lei-ming & Di Milia (in press, pl. 3, figs. 6–8; Pl. 4, fig. 11 herein), conceded by its authors to be a possible subspecies of *P. bergstroemii*, is characterized by consistently trilaminate processes with extremely thin laminae and non-flaring (i.e., tapering to uniform) trunks and is therefore specifically distinct from the latter. Specimens assigned by Lu Lichang (1987) to *P. bergstroemii* are clearly misidentified and seem close to *P. robustiramosum*. The same applies to the specimen attributed by Li Jun (1990, p. 151, pl. 5, fig. 7) to «*P. trifurcatum tipicum*».

Distribution – Baltic region: Ordovician glacial erratics (Eisenack, 1938, etc.). Sweden: Öland, middle Ordovician, Lasnamägi, upper Llanvirn, glacial erratic (Staplin *et al.*, 1965); Öland, lower Ordovician, upper Volkhov-lowermost Kunda, upper Arenig (Ribecai & Tongiorgi, in press; present study); Gotland, middle Ordovician (Kjellström, 1971a; as *P. trifurcatum*); Östergötland, middle Ordovician, upper Llanvirn (Kjellström, 1976; as *P.*

EXPLANATION OF PLATE 2

- Fig. 1 – *Peteinosphaeridium armatum* Tongiorgi, Yin Lei-ming & Di Milia, in press; ×600.
Figs. 2–6 – *Peteinosphaeridium bergstroemii* Staplin, Jansonius & Pocock, 1965 emend. 2) ×600. 3) ×600. 4a) ×600; 4b) detail of process and vesicle surface, ×1800. 5) ×600. 6) ×600.

For locality, stratigraphic, and curatorial details see Appendices 1, 2.



trifurcatum). Poland: middle Ordovician, upper Llanvirn (Górka, 1980). England: upper Ordovician, Caradoc (Turner, 1984; uncertain assignment). Bohemia: lower Ordovician, Arenig (Vavrdová, 1972; undescribed/unfigured, hence awaiting confirmation).

Stratigraphic range verified by co-occurrence of other fossils (Öland, Sweden) – (a) Lower limit: upper Volkhov, Langevoja (upper Arenig), *Microzarkodina parva* conodont Zone, Lepidurus Limestone, Horns Udde Quarry (Ribecai & Tongiorgi, in press). (b) Upper limit: lowermost Kunda, lower Hunderum (uppermost Arenig), lower *Amorphognathus variabilis* conodont Zone, Vaginatum Limestone, Horns Udde Quarry.

PETEINOSPHAERIDIUM EXIMIUM n. sp.
Pl. 3, figs. 1-6; Text-fig. 6C3

1969 *Peteinosphaeridium bergstromii* auct. non Staplin, Jansonius & Pocock, 1965 - GÓRKA, p. 53, pl. 14, fig. 8, ?7.

1991 *Peteinosphaeridium velatum* auct. non Kjellström - UUTELA & TYNNI, p. 106, pl. 24, fig. 255.

Diagnosis – Vesicle originally spherical, outline circular or subcircular. Vesicle wall 1-2.4 µm thick; essentially psilate, shagreenate, or punctate (?corrosion effect). Processes solid, more or less homomorphic, elongate, of gross cylindrical to slightly flared form, length 11/27 µm (but relatively uniform on given specimen); bases ca. 2.5-17 µm apart, infrequently with slight constriction; proximal contacts angular to slightly curved. Trunks quadrilaminate or trilaminate, consisting of 4 (rarely 3), relatively thin, longitudinally and radially disposed laminae; width of laminae fairly uniform on given process and within range of 1.5-5 µm for most of length to distal termination, where 4 (rarely 3) distinct branches developed, each ca. 3.5-8.5 µm wide, corresponding in position to a trunk lamina, and projecting at an angle usually > 90° to trunk. Branches invariably trilaminate, the component outer lamina of each being the extension of one trunk lamina. Proximal portions of inner laminae of

adjacent branches coalescent to form, at process extremity, a variably shaped (usually quadrangular) structure having markedly concave to near-planar surface. Distal portions of inner branch laminae prolonged as attenuated, simple or bifurcant, evexate or acuminate projections usually <4 µm long. Lamina edges predominantly psilate, but small echinae and/or bacula may project sparsely and irregularly; lamina surfaces psilate. Pylome circular to subcircular, with simple or slightly thickened and elevated margin; operculum essentially psilate.

Dimensions – Vesicle diameter 38 (57) 75 µm (60 specimens measured); pylome diameter 15 (21) 30 µm (53 specimens). Process length averages 30% of vesicle diameter (range 18-47%).

Holotype – Slide HUK13/50-1, L25; Pl. 3, fig. 1. Vesicle 56 µm in diameter, wall 1.5 µm thick, irregularly punctate; quadrilaminate processes numbering ca. 70, 18.5-25.5 µm in total length including distal branches 5-9.5 µm long; process bases 7-11 µm apart; laminae psilate, diaphanous, 1.5-2.5 µm wide at base, broadening progressively to ca. 4 µm at distal process extremity; circular pylome with internally displaced operculum 17 µm in diameter.

Type locality and stratum – Sweden, Island of Öland, northwest coast, Horns Udde Quarry, immediately south of Hornsudden; Lepidurus Limestone, 5.02-5.12 m above Flowery Sheet horizon, upper *Microzarkodina parva* conodont Zone; sample 13 (Ribecai & Tongiorgi, in press, fig. 2); lower Ordovician, Volkhov, Langevoja (upper Arenig).

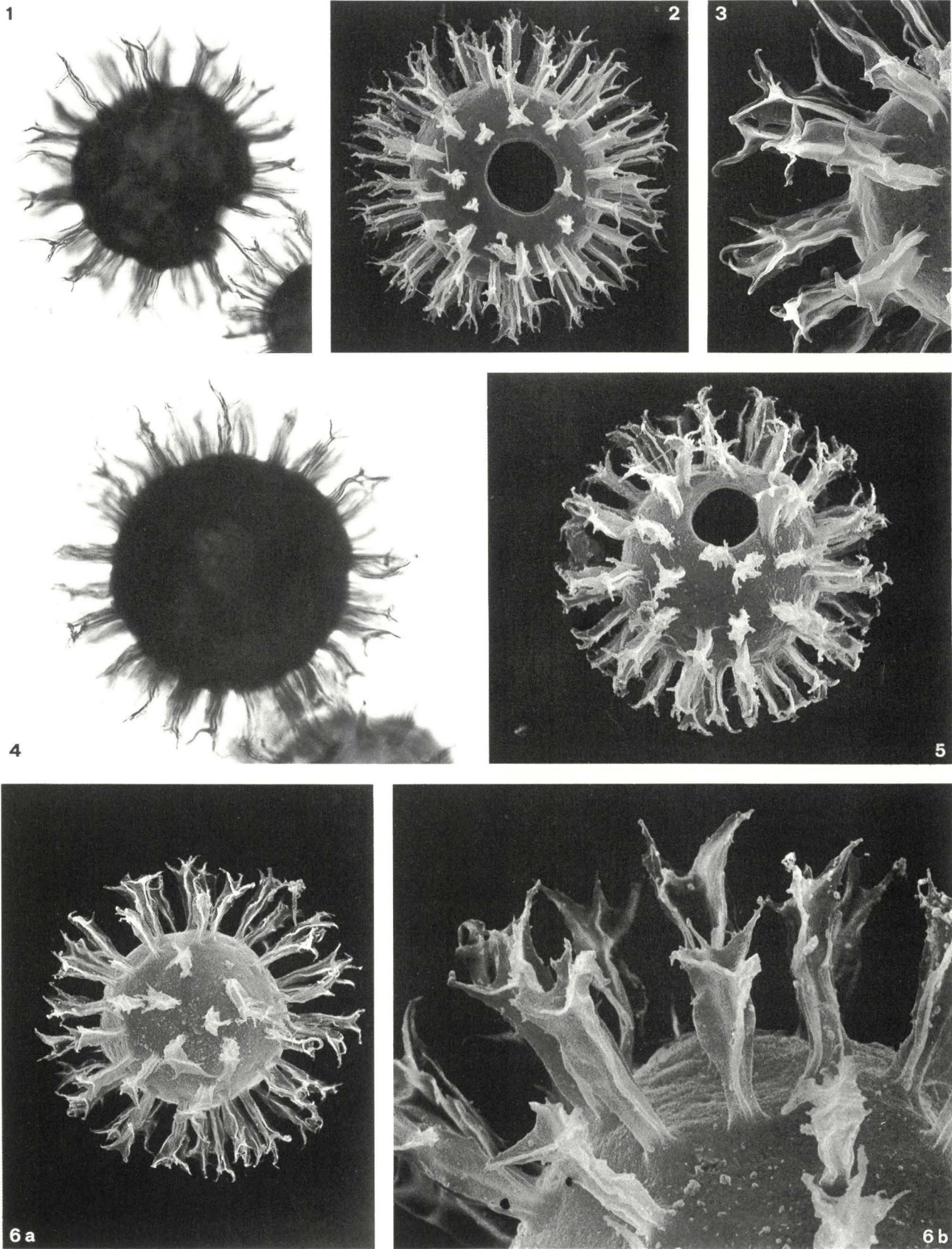
Etymology – Lat., *eximius* = excellent, remarkable.

Remarks – As noted previously under *Peteinosphaeridium bergstroemii*, neither of the illustrated Polish Arenig specimens of Górka (1969, pl. 14, figs. 7, 8) is considered identifiable with that species; at least one (see synonymy above) is referable to *P. eximium*. We also attribute to *P. eximium* a specimen recorded as *P. velatum* by

EXPLANATION OF PLATE 3

Figs. 1-6 - *Peteinosphaeridium eximium* n. sp. 1) holotype, ×600. 2) ×600. 3) detail of processes, ×1000. 4) ×600. 5) ×600. 6a) ×600; 6b) detail of processes, ×2000.

For locality, stratigraphic, and curatorial details see Appendices 1, 2.



Uutela & Tynni (1991, p. 106, pl. 24, fig. 255) from the lower Ordovician (Volkhov) of Estonia, on account of its unflared processes with distinctly ramified distal termini. An Öland Arenig specimen figured but not described by Ribecai & Tongiorgi (in press, pl. 2, figs. 1, 3) as *P. intermedium* is here assigned to *P. eximium* n. sp.

Comparison – *P. eximium* is distinguishable from *P. bergstroemii* chiefly in the overall cylindrical appearance of its processes; from *P. velatum* Kjellström, 1971 emend. in having elongate processes with more prominent, upwardly projecting branches; and from *P. hymeniferum* which features relatively simple and unbranched process termini.

Distribution – Sweden: Öland, lower Ordovician, Volkhov-uppermost Kunda, upper Arenig (Ribecai & Tongiorgi, in press, as *P. intermedium*; present study). Estonia: lower Ordovician, Volkhov, upper Arenig (Uutela & Tynni, 1991; as *P. velatum*). Poland: upper Arenig (Górka, 1969; as *P. bergstroemii*).

Stratigraphic range verified by co-occurrence of other fossils (Öland, Sweden) – (a) Lower limit: upper Volkhov, Langevoja (upper Arenig), upper *Microzarkodina parva* conodont Zone, Lepidurus Limestone, Horns Udde Quarry (Ribecai & Tongiorgi, in press). (b) Upper limit: lowermost Kunda, lower Hunderum (uppermost Arenig), lower *Amorphognathus variabilis* conodont Zone, Vaginatum Limestone, Horns Udde Quarry (Ribecai & Tongiorgi, in press).

PETEINOSPHAERIDIUM HYMENOFERUM
(Eisenack, 1938) Fensome *et al.*, 1990
Pl. 4, figs. 1-7; Text-fig. 6A2

1938 *Hystrichosphaeridium hymeniferum* EISENACK, p. 19, pl. 3, figs. 2-5.

1958 *Baltisphaeridium hymeniferum* (Eisenack) EISENACK, p. 400. [combination invalid: ICBN, Art. 33.2; moreover, generic name *Baltisphaeridium* not validly published until 1959].

1963 *Baltisphaeridium hymeniferum* (Eis. 1938) Eisenack 1958 - DOWNIE & SARJEANT, p. 90. [combination invalid: ICBN, Art. 33.2].

1969 *Peteinosphaeridium hymeniferum* (Eisenack) EISENACK, p. 254. [combination invalid: ICBN, Art. 33.2].

1973 *Peteinosphaeridium hymeniferum* (Eisenack) EISENACK *et al.*, pp. 903-904. [combination invalid: ICBN, Art. 33.2; neotype selected and refigured, see text below].

1974 *Peteinosphaeridium hymeniferum* (Eisenack) EISENACK, p. 293, fig. 48. [holotype refigured but stated to be lost].

1990 *Peteinosphaeridium hymeniferum* (Eisenack) FENSOME *et al.*, p. 390.

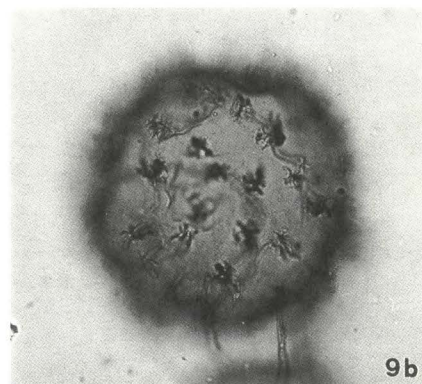
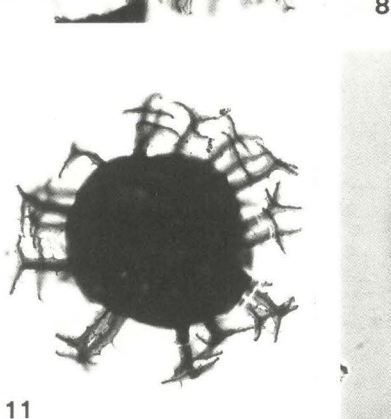
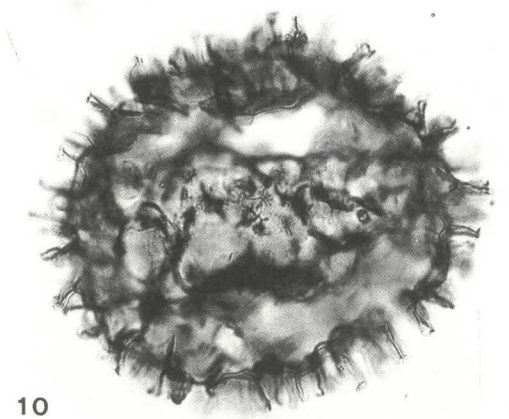
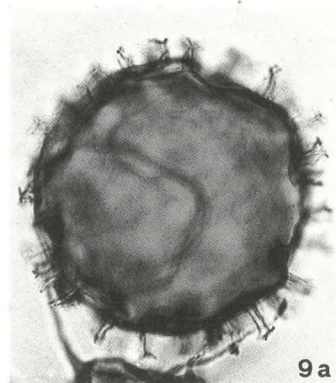
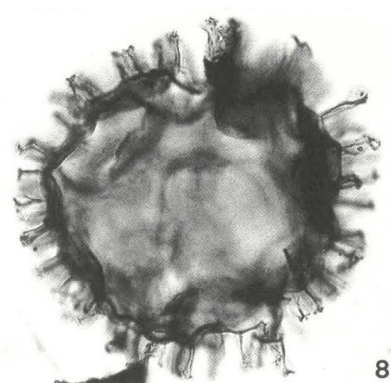
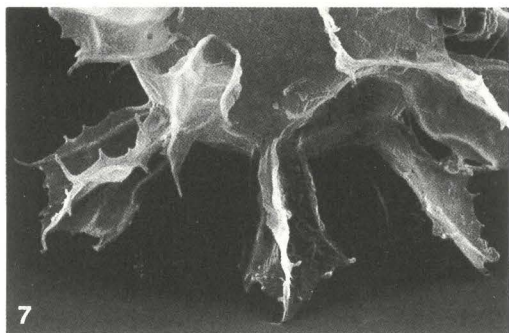
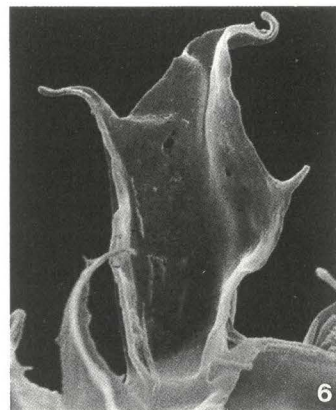
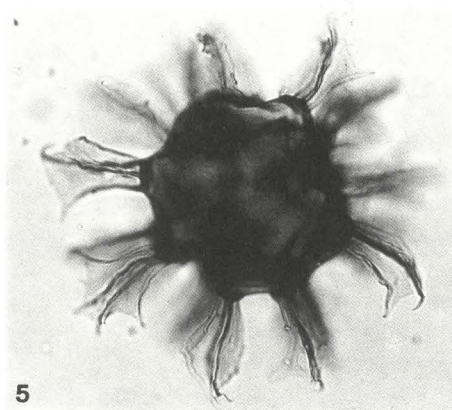
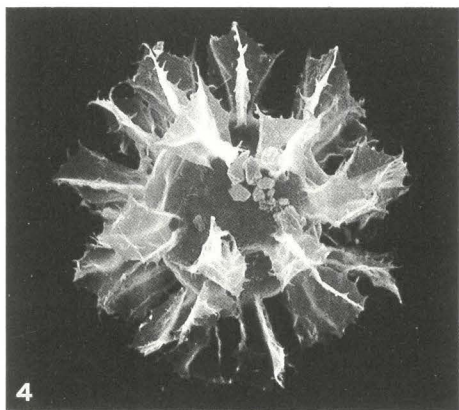
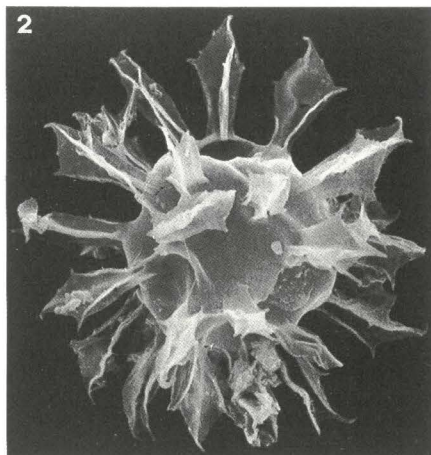
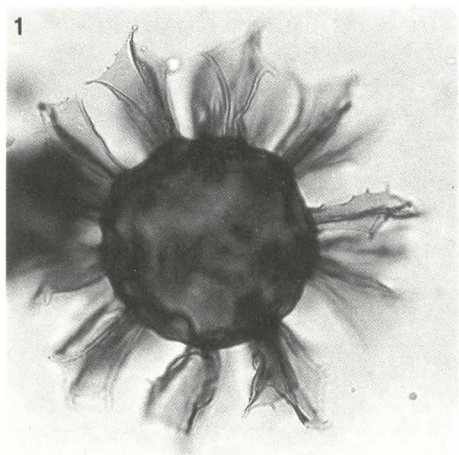
non 1991 *Peteinosphaeridium hymeniferum* Eisenack (1938) 1969 - UUTELA & TYNNI, pp. 104-105, pl. 24, fig. 250.

Amplification of diagnosis – Vesicle originally spherical, outline circular to subcircular; wall psilate, 1.1-2.4 µm thick. Processes solid, approximately homomorphic, elongate, unbranched, trilaminate, consisting of 3 relatively thin, longitudinally and radially disposed laminae, each 1.3-4.5 µm wide at process base, broadening gradually and uniformly to a maximum of 2.2-9.5 µm at about two-thirds of distance from base, then tapering distally to a common, acuminate to evexate point in the form of a central, elongate, spinelike projection. Distal radial corners of laminae attenuated and extended laterally, equally or unequally, each forming a conspicuous, relatively short, acuminate to evexate spine-like projection, ca. 2.5-12 µm long, typically non-recumbent (i.e., straight to slightly curved). Process length totalling ca. 15-35 µm, bases 4.5-18 µm apart, proximal contacts angular. Lamina surfaces psilate; edges characteristically bearing generally sparse, minute echinate projections, sometimes bifurcant and/or equipped with very fine, tenuous, thread-like apical extensions; sculpture tending to be more frequent distally, rare proximally (where lamina edges are normally psilate). Pylome circular to subcircular, with simple (unlipped) margin; operculum (rarely seen) psilate.

EXPLANATION OF PLATE 4

- Figs. 1-7 - *Peteinosphaeridium hymeniferum* (Eisenack, 1938) Fensome *et al.*, 1990. 1) ×600. 2) ×600. 3) detail of processes, ×1000. 4) ×600. 5) ×600. 6) detail of process showing basal coalescence of adjacent trunk laminae, ×1150. 7) detail of processes, ×1000.
Figs. 8, 9 - *Peteinosphaeridium micranthum* (Eisenack, 1959) Eisenack, Cramer & Diez, 1973. 8) ×600. 9a, 9b) different focus levels, ×600.
Fig. 10 - *Peteinosphaeridium* sp. cf. *P. micranthum* (Eisenack, 1959) Eisenack, Cramer & Diez, 1973; ×600.
Fig. 11 - *Peteinosphaeridium robustiramosum* Tongiorgi, Yin Lei-ming & Di Milia, in press; ×600.

For locality, stratigraphic, and curatorial details see Appendices 1, 2.



Dimensions – Vesicle diameter 38 (49) 64 μm (60 specimens measured); pylome diameter 10 (18) 25 μm (32 specimens). Process length averages 41% of vesicle diameter (range 28–58%).

Neotype – As the holotype slide (130 Nr 2; Eisenack, 1938, p. 19, pl. 3, fig. 2) is reportedly lost (Eisenack, 1974, p. 293), Eisenack *et al.* (1973, p. 903) selected a neotype (Eisenack, 1938, pl. 3, fig. 3; refigured in Eisenack *et al.*, 1973, p. 903, right-hand photomicrograph, erroneously cited in caption as «holotype»); slide 130 Nr 1, Geologisch-Paläontologisches Institut, Univ. Tübingen, Germany.

Type locality and stratum – Baltic region, glacial drift; Ordovician erratic.

Remarks – The process length tends to be relatively uniform on a given specimen but, as indicated above, shows considerable inter-specimen variation. Other variable attributes of *Peteinosphaeridium hymeniferum* (Eisenack, 1938) Fensome *et al.*, 1990 include: vesicle wall thickness (usually *ca.* 1.4 μm , but may attain as much as 2–2.4 μm on a few specimens); actual and spatial development of echinae on lamina edges (sparse and/or inconspicuous on some specimens; well-developed on others); and extent of the terminal process projections. The incidence of filose apical extensions to the echinae, or even of the echinae themselves, may be a manifestation of preservational quality, as the delicacy of these features would render them readily susceptible to degradation.

A Lower Ordovician specimen from North China identified by Hu Yunxu (1986, pl. 17, fig. 15) as *P. hymeniferum* appears to have process morphology distinct from the latter species. Uutela & Tynni's (1991) putative record of *P. hymeniferum* of Estonia cannot be sustained; as discussed under *P. angustilaminae* (above), their specimens (from the Estonian lower to middle Ordovician) are assignable to the latter species.

Comparison – See under *P. angustilaminae*.

Distribution – Baltic region: Ordovician glacial erratics (Eisenack, 1938, 1958). Sweden: Öland, lower Ordovician, Volkhov, upper Arenig (Ribecai & Tongiorgi, in press).

Stratigraphic range verified by co-occurrence of other fossils (Öland, Sweden) – (a) Lower limit: Volkhov, Langevoja (upper Arenig), *Microzarkodina parva* conodont Zone, Lepidurus Limestone, Horns Udde Quarry (Ribecai & Tongiorgi, in press). (b) Upper limit: upper Volkhov, middle Langevoja (upper Arenig), upper *Microzarkodina parva* conodont Zone, Lepidurus Limestone, Horns Udde Quarry.

PETEINOSPHAERIDIUM MICRANTHUM (Eisenack, 1959)

Eisenack, Cramer & Diez, 1973

Pl. 4, figs. 8, 9; Text-fig. 6C4

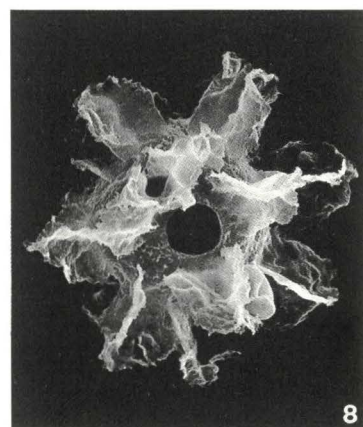
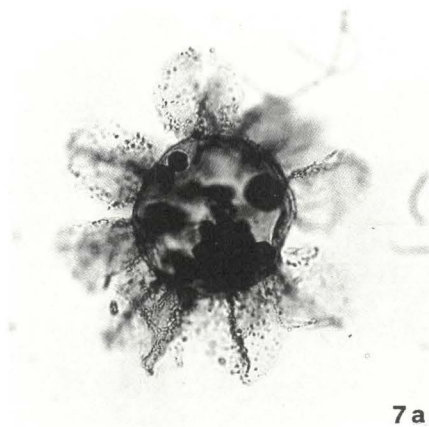
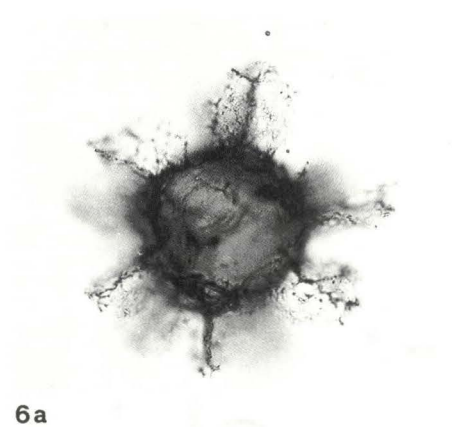
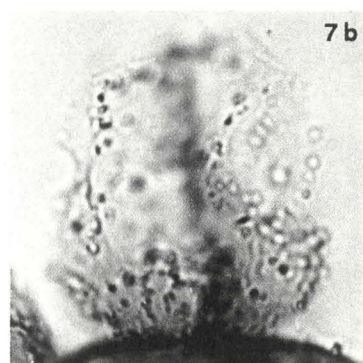
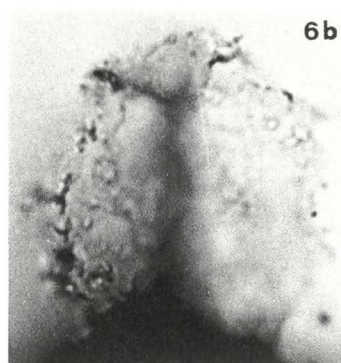
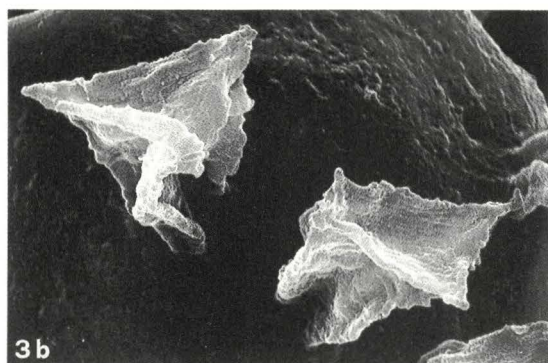
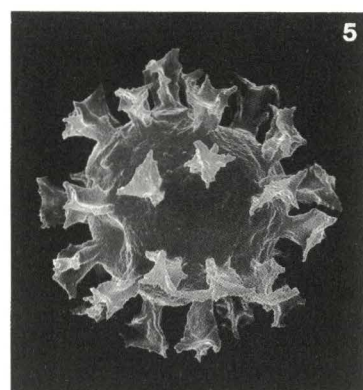
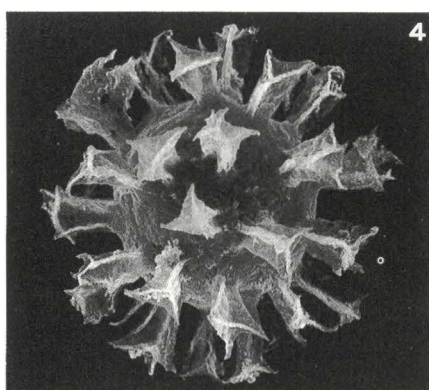
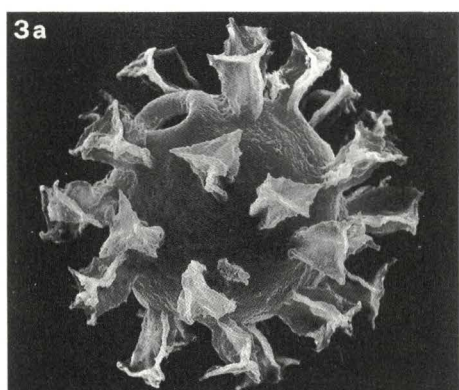
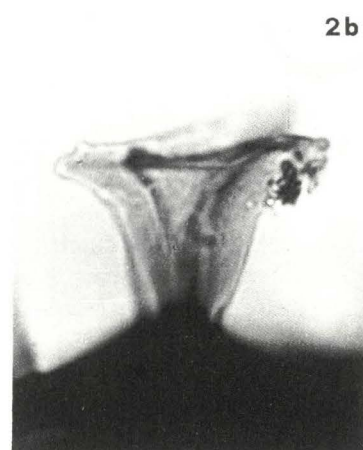
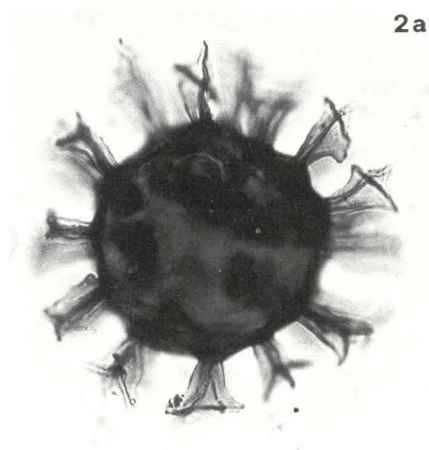
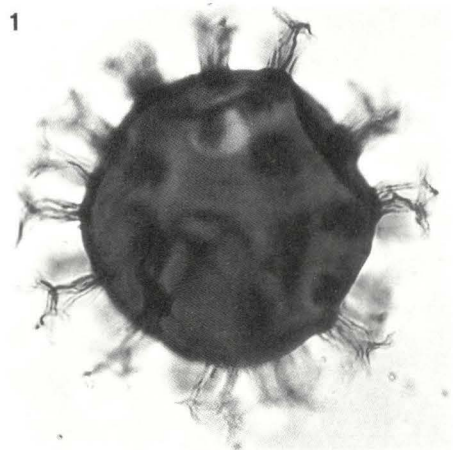
- 1959 *Baltisphaeridium micranthum* EISENACK, p. 203, pl. 17, figs. 13a, b.
- 1969 *Peteinosphaeridium micranthum* (Eisenack) EISENACK, p. 254. [combination invalid: ICBN, Art. 33.2].
- 1973 *Peteinosphaeridium micranthum* (Eisenack) EISENACK, CRAMER & DIEZ, pp. 913–914.
- non 1975 *Peteinosphaeridium micranthum* Eisenack - TYNNI, pp. 32, 34, fig. 4.
- non 1989 *Peteinosphaeridium micranthum* (Eisenack) - UUTELA, p. 36, pl. 8, fig. 68.
- non 1991 *Peteinosphaeridium micranthum* Eisenack - UUTELA & TYNNI, p. 105, pl. 24, fig. 252.

Description – Vesicle originally spherical, outline circular to subcircular. Vesicle wall thin (<0.5 μm thick); shagreenate to granulate. Processes solid, more or less homomorphic, uniformly and densely distributed, columnar or nearly so, distally truncate, numerous (*ca.* 80–150 per vesicle), short (3–12 μm in length); proximal contacts angular. Trunks trilaminate or quadrilaminate, consisting of 3 or 4, very thin (diaphanous), longitudinally and radially disposed laminae, each 1–3 μm in width; the latter

EXPLANATION OF PLATE 5

- Figs. 1–5 – *Peteinosphaeridium velatum* Kjellström, 1971 emend. 1) neotype, $\times 600$. 2a) $\times 600$; 2b) detail of process, $\times 2000$. 3a) $\times 600$; 3b) detail of processes showing microstriation, $\times 2000$. 4) $\times 600$. 5) $\times 600$.
- Figs. 6–8 – *Cycloposphaeridium auriculatum* Uutela & Tynni, 1991 emend. 6a) $\times 600$; 6b) detail of process, $\times 2000$. 7a) $\times 600$; 7b) detail of process, $\times 2000$. 8) $\times 600$.

For locality, stratigraphic, and curatorial details see Appendices 1, 2.



fairly uniform on given process from base to distal termination, where 3-4 branches are developed, each corresponding in position to a trunk lamina and typically projecting at right angles to trunk. Branch length approximating width of corresponding trunk lamina; branches invariably trilaminate, the outer lamina of each constituted by one trunk-lamina extension. Proximal portions of inner laminae of adjacent branches coalescent to form a small, variably shaped (mostly quadrangular), near-planar structure (i.e., the distal process truncation); corners of this structure (i.e., distal portions of inner laminae) infrequently produced as minute ($< 0.5 \mu\text{m}$), attenuated, simple or bifurcant, acuminate projections. Lamina surfaces psilate; edges psilate or, rarely, granulate. Pylome circular to subcircular with simple margin. Operculum not observed.

Dimensions – Vesicle diameter 54 (71) 95 μm (28 specimens measured); pylome diameter 14 (18) 22 μm (5 specimens). Process length averages 10% of vesicle diameter (range 3-18%).

Holotype – Eisenack (1959, pl. 17, figs. 13a, b); preparation E1, B₂ α , 1 Nr 4; Geologisch-Paläontologisches Institut, Univ. Tübingen, Germany.

Type locality and stratum – Estonia, Baltischport; lower Glaukonitkalk, lower Ordovician.

Remarks – Öland specimens of *Peteinosphaeridium micranthum* (Eisenack, 1959) Eisenack, Cramer & Diez, 1973, described above, concur with the five specimens described by Eisenack (1959), apart from having a greater range of vesicle diameter and a smaller pylome.

A few Öland specimens (e.g., pl. 4, fig. 10) bear processes of slightly different shape, with very gently tapering trunks; moreover, the processes are either unbranched or show very inconspicuous, rudimentary branching, with laminae attenuating distally and merging ultimately to form a more or less rounded process apex. Pending further studies, we provisionally regard these specimens as closely comparable to, but not necessarily identifiable with *P. micranthum*.

Reports of this species by Tynni (1975; from Ordovician erratic boulder, Bothnian Sea), Uutela (1989; also from Finnish offshore, Ordovician erratic), and Uutela & Tynni (1991; from lower to middle Ordovician, Estonia) are considered ill-founded (see synonymy above). Specimens briefly described and illustrated by Tynni (1975) possess furcant, weakly laminate processes, unlike those of *P.*

micranthum. Also distinct are the more elongate, furcant processes of specimens recorded by Uutela (1989) and Uutela & Tynni (1991). At least some of these specimens (particularly Uutela & Tynni's pl. 24, fig. 252) may be akin to the *P. macropylum* group, which, as noted previously herein, probably warrants separate generic recognition.

Hu Yunxu's (1986, pl. 17, figs. 10, 11) identification of *P. micranthum* in lower Ordovician material of north-central China needs confirmation from better-preserved and -illustrated specimens. Requiring similar scrutiny are Fournier-Vinas's (1985, table 1; pl. 4, fig. 15) record of this species from Tremadoc-Llanvirn strata of Morocco; an undescribed specimen figured by Chateauneuf *et al.* (1978, pl. 1, fig. 8; identified as *P. cf. «micracanthum»*) from the Caradoc of Iran; and Martin's (1978, fig. 12.3; pl. 12.1, fig. 20) specimen from the middle Ordovician of Newfoundland, Canada.

Comparison – *P. micranthum* is readily distinguishable from other members of the genus mainly by its densely distributed, squat, grossly cylindrical processes. The morphologically closest species, *P. trifurcatum* (Eisenack, 1931 ex Eisenack, 1938) Eisenack, 1969 [= *P. «breviradiatum»* (Eisenack, 1959 ex Eisenack, 1965) Eisenack, 1969], has yet to be defined adequately (cf. Eisenack, 1959, pp. 202-203, pl. 17, figs. 7a, b), but differs from *P. micranthum* in its generally smaller vesicle and pylome and its longer and fewer processes.

Distribution – Estonia: lower Ordovician, Volkhov, Arenig (Eisenack, 1959). Sweden: Öland, lower to middle Ordovician, Volkhov-Kunda, upper Arenig?-lower Llanvirn.

Stratigraphic range verified by co-occurrence of other fossils (Öland, Sweden) – (a) Lower limit: Volkhov, Langevoja (upper Arenig), *Microzarkodina parva* conodont Zone, Lepidurus Limestone, Horns Udde Quarry (present study). (b) Upper limit: lower Kunda, Hunderum (uppermost Arenig or lowermost Llanvirn), *Amorphognathus variabilis* conodont Zone, Vaginatum Limestone, Horns Udde Quarry.

PETEINOSPHAERIDIUM VELATUM Kjellström, 1971
emend.

Pl. 5, figs. 1-5; Text-fig. 6C6

1971 *Peteinosphaeridium velatum* KJELLSTRÖM, p. 58, pl. 4, fig. 8 [1971a].

non 1979 *Peteinosphaeridium velatum* Kjellström - BOCKELIE & KJELLSTRÖM, p. 214, figs. 16A, B.

non 1991 *Peteinosphaeridium velatum* Kjellström - UUTELA & TYNNI, p. 106, pl. 24, fig. 255.

1992 *Peteinosphaeridium bergstromii* ssp. *velatum* (Kjellstr.) comb. nov. (sic) - EISERHARDT, p. 70.

Emended diagnosis – Vesicle originally spherical; outline circular or subcircular. Vesicle wall psilate to shagreenate; 1.4–2.4 μm thick, may be locally thicker (up to 2.6 μm) about process bases. Processes solid, more or less homomorphic, elongate, flared. Trunks quadrilaminar or trilaminar, comprising 3–4 relatively thin, longitudinally and radially disposed laminae, each ca. 1.2–4 μm wide at process base, then showing more or less uniform and gradual expansion to maximum width (3.6–13 μm) at distal extremity, where 3–4 branches are developed, each corresponding in position to a trunk lamina and projecting at ca. 90° to trunk. Branch length about equal to width of corresponding trunk lamina; branches invariably trilaminar, the outer lamina of each being the extension of one trunk lamina. Proximal portions of inner laminae of adjacent branches coalescent to form a variably shaped (quadrangular or triangular), near-planar to moderately concave structure at process extremity; distal portions of inner laminae may or may not protrude as very short, infrequently furcate, spine-like elements. Length of processes totalling ca. 9.5–20.5 μm , but relatively constant on same specimen; proximal process contacts angular to slightly curved. Process bases 3.5–16 μm apart, some exhibiting short, divergent, root-like emanations. Edges of laminae psilate, rarely with very sparse, minute, sculptural projections (echinae or grana) that may feature drawn-out, thread-like apices; lamina surfaces characteristically with very minute sculpture (microstriae). Pylome circular to subcircular; with simple or slightly thickened margin that constitutes a slightly elevated circular band up to 3 μm wide; operculum (rarely seen) psilate.

Dimensions – Vesicle diameter 42 (58) 71 μm (34 specimens measured); pylome diameter 11 (16) 24 μm (26 specimens). Process length averages 27% of vesicle diameter (range 14–35%).

Holotype – The holotype (and sole originally figured specimen: Kjellström, 1971a, pl. 4, fig. 8; Geological Survey of Sweden slide no. 472: 1) is lost, according to Kjellström's written communication (1977) to S. R. Jacobson (see Jacobson, 1978, p. 297). Hence our designation of a neotype (below).

Neotype (here designated) – Slide HUQ14/50-1, D24/2; Pl. 5, fig. 1. Circular vesicle, diameter 65 μm ; psilate wall 1.4 μm thick; processes straight or

slightly curved, flared, 14.5–18 μm long, bases 6–14.5 μm apart; each process trunk consisting of 3, mostly 4, longitudinally-radially disposed, diaphanous laminae, smooth-edged, 1.5–3.5 μm wide basally, increasing uniformly to as much as 12.5 μm distally, where laminae conjoin to form moderately depressed to near-planar terminal structure; branch lengths approximating widths of corresponding trunk laminae; subcircular pylome, diameter 18 μm , margin slightly thickened.

Type locality and stratum (neotype) – Sweden, Island of Öland, northwest coast, Horns Udde Quarry, immediately south of Hornsudden; Lepidurus Limestone, 5.97–6.10 m above Flowery Sheet horizon, upper *Microzarkodina parva* conodont Zone; sample 14 (Ribecai & Tongiorgi, in press, fig. 2); lower Ordovician, Volkhov, Langevoja (upper Arenig).

Remarks – Augmenting the original circumscription of *Peteinosphaeridium velatum* Kjellström, 1971 are a few additional observations by Eiserhardt (1989, pp. 45, 47, pl. 6, figs. 1a–d). Those furnished by Bockelie & Kjellström (1979) and Uutela & Tynni (1991) are here discounted on the grounds of species misidentification. In the former paper, the single illustrated specimen (Bockelie & Kjellström, 1979, figs. 16A, B), from the Estonian middle Ordovician, bears processes with tapering trunks, projecting distal branches, and prominently sculptured lamina edges; this morphological combination precludes identification with *P. velatum*. Uutela & Tynni's (1991, pl. 24, fig. 255) illustrated specimen has slender, columnar, distally furcate processes quite dissimilar to those of *P. velatum* (but in fact consonant with *P. eximium*: see above).

The emended diagnosis, above, takes due cognizance of detailed process morphology and of the previously unrecorded mode of excystment. SEM observation of well-preserved specimens (e.g., Pl. 5, fig. 3b) reveals microstriate modification of lamina surfaces (not normally evident under light microscope). Contrary to Eiserhardt (1992, p. 70), the status of *velatum* as a species discrete from *bergstroemii* (rather than subspecifically within the latter) is endorsed here.

Comparison – See under *Peteinosphaeridium bergstroemii* (above). Illustrated, undescribed, tentative (cf.) records of *P. velatum* by Legault (1982, pl. 1, fig. 7) and Hu Yunxu (1986, pl. 17, fig. 3), from the upper Ordovician of offshore Newfoundland (Labrador Sea, eastern Canada) and the lower Or-

dovician (Arenig) of north-central China respectively, are not closely comparable with, indeed appear quite distinct from, *P. velatum*. The Labrador Sea specimen features numerous, relatively short and slender processes unlike those of *P. velatum*; and the Chinese specimen is dissimilar in bearing numerous, seemingly minute processes.

Distribution – Sweden: Gotland, middle Ordovician, Kunda, Valaste, lower Llanvirn (Kjellström, 1971a); Öland, lower Ordovician, Volkhov-Kunda, upper Arenig (Ribecai & Tongiorgi, in press). Estonia: lower Ordovician erratic boulder (Eiserhardt, 1989).

Stratigraphic range verified by co-occurrence of other fossils (Öland, Sweden) – (a) Lower limit: upper Volkhov, Langevoja (upper Arenig), upper *Microzarkodina parva* conodont Zone, Lepidurus Limestone, Horns Udde Quarry (Ribecai & Tongiorgi, in press). (b) Upper limit: lowermost Kunda, lower Hunderum (uppermost Arenig), lower *Amorphognathus variabilis* conodont Zone, Vaginatum Limestone, Horns Udde Quarry (Ribecai & Tongiorgi, in press).

Genus LILIOSPHAERIDIUM Uutela & Tynni, 1991
emend.

1991 *Liliosphaeridium* UUTELA & TYNNI, pp. 76-77.

Type species (by original monotypic designation) – *Liliosphaeridium kaljoi* Uutela & Tynni, 1991 emend.; from Ordovician, Volkhov-Kunda (upper Arenig-lower Llanvirn) of Estonia.

Emended diagnosis – Vesicle originally spherical or nearly so, with circular-subcircular outline. Vesicle wall relatively thin; two-layered, though stratification normally evident only where inner layer detached/contracted from outer to form a more or less distinct inner body. Wall commonly finely sculptured (shagreenate, granulate, rugulate); bearing conspicuous, elongate or squat, solid, essentially homomorphic processes. Trunks trilaminate or quadrilaminate, with 3 or 4, longitudinally and radially disposed, psilate laminae. Processes invariably discrete, each consisting of trunk surmounted by a generally well differentiated distal structure (calyx), which is prominently ramified, embodying branches corresponding in number and location to the main trunk laminae. Branches extending upward at an angle with the trunk exceeding 90°; each branch composed of 3 laminae, the outer being the exten-

sion of one trunk lamina; inner laminae of adjacent branches variably coalescent. Branches sometimes dichotomizing once or even twice, the dichotomies still retaining the trilamination. Relative development and differentiation of calyx and trunk variable. Sides of calyx continuous or incomplete; distal opening entire or variously embayed-lobate, characteristically with branched projections representing distal continua of branch laminae. Excystment structure, infrequently evident, consisting of pylome and operculum.

Discussion – Uutela & Tynni's (1991, pp. 76-77) diagnosis of *Liliosphaeridium* is sketchy, being supported only by two scanning-electron micrographs of one specimen, and providing scant information on process structure and none on excystment mode. They noted that «the processes do not communicate with the vesicle interior», thus implying hollowness of the processes. However, our observations of type species *L. kaljoi* (and of two other species of the genus reported herein) clearly indicate the solid, laminate nature of the processes. Detailed optical-microscopic and SEM examination of all three species, which are well-represented in the Öland material, constitutes the basis of the emended generic diagnosis presented above.

Comparison – *Liliosphaeridium* Uutela & Tynni, 1991 emend. and *Peteinosphaeridium* are closely comparable morphologically in that both are pylomate and, more particularly, possess laminate processes. However, the former is distinguishable in that its processes are modified distally in the form of a more or less distinct calyx. Furthermore, the vesicle wall of *Liliosphaeridium* is characteristically finely sculptured in contrast to the normally psilate wall of *Peteinosphaeridium*. Although both genera may have an inherently double-layered wall, the presence of a discrete inner layer, sometimes detached and contracted in part from the outer layer, has not been recorded in *Peteinosphaeridium*.

New combination – *Liliosphaeridium pennatum* (Deunff, 1977) n. comb.

Basionym – *Peteinosphaeridium pennatum* Deunff, 1977, p. 144, pl. 2, fig. 6.

Remarks – Deunff's (1977) diagnosis and sole photomicrograph of this species cannot be considered as providing adequate morphological detail. Nonetheless, the laminate processes with their calyx-like distal elaborations – shown also by Elaouad-Debbaj's (1984, pl. 3, figs. 3, 6) specimen

from Deunff's type locality and stratum – warrant the proposed new combination with *Liliosphaeridium*.

Occurrence – Morocco, lower Ordovician, upper Arenig (Deunff, 1977; Elaouad-Debbaj, 1984). Note that the latter author (p. 80) corrected the sample number/age from that stated originally by Deunff (1977).

LILIOSPHAERIDIUM HYPERTROPHICUM
(Eisenack, 1976) n. comb. et stat., emend.
Pl. 6, figs. 3-5; Pl. 7, fig. 1; Text-fig. 6D1

1976 *Peteinosphaeridium trifurcatum hypertrophicum*
EISENACK, p. 195, pl. 4, figs. 4-7.

non 1979 *Peteinosphaeridium trifurcatum hypertrophicum*
Eisenack - GÓRKA, pp. 369-370, pl. 17, fig. 5.

Emended diagnosis – Vesicle originally spherical, with circular to subcircular outline. Vesicle wall thin, 0.7-0.9 μm in thickness; mainly psilate but bearing scattered and irregularly distributed, low, hemispherical to craterlike grana and rugulae. Processes solid, numbering 20-32 (usually about 23), near-homomorphic, elongate, becoming distinctly funnel-shaped distally, where calyx developed; in profile, processes exhibiting clear trunk/calyx demarcation. Process length totalling 27 (36) 48 μm ; bases 5 (7.8) 10 μm in overall diameter, rarely with minor constriction; proximal contacts angular to slightly curved. Trunks quadrilaminar or trilaminar, consisting of 4 (rarely 3), longitudinally and radially disposed, thin, psilate laminae, individually 3.5-6 μm wide; trunks maintaining fairly constant width from base for ca. 70% of total process length, then, at calyx base, giving rise to 4 (rarely 3) branches, each corresponding in position to a trunk lamina and projecting at $>90^\circ$ to trunk. Each branch comprising 3 laminae, the outer constituting the extension of one trunk lamina and all progressively narrowing distally. Proximal parts of inner laminae of adjacent branches coalescing to produce, at calyx base, a variably shaped (mostly quadrangular), shallow, cup- or funnel-like structure, 1 (3) 6 μm deep, with distal opening 6 (11) 17 μm in diameter; margin regularly and conspicuously lobate, having 4 (rarely 3) embayments, infrequently sculptured with small flat projections or discrete simple spinae. Inner laminae of each branch coalescing distally to form a flat, fan-shaped projection, 6 (9) 13 μm in overall length, then dividing once or twice into 2-3, small, spine-like, evexate or acuminate elements rarely drawn out apically as thin, thread-like, non-

anastomosing termini. Pylome circular or subcircular; margin simple; operculum not observed.

Dimensions – Vesicle diameter 51 (58) 66 μm (24 specimens measured); pylome diameter 16-20 μm (4 specimens). Process length averages 61% of vesicle diameter (range 50-75%).

Holotype – Eisenack (1976, pl. 7, fig. 4); preparation 10, no. 7, catalogue no. 1487, Geologisch-Paläontologisches Institut, Univ. Tübingen, Germany.

Type locality and stratum – Sweden, Island of Öland, northern coastal section, Hälludden, ca. 2.9 km northeast of Byxelkrok; Raniceps Limestone, sample 10 (of Eisenack, 1976, table 1); middle Ordovician, Kunda, Valaste (lower Llanvirn).

Remarks – Reference to the description and illustrations furnished by Eisenack (1976) for his subspecies *hypertrophicum* – herein raised to specific status as *Liliosphaeridium hypertrophicum* (Eisenack, 1976) n. comb. et stat. – leaves no doubt as to the identity of the study specimens, which are well-preserved and often abundant in our Öland material, including samples from the Hälludden type locality. The above re-diagnosis provides, *inter alia*, more explicit information on process morphology, from both optical and scanning-electron microscopy. The terminal, albeit shallow calyx characteristic of the processes warrants reassignment of the taxon to *Liliosphaeridium*.

As in type species *L. kaljoi* Uutela & Tynni, 1991 emend. and in *L. intermedium* (Eisenack, 1976) n. comb., emend., a discrete inner body is evident in some specimens of *L. hypertrophicum*. This is regarded as signifying an inherently bilayered vesicle wall, the inner layer of which may, in rare circumstances, become at least partly detached and contracted from the outer layer. The inner layer, 0.3-0.4 μm thick, is usually slightly thicker than the outer, has a porous appearance, and is non-granulate. Although the trunk and constituent laminae typically show more or less uniform widths on a given process of *L. hypertrophicum*, slight tapering or slight near-central dilation is occasionally evident. The excystment opening is often strongly deformed and poorly defined.

A Polish Llanvirn specimen recorded by Górka (1979, pp. 369-370, pl. 17, fig. 5) as *Peteinosphaeridium trifurcatum hypertrophicum* is considered here to be representative of *L. intermedium* (see below).

Comparison – *Liliosphaeridium hypertrophicum* differs from *L. kaljoi* in having more numerous and slender processes, the trunks of which are longer than their suprajacent calices. Moreover, the processes of *L. hypertrophicum* are more distinctly differentiated from the calices, and the latter have more dissected margins. In comparison with *L. hypertrophicum*, *L. intermedium* features distinctly tapering and relatively narrower process trunks, together with more conspicuously dissected calices incorporating branches of greater intricacy.

Distribution – Sweden: Öland, lower to middle Ordovician, Volkhov-Kunda, upper Arenig-lower Llanvirn (Eisenack, 1976; Ribecai & Tongiorgi, in press; present study). Finland: Åland Islands, middle Ordovician (Tynni, 1982).

Stratigraphic range verified by co-occurrence of other fossils – (a) Lower limit: lowermost Kunda, lower Hunderum (uppermost Arenig), lower *Amorphognathus variabilis* conodont Zone, Vaginatum Limestone, Horns Udde Quarry, Öland, Sweden (Ribecai & Tongiorgi, in press). (b) Upper limit: Kunda, Valaste (lower Llanvirn), *Asaphus «raniceps»* trilobite Zone, *Amorphognathus variabilis* conodont Zone, Vaginatum Limestone, Hälludden, Öland, Sweden (Eisenack, 1976; for age see Stouge & Bagnoli, 1990).

LILIOSPHAERIDIUM INTERMEDIUM (Eisenack, 1976)
n. comb., emend.

Pl. 7, figs. 2-6; Pl. 8, figs. 1, 2; Text-fig. 6D2

- 1969 *Baltisphaeridium digitatum* (auct. non Eisenack, 1938) - GÓRKA (pars), pp. 22-23, pl. 1, fig. 6 (non pl. 1, figs. 2, 4; fig. 3).
1976 *Peteinosphaeridium trifurcatum intermedium* EISENACK, pp. 195-196, pl. 4, figs. 8-10 (non pl. 4, figs. 11a, b).
non 1978 *Peteinosphaeridium intermedium* Eisenack (sic) - JACOBSON, p. 297, pl. 1, figs. 10, 11, 14.
1979 *Peteinosphaeridium trifurcatum hypertrophicum* auct. non Eisenack, 1976 - GÓRKA, pp. 369-370, pl. 17, fig. 5.
non 1984 *Peteinosphaeridium trifurcatum intermedium* Eisenack 1976 - TURNER, pp. 132-133, pl. 9, figs. 1, 4-6.

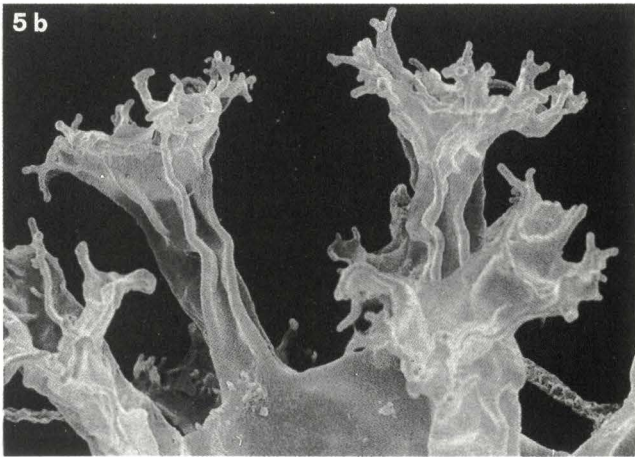
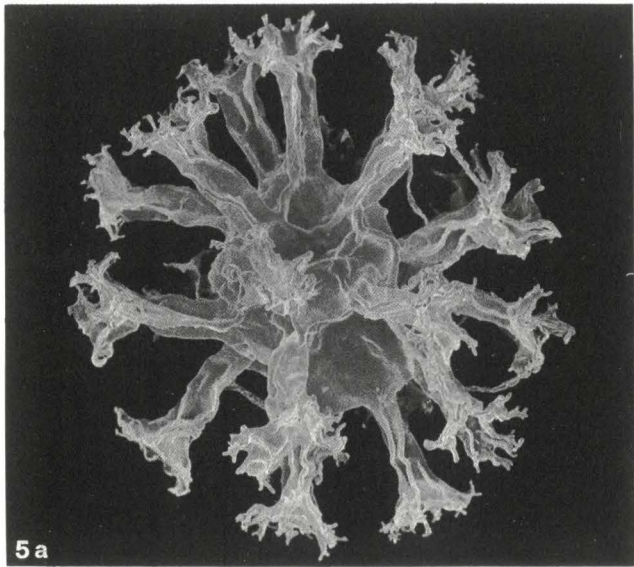
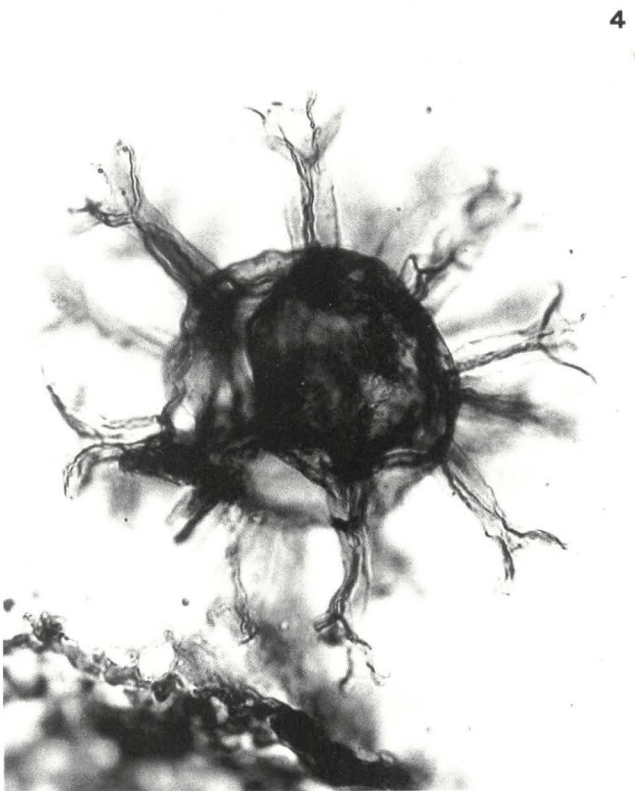
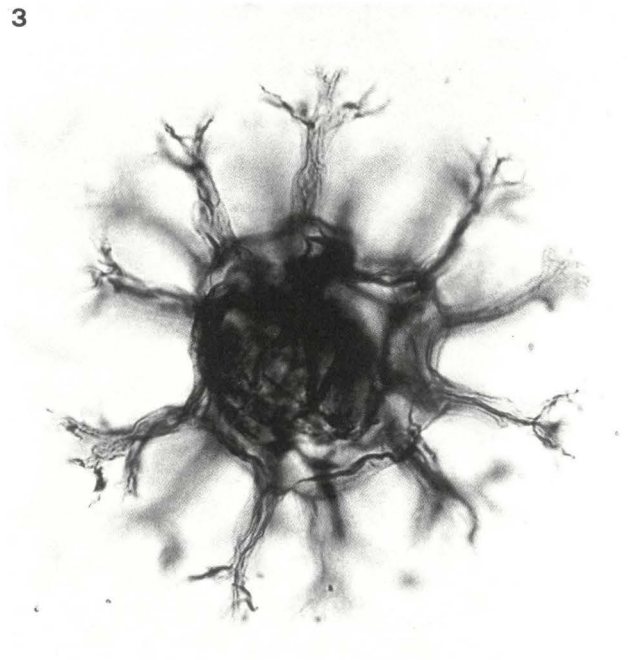
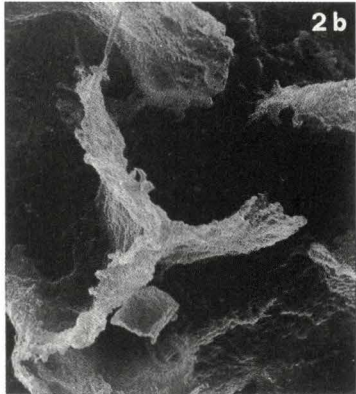
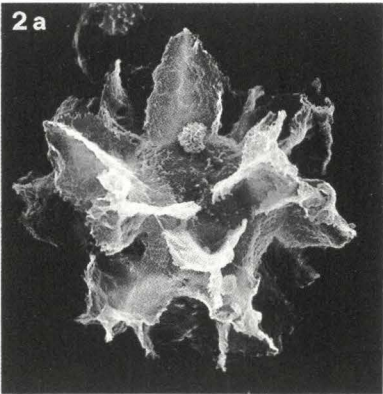
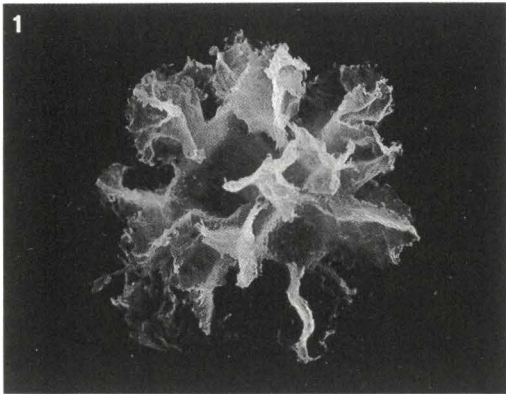
- non 1985 *Peteinosphaeridium intermedium* (Eisenack) Jacobson 1978 - JACOBSON & ACHAB, p. 190, pl. 7, fig. 5.
non 1987 *Peteinosphaeridium trifurcatum intermedium* Eisenack 1976 - LI JUN, pp. 619-620, pl. 71, fig. 9.
non 1990 *Peteinosphaeridium trifurcatum intermedium* Eisenack 1976 - LI JUN, p. 151, pl. 5, fig. 1.
non 1992 *Peteinosphaeridium trifurcatum intermedium* Eisenack 1976 - OTTONE, TORO & WASEFELD, pp. 107-108, pl. 4, figs. 1, 9.

Emended diagnosis – Vesicle originally spherical, with circular to subcircular outline. Vesicle wall thin (0.6-0.8 μ m thick), featuring fine, dense sculpture of discrete or coalescent grana, 0.5-0.8 μ m in diameter, with variable basal outlines (circular to roundly elongate or roundly polygonal) and characteristically showing slightly depressed surfaces (crater-like); locally, around process bases, variably delimited ring-like areas of vesicle wall typically psilate. Processes solid, more or less irregularly distributed, ca. 30-58 per vesicle (usually just over 40), near-homomorphic elongate, becoming funnel-shaped distally where calyx developed; trunk-calyx demarcation clearly evident in process profile. Length of processes 14 (25) 34 μ m (but fairly uniform on given specimen); bases non-constricted, 3 (6) 9 μ m in overall diameter; proximal contacts distinctly angular. Trunks quadrilaminar (rarely trilaminar), consisting of 4 (3) longitudinally and radially disposed, psilate laminae, individually 2-5 μ m wide at process base. Trunks constituting ca. 70% of total process length, tapering distally to calyx base, there giving rise to 4 (rarely 3) branches of 2 or 3 orders, each branch of the initial order coincident with a trunk lamina and projecting at ca. 130° to trunk. First order branches trilaminar, the outer lamina constituting extension of one trunk lamina and all 3 branch laminae progressively attenuating distally. Proximal parts of inner laminae of adjacent first order branches coalescing to produce, at calyx base, a small, variably shaped (mostly quadrangular), slightly concave structure. First order branches dichotomizing once or possibly twice, dichotomies still retaining trilamination, with the outer lamina of each successive branch con-

EXPLANATION OF PLATE 6

- Figs. 1, 2 - *Cycloposphaeridium auriculatum* Uutela & Tynni, 1991 emend. 1) $\times 600$. 2a) $\times 600$; 2b) detail of process, viewed superpositionally, showing trilaminar structure, $\times 2000$.
Figs. 3-5 - *Liliosphaeridium hypertrophicum* (Eisenack, 1976) n. comb. et stat., emend. 3) $\times 600$. 4) $\times 600$. 5a) $\times 600$; 5b) detail of processes, $\times 1400$.

For locality, stratigraphic, and curatorial details see Appendices 1, 2.



stituting extension of corresponding lamina from preceding parental order; inner laminae of adjacent branches partially coalescing in their proximal regions, thereby producing flat inter-branch connections. At calyx's distal limit, the 2 inner laminae of each ultimate branch coalescing, beyond the trilaminate branch apex, to form a flat, flared (fan-shaped) projection; the latter then forking up to 4 times, mostly by repeated dichotomy, to produce minute flexible spinae that often exhibit very fine, thread-like, non-anastomosing apical extensions. Overall diameter of calyx 7 (15) 23 μm distally. Pylome (rarely evident) circular to subcircular, margin simple; operculum (very rare) with psilate or faintly rugulate surface.

Dimensions – Vesicle diameter 50 (67) 84 μm (30 specimens measured); pylome diameter 18-27 μm (undeformed; 2 specimens); operculum diameter 18-24 μm (7 specimens). Process length averages 38% of vesicle diameter (range 26-57%).

Holotype – Eisenack (1976, pl. 4, fig. 8); preparation 11, no. 4, catalogue no. 1487, Geologisch-Paläontologisches Institut, Univ. Tübingen, Germany.

Type locality and stratum – Sweden, Island of Öland, northern coastal section, Hälludden, ca. 2.9 Km northeast of Byxelkrok; Raniceps Limestone, sample 11 (of Eisenack, 1976, table 1); middle Ordovician, Kunda, Valaste (lower Llanvirn).

Remarks – The revised specifications are based on optical and SEM observations of topotypic material; i.e., collected from the same section and horizons (at Hälludden, Öland) whence the original (Eisenack, 1976) specimens derived. We concur with Jacobson's (1978) proposal of elevation from subspecies (Eisenack, 1976) to species rank, even though, as discussed below, his illustrated specimens are considered misidentified. The new combination with *Liliosphaeridium* is warranted by the presence of a calyx, and indeed by Eisenack's (1976, pp. 195-196) own indication of similarities between the

subject species and *L. hypertrophicum* (see comparison below). As per above basionym citation, we formally exclude from *L. intermedium* (Eisenack, 1976) n. comb., emend. one of the four originally illustrated specimens, viz., Eisenack (1976, pl. 4, figs. 11a, b), by reason of its shorter and more numerous processes.

Vesicle diameter and process length and width (i.e., width of constituent laminae) vary fairly widely, albeit continuously, among specimens of *L. intermedium* obtained from the same sample and from different samples; but, normally, these values are comparatively uniform on any one specimen. Some samples from the uppermost Arenig of Öland yielded smaller specimens with shorter processes and shorter constituent branches. The distal filamentous projections form an intricate crown-like structure (e.g., Pl. 7, fig. 3; Pl. 8, figs. 1b, 2).

We refer to *L. intermedium* a specimen, from upper Arenigian beds of Poland, ascribed by Górka (1969) to *Baltisphaeridium digitatum* (Eisenack) Downie, 1959, now *Hoegklintia digitata* (Eisenack) Dörning, 1981. In having laminate processes, this specimen clearly differs from others correctly referred by Górka to the latter species. The tapering process trunks with branching distal process terminations warrant assignment of the specimen to *L. intermedium*. Also attributed herein to *L. intermedium* is Górka's (1979) Polish Llanvirn specimen identified by her as *Peteinosphaeridium trifurcatum hypertrophicum* Eisenack, 1976 but possessing, in accord with *L. intermedium*, tapering process trunks without strongly developed calices.

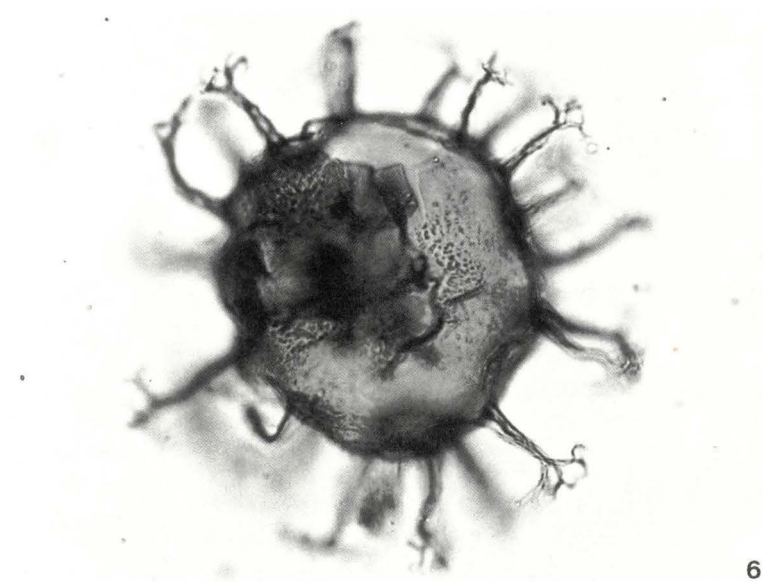
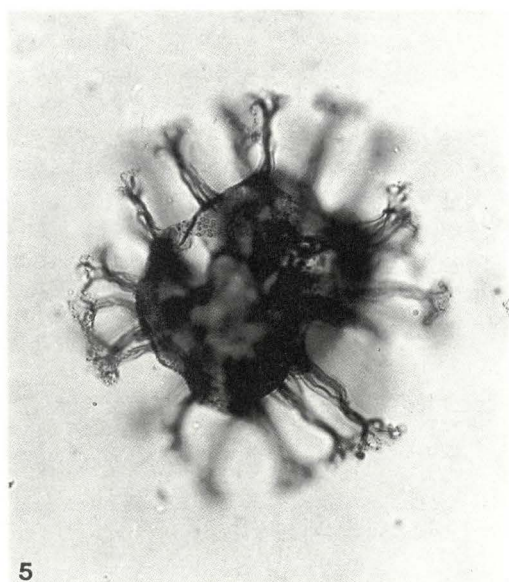
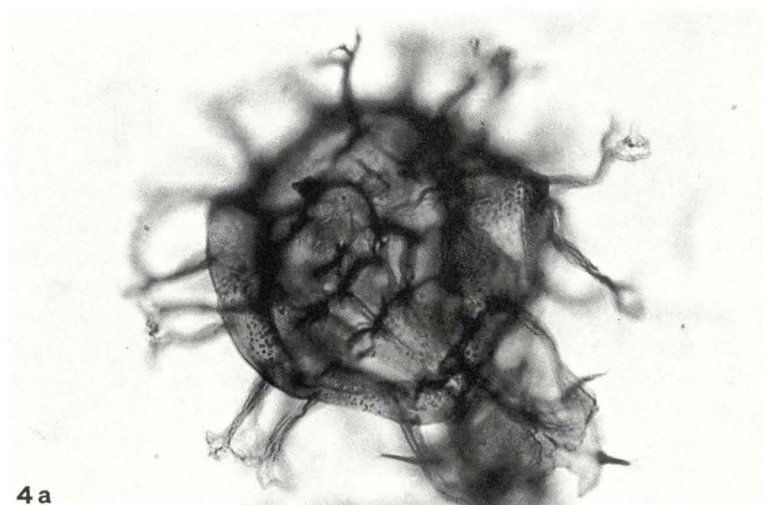
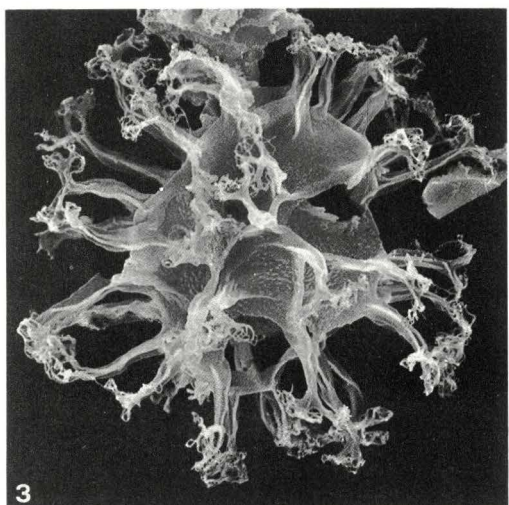
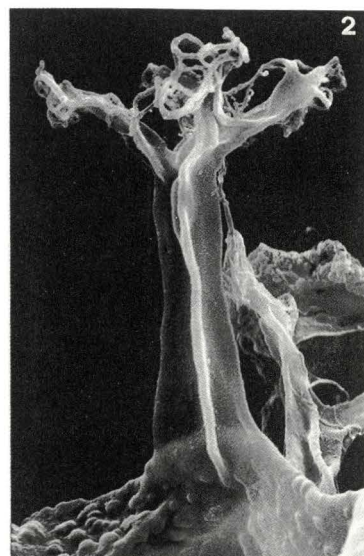
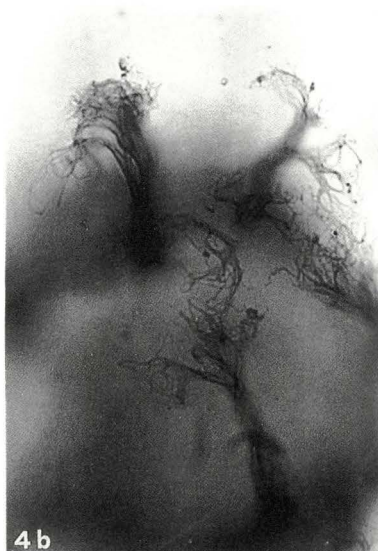
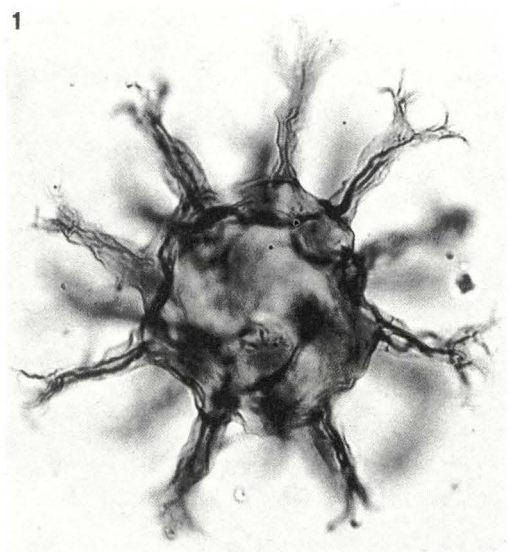
Upper Ordovician specimens from Kentucky, U.S.A., attributed by Jacobson (1978) to *P. intermedium*, are evidently wrongly identified, chiefly because the vesicle surface is psilate, the pylome has a distinctly everted lip, and the processes appear shorter than is usual for the species and are not multifurcant. English Caradocian specimens assigned by Turner (1984) to *P. trifurcatum intermedium* possess «distally trifurcate or quadrifurcate processes» that are relatively short (20-25% of vesicle diameter), together with highly variable pylome margins/collars; these attributes do not support identification with *L. intermedium*.

EXPLANATION OF PLATE 7

Fig. 1 - *Liliosphaeridium hypertrophicum* (Eisenack, 1976) n. comb. et stat., emend.; $\times 600$.

Figs. 2-6 - *Liliosphaeridium intermedium* (Eisenack, 1976) n. comb., emend. 2) detail of process and vesicle surface, $\times 3000$. 3) $\times 600$. 4a) $\times 600$; 4b) detail of distal ramifications of processes, $\times 1200$. 5) $\times 600$. 6) $\times 600$.

For locality, stratigraphic, and curatorial details see Appendices 1, 2.



Indifferently preserved Canadian Ashgillian specimens attributed by Jacobson & Achab (1985) to *P. intermedium*, and said to be possibly recycled, appear to be distinct from the latter, at least on the basis of the single photomicrograph (Jacobson & Achab, 1985, pl. 7, fig. 5) which depicts very short, relatively stout processes; moreover, the vesicle wall is stated to be unsculptured.

Li Jun's (1987, 1990) records of *P. intermedium* from South China (lower Ordovician, Arenig) should be disregarded, as the illustrated specimens differ from that species in possessing very slender and not multifurcate processes. Argentinian lower Arenig specimens attributed by Ottone *et al.* (1992) to *P. intermedium* appear closer to South China species such as *P. cruciatum* Lu Li-chang, 1987, owing to their somewhat tapering process trunks and their prominent distal, not multifurcate branches generally emanating at right angles to the trunk.

Comparison – *Liliosphaeridium intermedium* differs from *L. pennatum* (Deunff, 1977) n. comb. in possessing more numerous and narrower processes that are shorter compared to vesicle size; and from *L. hypertrophicum* in having a smaller, less depressed calyx basal structure, together with generally shorter, more numerous, and more conspicuously and intricately branched processes characterized by prominently tapering trunks. Contrary to Eisenack (1976, p. 195), we have observed no intergradational specimens linking *L. intermedium* with either *L. hypertrophicum* or *Peteinosphaeridium trifurcatum* (= *P. «breviradiatum»*).

Distribution – Poland: lower Ordovician, upper Arenig (Górka, 1969; as *Baltisphaeridium digitatum*); middle Ordovician, Llanvirn (Górka, 1979; as *Peteinosphaeridium trifurcatum hypertrophicum*). Sweden: middle Ordovician, Volkhov-Kunda, upper Arenig-lower Llanvirn (Eisenack, 1976; present study).

Stratigraphic range verified by co-occurrence of other fossils (Öland, Sweden) – (a) Lower limit: upper

Volkhov, Langevoja (upper Arenig), upper *Microzarkodina parva* conodont Zone, Lepidurus Limestone, Horns Udde Quarry (present study). (b) Upper limit: Kunda, Valaste (lowermost Llanvirn), *Asaphus «raniceps»* trilobite Zone, *Amorphognathus variabilis* conodont Zone, Vaginatum Limestone, Hälludden (Eisenack, 1976; present study).

LILIOSPHAERIDIUM KALJOI Uutela & Tynni, 1991
emend.

Pl. 8, figs. 3-6; Pl. 9, figs. 1-6; Text-fig. 6D3

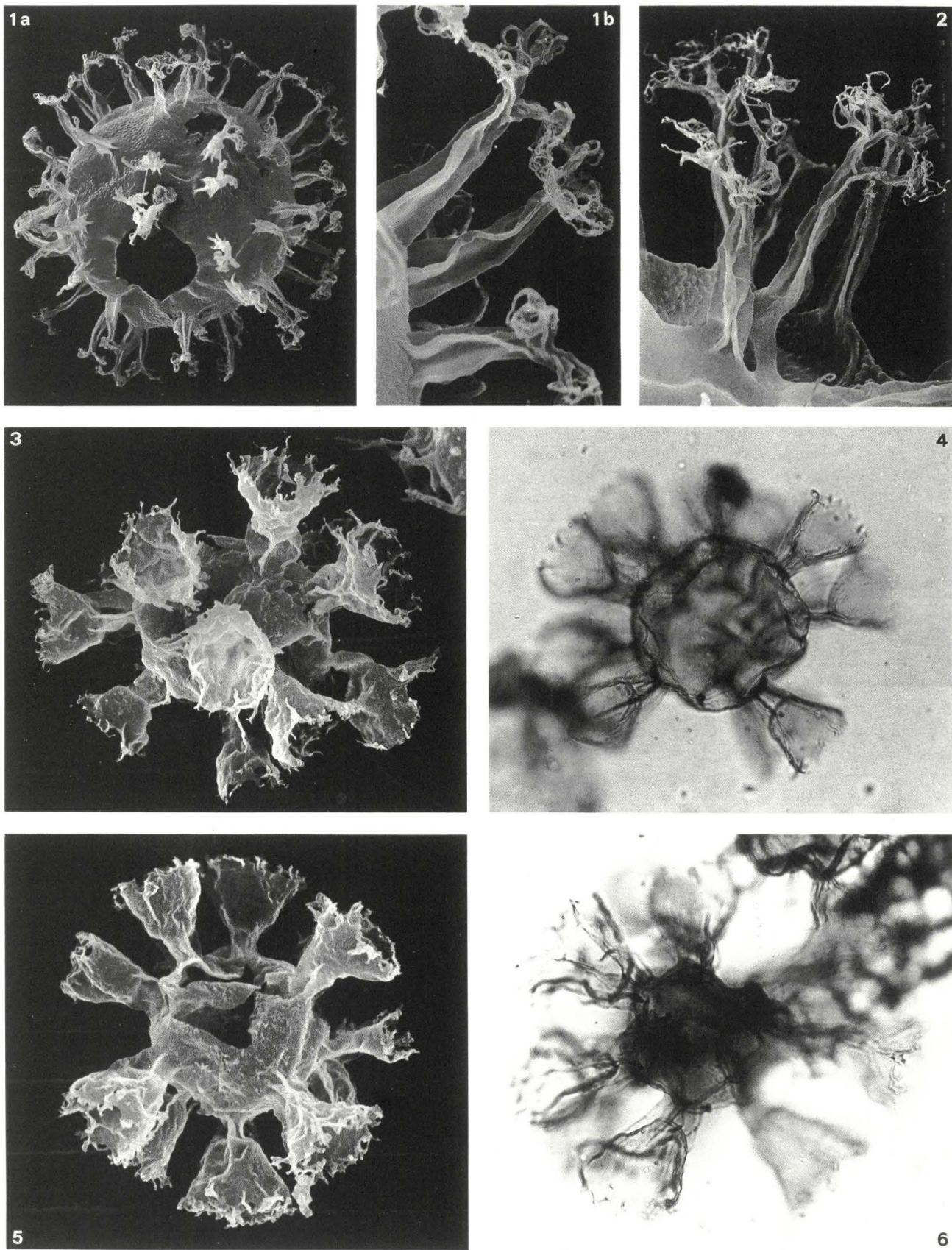
- ? 1975 *Hystrichosphaeridium anthophorum* auct. non Cookson & Eisenack forma *archaeoforme* TYNNI, p. 21, pl. 2, fig. 11.
1991 *Liliosphaeridium kaljoi* UUTELA & TYNNI, pp. 77, pl. 16, figs. 154a, b.

Emended diagnosis – Vesicle originally spherical; outline circular to subcircular. Vesicle wall thin (<0.5 µm thick); psilate or shagreenate to minutely sculptured with low, poorly defined rugulae and fine to medium-sized grana. Processes solid, squat, 8-17 per vesicle (usually about 13), near-homomorphic, becoming distinctly cup- or funnel-shaped distally where calyx developed; in profile, no abrupt trunk-calyx demarcation. Length of processes totalling 15 (31) 45 µm; bases 7-15 µm in overall diameter, mostly weakly constricted; proximal contacts angular to slightly curved. Trunks quadrilaminar (rarely trilaminar), comprising 4 (3) thin, longitudinally and radially disposed, psilate laminae, each 4-8 µm wide; a shorter subsidiary lamina may be developed between 2 adjacent main laminae; trunk showing slight, gradual flaring over its entire length (ca. 4-60% of total process length, usually <35%), then, at calyx base, giving rise to 4 or 3 branches, each contiguous with a trunk lamina and projecting at ca. 140-170° to trunk. Each branch trilaminar, the outer lamina being an extension of one main trunk lamina and narrowing rapidly on proximal part of calyx. Inner laminae of adjacent branches expanding and coalescing laterally and also distally (upwards) beyond the branch apex, thus producing well-defined, cup- or funnel-like structure (i.e., bulk of calyx), 4 (17) 27 µm deep, with distal

EXPLANATION OF PLATE 8

Figs. 1, 2 - *Liliosphaeridium intermedium* (Eisenack, 1976) n. comb., emend. 1a) note vesicle sculpture, ×600; 1b) detail of processes, showing at least two orders of trilaminar branches, ×2000. 2) process detail (as per fig. 1b), ×1400.
Figs. 3-6 - *Liliosphaeridium kaljoi* Uutela & Tynni, 1991 emend.; ×600.

For locality, stratigraphic, and curatorial details see Appendices 1, 2.



opening 12 (23) 37 μm in diameter. Margin of latter regularly lobate, with 4 (rarely 3) deep embayments separated by protrusions where the 2 inner laminae of each branch conjoin, thus forming flat, flared (fan-shaped) projections, 2 (6) 13 μm long, that repeatedly dichotomize to produce minute spinae often drawn-out apically as fine filaments. A subsidiary (often smaller) projection normally developed on embayment at junction of inner laminae of 2 adjacent branches. Pylome circular or subcircular; margin simple; operculum not observed.

Dimensions – Vesicle diameter 37 (53) 69 μm (46 specimens measured); pylome diameter 21 μm (2 specimens). Process length averages 60% of vesicle diameter (range 30–85%).

Holotype – Uutela & Tynni (1991, pl. 16, figs. 154a, b); Geological Survey of Finland preparation 1126 (SEM).

Type locality and stratum – Estonia, Rapla borehole, 189.0 m; Loobu Formation; lower or middle Ordovician, Volkhov-Kunda (upper Arenig-lower Llanvirn).

Remarks – Detailed examination of numerous well-preserved Öland specimens constitutes the basis of the above specific re-diagnosis, clarifying the original circumscription (Uutela & Tynni, 1991) that was founded on a more restricted number of specimens and was illustrated by two SEM images of one specimen. Consequently, we document *Liliosphaeridium kaljoi* Uutela & Tynni, 1991 emend. as a morphologically variable species, appreciably more so than originally defined. Contrary to the species definition (Uutela & Tynni, 1991, p. 77), it must be emphasized that the processes are solid. Process length does not exceed vesicle diameter, normally being about 60% of the latter. The calyx-depth : process-length ratio varies noticeably among different Öland samples; e.g., 0.5 (0.6) 0.8 (samples UQ14 and HL1; apart from one specimen only from latter sample at 0.3) down to 0.2 (0.4) 0.5 (sample HU654). Estimate of that ratio in

the holotype (Uutela & Tynni, 1991, pl. 16, fig. 154a) is 0.4. Processes of individual specimens are, however, more or less similarly proportioned; i.e., the calyx-depth : process-length ratio tends to be fairly consistent, as does gross process morphology. Specimens with deeper calices are mostly equipped with longer, more branching distal projections, sometimes showing filamentous ultimate apices. The pylome is often strongly deformed and poorly defined. Rare specimens of *L. kaljoi* possess a relatively dark, irregular, internal body, interpreted by us as detachment and contraction of the inner layer of an inherently bilayered vesicle wall.

Distribution – Estonia (Uutela & Tynni, 1991) and Öland, Sweden (Ribecai & Tongiorgi, in press; present study): lower to middle Ordovician, Volkhov-Kunda, upper Arenig-lower Llanvirn.

Stratigraphic range verified by co-occurrence of other fossils – (a) Lower limit: Volkhov, Langevoja (upper Arenig), upper *Microzarkodina parva* conodont Zone, Lepidurus Limestone, Horns Udde Quarry (Ribecai & Tongiorgi, in press). (b) Upper limit: Kunda, Valaste (lower Llanvirn), *Asaphus «raniceps»* trilobite Zone, *Amorphognathus variabilis* conodont Zone, Vaginatum Limestone, Hälludden.

Genus CYCLOSPHAERIDIUM Uutela & Tynni, 1991 emend.

1991 *Cycloposphaeridium* UUTELA & TYNNI, p. 55.

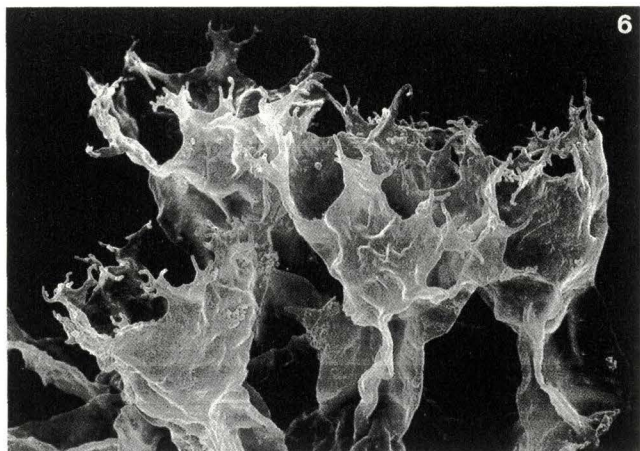
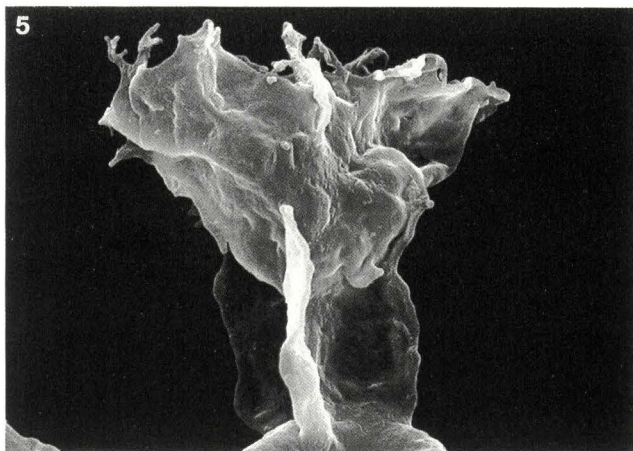
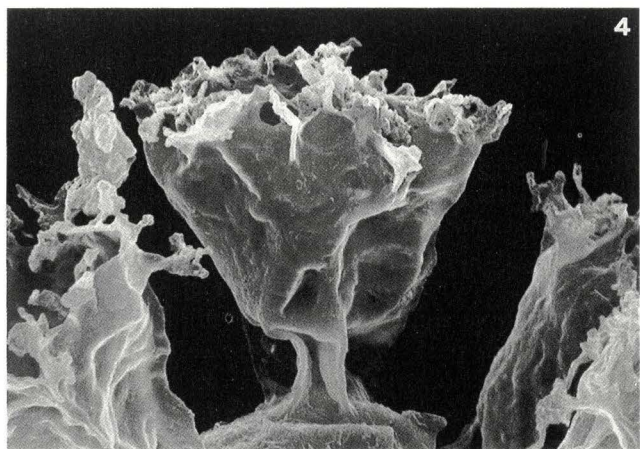
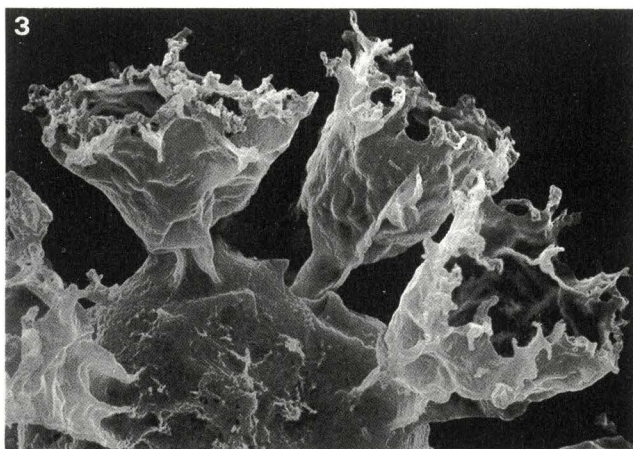
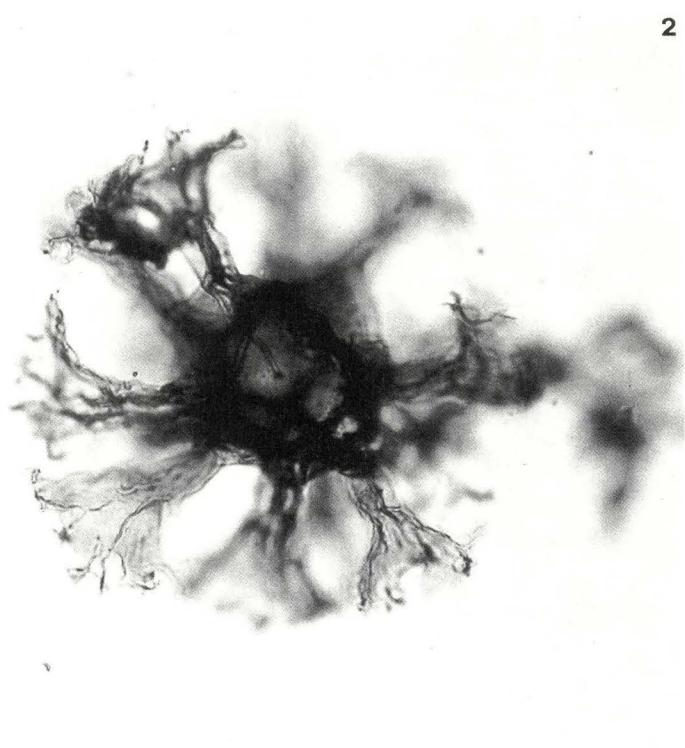
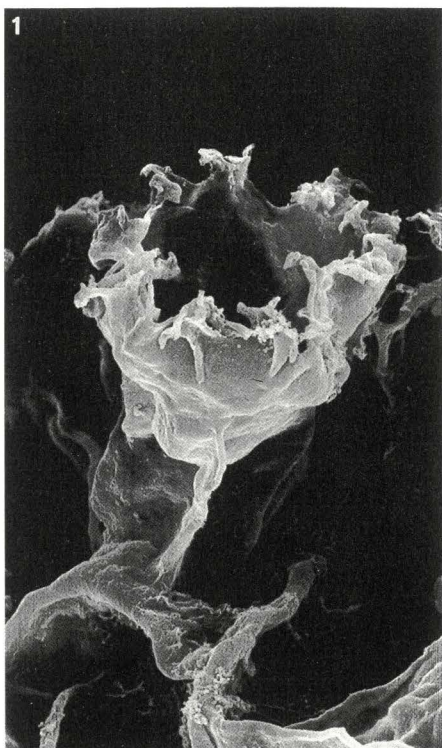
Type species (by original monotypic designation) – *Cycloposphaeridium auriculatum* Uutela & Tynni, 1991 emend.; from lower to middle Ordovician, Volkhov?-Aseri (uppermost Arenig-lower Llanvirn) of Estonia.

Emended diagnosis – Vesicle spherical to sub-spherical, with circular to subcircular outline. Vesicle wall normally very finely sculptured (e.g., granulate, echinate). Processes solid, laminate, consisting of longitudinally and radially oriented laminae, typically 3 per process, and having petaloid or phylloid profile in lateral aspect. Lamina surfaces

EXPLANATION OF PLATE 9

Figs. 1–6 – *Liliosphaeridium kaljoi* Uutela & Tynni, 1991 emend. 1) detail of process, $\times 1400$. 2) $\times 600$. 3) detail of processes, $\times 1000$. 4–6) detail of processes, $\times 1400$; note subsidiary trunk lamina (fig. 4) and embayments and projections on calyx margin (fig. 6).

For locality, stratigraphic, and curatorial details see Appendices 1, 2.



psilate or with minor sculpture; lamina edges characteristically finely sculptured similar to vesicle wall. Pylome with simple margin and operculum comprising excystment structure.

Discussion – The generic diagnosis is emended here to take account of the clearly laminate nature of the processes, in contrast to the «flat, membranous outer wall processes» reported by Uutela & Tynni (1991, p. 55). The type (and sole) species of the genus certainly displays three laminae composing each process (Uutela & Tynni, 1991, pl. 9, figs. 89a, b; holotype), as indeed do all Öland specimens of this species examined during the present study.

Comparison – *Cycloposphaeridium* Uutela & Tynni, 1991 emend. may be separated from *Asketopalla* Loeblich & Tappan, 1969 emend. Loeblich & Tappan, 1971 (p. 900) in being invariably unipylomate and in its essentially unified (non-stratified) vesicle-wall construction. Certainly, however, the processes of these two monotypic Ordovician genera are morphologically akin, albeit are appreciably smaller, more numerous, and essentially unsculptured in *A. formosula* Loeblich & Tappan, 1969 emend. Loeblich & Tappan, 1971. The gross (petaloid or phylloid) form of the processes of *Cycloposphaeridium* is the major factor permitting its segregation from both *Peteinosphaeridium* and *Liliosphaeridium*. Furthermore, process (lamina) surfaces are comprehensively sculptured in *Cycloposphaeridium*, psilate in *Liliosphaeridium*, and either psilate or very minutely sculptured (microstriate) in *Peteinosphaeridium*.

CYCLOPOSphaeridium auriculatum

Uutela & Tynni, 1991 emend.

Pl. 5, figs. 6-8; Pl. 6, figs. 1, 2; Text-fig. 6B

1991 *Cycloposphaeridium auriculatum* UUTELA & TYNNI, p. 55, pl. 9, figs. 89a, b.

Emended diagnosis – Vesicle originally spherical; outline circular to subcircular. Vesicle wall 0.5-1 µm thick; uniformly granulate to finely echinate (spinose); spinae diminutive but well-developed, very narrow, up to 1.5 µm long. Processes solid, conspicuous, discrete, 15-32 in number, homomorphic, invariably consisting of 3 longitudinally and radially disposed laminae, each reaching maximum width (4.5-12 µm) just above process base and then gradually decreasing in width to distal extremity, thus resulting in a broadly and uniformly curved,

petal- or leaf-like process profile in lateral aspect. Process length, fairly uniform on given specimen, within range of 8-25.5 µm; proximal contacts curved to angular; distal extremities obtusely rounded. Lamina surfaces psilate or, more commonly, with fine, irregularly distributed sculpturing elements (sparse faint rugulae and/or grana); lamina edges finely sculptured, more conspicuously in distal part of processes, with echinae/spinae (as vesicle wall) or bacula. Pylome circular to subcircular; margin simple; operculum finely echinate.

Dimensions – Vesicle diameter 22 (37) 48 µm (64 specimens measured); pylome diameter 7 (12) 18 µm (31 specimens). Process length averages 49% of vesicle diameter (range 33-62%).

Holotype – Uutela & Tynni (1991, p. 55, pl. 9, figs. 89a, b); Geological Survey of Finland preparation 1125 (SEM).

Type locality and stratum – Estonia, Rapla borehole, 188.6 m; lower or middle Ordovician; Volkhov?-Kunda (uppermost Arenig or lowermost Llanvirn).

Remarks – Emendation of the specific diagnosis results from reinterpretation of process morphology as evidenced by numerous, well-preserved Öland specimens. In the original circumscription, Uutela & Tynni (1991, p. 55) described their specimens as being equipped with flat, membranous processes. In contradistinction, however, the illustrated holotype (Uutela & Tynni, 1991, pl. 9, figs. 89a, b) shows distinctly trilaminate processes; this is confirmed by specimens of the present study.

Comparison – *Polyancistrodorus phylloides*, which is listed previously herein as a possible representative of *Peteinosphaeridium* and compared by its authors (Uutela & Tynni, 1991, p. 108, pl. 27, fig. 284) to their *Cycloposphaeridium auriculatum*, is clearly distinct from the latter in the gross form of its processes.

Distribution – Estonia: lower to middle Ordovician, Volkhov?-Aseri, uppermost Arenig-mid Llanvirn (Uutela & Tynni, 1991). Sweden: Öland, lower to middle Ordovician, Kunda, uppermost Arenig-lowermost Llanvirn (Ribecai & Tongiorgi, in press; present study).

Stratigraphic range verified by co-occurrence of other fossils (Öland, Sweden) – Lower Kunda, Hunderum (uppermost Arenig?-lowermost Llanvirn),

Asaphus expansus trilobite Zone, *Amorphognathus variabilis* conodont Zone, Vaginatum Limestone, Horns Udde Quarry and Hälludden (Ribecai & Tongiorgi, in press; present study).

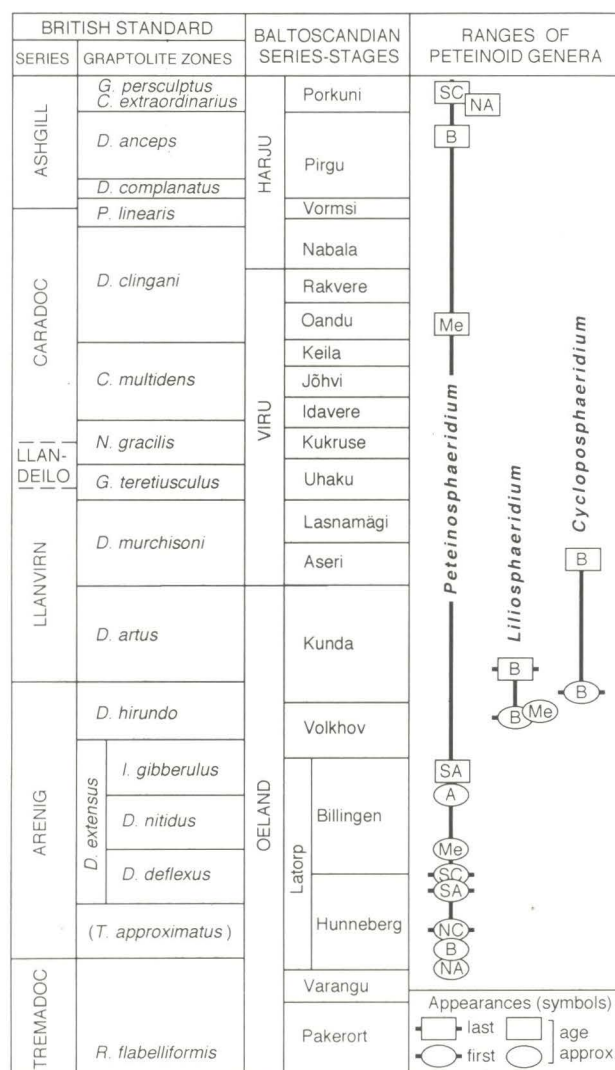
BIOSTRATIGRAPHY

The succeeding paragraphs provide a conspectus of the vertical distributions of the subject peteinoid taxa, at generic level (Text-fig. 8), based mainly on data given in the systematic text of this paper and in Tab. 1, and with limitations and reservations inherent in the available bibliographic data-sources as summarized in Text-fig. 10. Palaeoprovincial terminology accords with that adopted in the succeeding palaeogeographic section of this paper.

FIRST APPEARANCES OF PETEINOID GENERA

The oldest known, alleged peteinoid is that recorded by Yin Lei-ming (1986) as *Peteinosphaeridium* sp. from latest Cambrian beds (*Cordylodus proavus* conodont Zone) of Jilin Province, northeast China. However, the description and illustration furnished by Yin Lei-ming (1986, p. 352, pl. 90, fig. 15) are incongruent with *Peteinosphaeridium*, as the processes borne by the species are seemingly hollow [comparable with those of *Rhopaliophora palmata* (Combaz & Peniguel) emend. Playford & Martin, 1984], with simple or bifurcant/anastomosing distal termini. The lack of *Peteinosphaeridium* in the Cambrian-Ordovician beds of the Jilin Province is also confirmed by F. Martin (personal communication). It is perhaps noteworthy that no peteinoids were recorded in the upper Tremadoc-lower Arenig sequence of Jilin studied by Martin & Yin Lei-ming (1988); however, that paper is taxonomically selective and a more comprehensive account could conceivably disclose peteinoid presence. The first unequivocal record of peteinoids (i.e., *Peteinosphaeridium*) from North China is from lowermost Arenig (*Tetraraptus approximatus* graptolite Zone) strata of Shaanxi Province (Hu Yunxu, 1986).

From Australia, no data on Tremadoc palynofloras are yet available, though peteinoids had certainly appeared in northwestern Australia in the course of Arenig time (Playford & Martin, 1984). Based on inferred proximity of Australia and North China during the early Ordovician, one could anticipate more or less synchronous introductions of *Peteinosphaeridium* in those regions, where, however, the genus is evidently rare or infrequent in lower to middle Ordovician assemblages and (aside



Text-fig. 8 - Vertical ranges of *Peteinosphaeridium*, *Lilliosphaeridium*, and *Cycloposphaeridium*, shown provincially and *in toto*. Acritarch palaeoprovincial regions designated thus: A - Australia; B - Baltic; Me - Mediterranean; NA - North America; NC - North China; SA - South America; SC - South China.

from *Rhopaliophora* and *Polyancistrodorus*: Playford & Martin, 1984; Playford & Wicander, 1988) other laminate-processed genera are apparently absent.

In the Baltic Province, peteinoids have not been reported from Tremadoc strata, despite the fact that these latter have been extensively investigated (see, e.g., Volkova, 1993 and references cited therein). The youngest studied beds of the region's Tremadoc successions are referred to the middle to upper part of the series (Öland, Sweden: Tongiorgi *in* Bagnoli, Stouge & Tongiorgi, 1988) and to the upper part (easternmost Russian Platform, Aristova, 1980; Estonia and St. Petersburg region, Volkova, 1993;

Poland, Górka, 1967, 1969). In none of these strata were any peteinoids recorded; and this also seems to apply to the Baltic lower Arenig-lowest upper Arenig which appears to be mostly non-palyniferous, owing to primary oxidation of host rock. However, a recent short report (Paalits & Erdtmann, 1993; East European Platform) indicates the first appearance of *Peteinosphaeridium* (as *P. sp.*) slightly above the base of the *Paroistodus proteus* conodont Zone (lower Hunneberg) at a level which is referred by the above quoted authors as possibly lower Arenig, but which may in fact be uppermost Tremadoc. Confirmation of this report is desirable in the absence of description and illustration and of precise geographic and stratigraphic information. Definite peteinoids occur, quite profusely, close to the top of the Arenig (upper Volkhov) as representatives of both *Peteinosphaeridium* and *Liliosphaeridium* (see systematic section herein). The Baltic inception of these two genera can therefore be specified no more precisely than within the upper Tremadoc-upper Arenig interval. *Cycloposphaeridium* appears later (Uutela & Tynni, 1991; Ribecai & Tongiorgi, in press; present study), at the base of the Kunda (uppermost Arenig). It may well constitute a serviceable stratigraphic index for the Baltic Province, to which it is evidently endemic.

The oldest alleged peteinoids of the Perigondwana Province are Fournier-Vinas's (1978, pl. 2, figs. 18, 30) undescribed specimens, labelled *Peteinosphaeridium breviradiatum*, from possible Tremadoc strata of Montagne Noire (France) in the Mediterranean region. This report, however, is judged non-peteinoid, as the specimens concerned bear long, slender, non-laminate processes. The earliest authentic peteinoid record – of *Peteinosphaeridium* – in the Mediterranean region (and in Perigondwana as a whole) is that by Rauscher (1971) from slightly younger (early Arenig) sediments of Montagne Noire. Rauscher figured (without description) two different *Peteinosphaeridium* specimens: one identified as *P. trifurcatum* (his pl. 1, fig. 2; misidentified specifically); the other as *P. breviradiatum* (pl. 1, figs. 3-4; an unlikely representative of that species, but nevertheless genuinely referable to the genus). Therefore, the inception of *Peteinosphaeridium* in the Mediterranean area dates at least from the early Arenig. *Liliosphaeridium* is known from this region only as a single species (*L. pennatum*) from a single Moroccan sample of latest early Ordovician (late Arenig) age (Deunff, 1977; Elaouad-Debbaj, 1984).

In the South China area (northeastern Perigondwana), the oldest reported *Peteinosphaeridium* specimens occur in lower Arenig (*Didymograptus*

deflexus graptolite Zone) strata of Guizhou Province (Li Jun, 1987, pp. 619-620, pl. 71, fig. 7; misidentified specifically as *P. trifurcatum intermedium*). However, Tremadoc palynofloras of this area are as yet unrecorded.

From the even more sparsely studied South American sector of western Perigondwana, Ottone *et al.* (1992) have reported *Peteinosphaeridium*, with first appearance in the lower Acoite Formation, dated from graptolites as early Arenig (late Hunneberg; Toro, 1993), and extension into the formation's upper part («middle Arenig»). As with the southern Chinese record (above), the authors' identification of their specimens with *P. t. intermedium* (now *Liliosphaeridium intermedium*) is untenable, but attribution to *Peteinosphaeridium* is sustainable.

Available information indicates, therefore, that in the Perigondwana Province *Peteinosphaeridium* makes its debut within the earlier Arenig, while the sole record of *Liliosphaeridium* is considerably later, near the close of the Arenig. *Cycloposphaeridium*, seemingly endemic to the Baltic Province, is unknown from any Perigondwana region.

Very few data are currently available from the North American Province. Martin (*in* Dean & Martin, 1982, pl. 1, fig. 3; 1992, p. 27, pl. 8, figs. 5, 8, 11, 12) has reported *Peteinosphaeridium* (as *P. sp.* cf. *P. breviradiatum*) from the uppermost Tremadoc (trilobite zone F) of Alberta, Canada. According to Martin (1992), the oldest level with *Peteinosphaeridium* is in the top of trilobite Zone F. However, in the same reference (p. 14), zonal boundaries are said to be «drawn somewhat arbitrarily, notably between zones F and G». Identification of these specimens appears justified at generic level, but close comparison with *P. breviradiatum* seems unlikely, owing to the robust, distinctly echinate nature of the processes.

LAST APPEARANCES OF PETEINOID GENERA

Peteinosphaeridium typically occurs in Arenigian and middle Ordovician strata of all provinces. Its apparently greater frequency in the Baltic and Perigondwana Provinces cannot be adequately substantiated in view of shortcomings in global coverage, i.e., scant information on Ordovician palynofloras of Australia, North China, and the Americas. Notable post-Llanvirn decline of *Peteinosphaeridium* is discernible in most regions, though (on a cautionary note) the published database generally attenuates concomitantly.

Upper Ordovician acritarch assemblages are relatively poorly known: e.g., see Martin's (1988) review. Moreover, prevalence of acritarch reworking in regressive/transgressive sequences of this age (Tur-

ner, 1982; Vavrdová, 1982; Martin, 1988; Jacobson & Achab, 1985; Vavrdová, 1989; Tourneur *et al.*, 1993) creates obvious palynostratigraphic difficulties, with some occurrences being highly questionable in terms of their provenance. Nevertheless, *Peteinosphaeridium* seems to persist, albeit infrequently, into the upper Ordovician; in many cases, however, species identifications need confirmation.

Although there is scant documentation of palaeogeographic differentiation among later Ordovician acritarch palynofloras (Hill & Molyneux, 1988, p. 36), according to Elouadi-Debbaj (1981, pp. 79, 83) the provincialism evident in the early and middle Ordovician breaks down subsequently during the period, as indeed is the tendency with other marine fossil groups (e.g., Cocks & Fortey, 1990; Finney & Chen Xu, 1990). In the following brief review, therefore, late Ordovician occurrences of *Peteinosphaeridium* will be referred to geographical areas rather than to biogeographic provinces.

Near the end of the Ordovician, *Peteinosphaeridium* extends into Ashgill beds of South China (He Sheng-ce & Yin Lei-ming, 1993). From Europe, it has been recorded in the upper Ordovician of Bohemia as *Baltisphaeridium trifurcatum* (Konzalová-Mazancová, 1969; not described or illustrated) and as a figured but unnamed species (Vavrdová, 1982; possibly recycled); in the Caradoc of England (Turner, 1984; but reworking cannot be excluded – see Turner, 1982; Martin, 1988); in the Ashgill (and lowermost Silurian) of Belgium (Martin, 1974, but probably reworked *vide* Martin, 1974, 1988); and in the Caradoc of Montagne Noire, France, as an undescribed, unillustrated, «small sized» *Peteinosphaeridium* (Rauscher, 1974, p. 82). In Sweden (Gotland), *P. trifurcatum* was reported by Eisenack (1968b) from glacial erratics, Ashgillian in age (Eiserhardt, 1992; but note that this author's *P. breviradiatum* ssp. 1 from the same erratics is misidentified generically). As discussed above, under typification of *P. trifurcatum*, the age of specimens attributed by Eisenack to *P. trifurcatum breviradiatum* or to *P. breviradiatum* (now *P. trifurcatum*) are unlikely to postdate the late Caradoc. *P. trifurcatum longiradiatum* has been documented from both Baltic-Russian and southwestern European Caradoc rocks (see systematic section). This distinctive form, originating in the Llanvirn, is especially characteristic of Caradoc suites.

Most of the studied upper Ordovician sequences of north Africa are devoid of *Peteinosphaeridium* (see, e.g., Hill & Molyneux, 1988; Molyneux, 1988; Elouadi-Debbaj, 1988). The genus has been recorded, albeit rarely, only from Algeria (Caradoc-

Ashgill; Jardiné *et al.*, 1974, p. 104) and Libya (Ashgill; Molyneux & Paris, 1985, p. 11). The former report is of *P. trifurcatum* (undescribed, unfigured) and, according to Martin (1988, p. 301), it could represent recycling; the Libyan specimens were simply listed, without description, illustration, or specific identification [i.e., excluding *P. nudum*, now *Ordoviciidium nudum* (Eisenack, 1959) Loeblich & Tappan, 1978, recorded by Molyneux & Paris (1985) from an older, inferred Caradoc interval].

Upper Ordovician rocks from a few offshore and onshore locations in eastern Canada have produced somewhat equivocal records of *Peteinosphaeridium*. From Labrador Sea material reportedly of Caradoc-Ashgill age, Legault (1982) identified *P. breviradiatum* and *P. cf. P. velatum*; however, the former appears misidentified generically and specifically, while the latter seems not closely akin to *P. velatum*. Martin (1980) has recorded, without description, the presence of *P. breviradiatum* in upper Ordovician Quebec strata, though the specimen she illustrated (pl. 3, fig. 13; Ashgill) needs confirmation for specific identity. Also from Quebec (Ashgill, Anticosti Island), Jacobson & Achab (1985) described and illustrated putative, possibly remanié *P. intermedium*, but neither generic nor specific assignment is persuasive.

In eastern U.S.A., *Peteinosphaeridium* occurs in the upper Ordovician of Kentucky (Eden, upper Caradoc), reportedly (Jacobson, 1978) as *P. intermedium*, though the specific identification is erroneous (see systematic section herein); and also in Edenian rocks of Indiana, whence Colbath (1979) described *P. indianense* and *P. spiraliculum* (see also systematics, where the generic attribution of both is considered uncertain). Elsewhere (in Ohio, New York State), *Peteinosphaeridium* is said to be plentiful in middle and upper Ordovician strata (Jacobson, 1979). Miller & Wicander (1982) listed the genus as a component of a lower Richmondian (lower Ashgill) assemblage of Indiana.

Of the other peteinoid genera treated herein, *Cycloposphaeridium* is, comparatively speaking, very restricted stratigraphically, as well as being confined palaeogeographically to the Baltic Province. According to Uutela & Tynni (1991), this genus exits before the end of the Llanvirn (i.e., Aseri stage, about mid-Llanvirn). *Liliosphaeridium*, similarly limited vertically, is unrecorded post-Llanvirn. In the Baltic Province, last appearances are within the lower part of the Llanvirn (*L. hypertrophicum*, *L. intermedium*). The only reported Mediterranean occurrence (*L. pennatum*) is pre-Llanvirn (i.e., upper Arenig, Morocco).

Hence, on the basis of unequivocal iden-

tifications and demonstrably *in situ* occurrences, none of the subject peteinoid genera is known beyond the confines of the Ordovician system (Text-fig. 8). *Peteinosphaeridium*, which is diverse, abundant, and widespread in Arenig-Llanvirn times, then dwindles, both quantitatively and qualitatively, until its demise at or just prior to the close of the period; while both *Cycloposphaeridium* and *Liliosphaeridium* disappear within the middle Ordovician (Llanvirn). With respect to the upper age limitation of *Peteinosphaeridium*, the two-decades-old findings of Diez & Cramer (1974) still apply, even though many of the species they attributed to *Peteinosphaeridium* in their range chart have since been generically reassigned or are not here regarded as consonant with the genus.

PALAEOGEOGRAPHIC DIFFERENTIATION

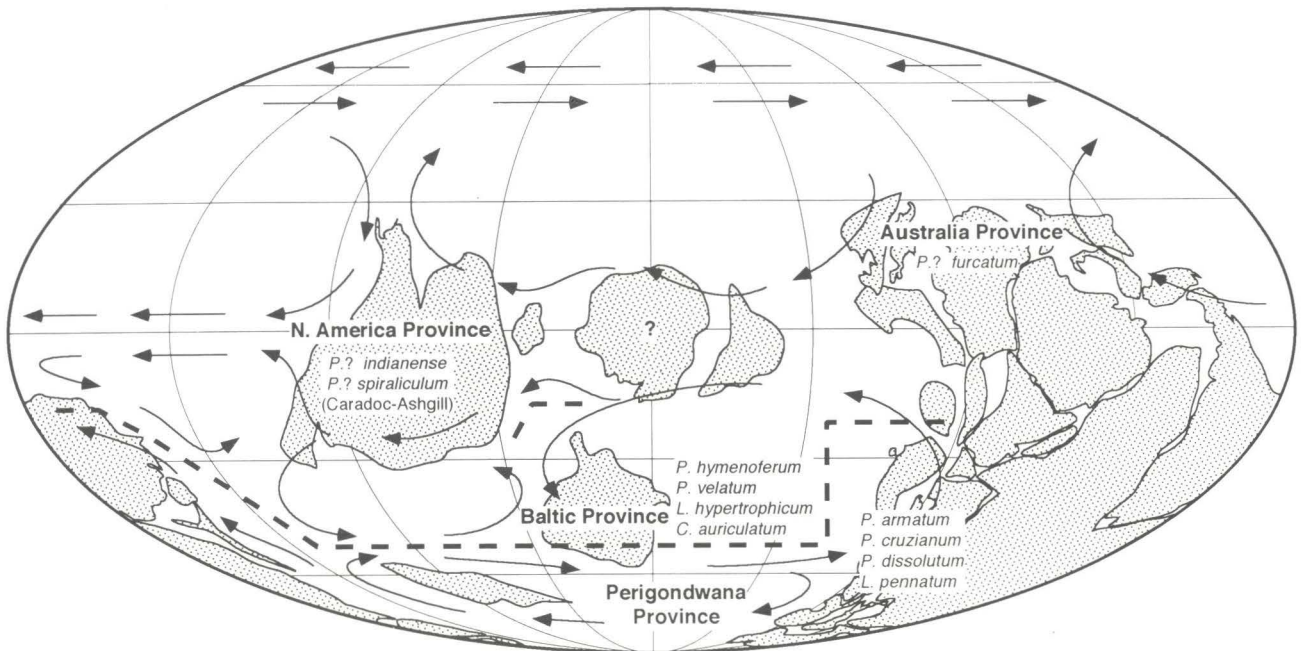
Although of inferred planktic habit (Tappan, 1980), acritarchs of the lower to mid Palaeozoic exhibit varying degrees of provincialism (Text-fig. 9), still incompletely documented and seemingly controlled chiefly by palaeotemperatures. Cramer & Diez (1974a, b) considered that acritarch-based palynofacies of Ordovician and Silurian epeiric seas appear to be delimited by palaeoisotherms, in turn paralleling palaeolatitudes. In his discussion of Silurian palynofacies, Cramer (1971) had conceded that oceanic circulation patterns can produce significant deviations in the latitudinal distribution of species, but he discounted the likelihood of strong currents in the broad Silurian epeiric seas. Therefore, with regard to then-known acritarch assemblages of the Ordovician and Silurian, the palaeoprovincial boundaries inferred by Cramer & Diez (1974a, b) relate basically to palaeolatitude. Colbath (1990) «viewed with some scepticism» Cramer's (1971) model of palaeolatitude-dependent palynofacies, which appeared not strongly consonant with more recent plate reconstructions for the early Palaeozoic. However, in analyzing the putatively diachronous distribution of the Ordovician acritarch genus *Frankea* Burmann, 1970 (see also Servais, 1993), Colbath (1990) still stressed palaeolatitude (in conjunction with plate dynamics) as the prime factor determining the spatial and chronological distribution of palynofacies. By contrast, Tongiorgi, Yin Lei-ming & Di Milia (in press) emphasize the influence of oceanic currents on palaeoisotherms, noting that the known global distribution of Arenigian acritarch palynofloras is in close accord with Wilde's (1991) reconstruction of early Ordovician oceanic current patterns (Text-fig. 9).

As discussed below, provincialism among early to middle Ordovician acritarch assemblages is endorsed herein, and palaeotemperature is acknowledged as the predominant, though not exclusive causative factor. While not intending to adopt an unduly partisan stance, we must take issue with the assertion of Fortey & Mellish (1992, p. 212) that «poor biogeographical discrimination is shown by acritarchs». That statement appears to have been engendered by the failure of Paris & Robardet (1990) to corroborate the notion of «Tornquist's Sea», which had been hypothesized by Cocks & Fortey (1982) as an early Ordovician seaway separating Baltica and Avalonia (viz., southern Britain and Lake District, eastern Newfoundland, and Nova Scotia: McKerrow & Cocks, 1986). Accordingly, Paris & Robardet (1990) continued to envisage Avalonia, not as a component of North Gondwana, but as a southwestern promontory of Baltica. Fortey & Mellish (1992) and Fortey & Cocks (1992) challenged the findings of Paris & Robardet (1990) on the grounds of the latter authors' supposed palynological (mainly chitinozoan) predilection. In fact, Paris & Robardet (1990) did attempt to take into account a whole range of available fossil and other (sedimentological, stratigraphic, tectonic) evidence. It is beyond the ambit of this paper to debate the merits and demerits of the Tornquist idea, but the acritarch testimony – incomplete as it admittedly is – does indicate the presence of manifestly different assemblages, presumably influenced mainly by palaeolatitude, in Baltica on the one hand, and in Avalonia and the Gondwanic-Mediterranean region on the other.

ORDOVICIAN ACRITARCH PROVINCES

Vavrdová (1974) introduced the concept of Ordovician palaeobiogeographic acritarch provinces in Europe by recognizing and defining the Mediterranean and Baltic provinces. The former (incorporating Belgium, France, Spain, northern Africa, Germany, central Bohemia, and Bulgaria) was characterized from the common and characteristic occurrence of diacromorphids. In contrast, the Baltic Province featured acanthomorphids as prevalent elements, and embraced the northern part of the former Soviet Union, Sweden, Poland, northern Germany, and «probably part of the British Isles» (not better defined). According to Vavrdová (1974), the two provinces were more clearly differentiated during early Ordovician time.

Concurrently, and though concerned primarily with Silurian acritarch suites, Cramer & Diez (1974a) produced a tentative palynoprovincial model for the early Ordovician plotted on an hypothetical



Text-fig. 9 - Lower to middle Ordovician acritarch provinces, with appended selection of peteinoid species characteristic of each. Plate tectonic reconstruction modified slightly from Scotese & McKerrow (1991, fig. 3). Oceanic current circulation based on Wilde (1991, fig. 3B).

world base map derived, with slight modification, from the «Bullard's fit» map (which portrays end-Palaeozoic palaeogeography). They distinguished, firstly, a *Coryphidium bohemicum* Province, which roughly corresponds to Vavrdová's (1974) Mediterranean Province with the addition of Arabia, southern Africa, and possibly southeastern Australia. Secondly, Cramer & Diez (1974a) referred to a North American Province with an acritarch content «profoundly distinct» from the *C. bohemicum* assemblages. It should be noted that at least some of the material utilized lacked rigorous stratigraphic control (Cramer & Diez, 1974a, p. 147).

Martin (1982) accepted Vavrdová's (1974) Mediterranean Province, but enlarged its boundaries appreciably to include the Anglo-Welsh area, eastern Newfoundland, and northwest Argentina. Li Jun (1987), in effect, redefined the Mediterranean Province taxonomically, based on the common occurrence of *Arbusculidium* Deunff, 1968, *Coryphidium* Vavrdová, 1972, and *Striatotheca* Burmann, 1970 (unknown from the Baltic Province), instead of the more generalized incidence-of-diacrodians criterion stated by Vavrdová (1974). It should also be noted that the latter group of acritarchs can no longer be regarded as principally diagnostic for the Mediterranean Province because some have been recorded from the Baltic Arenig-

Llanvirn (Uutela & Tynni, 1991; Ribecai & Tongiorgi, in press). According to Li Jun (1987, 1989, 1990) and Tongiorgi, Yin Lei-ming & Di Milia (in press), the composition of Arenigian acritarch floras of the Upper Yangtze Region (the Yangtze Platform) of South China facilitates inclusion of that region in the Mediterranean Province. Dean & Martin (1992) recognized typical Mediterranean taxa in both Tremadocian and Arenigian beds of central and eastern Taurus, southern Turkey. Early Arenigian assemblages from different outcrops in this latter region include *Arbusculidium*, *Striatotheca*, and *Coryphidium*, thus supporting the inclusion of southern Turkey in the Mediterranean Province (*sensu* Li Jun, 1987). Recently attributed to the same province is Karakorum (Pakistan), on the basis of Arenig acritarch assemblages reported therefrom (Tongiorgi, Di Milia, Le Fort & Gaetani, 1994).

Martin (1982, p. 38) alluded to «the resemblance between microfloras of eastern Newfoundland and the Mediterranean region, located around the periphery of Gondwanaland», a concept subsequently accepted and promulgated as «Perigondwanian Paleoprovince» by Albani (1989, p. 7) and adopted herein as Perigondwana Province (Text-fig. 9). This province is thus regarded as comprising a broad, latitudinally extensive, circumpolar, cold to cool-temperate, palaeogeographic belt along the northern

Gondwana border from Argentina through eastern Newfoundland, north Africa, central and southern Europe, and southern Turkey to South China. The name Mediterranean is accordingly applied here in a restricted palaeogeographic sense to the (subprovincial) Mediterranean area specified originally by Vavrdová (1974) with the subsequent additions (noted above) of the Anglo-Welsh area, Arabian peninsula, eastern Newfoundland, southern Turkey, and Karakorum (Pakistan).

In addition to the cold Perigondwana Province, we distinguish here the temperate Baltic Province (*sensu* Vavrdová, 1974; Tongiorgi, Yin Lei-ming & Di Milia, in press), and the warm North American (restricted to North American continent; partly corresponding to Cramer & Diez, 1974a), and Australian Provinces (*sensu* Tongiorgi, Yin Lei-ming & Di Milia, in press). The Ordovician of North China is virtually unexplored palynologically; it is here segregated from the other palynogeographic provinces largely for that reason. However, distinguishing warm, subequatorial North China (Sino-Korea) from the more temperate South China certainly accords with palaeofaunistic, tectonic, and palaeomagnetic data: see discussion in Scotese & McKerrow (1990, pp. 4-5; 1991, p. 276) and references cited therein. Conspicuous benthic faunal similarities between North China and Australia (Burrett *et al.*, 1990) may indicate close proximity of these intertropical regions in the middle Ordovician and thus point to their inclusion in the same acritarch province; however, the palynological data from these regions are clearly insufficient for this to be any more than a possible eventuality.

The other major group of early to mid Palaeozoic palynomorphs, i.e. chitinozoans, are common associates of acritarchs in Ordovician marine sedimentary rocks. For the Ordovician, Nölvak & Grahn (1993, pp. 246-247), among others, have noted significant differences between northern Gondwanan and Baltoscandian chitinozoan suites: particularly in the early and middle Ordovician, and thus more or less in concert with perceived, coeval acritarch provinciality.

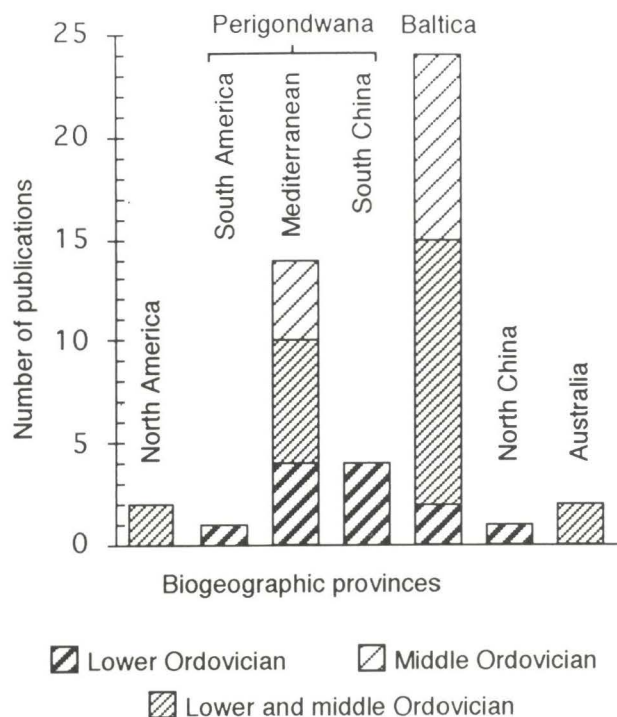
It is noteworthy that the trilobite fauna in the carbonates of southern Turkey (Sobova Formation) is of Baltic affinity, whereas the fauna and flora (acritarchs) of the more distal, offshore shaly facies indicate Mediterranean affinity (Dean & Martin, 1992). Thus, one may suppose that acritarch distribution is also controlled by a palaeoenvironmental (thermal?) gradient across continental margins. In other words, the Mediterranean-like acritarch assemblages may represent a widespread cold water flora which characterized the marginal ocean-facing deposits («Perigond-

wana oceanic Realm»), while relatively warm water shelf environments (Baltic Province, etc.) supported mostly endemic biotas. Unfortunately, there are no palynological data from the more proximal deposits of southern Turkey (Sobova Formation), nor from the (unknown) marginal deposits of Baltica. But a comparison is useful between Scandinavia and the Yangtze Platform (Lindström *et al.*, 1991; Tongiorgi, Yin Lei-ming & Di Milia, in press), both on cratons and at comparable latitude, and with a similar Ordovician facies evolution. These two regions show strong differences in the composition of Arenigian phytoplanktic communities, since in China the Mediterranean (Perigondwanan) taxa are spread deeply on-craton, while typical Perigondwana markers are completely lacking in the Baltic area. The oceanic current-dependent model we proposed above may better explain differences between South China and Baltica than the palaeoenvironmental gradient model.

EARLY-MIDDLE ORDOVICIAN PROVINCIALISM AMONG *PETEINOSPHAERIDIUM* AND RELATED GENERA

Text-fig. 10 is intended to place in realistic perspective the database currently available for consideration of both the palaeogeographic and the biostratigraphic significance of known occurrences of the subject peteinoid genera. Clearly, it is not to be regarded as a conspectus or inventory of all available acritarch literature covering the lower and middle Ordovician. For instance, some papers are overtly (if not covertly) taxonomically selective; i.e., they have not attempted to treat the acritarch assemblages comprehensively and hence may not record any actual peteinoid presence. Nevertheless, because most publications dealing with the time interval do, in fact, record peteinoid forms (predominantly species or subspecies of *Peteinosphaeridium*), the histogram representation does convey a reasonable indication of relative, and close to actual, numbers of publications focused on each region. Clearly then, for the lower and middle Ordovician, the Baltic Province and the Mediterranean subprovincial area have received the most attention; by contrast, data are most deficient from North China, Australia, and the Americas. Tab. 1 documents known lower and middle Ordovician occurrences of species and subspecies of the three peteinoid genera on a province-by-province basis.

From this critical literature survey together with our own observations, the following species appear to be confined to the Baltic Province: *Peteinosphaeridium angustilaminae*, *P. eximium*, *P.*



Text-fig. 10 - Numbers of publications containing reports of species/subspecies assignable, at least possibly, to the peteinoid genera *Peteinosphaeridium*, *Liliosphaeridium*, and *Cycloposphaeridium* from the various lower to middle Ordovician acritarch provinces.

granulatum, *P. hymeniferum*, *P. parvispinosum*, *P. velatum*, *Liliosphaeridium hypertrophicum*, *L. intermedium*, *L. kaljoi*, and *Cycloposphaeridium auriculatum*. Furthermore, *P. bergstroemii*, *P. dissimile*, *P. micranthum*, and *P. trifurcatum* (s. s.) are very likely Baltic-restricted, because specimens recorded from elsewhere are judged to be either misidentified or too poorly preserved for confident specific (or even generic) attribution. One of the subspecies of *P. trifurcatum* (*P. t. cylindroferum*) appears to be endemic to the Baltic Province. The other, *P. t. longiradiatum*, is dominantly Baltic (and later Ordovician), but is known also from one Mediterranean occurrence (Caradoc, Portugal).

The following species are confined to the Perigondwana Province: *Peteinosphaeridium armatum*, *P. cruciatum*, *P. cruzianum*, *P. dissolutum*, *P. exornatum*, *P. robustiramosum*, *P. strigosum*, *P. tenuifilosum*, and *L. pennatum*.

Peteinosphaeridium furcatum is known only from Western Australia and its generic assignment awaits confirmation. It can also be noted here that the upper Ordovician (upper Caradoc) species, *P. indianense* and *P. spiraliculum*, are unrecorded outside U.S.A. and they too are of equivocal generic attribution.

In summary, it is clear that the distribution of representatives of the peteinoid genera discussed herein connotes palaeogeographic differentiation in accordance with the recognized provincial categories. In other words, with remarkably few exceptions (and these subject to doubt or at least close scrutiny), species and subspecies attributable to the three genera evidently do not transgress the provincial boundaries. Reflecting the more intensive research in the Baltic Province, most known peteinoid species have been described from, and appear to be endemic to, that region; but an appreciable number are unrecorded outside the Perigondwanan Mediterranean area (Tab. 1). From a peteinoid and general acritarch standpoint, Australia, North China, and the Americas are relatively unexplored, and thus any palaeogeographic inferences concerning them in the earlier Ordovician remain highly speculative.

CONCLUSIONS

1. The Ordovician acritarch genera *Peteinosphaeridium*, *Liliosphaeridium*, and *Cycloposphaeridium* are linked as a morphologically coherent («peteinoid») grouping by their possession of conspicuous, typically elongate, solid processes constructed of longitudinally and radially oriented, blade-like laminae.

2. Four main categories of peteinoid laminate processes are distinguishable on the basis of gross process form and the unbranched or variously branching configuration of distal process termini. These distinctions – exemplified by the Öland material of this study – are manifested by taxonomic differentiation of the three genera, and, in further detail, at specific and subspecific levels.

3. A comprehensive survey of lower Palaeozoic acritarch literature discloses many peteinoid records needing careful re-evaluation in terms of generic and specific/subspecific assignments.

4. Notwithstanding the preceding paragraph, and with further limitations imposed by disparities in global coverage, palaeoprovincial differentiation of lower to middle Ordovician acritarch assemblages is reinforced by the currently known distribution of peteinoid species. More particularly, the majority of species belonging to the most widely disseminated (virtually cosmopolitan) genus – *Peteinosphaeridium* – occur, mutually exclusively, in either the Baltic province or the Mediterranean sector of the Perigondwana Province. The monotypic *Cycloposphaeridium* is endemic to the Baltic Province. *Liliosphaeridium* is also characteristically, though not solely Baltic, one of its four species being Mediterranean.

Species	Early to middle Ordovician biogeographic provinces						
	North America	Perigondwana			Baltic	North China	Australia
		S. America	Mediterran.	S. China			
<i>P. angustilaminae</i>					[44], ●		
<i>P. armatum</i>				38			
<i>P. bergstroemii</i>			(4)		(1), [8], [9], [19], [22], 36, 37, ✱		
<i>P. cruciatum</i>		[32]?		28, 38			
<i>P. cruzianum</i>			47				
<i>P. dissimile</i>					17	(21, cf.)	
<i>P. dissolutum</i>			3, [30]?, [35]?, [39]?, [34]?				
<i>P. eximium</i>					[17], [36], [44], ●		33,cf. ?
<i>P. exornatum</i>				38			
<i>P. furcatum</i>							?5
<i>P. granulatum</i>					?44		
<i>P. hymenoferum</i>					8, 36, ✱		
<i>P. micranthum</i>	(31)		(16)		9, ✱	(21)	
<i>P. parvispinosum</i>					?43		
<i>P. polyfurcatum</i>					?41		
<i>P. robustiramosum</i>				[26]?, [28]?, 38			
<i>P. strigosum</i>			46				
<i>P. tenuifilosum</i>				38			
<i>P. trifurcatum</i> (s. str.)			(39)	26?,28?	(1), 7, 8, [9], [10], 12, [13], [20], [23], [40], [41]?	(22,cf.)	
<i>P. t. cylindroferum</i>					11, 41		
<i>P. t. longiradiatum</i>					9, 10, 40		
<i>P. velatum</i>					22, 14, 36, ✱		
<i>P. xiphopterum</i>						21	
<i>L. hypertrophicum</i>					13, 18, 36, ✱		
<i>L. intermedium</i>					13, [17], [18], ✱		
<i>L. kaljoi</i>					36, 44, ✱		
<i>L. pennatum</i>			6, 15				
<i>C. auriculatum</i>					36, 44, ✱		

Tab. 1 - Distribution of peteinoid acritarch species attributable to *Peteinosphaeridium*, *Liliosphaeridium*, and *Cycloposphaeridium* in early to middle Ordovician acritarch provinces. Terminology for latter follows published sources cited in text. Records of species judged to be misidentifications are excluded from consideration, as are those unsubstantiated by descriptions or illustrations. Species doubtfully identified (with open nomenclature) are also excluded. See text for taxonomic details and for sources of data related to species occurrences. *Key to authors*: 1 - Aristova (1980); 2 - Bockelie & Kjellström (1979); 3 - Burmann (1970); 4 - Burmann (1973); 5 - Combaz & Peniguel (1972); 6 - Deunff (1977); 7 - Eisenack (1931); 8 - Eisenack (1938); 9 - Eisenack (1959); 10 - Eisenack (1965); 11 - Eisenack (1968a); 12 - Eisenack (1968b); 13 - Eisenack (1976); 14 - Eiserhardt (1989); 15 - Elaouad-Debbaj (1984); 16 - Fournier-Vinas (1985); 17 - Górka (1969); 18 - Górka (1979); 19 - Górka (1980); 20 - Górka (1987); 21 - Hu Yunxu (1986); 22 - Kjellström (1971a); 23 - Kjellström (1971b); 24 - Kjellström (1976); 25 - Li Jun (1987); 26 - Li Jun (1990); 27 - Lister & Holliday (1970); 28 - Lu Lichang (1987); 29 - Marhoumi *et al.* (1982); 30 - Martin (1969); 31 - Martin (1978); 32 - Ottone *et al.* (1992); 33 - Playford & Martin (1984); 34 - Rauscher (1971); 35 - Rauscher (1974); 36 - Ribecai & Tongiorgi (in press); 37 - Staplin *et al.* (1965); 38 - Tongiorgi *et al.* (in press); 39 - Turner (1985); 40 - Tynni (1975); 41 - Tynni (1982); 42 - Umnova (1975); 43 - Uutela (1989); 44 - Uutela & Tynni (1991); 45 - Vavrdová (1976); 46 - Vavrdová (1986); 47 - Vavrdová (1990). *Style of numerical citations and symbols*: 44 - includes original diagnosis/description of taxon; [23] - originally attributed to a different species; [41]? - idem, new attribution tentative; ?36 - generic attribution uncertain; 26? - species identification questionable; (31) - species identification awaiting confirmation (inadequate description, illustration); * - previously instituted species described herein; ● - new species instituted herein.

5. The three genera are confined to the Ordovician. On current knowledge, their respective stratigraphic ranges are: *Peteinosphaeridium*, lower to upper Ordovician (uppermost Tremadoc-upper Ashgill); *Liliosphaeridium*, upper lower to lower middle Ordovician (upper Arenig-lower Llanvirn); and *Cycloposphaeridium*, uppermost lower to middle Ordovician (uppermost Arenig-mid Llanvirn).

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APPENDIX 1

DATA ON SAMPLES STUDIED FROM NORTHWEST ÖLAND, SWEDEN

Text-figs. 1, 2 show collecting localities and sampling levels respectively.

a/b = metres above base of exposed stratigraphic section.

Locality	Sample no.	Strat. level	Strat. unit	Lithology
Horns Udde Quarry	HUQ12	0.12 a/b	Lepidurus Lst.	glauconitic lst.
	HUQ13	1.02 a/b	Lepidurus Lst.	glauconitic lst.
	HUQ14	1.98 a/b	Lepidurus Lst.	marly lst.
	HUQ15	2.96 a/b	Vaginatum Lst.	glauconitic lst.
	HUQ16	3.88 a/b	Vaginatum Lst.	glauconitic lst.
	HUQ17	4.50 a/b	Vaginatum Lst.	glauconitic lst.
Horns Udde	HU652	7.56 a/b	Lepidurus Lst.	glauconitic lst.
	HU654	8.50 a/b	Lepidurus Lst.	glauconitic lst.
	HU655	8.92 a/b	Lepidurus Lst.	glauconitic lst.
Hagudden	NH688	2.68 a/b	Vaginatum Lst.	glauconitic lst.
Hälludden	HL1	0.08 a/b	Vaginatum Lst.	glauconitic lst.
	HL4	0.46 a/b	Vaginatum Lst.	glauconitic lst.
	HL10	1.12 a/b	Vaginatum Lst.	glauconitic lst.
	HL14	1.50 a/b	Vaginatum Lst.	glauconitic lst.
	HL15	1.58 a/b	Vaginatum Lst.	glauconitic lst.

APPENDIX 2

REGISTER OF ILLUSTRATED SPECIMENS

All slides containing specimens illustrated herein are housed in the type collections of the Museo di Storia Naturale e del Territorio, Certosa di Calci, Pisa. Ho - holotype; Ne - neotype; Pa - paratype; To - topotype; Hy - hypotype. Sample numbers apply mainly to the northwest Öland sections at Horns Udde Quarry, Horns Udde, Hagudden, and Hälludden (Text-figs. 1, 2; Appendix 1). HD2 refers to sample from Daping section, South China (Tongiorgi, Yin Lei-ming & Di Milia, in press); and SJP refers to Öland topotypic sample of *Peteinosphaeridium bergstroemii* ex Staplin *et al.* (1965).

Species and type	Plate: figure	Sample number	Slide	England finder	Catalogue number
<i>Peteinosphaeridium angustilaminae</i>					
Ho	1:2a, b	HL10	HL10>50-1	S49/2	CPT103240-04
Pa	1:1a, b	HL10	HL10>50-2	Q50/4	CPT103240-05
Pa	1:3a, b	HUQ17	HQ17-stub1	P38	CPT103219-11
<i>Peteinosphaeridium armatum</i>					
To	2:1	HD2	HD2-tot3	F44	CPT701002-03
<i>Peteinosphaeridium bergstroemii</i>					
To	2:2	SJP	SJP>50-5	N37/1	CPT103300-07
Hy	2:3	HUQ14	HUQ14-stub2	O35/1	CPT103209-12
To	2:4a, b	SJP	SJP-stub1	L38/2	CPT103300-09
To	2:5	SJP	SJP>50-3	L36	CPT103300-05
To	2:6	SJP	SJP-stub1	N36/4	CPT103300-09
<i>Peteinosphaeridium eximium</i>					
Ho	3:1	HUQ13	HUQ13>50-1	L25	CPT103206-06
Pa	3:2	HUQ13	HUQ13-stub3	P39/2	CPT103206-13
Pa	3:3	HUQ13	HUQ13-stub4	R37/1	CPT103206-14
Pa	3:4	HUQ13	HUQ13>50-1	R23	CPT103206-06
Pa	3:5	HUQ13	HUQ13-stub3	R33	CPT103206-13
Pa	3:6a, b	HUQ13	HUQ13-stub4	O35	CPT103206-14
<i>Peteinosphaeridium hymeniferum</i>					
Hy	4:1	HUQ12	HUQ12>50-1	V37	CPT103202-06
Hy	4:2	HUQ12	HUQ12-stub3	M37	CPT103202-13
Hy	4:3	HUQ12	HUQ12>50-1	T28	CPT103202-06
Hy	4:4	HUQ12	HUQ12-stub3	O38/2	CPT103202-13
Hy	4:5	HUQ12	HUQ12>50-1	O33	CPT103202-06
Hy	4:6	HUQ12	HUQ12-stub3	N38/1	CPT103202-13
Hy	4:7	HUQ12	HUQ12-stub3	M38/4	CPT103202-13
<i>Peteinosphaeridium micranthum</i>					
Hy	4:8	HU652	HU652>50-2	Z28/4	CPT103165-07
Hy	4:9a, b	HU655	HU655>50-1	F45	CPT103168-06
<i>Peteinosphaeridium</i> sp. cf. <i>P. micranthum</i>					
	4:10	HU652	HU652>50-2	E51/3-F51/1	CPT103165-07
<i>Peteinosphaeridium robustiramosum</i>					
To	4:11	HD2	HD2-tot2	M37	CPT701002-02
<i>Peteinosphaeridium velatum</i>					
Ne	5:1	HUQ14	HUQ14>50-1	D24/2	CPT103209-04
Hy	5:2a, b	HUQ14	HUQ14>50-1	U38/4	CPT103209-04
Hy	5:3a, b	NH688	NH688-stub7	M39/2	CPT103091-23
Hy	5:4	NH688	NH688-stub10	O36/2-O37/1	CPT103091-26
Hy	5:5	NH688	NH688-stub9	N37	CPT103091-25
<i>Cycloposphaeridium auriculatum</i>					
Hy	5:6a, b	HL15	HL15>50-1	T41/2	CPT103245-04
Hy	5:7a, b	HL14	HL14>50-1	G30-2	CPT103244-04
Hy	5:8	HUQ17	HUQ17-stub5	O33/3	CPT103219-15
Hy	6:1	HUQ17	HUQ17-stub5	P32/4	CPT103219-15
Hy	6:2a, b	HUQ17	HUQ17-stub5	Q35/3	CPT103219-15

Liliosphaeridium hypertrophicum

Hy	6:3	HL4	HL4>50-2	H29/2-H30/1	CPT103234-05
Hy	6:4	HL4	HL4>50-2	O37/2	CPT103234-05
Hy	6:5a, b	HL4	HL4>50-3	Q37/1	CPT103234-09
Hy	7:1	HL4	HL4>50-1	Y49	CPT103234-04

Liliosphaeridium intermedium

Hy	7:2	HUQ13	HUQ13>50-3	N40/4	CPT103206-13
Hy	7:3	HUQ13	HUQ13>50-4	P36/1/4	CPT103206-14
Hy	7:4a, b	HUQ13	HUQ13>50-1	Q30/2	CPT103206-06
Hy	7:5	HUQ13	HUQ13>50-1	Y25	CPT103206-06
Hy	7:6	HUQ13	HUQ13>50-1	V28/4-V28/2	CPT103206-06
Hy	8:1a, b	HUQ13	HUQ13>50-2	M37/3-M37/4	CPT103206-12
Hy	8:2	HUQ13	HUQ13>50-4	N37	CPT103206-14

Liliosphaeridium kaljoi

Hy	8:3	NH688	NH688>50-3	O38/2	CPT103091-27
Hy	8:4	HL1	HL1>50-1	E50/3	CPT103231-04
Hy	8:5	NH688	NH688>50-7	P40/3	CPT103091-23
Hy	8:6	HL1	HL1>50-3	O39/1	CPT103231-06
Hy	9:1	NH688	NH688>50-13	N36/3	CPT103091-27
Hy	9:2	HL1	HL1>50-2	F32/4-G32/2	CPT103231-05
Hy	9:3	NH688	NH688>50-7	P40/3	CPT103091-23
Hy	9:4	NH688	NH688>50-7	P40/3	CPT103091-23
Hy	9:5	NH688	NH688>50-7	O39	CPT103091-23
Hy	9:6	NH688	NH688>50-13	P37/3	CPT103091-27

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